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Some considerations on Devonian miospore taxonomy

[Quelques considérations sur la taxonomie des miospores dévonniennes]

Pierre BREUER¹

John FILATOFF²

Philippe STEEMANS³

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Mots-Clefs : Taxonomie ; Dévonien ; miospores

Introduction

In order to be able to deal with objects human beings need to have name tags for them and to classify them in discrete boxes. It is primarily for this reason that miospore taxa are named using Linnaean-style Latinized binomial nomenclature, a system formally governed by the International Code of Botanical Nomenclature (ICBN). The purpose of formal nomenclature is to provide a precise, simple and stable system of unique names that can be used by scientists all over the world. This system must allow for expansion and refinement to accommodate increases in knowledge (see TRAVERSE, 1996). Currently however, Palaeozoic miospore taxonomy has become somewhat problematic. Indeed, the number of described species has become so enormous that it is difficult to cope with all of this information. In addition, each authors prefer to work with their own discriminatory criteria, so that each has a personnal conception of the miospore classification and so does not necessarily use the same discriminatory features when he erects a new taxon. Consequently comparisons between assemblages described by different authors are becoming more confusing. Also, many species have not been accurately described, either because the diagnosis is rather simplistic, or because it is based on but a few specimens resulting in an ignorance of their intraspecific

morphological variability. Furthermore, diagnoses based on poorly preserved specimens are not always precise and so are often unusable by other authors. Finally, species defined in journals with a limited circulation are unknown to many miospore researchers and are often described in other languages than English. Consequently, most of these species have been used only by the local authors and have been either completely unusable and/or overlooked by most of the palynologists. All these reasons have caused increased taxonomic chaos resulting in the overlapping diagnoses of some taxa. The intention of this extended abstract is not to resolve the problems related to miospore taxonomy but rather to highlight some of them by using selected examples from Devonian assemblages from Libya and Saudi Arabia.

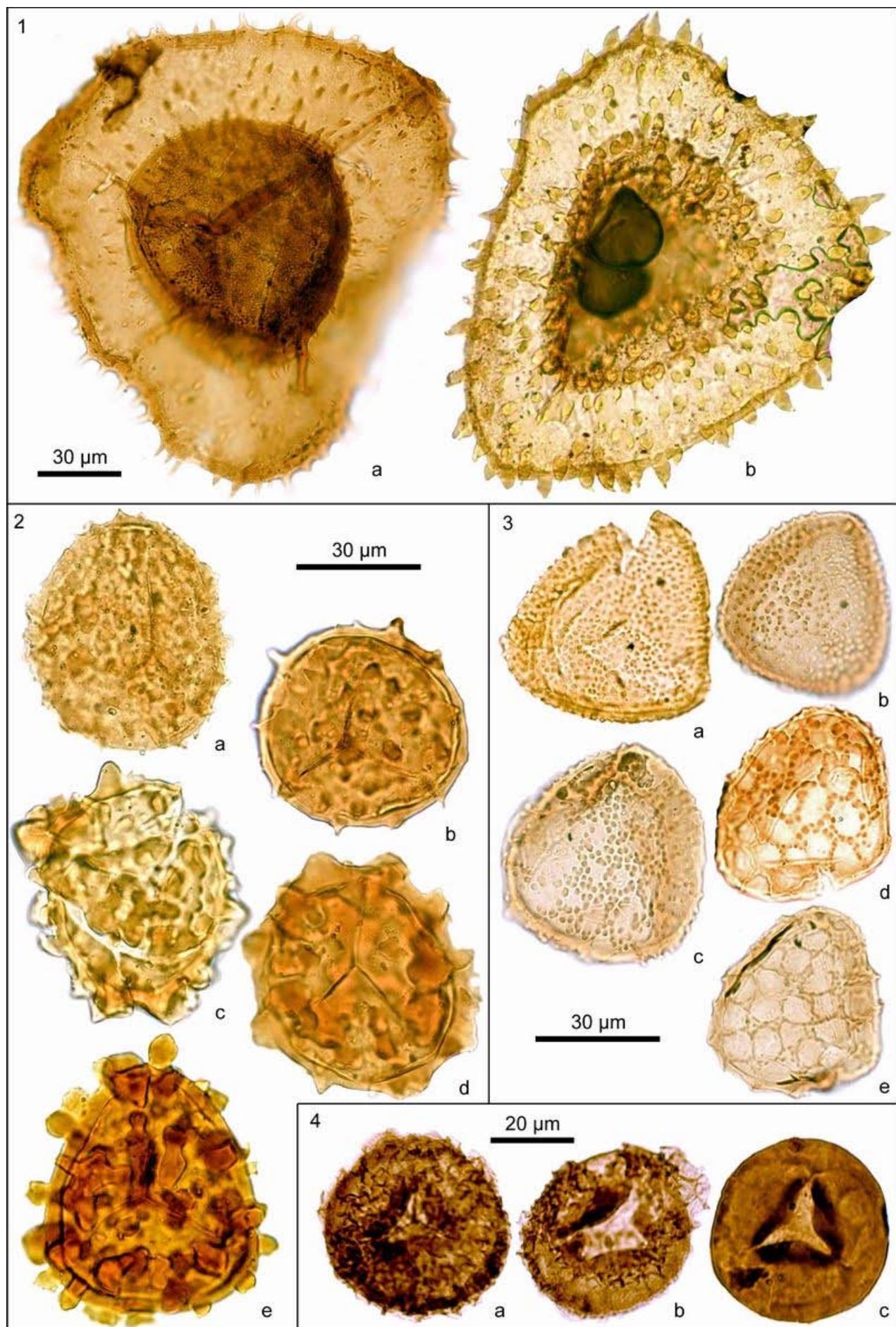
Discussion

The fact that miospores are generally retrieved from sediments after their dispersal from the parent plants often implies, at least for the Palaeozoic specimens, ignorance of their source and consequently for most, of the time their natural affinities. Therefore Palaeozoic miospore taxonomy is inevitably arbitrary and artificial. As the essential basis of palaeopalynology is dispersed spores, their morphology obviously provides the principal and unique basis for taxonomic discrimination.

¹ Laboratoire de Paléobotanique, Paléopalynologie et Micropaléontologie, Université de Liège, Allée du 6 août, B18, Sart-Tilman, 4000 Liège (Belgium)
piet79@yahoo.fr

² Geological Survey of Western Australia, Department of Industry and Resources, 100 Plain Street, East Perth, 6004 (Australia)
john.filatoff@aramco.com

³ Laboratoire de Paléobotanique, Paléopalynologie et Micropaléontologie, Université de Liège, Allée du 6 août, B18, Sart-Tilman, 4000 Liège (Belgium)
p.steemans@ulg.ac.be
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◀ **Figure 1:** Microphotographs of Devonian miospores.

- 1.a. *Grandispora libyensis*. Well A1-69, sample 1416', slide 26993, EFC O43.
- 1.b. *Grandispora libyensis*. Well A1-69, sample 1296', slide 62645, EFC G47/2.
- 2.a. *Dibolisporites farraginis*. Well A1-69, sample 1334', slide 27127, EFC L44.
- 2.b. *Dibolisporites uncatus*. Well A1-69, sample 1277', slide 62637, EFC V-W42.
- 2.c. *Verrucosporites scurruus*. Well A1-69, sample 1296', slide 62644, EFC P53/2.
- 2.d. *Verrucosporites scurruus*. Well A1-69, sample 1277', slide 62637, EFC W48/3.
- 2.e. *Verrucosporites premnus*. Well A1-69, sample 1277', slide 62636, EFC X41/4.
- 3.a. *Cymbosporites* sp. 1. Borehole BAQA-1, sample and slide 395.2', EFC G37/3.
- 3.b. *Cymbosporites* sp. 2. Borehole BAQA-1, sample and slide 395.2', slide, EFC X43/1.
- 3.c. *Cymbosporites?* sp. 3. Borehole BAQA-2, sample and slide 52.0', EFC N29/2.
- 3.d. *Dictyotrites biornatus*. Borehole BAQA-1, sample 308.3', slide 62243, EFC U38.
- 3.e. *Dictyotrites* sp. 1. Borehole BAQA-1, sample and slide 408.3', EFC G37/3.
- 4.a. sp. 1. Well UTMN-1830, sample 13689.7', slide 62317, EFC E33/4.
- 4.b. sp. 1. Well UTMN-1830, sample 13689.7', slide 62317, EFC Y42/1.
- 4.c. sp. 2. Well HWYH-956, sample 14195.2', slide 60550, EFC K35/1.

Therefore, miospores, as acritarchs, are classified into different groups by a simple morphological comparison. Indeed, miospore workers use form-genera and form-species ("parataxa"). At the suprageneric level, the completely informal subgroups of POTONIÉ (1956) are commonly used. His tural system, which has been revised several times in his Synopsis volumes (POTONIÉ, 1956, 1970) is a scheme for classifying fossil miospores according to their morphological characters. However, one can choose any version of POTONIÉ's system or indeed make up one's own, and as the individual units in the system are not subject to rules of priority (see TRAVERSE, 1988), this kind of classification will inevitably cause much confusion. Miospore genera are normally defined according to the general structural features of miospores, such as equatorial outline, wall stratification, wall sculpturing, and any structural modifications of the spore wall (e.g. cingulum, zona or patina). Miospore species are generally described on the basis of ornaments, such as their size, shape, and distribution. At the infraspecific level, the rank of variety is rarely used. Other methods of classifying miospores have been proposed (see TRAVERSE, 1996). HUGHES's biorecord (1975, 1991) scheme is a parataxonomy; he recognized that conventional taxa tend to be expanded by inclusion in them of newly discovered but slightly variant forms until the taxa are "balloon taxa" of little stratigraphic use. This biorecord system treats every newly described form as completely unchangeable and independent of others, thus preventing "ballooning". In summary, palynological parataxonomy produce groupings with common morphological features whereas a true taxonomy describes the hierarchy of groupings of plants and is indicative of presumed natural relationships (see TRAVERSE, 1996).

Some authors urge the stratigraphic utility of subdividing miospore groupings as much as possible; however, others note that gradations between taxa may be so subtle that intermediates can often be found between species, or even genera, commonly regarded as discrete. Many cases of such intergrading taxa are common in the fossil record (e.g. PLAYFORD,

1983; STEEMANS & GERRIENNE, 1984; RICHARDSON *et alii*, 1993; BREUER *et alii*, 2005). Such palynomorphs often transgress the taxonomical boundaries between genera and higher categories as they were originally defined and thus formed the bases of their taxonomy. That is why the concepts of palynodeme (VISSCHER, 1971) and morphon (VAN DER ZWAN, 1979) were introduced. A palynodeme defines a group of palynomorph species that intergrade and probably represent the palynological reflection of a known or hypothetical plant species (VISSCHER, 1971). As originally defined, this concept was also phylogenetic and referred to characters changing with time. In contrast, a morphon delimits a group of palynological species (form-species) simply united by a continuous variation of morphological characteristics (VAN DER ZWAN, 1979). However in practice the two concepts are considered by many as synonymous (TRAVERSE, 1988). We can reiterate the main idea of these concepts as follows: the apparent morphological continua may represent spore variation in a particular known or hypothetical natural plant species or group of related species. However, evolutionary convergence may cause morphological similarities between miospores that do not necessarily reflect links between their parent plants. During Palaeozoic times, different plant groups often produced miospores of very similar morphology (GENSEL, 1980; FANNING *et alii*, 1992). In contrast, a single sporangium can produce two different genera of trilete spore (HABGOOD *et alii*, 2002). In palynology, the palynodeme and morphon concepts are complementary to the typological approach of traditional taxonomy. They emphasize the continuity of the morphological characters more than the discontinuity. They integrate morphological trends which are space- or time-dependent but also sensitive to various environmental conditions. They may also facilitate the interpretation of the morphological variations in terms of natural variation. Unfortunately, studies treating of the environmental influences on miospore variability are rare or nonexistent. For Devonian miospores, McGREGOR and PLAYFORD (1992) have defined several morphons based on the

significant variation that has been observed in certain morphological characters. Those morphons are useful for comparison of assemblages on a second level (McGREGOR & PLAYFORD, 1992).

A few authors have mentioned phylogenetic miospore evolution in Palaeozoic sediments (e.g. BREUER *et alii*, 2005; MARSHALL, 1996; MAZIANE *et alii*, 2002; VAN DER ZWAN, 1979). Some of these authors have demonstrated continuous morphological intergradation among some dispersed spores that have previously been attributed to different form-species and even genera. However, the morphological signal presented by miospores may not reflect biological evolution alone. Indeed, it may be influenced locally by other parameters such as the state of preservation, sedimentary sorting (JÄGER, 2004) and/or reworking of simpler and older morphotypes into assemblages that contain more complex and younger forms (BREUER *et alii*, 2005).

Selected examples

In this section, three examples of continuous morphological intergradation are presented and one about a possible taphonomic problem. These specimens were isolated from Devonian core samples in Libya and Saudi Arabia. All material presented herein is housed in the collections of the Unit of "Paléobotanique, Palynologie et Micropaléontologie", University of Liège.

Continuous morphological intergradation within a unique form-species

Grandispora libyensis MOREAU-BENOIT, 1980 is a characteristic form found in the Middle Devonian sediments of Libya (see e.g. MASSA & MOREAU-BENOIT, 1976; LOBOZIAK & STREEL, 1989). This species of *Grandispora* is defined mainly by its equatorially thickened exoxine (3-7 µm thick) and its distal surface sculpture of spines or biform elements with 3-7 µm wide bulbous bases, commonly 3-10 µm high (rarely up to 13 µm); the rounded apices supporting a small spine. The ornament is usually densely spaced. After a study of some Libyan material, it appears that the specimens show a continuous morphological variation in ornamentation, intergrading from a morphotype with rather slender spines (Fig. 1.1.a) to one characterized by bulbous biform elements (Fig. 1.1.b). Although two end-members exist, all the intermediate forms are present. The morphotype characterized by the most massive sculptural elements seems to appear later than the morphotype with more slender ornaments, but in the youngest samples, the two-end members co-occur.

Continuous morphological intergradation within a unique form-genus

The genus *Verrucosiporites* is also a

significant form in Middle Devonian samples. In Libyan samples, this very confused group probably includes the following described species (Fig. 1.2): *V. premnus* RICHARDSON, 1965, *V. scurrus* (NAUMOVA) McGREGOR et CAMFIELD, 1982, *Dibolispores farraginis* McGREGOR et CAMFIELD, 1982 and *D. uncatus* (NAUMOVA) McGREGOR et CAMFIELD, 1982. Although the two latter species are included in the genus *Dibolispores*, many authors consider them to belong to *Verrucosiporites*. All of these described species co-occur and in most of the levels of Libya where they are common they can be discriminated only with difficulty. Indeed, this group of form-species have very similar diagnoses. Specimens herein assigned these species seems to form a more or less intergrading series from those with predominantly conate and small verrucose sculpture (*D. farraginis* and *D. uncatus*) to those with large verrucate sculptural elements, and thus conform rather closely to the diagnosis of *V. scurrus* and *V. premnus*. In addition, McGREGOR and PLAYFORD (1992) designated *D. farraginis* and *V. scurrus* as morphons when they noted morphological intermediates between them.

Continuous morphological intergradation between two form-genera

A continuous morphological intergradation between two genera has been highlighted in Early Devonian miospore assemblages from Saudi Arabia. The ornament and its organization on the spore distal surface varies between the two end-members which correspond to two distinct genera: *Cymbosporites* and *Dictyotriletes* (Fig. 1.3). All the intermediary forms between them co-occur in the assemblages. This "lineage" includes morphotypes undescribed in the literature except for *Dictyotriletes biornatus* BREUER *et alii*, in press. In the simplest form of the spore ornament, small cones are evenly distributed on the distal surface (*Cymbosporites* sp. 1). In the intermediary forms cones organize progressively and combine until they form a pseudo-reticulum, the walls of which are constituted by lines of discrete ornaments (*Dictyotriletes biornatus*). In the most complex spore form ornaments merge to form an elongated ornament which constitutes a perfectly closed reticulum (*Dictyotriletes* sp. 1). Thus a progressive organization of the ornamentation appears from the simplest spores to the most evolved ones. This example illustrates that the miospore taxonomy is artificial because the two end-members of this lineage belong to two distinct genera.

Taxonomical confusion as a result of preservation?

Finally, palynologists must be careful because morphological differences may depend on the state of preservation or the transport

undergone by the miospores, and hence not necessarily on the original features. In Saudi Arabia, two as yet unpublished Emsian form-species have been recognized. They can either co-occur in the same layers or they are found separately. The first species (sp. 1) is two-layered and rounded; the intexine has a dark triangular thickening of the proximal pole and the exoexine is very thin and strongly folded (Fig. 1.4.a). The second species (sp. 2) does not have an exoexine but has the same intexine as sp. 1 (Fig. 1.4.c). Although they can be clearly discrete morphologically, they may either represent two varieties of a single species of parent plant, or that one form (sp. 2) may result from the corrosion of the other (sp. 1). Indeed, a slight detachment of the exoexine can be seen locally on some specimens of sp. 1 (Fig. 1.4.b), thus the very delicate exoexine may have been torn off by sedimentary or taphonomic processes. This situation can be confusing when comparing different assemblages.

Conclusion

The examples of continuous intergrading morphological variation outlined above illustrate one of the major problems in miospore taxonomy: the morphological variability of each taxon, combined with the description of individual forms, that are rarely studied within large populations. In older papers the rather basic description of many new taxa does not meet the modern standards for palynology. Furthermore, new taxa are often illustrated by too few specimens. Most authors have preferred to place their new taxa into well-defined boxes rather than to introduce a palynodeme or morphon, which are concepts introduced for those species of miospore linked by a continuous variation of morphological characters. Ideally, in order to understand better the nature of a miospore taxon, larger populations and the relationships between the taxa should be studied. But in reality, the available material for study rarely allows the attainment of this level. The material can be badly preserved or is rare in most Devonian sediments. But these hindrances should not prevent improvement of our knowledge of palynological assemblages.

Another important factor in miospore taxonomy is the search for characters useful for the separation of taxa. We have to question the level at which such discriminatory criteria should be used: generic, specific or intraspecific. And their usage should be common to all authors in order to rein in the ongoing current taxonomical chaos.

The purpose of this short paper is neither to solve problems related to the somewhat chaotic miospore taxonomy nor to call into question the numerous stratigraphic correlations based on it, but rather to highlight some of these issues and

to encourage a common approach to systematics.

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**A classification of spores by support vectors
based on an analysis of their ornament spatial distribution –
An application to Emsian miospores from Saudi Arabia**

**[Classification de spores assistée par vecteurs de support
basée sur l'analyse de la distribution spatiale des ornements –
Une application à des miospores emsiennes d'Arabie Saoudite]**

Pierre BREUER¹

Godefroid DISLAIRE²

John FILATOFF³

Eric PICARD⁴

Philippe STEEMANS⁵

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Mots-Clefs : Phylogénie ; miospores ; analyse d'images ; histogrammes des sommes et différences ; classification de vecteurs à support

Introduction – Geological setting

Continuous morphological intergradations exist between two trilete spore taxa from the Jauf Formation (Early Devonian) of the Widyan and Tabuk basins (northwestern Saudi Arabia). The alternation of siliciclastics and carbonates in this unit has been used to subdivide it into five members: from bottom to top, the Sha'iba,

Qasr, Subbat, Hammamiyat and Muray members. The Jauf Formation in northwestern Saudi Arabia was deposited in a nearshore environment (AL-HAJRI *et alii*, 1999; AL-HAJRI & OWENS, 2000).

The latest study of miospores (BREUER *et alii*, 2005a, *in press*) suggests that the Jauf Formation is late Pragian to Emsian in age.

¹ Laboratoire de Paléobotanique, Paléopalynologie et Micropaléontologie, Université de Liège, Allée du 6 août, B18, Sart-Tilman, 4000 Liège (Belgium)
piet79@yahoo.fr

² Secteur de Géoressources Minérales et Imagerie Géologique, Université de Liège, Chemin des chevreuils 1, B52, Sart-Tilman, 4000 Liège (Belgium)
godefroid.dislaire@gmail.com

³ Geological Survey of Western Australia, Department of Industry and Resources, 100 Plain Street, East Perth, 6004 (Australia)
john.filatoff@aramco.com

⁴ Secteur de Géoressources Minérales et Imagerie Géologique, Université de Liège, Chemin des chevreuils 1, B52, Sart-Tilman, 4000 Liège (Belgium)
eric.pirard@ulg.ac.be

⁵ Laboratoire de Paléobotanique, Paléopalynologie et Micropaléontologie, Université de Liège, Allée du 6 août, B18, Sart-Tilman, 4000 Liège (Belgium)
p.steemans@ulg.ac.be

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Additional biostratigraphic evidence is provided by other fossil groups collected in outcrop (e.g. BOUCOT *et alii*, 1989; FOREY *et alii*, 1992). Among them, trilobites and conodonts indicate that the uppermost Sha'iba and Qasr members (lower Jauf Formation) are Pragian-early Emsian in age and brachiopods suggest that the Hammamiyat Member (upper Jauf Formation) is late Emsian in age.

The palynological material of this report comes from boreholes previously studied (see BREUER *et alii*, 2005a, in press). They are in two discrete areas about 350 km apart. Two of them (BAQA-1 and BAQA-2) are near Baq'a in the Widyan Basin, while JNDL-4 is near Domat Al-Jandal in the Tabuk Basin. The stratigraphic levels encountered in each locality overlap, and the correlations easily established using lithologic and wireline logs are confirmed by palynological data reported by BREUER *et alii* (2005a, in press). BAQA-1 and BAQA-2 cover an interval from the Sha'iba Member, through the Qasr and Subbat members to the lowermost Hammamiyat. The succession at JNDL-4 represents the upper part of the Subbat and the Hammamiyat Member.

Samples from BAQA-1, BAQA-2, and JNDL-4 were prepared in the Palynological Research Facility of the University of Sheffield. For this study additional slides from BAQA-1 were processed in the Laboratory 'Paléobotanique, Paléopalynologie et Micropaléontologie' of the University of Liège. All samples were prepared using standard palynological acid maceration techniques. A vast majority of the samples were productive and contain well-preserved organic matter. All material is housed in the Centre for Palynology of the University, Department of Animal and Plant Sciences, University of Sheffield and in the collections of the laboratory of 'Paléobotanique, Palynologie et Micropaléontologie', University of Liège.

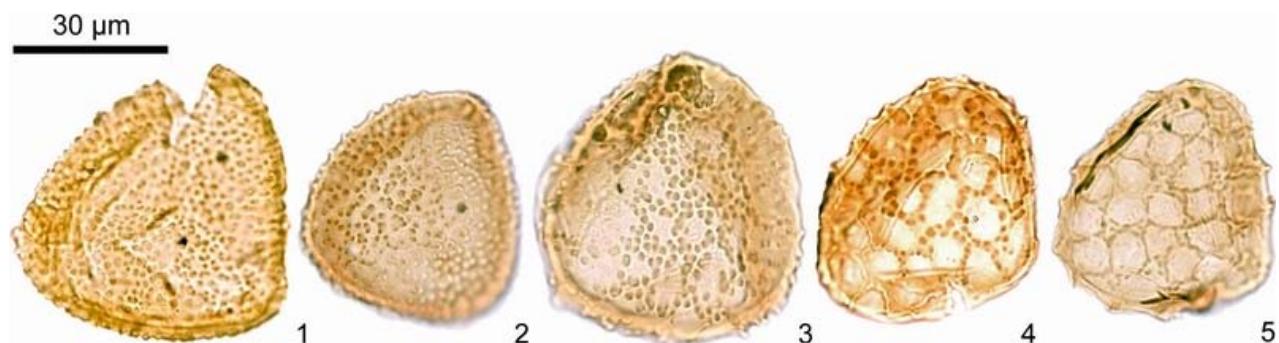


Figure 1: Microphotographs of the different morphotypes of the lineage.

Biostratigraphy

From a stratigraphic point of view, the range of the lineage is restricted to the Jauf Formation. Specimens occur first in the upper part of the Sha'iba Member and disappear in the upper part of the Hammamiyat Member. The spore assemblages from the upper part of the Sha'iba Member are considered to be in the PoW Oppel Zone of STREEL *et alii* (1987), based

Lineage

Palynologists have discussed only rarely the phylogenetic evolution of miospores in Palaeozoic sediments (e.g. VAN DER ZWAN, 1979; MARSHALL, 1996; MAZIANE *et alii*, 2002; BREUER *et alii*, 2005b). Some authors have demonstrated a continuous morphological intergradation among some dispersed spores that previously were attributed to discrete species. The morphological signal presented by miospores may not reflect only biological evolution, because it may be influenced locally by other parameters such as state of preservation, sedimentary sorting (JÄGER, 2004) and/or reworking (BREUER *et alii*, 2005b).

A possible phylogenetic lineage including several morphotypes (Fig. 1), one of which has been described in BREUER *et alii* (in press), is proposed here. The two end-members of this lineage are well differentiated; however all intermediary forms are present in the assemblages. The morphological variation concerns distal ornamentation. This ornamentation involves changes in the shape of small cones and their spatial distribution that vary progressively between the two end-members of the lineage. In the simplest morphotype ornaments are evenly distributed on the distal surface. In the intermediary morphotypes they combine progressively to form a pseudo-reticulum, the walls of which are constituted by the discrete ornaments. In the most complex morphotypes, ornaments merge to form elongated ridges which describe a completely closed reticulum. Thus a progressive change in ornamentation occurs: from the simplest spores (ornaments constituted by evenly distributed small cones) to the most complex ones (ornaments forming a reticulum).

on the general characteristics of the assemblages and the presence of typical taxa such as *Brochotriletes foveolatus* NAUMOVA, 1953, *Clivosispora verrucata* McGREGOR, 1973, *Dictyotriletes emsiensis* (ALLEN) McGREGOR, 1973, *D. subgranifer* McGREGOR, 1973, and *Verrucosporites polygonalis* LANNINGER, 1968 (Fig. 2) (BREUER *et alii*, 2005a, in press). The presence of *D. subgranifer* may indicate that they represent the uppermost interval of the

zone (Su Interval Zone) of the PoW Oppel Zone. The PoW Oppel Zone is of Pragian-earliest Emsian age, with the Su Interval Zone encompassing the latest Pragian-earliest Emsian. In the Qasr Member, the stratigraphically important spores *Emphanisporites schultzii* McGREGOR, 1973, and ? *Knoxisporites riondae* CRAMER et DÍEZ, 1975 (Fig. 2) make their first appearance. Similar spore assemblages are recovered throughout the Qasr Member and lower part of the Subbat Member. These assemblages are typical of those of Emsian age elsewhere and probably

belong to either the AB or to the lower FD Oppel Zones. These assemblages are constrained above by the first appearance of *Rhabdosporites minutus* TIWARI et SCHAARSCHMIDT, 1975 (Fig. 2) in the upper part of the Subbat Member. Its occurrence marks the base of the FD Oppel Zone (Min Interval Zone). The spore assemblages of the Hammamiyat Member are essentially similar throughout and also belong to the Min Interval Zone. That signifies that these assemblages are mid Emsian in age (BREUER *et alii*, 2005a, in press).

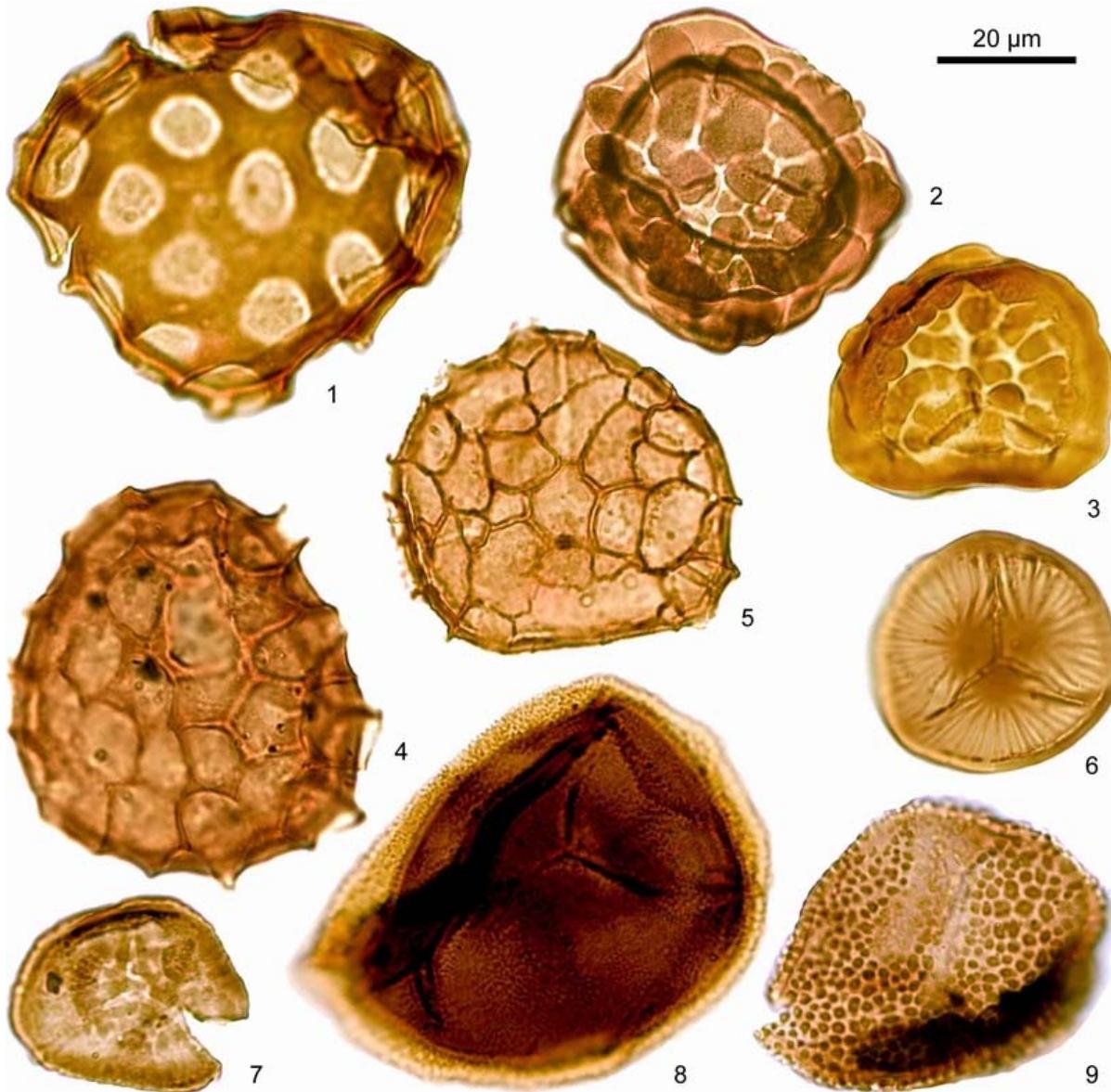


Figure 2: Microphotographs of characteristic miospores from the studied boreholes.

1. *Brochotriletes foveolatus*. Borehole BAQA-1, sample & slide 345.5', EFC H54/4.
2. *Clivosispora verrucata*. Borehole BAQA-1, sample & slide 395.2', F47/1.
3. *Clivosispora verrucata*. Borehole JNDL-4, sample & slide 87.2', F34/1.
4. *Dictyotriletes emsiensis*. Borehole BAQA-2, sample & slide 56.0', X46.
5. *Dictyotriletes subgranifer*. Borehole BAQA-1, sample & slide 366.9', O31.
6. *Emphanisporites schultzii*. Borehole BAQA-1, sample & slide 395.2', G50.
7. ? *Knoxisporites riondae*. Borehole BAQA-1, sample & slide 366.9', E27/4.
8. *Rhabdosporites minutus*. Borehole JNDL-3, sample & slide 368.8', H45/1.
9. *Verrucosporites polygonalis*. Borehole BAQA-1, sample & slide 371.1', R25/4.

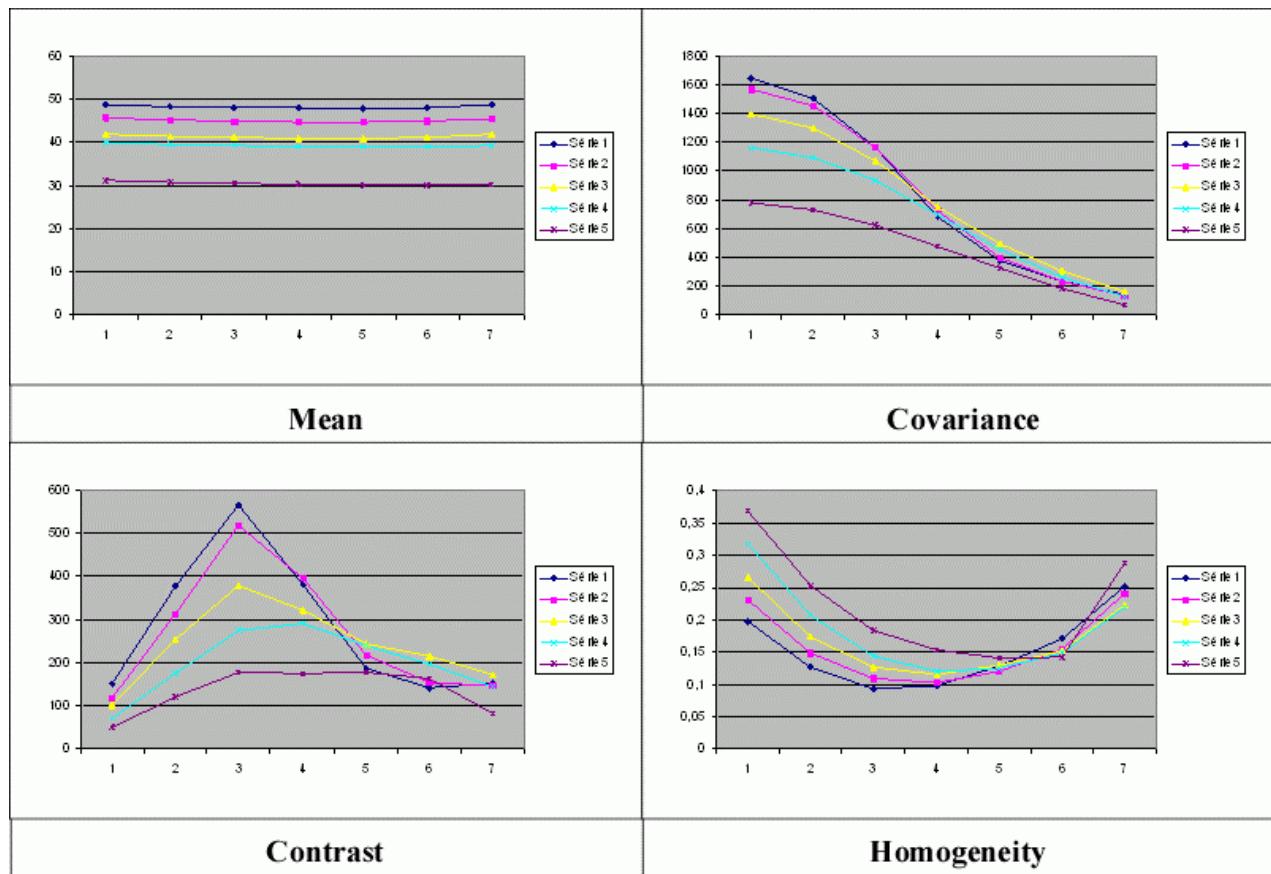


Figure 3: Mean, contrast, covariance and homogeneity for the 5 classes and for 7 decreasing scales.

Image analysis

The spore classification is based on the spatial distribution of the ornaments (from a simple pattern to a complex organization). Initially, we expect texture image analysis to provide a tool to gauge and thus to quantify morphological evolution and, eventually, to make automatic classification feasible. Both structural – extraction of texture elements and analysis of placement rules - and statistical methods – spatial statistics – are of interest in this case. Here we discuss only spatial statistics employing Sum and Difference Histograms.

Material

About 400 specimens of the miospore lineage defined here were found in more than 60 palynological slides but only half of the material was used for the image analysis. Excluded from the set are laterally compressed specimens and partial spore fragments.

A data set of region of interest (ROI) of 256x256 pixels was extracted from the original images in order to test the Spatial Vector Classification on SDH features (Fig. 3).

Sum and Difference Histograms (SDH)

Sum and Difference Histograms (SDH) are based on Co-occurrence Matrices (CoM) and are intended to make these matrices usable. Actually, CoM $P[d][z1][z2]$ are defined, for G grey level images, as the joint probability that a pair of point satisfying the dipole $d = (dx, dy)$ will have grey level values of $z1$ and $z2$. They display the image information as a co-occurrence of pixel pairs but although better-organized provide too much data. SDH (Unser, 1986) are often preferred to CoM and reduce the amount of data and computing time required. By writing $p(z, z')$ the probability of the pair of values z and z' at positions satisfying d , we define $p\Sigma(z + z')$ and $p\Delta(z - z')$ the probability of a sum and difference value for a given dipole.

HARALICK descriptors (HARALICK *et alii*, 1973) - mean, variance, contrast, energy, entropy and homogeneity - used to characterize a CoM have translations for SDH and results have shown that SDH are at least as efficient as co-occurrence matrices for classify textures.

$$\begin{aligned}
 Mean &= \sum_z \sum_{z'} z \cdot p(z, z') = \frac{1}{2} \sum_i i \cdot p_\Sigma(i) \\
 Variance &= \sum_z \sum_{z'} (z - \mu)^2 p(z, z') = \frac{1}{2} \left[\sum_i (i - 2\mu)^2 p_\Sigma(i) + \sum_j j^2 p_\Delta(j) \right] \\
 Covariance &= \sum_z \sum_{z'} (z - \mu)(z' - \mu') p(z, z') = \frac{1}{2} \left[\sum_i (i - 2\mu)^2 p_\Sigma(i) - \sum_j j^2 p_\Delta(j) \right] \\
 Contrast &= \sum_z \sum_{z'} (z - z')^2 p(z, z') = \sum_j j^2 \cdot p_\Delta(j) \\
 Energy &= \sum_z \sum_{z'} (p(z, z'))^2 \approx \sum_i p_\Sigma^2(i) * \sum_j p_\Delta^2(j) \\
 Entropy &= \sum_z \sum_{z'} -p(z, z') \log(p(z, z')) \approx -\sum_i p_\Sigma(i) \log(p_\Sigma(i)) - \sum_j p_\Delta(j) \log(p_\Delta(j)) \\
 Homogeneity &= \sum_z \sum_{z'} \frac{1}{1 + (z - z')^2} p(z, z') = \sum_j \frac{1}{1 + j^2} p_\Delta(j)
 \end{aligned}$$

This gives 7 values for the 65,535 pairs available in a 256x256 pixel image. Thereby, by keeping only one mean value by distance d and by selecting the distance as power of 2, this reduces data as 7 by 7 values when considering 7 scales ($d=1, 2, 4, 8, 16, 32, 64$) (Fig. 3).

Weighted Laplacian of Gaussian for ornament extraction

Classification based on Haralick features for the ROI data set gave results damaged by a large mean square error. Thereby, as only

ornaments are of interest in the classification, we first pre-processed the images in order to remove the background. Scale-Space theory (Lindeberg, 1994) advocated weighted Laplacian of Gaussian (wLoG) on increasing scales to capture blobs (the ornaments) independently of their sizes. An absolute value of the convolution of the ROIs by the wLoGs has been chosen to be independent of the fact that ornaments can appear black or white depending on the orientation of their relief (Fig. 4).

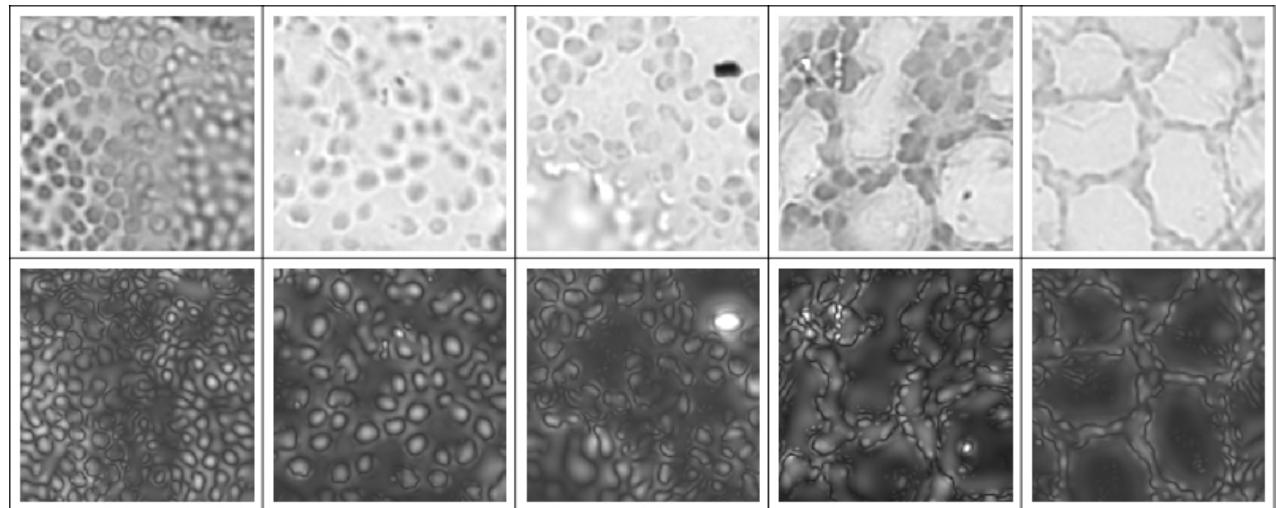


Figure 4: Regions of interest illustrating the 5 classes and their wLoG pre-processed version where background lighting is removed and ornaments highlighted.

Pattern classification

We used Support Vector Machine (CHANG & LIN, 2001; CORTES & VAPNIK, 1995; DUDA *et alii*, 2001; HASTIE *et alii*, 2001) to test a classification based on HARALICK descriptors on the original ROIs and on their wLoG version. A

classification task involves training and testing data. We used respectively 30, 30, 30, 40, 15 images for the training and 30, 20, 30, 30, 10 for the testing of the corresponding classes 1, 2, 3, 4, 5. Each instance in the training set contains one 'target value' – class label – and several 'attributes' – descriptors -. The goal of

SVM is to produce a model which predicts the target value of data instances in the testing set which are given only the attributes.

We selected the following attributes: the HARALICK descriptors for the scale 2 (7 attributes), the Contrast for the scale 3 and 4 and the Homogeneity for the scale 4 and 6 in order to exploit the differential scale dependency of these two last descriptors.

The model used is the nu Support Vector Classification with a linear kernel type.

The classification of the ROI gives an accuracy of 56% with a mean square error of 1.2 when the classification of the pre-processed ROI gives accuracy of 61% with a mean square error of 0.46 (Fig. 5).

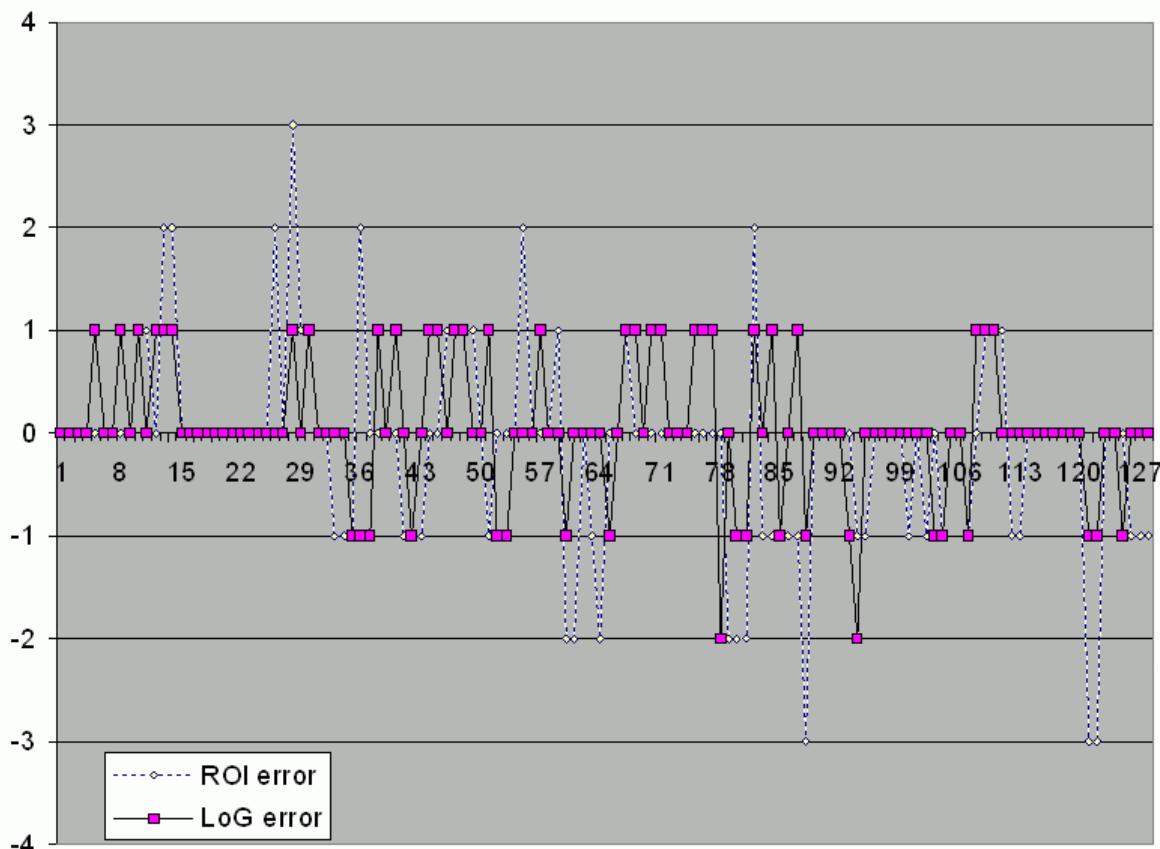


Figure 5: Classification error for the ROIs and the wLoG convolved ROIs.

Discussion

The accuracy of classification increases only from 56% to 61% when the ROI is pre-processed with the wLoG. But what is important is the reduction of the mean square error that balances the significance of the wrong classification. In fact, it drops so strongly that when a spore is misplaced it is reported only as being in a neighbouring class. In other words, if we accept the error of misplacing a spore in an adjacent class, the 'accuracy' of the classification increases from 85% to 98%.

In fact, the *a priori* human classification plays an important role as regards judgments of the accuracy and usefulness of computer-assisted classification. As classification by humans inevitably includes such types of error, we could adjudge this one test as equally subject to error but anticipate that a better-tuned training set would give better results.

Conclusion

Continuous morphological intergradations between two miospore taxa have been found in an Early Devonian miospore assemblage from Saudi Arabia. On the distal surface of these spores the ornaments and their organization show a gradual evolution in complexity between two end-members. All the intermediary forms co-occur in the assemblages. Thus there is a progressive evolution in the organization of the ornamentation ranging from the simplest spores to the most complex ones. This illustrates once again that miospore taxonomy is artificial because the two end-members of this lineage have been assigned to discrete genera.

Statistical texture image analysis provides a gauging tool to quantify morphological evolution and seems to allow assisted automatic classification. In this test case classification of spores by image analysis was

judged accurate in but 61% of the cases but rose to 98% if a misidentification to an adjacent class was accepted.

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We wish to express our gratitude to management of Saudi Aramco for permission to publish this paper. We acknowledge M. GIRALDO-MEZZATESTA (Liège) for the preparation of palynological slides. Thanks are also expressed to Y. GUÉDON (Montpellier, France) for the review of the paper. P. BREUER is supported by a F.R.I.A. grant.

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**Palyontology of Baudour Clays Formation
(Mons Basin, Belgium):
correlation within the "stratotypic" Wealden**
**[Palyntologie de la Formation des Argiles de Baudour
(Bassin de Mons, Belgique):
corrélation au sein du "Weald stratotypique"]**

Jean DEJAX¹

Élise DUMAX²

Freddy DAMBLON³

Johan YANS⁴

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Abstract: This article is a palyntological study of four clay samples from the dinosaur-bearing Wealden facies at Baudour (Belgium). Their microflora is compared to that found at Bernissart. The palyntomorphs of the four samples are of continental origin. The botanical affinities of the palyntological taxa are mainly ferns, gymnosperms and freshwater "algae". Also encountered are stratigraphically important angiospermous-like pollen grains (biorecord Superret-croton, probable paleotaxon Superret-subcrot and biorecord Retisulc-dentat); the aperture of the former is questioned ("variant forms").

Key Words: Belgium; Wealden facies; Baudour; palyntology; angiosperm pollen; dinosaur

Résumé : L'analyse palyntologique du faciès wealdien à dinosaures de Baudour (Belgique) est exposée et la microflore est comparée à celle de Bernissart. Les palyntomorphes des quatre échantillons d'argile sont d'origine continentale. Les affinités botaniques des taxons palyntologiques se partagent essentiellement entre les fougères, les gymnospermes et les "algues" d'eau douce. Des grains de pollen d'affinité angiospermienne possédant une importance stratigraphique ont été également observés (biorecord Superret-croton, probables paleotaxon Superret-subcrot et biorecord Retisulc-dentat) ; la nature de l'ouverture germinative du premier est discutée ("formes variantes").

Mots-Clefs : Belgique ; faciès wealdien ; Baudour ; palyntologie ; pollen d'angiosperme ; dinosaure

1. Introduction

The Wealden facies of the Mons Basin (Belgium) is well-known because of the exceptional fossil found in a coal mine at Bernissart during the years 1878-1881. At depths of 322 and 356 meters at least 29 complete specimens of *Iguanodon* were found, along with many fish, turtles, crocodiles, amphibians, insects and fragments of plants (see MARTIN & BULTYNCK, 1990, for a complete list of references). The palyntology of these

sediments has been reported on previously by DELCOURT and SPRUMONT (1955, 1956, 1959a, 1959b) and DELCOURT *et alii* (1963). Recently YANS *et alii* (2005, 2006) and DEJAX *et alii* (in press) analyzed the palyntological assemblage of the 322 meter level at Bernissart and focused their study on angiosperm pollen, found for the first time in the Belgian Wealden facies. Bernissart has long been considered as the only site yielding dinosaur bones from a Belgian Wealden facies. Recently, however, a fragment

¹ Muséum national d'Histoire naturelle, CNRS UMR 5143 (Paléodiversité : histoire et dynamique), Département "Histoire de la Terre", Case postale 38, 57 rue Cuvier, 75231 Paris Cedex 05 (France)
dejax@mnhn.fr

² Muséum national d'Histoire naturelle, CNRS UMR 5143 (Paléodiversité : histoire et dynamique), Département "Histoire de la Terre", Case postale 38, 57 rue Cuvier, 75231 Paris Cedex 05 (France)
elise.dumax@laposte.net

³ Institut Royal des Sciences naturelles de Belgique, rue Vautier 29, 1000 Bruxelles (Belgium)
Freddy.Damblon@naturalsciences.be

⁴ Facultés Universitaires Notre Dame de la Paix (FUNDP), rue de Bruxelles 61, 5000 Namur (Belgium)
Johan.Yans@fundp.ac.be

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of dinosaur bone has been identified in the Wealden facies of the Baudour quarry, located in the Mons Basin near Bernissart. We offer here the first palynological study of the Wealden facies of the Baudour site, and we compare its palynological assemblage with that at Bernissart.

2. Geological setting

The Baudour quarry is in the Mons Basin, Belgium (Fig. 1), which can be regarded as the northeastern part of the Paris Basin (see MARLIÈRE, 1970). The sedimentary succession of the Mons Basin begins with the Wealden facies and continues with Middle-Upper Albian, Upper Cretaceous and Cenozoic deposits (MARLIÈRE, 1970). The Wealden facies of Baudour is attributed to the Baudour Clays Formation (ROBASZYNSKI *et alii*, 2001).

3. Methods

For the purpose of palynological analysis, we processed four samples of grey clays from the collections of the Royal Belgian Institute of Natural Sciences (Brussels). The treatment involves the destruction of minerals with hydrofluoric acid (70 %), followed by a filtration using a 9 µm-mesh sieve.

The morphological classification and nomenclature of POTONIÉ and KREMP (1954 and subsequent papers), as improved by DETTMANN (1963), are followed herein. For the purpose in hand, another nomenclature *sensu* HUGHES and collaborators (see complete reference list in HUGHES, 1994) was also used for four taxa, two of which are discussed below.

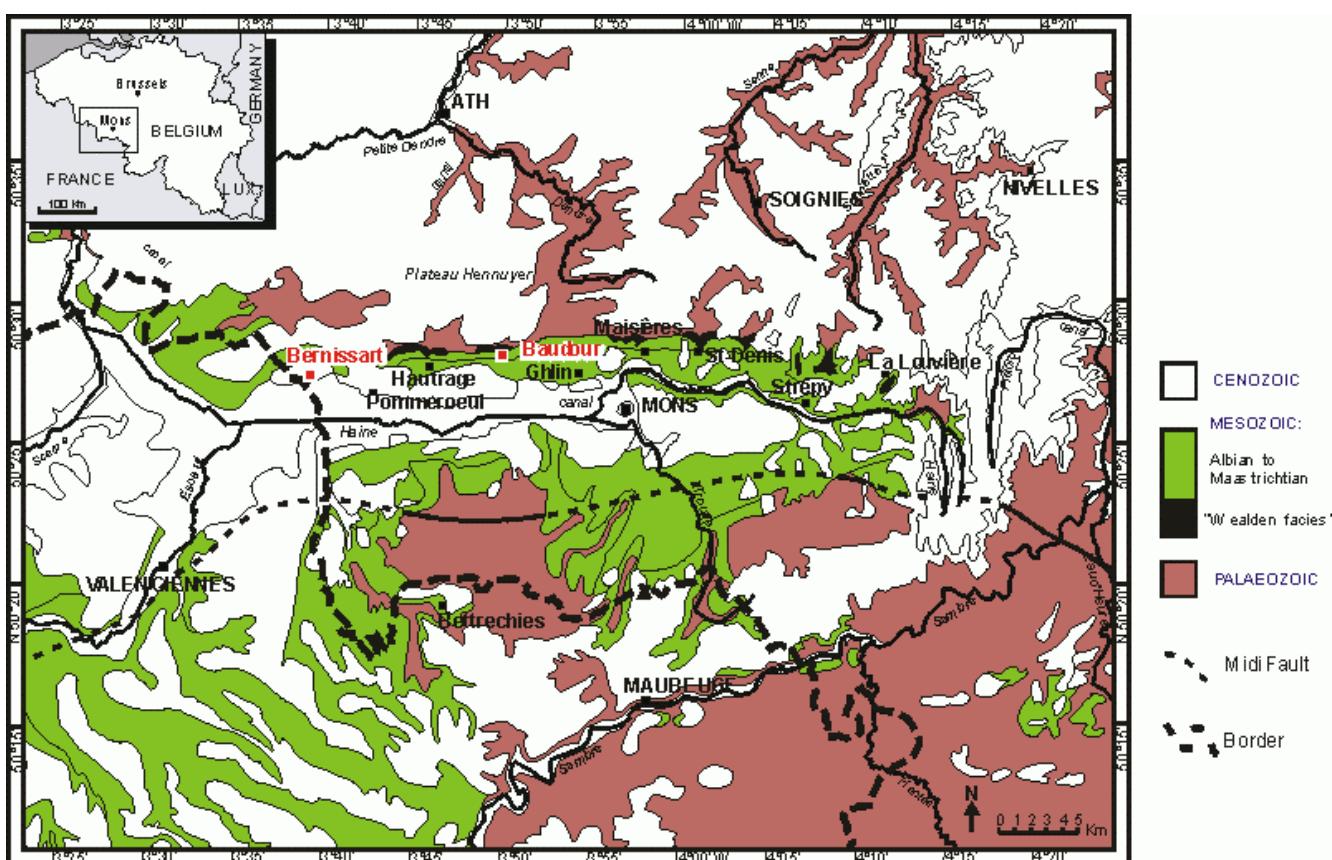


Figure 1: Simplified geological map of the Mons Basin. Location of Baudour, Bernissart and of the "pockets" filled with Wealden facies sediments (in black) on the northern border of the basin.

4. Palynological content

The palynological assemblage of Baudour quarry is very well preserved, suggesting that 1) most of the mother-plants grew close to the place where the palynomorphs were buried, and 2) diagenesis was minor. This assemblage is entirely continental in origin, quite similar to that at Bernissart, with the exception of differences in the relative abundances of some taxa. Fern spores (e.g. *Cicatricosporites brevilaesuratus*, *C. hallei*, *Deltoidospora minor*, *Dictyophyllidites harrisii* and *Trilobosporites*

hannonicus) and bisaccate pollen grains are a main feature of both assemblages; *Sciadopityaceae* (biorecord *Hauterivian-cactisulc*, alias *Cerebropollenites* sp.) and ephedroid pollen grains (*Ephedripites montanaensis*) are less numerous, but the angiospermous biorecord *Superret-croton* and its "variant forms" are more abundant than in Bernissart assemblage; freshwater "algae" zygospores (*Schizosporis reticulatus*) are also present.

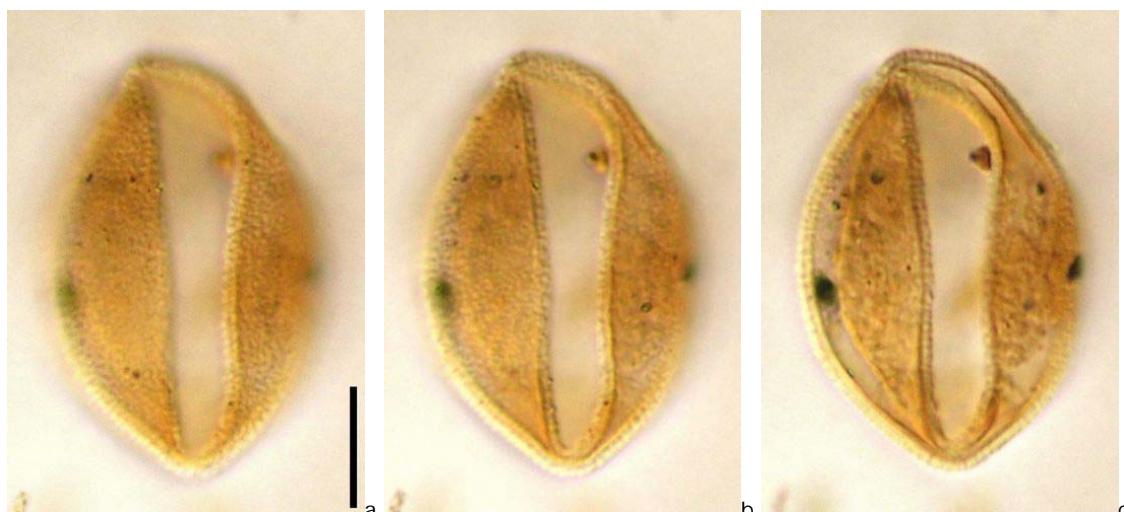


Figure 2: Biorecord Superret-croton, presumed distal face (slide Bau 2A – coordinates G37 - 1a, 2b and 2c: respectively high, less high and middle focus). Scale-bar is 10 µm.

5. Discussion

Many previous studies dealt with the palynology of the Wealden facies of northern Europe (DELCOURT & SPRUMONT, 1955, 1956, 1959a, 1959b; HUGHES, 1955, 1976, 1994; COUPER, 1958; LANTZ, 1958; DELCOURT *et alii*, 1963; VON DER BRELIE, 1964; DÖRING, 1964, 1965, 1966; BURGER, 1966; HUGHES & MOODY-STUART, 1967; NORRIS, 1969; KEMP, 1970; HERNGREEN, 1971; BATTEN, 1973; AMEROM *et alii*, 1976; DÖRHÖFER, 1977; HUGHES *et alii*, 1979; HUGHES & McDougall, 1987, 1990, 1994). The palynological assemblage of the Baudour quarry is typically "Wealden" in aspect: many of the palynomorphs identified have been reported elsewhere by DELCOURT and SPRUMONT (1955), DELCOURT *et alii* (1963) and others.



Figure 3: Biorecord Superret-croton, presumed distal face (slide Bau 3B – coordinates N44-4). Scale-bar is 10 µm.

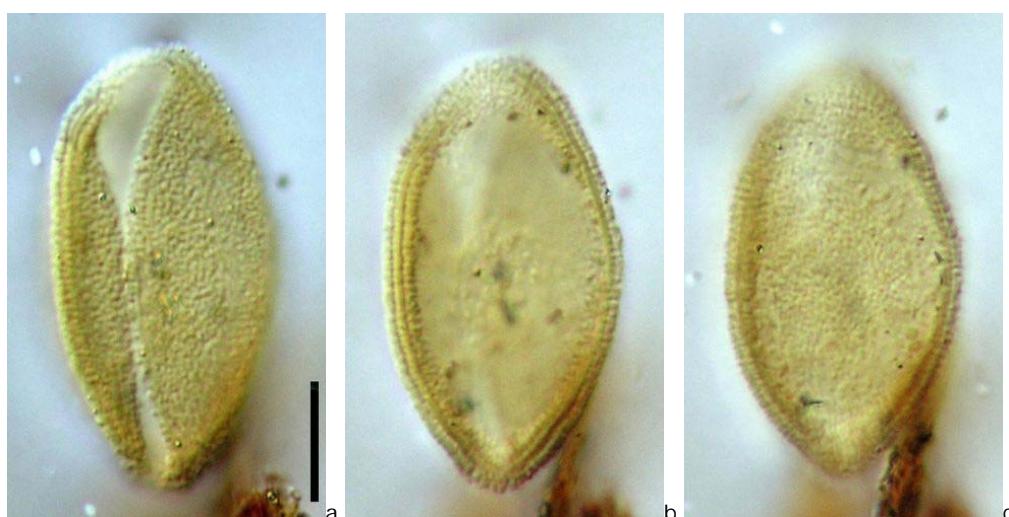


Figure 4: Biorecord Superret-croton (slide Bau 4B – coordinates T27-U27 – 4a, 4b and 4c: respectively high, average and low focus). Scale-bar is 10 µm.



Figure 5: Biorecord Superret-croton (slide Bau 4B – coordinates D28-2 – 5a and 5b: respectively low and high focus). Scale-bar is 10 µm. **Figure 6:** Biorecord Superret-croton, presumed distal face (slide Bau 2B – coordinates Q24-4/Q25-3). Scale-bar is 10 µm.

Because the biorecord Superret-croton, its "variant forms", the probable paleotaxon Superret-subcrot and the probable biorecord Retisulc-dentat are discussed below, a reminder of meanings of biorecord and paleotaxon is pertinent. Some palynomorphs have names that do not conform with classic palynological terminology: they are biorecords, *sensu* HUGHES (1976) and HUGHES *et alii* (1979), reiterated by PENNY (1991). Morphological taxa and biorecords are not true Linnean taxa, but parataxa or morphotypes which are *sporae dispersae* with no specific relationship to a mother-plant; in both biorecord and paleotaxon the *forms* are classified in an organizing chart developed in accordance with a descriptive pattern (a biorecord is generally more rigorously defined). A biorecord is considered here as a fundamental reference taxon, equivalent to the taxa defined through the use

of the conventional morphological scheme (HUGHES, 1976, p. 26; HUGHES *et alii*, 1979, p. 515); the word paleotaxon is here used in accordance with HUGHES' (1994) meaning, as qualifying a less rigorously defined taxon.

The goal of these concepts is to designate precisely what is recognized under the microscope, and so to make it useful for stratigraphic purposes; though the philosophies of "palynological language" may appear different on either side of the English Channel - as they concern the Lower Cretaceous - these "languages" have been so useful and so firmly established after several decades that there is no reason to reject one for the other, all the more that both may comply with the procedures of the Linnean Code [see HUGHES (1976, p. 29), who concludes as follows: "the two can be separate and complementary"].

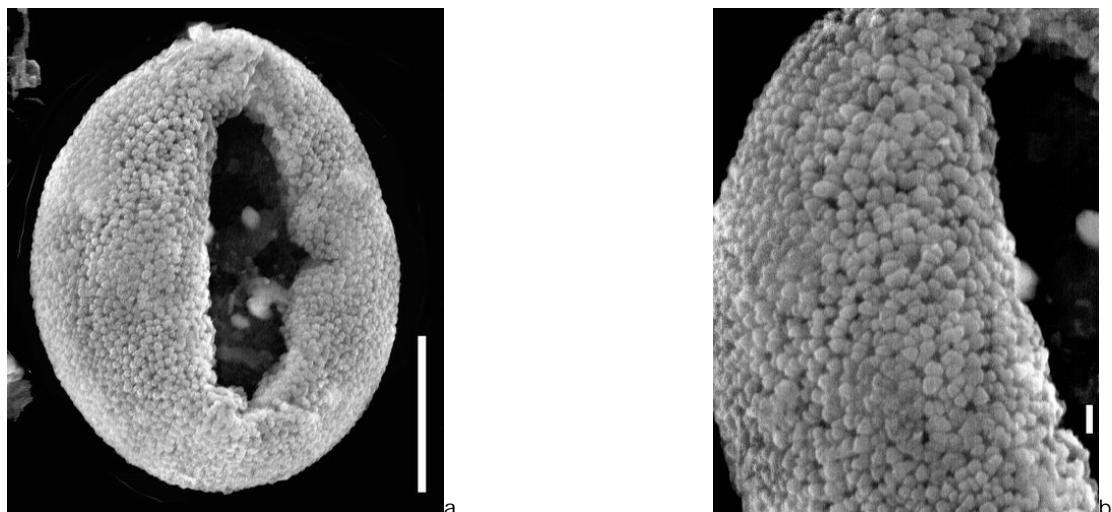


Figure 7: Biorecord Superret-croton, presumed distal face (glass stub 2/1 – 7a and 7b: whole specimen and detail). Scale-bar is 10 µm, except higher SEM magnification (1 µm).

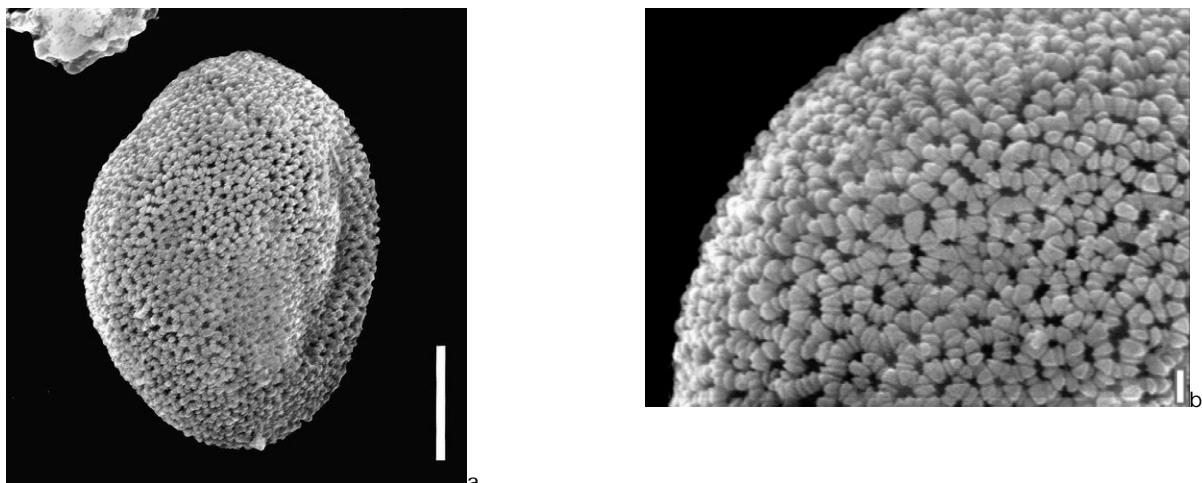


Figure 8: Biorecord Superret-croton, presumed proximal face (glass stub 2/1 – 8a and 8b: whole specimen and detail). Scale-bar is 10 µm, except higher SEM magnification (1 µm).

6. Stratigraphic implications

These three taxa (biorecord Superret-croton, probable paleotaxon Superret-subcrot and probable biorecord Retisulc-dentat) are of stratigraphic importance in the Baudour palynological assemblage.



Figure 9: Inaperturate "variant form": biorecord Inapert-croton, usual wrinkled specimen (slide Bau 4B – coordinates D43-E44). Scale-bar is 10 µm.

Biorecord Superret-croton (Figs. 2-8) was defined by HUGHES *et alii* (1979). In the "stratotypic" Wealden facies of the Weald and Wessex sub-basins, which is dated by interbeds with ammonites and dinoflagellate cysts (HARDING, 1986, 1990), the stratigraphic distribution of biorecord Superret-croton is attributed to MCT (Monosulcate Columellate Tectate) phases 3 to 5, ranging from the middle Barremian to the earliest Aptian (HUGHES, 1994). YANS *et alii* (2004) therefore suggested a

middle Barremian to earliest Aptian age for the sediments of Bernissart (at a depth of 322 m) and the same dating is proposed here for the Baudour Clays Formation. In the description of the species *Stellatopollis hughesii*, from the Upper Barremian (?) of Egypt, PENNY (1986) regarded it equivalent to biorecord Superret-croton.

Another peculiar palynomorph, very rare, is the probable paleotaxon Superret-subcrot (Fig. 16), which was defined by HUGHES *et alii* [1979, *sic*: SUPERRET-(CAND)SUBCROT] and reexamined by HUGHES (1994), using a scanning electron microscope. It is difficult to recognize with certainty under light microscopy; however its morphology appears to make it identifiable (shape, size, wall stratification and very small, numerous and closely packed crotonoid sculptural elements which are at the limit of the microscope's resolving power, so it is very difficult to produce convincing photographs). In the English Wealden, paleotaxon Superret-subcrot is reported from MCT phase 4, apparently restricted to one locality (Kingsclere borehole at a depth of 474 feet). Nevertheless, its scarcity renders impossible a more refined stratigraphic correlation than that mentioned above.

Lastly, another peculiar palynomorph, also very rare, is the probable biorecord Retisulc-dentat (Fig. 17), which was defined by HUGHES *et alii* (1979) then again by HUGHES (1994). In the English Wealden, the stratigraphic distribution of biorecord Retisulc-dentat (and similar forms) is attributed to MCT phases 2 to 4; its occurrence in the Baudour Clays Formation could be an argument to rule out the MCT phase 5. However, because of its rarity such a conclusion would be rash.

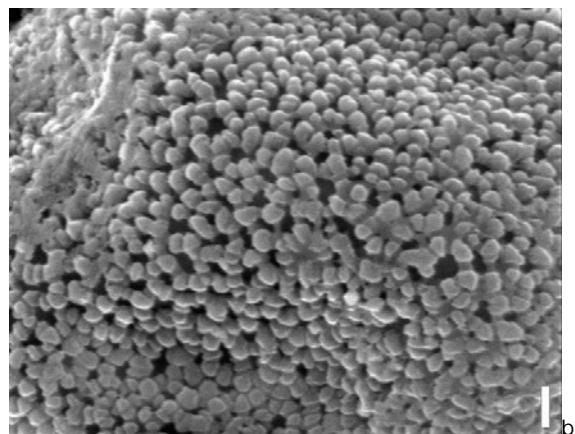
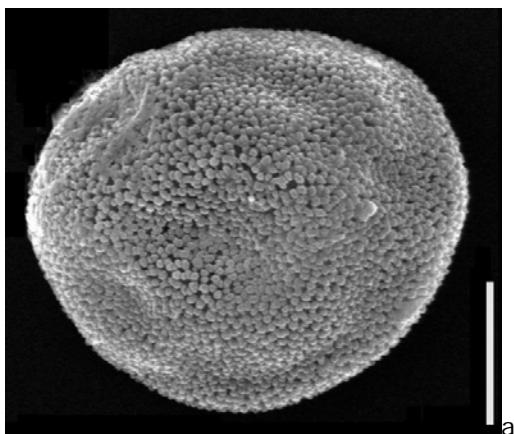


Figure 10: Inaperturate "variant form": biorecord Inapert-croton (glass stub 2/1 – 10a and 10b: whole specimen and detail). Scale-bar is 10 µm, except higher SEM magnification (1 µm).

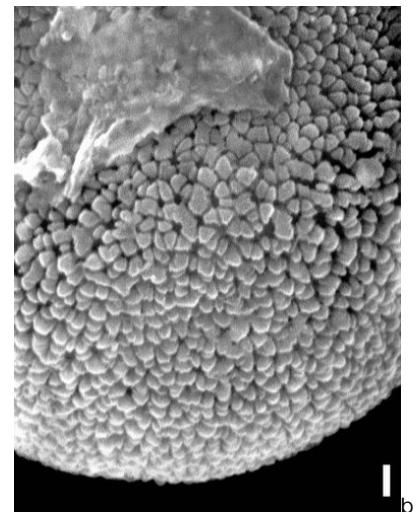
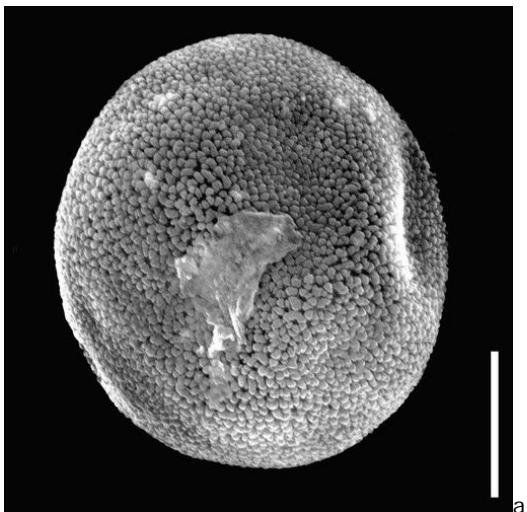


Figure 11: Inaperturate "variant form": biorecord Inapert-croton (glass stub 2/2 – 11a and 11b: whole specimen and detail). Scale-bar is 10 µm, except higher SEM magnification (1 µm).

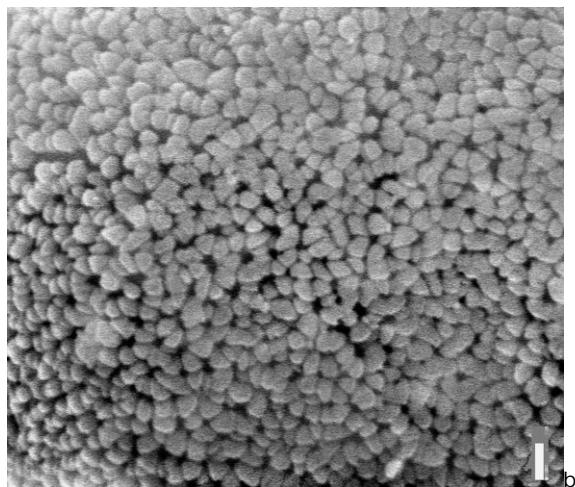
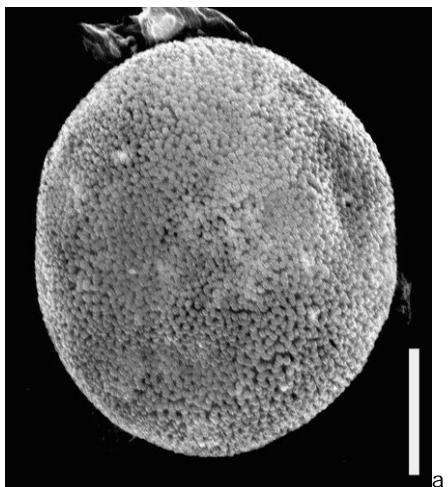


Figure 12: Inaperturate "variant form": biorecord Inapert-croton (glass stub 2/2 – 12a and 12b: whole specimen and detail). Scale-bar is 10 µm, except higher SEM magnification (1 µm).

7. Botanical affinity of these three guide-forms

HUGHES *et alii* (1979) and HUGHES (1994) highlighted the angiospermid characters of these three reference taxa: essentially they are the tectum structure (continuous reticulum) and the supratectal elements (particularly the crotonoid pattern exhibited by biorecord Superret-*croton* and paleotaxon Superret-*subcroton*). The crotonoid supratectal pattern is known in the following extant families: Euphorbiaceae (ERDTMAN, 1952; PUNT, 1962; ARCHANGELSKY, 1966; YBERT, 1975), Buxaceae and Thymelaeaceae (ERDTMAN, 1952; ARCHANGELSKY, 1966), Atherospermataceae (DOYLE *et alii*, 1975) and Liliaceae (ERDTMAN, 1952; ARCHANGELSKY, 1966; MULLER, 1970). Last, the biorecord Retisulc-*dentalis* is very similar to pollen grains of the extant Chloranthaceae family (see CHAPMAN, 1987).

8. About the aperture of biorecord Superret-*croton* and "variant forms"

After examination of numerous grains (several hundred) from the Baudour quarry samples, the presence of a definite sulcus is now certain, at least in a significant number: biorecord Superret-*croton* is undoubtedly monosulcate (Figs. 2-7). However, other grains with the same overall appearance (similar size and crotonoid pattern) differ with respect to the germinal aperture; these grains are here designed as "variant forms":

- a large proportion of these grains are undoubtedly inaperturate, their shape being

almost spherical instead of ellipsoidal (Figs. 9-12);

- some very rare grains seem to be tricolporate (Figs. 13-14) or are clearly trichotomosulcate (Fig. 15); these two early "variant forms" herald the diversification of apertures that began in strata of Early Aptian age.

These three "variant forms" may be due to some morphological intra-specific variability (CHAPMAN, 1987), or on the contrary may indicate the existence of different species of mother-plant.

In any event, as the grains are not monosulcate, these three "variant forms" cannot be referred to *Stellatopollis hughesii*, or to the Superret- genusbox (whichever "palynological language" is used). In order to remain logical and to avoid confusion, HUGHES' data-handling system (1976 and subsequent papers) must obviously be applied; these "variant forms" require discrete genusboxes which respectively are: Inapert- [proposed here, in accordance with the recommendations of HUGHES *et alii* (1979)], and Retitri- and Trichoto- (both established by PENNY, 1991). Logically too, trivial names can remain as -*croton*; thus, these "variant forms" belong respectively to these new taxa: biorecord Inapert-*croton*, biorecord (cand) Retitri-*croton* and biorecord (cand) Trichoto-*croton* ["cand" (*for candidate*) between brackets means that too few specimens are available to be acceptable as a full biorecord, after HUGHES *et alii* (1979) and PENNY (1991)].



Figure 13: Tricolporate "variant form": biorecord (cand) Retitri-*croton* (slide Bau 2A – coordinates N33-2). Scale-bar is 10 µm. **Figure 14:** Tricolporate "variant form": biorecord (cand) Retitri-*croton* (slide Bau 4B – coordinates F27-1 – 14a and 14b: respectively low and high focus). Scale-bar is 10 µm.

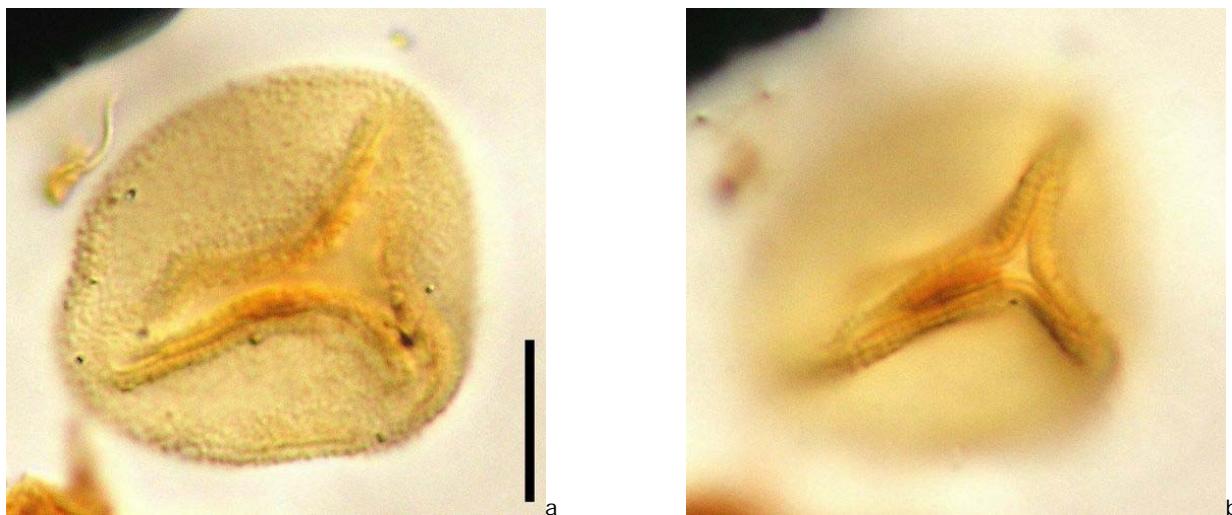


Figure 15: Trichotomosulcate "variant form": biorecord (cand) *Trichoto-croton* (slide Bau 2B – coordinates J31/K31 – 15a and 15b: respectively average and low focus). Scale-bar is 10 µm.

9. Implications about the formation of the Mons Basin

In the Mons Basin, the Wealden facies occur (ROBASZYNSKI *et alii*, 2001):

- in kilometric outcrops (also called "pockets") and in the northern part of this basin as shallow subcrops,
- as the infilling of several sinkholes developed in carbonates and siliciclastic sediments (for example at Bernissart),
- in the east as white sands and sandstones containing lignite and glauconitic material.

Recently YANS *et alii* (2005, 2006) demonstrated that the Wealden facies of the natural pit of Bernissart are of middle Barremian to earliest Aptian in age. A similar age is proposed for the Wealden facies of the "Baudour pocket". If so, subsidence responsible for both the Baudour pocket and the natural pit of Bernissart was contemporaneous and perhaps caused by the same genetic conditions. Deep boreholes drilled in the Mons Basin demonstrated partial and local dissolution of buried anhydrites immediately below the natural pits (DELMER *et alii*, 1982; DELMER, 1989; DUPUIS & VANDYCKE, 1989; ROUCHY *et alii*, 1993). As in other areas, the result of this partial dissolution of deeply buried anhydrites produces local repeated collapse in overlying rocks; this may cause geomorphological depressions or sinkholes at the surface (STANTON, 1966; GUTTIÉREZ, 1996; WARREN, 1999). So natural pits and "pockets" may be the surface expression of deep dissolution.

10. Conclusions

The palynological content of the dinosaur-bearing Wealden facies of the Baudour Clays Formation is reported for the first time. The palynomorphs are of continental origin. Ferns and gymnosperms are the dominant floristic groups. The occurrence of pollen grains of the angiospermous biorecord *Superret-croton*, probable paleotaxon *Superret-subcrot* and probable biorecord *Retisulc-dentat* [*sensu* HUGHES *et alii* (1979) and HUGHES (1994)] denotes a middle Barremian to earliest Aptian age for these sediments, and so they are confirmed to be of the same age as the Wealden facies sediments in the natural pit of Bernissart. This identity in age suggests that the natural pit of Bernissart and the "pocket" of Baudour are the result of the same mechanisms of subsidence, probably thus demonstrating a genetic relationship between natural pits and relatively large "pockets" in the Mons Basin.



Figure 16: Probable paleotaxon *Superret-subcrot* (slide Bau 4B – coordinates L32-L33 – assemblage of two photographs with different foci). Scale-bar is 10 µm.

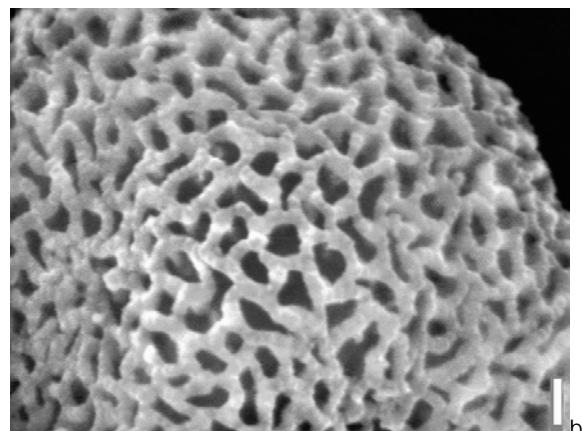
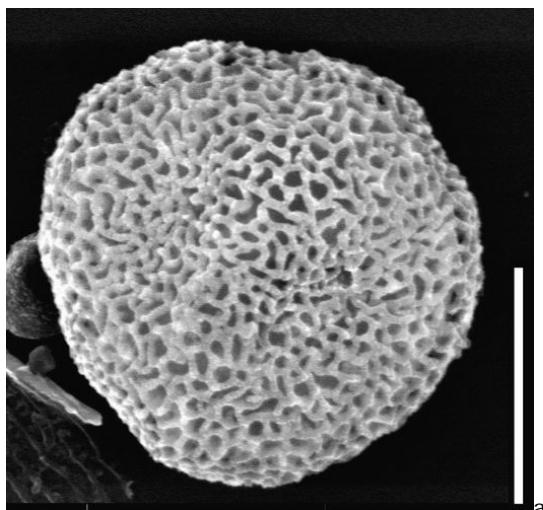


Figure 17: Biorecord *Retisulc-dentat*, presumed proximal face (glass stub 2/2 – 17a and 17b: whole specimen and detail). Scale-bar is 10 µm, except higher SEM magnification (1 µm).

Acknowledgments

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Remarks

The slides and glass stubs will be housed in the Institut Royal des Sciences Naturelles (Brussels).

Note about Figs. 2-6, 9 and 13-16: interferential- differential contrast after NOMARSKI, unmodified photographs; the position of the nine illustrated palynomorphs on each slide is given after the "England Finder".

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Taxa list

The taxa named here follow the morphological scheme instituted by POTONIÉ and KREMP (1954) and subsequently amplified by several palynologists. Biorecords and subordinate records are included, for in the authors' opinion there is no incompatibility.

SPORES AND POLLEN GRAINS

Anteturma Proximegerminantes POTONIÉ, 1970

Turma Triletes-Azonales (REINSCH, 1881) POTONIÉ et KREMP, 1954

Subturma Azonotriletes (LUBER, 1935) DETTMANN, 1963

Infraturma Laevigati, Quasilaevigati (BENNIE et KIDSTON, 1886) POTONIÉ, 1956

Biretisporites potoniaei (DELCOURT et SPRUMONT, 1955) DELCOURT, DETTMANN et HUGHES, 1963

Deltoidospora australis (COUPER, 1953) POCOCK, 1970

Deltoidospora minor (COUPER, 1953) POCOCK, 1970

Dictyophyllidites harrisii COUPER, 1958

Matonisporites equinoxinus COUPER, 1958

Infraturma Apiculati (BENNIE et KIDSTON, 1886) POTONIÉ, 1956

Subinfraturma Baculati DYBOVÁ et JACHOWICZ, 1957

Pilosporites trichopapillosum (THIERGART, 1949) DELCOURT et SPRUMONT, 1955

Subinfraturma Granulati, Scabratii DYBOVÁ et JACHOWICZ, 1957

Concavissimisporites verrucosus (DELCOURT et SPRUMONT, 1955) DELCOURT, DETTMANN et HUGHES, 1963

Subinfraturma Verrucati DYBOVÁ et JACHOWICZ, 1957

Leptolepidites tumulosus (DÖRING, 1964) SRIVASTAVA, 1975

Infraturma Murornati POTONIÉ et KREMP, 1954

Cicatricosisporites baconicus DEAK, 1963

Cicatricosisporites brevilaesuratus (COUPER, 1958) KEMP, 1970

Cicatricosisporites halleyi DELCOURT et SPRUMONT, 1955

Cicatricosisporites hughesi DETTMANN, 1963

Foveotriletes subtriangularis (BRENNER, 1963) PADEN PHILIPS et FELIX, 1970

Klukisporites foveolatus POCOCK, 1964

Retitriletes austroclavatidites (COOKSON, 1953) DÖRING, KREMP, MAI et SCHULZ in KREMP, 1963

Subturma Lagenotriletes POTONIÉ et KREMP, 1954

Infraturma Trifoliati, Barbatii POTONIÉ, 1970

Dijkstraisporites helios (Dijkstra, 1951) POTONIÉ, 1956

Turma Triletes-Zonales (BENNIE et KIDSTON, 1886) POTONIÉ, 1956

Subturma Auritotriletes POTONIÉ et KREMP, 1954

Infraturma Auriculati (SCHOPF, 1938) DETTMANN, 1963

Rouseisporites reticulatus POCOCK, 1962

Trilobosporites apiverrucatus COUPER, 1958

Trilobosporites hannonicus (DELCOURT et SPRUMONT, 1955) POTONIÉ, 1956

Infraturma Appendiciferi POTONIÉ, 1956

Appendicisporites erdtmanii POCOCK, 1965

Appendicisporites stylosus (THIERGART, 1954) DEAK, 1963

Infraturma Tricrassati DETTMANN, 1963

Camarozonosporites insignis NORRIS, 1967

Sestrosporites pseudoalveolatus (COUPER, 1958) DETTMANN, 1963

Subturma Zonotriletes WALTZ, 1935

Infraturma Cingulati (POTONIÉ et KLAUS, 1954) DETTMANN, 1963

Foraminisporis asymmetricus (COOKSON et DETTMANN, 1958) DETTMANN, 1963

Subinfraturma Euzonati, Coronati POTONIÉ, 1970

Aequitriradites spinulosus (COOKSON et DETTMANN, 1958) COOKSON et DETTMANN, 1961

Turma Vestitriletes POTONIÉ, 1970

- Suprasubturma Perinotrilites (ERDTMAN, 1947) DETTMANN, 1963
- Crybelosporites pannuceus* (BRENNER, 1963) SRIVASTAVA, 1975
- Anteturma Variegerminantes POTONIÉ, 1970
- Turma Saccites ERDTMAN, 1947
- Subturma Monosaccites (CHITALEY, 1951) POTONIÉ et KREMP, 1954
- Infraturma Saccizonati BHARADWAJ, 1957
- Applanopsis dampieri* (BALME, 1957) DÖRING, 1961
- Subturma Disaccites COOKSON, 1947
- Parvisaccites radiatus* COUPER, 1958
- Turma Aletes et Kryptoperturates POTONIÉ, 1966
- Subturma Azonoletes (LUBER, 1935) POTONIÉ et KREMP, 1954
- Infraturma Granulonapiti, Retinapiti (COOKSON, 1947) POTONIÉ, 1975
- Araucariacites australis* (COOKSON, 1947) COUPER, 1953
- Biorecord Inapert-croton (this study)
- Infraturma Circumpollini (PFLUG, 1953) KLAUS, 1960
- Classopollis* sp.
- Turma Plicates (NAUMOVA, 1939) POTONIÉ, 1960
- Subturma Costates POTONIÉ, 1970
- Infraturma Costati POTONIÉ, 1970
- Ephedripites montanaensis* BRENNER, 1968
- Ephedripites zaklinskaiae* AZÉMA et BOLTHAGEN, 1974
- Subturma Trichotomocolpates, Trichotomosulcates (ERDTMAN, 1954) POTONIÉ, 1970
- Infraturma Eutrichotomosulcati POTONIÉ, 1970
- Biorecord (cand) Trichoto-croton (this study)
- Subturma Monocolpates (Monosulcites) & Zonocolpates POTONIÉ, 1970
- Infraturma Quasilaevigati & Microsculptati POTONIÉ, 1970
- Cycadopites minimus* (COOKSON, 1947) POCOCK, 1970
- Infraturma Reticulati PONS, 1988
- Biorecord Retisulc-dentat (in HUGHES, DREWRY et LAING, 1979)
- Infraturma Sculptati POTONIÉ, 1970
- Biorecord Hauterivian-cactisulc (in HUGHES et McDougall, 1987)
- Biorecord Superret-croton (in HUGHES, DREWRY et LAING, 1979)
- Paleotaxon Superret-subcrot (in HUGHES, DREWRY et LAING, 1979)
- Subturma Tricolpates, Triptyches POTONIÉ, 1970
- Infraturma Heterotricolpati, Praecolpati POTONIÉ, 1970
- Eucommiidites minor* GROOT et PENNY, 1960
- Eucommiidites* sp. in KEMP, 1970
- Infraturma Isotricolpati POTONIÉ, 1970
- Biorecord (cand) Retitri-croton (this study)

VARIA

"Algae" zygosores:

Ovoidites parvus (COOKSON et DETTMANN, 1959) NAKOMAN, 1966

Schizosporis reticulatus (COOKSON et DETTMANN, 1959) PIERCE, 1976

Incertae sedis (perispore scrap ?):

Dictyothylakos sp. in SINGH, 1964

**Quelques implications paléoclimatiques
de l'observation de bois fossiles du Wealdien
du bassin de Mons (Belgique) - Résultats préliminaires**

**[Observations on Wealden fossilised wood from the Mons Basin (Belgium)
and their palaeoclimatic implications – Preliminary results]**

Thomas GERARDS¹

Johan YANS²

Philippe GERIENNE³

Citation: GERARDS T., YANS J. & GERIENNE P. (2007).- Quelques implications paléoclimatiques de l'observation de bois fossiles du Wealdien du bassin de Mons (Belgique) - Résultats préliminaires. In: STEEMANS P. & JAVAUX E. (eds.), Recent Advances in Palynology.- Carnets de Géologie / Notebooks on Geology, Brest, Mémoire 2007/01, Résumé 04 (CG2007_M01/04)

Mots-Clefs : Paléoclimatologie ; Crétacé ; Wealdien ; bois ; fossiles ; cernes

Abstract: Tree growth, including radial growth, is controlled by a complicated combination of climate-related factors. In seasonal climates many species of trees form clearly defined annual growth rings. Quantitative and qualitative analyses of growth rings are high resolution proxies of ancient environments, thus facilitating studies of past climates. We have applied this method to growth rings of early Cretaceous softwood branches from the Wealden facies of the Mons Basin, Belgium. Preliminary results confirm that during the early Cretaceous, the Mons Basin was located at 30-35°N, presumably in a tropical climate, with a succession of marked dry and wet seasons (KOEPPEN's climate type Aw). The Mean Sensitivity coefficient (the difference in a sequence of rings of the widths of consecutive ring pairs /average ring width) is high (above 0.4), and indicates unstable palaeoenvironmental conditions.

Key Words: Palaeoclimatology; Cretaceous; Wealden; wood; fossils; growth-rings

Introduction

La relation qui existe entre certains caractères du bois, et plus particulièrement les cernes de croissance, et le climat est connue depuis de nombreuses années (DOUGLASS, 1936). Les caractères des cernes de croissance peuvent donc être utilisés pour obtenir des informations climatiques (DOUGLASS, 1936 ; FRITTS, 1976). Le caractère le plus simple à observer est l'épaisseur de chaque cerne de croissance. Cette mesure permet de calculer la sensibilité moyenne (SM) du spécimen étudié, c'est-à-dire la variabilité interannuelle de la largeur des cernes (FRITTS, 1976). La SM nous donne des informations sur la variabilité de la croissance (essentiellement liée aux conditions climatiques) et se calcule selon la formule de la Figure 1.

$$SM = \frac{1}{1-n} \sum_{t=1}^{t=n-1} \left| \frac{2(X_t + 1 - X_1)}{X_t + 1 + X_1} \right|$$

Figure 1 : Formule de la sensibilité moyenne. SM est la sensibilité moyenne. X₁ est la largeur d'un cerne donné et X_{t+1} est la largeur du cerne qui le suit.

Figure 1: Calculation of mean sensitivity. SM is the mean sensitivity. X₁ is the width of a given ring and X_{t+1} is the width of the following ring.

Par ailleurs, CREBER et CHALONER (1984) ont défini 6 catégories de cernes de croissance en fonction du type de transition entre bois précoce (dans un cerne, bois produit en début de période de végétation) et tardif (dans un

¹ Laboratoire de Paléobotanique, Paléopalynologie et Micropaléontologie, Université de Liège, Allée du 6 août, B18, Sart-Tilman, 4000 Liège (Belgium)
tgerards@hotmail.com

² Facultés Universitaires Notre Dame de la Paix (FUNDP), rue de Bruxelles 61, 5000 Namur (Belgium)
Johan.Yans@fundp.ac.be

³ Laboratoire de Paléobotanique, Paléopalynologie et Micropaléontologie, Université de Liège, Allée du 6 août, B18, Sart-Tilman, 4000 Liège (Belgium)
p.gerrienne@ulg.ac.be

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cerne, bois produit en fin de période de végétation) et des proportions relatives de ces deux types de bois. Leur classification (Fig. 2) est basée sur la présence (Types A-E) ou l'absence (Type O) de cernes, sur le rapport d'épaisseur entre le bois précoce et le bois tardif et sur le mode de transition entre bois précoce et tardif (graduel ou abrupt). La distinction entre 6 types de cernes (comme préconisée par CREBER et CHALONER, 1984) est difficile et non essentielle pour tirer de leur observation des informations climatologiques. Le regroupement en supertypes semble plus judicieux. Ainsi, les types A-E peuvent être regroupés en 2 supertypes (sur base de la proportion bois précoce-bois tardif) en conservant le type O (BRISON *et alii*, 2001) :

- "Supertype ABC" : cerne dont la proportion bois tardif/ bois précoce est élevée
- "Supertype DE" : cerne dont la proportion bois tardif/ bois précoce est faible
- "Type O" : Pas de cernes

BRISON *et alii* (2001) ont étudié 643 spécimens de bois fossiles mésozoïques et ont montré qu'il faut tenir compte de l'affinité taxonomique des spécimens sur lesquels on réalise des études de cernes à des fins (paléo-) climatologiques. En effet, certains taxons (par exemple *Agathoxylon* (HARTIG)) présentent toujours le même type de cerne quelque soit le climat sous lequel ils ont poussé. Donc si la xyloflore est monogénérique à *Agathoxylon*, on aura aucun signal climatique quel que soit le nombre de spécimens observés. Si l'on veut s'affranchir de cette précaution, il faudra alors observer le type de cerne d'un grand nombre de spécimens appartenant à des genres différents d'une même localité pour en tirer des informations d'ordre climatique.

Cet article a pour objectif de donner quelques informations d'ordre paléoclimatologique tirées de l'observation de branches (ou axes de diamètre réduit) fossiles carbonisées du Crétacé inférieur de Belgique.

Contexte géologique et chronostratigraphique

Les bois fossiles carbonisés proviennent des sédiments argilo-sableux "à faciès wealdien" de la carrière Danube-Bouchon à Hautrage (Bassin de Mons, Belgique ; ROBASZYNSKI *et alii*, 2001 ; YANS, sous presse). Ces sédiments sont exclusivement continentaux. Aucun microfossile marin n'est présent dans ces sédiments (MARLIÈRE, 1946). Une étude palynologique de cette localité indique un âge barrémien moyen à aptien basal (YANS *et alii*, 2005, 2006 ; DEJAX *et alii*, sous presse).

Résultats et discussion

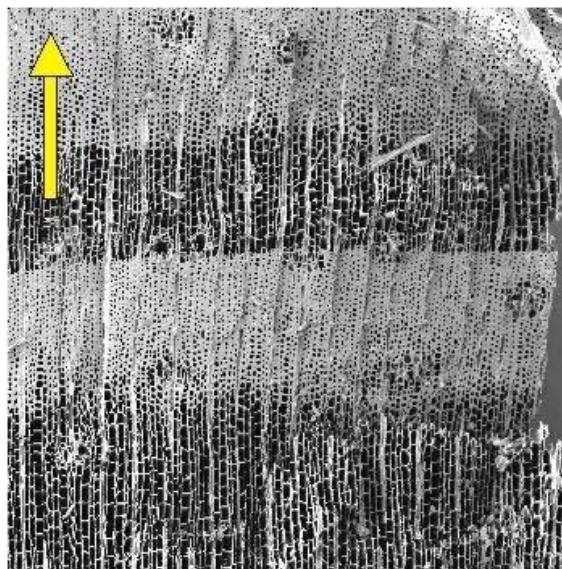
Quarante-deux spécimens de bois fossiles carbonisés ont été étudiés. La largeur moyenne des cernes est de 1,91 mm. Une majorité de spécimens présentent des faux cernes, dans un rapport moyen d'un faux cerne pour vingt vrais cernes. Deux spécimens (soit 4,76% des spécimens étudiés) ont des cernes de type ABC, trente-quatre spécimens (soit 80,95%) ont des cernes de type DE et 6 spécimens (soit 14,28%) ont des cernes de type O. Nous avons comparé (Fig. 3) la répartition des spécimens d'Hautrage parmi les 3 supertypes avec la répartition des différents supertypes en fonction de la paléolatitude au Crétacé inférieur proposée par BRISON *et alii* (2001). La proportion des trois supertypes de notre échantillonnage est intermédiaire entre la répartition caractéristique de latitude 25-35°N et de la répartition caractéristique de 35-45°N. La paléolatitude du bassin de Mons au Crétacé inférieur serait donc d'environ 35°N.

Par ailleurs, la présence de cernes de croissance chez plus de 85% des spécimens indiquerait plutôt un climat saisonnier. Dans 80,95% des cas, ces cernes sont de type DE caractérisés par un rapport bois tardif/ bois précoce très faible (plusieurs dizaines de rangées de cellules de bois précoce et 3 à 4 rangées de cellules de bois tardif). Ce type de cerne est généralement caractéristique d'arbre soumis à un climat à 2 saisons bien marquées (CREBER et CHALONER, 1984). Les seuls climats actuels qui comportent 2 saisons marquées sont les climats de type boréal et de type tropical. La paléolatitude du bassin de Mons au Crétacé était de 35° N (SCOTESE, 2000). Ceci permet d'écartier le climat de type boréal. Le climat qui régnait à Hautrage au Crétacé inférieur était donc vraisemblablement un climat de type tropical avec des saisons bien marquées : une saison des pluies et une saison plus sèche.

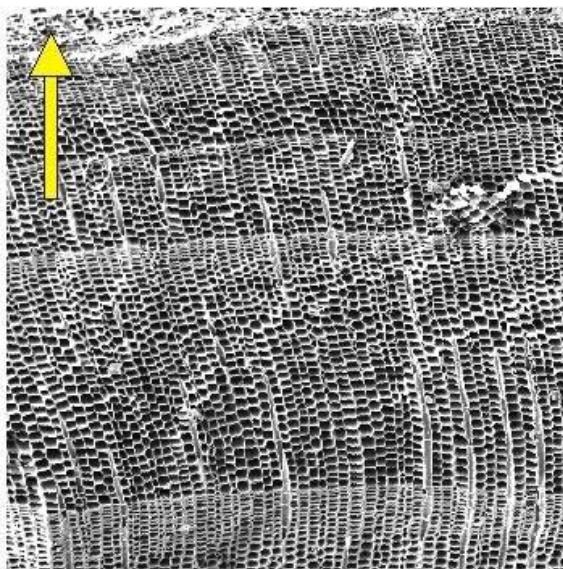
► **Figure 2** : Vues au microscope électronique à balayage des 6 types de cernes de croissance. Types A, B et C : cerne dont la proportion bois tardif/bois précoce est élevée ; types D et E : cerne dont la proportion bois tardif/bois précoce est faible ; type O : pas de cernes. Type A : *Keteeleria fortunei* HORT. (récolté en Chine), type B : *Cryptomeria japonica* D. DON. (Belgique), type C : *Thujopsis dolobrata* SIEBOLD et ZUCC. (Japon), type D : *Pilgerodendron uviferum* FLORIN (Chili), type E : *Fokienia hodginsii* A. HENRY et H.H. THOMAS (Chine).

Les flèches montrent l'extérieur des axes.

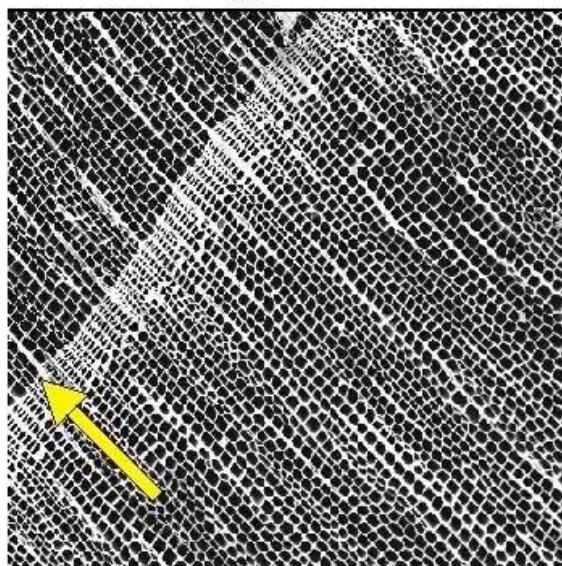
► **Figure 2:** Scanning electron microscope views of the six types of growth rings. Types A, B and C: rings in which the proportion of late wood to early wood is high; types D and E: rings in which the proportion of late wood to early wood is low; type O: no rings. Type A: *Keteeleria fortunei* HORT. (collected in China), type B: *Cryptomeria japonica* D. DON. (Belgium), type C: *Thujopsis dolobrata* SIEBOLD and ZUCC. (Japan), type D: *Pilgerodendron uviferum* FLORIN (Chile), type E: *Fokienia hodginsii* A. HENRY and H.H. THOMAS (China). The arrows indicate the exterior of the axes.



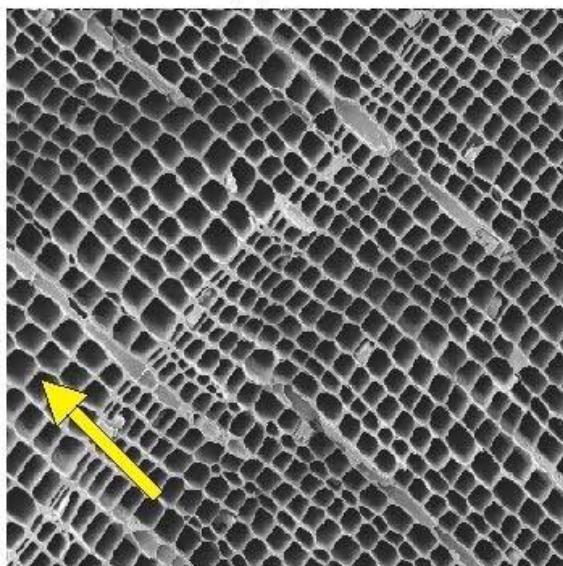
Type A



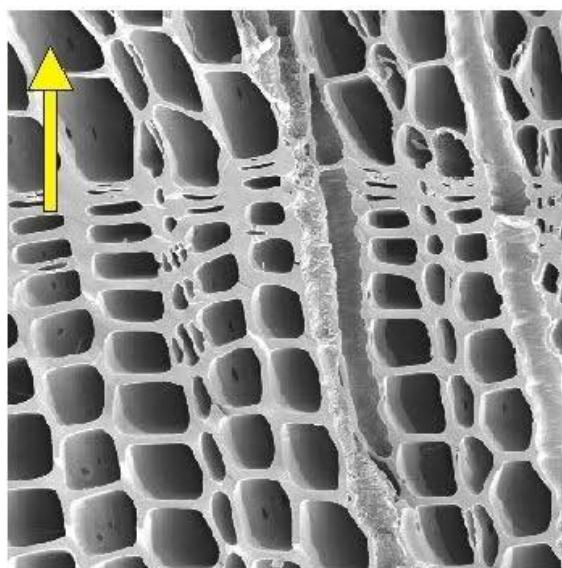
Type B



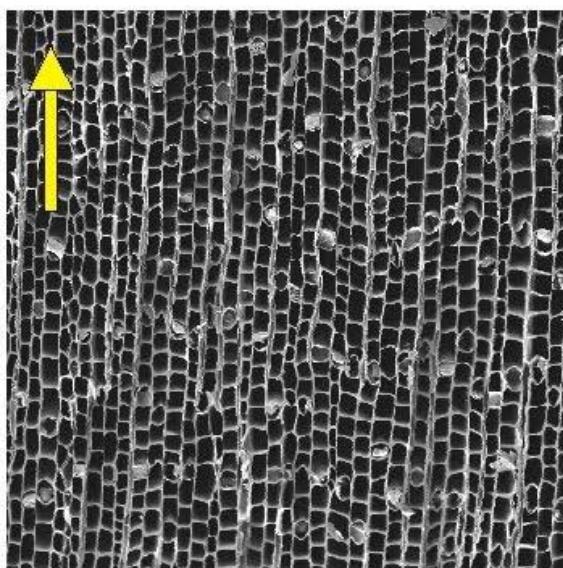
Type C



Type D



Type E



Type O

KÖEPPEN (1936) définit 3 sous-catégories de climats tropicaux : climat humide dépourvu de saisons (Af), climat de type "Savane" avec une saison sèche en hiver (Aw) et climat de mousson (Am). Le premier type de climat (Af) peut être écarté puisqu'il ne présente pas de saison et que 85,71% des bois d'Hautrage présentent des cernes de croissance. Les deux autres types de climat (type savane – Aw et type mousson - Am) présentent des saisons et peuvent être envisagés.

Aucune des conditions nécessaires à l'existence d'un climat de type mousson n'étaient réunies en Europe occidentale au Crétacé inférieur. En effet, la paléolatitude du Bassin de Mons au Crétacé inférieur est d'environ 35°N et non comprise entre 15 et 30°N. L'Europe à cette époque était un archipel et donc les masses continentale n'étaient pas suffisantes pour créer le gradient thermique indispensable à la formation des vents de moussons. Enfin, les reliefs ne dépassaient probablement pas 1000 m (Fig. 4). La thèse d'un climat de mousson semble être à écarter.

Reste le climat de type savane (au sens régime pluviométrique/ température). Cette hypothèse a, par ailleurs, déjà été émise par Bommer (*in* CASIER, 1978) qui évoque "une sorte de savane sur les grands plateaux houillers". Une végétation de type savane est propice aux incendies : la présence d'un biome

de type savane permettrait d'expliquer la grande quantité de restes végétaux carbonisés présents dans les sédiments wealdiens du Bassin de Mons.

Globalement, la sensibilité moyenne de nos spécimens est relativement élevée : 0,42. La valeur minimale de SM est de 0,32 et la valeur maximale calculée est de 0,55 (écart type : 0,09). Des arbres pour lesquels les valeurs de SM sont supérieures à 0,3 sont dits "sensibles" ; ceci témoigne d'une variabilité interannuelle importante de la largeur des cernes et donc de conditions climatiques relativement instables.

Contrairement à une idée largement répandue, les climats tropicaux (du moins aujourd'hui) sont très diversifiés. Seuls 10% des zones intertropicales sont recouverts par des forêts pluviales soumises à un climat dépourvu de saisons. Les 90% restants sont soumis à un climat saisonnier. Sous ces climats saisonniers tropicaux, le début d'une saison est peu prévisible et peut varier de plusieurs mois d'une année à l'autre. De plus, la pluviosité durant la saison des pluies peut varier du simple au double d'une année à l'autre (PFEFFERKORN, 1995). Il n'est donc pas étonnant que les arbres découverts à Hautrage aient, semble-t-il, grandi dans des conditions climatiques relativement instables.

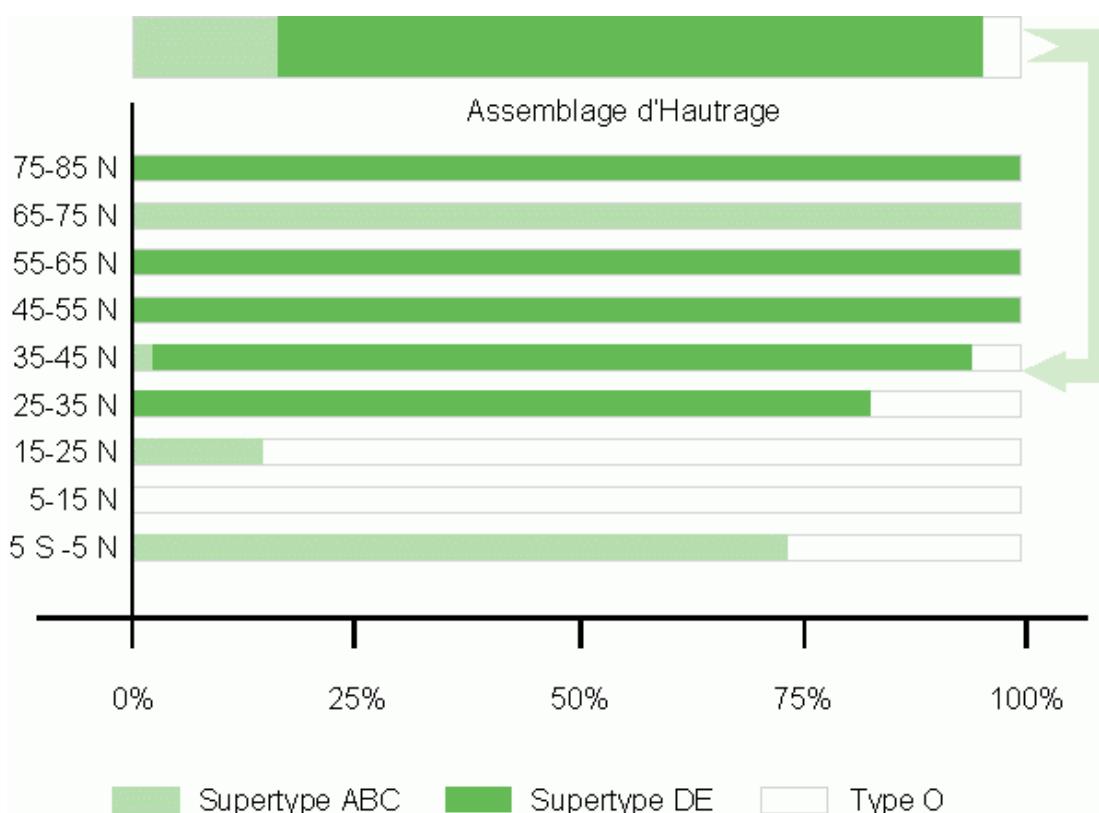


Figure 3 : Répartition des 3 supertypes de cernes de croissance en fonction de la paléolatitude au Crétacé inférieur (d'après BRISON *et alii*, 2001, modifié). Les proportions des différents supertypes de cernes observés sur les bois d'Hautrage indiquent une paléolatitude d'environ 35°N (cf. flèche).

Figure 3: Distribution of the 3 supertypes of growth rings in relation to their paleolatitude during the Early Cretaceous (after BRISON *et alii*, 2001, modified). The relative proportions of the several supertypes of rings in the woods from Haufrage indicate a paleolatitude of about 35°N (see arrow).

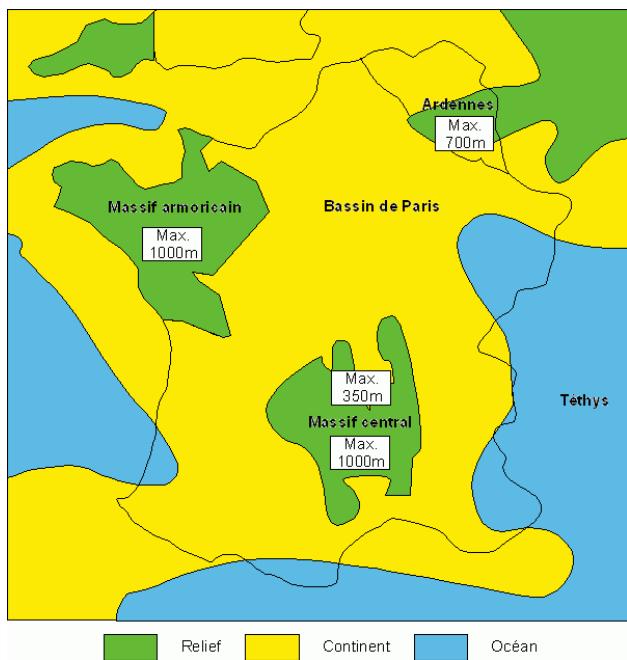


Figure 4 : Carte paléogéographique du Crétacé inférieur de l'Europe occidentale il y a 120 millions d'années (d'après THIRY *et alii*, 2006, modifiée). Cette carte montre les principaux reliefs de l'époque. Ces reliefs ne dépassent pas 1000 m d'altitude. Notez également l'invasion marine de l'océan Téthys.

Figure 4: Paleogeographic map of the lower Cretaceous of western Europe, 120 million years ago (after THIRY *et alii*, 2006, revised). This map shows the principal reliefs at that time. These reliefs do not exceed 1000 m in elevation. Also note the extent of the marine incursion of the Tethys ocean.

La présence de faux cernes chez les spécimens d'Hautrage renforce encore l'hypothèse d'un climat relativement instable. Sous ce type de climat soumis à une alternance marquée de saisons sèches et humide, la présence de faux cernes témoigne probablement de périodes relativement longues sans précipitations durant la saison des pluies. Enfin, la largeur moyenne des cernes tend à montrer que les arbres ont grandi dans de bonnes conditions. En effet, la valeur de largeur moyenne des cernes des spécimens d'Hautrage (1,91mm) est proche de la valeur moyenne de cernes de branches de *Pinus Sylvestris* modernes poussant en Ardenne dans des conditions favorables à environ 400m d'altitude (1,78mm, n=351, s=1,1 ; travail en cours à Liège).

Il est en théorie possible de tirer des informations d'ordre climatologique en comparant les associations végétales présentes à une période géologique donnée avec les associations végétales d'aujourd'hui. Ce concept repose sur l'hypothèse qu'un végétal fossile a probablement grandi, à l'époque, dans des conditions écologiques comparables à un végétal actuel taxonomiquement proche.

Les spécimens d'Hautrage ne sont pas tous déterminables, mais nous avons identifié les taxons ligneux suivants : *Agathoxylon* (HARTIG), *Circoporoxylon* (R. KRAUSEL) (taxonomiquement proche du *Podocarpoxylon* (W. GOTTHAN)), *Pinuxylon* (W. GOTTHAN), *Podocarpoxylon* (W. GOTTHAN) et *Taxodioxylon* (HARTIG). Cet assemblage est notamment proche de celui décrit par FALCON-LANG et CANTRILL (2000) sur le site d'Alexander Island (Antarctique, Albien supérieur), qui comporte les taxons suivants : *Araucarioxylon* (genre invalide), *Podocarpoxylon*, *Taxodioxylon*. Ceci suggérerie qu'au Crétacé inférieur, les climats de l'Antarctique et de l'Europe (alors à 35°N) étaient identiques. Ceci pourrait être expliqué par un effet de serre. En effet, durant une période à effet de serre, le climat de la planète est homogène et les zones à climat tropical s'étendent jusqu'aux régions boréales, au-delà de 60° N ou S (ZIEGLER, 1990). Cela semble avoir été le cas au milieu du Crétacé (*sensu* CROWLEY et NORTH, 1991), pendant lequel la concentration atmosphérique en CO₂ aurait été 5 à 10 fois plus importante qu'aujourd'hui (LEOPOLD, 1964 ; BERNER *et alii*, 1983 ; LASAGA *et alii*, 1985).

Conclusions

La paléolatitude déterminée sur base des assemblages de cernes est d'approximativement 35°N pour le Bassin de Mons au Crétacé inférieur. Ceci concorde avec les reconstitutions paléogéographiques communément admises (SCOTSESE, 2000). Le Bassin de Mons au Crétacé inférieur semble avoir été soumis à un climat tropical de type savane. Ce climat présentait deux saisons bien marquées : une saison sèche et une saison des pluies. Les conditions dans lesquelles ont grandi les arbres étaient relativement bonnes quoique relativement variables d'année en année. L'instabilité climatique peut s'expliquer par le fait que les saisons des climats tropicaux peuvent être extrêmement variables d'une année à une autre tant du point de vue temporel (début et fin des saisons) que du point de vue des régimes pluviométriques. Ce type de climat à une latitude aussi élevée peut s'expliquer par l'effet de serre très marqué auquel la Terre était soumise à cette époque.

Ce travail tend à montrer que l'observation des bois fossiles et plus particulièrement de leurs cernes de croissance permet de tirer des informations paléoclimatologiques même pour des temps aussi reculés que le Crétacé inférieur puisque les résultats obtenus concordent avec les reconstitutions paléogéographiques et paléoclimatologique de l'Europe occidentale au Crétacé inférieur de nombreux auteurs.

Remerciements

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Advances in Ediacaran biostratigraphy in Australia

[Récent développement dans la biostratigraphie de l'Édiacarien de l'Australie]

Kathleen GREY¹

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Key Words: Biostratigraphy; palynology; acritarchs; Ediacaran; Australia; Acraman impact

Mots-Clefs : Biostratigraphie ; palynologie ; acritarches ; Édiacarien ; Australie ; impact d'Acraman

Introduction

Despite the effort devoted to studying the Archean and Proterozoic fossil record, there has been only limited progress in developing zonal schemes similar to the ones well established for the Phanerozoic. In part, this reflects taxonomic uncertainty, morphological simplicity, slow rates of evolution, and sporadic distribution patterns during the Proterozoic, as well as perceptions that species diversity is restricted. However, the slow advance is also caused by a lack of rigorous biostratigraphic analysis. With the establishment of the Ediacaran System and Period, and recent discussions by the International Stratigraphic Commission to move away from the current chronometric scheme, the need for biostratigraphic subdivision has increased. In Australia, demands for improved Neoproterozoic correlation to assist the exploration industry and the discovery of well-preserved acanthomorphs in drill cores has encouraged biostratigraphic studies of Australian Ediacaran successions (GREY, 2005). This paper presents a review of some of the advances made to date.

Background

Analyses of more than 900 samples from 20 drillcores and 10 field sections in the Centralian Superbasin and Adelaide Rift Complex showed the feasibility of biostratigraphic correlation based on large, morphologically complex, acanthomorph acritarchs. Abundance, complex morphology, wide lithological and geographical distribution, and restricted time ranges make acritarchs ideal biostratigraphic tools.

Preparation techniques are critical to successful results. ZANG & WALTER (1992) demonstrated that samples need gentle treatment (i.e. minimal crushing and no centrifuging) to extract large (>200 µm in diameter), brittle process-bearing acritarchs. Zang obtained good assemblages by processing up to 1 kg of material per sample, but this approach has limitations for biostratigraphy and

taphonomic analysis. Refinement of techniques allowed preparation of smaller samples, enhanced specimen recovery, and provided tighter biostratigraphic and palaeoenvironmental control (GREY, 1999, 2005).

Results

Well preserved assemblages were obtained from the Officer and Amadeus Basins (Centralian Superbasin); less well preserved samples have been obtained from the Stuart Shelf. Unfortunately, all samples processed so far from the Adelaide Rift Complex, and in particular from the section above the Global Stratotype Section and Point (GSSP) for the Ediacaran showed high levels of thermal maturity and those from the Georgina Basin are badly oxidized. Seventy-one identifiable palynomorph taxa were recorded; 44 were fully identified and 27 were assigned tentatively or placed in open nomenclature. The 64 acritarch taxa consist of 49 acanthomorphs, 12 sphaeromorphs, and 4 coenobia. The 26 existing taxa were substantially emended, and 7 new combinations, 26 new species and 6 new genera were described (*Archaeotunisphaeridium*, *Australiastrum*, *Ceratosphaeridium*, *Labruscasphaeridium*, *Pennatosphaeridium*, and *Taedigerasphaera*). Remaining palynomorphs were filaments and problematica. More recent work by WILLMAN *et alii* (in press) has confirmed identifications and stratigraphic distributions in drill holes not previously studied in detail.

Range plots from several Centralian Superbasin drillholes produce consistent patterns suitable for zonation and 2 palynofloras and 5 assemblage zones were recognized by GREY (2005). The older palynoflora, the Ediacaran Leiosphere-dominated Palynoflora (ELP) consists of a single zone, the *Leiosphaeridia jacutica* – *Leiosphaeridia crassa* Assemblage Zone. A four-fold zonation is recognised in the Ediacaran Complex Acanthomorph-dominated Palynoflora

¹ Geological Survey of Western Australia, Department of Industry and Resources, 100 Plain Street, East Perth, 6004 (Australia)
kath.grey@doiwr.wa.gov.au
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(ECAP) consisting of the following (from oldest to youngest): the *Appendisphaera barbata* – *Alicesphaeridium medusoidum* – *Gyalosphaeridium pulchrum* Assemblage Zone; the *Tanarium conoideum* – *Schizofusa risoria* – *Variomargosphaeridium litoschum* Assemblage Zone; the *Tanarium irregulare* – *Ceratosphaeridium glaberosum* – *Multifronsphaeridium pelorum* Assemblage Zone; and the *Ceratosphaeridium mirabile* – *Distosphaera australica* – *Apodastoides verobturratus* Assemblage Zone. Zones are demonstrably independent of lithology, and can be recognised across the Officer and Amadeus Basins and Stuart Shelf despite taphonomic and palaeoenvironmental influences. The acanthomorphs show a marked and rapid increase in abundance, size, morphological complexity, and taxonomic diversity that indicate major diversification and significant evolutionary changes. The acanthomorphs appear to belong to a new, short-lived group of phytoplanktonic green algae that represent resting cyst stages and their first appearance lies about two thirds through the second rise in sea-level after the Marinoan glaciation. The late timing of the diversification suggests it is not an immediate consequence of Snowball Earth.

The possible role of the Acraman impact event

Officer Basin sedimentological studies show at least four, possibly five, basin-slope aprons, each consisting of a succession of fine-grained distal turbidite successions of monotonous mudstone and interbedded siltstone capped by shallow-water carbonate (AROURI *et alii*, 2000). In the second slope apron is an ejecta layer derived from the Acraman impact on the adjacent Gawler Craton (WILLIAMS & WALLACE, 2003). Initially, the ejecta layer was viewed simply as a significant synchronous marker to be used as datum for species distributions in biostratigraphic studies. However, as compilation progressed, a coincidence between the position of the ejecta layer and the first appearance of acanthomorphs became apparent. Lithology before and after the impact is remarkably uniform. An iridium anomaly is associated with the ejecta layer, and there is a marked, short-lived negative excursion in the $\delta^{13}\text{C}$ organic carbon curve that indicates a rapid fall in organic productivity. A subsequent positive excursion coincides with the diversification of the biota (GREY *et alii* 2003; CALVER & LINDSAY, 1998). The negative excursion is present not only in the Officer Basin, Stuart Shelf and Adelaide Rift Complex, where the ejecta layer is present, but also in the Amadeus Basin, where the layer itself has not been recognised. Furthermore, whole-rock organic geochemical analysis has identified significant changes in sterane patterns and series E and F highly branched alkanes (HBA) at the level of the ejecta layer (McKIRDY *et alii* 2006; WEBSTER

et alii 2006). The HBA appear to be molecular fossils of anaerobic fermenting bacteria, and their variable abundance in the Dey Dey Mudstone apparently records a short-lived collapse of primary productivity in the Ediacaran ocean soon after the Acraman impact. The probable encysting lifestyle of the acanthomorphs may account for their survival and subsequent proliferation, whereas leiospheres and bacterial mats were largely destroyed by the impact. The size of a dust cloud generated by the impact is of particular significance for such a scenario. In the case of the Acraman impact, this may have been exceptionally large because land areas were devoid of vegetation and continental surfaces would be more like those of the Moon or Mars.

Conclusions

Evidence of a relationship between the impact event and palynofloral diversification remains circumstantial, but supporting evidence is accumulating. Diversification of the algae, the base of the food chain, may have triggered other significant biotic changes, and further studies are indicated. A large impact could be a plausible explanation for dramatic biospheric changes that are otherwise difficult to explain.

Some taxa resemble those from probably coeval successions in China, Siberia, and northern Europe, suggesting that the proposed zonation scheme has good potential for global application. This zonation will serve as an important tool for the correlation of successions that at present lack both biostratigraphic and geochronological controls. Although there are still some gaps in the record (mainly resulting from barren samples or samples containing highly corroded organic matter), unequivocal evidence for the biostratigraphic usefulness of Australian Ediacaran acritarchs has emerged, and it should now be possible to apply the results on a broader scale in other parts of the world.

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Patterns of diversification in early eukaryotes

[Modes de diversification des premiers Eucaryotes]

Emmanuelle J. JAVAUX¹

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Key Words: Proterozoic; early eukaryotes; diversification

Mots-Clefs : Protérozoïque ; premiers eucaryotes ; diversification

1 - Introduction

The Precambrian includes: the Hadean (4.6 to 4 Ga), the period of solar system formation and Earth accretion; the Archean (4 to 2.5 Ga) when life appeared, and the Proterozoic (2.5 to 0.56 Ga) subdivided into the Paleo-, Meso-, and Neoproterozoic. During this major part of Earth history (about 90%), major environmental changes were registered in the geological record. These events include the step-wise oxygenation of the atmosphere and oceans, meteoritic impacts, supercontinent formation and breakup, and severe glaciations; they may have had a profound effect on the early evolution of the eukaryotes. Several lines of evidence from the geological record, the fossil history and molecular phylogenies can be used to decipher the early record of the domain Eucarya and its evolution.

Genetic material is rarely preserved in the rock record, so paleontologists have to rely on other features to identify microfossils as members of the domain Eucarya. Fossils provide direct evidence of early cells, and document steps in biological and biochemical innovations. Organisms can be preserved by a variety of processes in a range of substrates. Early eukaryotic fossils include: carbonaceous compressions (the organisms are preserved as a thin film of carbon); acritarchs (organic-walled vesicles with unknown biological affinities, they can be extracted from shales using strong acids, or observed in thin sections of shale, chert or phosphorite); multicellular organic-walled organisms (chert, shale); vase-shaped microfossils; molds and casts in sandstone or shale; skeletons preserved in carbonates or phosphorite; and phylogenetically informative molecules (biomarkers and biopolymers preserved in the rocks that provide information about past ecosystems and the evolution of biosynthetic pathways).

Molecular phylogenies yield important information or hypotheses about relationships between clades and their order of branching. However paleobiological data are essential for testing these trees and for constraining the (minimum age of) timing of diversification.

Fossils may also record ancestral forms (and steps in evolution) that might not have any extant relatives. The position of the root of the tree of life is not yet understood. Within the eukaryotic tree, the eukaryotes are divided into several supergroups whose relationships are not well resolved. Lineages thought to have branched early because they seemed to lack mitochondria, actually host derived mitochondrial organelles (EMBLEY & MARTIN, 2006). Nevertheless, calibration of phylogenies using dates from fossils, biomarkers, and isotopes, shows that a major diversification of extant clades occurred in the Neoproterozoic, preceded by a long evolution of eukaryotic fossils starting in the late Archean -as suggested by biomarkers- or in the late Paleoproterozoic, when the oldest eukaryotic microfossils are found (see reviews in JAVAUX, 2006; KNOLL *et alii*, 2006; PORTER, 2004). Superimposing the record of biological innovations and environmental changes on the fossil record might reveal possible explanations of the pattern of diversification in the middle Neoproterozoic, long after the origin of the domain and possible early divergence of major clades in the Paleo- and Mesoproterozoic when eukaryotic fossils of unknown biological affinities are preserved.

As discussed elsewhere (JAVAUX & MARSHALL, 2006; JAVAUX *et alii*, 2003, 2004; MARSHALL *et alii*, 2005), in order to determine the biological affinities of these fossils at the level of domain or beyond, we have defined a set of criteria to differentiate prokaryotic from eukaryotic microfossils and have formulated a methodology combining microscopy and microchemistry of single acritarchs. Fossils can display morphological and ultrastructural features showing a degree of complexity and/or particular features unknown in prokaryotic organisms, therefore pointing to a eukaryotic affinity. Indeed, the wall structure and ornamentation, the presence of processes that extend from the vesicle wall, the presence of excystment structures (openings through which cyst liberate their content), wall ultrastructure and wall chemistry can clarify the biological affinities of organic-walled microfossils at the

¹ Département de Géologie, Université de Liège, Allée du 6 août, B18, Sart-Tilman, 4000 Liège (Belgium)
EJ.Javaux@ulg.ac.be

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level of the domain, and in some cases even at the level of class. Microchemical analyses such as micro infra-red and Raman spectroscopy, secondary ion mass spectrometry, and other techniques applicable to very small samples such as one acritarch can be used to characterize the chemistry of organic microfossils and might even reveal biomolecules specific to extant clades.

One limitation of this approach is the limited knowledge that we have about extant organisms producing fossilizable structures and their morphological, ultrastructural and chemical properties. This approach requires investigation of preservable biological properties and comparative actualistic studies of taphonomic processes affecting diverse organisms in diverse environments (JAVAUX & MARSHALL, 2006).

2 - The fossil record of biological innovations in early eukaryotes

Fossils can inform about the evolution of biological innovations, regardless of their biological affinities, as briefly summarized below (see reviews in JAVAUX, 2006; KNOLL *et alii*, 2006 and reference therein).

- Biomarkers in 2.7 Ga kerogens of the Fortescue Group, Australia, indicate that contemporaneous cells were able to synthesize sterols, requiring a minimum of oxygen.

- Paleo- and Mesoproterozoic macroscopic compressions or mold and cast structures have been compared to algae but this interpretation remains controversial.

- The first ornamented acritarchs are populations of *Valeria lophostriata* recorded in the Paleoproterozoic of China (~1.8 Ga) and Australia (+1.65 Ga). Early Mesoproterozoic acritarchs *Shuiyousphaeridium macroreticulatum*, *Valeria lophostriata*, *Tappania plana*, and *Satka favosa* exhibits a complexity of form observed with TEM, SEM, and light microscopy that is unknown in prokaryotes. Prokaryotes can be large, they can have ornamentation, and they can have preservable walls (at least cyanobacterial sheaths), but no prokaryote currently known has all three (large size, ornamentation, preservable acid-resistant walls) at once. Many eukaryotes do. Therefore, these early microfossils display the characteristics of a eukaryotic grade of organization, and are interpreted as eukaryotes with a sophisticated cytoskeleton. These 1.65-1.3 Ga fossil assemblages record biological innovations such as reproduction by budding, complex ecology, vegetative and resting stages, synthesis of resistant polymers, synthesis of various wall ornamentation including processes, and a moderate diversity.

- The bangiophyte red alga *Bangiomorpha pubescens* is so far the oldest taxonomically resolved eukaryote, and records the evolution of complex multicellularity, cell differentiation, and sexual reproduction, eukaryotic photosynthesis, primary endosymbiosis of a chloroplast ancestor by 1.2-1 Ga. Note that these biological innovations are recorded in this one fossil population of bangiophyte red algae that chronostratigraphy dates at 1.2 Ga-750 Ma. Chemostratigraphy and lithostratigraphy indicate an age closer to 1.2 Ga. However other multicellular photosynthetic eukaryotes also appeared around 1 Ga.

- Upper Mesoproterozoic / Lower Neoproterozoic rocks (and possibly Paleoproterozoic rocks) have yielded biomarkers of alveolates (which include dinoflagellates and ciliates, among other groups).

- *Palaeovaucheria*, a 1 Ga xanthophyte alga, indicates the appearance of stramenopiles (which include diatoms, xanthophytes, and brown algae) and of secondary symbiosis (involving a red alga-like endosymbiont).

- The 750 Ma vase-shaped microfossils provide a firm calibration point for the opisthokonts, the clade that includes animals, fungi and the amoebozoans not to mention direct evidence for heterotrophic eukaryotes and eukaryotic biomineralization, and possibly predation. Cladophorales green algae also appeared, recording again multicellular photosynthetic eukaryotes, and implying earlier evolution and diversification of green algae, as clearly underlined by BUTTERFIELD *et alii* (1994), KNOLL (2003) and other Precambrian paleontologists, but recently misunderstood by TEYSSÈDRE (2006).

- The late Neoproterozoic appearance of animals preserved as calcareous skeletons forming large reefs or as possible animal embryos in phosphorites added another dimension to ecosystems and predation pressure.

- Florideophyte red algae at ~600 Ma record the evolution of a tissue-grade organization (cell differentiation in three dimensions to form a tissue with a specific function).

3 - Diversity patterns

So fossils do provide evidence for the evolution of eukaryotic biology, but their change in diversity might also tell us something about the factors controlling the patterns we see in the fossil record. What are those patterns?

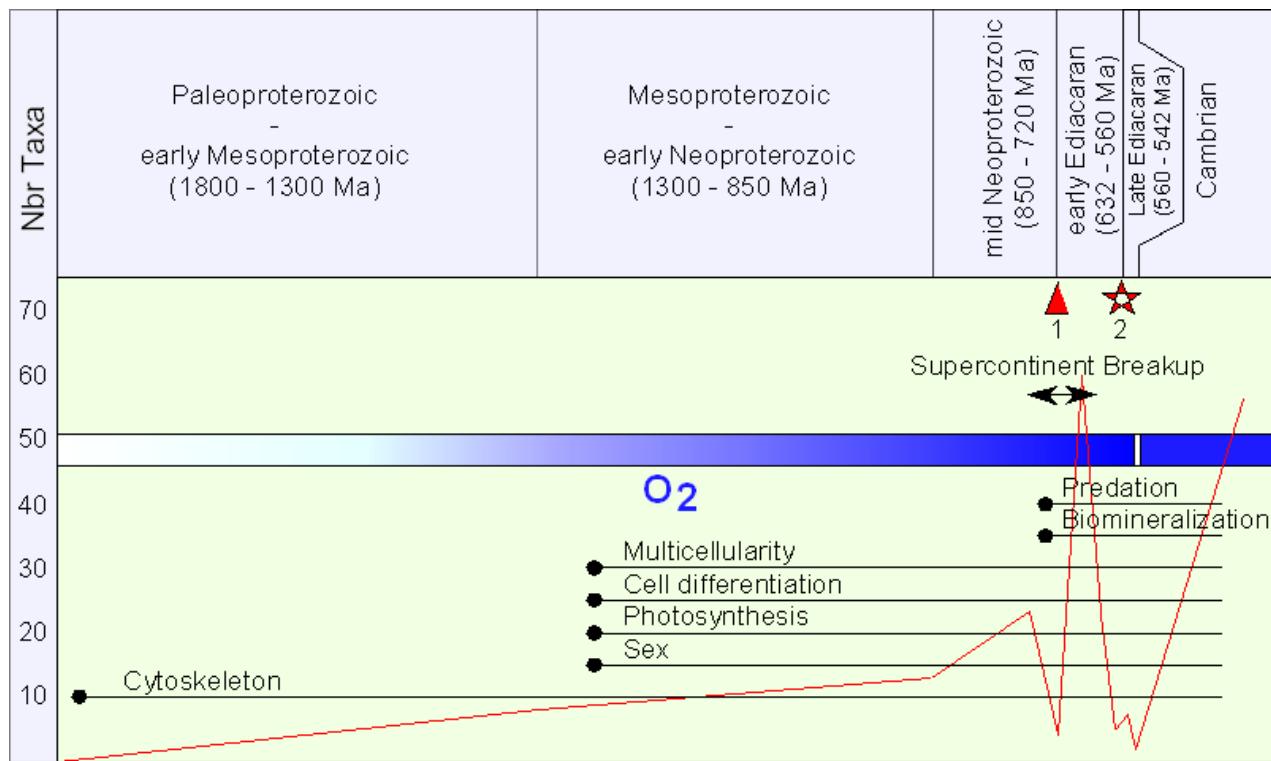


Figure 1: Patterns of early eukaryotic diversification, biological innovations and environmental changes (modified from KNOLL *et alii*, 2006).

This figure shows the general trend of variation in number of eukaryotic taxa (compilation of acritarchs, VSMs, multicellular fossils and macroscopic compressions, data in KNOLL *et alii*, 2006) through the Proterozoic, and the timing of major environmental changes (supercontinent formation and breakup, widespread glaciations, meteorite impact in Australia, and change in oxygenation), and of biological innovations evidenced by the fossil record (JAVAUX, 2006). 1: Glaciations. 2: Acraman impact.

The Figure 1 is a schematic curve drawn from a recent compilation of the number of taxa per assemblage throughout the Proterozoic, including the acritarchs, the VSMs, multicellular microfossils and macroscopic remains (data and references in KNOLL *et alii*, 2006). Of course, the fossil record is incomplete and more discoveries will undoubtedly improve our understanding. Nevertheless, there is a clear trend toward increasing diversity, starting with a low rate of diversity in the late Paleoproterozoic, a modest rate in the Mesoproterozoic-early Neoproterozoic, followed by a sharp increase in the mid and late Neoproterozoic (or early Ediacarian). In the late Ediacarian, diversity decreases before rising again at the Phanerozoic boundary. Between "global" glaciations, the fossil record is sparse and seems to show a big drop in diversity, although this might also result from insufficient sampling and/or gaps in the fossil record.

A closer look at the composition of acritarch assemblages (KNOLL *et alii*, 2006) reveals that earlier assemblages include mostly smooth and ornamented sphaeromorphs, along with a few forms with asymmetrically distributed processes whereas younger assemblages include more diversely ornamented acritarchs and acritarchs with symmetrically distributed processes. In the

Late Ediacarian, acanthomorphs disappear and large leiospheres dominate assemblages. Cambrian assemblages include a renewed diversity of ornamented forms and small acanthomorphs, generally assumed to represent planktonic algal cysts.

4 - Controls on diversification

To understand the factors controlling this pattern of fluctuations in diversity, we can superimpose on the diversity curve, the timing of environmental changes registered in the rock record and the timing of biological innovations evinced in the fossil record.

Three main factors are generally proposed to explain changes in diversity: genetic innovations, ecological innovations and environmental changes.

Since early cells had already all the eukaryotic features typical of their domain by the late Paleoproterozoic and possibly earlier, why did diversity stay modest until the mid-Neoproterozoic?

Sex, complex multicellularity (and cell differentiation) and eukaryotic photosynthesis appeared around 1.2 Ga, well before the increase in diversity around 850 Ma. Glaciations (poorly constrained at ~720-710 and 650-635

Ma) and possibly a transient shallow-water anoxia event at the Precambrian-Cambrian boundary might have cut down some of the diversity, but most clades (the red, green, xanthophyte algae, the fungi, and the amoebae) survived and diversified again in the Phanerozoic. Supercontinent breakup might have increased the surface area of epicontinental seas and modified the cycle of nutrients, thus providing new niches and altering the chemistry of the early oceans. Animal predation pressure might also have played a role in forcing diversification. Some authors suggested that spines on acritarchs could be a defense mechanism against metazoan grazers, and that the modest early acritarch diversity could have resulted from the absence of animals before the Ediacaran (PETERSON & BUTTERFIELD, 2005). However it is also possible that some of these acritarchs record directly the presence of animals as some of them resemble metazoan eggs (KNOLL *et alii*, 2006), but the wall of at least one species (*Tanarium conoideum*) was made of a biopolymer similar to algaenan, thus indicating a green algal affinity (MARSHALL *et alii*, 2005). Finally in Australia a meteoritic impact (so-called Acraman impact) occurred at ~570 Ma, and acritarch assemblages before and after the impact seem to differ (GREY, 2005).

So far, not any one event seems to explain the observed pattern of early eukaryote diversification. More precise dating constraints on environmental changes and the fossil record are needed before drawing conclusions, but probably the three factors (genetics, ecology, environmental changes) were involved.

5 - Conclusions

Early eukaryotes had developed many complex and characteristic cellular and molecular mechanisms by 1.2 Ga, but the diversity of microscopic forms increased only in the middle Neoproterozoic, and a high diversity of macroscopic forms appeared at the end of the Proterozoic era. Despite the unavoidable incompleteness of the fossil record, the observed pattern seems to reflect natural trends. The causes of this relatively late or delayed diversification are probably multiple, including changes in the chemistry of the early atmosphere and oceans and a lack of (or reduced) predation pressure until the Ediacaran when increased oxygenation permitted the evolution of animals (possibly already present) and consequently the complexification of ecosystems (see discussions in PORTER, 2005; PETERSON & BUTTERFIELD, 2005; KNOLL *et alii*, 2006). HUNTLEY *et alii* (2006) examined the evolution of variations in the morphology of acritarch vesicles, processes, process tips, and ornamentation: broadly correlating the observed pattern with environmental (glaciations) and ecological changes (appearance of Ediacaran metazoans and

"Cambrian explosion") but as pointed out above, cause-and-effects relationships may not be so closely connected. Moreover, the authors do not explain the rise in diversity around 850 Ma also detected in their study.

A multidisciplinary approach combining microscopy and microchemistry on both fossils and extant cells may permit a better understanding of the paleobiology of the fossils, and might clarify this pattern of diversification by identifying members of early and later clades, such as the late Neoproterozoic acritarchs (were they animal eggs and/or phytoplankton cysts or something else?). One crucial point to elucidate is whether or not the late diversification reflects diversification between or within clades. Collating the paleobiological data with information from geology and geochemistry regarding paleoenvironments and their evolution, and with insights from molecular phylogeny, we can better understand the evolution of life on our planet and characterize the biosignatures needed for paleobiology and astrobiology.

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Strud: old quarry, new discoveries.
Preliminary report
[Strud : Nouvelles découvertes dans une vieille carrière.
Étude préliminaire]

Cyrille PRESTIANNI¹

Maurice STREEL²

Jacques THOREZ³

Philippe GERRIENNE⁴

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Key Words: Famennian; biostratigraphy; fossil plants; Strud

Mots-Clefs : Famennien ; biostratigraphie ; plantes fossiles ; Strud

1. Introduction

The Strud quarry is located in the uppermost levels of the Dinant Synclinorium, Belgium. It exposes a part of the Upper Famennian (Upper Devonian) "Condroz sandstones", composed mainly of fine-grained, more or less micaceous, arkosic sandstones interlayered with thin shale or siltstone beds and, but rarely, with dolomite beds (these may occur either as evaporites or as immature dolcrete) (THOREZ & DREESEN, 1986).

In Belgium, most of the fossil-bearing beds in "Psammites du Condruz" are found in the Evieux Formation (FAIRON-DEMARET, 1996). The quarry was first investigated by Hock (1878). He mentioned only the presence of remarkably well-preserved specimens of *Rhacophyton condrusorum* CRÉPIN, 1875. STOCKMANS, in 1948, published a monograph on the Upper Devonian plants of Belgium. He described several localities, including Strud. The aim of the present study is to update the data set concerning Strud and to date the quarry correctly.

2. Biostratigraphy

The Strud quarry has been recently and densely sampled for miospores. Two samples have provided a miospore association that preliminary study has indicated surprisingly to be the Lower GF spore biozone characterized by *Grandispora gracilis*-*Grandispora famenensis*. Commonly, this biozone dates the Monfort Formation which in other areas of the Dinant Synclinorium lies below the Evieux Formation. Here, the Evieux Formation is dated by the slightly younger VCo (*versabilis cornuta*) biozone and by the lithology described above.

Taking into account the actual Strud lithology and its miospore association, one may conclude that the sequence exposed in the quarry is in reality facies of an Evieux type and does correspond biostratigraphically to the Evieux Formation as was thought previously: the data clearly demonstrate that the Evieux facies has a diachronous character dependent on Upper Famennian palaeogeography (THOREZ *et alii*, 2006).

¹ FRIA, PhD student, Laboratoire de Paléobotanique, Paléopalynologie et Micropaléontologie, Université de Liège, Allée du 6 août, B18, Sart-Tilman, 4000 Liège (Belgium)
cyrille.prestianni@ulg.ac.be

² Professeur honoraire, Laboratoire de Paléobotanique, Paléopalynologie et Micropaléontologie, Université de Liège, Allée du 6 août, B18, Sart-Tilman, 4000 Liège (Belgium)
maurice.streel@ulg.ac.be

³ Professeur émérite, Département de Géologie, Université de Liège, Allée du 6 août, B18, Sart-Tilman, 4000 Liège (Belgium)

j.thorez@ulg.ac.be

⁴ NFSR Research associate; Laboratoire de Paléobotanique, Paléopalynologie et Micropaléontologie, Université de Liège, Allée du 6 août, B18, Sart-Tilman, 4000 Liège (Belgium)
P.Gerrienne@ulg.ac.be

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3. Fossil remains

The quarry has yielded various fossil remains. An important vertebrate assemblage including a mandible of the early tetrapod *Ichtyostega* (CLÉMENT *et alii*, 2004) has been found. The palaeozoological material found in the quarry is currently under study by Gaël CLÉMENT (Museum d'Histoire Naturelle, Paris).

The outcrop has also yielded plant remains. The first collection was made by F. STOCKMANS before 1950 and is housed at the Institut Royal des Sciences Naturelles de Belgique. The fossils are preserved as strongly oxidized, red- to brown-coloured compressions. The state of preservation does not allow any anatomical study.

| | |
|---|--|
| Zosterophyllopside <i>Barinophyton citrulliforme</i> | Gymnospermes <i>Moresnetia zalesskyi</i> <i>Pseudosporogonites hallei</i> |
| Filicopsidae <i>Zygopteridale</i> <i>Rhacophyton condrusorum</i> | Incertae sedis Cf. <i>Calathiops</i> sp. |

Table 1: Paleofloristic assemblage of Strud as described by STOCKMANS (1948).

| | |
|---|--|
| Progymnospermes <i>Archaeopteris roemeriana</i> | Gymnospermes <i>Moresnetia zalesskyi</i> <i>Pseudosporogonites hallei</i> <i>Condrusia rumex</i> |
| Zosterophyllopside <i>Barinophyton citrulliforme</i> | |
| Filicopsidae <i>Zygopteridale</i> <i>Rhacophyton condrusorum</i> | Incertae sedis Cf. <i>Calathiops</i> sp. <i>Sphenopteris flaccida</i> <i>Sphenopteris modavensis</i> |

Table 2: Paleofloristic assemblage of Strud as determined in this work.

The new collection increases the floristic index of the locality to 9 taxa (Table 2). It shows the presence of nearly all important upper Devonian plant groups: Progymnosperms, Ferns, Gymnosperms and Barinophytes.

Progymnosperms:

Archaeopteris remains are the only representatives of this group (Pl. 1, fig. 1). In contrast with a number of Belgian localities (FAIRON-DEMARET, 1996), *Archaeopteris* remains are rare at Strud. Only three fragments have been recovered. The organisation of their axis and the shape of their leaves are characteristic of the species *Archaeopteris roemeriana* (GÖPPERT) *sensu* STOCKMANS, 1948. This species should probably be synonymised with *Archaeopteris halliana* (GÖPPERT) DAWSON, 1871 (FAIRON-DEMARET *et alii*, 2001).

Ferns:

This group is represented by *Rhacophyton condrusorum* (Pl. 1, fig. 4). It was the first plant to have been described from the quarry

The second collection (Pl. 1, figs. 1-7) is newly collected material and is housed in the collections of the University of Liège. The plants are less well-preserved than the older specimens. This can be explained by the fact that the Strud quarry has not been exploited for more than 100 years. The outcrop has thus been exposed to weathering processes for a long time.

STOCKMANS's floristic index mentions 5 taxa for the quarry. All are classical members of the "Evieux flora" (STOCKMANS, 1948; FAIRON-DEMARET, 1996). This index is summarized in Table 1.

Table 1: Paleofloristic assemblage of Strud as described by STOCKMANS (1948).

(Hock, 1878). The remains of this plant consist of large rachis without fertile parts or vegetative endings. In other beds from the same quarry, Hock (1878) described very fine and well preserved *Rhacophyton* fertile parts.

Spermatophytes:

They consist of three different taxa: *Moresnetia zalesskyi* STOCKMANS, 1948, emend. FAIRON-DEMARET et SCHECKLER, 1987 (Pl. 1, figs. 6-7), *Condrusia rumex* STOCKMANS, 1948 (Pl. 1, fig. 3) and *Pseudosporogonites hallei* STOCKMANS, 1948 (see STOCKMANS, 1948, Pl. XI, fig. 18). *Moresnetia* and *Pseudosporogonites* dominate this assemblage.

4. Discussion

Based on megafossils only, the locality is attributed to Famennian biozone number 7 of EDWARDS *et alii* (2000). If a palynological age of mid GF is confirmed, the locality would represent the earliest occurrence of cupulate early seed plants, if we exclude the poorly understood Russian *Moresnetia* mentioned by JURINA (1988) in the OG Russian Frasnian miospore zone.

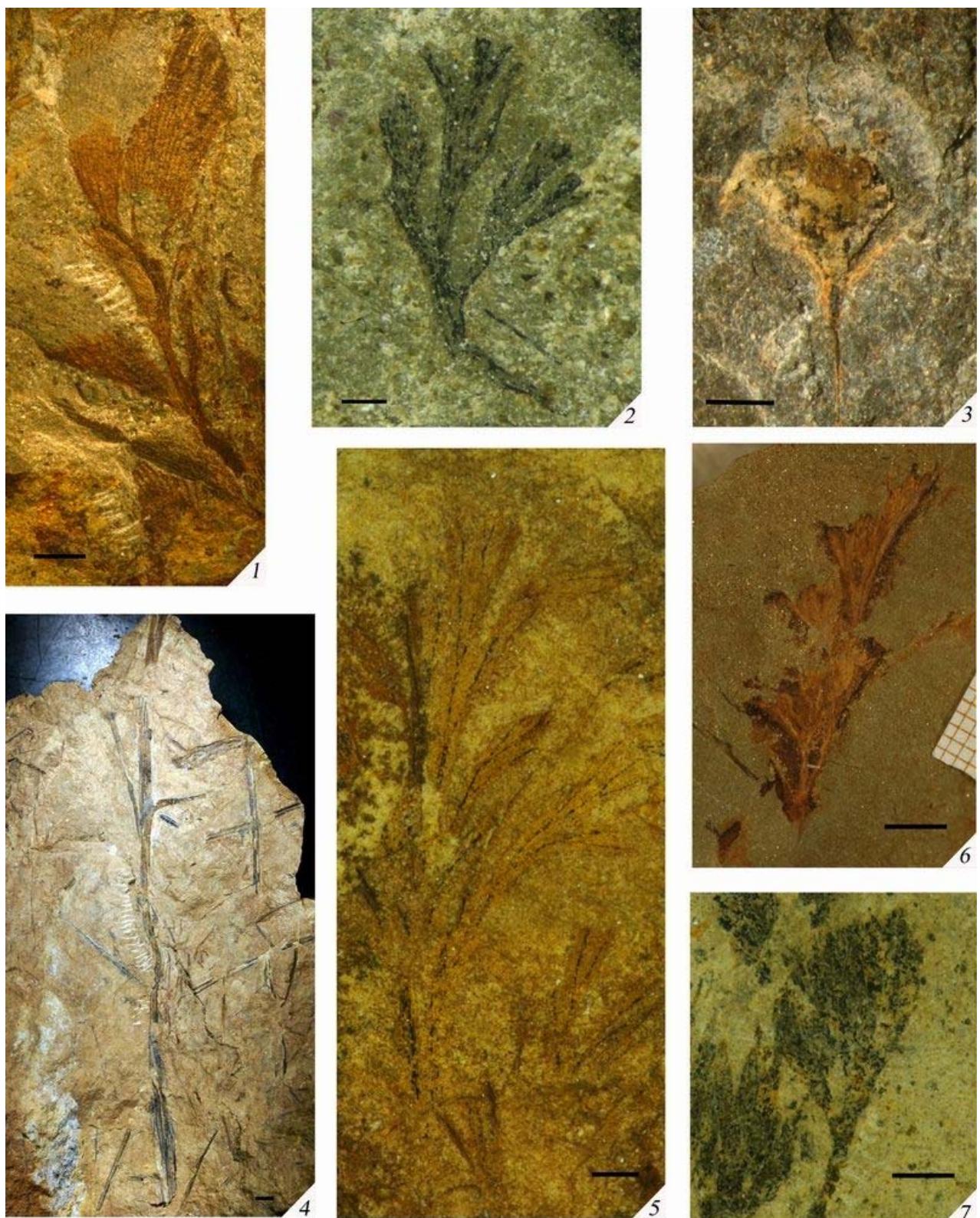


Plate 1:

figure 1. *Archaeopteris roemeriana* (GÖPPERT) STOCKMANS, ULg n° 15201, scale: 0.5 cm.
figure 2. *Sphenopteris modavensis* STOCKMANS 1948, ULg n° 15221, scale: 1 mm.

figure 3. *Condrusia rumex* STOCKMANS, ULg n° 15222, scale 1 mm.

figure 4. *Rhacophyton* sp. CRÉPIN, ULg n° 15203, scale 1 cm.

figure 5. *Sphenopteris flaccida* STOCKMANS 1948, ULg n° 15215, scale 5 mm.

figures 6-7. *Moresnetia zalesskyi* STOCKMANS, ULg n° 15216 and 15217, scales 0.5 mm.

The greatest diversity among the plants observed in the quarry is found in the spermatophytes, represented by 3 very different genera: the classical *Moresnetia zalesskyi*, and the less well-known *Condrusia rumex* and *Pseudosporogonites hallei*. These three seed-plant genera illustrate a wide range of morphological variation both in the cupule and in the integument (FAIRON-DEMARET & SCHECKLER, 1987; PRESTIANNI, 2005; PRESTIANNI *et alii*, 2006a), representing three distinct architectural schemes (HILTON, 1999; PRESTIANNI, 2005).

Such diversity in a group suggests a long evolutionary story. The origin of seed plants is thus presumably to be found earlier in the geological record. The description of the proto-seed *Runcaria heinzellinii* (GERRIENNE *et alii*, 2004), the discovery of a highly diversified Givetian megaspore assemblage (PRESTIANNI *et alii*, 2006b; VILLE de GOYET *et alii*, 2007) and the two seed megaspores *Spermasporites allenii* MARSHALL et HEMSLEY, 2003 and *Granditetrasperites zharkovae* ARKHANGELSKAYA et TURNAU, 2003 are all supplementary indications of the probable Middle Devonian origin of the seed plant lineage.

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PalyWeb: A palynomorph database project on the web

[PalyWeb : un projet de banque de données de palynomorphes sur le web]

Philippe STEEMANS¹

Pierre BREUER²

Key Words: Palynology; database; Internet

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Mots-Clefs : Palynologie ; banque de données ; Internet

Introduction

Since the sixties, palaeopalynology has been experiencing a spectacular growth. Already by the end of 1966, KREMP (*in LENTIN et alii*, 1996) had calculated that about 330 new articles on palynology were published each year in more than 200 journals, and about 4200 had already been published. In a paper published during the 90's, JANSONIUS and MCGREGOR (1996) made an estimation of the number of palynological papers published each year. Although they noted that data are incomplete, around 400 new articles are published annually. Because of this, palynology is a victim of the abundance of published information, which has created taxonomic chaos in some palynological groups. In addition, numerous palynomorphs have been published invalidly, some with redundant names. Several taxa have been described in publications with a limited distribution in other countries or in languages not accessible to most palynologists. Therefore, palynologists were soon convinced that an urgent need existed to create catalogues, or large datasets to manage this mountain of data. The first of these were in a paper format but it rapidly became clear that the solution to the management of palynological data is the use of personal computers. The better known applications for this purpose, like PALYNODATA, DinoSys, etc. are briefly described in LENTIN *et alii* (1996), but there are other projects: for the Palaeozoic, Phytopal for acritarchs and Chitinovosp for Chitinozoans.

The MediaWiki technology

Originally written for the well-known Wikipedia encyclopaedia, MediaWiki is free software accessible on the Internet (<http://en.wikipedia.org/wiki/>), but is now run on other projects of the non-profit Wikimedia Foundation (http://en.wikipedia.org/wiki/Wikimedia_Foundation) and many other wikis. The term wiki is a short form of "wiki wiki" which means something quick or fast in Hawaiian. On the Internet, a wiki is a website that allows users to add, remove, or edit content very quickly and easily.

PalyWeb is a new palynomorph database project based on MediaWiki technology. It is a web-based open-access, free-content palynological database. To our knowledge, it is alone in its mode of data acquisition and management for palynology. It is also the only one to have as an objective the presentation in one dataset of all fossilised palynomorph taxa. Its conception is similar to that of the Wikipedia encyclopaedia, so it can be considered a wiki website. The ease of interaction and operation makes a wiki website an effective tool for collaborative scientific writing. **PalyWeb** is designed to be a database compiled collaboratively by volunteers, and allows most articles to be changed by anyone with access to a computer, a web browser and an Internet connection. However, users must be logged in to avoid vandalism and inconsistency. **PalyWeb** is built with the expectation that over time collaboration among users will improve the quality of the articles.

¹ Laboratoire de Paléobotanique, Paléopalynologie et Micropaléontologie, Université de Liège, Allée du 6 août, B18, Sart-Tilman, 4000 Liège (Belgium)

p.steemans@ulg.ac.be

² Laboratoire de Paléobotanique, Paléopalynologie et Micropaléontologie, Université de Liège, Allée du 6 août, B18, Sart-Tilman, 4000 Liège (Belgium)

piet79@yahoo.fr

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Tetrahedraletes medinensis - PalyWeb - Mozilla Firefox

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Tetrahedraletes medinensis

Tetrahedraletes medinensis Strother & Traverse 1979 [edit]
emend. Burgess 1991, p. 580

This species has been subdivided into two varieties based on size because the original specimens (Strother & Traverse 1979) are much larger than those recorded from the late Ordovician and early Llandovery (e.g. Gray 1988).

Tetrahedraletes medinensis Strother & Traverse 1979, p. x, Pl. X [edit]

Diagnosis: Diagnosis: As for genus but with the added size restriction of 35 to 70 µm tetrad diameter and psilate wall surface.

Type specimen: Slide no. 75-4/ A3, location on slide 43.Bx 107.9mm, reference point 13.3x 109.2mm; Harvard Paleobotanical Collections no. 60289; Plate 1, Figure 5. Collected from Mann Narrows along route 322, northwest of Bumham, Mifflin County, Pennsylvania.

Name derived from the Medina Group of New York State where this species was first found.

Range and Distribution: Power Glenn Formation, Niagara Falls, New York (Gray and Boucot, 1971, Figure 1(h) and Figure 2). Tuscarora Formation. Llandoverian age.

Discussion: Two sample populations were measured from the type slide. Sample 1 (N = 29) had a mean of 54 µm, sample deviation of

Tetrahedraletes medinensis varietes [edit]

Tetrahedraletes medinensis var. *medinensis* Burgess 1991

Tetrahedraletes medinensis var. *parvus* Burgess 1991

Catégories: Cryptospore

This page was last modified 22:47, 9 Apr 2005. This page has been accessed 47 times. About PalyWeb Disclaimers Powered By MediaWiki

Figure 1: Example of a **PalyWeb** page containing the description of the *Tetrahedraletes* genus. Bleu words inside of the descriptive text are links to other pages (bibliographic references or genus description pages).

The **PalyWeb** project is housed on the web server of the University of Liège. A daily backup is carried out to safeguard all information in the event of failure of the system. Its Internet address (URL) is: <http://www.palyweb.ulg.ac.be/wiki/>. To give an estimation of the volume of information that the operating system can manage, the Wikipedia website provides some statistics: on May 2006, Wikipedia had 1,122,525 articles. That number excludes redirects, discussion pages, image description pages, user profile pages, templates, help pages, portals, articles without links to other articles, and pages about Wikipedia. Including these, Wikipedia has 4,154,971 pages. Users have made 53,926,940 edits, an average of 12.98 per page, since July 2002. At that time Wikipedia had 1,395,387 registered user accounts.

The PalyWeb project

PalyWeb is designed to accept the descriptions of a maximum number of published palynomorph taxa available from conventional scientific reviews in accordance with the Botanical and Zoological Nomenclature Codes. **PalyWeb** has been deliberately limited to pre-Mesozoic palynomorphs, the field of research of the authors. It was presented to the scientific community officially at the General meeting in Prague (2006) of the "Commission Internationale de la Microflore du Paléozoïque" (<http://www.cimp.ulg.ac.be/>). **PalyWeb** is not an online medium for publication. New taxa cannot be presented on its website. However, concerning a published species there is no limitation in the number of pages or their length. Text, figures and pictures may be up- and downloaded. Of course, to avoid long delays, pictures may be compressed. It is forbidden to up-load pictures protected by copyright. Navigation through pages may be done by clicking on internal links or by typing keywords in the search engine (e.g. the name of species, etc.).

A screenshot of a Mozilla Firefox browser window displaying the history page for the taxon 'Ambitisporites' on the PalyWeb wiki. The title bar reads 'Ambitisporites - History - PalyWeb - Mozilla Firefox'. The main content area shows a list of 15 previous versions, each with a timestamp, author, and a link to the specific version. The most recent version is by Mariella G. on April 22, 2005. The left sidebar includes a navigation menu with links like 'Main Page', 'Community portal', and 'Recent changes', and a search bar.

| Author | Date | Comments |
|-------------|--------------------|--|
| Mariella G. | 15.21, 22 Apr 2005 | (→ "Ambitisporites" species) |
| Breuer | 12:16, 14 Apr 2005 | |
| | 15:28, 13 Apr 2005 | Palyweb (→ "Ambitisporites" species) |
| | 15:22, 13 Apr 2005 | Palyweb (→ "Ambitisporites" species) |
| | 14:55, 13 Apr 2005 | Palyweb (→ "Ambitisporites" species) |
| | 23:04, 9 Apr 2005 | Palyweb m |
| | 18:36, 7 Apr 2005 | Palyweb m |
| | 10:58, 7 Apr 2005 | Breuer (→ Genus "Ambitisporites" Hoffmeister 1959) |
| | 21:06, 31 Mar 2005 | Palyweb m |
| | 14:41, 30 Mar 2005 | Breuer |
| | 13:44, 30 Mar 2005 | Breuer |
| | 13:43, 30 Mar 2005 | Breuer |
| | 13:41, 30 Mar 2005 | Breuer |

Figure 2: Example of an historic page with the date and the author of the modifications.

At the moment, the database is organized in three sections: the main one hosts the descriptions of taxa previously published in scientific reviews, the second concerns unpublished taxa left in open nomenclature for which information from the **PalyWeb** community is requested, and the third is devoted to enigmatic palynomorphs. The second and third are actually discussion forums, not a part of the database. Of course, this structure is tentative, and can be debated and easily modified. Such flexibility is one of the advantages of a wiki-type website. Each page (article) is articulated around four main components. The first is the "page" itself (Fig. 1) with a title, a name at the top of the screen. The second component is obtained by selecting the heading "to modify" (edit page), where upon the page can be changed immediately, without restrictions. A third component is the heading "discussion", where **PalyWeb** users can exchange their ideas on the contents of the pages. The last component is the "history" of pages (Fig. 2). All former versions of the pages are stored with the user names, the authors of its modifications. Each previous version can be restored (a very useful tool as this procedure

prevents mistakes and allows the evolution of the page content to be followed in accordance with modifications made by various contributors).

The general architecture of the website is illustrated on Figure 3 using as an example the organization of a page concerning the cryptospore genus *Tetrahedraletes*. The words in blue are internal links to existing pages. The words are in red when a link has been created but the page to be linked does not yet exist. All words useful for indicating relationships within the database can be converted into links to other **PalyWeb** pages (external links are also possible). Most of the connexions in the example link to taxonomic pages, but it is possible to link to pages of other subjects, for example, pages with bibliographic references, personal pages, etc. Each page can be classed in several categories. This is a very important tool, not only as an aid to navigation through the website, but also to organize pages in relation to several discrete criteria. It is particularly interesting to group taxa by morphological characteristics, by stratigraphic levels (Fig. 4), by geographic distribution and

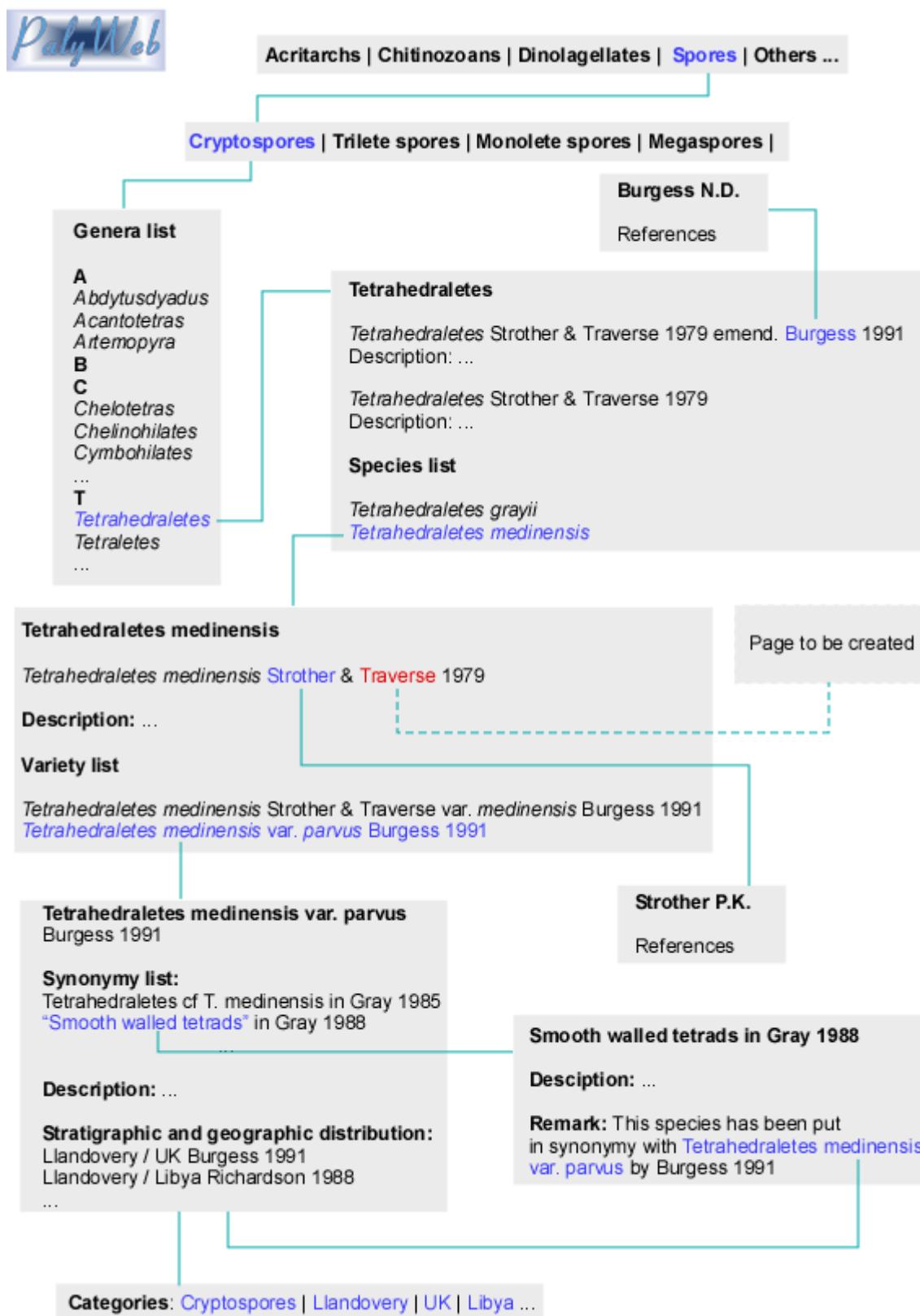


Figure 3: General architecture of PalyWeb based on the example of the *Tetrahedraletes* cryptospore genus.

so on. Categories make this possible for the application groups pages automatically and alphabetically by the several criteria. One page can be assigned to several different categories. Categories can be created or modified like a conventional page. However, the great flexibility of a database of this kind could

generate problems. To avoid inconsistency, it is important that syntactical rules be established for naming the internal links. For example, in **PalyWeb**, "cryptospore" and "cryptospores" are discrete pages. Therefore, it is necessary to be strict in the way one contributes to the database.

The screenshot shows a Mozilla Firefox browser window with the title "Category:Llandovery cryptospore - PalyWeb - Mozilla Firefox". The address bar displays the URL http://www.palyweb.ulg.ac.be/wiki/index.php?title=Category:Llandovery_cryptospore. The main content area is titled "Category:Llandovery cryptospore" and contains a list of spore genera and species. A sidebar on the left includes links for Main Page, Community portal, Current events, Recent changes, Random page, and Help. A search bar is also present. The bottom of the page includes standard Wikipedia-style footer links for About PalyWeb and Disclaimers.

Figure 4: Example of a category page based on the example of Llandovery cryptospores already introduced in the PalyWeb database.

The advantages of PalyWeb

The advantages of such a database are numerous. The whole palynological community has free access to the website and everybody is allowed to improve or to add to its contents. The free distribution, constant updates, diverse and detailed coverage, by numerous professional palynologists guarantees the high quality of data. The database is accessible by any computer with an Internet connexion (Windows, Mac, Linux). Common web browsers are adequate for work with the database (Internet Explorer, Firefox, etc.). Therefore, it is not necessary to buy new software and to keep it up to date. The database is accessible from wherever you are. To work with a colleague in a foreign country, a copy of the database in your computer is not needed and there is no problem of cross-platform incompatibility. Information introduced into the database is immediately available to all. Unlike other databases, it is not necessary to wait until the database is considered complete before it becomes accessible. In addition, as new palynological data are available continually, databases may be constantly and immediately upgraded. Wait for the new version of a database (usually obsolete in a short time) is eliminated. There is

no limitation on size or contents (except the capacity of the disk on which the information is stored). The content of the database is highly flexible and it was conceived to facilitate discussion. The website was not conceived and built by a pugnacious individual or a small group; it is the result of the worldwide collaboration of the whole palynological community. Meetings for the exchange of information are no longer necessary, and in any event, were commonly restricted in number to those with travel subsidies.

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Palynological and geochemical data in peat sediments alongside an old (Roman or Merovingian) paved road in the Hautes-Fagnes

[Données palynologiques et géochimiques de sédiments provenant de tourbières en bordure d'une ancienne route pavée, romaine à/ou mérovingienne, dans les Hautes-Fagnes]

Maurice STREEL¹

Virginie RENSON²

François de VLEESCHOUWER³

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Key Words: Palynology; geochemistry; peat; Holocene; Belgium; Roman; Merovingian; road

Mots-Clefs : Palynologie ; géochimie ; tourbe ; Holocène ; Belgique ; Romain ; Mérovingien ; route

Introduction

In 1768, a report to her Majesty Empress Marie-Thérèse of Austria, concerning the Duchies of Limburg and Luxemburg, indicated that an old paved road, then covered by peat and vegetation, linked the regions of Eupen and Sourbrodt (now in area called Hautes-Fagnes, in the province of Liège in eastern Belgium). At that time, only a bad trail wound across the region and the users of this trail were obliged to pay toll to the Liège Principality. The paved road, after restoration, would have allowed direct communication between the duchies (Fig. 1).

The paved road, traditionally known to the local inhabitants as the "Pavé de Charlemagne", was never restored and its detailed layout was forgotten until the early 1930's when the abbot J. BASTIN rediscovered and described (BASTIN, 1934) its remarkable structure between the sites of "Croix Mockel" and "Wez" (Fig. 1).

The road was believed to have a Roman origin until several ^{14}C dates obtained at the "Croix Mockel" site (CORBIAU, 1981) suggested a Merovingian age (between A.D. 460 and A.D. 885). Pollen analyses performed in the Wez site

(Fig. 2) by DRICOT (1960), DALEMANS & STREEL (1986) and more recently by STREEL *et alii* (2005) generated contradictory conclusions. DRICOT (1960) concluded that the pollen analysis of the peat below the road suggested an age considered to be too old for, but one ^{14}C date supported a Roman age. DALEMANS & STREEL (1986), introduced a new method of dating by pollen analysis of the peaty layers contaminated by mineral dust alongside the road and proposed a Merovingian age. The latest contribution was obtained from a trench made perpendicular to, but alongside the paved road, in a new site investigated by CORBIAU (2005) near the southern border of the Wez. Two profiles were studied (W A and W B) using geochemical (RENON *et alii*, 2005) as well as palynological (STREEL *et alii*, 2005) techniques on the samples. Helped by several ^{14}C dates, they came to the conclusion that the road was built between A.D. 210-390 and A.D. 380-540, using calibration method Oxcal 3.8. These two dates were then recalibrated using the calibration method Oxcal 3.10 to give an interval ranging from A.D. 130-380 to A.D. 350-540. It was then decided to use the same techniques on a new core (W VI) taken at the site investigated by DALEMANS & STREEL (1986).

¹ Laboratoire de Paléobotanique, Paléopalynologie et Micropaléontologie, Université de Liège, Allée du 6 août, B18, Sart-Tilman, 4000 Liège (Belgium)
maurice.streel@ulg.ac.be

² URAP, Department of Geology, DGLG-WE-Vrije Universiteit Brussel, Pleinlaan 2, B-1050 Brussels (Belgium)
vrenson@vub.ac.be

³ Unité de Recherche Argiles et Paléoclimats, University of Liège, Allée du 6 Août B18, Sart Tilman, B-4000 Liège 1 (Belgium)
fdevleeschouwer@student.ulg.ac.be

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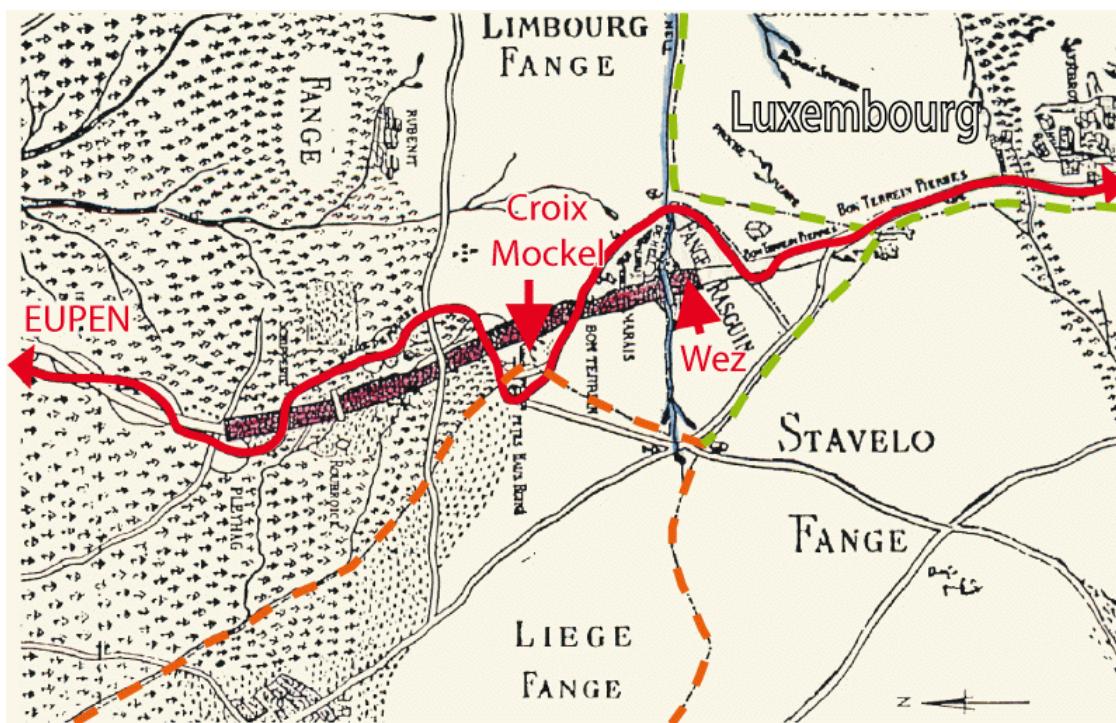


Figure 1: Map drawn by Cornelius LEURS in 1778 (after FAUCHAMPS, 1950). Dotted lines: boundaries between the four Duchies and Principalities which were meeting in the Hautes-Fagnes. The toll fees were to be paid at the site named here "Croix Mockel".

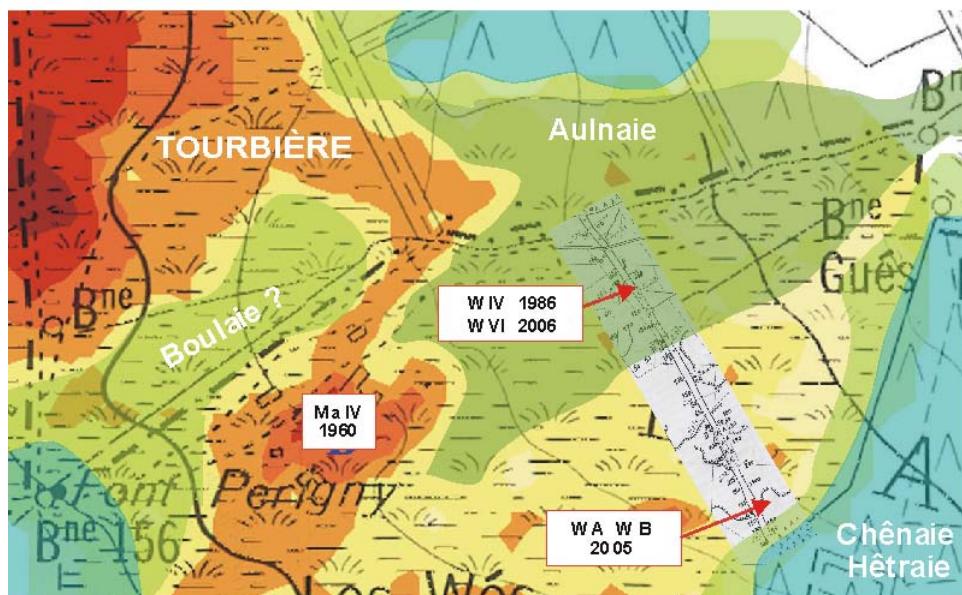
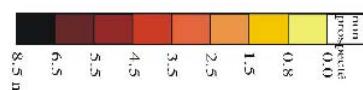


Figure 2: The site "Les Wés" or "Wez" on the right side of the small brook "Helle". Grey shaded area: layout of the paved road (BOLLINNE & STREEL, 1998). Other colours: hypothetical vegetation cover before the road building, based on the soil characteristics and on pollen data. "Aulnaie", "Boulaie", "Chênaie", and "Hêtraie" are woods dominated respectively by *Alnus*, *Betula*, *Quercus* and *Fagus*. Investigated sites are reported (see text for details).

Impact of environment on the pollen rain

It is important to note the environmental differences between the site of profiles W A and W B and the site of cores W IV and VI when the road was built. *Alnus* (alder) makes up to 50% of the total pollen sum in the lower part of W IV and W VI (Figs. 4 - 5) but is smaller in amount and range of variation in profiles W A and W B.

However for dating purposes, the regional pollen rain is of the greatest importance as shown by DRICOT (1960) in his profile Ma IV. Taken in a non-wooded raised bog, regional pollen rain is assumed to be at a maximum.

Dricot (1958)1960
Ma IV % Fagus-Carpinus-Alnus / AP
% Poaceae / AP

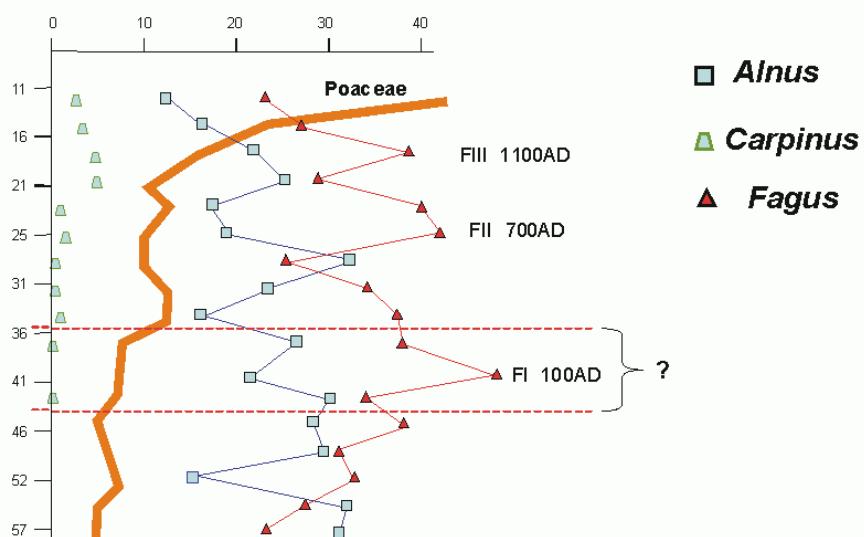


Figure 3: Simplified 5 cm interval pollen diagram Ma IV (DRICOT, 1960) with percentages calculated on arboreal pollen sum (AP). Dates of maxima of *Fagus* pollens based on the pollen analysis of another peat bog, 10 km to the north (PERSCH, 1950). The "?" indicates a possible equivalent of core W VI as explained in text.

The new core W VI (Fig. 4) compared to the old core W IV (Fig. 5)

Core W IV was sampled at 2.5 cm intervals and macerated for pollen analysis, for recording of ash weight/dry peat weight and for isolation of the first occurrence of small (1mm or less) fragments of quartzite in the calcined peat. The new core W VI was sampled every cm and treated like W IV. The same samples were analyzed by geochemistry for later comparison with the data observed in profile W B.

In core W IV, the sudden decline in the percentage of *Alnus* pollen was explained by DALEMANS & STREEL (1986) as the result of the opening of the paved road through the wooded peat-bog associated with the Helle brook. The sudden decline is indeed accompanied in the core by an increase of ash content and by the first occurrence in the calcined peat of small (1 mm or less) fragments of quartzite. It was

DRICOT (1960) identified 3 of the 4 maxima of *Fagus* (beech) pollen (Fig. 3) recorded by PERSCH (1950) in another peat-bog some 10 km to the north. However, the dates given by PERSCH (1950) were interpolated without ¹⁴C control, assuming a constant accumulation rate of the peat and therefore are of low reliability. Therefore, the correlation made by DRICOT (1960) and the dates given (Fig. 3) are also of low reliability. The presence/absence or frequency of *Carpinus* (hornbeam) is the only criterion for discriminating between FI, FII and FIII. DRICOT (1960) calculated all the percentages on the sum of arboreal pollen (AP).

also considered that the paved road was built there for the first time. In core W VI the decline in the percentage of *Alnus* pollen is again taken to indicate the construction of the new road. However, the decline is more gradual than in W IV because of the closer sampling.

The abundance of *Alnus* pollens in this site along the Helle had to be taken into account when calculating the percentages of pollen from other tree species provided by forests dominating the landscape outside the peat-bogs. Not only is the *Alnus* pollen rain locally more abundant than the regional pollen rain from the surrounding forests, but also the local density of *Alnus* trees may have acted as a shelter from the regional pollen rain. We have therefore recalculated in both cores the percentages of *Fagus* and *Carpinus* in the arboreal pollen sum less *Alnus* in order to reduce the importance of non-arboreal and local pollen rain. This was not done by DALEMANS & STREEL (1986) who had come to the conclusion

that the *Fagus* maximum above the decline of *Alnus*, as it was less important than the maximum visible below the decline of *Alnus*, corresponded to the FII of DRICOT (1960). The recalculation of DALEMANS & STREEL's (1986) diagram however shows (Fig. 5) that this *Fagus* maximum could also correspond to the FI.

The *Fagus* maximum in the new core W VI, immediately above the *Alnus* decline might therefore correspond to the FI of DRICOT (1960), here called zone A (Fig. 4). If so, the opening of the road through the *Alnus* wooded peat-bog might be Roman, not Merovingian.

However the drastic increase of ash content (> 50 %) in dry peat is clearly above that of the *Fagus* maxima in both cores. Above the *Fagus* maximum in the new core W VI, identified now as zone B (Fig. 4), a continuous occurrence of Filicales spores implies a superficial more mineralized peat. At the same level occur very abundant cenospheres. They are known to be ash particles resulting from incomplete high-temperature combustion of peat (MILLER & JANSONIUS 1996; GRIFFIN & GOLDBERG, 1979).

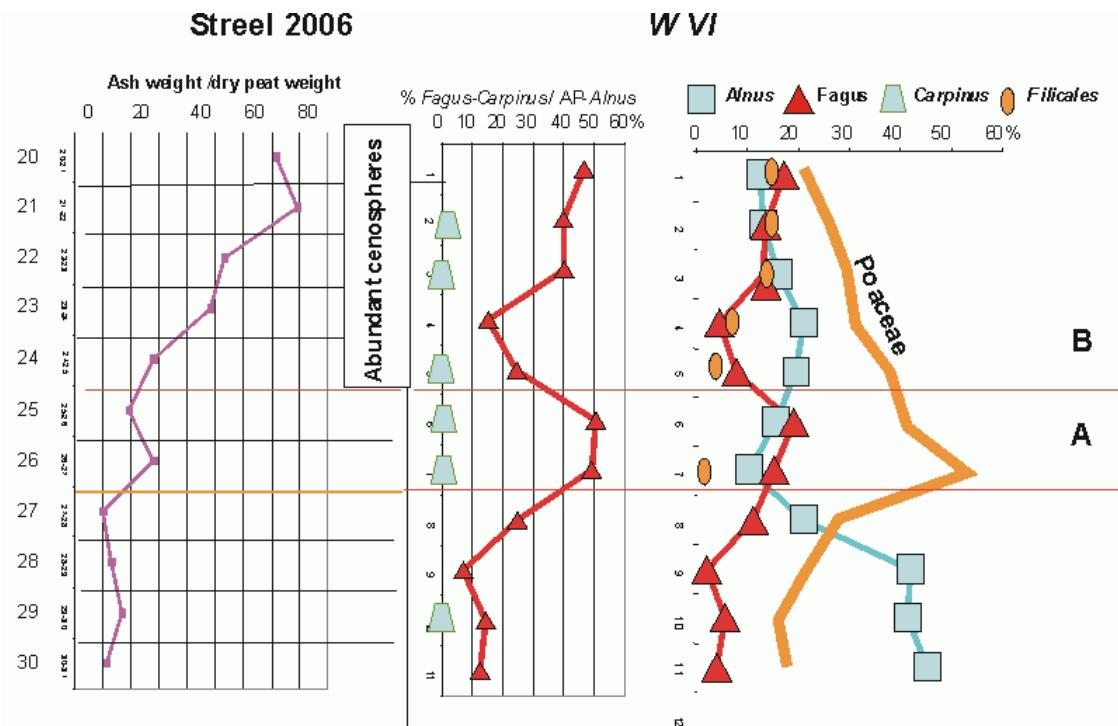


Figure 4: On the right: simplified pollen diagram of core W VI (percentage calculated on total pollen sum). On the left: percentages of ash in dry peat, and levels with abundant cenospheres. In the middle: percentages of *Fagus* and *Carpinus* recalculated on arboreal pollen sum less *Alnus* in order to reduce the importance of non-arboreal and local pollen rain.

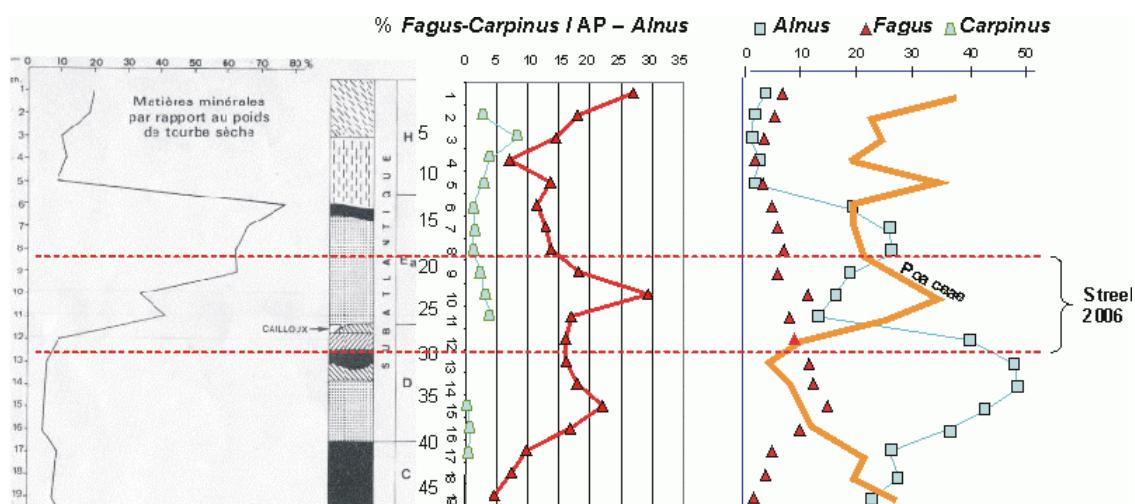


Figure 5: On the right: simplified pollen diagram of core W IV (after DALEMANS & STREEL, 1986) (percentage calculated on total pollen sum). On the left: percentages of ash in dry peat. In the middle: percentages of *Fagus* and *Carpinus* recalculated on arboreal pollen sum less *Alnus* in order to reduce the importance of non-arboreal and local pollen rain.

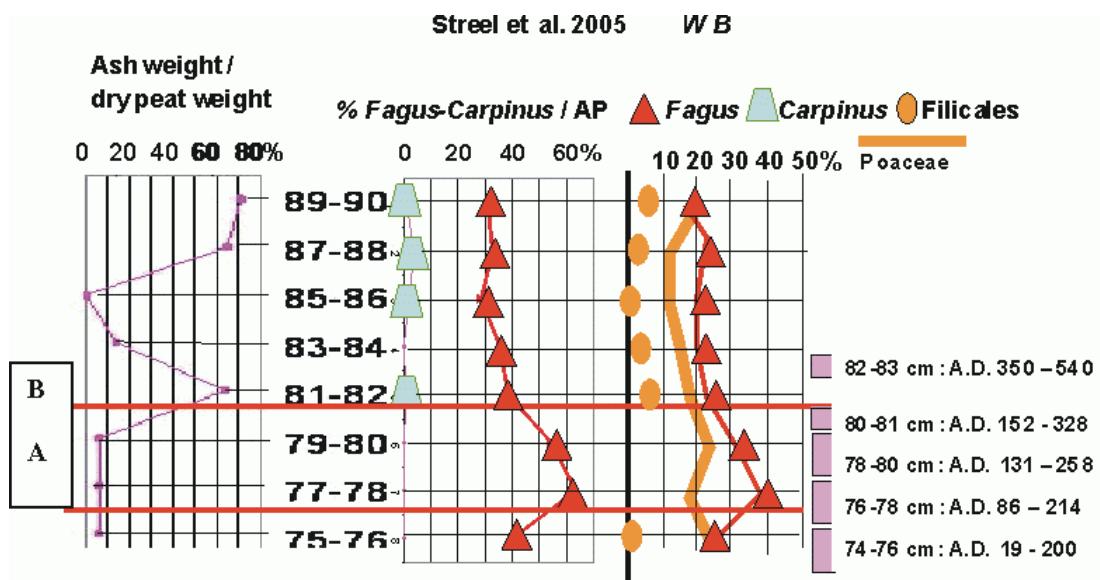


Figure 6: On the right: simplified pollen diagram of profile W B (STREEL *et alii*, 2005) (percentage calculated on total pollen sum). On the left: percentage of ash in dry peat and calibrated ^{14}C intervals. In the middle: percentages of *Fagus* and *Carpinus* recalculated on arboreal pollen sum in order to reduce the importance of non-arboreal pollen rain. Note that the samples in profile W B are measured from the base of the peat layer.

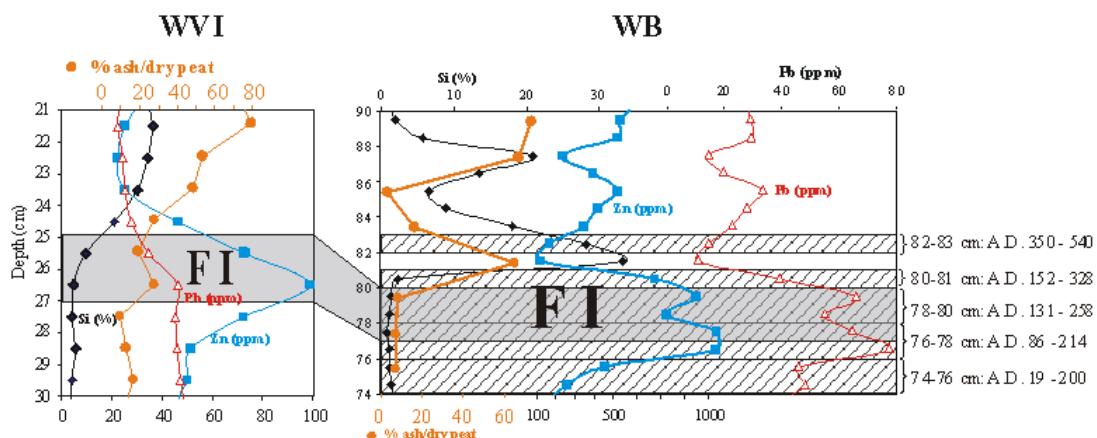


Figure 7: Comparison of geochemical data in new core W VI and profile W B (RENNON *et alii*, 2005) in the case the maximum of *Fagus* FI is confirmed in W VI.

The new core W VI (Figs. 4 & 7) compared to the profile W B (Figs. 6 - 7)

In Figure 6 (a simplified diagram of profile WB), the pollen percentages of *Fagus* and *Carpinus* were recalculated on the arboreal pollen sum only, to reduce the local importance of non arboreal pollen rain in the pollen diagram. This profile W B has been dated by five successive ^{14}C dates. The four lower dates, being very close, allowed recalibration using the wiggle-match dating program Bcal (Figs. 6 - 7). The maxima of *Fagus* were attributed to the FI based on their calibrated ^{14}C age interval of A.D. 86 – A.D. 258. The site W B was not situated in an *Alnus* wooded peat-bog and therefore the supposed man-made *Alnus* decline could not be detected. The ash content in dry peat increases suddenly between 79-80cm and 81-82cm *i.e.* within the time limit of A.D. 131 and A.D. 540.

The drastic increase of silica content between 81 and 82 cm (between A.D. 152 and A.D. 540) in the W B profile attests the presence of quartzite fragments linked to the building of the paved road and the beginning of its use (Fig. 7). This characteristic is also present in W VI although the Si increase in W VI is more progressive than in W B. Moreover, the appearance of Filicales is abrupt in W B while progressive in W VI. These discrepancies between W B and W VI profiles suggest either a difference in the accumulation rate of peat, or a difference in the recording of quartzite fragments. Indeed, the deposition of quartzite fragments on a peat surface is completely chaotic. It is thus possible not only to have a difference in quantity but also in size (small then large in W VI, while all are large in W B) of quartzite fragments, resulting in a difference in Si profiles. However, to clarify this point ^{14}C dating needs be performed in W VI.

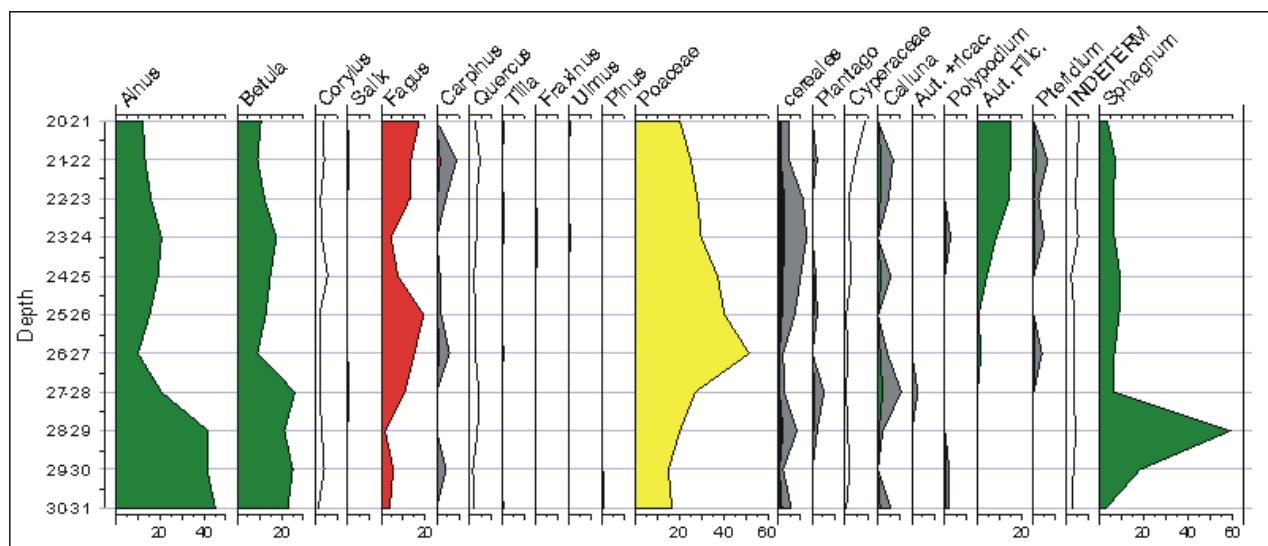
Trace element geochemistry shows significant increases in lead and zinc beginning at 70 cm in W B and at 29 cm in W VI. Lead isotopes analyses were performed on some samples presenting high concentrations of lead and zinc (between 70 cm and 94 cm in W B). These samples show isotopic ratios similar to isotopic ratio of lead-zinc ores located approximately 15-20 km to the north-northwest, in the Verviers synclinorium. Therefore, it is possible to suggest the hypothesis that the road could have been used to carry lead-zinc ores from the Verviers-Aachen area through the Hautes-Fagnes region, and then perhaps south-southwest to Trier, an important metal working centre at these times.

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Addendum: Pollen diagram of core W VI. Percentages of all pollens and spores (except *Sphagnum*) on the total sum. Curves of pollens from *Carpinus*, *Cerealia*, *Plantago*, *Calluna*, other Ericaceae and spores of *Polypodium* and *Pteridium* are 5x exaggerated.

**Chitinozoans of the lower Llanvirn Huy
and the middle Caradoc Sart-Bernard formations
(Middle to Upper Ordovician):
implications for the stratigraphy
of the Condroz Inlier (Belgium)**

**[Les chitinozoaires des formations de Huy, Llanvirnien inférieur,
et de Sart-Bernard, Caradocien moyen
(Ordovicien moyen et supérieur) :
implications stratigraphiques pour le Massif du Condroz (Belgique)]**

Jan VANMEIRHAEGHE¹

Citation: VANMEIRHAEGHE J. (2007).- Chitinozoans of the lower Llanvirn Huy and the middle Caradoc Sart-Bernard formations (Middle to Upper Ordovician): implications for the stratigraphy of the Condroz Inlier (Belgium). *In: STEEMANS P. & JAVAUX E. (eds.), Recent Advances in Palynology.- Carnets de Géologie / Notebooks on Geology*, Brest, Memoir 2007/01, Abstract 10 ([CG2007_M01/10](#))

Abstract: This paper reports on chitinozoans from the early Llanvirn (mid Darriwilian) Huy Formation found at three localities in the central Condroz Inlier: the Huy and Sart-Bernard railway sections and the Wépion borehole. In addition, it presents data on chitinozoans from the middle Caradoc (upper Sandbian to lower Katian) Sart-Bernard Formation, known from the eastern Sart-Bernard railway section and historically confused with the Huy Formation. We confirm the distinct palaeontological and lithological differences between the two formations, already noted by some authors. Our data, however, suggest that the Huy Formation is probably absent in the eastern Sart-Bernard section and demonstrate that the supposed stratigraphic hiatus between the Huy and Sart-Bernard formations is at least partly occupied by the soon-to-be-defined Chevreuils Formation. The chitinozoans indicate an early Abereiddian (early Llanvirn, mid Darriwilian) age for the Huy Formation and a Burrellian-Cheneyan age (middle Caradoc, late Sandbian to early Katian) for the Sart-Bernard Formation, thus narrowing the known stratigraphic range of these units. The chitinozoans of the Huy Formation have a northern Gondwana signature, whereas those of the Sart-Bernard Formation show clear Baltoscandian affinities.

Key Words: Biozonation; chitinozoans; Condroz Inlier; Llanvirn; Caradoc; Ordovician

Résumé : Les chitinozoaires du Llanvirnien inférieur (Darriwilien moyen) de la Formation de Huy ont été étudiés dans trois localités de la partie centrale de la Bande de Sambre-et-Meuse : les coupes de la voie de chemin de fer de Huy et de Sart-Bernard, ainsi que le sondage de Wépion. De plus, de nouvelles données sont ici présentées sur les chitinozoaires du Caradocien moyen (Sandbian supérieur à Katien inférieur) de la Formation de Sart-Bernard dans la coupe est de la voie de chemin de fer à Sart-Bernard, historiquement confondue avec la Formation de Huy. Nous confirmons l'existence de différences paléontologiques et lithologiques nettes entre les deux formations ainsi que cela a déjà été noté précédemment par certains auteurs. Nos résultats, cependant, suggèrent l'absence probable de la Formation de Huy dans la section est de Sart-Bernard et démontrent que l'hiatus stratigraphique supposé entre les Formations de Huy et de Sart-Bernard est occupé par au moins la Formation des Chevreuils qui sera définie bientôt. Les chitinozoaires indiquent un âge Abereiddien inférieur (Llanvirnien inférieur, Darriwilien moyen) pour la Formation de Huy et un âge Burrellien-Cheneyen (Caradocien moyen, Sandbian supérieur à Katien inférieur) pour la Formation de Sart-Bernard, précisant ainsi la position stratigraphique de ces unités. Les chitinozoaires de la Formation de Huy montrent une affinité nord-gondwaniennes alors que ceux de la Formation de Sart-Bernard montrent des affinités baltoscandinaviennes claires.

Mots-Clefs : Biozonation ; chitinozoaires ; Bande du Condroz ; Llanvirnien ; Caradocien ; Ordovicien

1. General geological information

1.1. The Huy Formation

The Huy Formation was defined as the "Assise de Huy" by MALAISE (1909). We describe its lithology as slightly micaceous dark grey or black mudstone, with intercalated millimetric grey (fine-grade) siltstone beds, mostly with

diffuse limits, and a few fine-grade sandstone beds. Its base was observed in the Wépion borehole. It is a 5 cm thick pebble-supported conglomerate, disconformably overlying the Tremadocian Chevripont Formation (*cf.* GRAULICH, 1961). The supposed transitional contact of the Huy Formation with the grey siltstones of the overlying Sart-Bernard

¹ Research Unit Palaeontology, Department of Geology and Pedology, Ghent University, Krijgslaan 281/S8, B-9000 Gent (Belgium)

Jan.Vanmeirhaeghe@UGent.be

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Formation was reported from the eastern Sart-Bernard railway section (km 73.110) by MAILLIEUX (1939). As we shall show no such contact is likely to be present.

The macrofauna of the Huy Formation consists of graptolites, trilobites, lingulid brachiopods, crinoids, molluscs, orthocone nautiloids and caryocarids (arthropod zooplankton), along with trace fossils and coprolites. SERVAIS & MALETZ (1992) reviewed the graptolites of the Huy Formation and assigned them to the lower Abereiddian (lower Llanvirn) *D. artus* (= *D. bifidus*) Zone.

Estimates of the thickness of the Huy Formation range from more than 150 m (MICHOT, 1957) to more than 120 m in the Wépion borehole (GRAULICH, 1961). Disregarding the faults, which have an unknown displacement, the thickness of the Huy Formation in the western Sart-Bernard railway section is estimated by us at 100 m.

1.2. The Sart-Bernard Formation

The Sart-Bernard Formation, defined by MAILLIEUX (1939) as the "Assise de Sart-Bernard" is known only from the eastern portion of the Sart-Bernard railway section (east of km 73.110), which is also its type locality (MARTIN, 1969). It consists of grey micaceous siltstones, with a few grey micaceous sandstone beds and a nodule

horizon. The macrofauna comprises gastropods, bivalves, hyolites, brachiopods, trilobites and crustaceans (MAILLIEUX, 1939). It was originally dated as lower Llandeilian (MAILLIEUX, *ibid.*), but OWENS & SERVAIS (*in press*) mention a late Llanvirn (late Darriwilian) to Chenyan (early Katian) age, with a preference for an early to middle Caradoc age interval (Sandbian to early Katian), on the basis of trilobite, graptolite and unpublished chitinozoan data (now published herein). We estimate the stratigraphic thickness of the Sart-Bernard Formation as between 80 and 115 m, but we saw neither the base nor the top of the formation.

1.3. The erroneously ascribed Huy Formation in the eastern Sart-Bernard railway section

MAILLIEUX (1939) reported the *D. bifidus* Zone from one fossil-bearing level (Naninne 2a), situated at km 73.078, a finding confirmed by BULMAN (1950). Consequently, MAILLIEUX (*ibid.*) considered the whole (poorly exposed) interval between km 73.0 and km 73.110 as the Huy Formation. This view was followed by later authors, because the lithology of the best exposed part of the sequence just west of km 73.110 resembles that of the Huy Formation. Our palaeontological results contradict the presence of the Huy Formation in the eastern Sart-Bernard railway section (see 5.2).

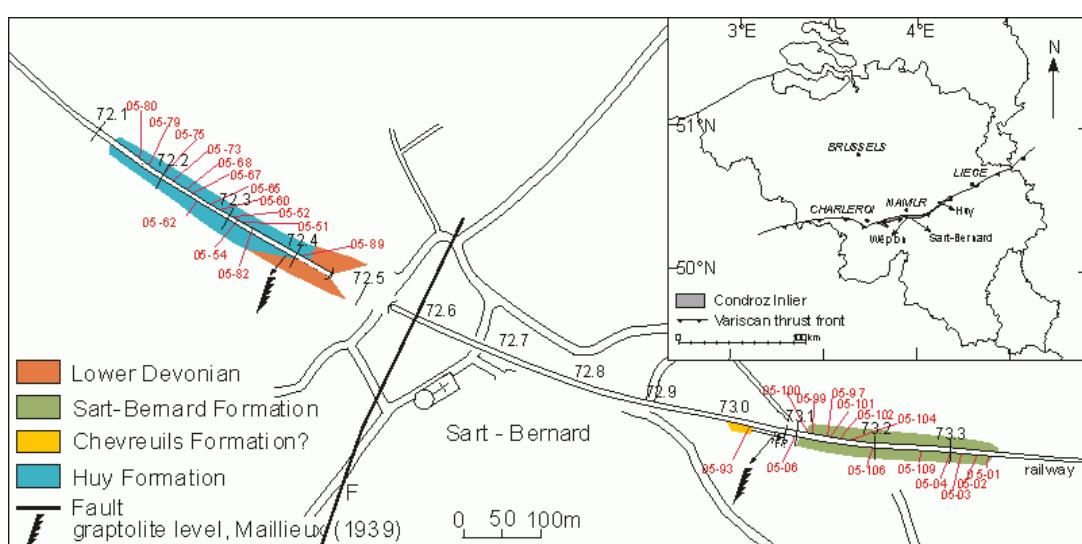


Figure 1: Location of the Condroz Inlier and the Sart-Bernard sections, with sample sites indicated. The map reflects a new geologic interpretation, in agreement with data in the text regarding chitinozoans and lithology.

1.4. The Huy and Sart-Bernard formations: the confusion

In his summary of the Ordovician and Silurian rocks of Belgium, MICHOT (1954) recognized the black shales of the Huy and Sart-Bernard sections as the "Assise de Huy" (MICHOT, 1954, p. 47), but in his summarising stratigraphical chart he named it erroneously as the "Assise de Sart-Bernard" (MICHOT, 1954, p.

75). Unfortunately, MAILLIEUX (1939) had already assigned this name to the grey siltstones of the eastern Sart-Bernard railway section. MICHOT (1954) incorporated this unit into his "Assise de Vitrival-Bruyère", but his assignment was not accepted by other authors.

MARTIN (1969) recognized a distinction between the "Assise de Huy" and the "Assise de Sart-Bernard", but erroneously referred the

whole eastern Sart-Bernard railway section to the "Assise de Sart-Bernard" (MARTIN, 1969, p. 32). As BULMAN (1950) attributed the graptolite horizon at km 73.078 to the *D. bifidus* Zone, MARTIN (*ibid.*) attributed an early Llanvirn age to the "Assise de Sart-Bernard". As a consequence, VERNIERS *et alii* (2001) doubted whether the Huy and Sart-Bernard formations are synonyms in the central Condroz Inlier, and considered both of them to be of Abereiddian

(early Llanvirn, mid Darriwilian) age. OWENS & SERVAIS (in press) pointed out the difference in the ages of the Huy and Sart-Bernard formations, and inferred a stratigraphic gap, which includes at least the middle Llanvirn (middle Darriwilian), but probably also parts of the upper Llanvirn (upper Darriwilian). As we show below (2.2), our chitinozoan data confirm that the two formations differs in age, but do not indicate the existence of a large hiatus.

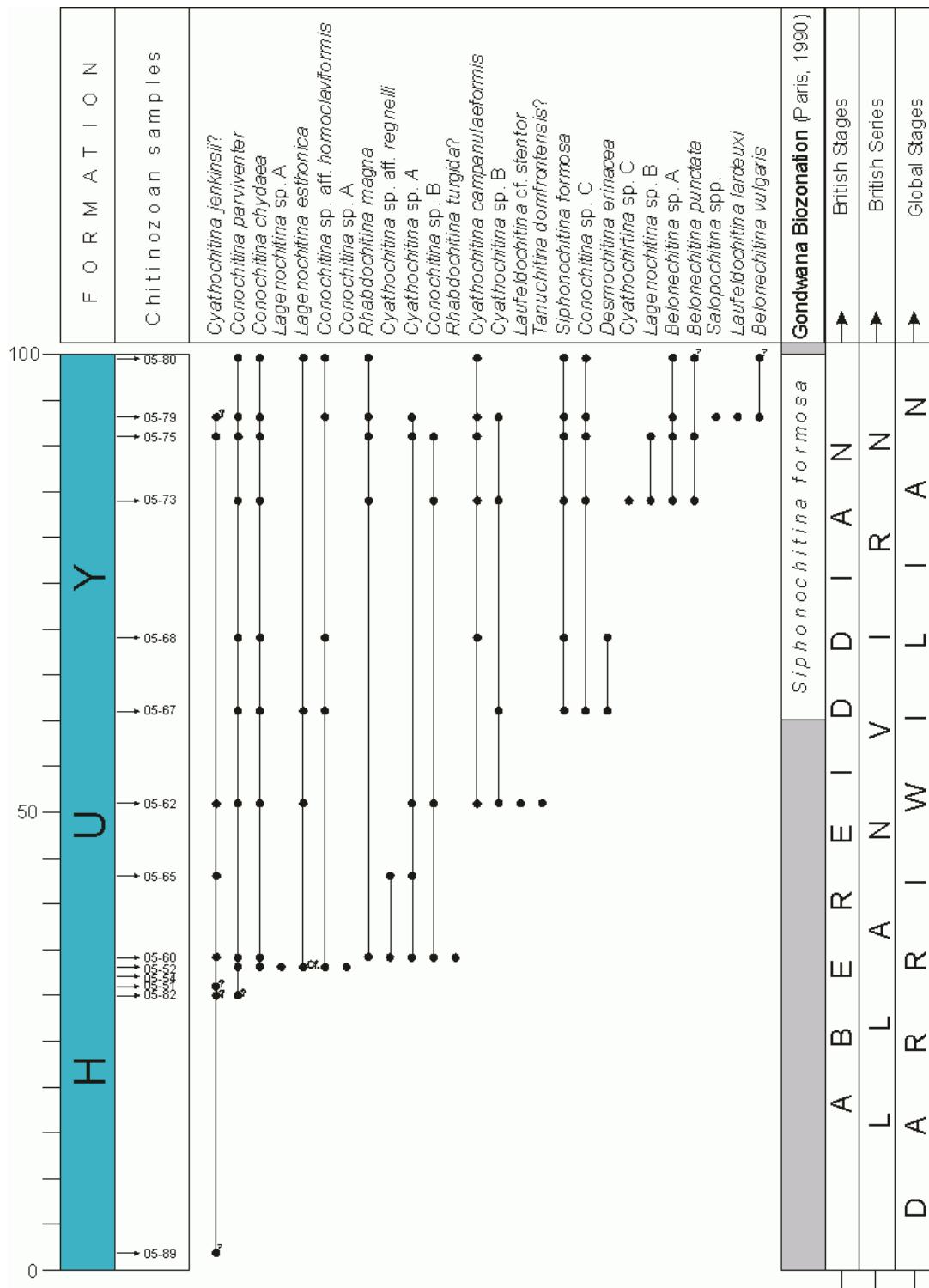


Figure 2: Chitinozoan distribution, biozonation and age assignment of the Huy Formation in the western Sart-Bernard section. The thickness and stratigraphic position of the samples are based on work in the field.

2. Chitinozoan biostratigraphy (Pl. 1)

2.1. Huy Formation (Fig. 2)

In the samples from the western Sart-Bernard railway section, the species of greatest value stratigraphically are *Cyathochitina jenkinsi?* (also found in the Huy and Wépion sections), *Cyathochitina aff. varenensis*,

Lagenochitina esthonica (also present in the Wépion and ?Huy sections), *Siphonochitina formosa* (also found in the Huy and Wépion sections), *Fungochitina vulgaris* (also ?Wépion), *Belonechitina punctata* (also ?Wépion) and *Laufeldochitina lardeuxi* (also Wépion). All but the two last-mentioned species were encountered by JENKINS (1967) in the Hope Shales (Shropshire, U.K., Avalonia), where

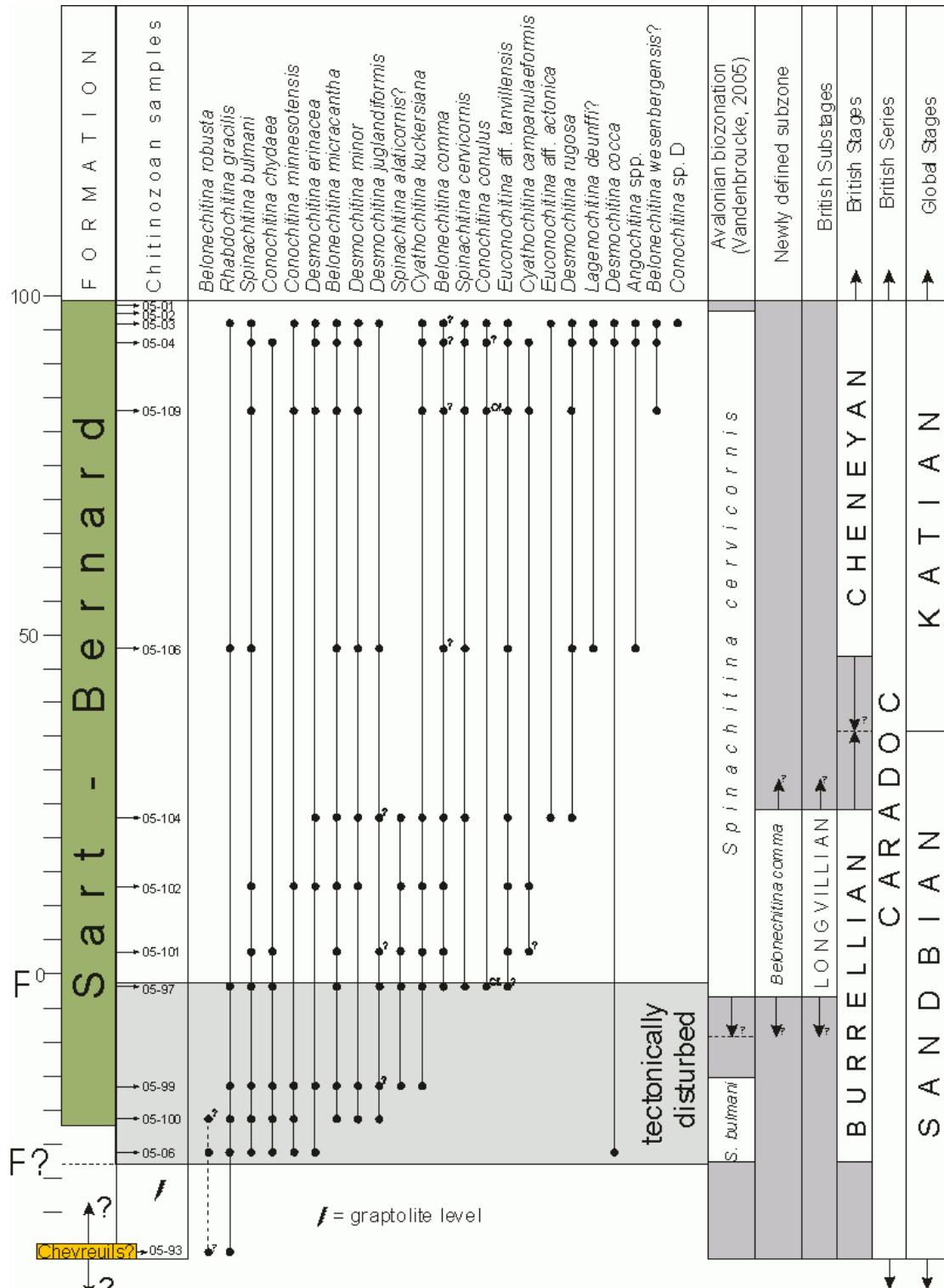


Figure 3: Chitinozoan distribution, biozonation and age assignment of the ?Chevreuil and Sart-Bernard formations in the eastern Sart-Bernard section. The indicated thickness and stratigraphic position of the samples are based on field work.

graptolites suggest an early Llanvirn age (STRACHAN, 1986). Our specimens of *C. jenkins?* are very similar to those in the Hope Shales assigned to *C. calix* by JENKINS (*ibid.*). We opt for a different identification, as various aspects of our specimens differ slightly from those of the Gondwanan index species *C. calix* (*sensu stricto*).

The chitinozoan fauna clearly has northern Gondwanan affinities (Fig. 4). With the exception of *C. jenkins?* and *C. parviventer*, all the species listed above are found in northern Gondwana in Llanvirn (middle to upper Darriwilian) strata (PARIS, 1981), and the ranges of some of them are restricted to that interval of time. In northern Gondwana, *Siphonochitina formosa* is the index species of the eponymous total-range zone (PARIS, 1990). The *S. formosa* Zone is correlated with the upper half of the *D. artus* graptolite Zone (WEBBY *et alii*, 2004).

An eye-catching species, *Salopochitina* sp. A (Plate 1.12), occurs in both the Huy and the western Sart-Bernard railway sections. This genus was formerly thought to be confined to the Wenlock-Ludlow interval, but may be used as guide fossil for a biozone situated in the *Siphonochitina formosa* Zone. PARIS *et alii* (in press) also did report the genus from the dark shales of the Sabova Formation of Turkey, which is attributed to the middle to late Darriwillian (Abereiddian). As is the case with our specimens, the *Salopochitina* specimens of PARIS *et alii* (in press) have a longer neck than the Silurian ones.

Our chitinozoan findings corroborate the presence of the lower Llanvirn (mid Darriwilian) *D. artus* graptolite Zone in the Huy Formation (SERVAIS & MALETZ, 1992), but *Cyathochitina protocalix* and *Cyathochitina calix*, in northern Gondwana known to occur in the lower part of this biozone, are not recognised in our samples.

2.2. Eastern Sart-Bernard section, west of km 73.110: partly Chevreuils Formation? (Fig. 1 & Fig. 3)

The assemblage of chitinozoans from the samples of what had been called the Huy Formation in the eastern Sart-Bernard railway section is different from that of the western section. The chitinozoans in sample JVM 05-93 (km 73.038, see Fig. 1) are poorly preserved, but *Rhabdochitina gracilis* and *Belonechitina robusta?* were recognised. The assemblage is completed by *Lagenochitina* spp. and *Siphonochitina* spp. The presence of *Siphonochitina* spp. and the absence of *Spinachitina* spp. and *Desmochitina* spp. suggest a pre-Burrellian (pre-late Sandbian) age. If so, the sample should be situated in the interval upper Abereiddian (above the *D. artus*

Zone) to Aurelucian, with a preference for the Aurelucian because of the presence of specimens resembling *B. robusta*.

In sample JVM 05-06 (km 73.097, see Fig. 1), *Spinachitina bulmani*, *Belonechitina robusta*, *Rhabdochitina magna*, *Desmochitina erinacea*, *Desmochitina coca* and *Conochitina minnesotensis* occur. This assemblage is typical for the Burrellian (upper Sandbian – lower Katian) of the Onny Valley (*cf.* JENKINS, 1967; VANDENBROUCKE, 2005). An age older than Burrellian (late Sandbian) is excluded; in Baltoscandia as well, *B. robusta* first occurs in the Idavere strata (NÖLVAK & GRAHN, 1993), that are roughly correlative with the basal part of the Burrellian (WEBBY *et alii*, 2004).

Our chitinozoan data confirm a difference in the ages of the Huy and Sart-Bernard formations, but do not support the existence of a large hiatus between them. Indeed, the chitinozoan content of sample JVM 05-93, formerly considered to be situated in the upper part of the Huy Formation, is instead late Abereiddian to Aurelucian (late Darriwilian to early Sandbian), much younger than the early Llanvirn (mid Darriwilian). The lithology of this sample is strongly-burrowed, dark grey shale with small silt- and sandstone lenses and thus resembles the lithology of the soon-to-be-defined upper Llanvirn to lower Caradoc Chevreuils (upper Darriwilian to lower Sandbian) Formation (*cf.* VANMEIRHAEGHE, 2006a). Immediately below the base of the Sart-Bernard Formation as previously defined (at km 73.110), the Burrellian (upper Sandbian – lower Katian) is demonstrated in JVM 05-06. Therefore, the graptolite identifications of MAILLIEUX (1939) and BULMAN (1950) of the specimens collected at km 73.078, which they assigned to the lower Llanvirn (middle Darriwilian) *D. bifidus* Zone, need reconsideration, for in all probability the Huy Formation is absent in the eastern Sart-Bernard railway section.

These results imply the presence of a fault between JVM 05-93 (Chevreuils Formation?) and JVM 05-06 (Burrellian, upper Sandbian – lower Katian) (Fig. 1 & Fig. 3). Indeed, in the central Condroz Inlier, the Vitrival-Bruyère Formation (its base with thick sandstone beds) is inferred to occur between the Chevreuils and the Sart-Bernard formations, for it is correlated with the *Laufeldochitina stentor* Zone (~upper Llanvirn to Aurelucian, upper Darriwilian to lower Sandbian), of which it probably represents the uppermost element (Fig. 4). Because the upper boundary of Vitrival-Bruyère Formation is Onnian (late Streffordian, mid Katian) (VANMEIRHAEGHE, 2006b), the equivalent of the Sart-Bernard Formation must exist within the Vitrival-Bruyère Formation (Fig. 4). This



Plate 1: SEM microphotographs of chitinozoans of the Huy and Sart-Bernard Formations from the Sart-Bernard sections. All measurements in microns ($L \times D_p \times D_c$) or ($L \times D_p \times D_c \times D_b$), with L = total length; D_p = width of the chamber; D_c = width of the neck; D_b = width at the base;

figure 1. *Lagenochitina esthonica*. $600 \times 275 \times 135$. JVM 05-80; 05-1546. Huy Formation;

figure 2. *Lagenochitina esthonica*. $660 \times 235 \times 110$. JVM 05-80; 05-1546. Huy Formation;

figure 3. *Cyathochitina jenkinsi?* $250 \times 160 \times 90 \times 130$. JVM 05-75; 05-1542. Huy Formation;

figure 4. *Cyathochitina jenkinsi?* $240 \times 120 \times 70 \times 100$. JVM 05-75; 05-1542. Huy Formation;

figure 5. *Lagenochitina* sp. A. $130 \times 80 \times 45$. JVM 05-73; 05-1541. Huy Formation;

figure 6. *Fungochitina* aff. *tanvillensis*. $100 \times 72 \times 25$. JVM 05-106; 05-1566. Sart-Bernard Formation;

- figure 7.** *Fungochitina vulgaris*. 100 x 60 x 40. JVM 05-79; 05-1544. Huy Formation;
- figure 8.** *Cyathochitina aff. varenensis*. 165 x 135 x 60. JVM 05-73; 05-1541. Huy Formation;
- figure 9.** *Conochitina parviventer*. 350 x 90 x 60. JVM 05-67; 05-1538. Huy Formation;
- figure 10.** *Conochitina parviventer*. 450 x 90 x 65. JVM 05-62; 05-1537. Huy Formation;
- figure 11.** *Desmochitina juglandiformis*. 1 specimen: 70 x 60. JVM 05-106. Sart-Bernard Formation;
- figure 12.** *Salopochitina* sp. A. 160 x 85 x 40. Length appendix: 160 µm. JVM 05-79; 05-1544. Huy Formation;
- figure 13.** *Spinachitina cervicornis*. 145 x 82 x 45. JVM 05-97; 05-1569. Sart-Bernard Formation;
- figure 14.** *Spinachitina bulmani*. 110 x 75 x 35. JVM 05-101; 05-1571. Sart-Bernard Formation;
- figure 15.** *Siphonochitina formosa*. Without siphon: 270 x 65 x 40 x 45. Siphon: 140 x 75 x 45. JVM 05-73; 05-1541. Huy Formation;
- figure 16.** *Siphonochitina formosa*. Without siphon: 310 x 60 x 32 x 42. Siphon: 120 x 60 x 40. JVM 05-73; 05-1541. Huy Formation;
- figure 17.** *Rhabdochitina magna*. 1100 x 115 x 90. JVM 05-73; 05-1541. Huy Formation;
- figure 18.** *Spinachitina cervicornis*. 145 x 80 x 40. JVM 05-97; 05-1569. Sart-Bernard Formation;
- figure 19.** *Cyathochitina* sp. C. 350 x 130 x 75 x 95. JVM 05-73; 05-1541. Huy Formation;
- figure 20.** *Belonechitina comma*. 230 x 60 x 30. JVM 05-104; 05-1572. Sart-Bernard Formation;
- figure 21.** *Belonechitina comma*. 230 x 60 x 30. JVM 05-104; 05-1572. Sart-Bernard Formation.

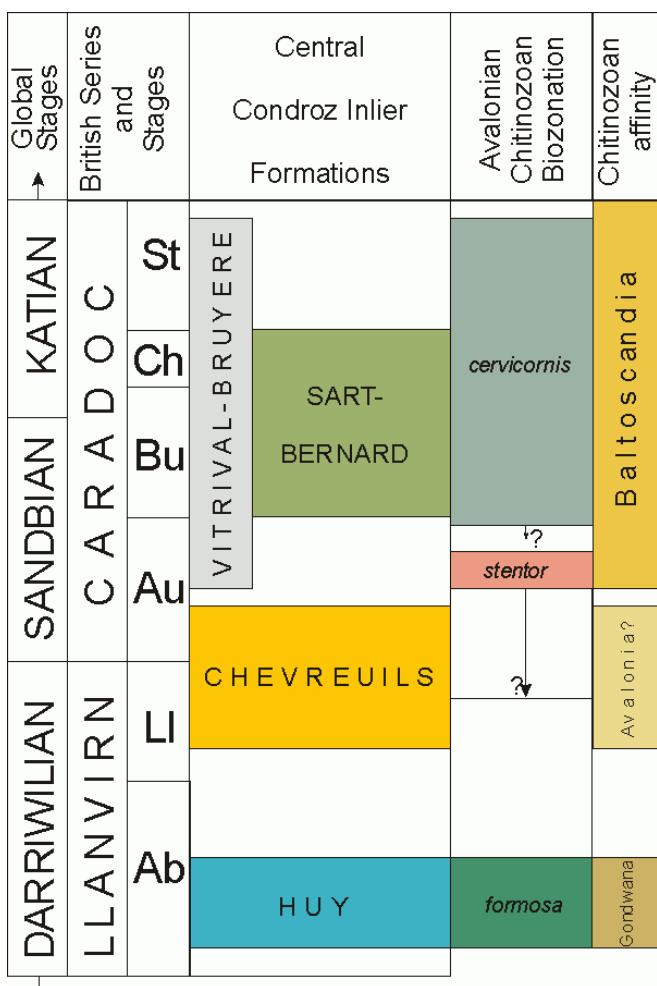


Figure 4: Stratigraphic position of the formations of the central Condroz Inlier, as discussed in the text. On the right, Avalonian chitinozoan biozones found in the central Condroz Inlier and their affinities with other palaeocontinents. The base of the Vitrival-Bruyère Formation is indicated as in the *L. stentor* Zone, but might be lower, given the range of the index species on Baltoscandia (NÖLVAK & GRAHN, 1993). However, the Chevreuil Formation in its type locality is situated in the upper Llanvirn to lower Caradoc interval. No specimens of *L. stentor* were seen in samples from that section. Possibly, this absence was caused by chitinozoan-endemism in Avalonia during late Llanvirn – early Caradoc times. Ab: Abereiddian; Li: Llandeilian; Au: Aurelucian; Bu: Burrellian; Ch: Cheneyan; St: Streffordian.

conclusion is supported by the existence of a thick siltstone interval with a few sandstone interbeds in the type section of the Vitrival-Bruyère Formation.

2.3. Sart-Bernard Formation (Fig. 4)

Stratigraphically important species in the Sart-Bernard Formation are *Spinachitina bulmani*, *Spinachitina cervicornis*, *Desmochitina juglandiformis* and *Belonechitina comma*. The chitinozoan fauna is similar to that of British Avalonia (VANDENBROUCKE, 2005) and has a clear Baltoscandian signature.

VANDENBROUCKE's (2005) data from British Avalonia suggest that the FAD of *S. bulmani* must be situated somewhere in the *D. foliaceus* graptolite Zone, which taken largely, corresponds to the Burrellian (upper Sandbian – lower Katian). In Avalonia, *S. cervicornis* ranges from the Cheneyan (lower Katian) to the Actonian (lower Streffordian, middle Katian), but its lowermost occurrence might be in the lower Burrellian (upper Sandbian), if the long-spined specimens attributed to *S. bulmani* are within the scope of the variations of *S. cervicornis* (VANDENBROUCKE, 2005). In any event, *S. cervicornis* co-occurs in some of our samples with *Desmochitina juglandiformis*, which in Baltoscandia has more or less the same range as *S. cervicornis*. In Baltoscandia, the *S. cervicornis* (total-range) Zone occupies the late Idavere-early Oandu time interval (NÖLVAK & GRAHN, 1993), and thus is of the age interval Burrellian (except for the basal part) to early Cheneyan or the late Sandbian – early Katian global Stages (WEBBY *et alii*, 2004; BERGSTRÖM *et alii*, 2005). *Belonechitina comma* is characteristic of the Jöhvi to Keila stages (NÖLVAK & GRAHN, 1993), that correlate with the middle to upper Burrellian (upper Sandbian – lower Katian).

In summary, the chitinozoans of the Sart-Bernard Formation correlate with the middle Burrellian to (lower) Cheneyan (upper Sandbian – lower Katian) and have a Baltoscandian signature (Fig. 4); the interval between and including JVM 05-97 and JVM 05-104 has a

middle to late Burrellian (~Longvillian, late Sandbian – early Katian) age (Fig. 3). From JVM 05-106 upward, it is quite probable that the strata are Cheneyan (early Katian). So chitinozoan data narrow the late Llanvirn (late Darriwilian) to Cheneyan (early Katian) age proposed by OWENS & SERVAIS (in press).

3. Conclusions

Chitinozoans from the Huy and Sart-Bernard formations, two units of the Lower Palaeozoic Condroz Inlier, Belgium, were collected and studied. The occurrence of the *Siphonochitina formosa* Zone in the Huy Formation is in agreement with the previously obtained graptolite data that assigned an early Llanvirn (mid Darriwilian) age to this formation. In the eastern Sart-Bernard section, the Huy Formation is absent in all probability, as the chitinozoans from two samples indicate a late Abereiddian to Aurelucian (late Darriwilian to early Sandbian) and a Burrellian (late Sandbian – early Katian) age. The western part of the eastern Sart-Bernard section might represent the late Darriwilian to early Sandbian Chevreuil Formation. The chitinozoans of the Sart-Bernard Formation are assigned to the *Spinachitina cervicornis* Zone and are shown to have a middle Burrellian to (early) Cheneyan (late Sandbian – early Katian) age, narrowing the previously proposed late Llanvirn (late Darriwilian) to Cheneyan (early Katian) range in age.

The chitinozoans show that Avalonia moved northward from Gondwana to Baltica during Ordovician times. The early Llanvirn (mid Darriwilian) chitinozoan assemblages of the Huy Formation are very similar to those of the same age in Gondwana, whereas those of the Burrellian-Cheneyan (late Sandbian – early Katian) have Baltoscandian affinities. Chitinozoans from the type locality of the Chevreuil Formation have no obvious similarities with contemporaneous assemblages on other palaeocontinents. We suggest that during late Darwillian to early Sandbian times, the age of the Chevreuil Formation, Avalonia was at a latitude intermediate between that of Gondwana to the south and that of Baltica and Laurentia to the north. Furthermore, the lack of thermohaline circulation during the Early and Middle Ordovician and the peculiar position of the palaeoplates were conditions favourable to endemism (see references in ACHAB & PARIS, in press).

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Middle Devonian (Givetian) megaspores from Belgium (Ronquières) and Libya (A1-69 borehole)

[Les mégaspores du Dévonien moyen (Givetien)
de Belgique (Ronquières) et de Libye (sondage A1-69)]

Frédéric de VILLE de GOYET¹

Pierre BREUER²

Philippe GERRIENNE³

Cyrille PRESTIANNI⁴

Maurice STREEL⁵

Philippe STEEMANS⁶

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Mots-Clefs : Mégaspores ; Dévonien moyen ; Givetien ; Belgique ; Libye ; biodiversité

1 - Introduction

Preliminary results are presented on newly discovered megaspore assemblages recovered from Givetian localities at Ronquières, Belgium, and a borehole (A1-69) drilled in the Ghadames Basin, Libya, by SHELL in 1959. The miospore biostratigraphy of the Ronquières and of A1-69 borehole sections has been published (VILLE de GOYET, 2005; GERRIENNE *et alii*, 2004; LOBOZIAK & STREEL, 1989; LOBOZIAK *et alii*, 1992; STREEL *et alii*, 1990).

2 - Material and methods

Thirty-six samples have been studied to date. Eighteen are from the "Plan Incliné de Ronquières" section. Their weight ranged

between 60 to 75 g. Most of the samples found productive are grey sandstone. The eighteen Libyan samples are from the collections of the University of Liège. Their weight ranged from 4 to 23 g. They are grey sandstone and sandy clay.

The Libyan samples were immersed in 40% hydrofluoric acid for 3 to 5 days and the Belgian sediments from 5 to 13 days. The rock dissolution was facilitated by a 0.5-1 mm sieve placed under the sample. In consequence, the sediments were constantly surrounded by acid, and the acid insoluble residue dropped through the sieve mesh to the bottom of the container during processing. The sample is thus not coated by acid-insoluble material.

¹ Laboratoire de Paléobotanique, Paléopalynologie et Micropaléontologie, Université de Liège, Allée du 6 août, B18, Sart-Tilman, 4000 Liège (Belgium)
F.deVilledeGoyet@skynet.be

² Laboratoire de Paléobotanique, Paléopalynologie et Micropaléontologie, Université de Liège, Allée du 6 août, B18, Sart-Tilman, 4000 Liège (Belgium)
piet79@yahoo.fr

³ NFSR Research associate; Laboratoire de Paléobotanique, Paléopalynologie et Micropaléontologie, Université de Liège, Allée du 6 août, B18, Sart-Tilman, 4000 Liège (Belgium)
P.Gerrienne@ulg.ac.be

⁴ Laboratoire de Paléobotanique, Paléopalynologie et Micropaléontologie, Université de Liège, Allée du 6 août, B18, Sart-Tilman, 4000 Liège (Belgium)
cyrille.prestianni@ulg.ac.be

⁵ Laboratoire de Paléobotanique, Paléopalynologie et Micropaléontologie, Université de Liège, Allée du 6 août, B18, Sart-Tilman, 4000 Liège (Belgium)
maurice.streel@ulg.ac.be

⁶ Laboratoire de Paléobotanique, Paléopalynologie et Micropaléontologie, Université de Liège, Allée du 6 août, B18, Sart-Tilman, 4000 Liège (Belgium)
p.steemans@ulg.ac.be

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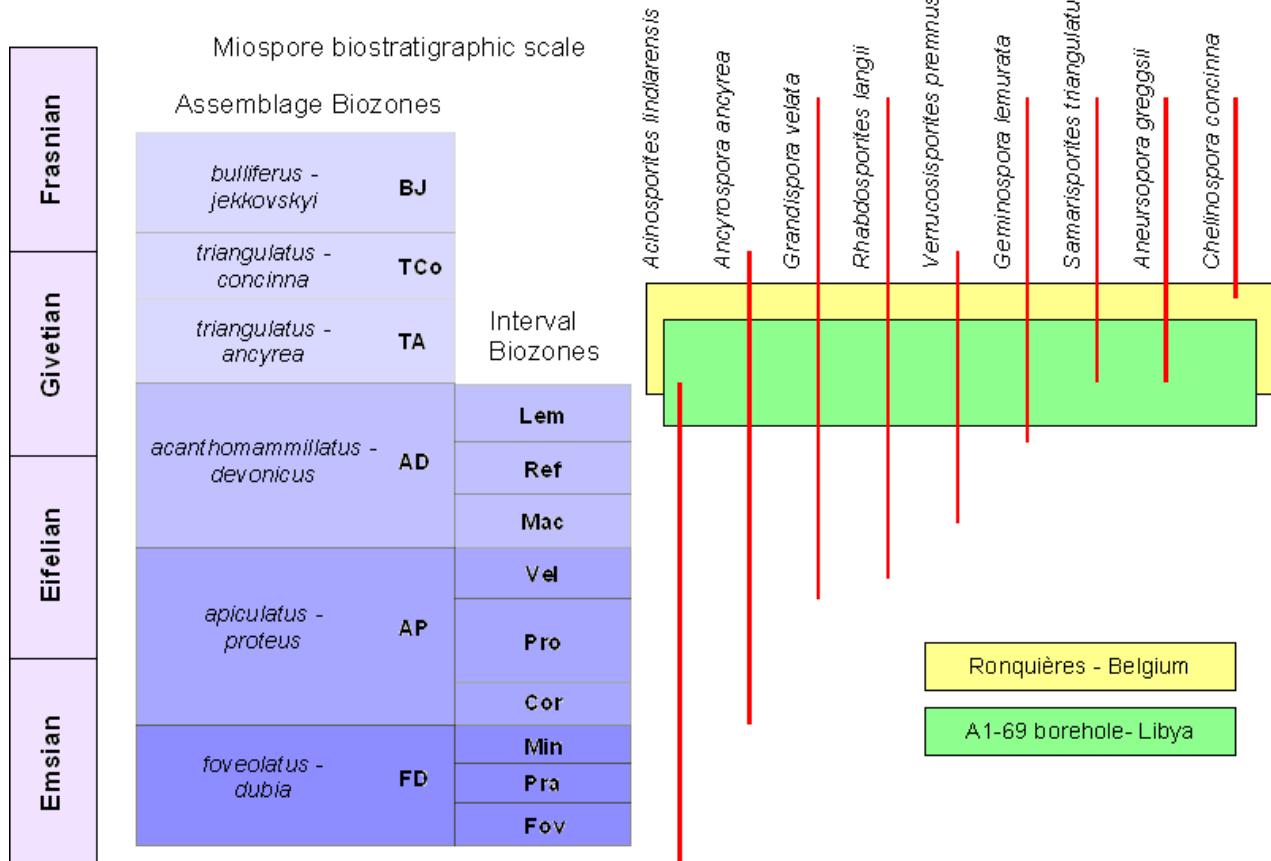


Figure 1: Biostratigraphic extension of selected species observed in the Ronquières and A1-69 borehole sections. The green and yellow rectangles represent the stratigraphic range of the samples containing megaspores. Biostratigraphic scale after STREEL *et alii* (1987).

All residues were washed through a 150 µm sieve. The fraction of the residue less than 150 µm in diameter was re-sieved in order to collect miospores.

Megaspores were located using a dissecting microscope at high magnification (up to 70x). They were picked with a pipette and then placed over a slide on which lines had been engraved. After examination of the upper surface of the megaspore using the SEM, a drop of water was placed on the specimens. This induced the formation of an air bubble under the specimens; so they could be turned over to observe the opposite surface.

3 - Results

3.1. Ronquières

3.1.1. Geographical and geological data

Ronquières is located in the Walloon Brabant Province between the cities of Braine-le-Comte and Nivelles ($x=50^{\circ}36'30''N$, $y=4^{\circ}13'30''E$). The section is situated at the "Plan Incliné de Ronquières".

The sediments of the Givetian at Ronquières are on the northern flank of the Namur Syncline. The megaspores were isolated from grey sandstones in the Bois de Planti Member of the Bois de Bordeaux Formation (BULTYNCK &

DEJONGHE, 2002; HENNEBERT & EGGERMONT, 2002). Most of these sediments were deposited in a fluvial to near-shore environment. One megaspore-rich level also yielded the proto-ovule *Runcaria* STOCKMANS, recently redescribed by GERRIENNE *et alii* (2004). This level is no longer accessible.

During Middle Devonian times Belgium was in the Southern Hemisphere on the Euramerican Plate at 20°S.

3.1.2. Stratigraphic palynology

The stratigraphic range of the biostratigraphically most characteristic miospores from the "Plan Incliné de Ronquières" are illustrated in Figure 1. The miospore assemblage includes, among other species, *Acinosporites lindlaensis* RIEGEL 1968, *Ancyrospora ancyrea* var. *ancyrea* RICHARDSON 1965, *Grandispora velata* (EISENACK) PLAYFORD 1971, *Rhabdosporites langii* (EISENACK) RICHARDSON 1960, *Verrucosporites prenus* (RICHARDSON) RICHARDSON 1965, *Geminospora lemurata* BALME 1962, *Chelinospora concinna* ALLEN 1965, *Samarisporites triangulatus* ALLEN 1965 and *Aneurospora greggsii* (McGREGOR) STREEL 1974.

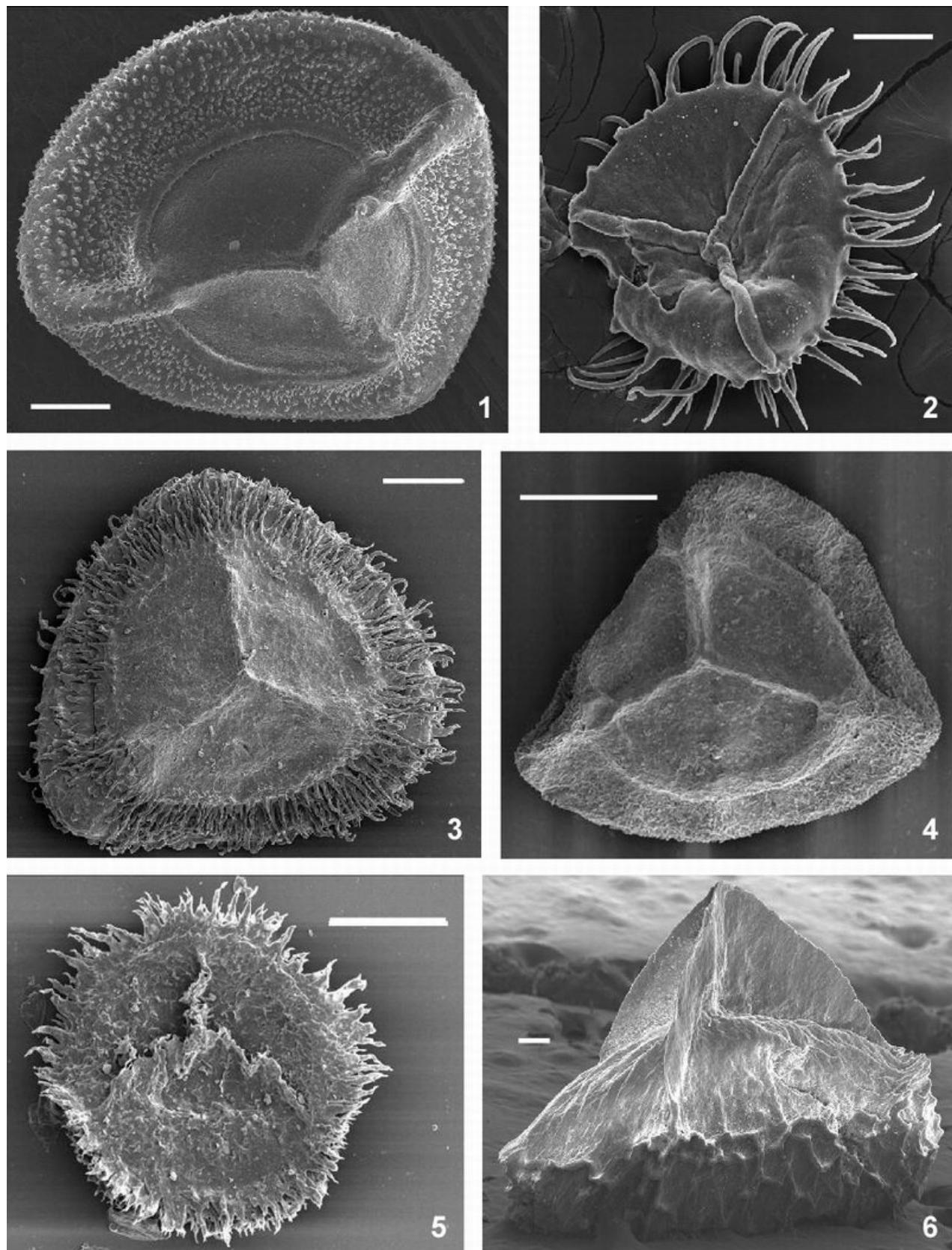


Plate 1: Some selected miospores from the Ronquières and A1-69 borehole sections (scale bars = 100 μm):
figure 1. *Contagisporites optivus* (CHIBRIKOVA 1959) var. *optivus* OWENS 1971. Libyan specimen;
figure 2. *Heliotrilletes longispinosus* FUGLEWICZ et PREJBISZ 1981. Libyan specimen ;
figure 3. *Biharisporites* sp. Belgian specimen;
figure 4. *Contagisporites optivus* (CHIBRIKOVA 1959) var. *optivus* OWENS 1971. Belgian specimen;
figure 5. *Corystisporites multispinosus* RICHARDSON 1965. Belgian specimen;
figure 6. Undetermined specimen showing a large gula. Libyan specimen.

Those species indicate that the sediments of Ronquières range from the uppermost part of the Lem Interval Zone (*G. lemurata* Interval Zone) of the AD Oppel Zone (*A. acanthomammillatus* - *D. devonicus* Oppel Zone) to the lowermost part of the TCo Oppel Zone (*S. triangulatus* - *C. concinna* Oppel Zone) (STREEL *et alii*, 1987). The Ronquières locality is thus middle to late Givetian in age.

3.1.3. Megaspore assemblage description

Nineteen megaspore morphotypes were recognized. The specimens are black and have been altered by thermal diagenesis and damaged by pyritization. This megaspore assemblage is the richest ever described of Givetian age (VILLE de GOYET, 2005).

The megaspores are 200 to 800 µm in diameter. Most are circular; a few others are subtriangular in outline. The labra of the trilete mark can be very high (up to 35 µm) to nonexistent and curvatura may or may not be present. Their ornamentation can consist of grana, coni, spinae, large appendices, or of a reticulum. The maximum length of the ornamentation ranges from 1.5 to 71.6 µm.

Contagisporites optimus (CHIBRIKOVA) var. *optimus* OWENS 1971 (Pl. 1, fig. 4), and *Corystisporites multispinosus* RICHARDSON 1965 (Pl. 1, fig. 5) have been identified from this assemblage.

3.2. Borehole A1-69

3.2.1. Geographical and geological data

The A1-69 borehole is located in the Ghadames Basin of northwestern Libya (X=29°03'50", Y=13°40'13"E). The 18 samples studied are from the interval 1,074 feet (327 m) to 1,486 feet (453 m).

The samples are from the Ouenine II Formation of the Aywanat Wanin Group (MASSA, 1988). The Ouenine II Formation consists of more than 80 m of a greyish green finely bedded argillaceous sequence with three interbedded sandy units. It is a typical deltaic facies.

The paleogeographic position of Libya during the Middle Devonian was at 40°S on the northern margin of the Gondwana plate.

3.2.2. Stratigraphic palynology

The stratigraphic range of the most characteristic miospores in borehole A1-69 is shown on Figure 1.

The miospore assemblage includes, among other species, *A. lindlarensis*, *Grandispora protea* (NAUMOVA) MOREAU-BENOIT 1980, *Emphanisporites rotatus* (MCGREGOR) MCGREGOR 1973, *Grandispora megaformis* (RICHARDSON) MCGREGOR 1973, *R. langii* (EISENACK) RICHARDSON

1960, *Grandispora libyensis* MOREAU-BENOIT 1980, *V. premnus* (RICHARDSON) RICHARDSON 1965 and *S. triangulatus*. This indicates that the Libyan sediments range from the uppermost part of the Lem Interval Zone to the TA Oppel Zone (*S. triangulatus* - *A. ancyrea* Oppel Zone). They are thus middle to late Givetian in age. Hence the samples from Ronquières and Libya are contemporaneous.

3.2.3. Megaspore assemblage description

Twelve megaspore morphotypes have been differentiated. Megaspores range in color from light orange to dark brown and are very well preserved. A few specimens have been altered by pyrite.

Most of the megaspores are circular, but some are subtriangular in outline. The labra of the trilete mark of some specimens are very high (up to 47.9 µm). The contact area is either poorly defined or is well marked by a circular thickening, a depression, or ornamentation. All megaspores from this borehole are ornamented. The length of the ornament ranges from 3.6 to 186.3 µm.

Only *Contagisporites optimus* var. *optimus* (Pl. 1, fig. 1) and *Heliotriletes longispinosus* FUGLEWICZ et PREJBISZ 1981 (Pl. 1, fig. 2) have been identified. Some megaspores from this borehole are so well preserved that we are able to see the ultrastructure of the outer wall and to distinguish differences between the exine layers.

We found some very large megaspores with a maximum diameter of 1000 µm and a length of up to 2000 µm. Some of these megaspores possess a hologula that may reach 1000 µm. They have a spinate or reticulate ornamentation on the central body. The hologula is smooth (Pl. 1, fig. 6).

4 - Discussion

Sediments from both localities are coeval and deposited in very similar paleoenvironments: continental to deltaic for Ronquières and clearly deltaic for the A1-69 borehole. The palaeoclimate of each region was discrete, however, warm and arid in Belgium and warm temperate and wet in Libya (SCOTESE, 2001).

Cross-plot of maximum ornamentation length / maximum diameter of the megaspores from the two areas reveal marked differences. Most of the Libyan megaspores are located in a group characterised by large scale ornamentation (above 50 µm) and sizes ranging from 300 to 450 µm, while in most of the specimens of the Belgian material the length of the ornament ranges from 0 to 50 µm.

The megaspore assemblages from the 2 localities contain many morphotypes as yet

undescribed. And they are very different from each other. Indeed, *C. optivus* var. *optivus* is the only species present in both localities. In contrast to the disparate megaspore assemblages, there are many more correspondences in the respective miospore assemblages (42% of miospore species of Ronquières were also recovered from the Libyan borehole). The coefficient of similarity (CLARK & HARTEBERG, 1983) is moderate to high for miospores (20.83%), but very low for megaspores (3.23%). As the two localities are on widely separated palaeoplates, this difference in coefficients could reflect the fact that because of their smaller size miospores are more easily transported by wind. DILCHER *et alii* (1992) concluded that many Devonian heterosporous plants were probably aquatic. On the contrary, miospore-producers lived in many different biotopes ranging from dry to humid. The fact that megaspores are rarely transported by wind and that they may be produced by a plant living in a restricted aquatic biotope might force a high level of endemism. The presence of processes (spinate, bifurcate processes) on most of them (81% of all specimens) may corroborate the hypothesis regarding functional morphology proposed by DILCHER *et alii* (1992) for the processes of Devonian spores. They suggest that the morphological characters of megaspores may have been developed to provide buoyancy, movement or attachment for some plants living permanently, temporarily or for a particular phase of their life cycle in an aquatic environment. Alternatively, these processes may have been used to facilitate the adherence of the microspores.

Very large megaspores, comparable to those we collected from the Libyan borehole, are extremely rare in sediments older than Carboniferous (CHALONER, 1967; TRAVERSE, 1988) with the exception of that reported in the Bois de Bordeaux Formation by STOCKMANS and STREEL (1969). TEM study of specimens will help to determine whether or not our megaspores possess an ultrastructure indicating lycopsid affinities (CHALONER, 1980; BRACK-HANES, 1981).

5 - Conclusions

Those results show that:

- 1) static dissolution of sediments allows isolation of some fragile large palynomorphs;
- 2) the biodiversity of Givetian megaspores is greater than that assumed previously. A total of 30 different morphotypes have been recognized from Ronquières and from the borehole A1-69 from Libya, with only one species common to both localities;
- 3) evolution in the size of megaspores occurred earlier and took place more rapidly than expected;
- 4) process morphology could be either an adaptation to an aquatic environment (DILCHER

et alii, 1992) and/or due to climatic factors.

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