The plant remains from the Late Famennian of Belgium: A review

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A short survey of the plant lineages represented in the Late Famennian "Evieux flora" in Belgium is provided. Recent data about the taxonomy of these fossil remains are gathered and the morphological diversity of the early seed plants is emphasised. The climatic conditions prevailing in Belgium at that time are briefly considered.

Key -words—Evieux flora, Cupule systems, Palaeoclimate, Famennian, Belgium.

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सारांश

बेल्जियम के अनंतिम फामेनियन से पादप अवशेष : एक समीक्षा

मुरियल फेयरॉन-डेमरॅट

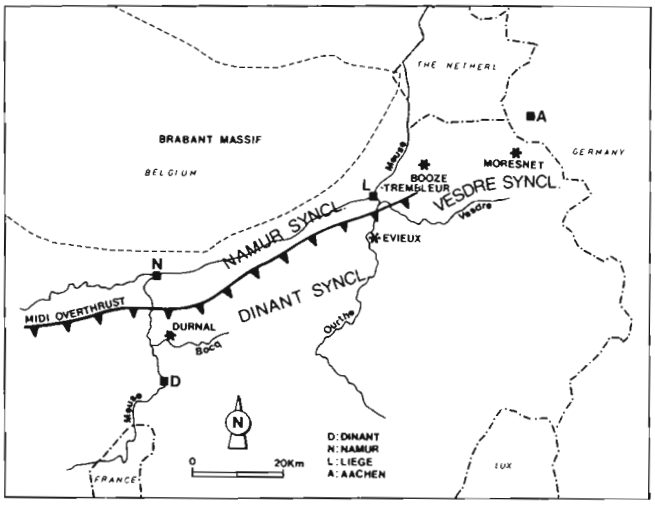
बेल्जियम में अनंतिम फामेनियन "एवियॅक्स वनस्पतिजात" में मिले पादप अवशेषों की समीक्षा की गई है। इन पादप-अवशेषों के वर्गिकीय आँकड़े एकत्र किये गये हैं तथा प्रारम्भिक बीज वाले पौधों की आकारिकीय विभिन्नता पर बल दिया गया है। इस समय बेल्जियम में जलवायवी परिस्थितियों के बारे में भी संक्षिप्त विवेचना की गई है।

IN Belgium, most, if not all the Late Famennian fossiliferous outcrops belong to the Evieux Formation of the upper part of the Condroz Sandstone Group or "Psammites du Condroz". They always yield numerous specimens which, however, usually represent a rather monotonous assemblage dominated by remains of *Archaeopteris* or *Rhacophyton*. Diversified plant remain associations are uncommon but they contain rare sphenopsids and lycopods and more especially early seed plant preovulate structures, sometimes together with detached pinnules fragments. Since the pioneering work of Crépin (1874) and Gilkinet (1875, 1922) these plant assemblages collected in the Evieux Formation are collectively designated as the "Evieux flora".

The most extensive account on the "Evieux flora" still remains the publication of Stockmans (1948) who described 25 different taxa collected from a variety of deposits outcropping in the then called "Assise d'Evieux". In the early fifties Leclercq brought also her contribution to the study of these Upper Devonian plant remains with in depth revisions and extension of some of the Stockmans' descriptions. Several contributions appeared during the last ten years and the discovery of new well preserved specimens of early seed plant fossils renewed interest in the "Evieux flora". The purpose of this short paper is to gather the information about this "Evieux flora" which are dispersed in the literature and to provide an up-to-date overview of the taxonomy of these remains and the recent data about the their palaeoenvironment.

GEOLOGICAL SETTING, STRATIGRAPHY AND DATATION

The "Psammites du Condroz" outcrop in three main tectonic units: the allochthonous Dinant Synclinorium and the autochthonous Namur and Vesdre Synclinoria, all located south or south-east of the London-Brabant Massif (Text-figure 1). The



Text-figure 1— Geographical location of the important localities in the "Psammites du Condroz".

Namur and Dinant Synclinoria are separated by the Midi-Eifel-Aachen Over thrust. The latter Synclinorium, the width of which is 20-30 km, measured at a right angle to the Midi-Eifel-Aachen Over thrust is by far, the most productive area. Two decades ago, numerous quarries were still extracting the micaceous "sandstone" beds along the main river valleys such as the Ourthe, Hoyoux, Bock, Meuse, and Lesse valleys (see Thorez & Dreesen, 1986, fig. 1 for location map of the studied outcrops in the Dinant Synclinorium).

Several localities in the Evieux Formation (indicated in Text-figure 1) are particularly rich in plant remains: e.g., Evieux in the Ourthe valley, Pontde Bonne in the Hoyoux valley and Durnal in the Bocq valley belong to the Dinant Synclinorium. Moresnet, Booze-Trembleur and Foret-Trooz are located in the Vesdre Synclinorium.

Intensive studies have been conducted simultaneously into the lithostratigraphy, biostratigraphy and sedimentology of the Condroz Sandstones. They demonstrate the progradational (regressive) pattern of the group which displays a complex interfingering of depositional environments. These developed during the progradation of siliciclastic sediments onto the Condroz shallow marine shelf area (Bouckaert *et al.*, 1968; Thorez *et al.*, 1977, 1988; Thorez & Dreesen, 1986; Dreesen *et al.*, 1988). Each of these environments is evidenced by its rhythmic construction, by the distribution and abundance of associated sedimentary structures or by the presence of particular organisms. Plant remains occur in the upper part of the Condroz Sandstones in fluvial deltaic (with red beds and dolocretes) to distal alluvial, alluvio-lagoonal with tidal delta, point bar or estuary channel and near shore sandy barrier settings (Thorez *et al.*, 1988, Dreesen *et al.*, 1993).

Lithostratigraphic correlations have been controlled by micropalaeontological data (spores, conodonts, ostracods) in some strategic outcrops. These provided the so-called 'Micropalaeontological Guide Marks'(mgm; Streel *et al.*, 1975) which combine microfossil zonal ranges into a calibration of multiple zonal schemes for both local (in-valley) and intrabasinal (valley-to-valley) correlations. Recent works on spores and conodonts have provided a refined biostratigraphic scheme (Dreessen *et al.*, 1988, 1993). Palynological assemblages obtained from the "Evieux flora" embedding sediments belong to the VCo (*versabilis-cornuta*) Spore Zone (Paproth *et al.*, 1986; Clemente, 1985; Streel *et al.*, 1987) and most of the outcrops are in the lower part of this Zone (Streel & Scheckler, 1990). The "Evieux flora" is thus often regarded as lower Fa2c in age. However, when compared to the conodont based biostratigraphy, the base of the VCo Spore Zone is not precisely positioned, occurring somewhere within the *trachytera* and *postera* zones of the standard Conodont Zones of Ziegler and Sandberg, 1990 (Streel & Meziane in Dreesen *et al.*, 1993). Accordingly a Fa2b/Fa2c chronozone limit may not be characterised any more by the base of the VCo Spore Zone. Consequently these chronozone connotations should be avoided, the lower age limit of the Evieux flora being still not assessed with accuracy.

GENERAL COMPOSITION OF THE "EVIEUX FLORA"

All the main plant lineages are represented in the "Evieux flora", as demonstrated by a survey of the most productive localities mentioned above.

Progymnosperms

Archaeopteris-Callixylon remains are present in almost every plant locality (Stockmans, 1948). Concentration of drifted logs of *Callixylon* are not rare (Fairon-Demaret, 1986).

The Vesdre Synclinorium yields the first *Archaeopteris* specimens ever mentioned in the literature (Göppert, 1874). Specimens of *A. roemeriana* (Göppert) sensu Stockmans 1948 collected by Gilkinet (1922), Stockmans (1948) and new material from the Bocq Valley have been analysed recently. In the vegetative ultimate axis, the leaf size polymorphism and the bilateral symmetry of the vascular tissues in transverse section is demonstrated. The fertile ultimate branches on the other hand, show radial symmetry, similar size of leaves on opposite sides of the axes and greater number of fertile leaves and orthostiches per unit length of axis (Kenrick & Fairon-Demaret, 1991). Actually, *A. roemeriana* and *A. macilenta* are similar in these respects and a re-evaluation of these two species is obviously necessary.

Aneurophyton olnense Stockmans 1948, occurring in one locality only is usually considered as another member of the Progymnosperms. A recent re-examination of the type specimens suggests they should not be included in the genus *Aneurophyton*. Its affinities remain pending.

Zygopteroid ferns

Rhacophyton condrusorum was the first plant to be described (under the combination *Sphenopteris condrusorum* Crépin, 1875) from the "Evieux flora". *Rhacophyton* is well represented in the Belgian Upper Famennian plant assemblages but is not as widespread as *Archaeopteris-Callixylon* fragments. Its remains which usually depict almost pure stand, as already mentioned by Leclercq (1951), appear tightly facies-bound, occurring only in siltstone and mudstone lenses. Knowledge of the habit of the plant and of its zygopteroid anatomy result from the detailed studies of Leclercq (1951) who established the second species *R. zygopteroides*. In fact, *R. zygopteroides* and *R. condrusorum* share many characters in common, differing mainly in size. *Rhacophyton* is the only coloniser of the Late Famennian swamps but it was also a tolerant plant growing on more drier sites too (Scheckler, 1986a). Differences in size, particularly of the fertile aggregates, might be related to divergence of species from wet and drier habitats, from swampy and flood plain environments (Scheckler, 1986a). Moreover as detailed comparative studies are still lacking *R. zygopteroides* and *R. condrusorum* are presently, better kept separate.

Sphenophytes

Sphenopsid remains are rare in the Condroz Sandstones. They always demonstrate obvious transportation. For example in the Hoyoux Valley, rare, detached, shaggy *Eviostachya* cones were washed within the delicately preserved remains of *Rhacophyton zygopteroides*. The study by Leclercq (1957) of these tiny cone of *Eviostachya* still remains an example of successful application of adequate techniques, with the demonstration of eleven whorls of sporangiophores spaced 2-3 mm apart; each whorl consisting of 6 sporangiophores given off in pairs; each sporangiophore is divided into three segments which divided in turn into three lesser segments; each of these segments bears three terminal, recurved sporangia (27 per sporangiophore). Recently occurrence of *Eviostachya,* which formerly appeared restricted to the Belgian Late Famennian is demonstrated in China (Wang, 1993), from strata in the Wutung Formation, which might be equivalent in age (Lu, 1994). *Sphenophyllum subtenerrimum* illustrated by Ledoux-Marcelle (1927) in the Ourthe Valley was recently observed again in the Trooz quarry, Vesdre Valley, where several macerated twigs of *Sphenophyllum* cf. *subtenerrimum* occur within drifted plant remains, fish scales and, more significantly, inarticulate brachiopods of the Orbiculoidea group, indicating a marine environment of deposition (Fairon-Demaret, in press).

Lycophytes

While several thousands of plant remains were collected in the Evieux Formation, only a dozen of fragments are assignable to the lycopods. Most of them come from the Evieux locality in the Ourthe Valley; one specimen, severely macerated but with permineralised internal structure, occurred, washed in the *Rhacophyton zygopteroides* remains in the Hoyoux Valley. These lycopod fragments have been successively compared to the Scottish *Archaeosigillaria* (Walton, 1931) or to *Cyclostigma brevifolium* (Stockmans, 1948). Recently most of them were demonstrated to be fertile and combination of new

data on their external morphology, anatomy and spores led their assignation to a new genus and species, *Barsostrobus famennensis* Fairon- Demaret 1991.

Barinophytes

Barinophyton citrulliforme is recorded from many localities (Gilkinet, 1922; Stockmans, 1948) where rare isolated fragments are observed in a variety of lithologies, from mudstone to micaceous arkosic sandstones (in the latter case *Barinophyton* remains consists of impressive pyritized carbonaceous fragment). According to Scheckler (1986a), *Barinophyton* is interpreted as a shore adapted plant, a deduction that is not challenged by the depositional settings of its occurrences in the Evieux Formation.

Frond remains

A variety of frond and pinnule remains have been collected and attributed to six different species of *Sphenopteris* by Stockmans (1948), the most common being the polymorph *S. flaccida* Crépin 1874 which is present in at least ten localities. *Sphenocyclopteridium belgicum* Stockmans 1948 (ex *Triphyllopteris elegans* Crépin, 1874) is less widely distributed in the plant assemblages. All these *Sphenopteris* and *Sphenocyclopteridium* remains are fragmentary and their eventual relationships with the early seed plants still remain to be demonstrated: even if both detached pinnules and cupulate structures are on very rare occasions, observed associated on the same bedding plane, up to now, connections are still missing.

Ovulate or preovulate structures

Early seed plant remains are abundant in several localities of the Evieux Formation. They consist mostly of remains of cupulate structures. The most common belong to *Moresnetia zalesskyi* Stockmans 1948 (Pl. 1, figs 1-5). The best, most impressive specimens which allowed a good understanding of the terminal branching system and of the cupulate structure of this early seed plant, are collected in the Bocq Valley. They occur in grey to dark mudstone filling an estuary channel, within characteristic lenticular sandstones, the overall architecture of which corresponds to a point bar (Thorez, personal comm.). *M. zalesskyi* with cruciately forking systems of cupules enclosing preovules with hydrasperman reproduction (Fairon-Demaret & Scheckler, 1987), shares the same overall design of cupule and preovule morphology as *Elkinsia polymorpha* Rothwell *et al.* and might be included within the Elkinsiales, as advocated by Serbet and Rothwell (1991). Both early seeds differ in the degree of fusion of the integumentary lobes, almost free from their base in *M. zalesskyi* and fused up to about one third of their length in *E. polymorpha,* a character which is very difficult to demonstrate on compressions (Pl. 1, figs 3, 5). More readily noticed, is the strong overtopping (Pl. 1, figs 1, 3) of the cupule

PLATE 1

1-5. *Moresnetia zalesskyi*

1. General aspect of the cupules at the tip of the axes. ULg 12953. x 2,5.
2. Detail of a cupule split open and showing one enclosed seed (s). ULg 12984. x 4.
3. Detail of figure 2; i: integument lobe; mg: megaspore; l: lagenostome.
4. General view of a branch system with numerous overtopped cupules. ULg 12.934. x 1.
5. Detail of a cupule split open, with two enclosed seeds; the integumentary lobes are exposed. ULg 13.03. x 8.

6-9. *Dorinnotheca streelii*

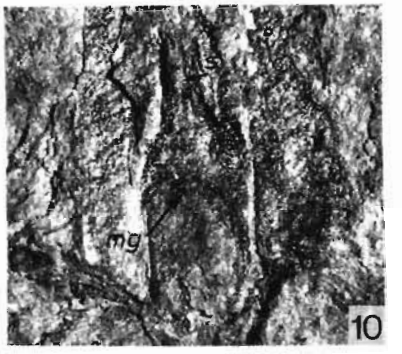
6. Detached seed showing three integumentary lobes, 1, 2, 3, and recurved cupule elements; under integumentary lobe 2, the tubular, salpinx-like extension of the nucellus (s) is visible. ULg 13217a.
7. Cupule observed spread on the fracture plane. 8 dissected segments are exposed. ULg 13245a. x 4.
8. Detail of the counter-part of the specimen illustrated in fig. 7. The 8 cupule segments are proximally fused. The conical projection in the centre of the fig. corresponds to the stalk. ULg 13245b. x 10.
9. General view of a detached cupule split open. Two integumentary lobes look like narrow thick triangles on both sides of the nucellus (n). ULg 13470. x 4.
10. Detail of fig. 9 showing the nucellus and its salpinx-like extension (s). The top of the megaspore is indicated by a slight difference of level (mg). x 10.
11. General view of another detached cupule split open. ULg 13470. x 4.

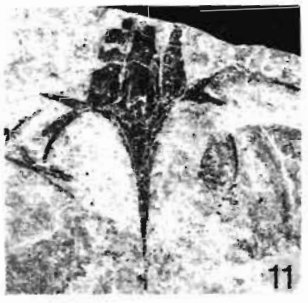
12-13. *Moresnetia* sp.

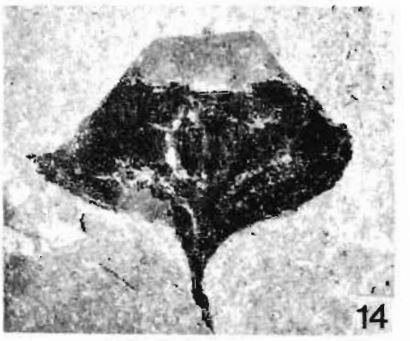
12. General view of a detached cupule. ULg 13509. x 4.
13. Bouquet of cupules. ULg 13510. x 4.

14-15. *Condrusia rumex*

14. Detached seed with brittle carbonaceous remains. ULg 13065. x 4.
15. Another detached seed preserved as an impression on the sediment. ULg 13060/8. x 4.







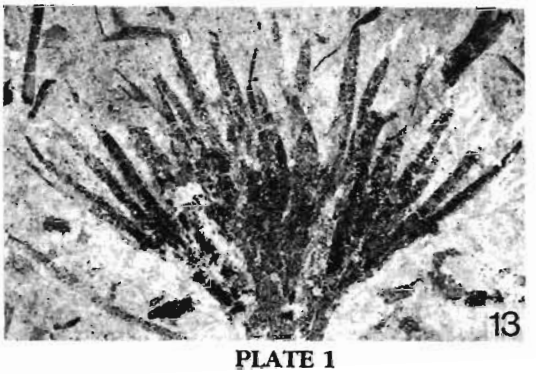


PLATE 1

systems of *M. zalesskyi* which gives an unique appearance to the remains of the plant.

Another species of cupulate preovulate structures has been recently discovered in Foret-Trooz, Vesdre Valley. It apparently shares the same general organisation as *M. zalesskyi* but differs from the latter by the much more regularly arranged cupule lobes (Pl. 1, figs 12, 13); the bouquets of cupules at the tip of the branches systematically gather four cupules and these show almost no sign of overtopping at all. These new specimens that are currently under study, are associated with "regular" *M. zalesskyi* and are readily distinguishable from it.

Remains of still another early seed plant were also discovered in the same locality. They also are collected in the Ourthe and in the Bocq valleys where they occur on the same slab as *Moresnetia zalesskyi* remains. *Dorinnotheca streelii* Fairon-Demaret (in press) bears cupules hanging singly at the tips of the slender ultimate axes of a pinnately branched system. Each cupule encloses a single, centrally located preovule protected by sturdy, free, integumentary lobes, only four in number (Pl. 1, figs 6, 9, 11). At the base of the fertile unit, the cupule segments are fused (Pl. 1, figs 7, 8) for a quarter of their total length; higher up they are free, recurved and highly dissected (Pl. 1, figs 5, 9, 11). The integumentary lobes and the fused part of the cupule segments appear joined. The preovule is sessile. At the top, the nucellus shows occurrence of a pollen chamber, most probably of the hydrasperman type, with a long, tubular, salpinx-like extension (Pl. 1, 7 figs 10, 11). *Dorinnotheca illustrates* a morphology that deviates from the cruciately forking cupule systems which are regarded as " characterising virtually all the well known seed megasporangiate fructifications from Upper Devonian" (Rothwell & Scott, 1992, p. 283). None of the coeval or slightly younger previously described form display preovules which occur singly in the centre of the proximal, fused, cup-like part of a dissected cupule. On the other hand, the long tubular extension of the top of the nucellus appears as a specialised, adaptive character. The organisation of this preovulate structure doesn't appear primitive. It is postulated that this salpinx-like extension of the apex of the nucellus, by preventing desiccation of the pollen chamber area, might be an adaptive response to a very dry living environment (Fairon-Demaret, in press).

From two localities in the Evieux Formation, Stockmans (1948, pl. XI, figs 14-17) illustrated still another type of early seeds he designated as a new species of *Xenotheca, X. bertrandii* Stockmans, because he thought they were cupulate. Their attribution to the genus *Xenotheca* is challenged by Fairon-Demaret and Scheckler (1987). They most probably belong to still another type of early seeds.

Most intriguing and still different, *Condrusia rumex* Stockmans 1946 and *Condrusia minor* Stockmans 1948 are presently under study. Many new specimens have been collected in the Bocq Valley. Most often they are preserved as brittle, carbonaceous compressions (Pl. 1, fig. 15) or as impressions (Pl. 1, fig. 16). Despite the appearances, up to now, the bilateral nature of the whole structure can't be assessed, nor the number and details of the enclosed ovule(s), nor the organisation of the enclosing? foliaceous appearing structures. Such specimens address more questions than they solve.

The "Evieux flora" yields thus at least five different species of early seeds. Among these, four taxa exhibit strikingly different morphologies. They demonstrate evolved, specialised stages of diversification that imply the existence of pre-late Famennian more primitive forms.

PALAEOENVIRONMENTAL CONSIDERATIONS

During Famennian times the Rheno-hercynian realm was occupied by a shallow epicontinental sea bordering a northern, deeply eroded, Old Red Continent. The "Psammites du Condroz" were deposited in an area which corresponds now to the Belgian Ardenne (Paproth *et al.*, 1986). It was located in the then southern hemisphere between latitudes 20° and 15°S (Streel, 1986; Scheckler, 1986b; Dreesen *et al.*, 1988). The Condroz shelf was submitted to westerly tropical winds and storms and such a situation provided a relatively arid to sub-arid climate (Paproth *et al.*, 1986; Dreesen *et al.*, 1988). The characteristics of the sediment (occurrence of fresh arkosic sandstones) and the episodic, rhythmic development of evaporitic dolomites assemblages, demonstrated from multidisciplinary analyses, are in agreement with such palaeoclimatic conditions. The fluvial sys-

tem draining the hinterland was characterised by strong, flash floods (Streel & Scheckler, 1990), as evidenced, among other arguments, by episodic influxes of alluvial discharges (Paproth *et al.*, 1986).

The probably slightly younger assemblage (upper VCo Spore Zone containing *Vallatisporites hystricosus*, Streel & Scheckler, 1990) from the Hampshire beds in West Virginia and Virginia (U.S.A.), which occurs in mainly alluvial and fluvial facies (Scheckler, 1986a, b), yields plant species similar or closely related to those of the Belgian lower VCo localities. The sediments from both areas also contain very similar assemblages of miospores (Streel & Scheckler, 1990). Nevertheless, the Famennian deposits of Appalachian North America are rich in arborescent lycopod fragments, all the data suggesting that these lycopod trees were growing near the *Rhacophyton* swamps, depicting "inland fringes" (Scheckler, 1986a, p. 220). In the Evieux Formation the scarcity of lycopod remains is a general phenomenon. This difference might result from different palaeoclimatic conditions on both sides of the Acadian mountains. The American Appalachian basin was located on the windward, rainy side of the Acadian mountains where the climate was probably less arid. Nevertheless, in the Evieux Formation the plant bearing strata correspond to distal alluvial and usually near shore environments; no remains of *in situ*, rooted, plant communities in the hinterland are known up to now. In both areas the environments of deposition remaining to-day are not similar and on taphonomic grounds preclude valuable global comparisons between their macrofossil content.

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