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Typification and redescription of *Moresnetia zalesskyi* STOCKMANS, 1948, an early seed plant from the Upper Famennian of Belgium

by Muriel FAIRON-DEMARET and Stephen E. SCHECKLER

Abstract

A lectotype is chosen for STOCKMANS' genus and species *Moresnetia zalesskyi* now shown to be a cupulate seed plant. Analysis of new collections from the Bocq Valley and restudy of STOCKMANS' specimens from several localities in the Dinant Synclinorium (material of both origins has been collected in the Evieux Formation = Fa2c) demonstrate the details of seed and cupule structure as well as the general organization of the terminal branchlets of *Moresnetia zalesskyi* which is one of the earliest seed plants. The characters that distinguish it from all other Late Devonian seed plants are discussed, e.g., *Archaeosperma arnoldii* PETTITT & BECK, 1968; *Xenotheca devonica* ARBER & GOODE, 1915; *Hydrasperma tenuis* LONG, 1961 emend. MATTEN, LACEY & LUCAS, 1980; *Spermolithus devonicus* JOHNSON, 1917; and the new plant of GILLESPIE, ROTHWELL & SCHECKLER, 1981.

Key-words: *Moresnetia* - seeds and cupules - Famennian - Belgium.

Résumé

Un lectotype est sélectionné pour le genre et l'espèce *Moresnetia zalesskyi* de STOCKMANS dont la nature de plante à graines cupulées est maintenant démontrée. L'analyse de nouvelles collections de la Vallée du Bocq et le réexamen des spécimens de STOCKMANS de diverses localités du Synclinorium de Dinant (le matériel des deux provenances a été récolté dans la Formation d'Evieux = Fa2c) mettent en évidence les détails de la structure des graines et des cupules ainsi que l'organisation générale des rameaux terminaux de *Moresnetia zalesskyi* qui est l'une des plus anciennes plantes à graines. Les caractères qui la distinguent de toutes les autres plantes à graines du Dévonien Supérieur, à savoir *Archaeosperma arnoldii* PETTITT & BECK, 1968; *Xenotheca devonica* ARBER & GOODE, 1915; *Hydrasperma tenuis* LONG, 1961 emend. MATTEN, LACEY & LUCAS, 1980; *Spermolithus devonicus* JOHNSON, 1917; et la nouvelle plante de GILLESPIE, ROTHWELL & SCHECKLER, 1981, sont discutés.

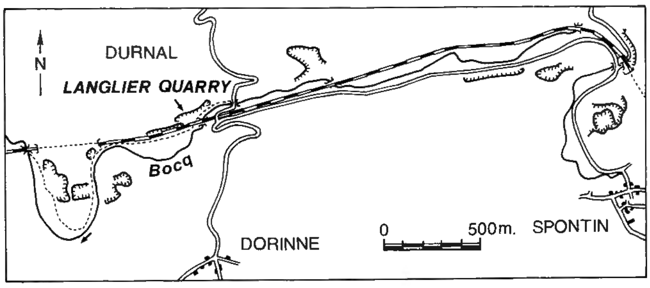
Mots-clefs: *Moresnetia* - graines et cupules - Famennien - Belgique.

Introduction

In 1946 F. STOCKMANS briefly described the fossil plants of Belgium. In his description of the Late Famennian plants, he introduced two new names (*Moresnetia zalesskyi* and *Condrusia rumex*) for plant fossils that had not previously been recognized. These were accompagnied by two drawings. Although this marks the effective publication of these names, no diagnoses nor descriptions nor comparisons with similar forms were given so that these are *nomina nuda* (Articles 29, 32 and 34, International Code of Botanical Nomenclature). STOCKMANS (1948) published detailed descriptions of the Belgian Late Famennian flora in which diagnoses, descriptions, comparisons and photographic illustrations of *Moresnetia zalesskyi* and *Condrusia rumex* (and *C. minor*) were given. This constitutes valid publication so that these names date from 1948 instead of 1946 (Articles 11, 12, 32, International Code of Botanical Nomenclature). At this time STOCKMANS regarded *Moresnetia* as an axis repeatedly divided by dichotomies "dont les ultimes passent insensiblement à des feuilles de contour général triangulaire, bifides, à dents largement effilées" (STOCKMANS, 1948, p. 55), the apical, assymetric, bouquet of forked leaves having a "faux aspect de cupule".

Since that time, seed-bearing cupule systems have been discovered from strata of similar or slightly younger age and have extended considerably our knowledge of the earliest seed plants (PETTITT & BECK, 1968; PETTITT, 1970; MATTEN *et al.*, 1980; GILLESPIE *et al.*, 1981; MATTEN *et al.*, 1984). Several authors (ANDREWS, as early as 1966; PETTITT & BECK, 1968; PETTITT, 1979; GILLESPIE *et al.*, 1981; GENSEL & ANDREWS, 1984) have commented on the similarity of their seed plant fossils with *Moresnetia zalesskyi.* Spurred by these discoveries and comments, we have re-investigated STOCKMANS' *Moresnetia*; similar fossils, such as *Xenotheca devonica* (ARBER & GOODE, 1915; ROGERS, 1926) and STOCKMANS' (1948) *X. bertrandii* have also been examined for evidence of their possible seed plant affinity (SCHECKLER, 1985; FAIRON-DEMARET, 1986; FAIRON-DEMARET & SCHECKLER, 1986).

We have restudied STOCKMANS' (1946, 1948) illustrated specimens of *Moresnetia* as well as the several thousand more, collected by STOCKMANS, that are housed at Brussels in the Royal Institute of Natural Sciences of Belgium according to the locality from which they come. Important new collections and preparations of *Moresnetia* from the Bocq Valley,



Text.-fig. 1. *Location of Langlier Quarry, in the Bocq Valley, that yielded numerous specimens of* Moresnetia zalesskyi. *(1/10.000 topographic map of Belgium 53/4 - 54/1).*

Langlier Quarry (Text.-fig. 1), near Dorinne and Spontin (Province of Namur, Belgium) supplement STOCKMANS' specimens so that we now have a good understanding of this plant.

From STOCKMANS' and our new material we are able to demonstrate that *Moresnetia* is another Late Devonian seed plant, the cupules of which are borne on the terminal axes of a large, three-dimensionally forked, branch system. The seeds of *Moresnetia zalesskyi* are more primitively organized than those of any other Devonian seed plant yet described and resemble those of *Genomosperma kidstonii* from the latest Tournaisian and earliest Visean, which are often cited as showing archaic seed organization (LONG, 1960 a & b, 1961; ANDREWS, 1963; SCOTT, GALTIER & CLAYTON, 1984).

Not only is *Moresnetia zalesskyi* an important milestone in our discovery of early seed plants, but many of the exposures of the Evieux Formation from which it comes have been precisely dated biostratigraphically by the use of microfossils and the depositional settings of this time-trangressive formation have been described (STREEL *et al.*, 1975; THOREZ *et al.*, 1977; THOREZ & DREESEN, 1986; STREEL, 1986).

Unfortunately, STOCKMANS (1946, 1948) failed to designate a holotype as required by Article 23 of the International Code of Botanical Nomenclature. Accordingly, we have restudied all of his syntypes and selected as the lectotype the specimen on which STOCKMANS based most of his understanding of this plant. This specimen, first figured in 1946 (fig. 1), was the first one found by STOCKMANS in 1936 at Moresnet. Its preparation revealed the form of what we know to be the cupule lobes and these data formed the base for most of STOCKMANS' (1948, p. 55) description. We have found that the form of the cupule lobes is an important character that identifies the other Devonian cupulate seed plants [*Archaeosperma arnoldii* (PETTITT & BECK, 1968), *Xenotheca devonica* (ARBER & GOODE, 1915; ROGERS, 1926), *Hydrasperma tenuis* (of MATTEN, LACEY & LUCAS, 1980), and the new plant of GILLESPIE *et al.*, 1981) in addition to seed and cupuliferous axis morphology. Several important features of cupule morphology are well shown by this specimen which we here select as the lectotype.

We provide below a brief description of our new findings and illustrate those of critical importance to re-defining this Late Devonian seed plant, compare *Moresnetia zalesskyi* with other Devonian seed plants, and give emended generic and specific diagnoses.

Description

1. *Seed morphology.*

Proof that the "asymmetric bouquet of leaves" are really seed plant cupules comes from our discovery of their seeds. Among the syntypes seeds are shown inside several cupules from Assesse (STOCKMANS, 1948, Pl. 9, fig. 7-7a) and we have seen many others in STOCKMANS' unillustrated specimens from Assesse also (i.e. this paper Pl. 3, Fig. 3), from Moresnet, Hamois (Pl. 1, Figs. 1, 2), Evrehailles and Strud-Haltinne (Pl. 1, Fig. 7), but our best specimens come from the Bocq Valley (i.e. Pl. 1, Fig. 4).

Seeds are variable in size ranging from 2.5 mm to 4 mm long with a few being as small as 1 mm and others up to 5 mm long. They attach by a very short stalk, that usually appears as a constriction of the base of the chalaza (Pl. 1, Fig. 3, 6), to the inner facing surface of cupule segments. This stalk is seen mainly as an abrupt constriction (circa 0.5 mm in diameter) at the point of attachment while the chalaza itself is expanded to about 1 mm wide (Pl. 1, Figs. 3, 6). Seeds may be wider (slightly more than 1.0 mm) near their middle (Pl. 1, Figs. 3, 9, 10; Pl. 2, Figs. 2, 3; Pl. 3, Fig. 5) or their apex (Pl. 1, Fig. 4; Pl. 2, Fig. 15) depending on the degree of spreading of the free portion of the integument lobes.

The integument consists of 8 to 10 thin lobes that seem to be fused to one another or to the nucellus only at the chalaza. Some compressions suggest this separation of lobes well (Pl. 1, Figs. 4, 6) while others could be interpreted as ridged seeds with only the tips of the integument free (Pl. 1, Figs. 3, 8, 10-12; Pl. 2, Figs. 8-11, 14, 15; Pl. 3, Fig. 5). Fortunately many cupules and the enclosed seeds are petrified in our specimens from the Bocq Valley. Preparations show little histological detail, but do confirm that the integument separates into free terete lobes within 1 mm or less from the base of the chalaza (Pl. 1, Fig. 13). Our anatomical preparations reveal little so far about the nucellus. But by carefully removing the overlying sediment and integument lobes with needles, we can show that the nucellus is about 3/4 the length of a seed, is free from the integument except at the chalaza, and has a large rounded distal tip from which extends a large conical lagenostome (= salpinx of some authors) (Pl. 2, Figs. 2, 3). Further uncovering has revealed the seed megaspore inside the nucellus (Pl. 1, Fig. 9; Pl. 3, Fig. 5) so that there can be no doubt that we have correctly identified these structures as seeds. The functional megaspore is elongate and tapers distally to a point (chalazal end of nucellus). The proximal end (apex of nucellus) is covered by three small bumps which represent the aborted megaspores of the tetrahedral tetrad (Pl. 3, Fig. 5).

2. *Cupule morphology.*

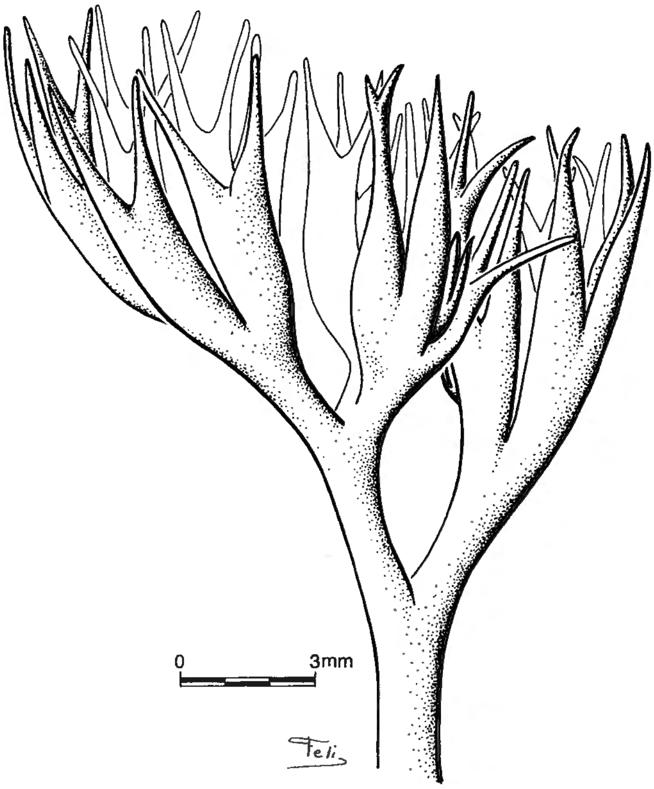
Cupule form and arrangment are the most visible characters of *Moresnetia* by which all the specimens are recognized.

Cupules appear to be borne in pairs, on top of short terete bifurcating axes which fork at narrow angles (Pl. 1, Figs. 1, 2, 5; Pl. 2, Figs. 4-15; pl. 3, Figs. 1, 2, 4). The apparent pairs of cupules are markedly asymmetric with one member being narrower and overtopped by the other which is sustained by a longer stalk (Pl. 2, Figs. 4-14). This taller member of the conspicuous pair is actually more complicated than it appears, consisting in fact, of two tightly appressed individual cupules borne each on a very short stalk. These two stalks may be more or less equal in length (Pl. 2, Figs. 12, 13) or one may be longer than the other so that the terminal bouquet of cupules shows three main units (Text.-fig. 2) with the more distal one overtopping the others (Pl. 1, Fig. 5; Pl. 3, Fig. 1, on the right). Definite pairs with only two cupules are most often encountered at or very near the top of the branch system (Pl. 1, Fig. 5, on top of the specimen).

At the base of each individual cupule the stalk forks cruciately twice into four main parts, or cupule quarters (which are indicated by Roman numerals on Pl. 2, Figs. 4-15), that surround a central space. The cupule quarters are further divided by two dichotomies (third and fourth levels of forking) which are successively oriented tangentially and radially with respect to the central space the cupule quarters enclose. These four successive forkings result in a maximum of 16 tips per individual cupule.

The divisions of an identical level of dichotomy do not occur simultaneously in each of the cupule quarters: they are delayed in the more distal ones (which are not facing the opposite cupules of the bouquet) where the tips, as a consequence, are longer, overtopping the others (Pl. 2, Figs. 11, 13, 14).

The width of the cupule segments formed by the repetitive forking can vary markedly. Some (e.g. STOCKMANS, 1948, Pl. 9, figs. 2-2a, 3-3a; this paper Pl. 1, Figs. 8, 11, 12; Pl. 2, Fig. 7) are noticeably wider just before the terminal fork that produces the finely tapered tips. Others (STOCKMANS, 1948, Pl. 9, figs. 4-4a, 5-5a, 7-7a; this paper Pl. 2, Figs. 4 to 6) are narrower and still others (STOCKMANS, 1948, Pl. 9, fig. 1-1a) are narrow throughout. Anatomical preparations of cupules from Assesse and the Bocq Valley show that the cupule lobes are terete except at the points of forking where they are temporarily elliptical or clepsydroid in cross section. The expansion of cupule quarters just before their distal forking into finely tapered tips, especially, is cylindrical instead of laminated and leaflike as might otherwise be suggested by the compressions.



Text.-fig. 2. *Reconstruction of a cluster of three cupules.*

3. *Seed position and number within cupules.*

Cupules readily showing several seeds are not very common. Most often a single seed is seen near the base of the cupule, slightly protruding from one edge of its inner facing side (Pl. 1, Figs. 8, 11, 12; Pl. 2, Fig. 5 and Text.-fig. 3). Further preparation, however, not exceptionnally reveals several additional seeds. A maximum of four seeds has been observed within a single cupule but three seeds are usually counted (Pl. 1, Figs. 3, 4). They appear characteristically attached in an obliquely vertical series rather than all at the same level. Characteristically also the cupules enclosing the highest number of seeds (4 or 3) are the less bushy; they invariably show a lower number of tips than those that are less productive.

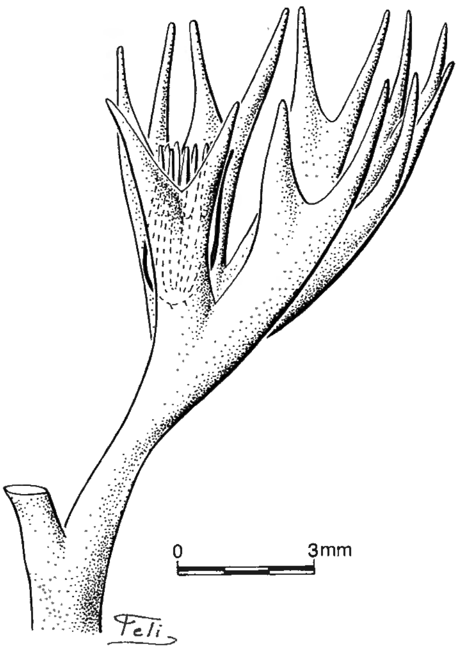
By uncovering numerous cupules it can be demonstrated that one seed may be produced each time the third, tangentially oriented division, takes place within a cupule quarter. That tangential division results in an inner part which yields one seed when fertile, and in an outer lobe which divides once more, radially, giving two acute, tapering or notched tips. When no seed is produced, the inner oriented lobe divides one more so that the sterile cupule quarter counts four tips while a fertile one has only two. A cupule that encloses three seeds presents ten tips; a sterile cupule counts up to sixteen tips (Pl. 2, Figs. 12 and 13). Most of the cupules, however, show only between four (e.g. Pl. 2, Fig. 7) and eight (e.g. Pl. 1, Figs. 11, 12) tips when exposed by the rock fracture. The asymmetry, plus the three dimensional arrangement of the rigid cupule tips and the tendency of the rock fracture to pass over the outer surface of one of the cupule quarters, account for the reduced number of tips readily visible. It also makes precise measurements difficult since whole cupules are almost never seen. Most exposures of cupules, therefore measure 0.8 - 1.0 cm long by 0.4 - 0.8 cm wide. Uncovered cupules reach a width of 1.0 - 1.2 cm.

Owing to the general overtopping by the distally located cupule lobes, the tangential, seed producing division occurs earlier in the proximal quarter (which is adjacent to the opposite cupule in a bouquet) which, therefore, bears on its inner side the lowest seed seen in an obliquely vertical row.

Invariably the seeds of such an obliquely vertical series show a gradient of size, the smallest being located more distally. The latter also often show the greatest apical flaring of the integument lobes (Pl. 1, Figs. 3, 4). These differences in integument morphology may reflect: relative stages of maturity or pre-pollination/post-pollination with the smaller seeds being younger; or the determinate growth of the cupule so that all the seeds are equally mature, but those produced first are the larger.

4. *Cupuliferous branch system.*

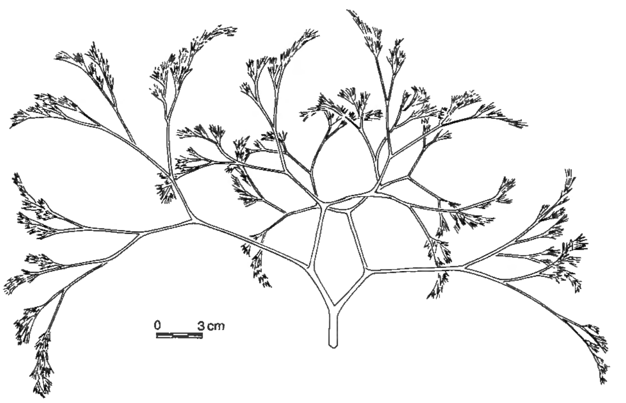
In addition to the pronounced asymmetry of individual cupules, the terminal forking branch system that bears clusters of cupules is also strongly overtopped (Pl. 1, Fig. 5; Pl. 3, Figs. 1, 2). This is well shown by Stockmans' figs. 3-3a, 5-5a and 7-7a (1948, Pl. 9) and results from the unequal forking of the cupuliferous branch system that is most pronounced in the cupule-bearing terminal branchlets. Upon the forking of these terminal cupuliferous branches, one half is short and terminates in a pair, or most often in a bouquet of three cupules, while the other half continues and forks again to produce another shorter-stalked terminal bouquet and a continuing axis. This produces a strongly overtopped, raceme-mike (or panicle-like) aggregate of cupules, on progressively shorter stalks, at the terminal end of a much larger forked branch system. The number of cupules in these terminal, raceme-like aggregates varies but is in the order of 5-15.



Text.-fig. 3. *Reconstruction of a cupule with one ovule.*

Stockmans (1948) attributed a forked axis system from Hamois (Pl. 9, fig. 6) to *Moresnetia.* This specimen has no cupules at the termini of its branches, but other specimens from Hamois (e.g. I.R.Sc.N.B. n° b 1843) and from the Bocq Valley, however, show that similar large forked systems terminate in aggregates of cupules. Although Stockmans' (1948) figure 6 on plate 9 is probably a cupuliferous truss of *Moresnetia,* we exclude this specimen from the syntypes because it has no cupules by which we can identify it and similar forked branch systems can be found in other plants from the Evieux flora (Fairon-Demaret, work in progress). One large specimen from Hamois (I.R.Sc.N.B. n° b 1843) shows a three-dimensionally forked system that divides seven times before terminating in a cluster of cupules (Pl. 3, Fig. 4). The divisions diverge at generally wide angles near the base (55-70°), even wider angles near the middle (70-110°) and become narrower (45-20°) in the distal parts. Similarly the axes produced are long in the proximal parts (3.0 - 5.0 cm), longer in the middle (5.0 - 8.0 cm) and shorter in the distal parts (1.5 - 3.5 cm). This specimen, and others from the Bocq Valley (Pl. 3, Figs. 1, 2), show strong bilateral, mirror-image symmetry with right and left halves being mirror-images and each half then showing some overtopping in the successive divisions. Many of the divisions are at right angles to those before and after so that the whole system is three-dimensional. The total of raceme-like cupule clusters was apparently from 64-128 so that the total number of cupules borne by such a system was at least 320 and could have been many more (Text.-fig. 4).

Since the cupules are borne only by the distal-most forks of the cupuliferous truss, the three-dimensional branch angles of which decrease distally, the overall arrangement of the raceme-like clusters of cupules formed a complex topography at the distal surface of a hemispherical tuft of branchlets with a radius of 20-30 cm. This surface appears to have been covered with conical branchlet projections so that the raceme-like aggregates of cupules formed the surface of the



Text.-fig. 4. *Reconstruction of the cupuliferous branch system.*

cones. Alternatively, the cupuliferous truss surface could have been indented by conical cavities, the surfaces of which were covered by cupules. If the topography of the cupuliferous surface was related to capture of wind-borne pollen, then the shapes of individual cupules on this surface might also have been related to pollination (e.g., NIKLAS, 1981a, 1981b). Thus the strong overtopping seen within individual cupules, so characteristic of *Moresnetia,* may correlate with the strong overtopping of the distal cupuliferous axes that forms raceme-like clusters of cupules.

Indeed, the terminal cupules of these clusters, which occur either at the tops of conical projections or the edges of conical identations, show the least overtopping of their lobes (Pl. 1, Fig. 5, compare the shape of the individual cupules at the top and at the base of the specimen). That the shapes of individual cupules seem to correlate with their overall position in the cupuliferous truss may support our conjecture that cupule shape, positions of ovules, and cupule display within the truss relate to the aerodynamics of wind pollination of *Moresnetia.*

Comparison with other late Devonian seed plants

Experience has shown that while only one organ (seed or cupule) may be enough for a tentative identification, confirmation requires knowledge of and consideration of the whole set of characters. With the exception of the peculiar *Spermolithus,* all late Devonian seed plants so far described share a similar overall pattern or organization of seeds and cupules. Nevertheless the seeds of *Moresnetia,* with their integument of 8-10 virtually unfused terete lobes that flare away from the nucellar apex, and the asymmetric cupules borne in asymmetrical overtopping pairs or bouquets of three in raceme-like clusters, are clearly distinct from those of all other early seed plants.

Individual seeds of *Moresnetia zalesskyi* are similar to those of *Genomosperma kidstonii* (LONG, 1960a, 1961) recorded in Scotland from several localities stratigraphically within the Cementstone Group (CM to PU spore zones; Late Tournaisian to Earliest Visean, SCOTT *et al.,* 1984): both seeds are radially symmetrical, their overall dimensions compare well and they possess an integument consisting of 6-11 (but most specimens with 8) free lobes that surround the nucellus and flare out distally; no micropyle is formed. In both cases the nucellus and integument are fused only at the base. A seed of *G. kidstonii,* however, is borne on a pedicle while the seed of *M. zalesskyi* is almost sessile. The lagenostome of *G. kidstonii* encloses a central parenchymatous core, the occurrence or absence of which cannot be ascertained in *M. zalesskyi* owing to the different mode of preservation. No cupule-like structure has been found associated with *G. kidstonii* and no further comparison is possible. That the seeds of *Moresnetia* resemble those of *G. kidstonii* is a confirmation of earlier deductions of "primitive" seed morphology based on comparisons of younger Lower Carboniferous seeds (LONG, 1960b, 1961, 1966; ANDREWS, 1963). *Moresnetia* is as old as or older than any other early seed plant. Numerous, free, terete integument lobes that flare away from the rounded nucellar apex with its large conical lagenostome are now shown to be archaic features of early seed plants. Although integument morphology may have helped guide pollen flow, pollen was directly captured by the lagenostome, since no micropyle was formed by the integument of *Moresnetia.*

Archaeosperma arnoldii (PETTITT & BECK, 1968) from the Oswayo Formation in Eastern Pennsylvania was the first Late Devonian cupulate organ in which occurrence of seeds had been demonstrated . The Oswayo microflora (from adjacent stratigraphic sections in New York State) is not older than Fa2d (PLi = lower LV spore zone in STREEL *et al.,* 1987; GILLESPIE *et al.,* 1981). *Archaeosperma arnoldii* is thus slightly younger than *Moresnetia zalesskyi* from beds of the Evieux Formation with lower VCo spore zone microflora and Fa2c in age. The holotype (ARNOLD, 1935) and paratypes (PETTITT & BECK, 1968) were re-examined by SCHECKLER in 1984 and 1985. The seeds of *Moresnetia* differ from those of *Archaeosperma* by their lack of integument fusion, greater number of integument lobes and their divergence away from the nucellar apex so that a true micropyle is not formed. Seeds of *Archaeosperma* show extensive fusion of the 5-6 parted integument so that only the apical tips are free. The nucellar apex is not preserved in *Archaeosperma* but the rest of the nucellus was apparently fused at the middle and base to the integument, the outer surface of which is covered by small spines. The nucellus of *Moresnetia* is virtually unfused to the integument which appears smooth externally, and extends to a large conical lagenostone. The functional megaspores of each taxon taper distally into a pointed tip at the chalaza and were produced by a tetrahedral meiotic division so that the thee aborted megaspores are arranged at the nucellar apex.

The details of the morphology are, however, better known for *A. arnoldii* megaspore tetrads that were extracted from the seeds. Although interpreted and reconstructed by its authors as a pair of two seeded cupules with flattened, leaf-like lobes, the dichotomous cupule of *Archaeosperma* can also be regarded as a four seeded structure with terete lobes, as already suggested by MATTEN *et al.* (1980). Interpreted this, an *A. arnoldii* cupule is similar in overall design to one of a pair or group of three *Moresnetia* cupules. PETTITT & BECK (1968) were convinced of the seed plant nature of *Moresnetia* but failed to detect seeds within the cupules of the few STOCKMANS' specimens they received on loan. Nevertheless, they pointed to the obvious similarity between the cupule lobe morphology in both *Archaeosperma* and *Moresnetia* as well as to the difference in cupule postion — terminal only versus terminal and lateral on the axes — of both taxa. Nothing is known of the arrangement of *Archaeosperma* cupules on a larger branch system but, if our interpretation is correct, the symmetrical forking of its cupules suggests that they were borne in less overtopped, more corymbose aggregates that were less crowded than the raceme-like grouping of paired (or units of three) overtopped, asymmetric cupules of *Moresnetia.*

The same overall design of cupule morphology is also shared by the new seed plant that was briefly described by GILLESPIE *et al.* (1981) from the Hampshire Formation of eastern West Virginia. At this location, the Hampshire yields a spore flora suggestive of the VUi (= VCo; lower Fa2c) spore zone which is about the same age as the Evieux Formation of Belgium (FAIRON-DEMARET, 1986; THOREZ & DREESEN, 1986). The new taxon is represented by numerous cupules with seeds, some of which are petrified (a more complete description, including larger pieces of the cupuliferous branch system, will be published soon by ROTHWELL, SCHECKLER & GILLESPIE): it has symmetrical cupules, the quarters of which divide twice into 16 tips and usually bear four seeds to the interior. The seeds have 4-5 integument lobes that are fused to each other in the basal third and to the nucellus up to and including the basal half (GILLESPIE *et al.,* 1981), and that curve inward at the seed apex. Cupules are borne terminally on long branchlets of the overtopped cupuliferous branch system so that they are arranged in a loose corymbose tuft. *Moresnetia* differs by the asymmetry of its cupules, the greater number and apical divergence of its nearly free integument lobes, and the raceme-like aggregations of its short-stalked cupules.

Xenotheca devonica (ARBER & GOODE, 1915; ROGERS, 1926) was long ago proposed as a seed plant cupule system from the Baggy beds (= Marwood Fm.) of south-western England. GOLDRING (1970, 1971) analyzed the depositional settings of the Baggy Beds and found that ARBER and GOODE's and ROGERS' plant collections all came from one thin lens of silt and shale of Hoe facies in the disused quarry of Timber facies at Croyde Hoe Farm, near Barnstable. GOLDRING (1971) assumed that the Baggy beds were more or less equivalent in age to the Wocklumerian Substage of the German Nomenclature. Spore analyses of these beds (DOLBY, 1970; HIGGS & CLAYTON, 1984) led FAIRON-DEMARET (1986) to conclude that the flora is Strunian (Fa2d - Tn1b lower). *Xenotheca devonica* is thus slightly younger than *Moresnetia.* Its cupules are the same size, fork similarly into 8-16 tips, and are also asymmetrical like those of *Moresnetia.* Neither ARBER & GOODE (1915) nor ROGERS (1926), who described additional specimens from the type locality, were able to demonstrate seeds of *Xenotheca devonica* so that their attribution of seed plant affinity was made by comparison with younger Carboniferous examples. Re-examination of ARBER & GOODE's syntypes and ROGERS' specimens by SCHECKLER (1985) reveals that several of ROGERS' specimens, now at the British Museum (Natural History), contain seeds.

STOCKMANS (1948) briefly mentioned *Xenotheca devonica* in his comments on *Moresnetia* and more extensive comparisons in his section on *Xenotheca bertrandii.* In the first instance he claimed that some *X. devonica* resembled the "leaves" of his *M. zalesskyi* (1948, p. 57). In the second case, he claimed that other imprints of *X. devonica* were identical to the "cupuliform" organs for which he erected *Xenotheca bertrandii.*

ARBER & GOODE's (1915) syntypes, however, show more of the overall organization of the cupuliferous branches and cupules than is suggested by their drawings. We confirm that ROGER's (1926) illustrated and other unillustrated specimens, which are better preserved than those of ARBER & GOODE, are the same plant and show even more of its organization as well as portions of several seeds. Our new knowledge of *Moresnetia* and better understanding of *Xenotheca devonica* compel a more thorough comparison. Cupules of both plants are borne terminally on the shorter halves of an overtopped, forked branch system. But individual cupules of *Moresnetia* show much more asymmetry than those of *X. devonica* and their arrangement into raceme-like clusters of pairs or groups of three is quite different from the corymbose arrangements of cupules seen in ARBER & GOODE's and ROGERS' specimens.

Seeds are incompletely preserved in ROGERS' *Xenotheca devonica,* but seem to have four to five erect and stout integument lobes that appear to be fused at the base (SCHECKLER, 1985). Details of the nucellus are unknown. Seeds of *Moresnetia* are much better known; their 8-10 integument lobes are free nearly to the chalaza and diverge from the micropylar region. The nucellus has a rounded apex with a large elongate lagenostome. *Moresnetia* is thus a different seed plant even though many features of cupule morphology are superficially similar to *X. devonica.*

STOCKMANS' (1948, Pl. 11, figs. 14-17) *Xenotheca bertrandii* was re-examined by SCHECKLER in 1984 and found to be either indeterminable or possibly aborted young cupules or portions of cupules of the *Moresnetia* type. One specimen (STOCKMANS, 1948, Pl. 11, fig. 14) resembles a possible stalked, fourlobed "seed". A similar "stalked seed" was shown by BASSETT & EDWARDS (1982, p. 14). From the same Upper Old Red Sandstone beds (? Latest Strunian) of Tongwynlais, near Cardiff, Wales, BASSETT & EDWARDS (1982) also illustrated a microsporangiate cupule they referred to *Xenotheca* sp. This cupule however, shows little of the overtopping that characterizes ARBER & GOODE's (1915) *X. devonica* and looks more similar to the ovulate cupules of GILLESPIE *et al.* (1981).

Hydrasperma tenuis of MATTEN *et al.* (1980) and MATTEN *et al.* (1984) comes from Strunian rocks (Tn1a-lower Tn1b) of the Coomhola Formation of southern Ireland. This plant is preserved mainly as petrifactions and its cupules ans seeds have been reconstructed from serial preparations. Some partly permineralized compressions exist and confirm the reconstructions. Cupules fork similarly and are divided into terete lobes like those of *Moresnetia.* But *Moresnetia* cupules fork throughout and are strongly overtopped while those of MATTEN *et al.*'s (1980, 1984) *H. tenuis* branch "pinnately" and are essentially symmetrical overall. Seeds of *Moresnetia* show virtually no fusion of the 8-10 integument lobes while those of *Hydrasperma* are fused to each other for more than half the total length of the seed and to the nucellus from the chalaza to just below the pollen chamber and are generally fewer in number (8-10 but usually 8). Cupuliferous branches are only partly known, but seem to fork into equal halves so that an umbel-like cluster might have been produced.

Many specimens of apparent cupules and cupuliferous axes have been recognized from various Late Devonian strata in the Soviet Union and attributed to STOCKMANS' *Moresnetia zalesskyi* (LEPEKHINA, PETROSYAN & RADCHENKO, 1962; PETTITT, 1970). Now that the seed-bearing nature of STOCKMANS' plant is known and its fertile morphology is well understood, we are better able to evaluate these attributions. The specimens of LEPEKHINA *et al.* (1962) are forked axes similar to the basal part of *Moresnetia* and other early seed plants. Without knowledge of cupules and seeds, however, these specimens must be excluded from *M. zalesskyi* or any other "species" of the genus (i.e., *M. krystofovichii* RADCHENKO, 1962 and *M. sibirica* PETROSYAN, 1962, *in* LEPEKHINA *et al.*, 1962).

PETTITT (1970, Pl. 6, fig. 1) illustrated another Soviet *"Moresnetia zalesskyi"* from the British Museum (Natural History) collections that he called a "seed-like fossil". This specimen [B.M. (N.H.) V. 44778] is now missing from the British Museum, but SCHECKLER studied other Soviet specimens, apparently from the same locality, at the B.M. (N.H.) in 1984. At least one [B.M. (N.H.) V44784] seems to contain a fragmentary seed so that their identity as seed plant cupules is likely. Other floral associates from this locality include, according to SCHECKLER, a sporangial cluster of *Rhacophyton* sp. cf. *R. condrusorum* CREPIN, 1875, *Archaeopteris halliana* (GOEPPERT) DAWSON, 1891 and *Sphenopteridium* sp. cf. *S. rigidum* (LUDW.) POTONIÉ, 1899 which suggest a Late Famennian to Strunian age.

The identity of these seed plant cupules, however, remains to be determined. The cupules are smaller, about half the size of those of *Moresnetia,* fork into just barely overtopped quarters, and terminate an only slightly overtopped, corymbose, forked branch system. Although their overall morphology is similar to Belgian *Moresnetia zalesskyi,* the Soviet specimen illustrated by PETTITT (1970), as well as the others at the British Museum (Natural History), must be kept separated from STOCKMANS' genus since we now know several other genera of Late Devonian seed plants that also differ from *Moresnetia* in similar subtle ways.

Spermolithus devonicus JOHNSON, 1917 from the late Strunian (Tn1a - lower Tn1b) Kiltorcan Beds of Southern Ireland was recently redescribed by CHALONER, HILL & LACEY (1977) from new specimens and interpreted as isolated, dispersed platyspermic seeds. The presumed integument of *Spermolithus* appears fused and, if so, is quite different from the numerous free lobes of the integument of radiospermic *Moresnetia* seeds.

All of these Late Devonian seed plants (*Moresnetia, Archaeosperma,* the new plant of GILLESPIE *et al.*, 1981, *Xenotheca,* and *Hydrasperma*) have an overall similar pattern of seed, cupule, and cupuliferous branch system morphology (except *Spermolithus*) which demonstrates the closeness of their relationship. But each has its own unique constellation of characters such that they are readily recognized as five (or six including *Spermolithus*) distinct genera. They are not known equally, however. Some are known only from compressions or preparations of compressions (*Xenotheca* and *Archaeosperma*), others from mostly petrifactions (*Hydrasperma*), and some from both (*Moresnetia* and GILLESPIE *et al.*'s new plant). Therefore, the characters that we are able to use for comparison of *Moresnetia* with other Devonian seed plants vary with each case. Of all these, *Moresnetia zalesskyi* is the best known.

Typification and diagnoses

Moresnetia zalesskyi STOCKMANS, 1948

1946 STOCKMANS, F. Tour d'horizon paléobotanique en Belgique. Bulletin de la Société «Les Naturalistes Belges». Société de Diffusion Scientifique. 27 (7-8): 82-87. Bruxelles. Page 82, figure 1.

1948 STOCKMANS, F. Végétaux du Dévonien Supérieur de la Belgique. Mémoires du Musée Royal d'Histoire Naturelle de Belgique. 110: 1-85, Pl. I-XIV. Bruxelles. Pages 55-57, Planche IX, figures 1-1a, 2-2a, 3-3a, 4-4a, 5-5a, 7-7a.

1968 PETTITT, J.M. & BECK, C.B. *Archaeosperma arnoldii* a cupulate seed from the Upper Devonian of North America. Contributions from the Museum of Paleontology, The University of Michigan. 22 (10): 139-156. Pl. 1-6, Text-figs. 1-3. Ann Arbor. Plate 5, figures 3-4.

Excludenda

1948 Planche IX, figure 6 of STOCKMANS, F. Végétaux du Dévonien Supérieur de la Belgique. Mémoires du Musée Royal d'Histoire Naturelle de Belgique. 110: 1-85, Pl. I-XIV. Bruxelles.

1970 Plate 6, figure 1 of PETTITT, J. Heterospory and the origin of the seed habit. Biological Review 45: 401-415, Pl. 1-6. Cambridge.

All other attributions of *Moresnetia* from non-Belgian material are excluded.

LECTOTYPE

Specimen *I.R.Sc.N.B. N° b1832* (= n° 25.596 of STOCKMANS), figured as fig. 1 in STOCKMANS, 1946 and fig. 4-4a, Pl. IX in STOCKMANS, 1948.

SYNTYPES

Specimen *I.R.Sc.N.B. N° b1833* (= n° 44.140 of STOCKMANS) and *N° b1834* (= n° 25.591 of STOCKMANS) from Moresnet, illustrated respectively, fig. 1-1a and 2-2a, Pl. IX, in STOCKMANS 1948) *N° b1835* (= n° 29.814 of STOCKMANS), *N° b1836* (= n° 29.703 of STOCKMANS) and *N° b1837* (= n° 29.961 of STOCKMANS) from Assesse, illustrated respectively, fig. 3-3a, fig. 5-5a and fig. 7-7a, Pl. IX, in STOCKMANS 1948.

TYPE LOCALITY

Moresnet, Belgium, 60 m east of the church along the road embankment (fig. 4-4a, 2-2a, Pl. IX, STOCKMANS, 1948).

OTHER LOCALITIES

STOCKMANS (1948) mentions that he had also collected *Moresnetia* from the old Suerdmondt quarry also in Moresnet, from Hun Annevoie (Beaupère Quarry), Assesse (railway trench), Strud-Haltinne (in an outcrop) and Hamois (disused quarry at the railway station). Our examination of his collections confirms these identifications and shows that *Moresnetia* occurs also at Evrehailles; we have newly collected this plant from the Bocq Valley, in the Langlier quarry near Dorinne, Belgium (Texte fig. 1).

TYPE FORMATION

Evieux Formation.

BIOSTRATIGRAPHIC HORIZON

Lower part of the VCo spore zone which is Famennian 2c in the type Belgian Famennian chronozones. This miospore zone is characterized in the considered region of Belgium by a maximum of regression and by the joint first appearance of *Grandispora cornuta* HIGGS, 1975, *Rugospora flexuosa* (JUSCHKO) STREEL in BECKER *et al.*, 1974 and *Retusotriletes phillipsii* CLENDENING *et al.*, 1980 according to STREEL *et al.* (1987) and FAIRON-DEMARET (1986).

Emended diagnoses

GENERIC DIAGNOSIS

Moresnetia STOCKMANS, 1948.
Only reproductive axes known. Raceme-like clusters of cupules produced by the strongly overtopped terminal branchlets of a large unequally and cruciately forked branch system. Cupules borne in pairs or groups of three on short erect axes. Asymmetric cupules fork cruciately into four unequally sized main parts, the dichotomous terminations of which form long tapered, pointed or notched tips. Up to four ovules per cupule, sessile or attached by short stalks in an oblique vertical series from the inner side of main cupule parts. Integument divided into 8-10 thin terete lobes, fused only at the chalaza and flared outward apically; no micropyle is formed. Nucellus free from integument except at the chalaza and terminated by a large rounded tip from which extends a conical lagenostome (= salpinx). Functional megaspore of the tetrahedral tetrad elongate and tapered to a distal point. Three aborted megaspores cover the proximal end.

SPECIFIC DIAGNOSIS

Moresnetia zalesskyi STOCKMANS, 1848.
Characters the same as the genus. Proximal axes of 7 - 8 times forked cupuliferous branch system are 3 - 5 mm in diameter and short (3 - 5 cm), middle axes are narrower 1,5 - 2 mm diameter) but longer (5 - 8 cm) and distal axes are narrowest (0,5 - 1 mm) and progressively shorter (3,5 - 1,5 cm) until their terminal raceme-like clusters of cupules are reached. Cupules are 8 - 10 mm long and 7 - 12 mm wide when complete and have 8 - 16 pointed ot notched tips (8 tips when four seeds are produced; 10 tips when three seeds are present; 16 tips when the cupule is sterile). Ovules from 2,5 - 4 mm long (with a few as small as 1 mm and others exceptionnaly up to 5 mm long) and 0,5 mm wide at the chalaza to 1 mm near the middle or at the apex. Nucellus 2 - 3 mm long and 0,5 - 0,8 mm wide. Functional megaspore 1 - 1,5 mm long by 0,2 - 0,3 mm wide.

Conclusion

Our new information demonstrates that *Moresnetia zalesskyi* is one of the oldest and best known early seed plants. Its asymmetric cupules and archaic ovules provide a unique assemblage of characters so that *Moresnetia zalesskyi* can be easily distinguished from other Late Devonian cupulate seed plants, such as *Xenotheca devonica* (ARBER & GOODE, 1915; ROGERS, 1926), *Archaeosperma arnoldii* (ARNOLD, 1935; PETTITT & BECK, 1968), *Hydrasperma tenuis* (MATTEN, LACEY & LUCAS, 1980; MATTEN *et al.*, 1984) and the new plant of GILLESPIE, ROTHWELL & SCHECKLER (1981). As the pollination biology, growth habits and ecology (SCHECKLER, 1986a, 1986b) of early seed plants become better known, their diversification in the Famennian might be understood as the expected response to reproductive selection and habitat invasion. Clearly, *Moresnetia* will be important to our interpretations of primitive states of seed and cupule organization and the reproductive biologies that these imply. This brief note is intended to bring our rapidly expanding knowledge of one of these early seed plants to the attention of botanists, paleontologists and geologists. A more complete description of the anatomy morphology and geological setting of *Moresnetia zalesskyi* will follow.

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FAIRON-DEMARET, Muriel
Paléobotanique et Paléopalynologie
Université de Liège
7, Place du XX Août.
B-4000 LIEGE (Belgique)

SCHECKLER, Stephen E.
Department of Biology
Virginia Polytechnic Institute
and State University
BLACKSBURG, Virginia 24061
(U.S.A.)


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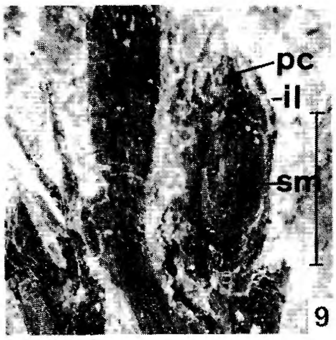
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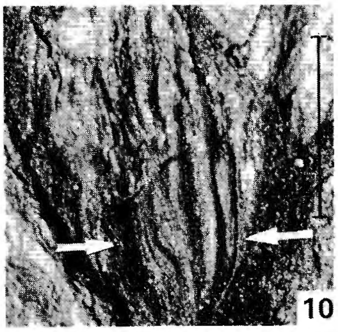
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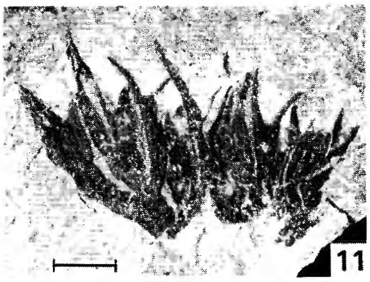
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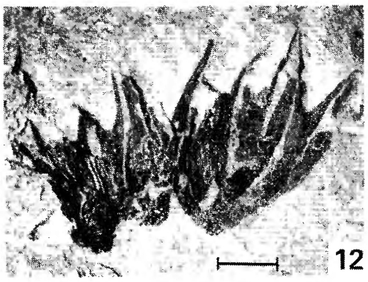
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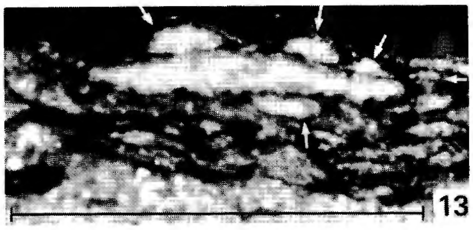
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PLATE 1

Scale bar = 2 mm except on figure 13 where it corresponds to 1 mm.
When not otherwise stated, the specimens come from the Bocq Valley, near Dorinne (Province of Namur, Belgium).

Figs. 1 and 2.	*Part and counter-part of a pair of cupules from Hamois with long acute tips. s: seed. I.R.Sc.N.B. N° b 1845 (a, b).*
Fig. 3.	*Cupule with three seeds, one of which clearly showing its attachment to the inner facing side of a cupule lobe. I.R.Sc.N.B. N° b 1855.*
Fig. 4.	*Detail of another cupule with three seeds; it has been exposed by the rock fracture in a plane perpendicular to the one of the cupule illustrated Fig. 3; the three seeds are in an oblique vertical series and show the flaring of the integument lobes. I.R.Sc.N.B. N° b 1852a.*
Fig. 5.	*General view of the top of a fertile branch system. a: cupule detailed on Fig. 4, same plate. b: pair of cupules illustrated Fig. 7, plate II. I.R.Sc.N.B. N° b 1852a.*
Fig. 6.	*Detail of one cupule quarter and its seeds with free integument lobes; a second cupule quarter is partly shown. I.R.Sc.N.B. N° b 1854.*
Fig. 7.	*Detail of a seed from Strud-Haltinne; some of the free integument lobes have been taken away in order to show the pollen chamber (p c). il: integument lobe; s m: seed megaspore. I.R.Sc.N.B. N° b 1846.*
Fig. 8.	*An almost complete cupule more or less flattened on the sediment and enclosing a "ridged" seed (s). I.R.Sc.N.B. N° b 1848 (b).*
Fig. 9.	*Detail of a seed treated as the one on Fig. 7, same plate. il: integument lobe; s m: seed megaspore; p c: pollen chamber. I.R.Sc.N.B. N° b 1852 (b).*
Fig. 10.	*Close up of a seed ridged in aspect; note the flaring of the tips of the integument lobes; the arrows indicate the level of the transverse section illustrated Fig. 13. I.R.Sc.N.B. N° b 1850.*
Figs. 11 and 12.	*Part and counter-part of a pair of cupules, a detail of which is illustrated Fig. 8, same plate. s: seed. I.R.Sc.N.B. N° b 1848 (a, b).*
Fig. 13.	*Transverse section through the seed illustrated Fig. 10; several sections through the free integument lobes (arrows) are visible.*

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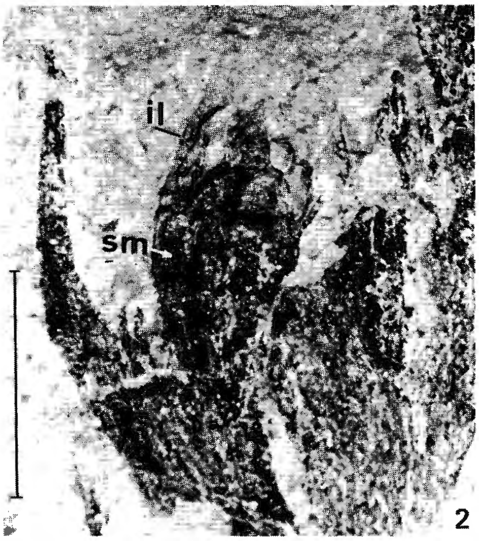

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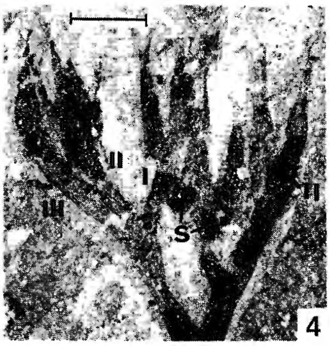

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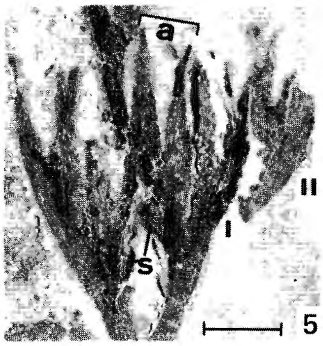

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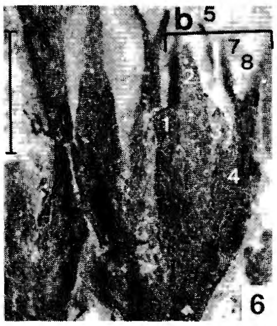

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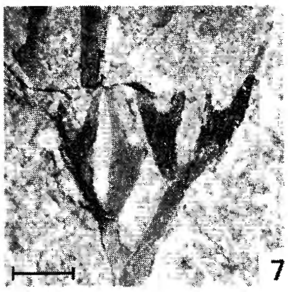

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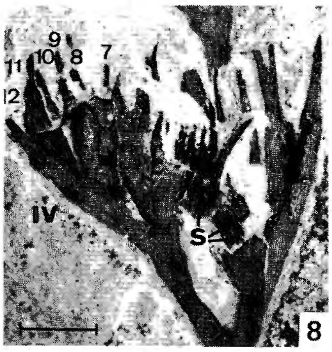

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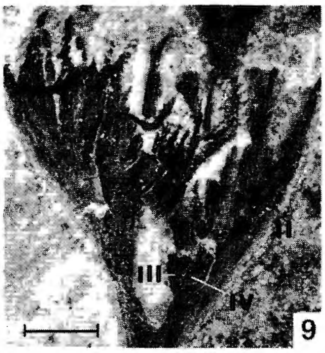

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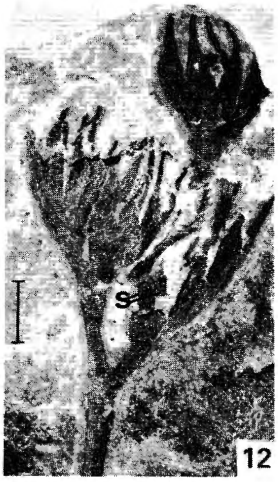

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PLATE 2

Scale bar = 2 mm.
The illustrated specimens have been collected in the Bocq Valley, near Dorinne (Province of Namur, Belgium).

Fig. 1. *General view of specimen I.R.Sc.N.B. N° b 1855 (a).*

Fig. 2. *Seed uncovered on the counter-part of specimen I.R.Sc.N.B. N° b 1855 (b). la: lagenostome; pc: pollen chamber; il: integument lobe.*

Fig. 3. *Detail of Fig. 2.*

Fig. 4. *Group of three cupules appearing as a pair when the sediment was split; the Roman numerals indicate the cupule quarters. I.R.Sc.N.B. N° b 1849 (a).*

Fig. 5. *Counter-part I.R.Sc.N.B. N° b 1849 (b) during the uncovering process. a: a quarter of one of the two tightly appressed cupules that looked like a single entity on the splitting of the rock; I and II indicate two quarters belonging to the second cupule; s: base of the seed enclosed in cupule a.*

Fig. 6. *Detail of Fig. 5. Eight tips of the cupule b are numbered. s: base of the seed in cupule a.*

Fig. 7. *A pair of cupules as they usually appear when the sediment is split. I.R.Sc.N.B. N° b 1852 (a).*

Fig. 8. *Further uncovering of I.R.Sc.N.B. N° b 1849 (a). The seed of cupule a is shown as well as additional lobes at a deeper level of cupule b, belonging to the quarter IV; two small seeds are also present in the right hand cupule. Polarized light.*

Fig. 9. *Same as Fig. 8, unpolarized light in order to enhance the different levels in each cupule. On the right cupule, an almost complete quarter (II) and the base of two additional ones (III, IV) can be seen.*

Fig. 10. *A two seeded cupule. The attachment of one of the seeds to the inner facing side of its cupule lobe is well seen. la: lagenostome. I.R.Sc.N.B. N° b 1854.*

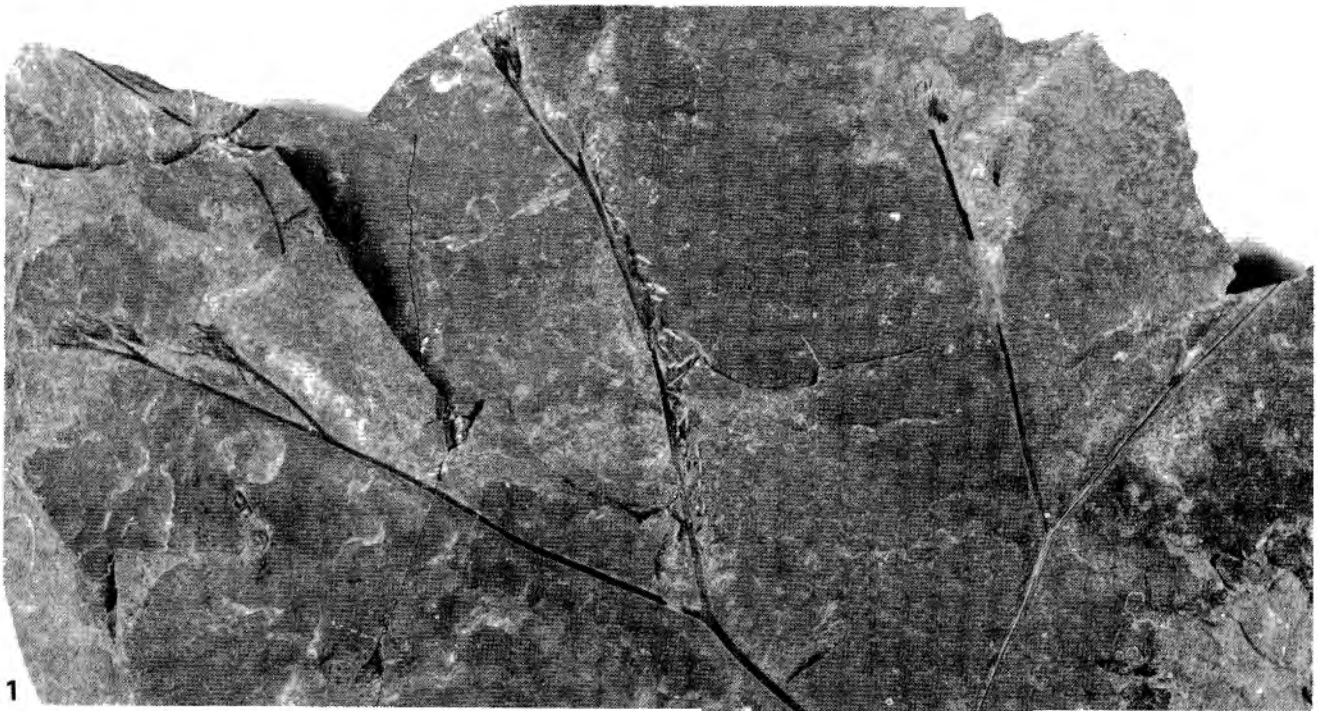
Fig. 11. *Uncovering of the pair of cupules on I.R.Sc.N.B. N° b 1852 (b). A seed is present in the left cupule; the right cupule counts more segments than previously shown (compare with Fig. 7, same plate).*

Fig. 12. *Further uncovering of I.R.Sc.N.B. N° b 1849 (a). The seed enclosed in cupule a has been removed in order to demonstrate the occurrence of cupule lobes lying behind it; the two small seeds (s) of the right cupule are still present.*

Fig. 13. *Detail of the pair of tightly appressed cupules at the end of the uncovering. The visible tips of the more distal cupule, b, are numbered. I.R.Sc.N.B. N° b 1849 (a).*

Fig. 14. *Further uncovering of I.R.Sc.N.B. N° b 1852 (b) showing the superposed tips in the distal part of the left cupule and the base of the cupule quarters III and IV of the right cupule.*

Fig. 15. *Detail of Fig. 11, same plate.*



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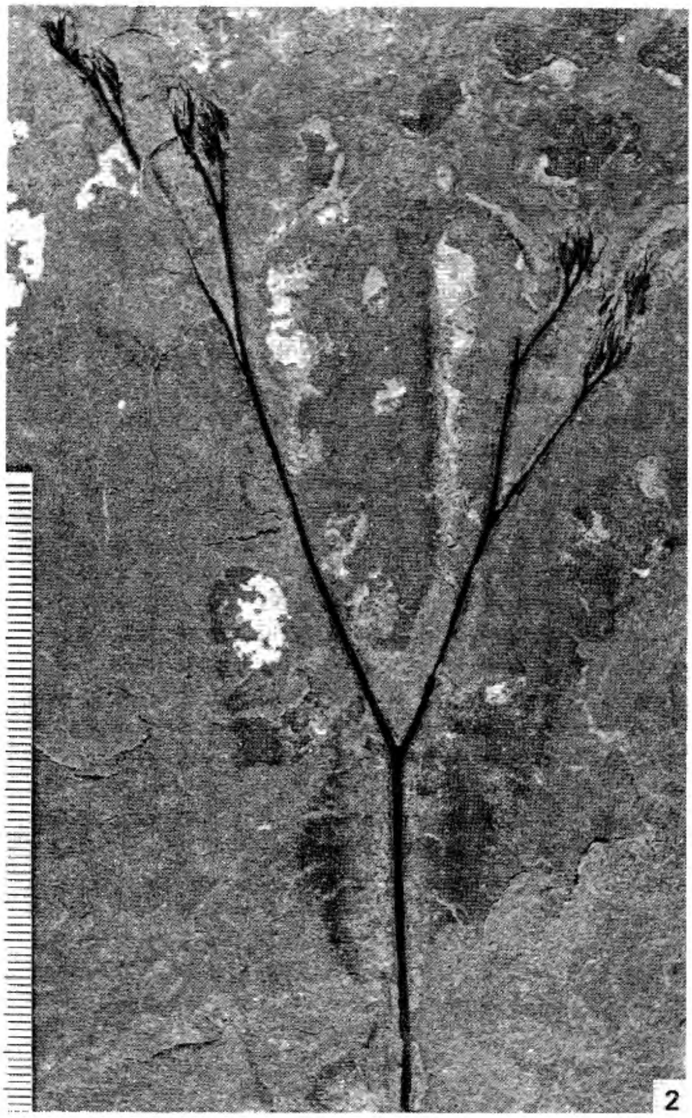

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PLATE 3

Scale bar, when present = 2 mm.

Fig. 1. *General view of the top of a fertile branch. Bocq Valley. I.R.Sc.N.B. N° b 1851 (a).*

Fig. 2. *Raceme-like termini of a fertile branch. Bocq Valley. I.R.Sc.N.B. N° b 1847 (a).*

Fig. 3. *Cupules laterally compressed; two seeds at least (s) are present. Assesse. I.R.Sc.N.B. N° b 1844 (b).*

Fig. 4. *Cluster of cupules terminating the three-dimensionnaly forked branch system of Hamois. I.R.Sc.N.B. N° b 1843.*

Fig. 5. *Detail of one seed from the Bocq Valley; the seed megaspore is visible (sm); note the three bumps — arrows — on top of it, most probably representing the aborted megaspores of the tetrad. I.R.Sc.N.B. N° b 1853.*