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## Early diversification of seeds and seed-like structures.

### [Diversification précoce des graines et structures assimilées]

Cyrille PRESTIANNI<sup>1</sup>

**Key Words:** Seeds; diversity; Devonian; Lower Carboniferous; evolution

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**Mots-Clefs :** Graines ; diversité ; Dévonien ; Carbonifère inférieur ; évolution

The seed habit is one of the most important evolutionary acquisition in plant evolution. It allowed colonisation of new ecological niches, leading to a level of diversification never observed before. The seed habit involves occurrence of a single functional megaspore within an indehiscent megasporangium (nucellus), development of an endosporic megagametophyte, enclosure of the nucellus by an integument, and capture of pollen before dispersal from the sporophyte.

Early ovulate structures are better regarded as preovules (*sensu* STEWART & ROTHWELL, 1993) as their nucellus is surrounded by unfused or partially fused integumentary lobes, and they consequently lack a well-defined micropyle. The functions of the micropyle were then assumed by modifications of the nucellar apex.

Many preovules are known from Upper Devonian deposits (see Fig. 1). They show a variety of morphologies, but they all share the same set of modifications of the nucellar apex: the hydrasperman syndrome (ROTHWELL, 1986; ROTHWELL & SCHECKLER, 1988). The nucellar apex is modified into a pollen chamber (*sensu* GORDON, 1941) closed by a plinth (*sensu* GORDON, 1941) and extended by a cylindrical structure (HILTON, 1996), the salpinx (*sensu* GORDON, 1941). The pollen chamber contains a central parenchymatous column. We here call lagenostome (*sensu* SCOTT, 1917) the whole modification of the nucellar apex, pollen chamber plus apex.

All these Upper Devonian types show various degrees of fusion of the integumentary lobes and/or characteristics of the cupule, a set of vegetative segments that usually encloses the pre-ovulate structure. On the basis of the characteristics of these parts, the Upper Devonian preovules can be classified in the following types.

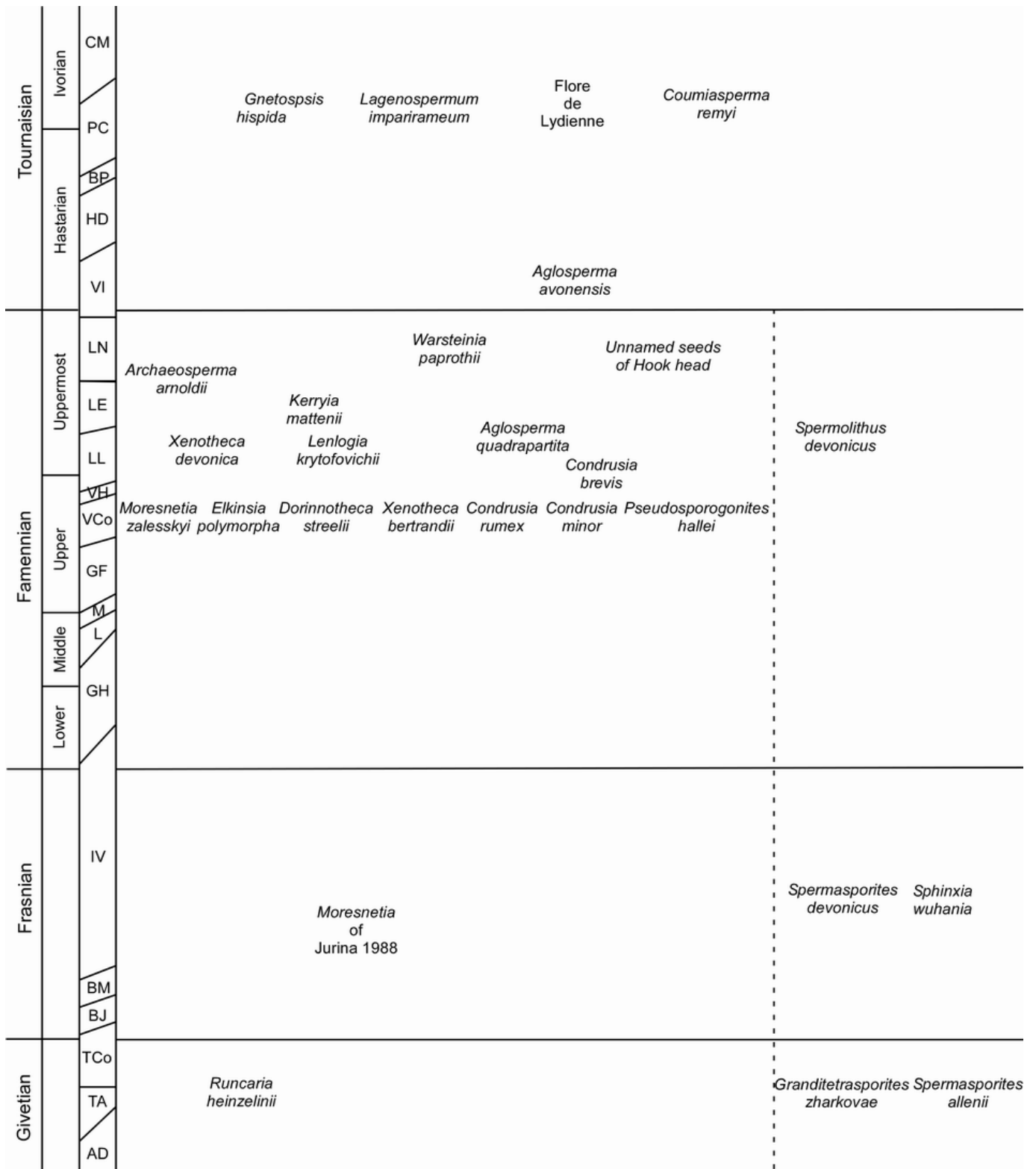
#### A. *Moresnetia*-type

The first type of preovule is the *Moresnetia*-type. It is characterised by a four unit cupule formed by two successive cruciated dichotomous divisions. Within this group, we notice a progressive fusion of the integumentary lobes, ranging from completely dissected in the Belgian taxon *Moresnetia zaleskyi* STOCKMANS (1948), emend. FAIRON-DEMARET et SCHECKLER (1987) [West European VCo biozone] to a nearly completely fused integument in *Archaeosperma arnoldii* PETTITT et BECK (1968) [North American LE-LN biozone]. *Xenotheca devonica* ARBER et GOODE (1915), emend. HILTON et EDWARDS (1999) [West European LL biozone] and *Elkinsia polymorpha* ROTHWELL *et alii* (1989), emend. SERBET et ROTHWELL (1992) [North American VH biozone] have an intermediate degree of fusion. The degree of fusion of the integument can be observed only on perfectly preserved specimens. This led HILTON (1999) to doubt the justification of a distinction between the genera *Moresnetia*, *Elkinsia* and *Xenotheca*.

We also include in the *Moresnetia*-type two slightly different taxa: *Kerrya mattenii* ROTHWELL et WIGHT (1989) [West European LE/LN biozone] and *Lenlogia krystofovichii* PETROSYAN *in* LEPEKHINA *et alii* (1962) emend. KRASSILOV et ZAKHAROVA (1995) [LL Biozone]. *Kerrya mattenii* possesses a six unit cupule, but its overall organisation conforms to the *Moresnetia*-type. *Lenlogia krystofovichii* is poorly understood, but may be provisionally included in this group because of its apparent structural resemblance.

The *Moresnetia*-type comprises the most ancient type of preovules. Its first representatives are found in the upper Frasnian of Russia (IURINA *et alii*, 1988). This early occurrence may be a partial explanation for its wide geographic distribution by late Famennian times (see Fig. 2). This type ranged across the D/C boundary, for it is represented by the Carboniferous lagenostomalean seeds ovules (CLEAL, 1993; LONG, 1975).

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**Figure 1:** Stratigraphic distribution of Devonian and Lower Carboniferous ovules and ovule-like structures. Dotted line separates preovules (left) from ovule-like structures (right). See text for references. Stratigraphic scale modified from DREESEN *et alii* (1993) and STREEL *et alii* (1987). AD. *Acinosporites acanthomammilathus* - *Densosporites evonicus*; BJ. *Verrucosporites bulliferus* - *Cirratriradites jekhowskyi*; BM. *Verrucosporites bulliferus* - *Lophozonotriletes media*; P. *Spelaeotrilete balteatus* - *Rugospora polyptycha*; CM. *Schopfites claviger* - *Auroraspora macra*; GF. *Grandispora gracilis* - *G. famenensis*; GH. *Grandispora gracilis* - *A. hirtus*; HD. *Kraeuselisporites hibernicus* - *Umbonatisporites distinctus*; LE. *Retispora lepidophyta* - *Indotriradites explanatus*; LL. *Retispora lepidophyta* - *Knoxisporites literatus*; TA. *Samarisporites triangulatus* - *Acyspora* var. *ancyrea*; TCo. *Samarisporites triangulatus* - *Chelinospora concinna*; L; M; PC. *Spelaeotriletes pretiosus* - *Raistrickia clavata*; VCo. *Diducites versabilis* - *Grandispora cornuta*; VI. *Vallatisporites allatus* - *Retusotriletes incohatus*; LN. *Retispora lepidophyta* - *Verucosporites nitidus*; VH. *Apiculiretusispora verrucosa* - *Vallatisporites hystricosus*.

**B. Aglosperma-type**

The second type of preovule is the acupulate *Aglosperma*-type. It includes: *Aglosperma quadrapartita* HILTON et EDWARDS (1996) [West European LL-LE biozone] and *Aglosperma avonensis* HILTON (1998) [West European VI Biozone]. Their integument is formed by three to four flat lobes fused up to their lower third.

**C. Warsteinia and Dorinnotheca-types**

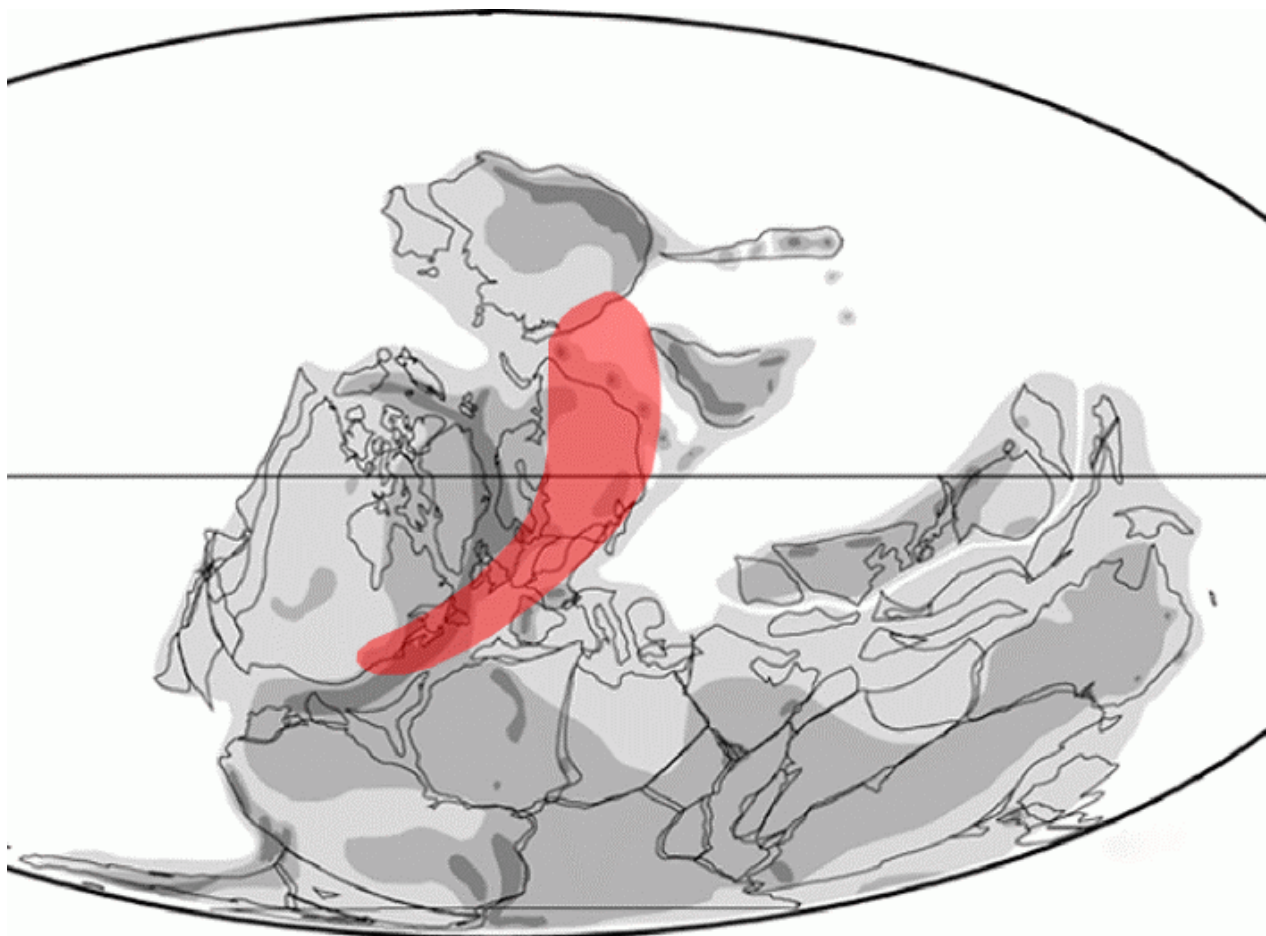
An adaptation to anemochory may be observed in the third and fourth types: the *Warsteinia*-type and the *Dorinnotheca*-type. *Warsteinia paprothii* ROWE (1997) [West European LE biozone] is acupulate. Its integument is made of four winged lobes adnate or fused to the nucellus. The *Dorinnotheca*-type, represented by *Dorinnotheca streelii*, FAIRON-DEMARET (1996) [West European VCo], is putatively anemochoreous too. Its cupule is composed of eight parts fused proximally so that they form a cup, the segments of which divide to form at least 40 free endings. Each cupule contains only one central ovule. The integument is composed of four free terete lobes (FAIRON-DEMARET, 1996).

**D. Condrusia-type**

The fifth type is the *Condrusia*-type represented by three described species, *C. rumex* STOCKMANS (1948), *C. minor* STOCKMANS (1948) and *C. brevis* PETROSYAN in LEPEKHINA et alii (1962). They differ from all the others in the characteristics of their cupule which is composed of two flat bilaterally symmetrical wings adressed against each other. In the two species currently under investigation, *C. rumex* and *C. minor*, the integument is not dissected into lobes and shows a complex organisation with three layers, the middle one consisting of large sclerified cells. The nucellus appears to be fused with the integument. Its apex is modified into a very long salpinx protruding above both the integument and the cupule wings.

**E. Other preovules and seed-like structures**

In addition, two new types of preovules occur in the Irish Hook Head locality (KLAVINS & MATTEN, 1999; KLAVINS, 2000). They are both radially symmetrical and present the hydrasperman-type of reproduction. Their integument is made of four lobes fused basally and curving inward over the ovule apex. One of



**Figure 2** (modified from SCOTESE, 2002): In red the geographic area covered by the *Moresnetia*-type during the late Famennian. Data from PETTITT & BECK (1968), FAIRON-DEMARET & SCHECKLER (1987), IURINA (1988), ROTHWELL et alii (1989), ROTHWELL & WIGHT (1989), KRASSILOV & ZAKHAROVA (1995) and HILTON & EDWARDS (1999).

the two new preovules presents an integument composed of three distinct layers. However, without published description or illustration, further discussion is impossible.

Some Upper Devonian seed-like structures are not understood well enough to be placed in one or another group. They are provisionally included in an heterogeneous type containing the Frasnian seed-like structure *Sphinxia wuhania* LI *et alii* (1997), the enigmatic *Spermolithus devonicus* JOHNSON (1917) and the two poorly described Belgian seeds "*Xenotheca bertrandii* STOCKMANS (1948) and *Pseudosporogonites hallei* STOCKMANS (1948).

#### F. The earliest representatives

Contrary to earlier opinion, the preovules of the Upper Devonian are very diverse. This diversity, as well as the sophistication of the hydrasperman reproduction, strongly suggests an origin for early seeds older than the Frasnian. The Givetian taxon *Runcaria heinzelinii* STOCKMANS 1948, emend. GERRIENNE *et alii* 2004, probably represents one of the early stages in this evolution (GERRIENNE *et alii*, 2004). This taxon already possesses most of the characteristics of the Upper Devonian preovules (see above). It consists of a short basal cuplike cupule made of four segments. This cupule contains a radially symmetrical megasporangium surrounded by an integument comprising at least 16 free lobes. The megasporangium bears a long distal extension emerging above the integument and enlarged at the top. The apical extension of the megasporangium probably played a role in the capture of microspores. Consequently, the reproductive biology of *Runcaria* putatively included anemophilous pollination and dissolution of sporangial cells to allow fertilization (GERRIENNE *et alii*, 2004). The morphology of its megasporangium and its presumable particular type of reproduction distinguishes *Runcaria* from all the Famennian early seeds.

MARSHALL and HEMSLEY (2003) described *Spermasporites allenii*, a Givetian seed-megaspore. The "seed-megaspores" are obligatory tetrads, with a unique functional and three aborted megaspores. *Spermasporites allenii* seems to be enclosed in a sporangium. Whether or not this sporangium is indehiscent remains unknown. The relative ultrastructural simplicity of the outer megaspore layer and the presence of monomegaspority (*sensu* BATEMAN & DiMICHELE, 1994) led MARSHALL and HEMSLEY (2003) to suggest gymnospermous affinities for *Spermasporites*. As the sporangium contains both micro- and megaspores, the structural differences and the uncertainties about dehiscence seem to us rather suggestive of a lineage discrete from that of the seed plants. This taxon might be another example of the

iterative (*sensu* BATEMAN & DiMICHELE, 1994) aspect of heterospory.

#### G. The Early Carboniferous representatives

After Devonian times, a gap is observed in the seed record. This remains enigmatic (it was probably related to lack of adequate deposits) for a lot of vegetative parts assignable to seed-plants are found, but reproductive organs are recorded either not at all or very rarely (GALTIER, pers. com.). It is only at the PC biozone that an increase in the seed record is observed. A very peculiar type of seed, *Coumiasperma remyi* (GALTIER *et* ROWE, 1991) has been reported once. It is atypical because the usual hydrasperman nucellar apical modification is absent. This ovule is interpreted as showing adaptation to aquatic dispersal (GALTIER & ROWE, 1991). More classical hydrasperman types are also described as *Gnetopsis hispida* GENSEL *et* SKOG (1977) and *Lagenospermum imparirameum* ARNOLD (1939) emend. GENSEL *et* SKOG (1977). Some other taxa of the Lydienne Formation are also mentioned (ROWE & GALTIER, 1990; UNGER, 1856; MEYER-BERTHAUD & ROWE, 1997), but their affinities remain uncertain. However, some have been compared to the *Moresnetia* morphological group (ROWE & GALTIER, 1990) or to some Carboniferous genera.

After the CM biozone [Lower Carboniferous], we observe a rapid and important expansion of the seed plants. The number of genera for isolated seeds increases (LONG, 1975); a lot of types are known. This is the beginning of the worldwide dominance of seed plants.

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