Early diversification of seeds and seed-like structures.

[Diversification précoce des graines et structures assimilées]

Cyrille PRESTIAANNI 1

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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 than 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 & SHECKLER, 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 zallesskyi STOCKMANS (1948), emend. FAIRON-DEMARET et SHECKLER (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 PETROVSKII et 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).

1 Doctorant F.R.I.A., Département de Géologie, Laboratoire de Paléobotanique, Paléopalynologie et Micropaléontologie, Université de Liège, Allée du 6 août, B18, Sart-Tilman, 4000 Liège (Belgium)
cyrille.prestianni@ulg.ac.be
**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 DRESENE et allii (1993) and STREEL et allii (1987). AD. Acinosporites acanthomamillatus - Densosporites eonicus; BJ. Verrucosporites bulliferus - Cirratiradites jekhowskyi; BM. Verrucosporites bulliferus - Lophozonotriletes media; P. Spelaeotriletes balteatus - Rugospora polypticha; CM. Schopfites claviger - Auroraspora macra; GF. Grandispora gracilis - G. famenensis; GH. Grandispora gracilis - A. hirtus; HD. Kraeuzelisporites hibernicus - Umbonatisporites distinctus; LE. Retispora lepidophyta - Indotiradites explanatus; LL. Retispora lepidophyta - Knoxisporites literatus; TA. Samarispores trianulatus - Acyspora var. ancrea; TCo. Samarispores trianulatus - Chelinospora concinna; L; M; PC. Spelaeotriletes pretiosus - Raistrickia clavata; VCo. Diducites versabilis - Grandispora cornuta; VI. Vallatisporites allatus - Retusotriletes incohatus; LN. Retispora lepidophyta - Verrucosporites 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 adpressed 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 hydasperman-type of reproduction. Their integument is made of four lobes fused basally and curving inward over the ovule apex. One of

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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 Sphinctia wuhania Li et alii (1997), the enigmatic Spermolitthus 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 heinzeliini Stockmans 1948, emend. Gernienne et alii 2004, probably represents one of the early stages in this evolution (Gernienne 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 (Gernienne 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 Spermaspores alleni, a Givetian seed-megaspore. The "seed-megaspores" are obligatory tetrads, with a unique functional and three aborted megaspores. Spermaspores alleni 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 monomegasporous (sensu Bateman & Dimichele, 1994) led Marshall and Hemsley (2003) to suggest gymnosperous affinities for Spermaspores. 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 reymi (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 impirirameum Arnold (1939) emend. Gensel et Skog (1977). Some other taxa of the Lydiennne Formation are also mentioned (Rowe & Galtier, 1990; Unger, 1956; 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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