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Early diversification of seeds and seed-like structures.

[Diverrsification précoce des graines et structures assimilées]

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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 & 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 zallesskyi 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 Lenologia krystofovichii PETROSVAN IN LEPEKHINA et alii (1962) emend. Kрасилоv et ZAKHAROV (1995) [LL Biozone]. Kerrya mattenii possesses a six unit cupule, but its overall organisation conforms to the Moresnetia-type. Lenologia 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 lagenostomal seeds ovules (CLEAL, 1993; LONG, 1975).
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 acanthomammilatus - Densosporites evinicus; BJ. Verrucosporites bulliferus - Cirratiradites jekhowskyi; BM. Verrucosporites bulliferus - Lophozonotriletes media; P. Spelaeotriletes baltatus - Rugospora polyptycha; CM. Schopfites claviger - Auroraspora macra; GF. Grandispora gracilis - G. famenensis; GH. Grandispora gracilis - A. hirtus; HD. Kraeuzelisporites hibernicus - Umbonatisporites distinctus; LE. Retispora lepidophyta - Indotriradites explanatus; LL. Retispora lepidophyta - Knoxisporites literatus; TA. Samarisorites triangularus - Acyspora var. ancyrea; TCo. Samarisorites triangularus - Chelinospora concinna; L; M; PC. Spelaeotriletes pretiosus - Raistrickia clavata; VCo. Diducites versabilis - Grandispora cornuta; VI. Vallatisporites allatus - Retusotriletes incoha; LN. Retispora lepidophyta - Verrucosporites nitidus; VH. Apiculiretusispora verrucosa - Vallatisporites hysteriosus.
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 hydrasperman-type of reproduction. Their integument is made of four lobes fused basally and curving inward over the ovule apex. One of
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 "Xenothea" 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 hydrasperm reproduction, strongly suggests an origin for early seeds older than the Frasnian. The Givetian taxon *Runcaria heinzellini* 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 monomegasporous affinities (sensu Bates & 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 Bates & 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 hydrasperm nucellar apical modification is absent. This ovule is interpreted as showing adaptation to aquatic dispersal (Galtier & Rowe, 1991). More classical hydrasperm 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, 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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