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Merging concepts: The role of self-assembly in the development of pollen wall structure

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Abstract

In this article, we analyse established details of exine development from a perspective that favours the integration of self-assembly. We isolate those intervals in development in which genomic control is exercised and offer a number of scenarios, which show how self-assembly can build upon a genetic basis to give rise to the fundamental pollen exine structure. This paper is a synthesis of a new concept and a detailed review of achievements in the field of developmental palynology. It seeks to link what is known regarding development with the liquid crystal realm of colloid chemistry.

Keywords: exine; glycocalyx; callose; self-assembly; pollen wall development

1. Introduction

The belief that self-assembly of components plays an important role in the production of exine structure and sculpture is not new. However, in recent years, a number of attempts have been made to define the mechanisms that may be involved in the generation of species-distinct patterning. These mechanisms must unite what is known about the ultrastructural aspects of exine development with an understanding of the macromolecular interactions likely at the scale considered.

In the past decade, a considerable body of information has been accumulated regarding the formation of the pollen wall, its development and chemistry. A diversity of plant groups have been investigated using ultrastructural techniques (see Table 1) and the nature of sporopollenin has been explored using a range of analytical methods (summarised by Van Bergen et al., 2004). Advances have been made in our understanding of wall development in the earliest fossil spores as well as those of extant species. Although this body of information is far from complete, we believe sufficient is now available for us to hesitantly offer a generalised scheme of pollen wall development. The scheme we propose includes particular reference to functions and mechanisms, and especially to those involved (we believe) in the formation of wall sculpturing.

Numerous authors have speculated on the role of self-assembly in the formation of the pollen wall (exine) (Heslop-Harrison, 1972; Gerasimova-Navashina, 1973; Gabarayeva, 1990b, 1993, 2000; Van Uffelen, 1991; Hemsley et al., 1992; Collinson et al., 1993; Hemsley et al., 1994, 1996, 1998, 2000, 2004; Borsh and Wilde,

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Table 1
Differences between the principal plant groups concern mainly stage 1 (the appearance of callose) and stage 3 (initial sporopollenin (SP) accumulation). The data for spore-producing plants is limited and many do not show callose around tetraspores. Callose was shown around SMC (spore mother cell) in at least one stage of sporogenesis for the Bryophyta (Hepaticopsida: *Anthoceros*, *Geothallus*, *Riccia*; Bryopsida: *Mnium*), but not for *Riccardia* (see review of Waterkeyn and Bienfait, 1971; Horner et al., 1966). An acid polysaccharide special wall around the tetrad has been demonstrated in Bryophytes (Bienfait and Waterkeyn, 1976—*Brachythecium velutinum*, *Brachythecium rutabulum*, *Leptobryum piriforme*). Callose is absent in the Pteridophyta, with exception of the microspores of *Selaginella*, where there is a transitional stage of callose around SMC (Waterkeyn and Bienfait, 1971, 1972; Buchen and Sievers, 1978). A non-callosic thick special wall occurs around the tetrad in homosporous lycopsids (Bienfait and Waterkeyn, 1976—*Lycopodium squarrosum*); although there are contradictory test results for lycopsids (Lugardon, pers. comm., 2004), no callose and a very short tetrad period in *Equisetum* (Uehara and Kurita, 1989a; Lugardon, 1990), small amounts of callose under fluorescence test in the central area of tetrads (Lugardon, pers. comm., 2004) and no data on tetrad wall in eusporangiate ferns (Pettitt, 1979—*Botrychium lunaria*; Uehara and Kurita, 1989b—*Ophioglossum thermale*). A polysaccharide special wall was demonstrated around the tetrad for homosporous leptosporangiate ferns (Lugardon, 1990—*Oreopteris limbosperma*), positive fluorescence reaction with aniline blue fluorochrome (test for callose) in the cell plate separating the tetraspores (Lugardon, pers. comm., 2004—*Osmunda regalis*), and the absence of the tetrad period (isolation of tetraspores by plasmodial tapetum at early tetrad stage) for heterosporous leptosporangiate ferns (Lugardon, 1990—*Azolla filiculoides*). However, callose special cell wall around microspores is fact confirmed histochemically in Cycads, Gnetopsids, Conifers, Angiosperm magnoliid and eumagliids.
A glycoprotein glycocalyx was first shown in liverworts (Marchantiopsida) by Horner et al. (1966—*Riccardia pinguis*), but for the mosses (Bryopsida) the situation is more complicated: authors (Brown and Lemmon, 1980—*Ditrichum pallidum*; Brown et al., 1982—*Sphagnum lescurii*) have found a fibrillar layer around the tetraspores (no histochemical data available), but concluded that this layer is not glycocalyx (or primexine, as they called it). The glycoprotein glycocalyx on the sporocytes and spores for other Bryophyta (*Anthoceros punctatus*, *Phaeoceros laevis*), eusporangiate ferns (*Botrychium lunaria*, *Ophioglossum palmatum*, *Marattia salicinia*), Psilotophyta (*Tmesipteris tannensis*, *Psilotum nudum*), homosporous lycopsids (*Lycopodium gnidioides*) and heterosporous lycopsids (*Selaginella sulcata*, *Isoetes lacustris*) was demonstrated and histochemically confirmed by Pettitt and Jermy (1974) and Pettitt (1979), by Rowley and Morbelli (1995—*Selaginella*). A glycocalyx would seem to be responsible for exospore development in homosporous lycopsids (*Lycopodium clavatum*), which resembles, in the opinion of the author (Lugardon, 1990), a seed plant glycocalyx, but with differ functioning. This is comparable to para-exospore development in heterosporous lycopsids (*Isoetes durieui*) where the fibrillar layer is reminiscent of the glycocalyx.
A fibrillar layer has been demonstrated around tetraspores by Uehara and Kurita (1989b—*Ophioglossum thremale*, 1991—*Lycopodium clavatum*), and its glycoprotein status was histochemically confirmed for *Equisetum arvense* by Uehara and Kurita (1989a). A fibrillar layer was also shown for homosporous leptosporangiate ferns by Surova (1981—*Anemia phyllitidis*), which, on the opinion of this author (but without histochemical confirmation), corresponds to the glycocalyx. Lugardon (1990, pers. comm., 2004) has generated and summarised many results and has shown a fibrillar layer for perispore development in homosporous leptosporangiate ferns (*Oreopteris limbosperma*), but which the author, however, considers to be most probably not glycocalyx. Extra-exospore development in heterosporous leptosporangiate ferns (Lugardon, 1990—*Azolla filiculoides*) probably involves a glycocalyx and the same would appear to be true for epispore and elater development in *Equisetum ramosissimum*.
A glycocalyx has been demonstrated in Cycads by Audran (1981—*Ceratozamia mexicana*) and Gabarayeva and Grigorjeva (2002—*Stangeria eriopus*, in press—*Encephalartos altensteinii*); in Conifers: Willemse (1971—*Pinus sylvestris*), Rohr (1977—*Taxus baccata*), Pennell and Bell (1986—*Taxus baccata*), Kurmann (1989, 1990a—*Abies concolor*, *Tsuga canadensis*), Rowley et al. (2000—*Pinus sylvestris*), Lugardon (1995—*Chamaecyparis lawsoniana*); in Gnetopsids: Kurmann (1990b—*Cunninghamia lanceolata*).
The presence of glycoprotein glycocalyx in Angiosperm magnoliid and many Angiosperm eumagnoliid has been demonstrated by many authors (see main text).
Stage 3–initial sporopollenin accumulation–is probably different in spore and seed plants. It seems that, in the groups of seed plants (Cycads, Conifers, Angiosperms), initial sporopollenin accumulates on SAPs (Skvarla and Rowley, 1987—*Poinciana*; Rowley et al., 1995, 1999a—*Nuphar*, *Pinus*; Rowley et al., 1999b—*Borago*; Gabarayeva and Grigorjeva, 2002—*Stangeria eriopus*; Gabarayeva et al., 2003c—*Lavatera arborea*; Gabarayeva et al., 2003a—*Cabomba aquatica*; Gabarayeva and Grigorjeva, 2004—*Enchephalartos altensteinii*). There is little data on Gnetopsids. SAPs have not been observed in the Bryophyta or Pteridophyta. The supposition is therefore that SAPs are inherent in seed plants only (Gabarayeva, 2004).

	Stage 1	Stage 2	Stage 3	Stage 4	Stage 5
Bryophytes	Callose around SMC	Glycocalyx	Initial SP accumulation without SAPs	Further SP accumulation	Massive SP accumulation
Homosporous lycopsids	No callose	Glycocalyx	Initial SP accumulation without SAPs	Further SP accumulation	Massive SP accumulation
Heterosporous lycopsids	Callose around SMC	Glycocalyx	Initial SP accumulation without SAPs	Further SP accumulation	Massive SP accumulation
Equisetum	No callose	Glycocalyx	Initial SP accumulation without SAPs	Further SP accumulation	Massive SP accumulation
Eusporangiate ferns	No callose	Glycocalyx	Initial SP accumulation without SAPs	Further SP accumulation	Massive SP accumulation
Homosporous leptosporangiate ferns	No callose?	Fibrillar layer (no histochem. data)	Initial SP accumulation without SAPs	Further SP accumulation	Massive SP accumulation