Synaptospory: a hypothesis

A possible function of spore sculpture in pteridophytes

by

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Summary

Part of the spore output of some ferns is shed in groups of spores, sometimes still contained within the sporangium. It is theorized that spore sculpture, particularly a distinct, strongly sculptured perispore, plays a part in keeping, or bringing, spores together. This is important for increasing the chance for intergametophytic fertilization. The want of a pronounced spore sculpture in most epiphytic ferns and the strongly sculptured spores of heterosporous pteridophytes are brought in connexion with the phenomenon, tentatively called synaptospory.

Until recently, pteridologists used to distinguish between fern taxa (genera or groups of higher rank) with a perispore and taxa without one, and much taxonomic value was attributed to this character (e.g., Kramer in Lanjouw & collab., 1968; Wagner, 1974). Through Lugardon's fundamental work (e.g., 1971, 1972a, 1974) it has now become known that the perispore is apparently of universal occurrence in ferns, and it has also been found in so-called fern allies (e.g., Lugardon 1969, 1972b, 1973). It is therefore no longer correct to speak of ferns with and ferns without a perispore. Instead, one should distinguish between spores having a perispore that is firmly appressed to the exospore, and others where the perispore forms a distinct, usually strongly sculptured layer. To avoid this awkwardness in expression I shall continue to speak below of spores with and spores without a perispore, being, of course, fully aware of the incorrectness of these terms.

In most cases a strongly developed surface sculpture of a spore was attributed to the perispore although in some cases the exospore was held responsible for the surface features. It now seems as if in all these cases a perispore is present, but where it seemed to be absent it firmly adheres to the exospore and cannot readily be distinguished except in cross-sections examined with the transmission electron microscope.

Whatever the morphological interpretation, the function of this surface sculpture has remained a matter of conjecture, not to say an enigma, as it remains to this day, to a certain extent and largely as to details, in the pollen grains of seed plants. In the following I want to put forward a hypothesis that tries to account for the presence of spore sculpture in pteridophytes. I wish to stress that it may only be one of several possible functions, and that the attempt at an explanation is no more than a hypothesis, as for the moment it rests on too few observational data. I hope, though, that it may lead to further experimental work and will either be confirmed or, if disproved, will show to have been a stimulating error.

When we review the "presence" or "absence" of a perispore (inverted commas because of the restrictions stated above), or, more generally, of a pronounced external sculpture in the spores of modern ferns, it becomes immediately apparent that large groups are without such sculpture and other, equally large and as a rule

very naturally defined ones, possess it. Wagner (l.c.) regarded the groups with a pronounced perispore as derived ones, and the perispore in general as a specialization, whatever its function. It seems to me that there is another striking correlation, namely between the "presence" or "absence" of a perispore and the habitat of the fern, that has, to my knowledge, not been reported before.

If we regard the spore wall of taxa of higher order among the modern ferns, it springs to the eye that epiphytic genera, genus groups, etc., in most cases have more or less smooth, "perisporeless" spores: Vittarioids, Davallioids, Grammitidoids, Polypodioids, Hymenophyllaceae. Minor exceptions can be found with ease, e.g. in the Polypodioids in *Drymoglossum* (see Wagner, l.c., fig. 2), in the Davallioids in *Gymnogrammitis* (see Ching, 1966, and Sen & Sen, 1971), etc., and there is one important major exception: the genus *Elaphoglossum*. This, though containing some terrestrial species, as do indeed most epiphytic groups, consists almost entirely of epiphytes; but its alliance is with a group of terrestrial or scandent genera known as the Lomariopsidoid ferns or Lomariopsidaceae*). "Perispore-less" spores occur, of course, in a considerable number of essentially or entirely terrestrial fern groups. Examples are Osmundaceae, Plagiogyriaceae and Dennstaedtioids.

A second observation, of high relevancy in this context, was recently published by Schneller (1975). It has nearly always been assumed, explicitly or tacitly, that fern spores are scattered invidually as far as possible. Schneller showed that in *Dryopteris* spp. a not inconsiderable part of the spores is shed in groups of two, three, four, or more.

According to Gastony's findings (1974), in certain tree-ferns not the spore but the sporangium, with its complete spore-content, is the unit of dispersal. The spores germinate whilst held together by the sporangium. I have the strong impression that at least partial retention of spores in the sporangium, with subsequent shedding of the entire structure, is not a rare phenomenon in ferns.

The pioneer work by Näf (1961) and Voeller (1971) has shown that the development of gametophytes and their sex organs is a process subject to physiological interaction between closely associated prothalli. These interactions greatly tend to favour intergametophytic fertilization and hence gene exchange. Various authors have reported on the much greater viability of fern sporophytes produced by intergametophytic as opposed to intragametophytic fertilization (e.g., Lloyd, 1974).

Terrestrial ferns by and large may be supposed to grow in an essentially stable environment (there are, of course, exceptions like pioneers on bare soil, lava flows, etc.) where the rate of mortality of individual plants is relatively low. Once they are mature, individual plants often grow slowly and are supposed to be potentially very long-lived, e.g., in *Osmunda regalis*. Except when new habitats are colonized, sexually produced new generations will follow each other at rather long time intervals, and it must be of great importance for the plants to maintain their genetic variability, and to avoid the influence of recessive deleterious genes, by increasing the chance for cross-fertilization when new plants are sexually produced from prothalli. The coherence of some spores, whether through the action of the spore wall or by retention in the sporangium, must greatly enhance this chance, and external spore sculpture may be one mechanism by which the former is achieved. Spores from one sporangium will not be all genetically identical, unless the mother plant is one hundred percent homozygous. Schneller (l.c.) found many groups of more than four spores being dispersed as a unit, so the tetrad is certainly not the

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* On the evidence available at present I find myself unable to agree with Tutin (1964) and Pichi Sermolli (1968) who distinguish a family Elaphoglossaceae comprising only *Elaphoglossum* and satellite genera.

limit beyond which the spores do not cohere. And there seems no reason to suppose why spores produced by different plants from one colony, and even from different ones, could not meet after having been dispersed by air currents, runoff water, etc., for instance, in a surface-film of rainwater, cohere, and germinate together, with subsequent cross-fertilization.

In contrast, most epiphytes inhabit a very unstable *milieu*. The branches and twigs they colonize have but a limited life-span, and they are thus bound to colonize new places continuously in order to survive as a species. Many do this by producing long-creeping, branching rhizomes, or sometimes runners, and such ferns very often inhabit the smaller branches and twigs of trees and shrubs, as I observed myself in some parts of tropical America, and as can be deduced from de la Sota's diagram (1971, fig. 13) illustrating Costa Rican fern epiphytes; see also Johansson (1974). The epiphytes with short rhizomes, often more massive, or even forming so-called nests, favour the more stable habitats of the main trunks and crotches of larger branches.

For colonizing new stations, these, as it were, pioneer epiphytes thus depend to a great extent on spore dispersal, which must be sufficient and efficient in order to ensure maintenance of a sufficiently large population, in spite of considerable turnover. This must largely be achieved by dispersing individual spores, and self-fertilization in lone prothalli originating from singly spread spores should be much more common in these plants. Indeed, coherence of spores in groups would impede dispersal. Wagner (l.c.) suggested that the lack of a perispore in Davallioid ferns should be regarded as a result of secondary loss of this organ, and if that is true, it might be regarded as an adaptation to epiphytism. With the comparatively rapid succession of sexually produced generations, occasional cross-fertilization would suffice for maintaining genetic variability.

In this connexion it is, I think, significant that so very few natural hybrids of epiphytic fern species have been reported, in contrast to the many terrestrial hybrids known. This may be due in part to the physical inability of the researcher to sample populations of epiphytes in the same way as of terrestrial or epilithic species, but it can hardly account for the fact as a whole. The regular development of single, self-fertilized prothalli may well be the reason for a greatly reduced chance for interspecific cross-fertilization.

The phenomenon of coherence of spores by means of cohering or interlocking surface structures may be called "synaptospory", analogous to what has been called "synaptospermy" in seed plants, after Murbeck (see, for instance, Zohary, 1962, p. 180, and van der Pijl, 1969, p. 77). Further research will have to show whether it exists as a widespread phenomenon.

One general feature observed in terrestrial heterosporous lycopodiophytes seems to point in the same direction. The great majority of *Selaginella* species, and many species of the partly terrestrial genus *Isoetes*, have strongly sculptured spores. For illustrations, see, for instance, Knox (1950) and Hellwig (1969). For sexual reproduction these plants are, of course, entirely dependent on germination of spores producing gametes of opposite sex in very close proximity. The surface sculpture may here, too, serve to enhance the chance for this to occur.

Equisetum is probably another case in point. The perispore here dissolves into hygroscopically moving bands, somewhat unfortunately termed elaters, which loosen the spore mass but also become entangled, leading to distribution of spores in groups. The prothalli are at least very often functionally unisexual (Sporne, 1952, p. 112; Duckett & Duckett, 1974).

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