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SYNAPTOSPORY IN THE FERN GENUS PYRROSIA (POLYPODIACEAE)

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SUMMARY

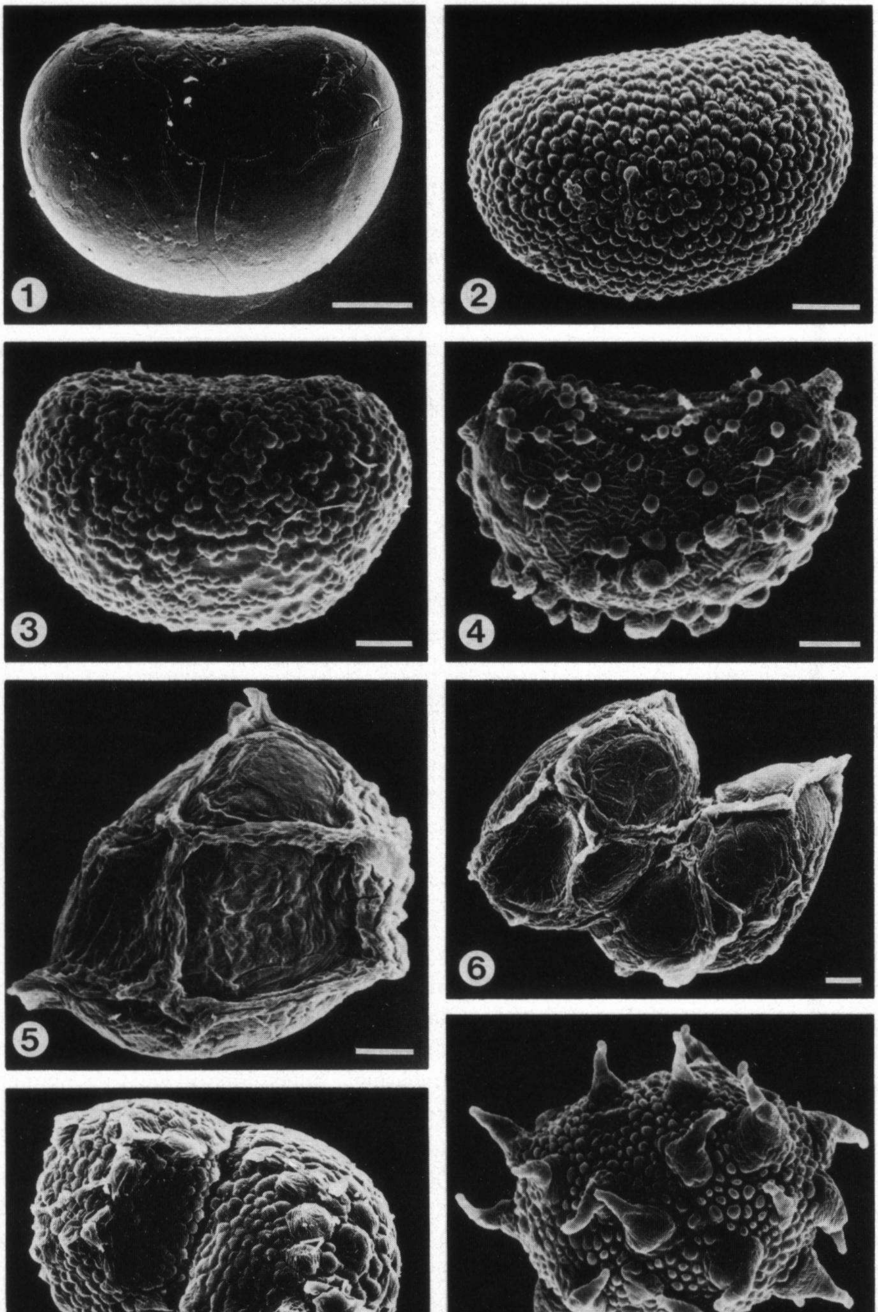
The correlation between sporoderm sculpture and life form of the sporophyte as postulated by Kramer (1977) is investigated for the fern genus *Pyrrosia*. This correlation is not found in *Pyrrosia* but may be present in other fern groups.

INTRODUCTION

An interesting hypothesis is put forward by Kramer (1977), who states that sporoderm sculpture may be correlated with dispersal ecology. According to this hypothesis epiphytic groups have more or less smooth spores, unable to stick together in order to spread easily to other trees that may be some distance away. On the other hand, terrestrial groups live in a more stable environment and have no immediate need of a wide dispersal, therefore they may have larger dispersal units like a number of spores kept together by means of their sculptured surfaces (*Dryopteris:* Schneller, 1975) or whole sporangia (Cyatheaceae: Gastony, 1974, and an example not mentioned by Kramer, *Lecanopteris:* Docters van Leeuwen, 1929*). This phenomenon is called synaptospory by Kramer, in analogy to synaptospermy in seed plants, and is supposed to enhance cross-fertilization. Although Kramer suggests these differences in dispersal ecology and sporoderm sculpture to exist between larger groups (genus level and higher), it may be interesting to examine the relation between sporoderm sculpture and substrate of the sporophyte in a single genus. Firstly, whether Kramer's hypothesis covers the situation in the genus as a whole and secondly, whether it holds for species groups within the genus.

As data about spores and ecology of *Pyrrosia* Mirbel (Polypodiaceae) have recently become available (Hovenkamp, in prep.; Van Uffelen & Hennipman, in press), this genus is chosen as the object of study. The genus *Pyrrosia* also contains the species formerly attributed to the genera *Saxiglossum* Ching and *Drymoglossum* Presl. Kramer mentions the genus *Drymoglossum* in his publication and states it to be an exception to his proposed rule.

* See also Tryon (1985) and Walker (1985).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MATERIAL AND METHODS

The spores of all species in the genus *Pyrrosia* Mirbel (Polypodiaceae) have been studied by Van Uffelen and Hennipman (l.c.) in connection with a revision of *Pyrrosia* by Hovenkamp (l.c.). The five species formerly placed in *Drymoglossum* have elaborately sculptured perispores showing two different spore types, while the one species formerly placed in *Saxiglossum* shows yet another type of spore. In all, Van Uffelen and Hennipman distinguish five spore types within the genus *Pyrrosia*, mainly based on perispore ornamentation.

One may roughly arrange the spore types according to perispore sculpture, from absent to pronounced, as follows: 1) the *P. princeps*-type, characterized by a very thin perispore that adheres tightly to the exospore surface (figs. 1, 2), 2) the *P. subfurfuracea*-type, characterized by a rather thin perispore containing spherical bodies (fig. 3), 3) the *P. christii*-type, characterized by a hatch in the perispore over the laesura and the presence of spherical bodies, together with large and solitary verrucae in some species (fig. 4), 4) the *P. nummulariifolia*-type, characterized by cristae and/or verrucae (figs. 5, 6), and 5) the *P. rupestris*-type, characterized by a bisculptate perispore with colliculate smaller warts and solitary large verrucae or echinulae (figs. 7, 8).

In *P. princeps*-type spores the exospore may be ornamented (fig. 2) but not to such an extent that they will as easily cohere as spores with an elaborately ornamented perispore.

RESULTS AND DISCUSSION

Spores and substrate of the species in Pyrrosia. — Species in the genus *Pyrrosia* are known to be epiphytes generally, but the labels of the 123 specimens studied indicate that rather a large number of them were terrestrial or epilithic. Forty-three of the labels do not indicate the place of growth; whether this means the specimen was terrestrial (like most plants) or epiphytic (supposed to be usual in *Pyrrosia*) is impossible to assess.

Of the remaining 80 specimens, 52 were epiphytic, 2 were growing on dead wood, 20 were epilithic and 3 terrestrial; 3 were found growing on tree trunks as well as on rocks or on the ground. These last specimens indicate that in some species the preference for a certain substrate is not very distinct. Besides, in 9 of the 31 species of

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Fig. 1–8. Spore types in *Pyrrosia*; scale represents 10 µm. – 1: *P. princeps* (Mett.) Morton (*Damask 7*, L), lateral view. – 2: *P. schimperiana* (Kuhn) Alston (*Maas Geesteranus 6270A*, L), lateral view. – 3: *P. subfurfuracea* (Hooker) Ching (*Tsai 53252*, A), lateral view. – 4: *P. christii* (Giesenh.) Ching (*Nooteboom 1227*, L), approx. lateral view, showing the hatch over the laesura. – 5: *P. nummulariifolia* (Swartz) Ching (*cult. Kew 685-69 6337*), general view. – 6: *P. novoguineae* (Christ) Price (*Brass 27921*, L), two spores. – 7: *P. niphoboloides* (Baker) Price (*Humbert 5831*, K), two spores. – 8: *P. piloselloides* (L.) Price (*Phengklai 1130*, L), general view.

Table 1. Substrates on which the species in *Pyrrosia* as recognized by Hovenkamp (in prep.) have been found.

Species	A	B	C	D	E	F	G	H
P. abbreviata	4	+	–	–	+	+	5	epiphytic or epilithic
P. africana	1	+	–	–	–	–	1	epiphytic, sometimes epilithic
P. albicans	4	+	–	–	–	+	2	epiphytic, occ. terrestrial or epilithic
P. angustata	4	+	–	–	–	–	1	epiphytic, also epilithic or terrestrial
P. angustissima	3	–	–	+	–	–	2	epiphytic or epilithic
P. assimilis	2	–	–	–	+	–	1	epilithic, occ. epiphytic
P. asterosora	4	–	–	–	–	+	2	epiphytic
P. boothii	2	+	–	–	–	–	1	epilithic or epiphytic
P. ceylanica	5	–	–	+	–	+	2	epiphytic or epilithic
P. christii	3	+	–	–	–	+	2	mainly epiphytic
P. confluens	5	+	–	–	–	+	3	epiphytic, sometimes epilithic
P. costata	1	–	–	+	–	–	1	epiphytic or epilithic
P. distichocarpa	4	–	–	–	–	+	2	epiphytic, occ. epilithic
P. drakeana	2	+	–	–	–	–	1	epilithic or terrestrial, sometimes epiphytic
P. eleagnifolia	5	+	–	–	+	+	2	epiphytic or epilithic, sometimes terrestrial
P. fallax	5	+	–	–	–	–	1	mostly epiphytic
P. flocculosa	2	+	–	–	–	+	2	mostly epiphytic, sometimes epilithic
P. foveolata	5	+	–	–	–	–	4	epiphytic, occ. epilithic
P. gardneri	3	+	–	+	–	+	4	epiphytic or epilithic
P. hastata	2	–	–	+	–	–	2	mostly epilithic, sometimes epiphytic
P. heterophylla	5	+	–	–	–	–	1	epiphytic or epilithic
P. kinabaluensis	4	+	–	–	–	–	1	epiphytic, sometimes epilithic
P. laevis	3	–	–	–	–	+	3	probably mostly epiphytic
P. lanceolata	5	+	–	+	–	+	13	mostly epiphytic, sometimes epilithic
P. linearifolia	2	+	–	–	–	–	2	epiphytic or epilithic
P. lingua	3	+	–	+	–	–	3	epiphytic or epilithic, sometimes terrestrial
P. longifolia	5	+	–	–	–	–	2	epiphytic, rarely epilithic or terrestrial
P. mannii	2	+	–	–	–	–	1	mostly epiphytic, sometimes epilithic

(Table 1 continued)

Species	A	B	C	D	E	F	G	H
P. niphoboloides	5	–	–	–	–	+	2	epiphytic or epilithic
P. novo-guineae	4	+	–	–	–	–	1	epiphytic
P. nummulariifolia	4	–	+	–	–	+	2	epiphytic
P. pannosa	2	–	–	+	–	–	2	few data, mainly epilithic
P. penangiana	2	–	–	–	–	+	1	mostly epiphytic, also epilithic
P. petiolosa	3	–	–	+	–	+	3	epilithic, rarely epiphytic
P. piloselloides	5	+	–	–	–	–	1	epiphytic, sometimes epilithic
P. platyphylla	1	–	–	–	–	+	1	epiphytic or epilithic
P. polydactyla	2	–	–	–	–	+	1	epilithic, terrestrial or epiphytic
P. porosa	2	+	–	–	–	+	7	epilithic or epiphytic, sometimes terrestrial
P. princeps	1	+	–	+	+	+	6	mostly epilithic or terrestrial, also epiphytic
P. rasamalae	4	+	–	–	–	–	1	epiphytic, occ. epilithic or on earth banks
P. rhodesiana	2	+	–	+	–	+	6	epiphytic or epilithic
P. rupestris	5	+	–	–	–	–	1	epilithic, also on trees and logs
P. samarensis	4	+	–	–	–	+	2	epiphytic
P. schimperiana	1	+	+	–	–	+	5	epiphytic, also epilithic
P. serpens	5	+	–	–	–	–	1	epiphytic, sometimes epilithic
P. sheareri	2	+	–	+	–	–	2	epilithic, less often epiphytic
P. sphaerosticha	4	+	–	–	–	+	3	epiphytic, occ. epilithic
P. splendens	1	–	–	–	–	+	1	few data, mostly epiphytic
P. stigmosa	1	–	–	+	–	–	1	epilithic or epiphytic
P. stolzii	2	+	–	–	–	+	4	epiphytic
P. subfurfuracea	2	+	–	+	–	–	2	epilithic, occ. epiphytic

A: Spore type (Van Uffelen & Hennipman, in press). – B: Epiphytic. – C: On dead wood. – D: Epilithic. – E: Terrestrial. – F: Unknown. – G: Number of specimens studied. – H: Substrate preference as described by Hovenkamp (in prep.).

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which more than one specimen was studied, epiphytic (incl. those on dead wood) as well as terrestrial or epilithic specimens were found (table 1). Nevertheless, as over half of the specimens of which the place of growth is known were epiphytes, the image of *Pyrrosia* as an epiphytic genus still appears to agree with the facts. The elevation of sporoderm sculpture in some species of *Pyrrosia*, especially in *P. rupestris*-type spores, therefore contradicts Kramer's hypothesis about the correlation between pronounced sporoderm sculpture and a terrestrial mode of life.

As the elevation of sporoderm sculpture differs very much between spore types in *Pyrrosia*, Kramer's hypothesis may still hold for these smaller groups. Table 2 gives the numbers and percentages of specimens studied of the different spore types, arranged according to substrate. These data show clearly that more epiphytes are found among species having spores with very pronounced sporoderm sculpture (*P. nummulariifolia*- and *P. rupestris*-type) than in species with other types of spores.

As the percentage of specimens of which the substrate is unknown is very high, no valid conclusions can be drawn. However, this set of specimens does certainly not confirm Kramer's hypothesis and it seems that not only the species formerly attributed to *Drymoglossum*, but the genus *Pyrrosia* as a whole is an exception to his proposed rule.

Cohesion of spores. — The hypothesis of synaptospory is based on the assumption that the degree to which spores tend to cohere is highly correlated with the elevation of sporoderm sculpture. I found spores cohering in *P. novo-guineae* (fig. 6), *P. samarensis, P. rasamalae* and *P. niphoboloides* (fig. 7), species with a pronounced sporoderm sculpture. I never found more than two or three spores cohering and in the cases observed the perispores fitted so closely together that perispore formation must have taken place with the spores in this position. This agrees with the ideas of Hennipman (1977) about the origin of perisporal cristae in some species of *Bolbitis*, although Lugardon (1981) states that in most ferns adjacent spores are probably separated from each other during development by some kind of barrier, preventing perispores from merging together.

Table 2. Numbers of specimens studied of the different spore types arranged according to substrate.

Spore type*	A		B		C		D		E		Total	
	nr.	%	nr.	%	nr.	%	nr.	%	nr.	%	nr.	%
Epiphytic	4	25	14	40	2	12	11	50	21	64	52	42
On dead wood	1	6	–	–	–	–	1	5	–	–	2	2
Epilithic	3	19	8	23	7	41	–	–	2	6	20	16
Terrestrial	1	6	1	3	–	–	1	5	–	–	3	2
Variable	–	–	–	–	1	6	–	–	2	6	3	2
Unknown	7	44	12	34	7	41	9	41	8	24	43	35
Total number of specimens	16		35		17		22		33		123	

* A: *P. princeps*-type. – B: *P. subfurfuracea*-type. – C: *P. christii*-type. – D: *P. nummulariifolia*-type. – E: *P. rupestris*-type.

As the spores that I observed cohering must have lain side by side at the beginning of perispore formation, it is probable that many of the spores thus hanging together in twos and threes have arisen from the same tetrad, unless it is assumed that the spores leave the tetrad figure and get mixed up after exospore formation. It follows that in *Pyrrosia* even spores with a pronounced perispore sculpture have rarely been observed to cohere in the haphazard way that is supposed to enhance cross-fertilization between the subsequent gametophytes. Cohesion of spores from the same tetrad actually prevents the recombination of genetic material: within one tetrad there are two pairs of genetically identical spores, each pair complementary to the other; intergametophytic selfing (Klekowski, 1969) between genetically identical gametophytes would result in homozygotic sporophytes, intergametophytic selfing between complementary gametophytes would result in exact copies of the plant that produced the spores in the first place. In both cases, very little recombination would take place, although it would not be impossible, especially in polyploids (Klekowski, 1973). Recombination in ferns as a result of synaptospory can usually only follow if spores from different tetrads or different sporophytes are involved.

CONCLUSION

Synaptospory as observed in *Pyrrosia* does not serve a clear purpose, but seems to be an accidental remaining together of intricately sculptured perispores. As the amount of variation in perispore sculpture found in *Pyrrosia* indicates the unique position of this genus with respect to the spores and as Kramer already refers to *Drymoglossum* (= *Pyrrosia*) as an exception to his hypothesis, I do not suggest the hypothesis as such should be rejected. It could still cover the situation in many other groups that are more consistent with regard to sporoderm sculpture and ecology.

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