BLUMEA 37 (1993) 529-561

SPOROGENESIS IN POLYPODIACEAE (FILICALES). III. SPECIES OF SEVERAL GENERA. SPORE CHARACTERS AND THEIR VALUE IN PHYLOGENETIC ANALYSIS

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SUMMARY

Mature spores were studied in more than 30 species from sixteen genera of Polypodiaceae. Of ten of these species sporogenesis was also studied, after the application of conventional fixation techniques for transmission electron microscopy, or of freeze fracturing for scanning electron microscopy. For the species studied here and for those described earlier in this series of publications, the possible value of spore characters in phylogenetic analysis is discussed.

INTRODUCTION

This is the third publication in a series treating sporoderm development in the fern family Polypodiaceae. In the first publication the development of the spore wall in *Drynaria sparsisora* has been described (Van Uffelen, 1990), in the second its development in species of *Microgramma* and *Belvisia* (Van Uffelen, 1992). The present study includes observations on spores and sporogenesis of a wide range of polypodiaceous species in order to build a picture of this character complex in Polypodiaceae that is as complete as possible at this moment.

Comparative study of sporoderm development in species of Polypodiaceae with transmission electron microscopy (TEM) did not show any differences between species during the first stages of sporogenesis (Van Uffelen, 1985a, 1990, 1992). They all produce similar spore mother cells, meiosis looks similar, and deposition of the thin and smooth inner exospore layer is also similar, as well as formation of the apertural fold. Finally, deposition of the first lumps of the outer exospore layer looks identical in all species. However, as soon as the young spores are completely covered with the first thin layer of outer exospore, differences become apparent.

As it is difficult to interpret the sequence of different exospore patterns with two-dimensional TEM micrographs only, I applied a technique developed by Blackmore & Barnes (1985). It involves the freeze fracturing of whole sori, and the study of the fractured sporangia in different stages with scanning electron microscopy (SEM).

Mature spores of many species of Polypodiaceae have also been depicted in other publications by contributors of the Polypodiaceae project: Van Uffelen & Hennipman (1985: *Pyrrosia*), Hennipman (1990), and Hensen (1990: *Polypodium loriceum*-complex), and the spores of some species in the revisions of the genera *Platycerium* (Hennipman & Roos, 1982), *Drynaria* and *Aglaomorpha* (Roos, 1986), *Goniophlebium* (Rödl-Linder, 1990), and *Microsorum* (Bosman, 1991).

Table 1. Specimens studied.

Species	Origin of material	Sd.	Sm.	Td.	Tm.
Arthromeris lehmannii	Mann s.n. VII 1890 (L)	–	+	–	–
Campyloneurum angustifolium	LEI 21566	–	+	–	–
Crypsinus bakeri	De Wilde & Duyfjes 13244 (L)	–	+	–	–
Crypsinus enervis	LEI 21196	–	+	–	–
Crypsinus simplicissimus	LEI 21666	–	+	+	+
Crypsinus veitchii	Togashi 400 (U)	–	+	–	–
Dictymia brownii	Hennipman 6411 (L)	–	+	–	–
Goniophlebium korthalsii	Kato, Murata & Mogea B3729 (L)	–	+	–	–
Goniophlebium percussum	Rödl-Linder 194 (HBU)	+	+	–	–
Goniophlebium persicifolium	LEI 22210	–	+	–	–
Lecanopteris celebica	Hennipman 5993 (L)	–	+	–	–
	Hennipman 5665 (L)	–	+	–	–
Lecanopteris darnaedii	Hennipman 5322 (L)	–	+	–	–
Microsorum linguiforme	LEI A00971	–	+	–	–
Microsorum punctatum	LEI 560031	–	+	–	–
Neocheiropteris ensata	Tagawa 3011 (P)	–	+	–	–
Neocheiropteris normalis	Trotter s.n. 26/30-4-1887 (P)	–	+	–	–
Neocheiropteris ovatus	Esquirol 1105 (P)	–	+	–	–
Neocheiropteris palmatopedata	Ducloux 6367 (P)	–	+	–	–
Neocheiropteris spec. [= *Microsorum pappei*]	84GR00043 (HBU)	–	+	–	–
Niphidium crassifolium	LEI 298A	–	+	–	–
Paragramma longifolia	LEI 23041	–	+	–	–
	LEI 23306	–	+	–	–
Pecluma singeri	LEI 21595	+	+	–	+
Phymatosorus commutatus	82GR00146 (HBU)	+	+	–	–
	Buwalda 3772 (L)	–	+	–	–
	LEI 21238	–	+	+	+
Phymatosorus diversifolius	Constable P8264 (U)	–	+	–	–
	Philipson 10073 (L)	–	+	–	–
Phymatosorus longissimus	Amdjah 129 (L)	–	+	–	–
Phymatosorus scolopendria	LEI 20345	–	+	–	–
Platycerium alcicorne	LEI 19726	–	+	–	–
Pleopeltis lanceolata	LEI 21967	–	+	–	–
Pleopeltis percussa	86GR0101 (HBU)	+	+	–	–
Polypodium australe	P208 ex Newcastle	–	–	+	+
Polypodium fraxinifolium	LEI 21179	–	+	–	–
	LEI 23479	–	+	+	+
Polypodium hirsutissimum	LEI 20348	–	+	–	–
Polypodium levigatum	Herb. Christ, L81347	–	+	–	–
	LEI 21902	–	+	–	–
Pyrrosia angustata	LEI 19713	–	+	–	+
	Meijer 2196 (L)	–	–	–	+
Pyrrosia gardneri	LEI 22359	–	+	–	+
Pyrrosia polydactyla	LEI 21249	+	+	+	+
	LEI 21440	+	+	–	–
Pyrrosia princeps	LEI 20608	–	+	+	+
Pyrrosia rupestris	LEI 21551	–	+	+	+
	Schodde 3242 (L)	–	–	–	+

Sd. = SEM study of spore development. — **Sm.** = SEM study of mature spores. — **Td.** = TEM study of spore development. — **Tm.** = TEM study of mature spores.
LEI = Botanic garden of Leiden University. — HBU = Botanic garden of Utrecht University.
(L) = Herbarium Leiden. — (P) = Herbarium Paris. — (U) = Herbarium Utrecht.

MATERIAL AND METHODS

The same methods have been used here as previously described by Van Uffelen & Hennipman (1985) for the study of mature spores with SEM, and by Van Uffelen (1990) for the study of mature spores with TEM and of spore wall development with both SEM and TEM.

Mature spores were collected from herbarium specimens or from living plants, usually grown in the Botanic Gardens of Leiden or Utrecht. Material for the study of spore wall development was taken from living plants. A list of all material studied is shown in Table 1.

RESULTS

The results are presented in systematic order, following Baayen & Hennipman (1987), except in the case of *Pleopeltis percussa*. Unless stated otherwise, only mature spores of a species have been studied, with SEM. Text between square brackets refers to micrographs published elsewhere. The abbreviation T&L refers to Tryon & Lugardon (1991).

Subfamily Platycerioideae

The exospore of *Platycerium alcicorne* Desv. is smooth with a short, narrow laesura of c. 17 μm long, and with one or more rows of very small spherical bodies parallel to it. The perispore is thin (c. 0.2 μm) and granular with groups of small spherical bodies, which are c. 0.4–1.0 μm ø (Plate I-1). Spore length c. 50 μm, height 33 μm, width 35 μm.

[For TEM, see Lugardon (1974, Pl. XV) and T&L (p. 304)]

Van Uffelen & Hennipman (1985) distinguished five spore types in the genus *Pyrrosia*, based on observations with SEM. Of each of these spore types a representative has now been studied with TEM. The types are mainly based on perispore characters.

Mature spores of *Pyrrosia angustata* have a smooth exospore and a very thick perispore with ridges more or less parallel to the laesura. If the perispore breaks, it often does so along the ridges, which are usually, but not always solid. The exospore is c. 1.2–1.6 μm thick, the perispore more than 1 μm thick in its thinnest parts, on the ridges up to 10 μm (Plate I-5). The perispore has a fibrillar structure, with a repetitive arrangement of substructures (Plate I-6), which is interrupted near some of the ridges in order to provide a rupture site.

[SEM in Van Uffelen & Hennipman (1985, Pl. VII-1), in Hennipman (1990, fig. 2.6.e), and in T&L (p. 307); TEM in Hennipman (1990, fig. 2.6.g)]

Pyrrosia gardneri (Mett.) Sledge has spores with a smooth exospore and a perispore with scattered small and large verrucae with a thinner, oval 'hatch' over the laesura. The exospore is at least 1.5 μm thick, with many channels around the laesura and none distally (Plate I-4). The exospore is not quite homogeneous but shows tangential bands of different electron opacity. The perispore is very thin over the laesura, consisting of only a few membranes. It is thicker (at least 0.2 μm) but not always solid on the rest of the spore, with verrucae of up to 4 μm high, which often contain a spherical body of up to 1.7 μm ø. The surfaces of mature perispores of adjacent spores often fit neatly into each other.

[SEM in Van Uffelen & Hennipman (1985, Pl. VI-4–7)]

Pyrrosia polydactyla (Hance) Ching has a smooth exospore and a perispore containing so many spherical bodies that they sometimes form ridges. On SEM the smooth exospore may show slight depressions caused by spherical bodies contained in the perispore, and flakes of perispore material may remain after the brittle perispore has broken away. The exospore is at least 1.2 μm thick. The perispore is thick and electron opaque in its basal part (up to c. 1.8 μm thick), thin and flaky under the embedded spherical bodies, somewhat thicker over them. The up to 1 μm thick outermost part of the perispore, which is much less electron opaque, probably is a TEM fixation artifact, as it appears to be thin and closely following the contours of the spherical bodies on SEM. The numerous spherical bodies are up to c. 2 μm ø (Plate I-3).

[SEM in Van Uffelen & Hennipman (1985, Pl. III-3)]

Mature spores of *Pyrrosia princeps* (Mett.) Morton are entirely smooth. The exospore is c. 1.25 μm thick, the perispore very thin (Plate I-2). Observation of spore wall development with TEM shows a succession of different verrucate and almost smooth patterns.

[SEM in Van Uffelen & Hennipman (1985, Pl. I-1 & 2)]

Mature spores of *Pyrrosia rupestris* (R. Br.) Ching (Plate I-7) have a slightly colliculate (Van Uffelen & Hennipman, 1985) exospore surface. A profusion of channels is present around the laesura. The exospore is c. 1.2–1.4 μm thick, the perispore is at least 0.5–1 μm thick (Plate I-8), with a basal pattern of wrinkled, colliculate verrucae of c. 2–3 μm ø, and with large verrucae of up to 15 μm ø and 8 μm high, which are also wrinkled and appear to be arranged in rows.

Subfamily Polypodioideae

Tribe Selligueinae

On SEM micrographs of *Arthromeris lehmannii* (Mett.) Ching (Plate II-1) the exospore is smooth, the laesura inconspicuous. The perispore is rather thick, at least 1 μm, coarsely rugate/verrucate, the rugae c. 4 μm broad and 1–2 μm high, with occasional blunt spines (up to 2 μm high), and many small spherical bodies (< 1 μm ø). The spores are 40 μm long and 24 μm high.

[SEM of mature spores and a perispore detail, and TEM of the exo- and perispore in T&L (p. 355)]

Spores of *Crypsinus bakeri* (Luerss.) Tagawa (Plate II-2) have a finely verrucate perispore, which is c. 1 μm thick. The small verrucae are colliculate and smaller than 1 μm ø. Both spines and spherical bodies (< 1 μm ø) are present on the perispore. The spines are up to 4(–7) μm long and often apparently consist of a small tower of spherical bodies, but are sometimes more or less cylindrical, and sometimes topped with a globule. The spores are 68 μm long, 46 μm high and c. 50 μm wide. The laesura is c. 44 μm long.

Spores of *Crypsinus enervis* (Cav.) Copel. (Plate II-4) have a finely verrucate perispore, with many small spherical bodies (up to 1 µm ø), and some spines consisting of spherical bodies, the spines up to 3(–7) µm long. The verrucae are colliculate, and smaller than 1 µm ø. The spores are 63 µm long, c. 38 µm high and c. 52 µm wide. The laesura is a conspicuous ridge, covered with a similarly patterned perispore as the rest of the spore, c. 26 µm long.

Mature spores of *Crypsinus simplicissimus* (F.Muell.) S.B. Andrews have been studied with SEM and TEM. They have a slightly colliculate exospore, and a thin, more distinctly colliculate perispore (Plate II-5), the verrucae c. 1–1.5 µm ø. The spines (Plate II-7) on the perispore are usually tapering, up to c. 10 µm long and 1.5 µm wide at the base, and sparse; they are mainly placed at the spore ends, some distally. Some spherical bodies (< 1 µm ø) are present. Spherical bodies also appear to be included in the spines, and some spines are topped with a globule. The spores are 58 µm long and 40 µm high. The laesura is conspicuous, c. 34 µm long. With TEM both sporogenesis and mature spores have been observed. During exospore formation a series of alternating smooth and verrucate patterns follow each other. The exospore thickness varies from 1–1.5 µm in the later stages of its formation, but in mature spores with a completed perispore it is usually thinner than 1 µm. Many blobs (Plate II-6) are involved in perispore formation. Although in the species of *Crypsinus* studied here with SEM the spines seem to be assembled out of spherical bodies, on TEM it is to be postulated that, at least in *C. simplicissimus*, both the basal layer and the spines are assembled out of lamellae (Plate II-6), and that the spines are entirely continuous with the perispore base at maturity (Plate II-8). The perispore base is c. 0.6 µm thick.

Spores of *Crypsinus veitchii* (Baker) Copel. have a slightly colliculate exospore, and a distinctly colliculate perispore (Plate II-3), the verrucae up to c. 2 µm ø. The perispore is c. 0.5 µm thick, echinate, the spines slightly tapering, up to c. 5 µm long, sometimes topped with a globule. The spores are 56 µm long and 38 µm high. The laesura is 36 µm long, tightly covered with perispore.

[SEM as *Selliguea* spec. in Hennipman (1990, fig. 2.5.d)]

Tribe Lepisorinae

The spores of *Paragramma longifolia* (Blume) Moore are neatly plano-convex with a rather long, conspicuous laesura. The exospore surface is verrucate, the verrucae small, c. 1.5–2 µm ø, and fused into long, distinct ridges, most of which run more or less parallel to each other from the laesura towards the distal pole. The perispore is inconspicuous. The spores are c. 55 µm long, 36 µm high, and the laesura is c. 30 µm long.

[SEM published by Hennipman (1990) as fig. 2.3.f]

Tribe Microsorinae

The exospore surface of *Dictymia brownii* (Wikstr.) J. Smith is faintly verrucate, the verrucae often united into short rugae, of the same size all over the spore, c. 1.5–3 µm ø. The perispore is not very thin, but it follows exactly the contours of the exospore (Plate III-1) and is rather fragile; its thickness is difficult to assess on SEM micrographs. The spores are c. 53 µm long, 32 µm high and 36 µm wide. The laesura, which is not conspicuous, is c. 23 µm long.

The spore shape of *Lecanopteris celebica* Hennipman is not beanlike as in most polypodiaceous spores, but rather angular (T&L, p. 322: 'fusiform'): rhomboid in proximal view and markedly concavo-convex in lateral view (Plate III-5). The exospore is smooth, the perispore thin and granular, in some spores with spherical bodies of 1–2 µm ø scattered over the surface. A flaky perisporal mass is present on the proximal face over the laesura, usually covering the entire laesura. The spores are c. 60 µm long, 33 µm high and 34 µm wide.

The spores of *Lecanopteris darnaedii* Hennipman are neatly biconvex. The exospore is rather smooth and thin, c. 1 µm thick, with many small depressions (Plate III-3 & 4). The perispore is smooth and flaky, usually forming a most conspicuous flaky perisporal mass over the laesura, where it may be more than 10 µm high. Few spherical bodies of c. 1 µm ø are present. The spores are 57 µm long, 42 µm high and 42 µm wide. The laesura is inconspicuous and c. 11 µm long.

[SEM and TEM in Hennipman (1990) as figs. 2.5.a and 2.1.b]

In both species of *Lecanopteris* studied here, the spores often stay together in pairs or tetrads, apparently kept together by the perisporal mass over the laesura (see Plate III-5: tetrad of *L. celebica*).

The exospore surface of *Microsorum linguiforme* (Mett.) Copel. is smooth. The perispore has many small spherical bodies, which are much less than 1 µm ø. The laesura is inconspicuous, c. 17 µm long, but lies sometimes on a prominent ridge. The spores are 59 µm long, 37 µm high, and 37 µm wide.

[SEM of a mature spore published in Bosman (1991, p. 39)]

The spore surface of *Microsorum punctatum* (L.) Copel. is almost smooth, scabrate, with some very small spherical bodies. The laesura is inconspicuous. Both large and small spores were present in the sample. The small spores are c. 50 µm long and 20 µm high, the large ones are c. 65 µm long and 33 µm wide, with a c. 27 µm long laesura.

[See T&L for SEM (p. 327) and TEM (p. 329)]

The spore surface of *Neocheiropteris* spec. [= *Microsorum pappei* (Kuhn) Tardieu-Blot; see Bosman, 1991] is slightly verrucate, with a pattern of which it is difficult to say which are more conspicuous: the verrucae or the depressions in between (Plate III-6). The verrucae are up to c. 2 µm ø. The spores are 52 µm long and 34 µm high, the laesura is slight, c. 26 µm long.

Neocheiropteris ensata (Thunb.) Ching has spores with a slightly colliculate surface. The verrucae are small, c. 1 µm ø, up to 2.5 µm ø, the few spherical bodies on the spore surface are up to 2 µm ø. The exospore is c. 1 µm thick. The spores are c. 51 µm long, 37 µm high, the laesura is c. 20 µm long.

[For SEM, see T&L (p. 330)]

The spores of *Neocheiropteris normalis* (Don) Tagawa (Plate III-7) are slightly verrucate. The verrucae are small, c. 1(–1.5) µm ø, not touching each other, but sometimes fused to form irregular short ridges. The laesura itself is inconspicuous and 9–26 µm long, but it lies occasionally on a large ridge, which is c. 47 µm long. The spores are c. 64 µm long and 38 µm high.

The spores of *Neocheiropteris ovatus* (C. Presl) Nayar & Kaur (Plate III-8) are rather distinctly verrucate, the verrucae more distinct away from the laesura, > 1.25 µm ø, in many places joining to form a pattern with ridges. Verrucae just as conspicuous as the depressions in between. Some spherical bodies are present, up to 1 µm ø. The laesura is slight, 19 µm long, but lies on a conspicuous, c. 36 µm long ridge, running almost the entire length of the spore. The spores are 50 µm long.

Neocheiropteris palmatopedata (Baker) Christ has spores with an almost smooth, barely verrucate surface, on which quite a number of small spherical bodies, smaller than 1.2 µm ø, are present. The exospore is c. 1 µm thick, not smooth on the inside. The laesura is c. 19 µm long and lies on a very slight ridge. Perispore inconspicuous. The spores are c. 44 µm long, 36 µm high, and 32 µm wide.

[For SEM of a mature spore, see T&L (p. 330)]

Of *Phymatosorus commutatus* (Blume) Pichi Serm. both mature spores and spore wall development have been studied with SEM as well as with TEM. The developing spores show a succession of verrucate patterns, which results in a smooth exospore.

At the beginning of outer exospore formation (Plate IV-1, 5), the inner exospore is 0.03 µm thick, the outer exospore 0.01–0.05 µm thick, the verrucae ('units') c. 0.05–0.1 µm broad.

In a slightly later stage (Plate IV-6) the spores are c. 33 µm long and the verrucate pattern is of a larger scale, more so on the distal part of the spore than on the proximal side.

The exospore gets thicker and the verrucae larger both as to height and basis; the surface covered by a verruca is up to 1 µm ø in Plate IV-2, where the exospore is distinctly verrucate and 0.3–1.2 µm thick.

In a slightly later stage, the exospore is 0.8–1.8 µm thick, and there are many channels present around the laesura, but only a few in the more distal part of the exospore (Plate IV-3). The cavities in the exospore around the laesura may result from former verrucate patterns.

The exospore surface gets smoother (Plate IV-7), with a shallow, colliculate surface pattern with verrucae of up to 2 µm ø.

Mature spores have a smooth, c. 1 (0.6–1.3) µm thick exospore, which may bear distinct impressions of perisporal spherical bodies or spines. The perispore is thin, c. 0.15 µm thick, sparsely to very densely set with spherical bodies of c. 0.5 (up to 1.25) µm ø, sometimes also with short, up to 1 µm long spines (Plate IV-8, 82GR00146). The laesura is short, c. 14 µm long. The spores are c. 45 µm long and 31 µm high. Larger spores of c. 65 µm long were present in one of the samples (LEI 21238).

Plate IV-4 shows a germinating spore, therefore it must be mature. Its exospore is thinner (0.8–1.2 µm thick) than found in a late stage of outer exospore formation, indicating that consolidation of exospore material takes place at the time of maturity.

[For SEM (LEI 21238) see Hennipman (1990, fig. 2.1.e)]

Spores of *Phymatosorus diversifolius* (Willd.) Pichi Serm. have a verrucate surface, the verrucae becoming larger towards the distal pole and the spore ends. The verrucae are often rounded/half-globular, and up to 1–3 µm high, up to 3–5 µm ø. The laesura is conspicuous, the perispore is not. The spores are c. 47 µm long, 27 µm high, and 29 µm wide. The laesura is c. 23 µm long.

[For SEM of a mature spore, see Hennipman (1990, fig. 2.3.g)]

The exospore of *Phymatosorus longissimus* (Blume) Pic.Serm. is smooth with very small holes, the perispore thin with numerous small (c. 0.5 µm ø) and some larger (up to 3 µm ø) spherical bodies. The laesura is inconspicuous. Small, pointed spines of up to 2 µm long are also present on the perispore. The spores are c. 40 µm long.

[See Hennipman (1990), fig. 2.4.f (SEM) and fig. 2.4.g (TEM); SEM also in T&L (p. 332)]

The exospore surface of *Phymatosorus scolopendria* (Burm.) Pic.Serm. is almost smooth, very slightly colliculate, with numerous very small holes. The laesura is rather conspicuous, 17 µm long. The perispore is inconspicuous. The spores are c. 42 µm long and 31 µm high.

[For SEM of a mature spore, see T&L (p. 332)]

Tribe Polypodiinae

Campyloneurum angustifolium (Sw.) Fée has spores with a colliculate surface, the verrucae being very low and rounded, c. 2–3 µm ø. The laesura is conspicuous and c. 30 µm long. The perispore is very thin, closely adhering to the exospore surface, with a few spherical bodies of up to 2 µm ø present. The spores are c. 68 µm long, 47 µm high and 44 µm wide.

[For SEM, see Hennipman (1990, fig. 2.1.f), and T&L (p. 334)]

The exospore surface of *Niphidium crassifolium* (L.) Lell. is almost smooth, dotted with numerous very small depressions (Plate V-1). Small spherical bodies (< 1 µm ø) are present on the spore surface. The spores are c. 58 µm long and 37 µm high. The laesura is not very prominent.

[SEM published by T&L (p. 340), TEM by Hennipman (1990) as fig. 2.4.b]

In *Pecluma singeri* (de la Sota) Price both mature spores and some stages in sporoderm development have been studied. SEM has been applied in order to study spore wall formation, during which several more or less pronounced verrucate patterns succeed each other.

Plate V-2 shows a cross section of a developing spore with a mass of verrucae around the laesura. The spaces between some of these large verrucae probably form the cavities as observed in TEM of mature spores. The exospore is 0.35–1.9 µm thick. The spores are rather long, 36 µm. Spherical bodies are present on some of the spores.

A large number of spherical bodies is present in most stages of development (e.g., Plate V-3, spherical bodies 1.7–3.4 µm ø). Their role is not easy to interpret, as it often seems as if they are added on to the surface to form verrucae (Plate V-4), which is difficult to reconcile with the homogeneous aspect of the mature exospore on TEM micrographs.

After its formation the perispore peels off very easily, leaving the exospore surface bare, slightly colliculate and smooth, or verrucate with a very fine pattern.

Mature spores of this species as observed with SEM (Plate V-5) have a colliculate surface, with low and rounded verrucae, which become more elongated towards the distal pole. Their size ranges from 2 μm ø to c. 9 μm long. In some spores the verrucate surface is covered with very small (0.5–1.0 μm ø) pustules, formed by the very thin perispore, which abrades easily. The spores are c. 44 μm long, c. 34 μm high, and c. 37 μm wide; the laesura is c. 18 μm long.

On TEM (Plate V-6) the mature exospore is homogeneous, thick (at least 2.1 μm) and colliculate, the verrucae are up to 3 μm ø (smallest dimension). Some traces of former verrucate surfaces during exospore development are visible as darker lines in the mature exospore. Large channels, even cavities, show electron transparent around the laesura, running from both the outer and the inner exospore surface. In the rest of the exospore thin, electron opaque, branched channels are visible. The perispore is granular. Tapetal blobs may be involved in its formation, as in many other species of Polypodiaceae studied. There are some spherical bodies present in the tapetum, of at least 1.25 μm ø.

The exospore surface of *Pleopeltis lanceolata* (L.) Kaulf. is colliculate with very low, rounded verrucae of up to 3 μm ø. The laesura is conspicuous and c. 27 μm long. The perispore is inconspicuous. The spores are c. 45 μm long, 31 μm wide and high (Plate V-8).

Of *Pleopeltis percussa* (Cav.) Hook. & Grev. both mature spores and sporogenesis have been studied with SEM. Only a few stages of exospore formation have been found, e.g., Plate V-7, where the laesural fold is not yet entirely covered with exospore material, and channels are visible around the laesura. The exospore surface is very slightly colliculate, with traces of tapetum. The spores are c. 40.5 μm long. In this stage the exospore is c. 0.6–1.1 μm thick.

Mature spores are very slightly colliculate, the verrucae up to 5 μm ø. The laesura is inconspicuous and c. 19 μm long. The perispore has a few slight spines of up to 1.25 μm long. The spores are c. 55 μm long, 39 μm high, and 38 μm wide.

[For SEM of a mature spore, see T&L (p. 341)]

The study of spore development with TEM of *Polypodium australe* Fée did not show any features that have not already been observed in other species of Polypodiaceae (Van Uffelen, 1990, 1992). In mature spores the exospore is rather thick, from 2.2 μm between verrucae to 4.0 μm at the verrucae, which are up to c. 7 μm wide. The inner exospore is c. 0.07 μm thick. Exospore channels were not clearly visible, except near the laesura. The perispore is inconspicuous.

[TEM published by Lugardon (1974, Pl. XV as *P. serratum*)]

Mature spores of *Polypodium fraxinifolium* Jacq. have a colliculate exospore, with distinct verrucae that are small and low around the laesura, and larger towards the distal pole. The verrucae are up to c. 5 μm ø and 2.5 μm high. The perispore is thin and inconspicuous, and peels off easily. The laesura is quite prominent, often on a ridge. The spores are c. 42 μm long, 30 μm high, the laesura is c. 17 μm long and up to 3 μm high. In one sample (LEI 23479) some larger spores have been found of up to 70 μm long.

Plate VI-1 shows an immature spore. The laesural fold is not yet entirely covered with exospore material, but the basis of the mature spore surface is already there: the spore surface is covered with colliculate verrucae, those around the laesura smaller and higher, becoming lower and broader towards the distal pole. In this stage the spores are c. 35 µm long.

TEM also shows a succession of verrucate spore surfaces during outer exospore formation. Plate VI-2 shows a spore where the apertural fold is not yet covered with exospore material. The exospore is 0.1–0.4 µm thick, its surface covered with verrucae of up to 1 µm ø. Plate VI-4 shows a mature spore with a verrucate exospore, which is 1.0–1.8 µm thick, the verrucae up to 4 µm ø. A darker tangential band runs in the lower part of the exospore. Channels are only present around the laesura. The perispore is c. 0.04 µm thick and, as in many other species studied, tapetal blobs are probably involved in its formation (Plate VI-3).

[For SEM of mature spores, see Hennipman (1990, fig. 2.2.h) and Hensen (1990, figs. 45 & 46)]

Spores of *Polypodium hirsutissimum* Raddi (Plate VI-5) have a very conspicuous perispore. The exospore is colliculate with shallow verrucae, and the spore without perispore is c. 43 m long. The perispore consists of a basal layer almost entirely covered with 1–3 µm high papillae and spherical bodies, which are c. 1.5–3 µm ø. The papillae have a smooth surface, the spherical bodies are very finely patterned. The inside of the perispore is not smooth, but patterned, looking like a mesh of small, long structures. The spores are c. 61 µm long, 37 µm high and 41 µm wide. The laesura is very conspicuous and c. 35 µm long.

[SEM and TEM in Hennipman (1990, fig. 2.7.b, d, e)]

Spores of *Polypodium levigatum* Cav. have a colliculate exospore surface with distinct, broad verrucae and a conspicuous laesura. The exospore is 2–3 µm thick and rather smooth on the inside. The perispore is inconspicuous. The spores are c. 50 µm long, c. 32 µm high and wide, the laesura is c. 28 µm long.

[For SEM, see Hennipman (1990, fig. 2.2.g) and Lloyd (1981, fig. 23)]

SEM micrographs of mature spores of *Goniophlebium korthalsii* (Mett.) Bedd. show a smooth exospore. The spore (without perispore) is c. 45 µm long. The perispore is smooth with low, 2–3 µm broad, rounded ridges running parallel to the laesura, and very conspicuous, up to more than 50 µm long excrescences at the spore ends, making the spores look like wrapped toffees.

[For SEM, see Hennipman (1990), fig. 2.6.a]

Of *Goniophlebium percussum* (Cav.) Wagner & Grether both sporogenesis and mature spores have been studied with SEM.

Of the outer exospore formation, only the later stages have been observed. Plate VI-6 shows two slightly colliculate spores that are c. 32 µm long, and of which the laesural fold is not yet entirely covered with exospore material. Channel openings are abundant around the laesura. Plate VI-7 shows a slightly later stage, still with a slightly colliculate exospore surface, but here the laesural fold is almost completely covered with exospore material, and the spores are 37 µm long.

Mature spores are up to c. 50 µm long, with an almost smooth exospore and a slight laesura of c. 20 µm long. The perispore features ridges of up to 3 µm high, which run parallel to the laesura and form short appendages at the spore ends. The perispore is rather fragile, breaking most easily along or parallel to the ridges. Its structure is fibrillar, which is visible where the perispore is torn (e.g., Plate VI-8), and small fibres are also joining the exo- and perispore together. It consists of two layers: a basal one, and a superimposed layer featuring the ridges. The perispore is at least 0.3–0.6 µm thick.

[For SEM of mature spores, see Rödl-Linder (1990, p. 368), Hennipman (1990, fig. 2.6.c) and T&L (p. 351)]

Mature spores of *Goniophlebium persicifolium* (Desv.) Bedd. have a very slightly colliculate exospore surface, and the exospore is c. 0.6 µm thick. Spore (without perispore) c. 45 µm long. Perispore almost smooth with rounded ridges, which are higher than those of *G. korthalsii*, not all of them running parallel to the laesura. The basal perispore layer is rather thin, c. 0.3 µm. Inconspicuous excrescences are present at the spore ends.

[For SEM, see T&L (p. 351)]

DISCUSSION

In his character analysis of spores of Polypodiaceae Hennipman (1990) published many micrographs of polypodiaceous spores, which have been referred to in the section on results of the present paper. He distinguished four exospore types and two perispore types, which will often be referred to in the following section.

Exospore types:

The *Blechnum spicant* type of exospore is named after the 'exospore blechnoïde' as described by Lugardon (1971, p. 248; 1974, p. 212) in *Blechnum spicant* and regarded as synonymous with it by Hennipman (l.c.). After studying the spores of many species with TEM, Lugardon (1974) postulated that all ferns belonging to the Filicales (except Gleicheniaceae) have this type of exospore. He regards this type of exospore as 'simplifiée l'extrème', and the Filicales (Gleicheniaceae excluded) as 'un ensemble très homogène'. As he only studied two species of Polypodiaceae s.str. (*Platycerium alcicorne* and *Polypodium australe*), it is not surprising that he did not spot all the variation in spore morphology in this family. However, Hennipman should not have coined the term '*Blechnum spicant* type' (referring to Lugardon, 1971, and citing it as a synonym of his 'exospore blechnoïde') for only part of the species that Lugardon described as blechnoid. It is also rather confusing that one of the main exospore types in the family Polypodiaceae is named after a species belonging to another family (Blechnaceae).

The *Blechnum spicant* type features a rather thin (c. 1 µm thick), smooth or slightly colliculate exospore, with microchannels and a straight distinct laesura of various length. It occurs in all the major groups of Polypodiaceae except the Lepisorinae.

The *Polypodium vulgare* type of exospore is c. 2.5–4.5 µm thick and distinctly verrucate, with verrucae of various size, which often decrease in size towards the usually long and prominent laesura. Microchannels are prominent near the laesura, but absent in the distal part of the exospore. This type occurs in different subfamilies of the Polypodiaceae, and is common in the Polypodiinae.

The *Belvisia* type of exospore is 3–8.5 µm thick and distinctly verrucate, fissured, or cerebriform. It features a short laesura, the *Belvisia* type of microchannels, and tangential bands on TEM. It is confined to the Lepisorinae, *Microsorum* p.p., and *Microgramma megalophylla.*

The *Microsorum membranaceum* type has a 2–4 µm thick, verrucate, deeply fissured exospore and a short, indistinct laesura, without microchannels or tangential bands. It is confined to *M. membranaceum.*

Perispore types:

Of the two perispore types distinguished by Hennipman (l.c.), the first (A) has an indistinct perispore, composed of one or more unit membranes, closely adhering to the exospore surface. Perispores belonging to the second type (B) are more distinct and much more variable; therefore this type is divided into six 'phenetical' types (Ba–Bf).

Subfamily Platycerioideae

Spores of *Platycerium alcicorne* have been observed with TEM (Lugardon, 1974; Tryon & Lugardon, 1991). The micrographs show captive spherical bodies contained in the perispore. The exospore is rather thin, and obviously of the *Blechnum spicant* type (Hennipman, 1990). In the genus *Platycerium* there appears to be very little variation in spore morphology, so that spore characters have not been used in reconstructing relationships within the genus (Hennipman & Roos, 1982), except for the flaky perispore in *P. coronans* and *P. ridleyi,* which has been interpreted as an apomorphy for the group formed by these two species. The simplicity of both exo- and perispore neither contradicts nor confirms the close relationship with the genus *Pyrrosia,* which is firmly based on other characters (see, e.g., Hovenkamp, 1986).

The mature spores of all 51 species of *Pyrrosia* (Hovenkamp, 1986; Ravensberg & Hennipman, 1986) have been studied with SEM (Van Uffelen & Hennipman, 1985). They distinguished five spore types, which are mainly based on perispore characters. The astounding variation in perispore morphology in this genus is unique in the family Polypodiaceae s.str. According to Hennipman (1990) all species of *Pyrrosia* have a *Blechnum spicant* type of exospore.

In all spore types, except the *P. princeps* type, the exospore surface is smooth, sometimes only slightly colliculate, or with slight depressions caused by spherical bodies contained in the perispore.

Pyrrosia angustata has spores of the *P. nummulariifolia* type, which is characterized by a perispore with large ridges. The repetitive arrangement of substructures in the perispore of *P. angustata* suggests a helicoidal arrangement of the microfibrils, in discrete layers (Neville & Levy, 1984). The fairly thin, homogeneous and smooth exospore is of the *Blechnum spicant* type, the thick and cristate perispore is depicted and described by Hennipman as a type occurring in the distantly related polypodiaceous genera *Pyrrosia* and *Goniophlebium.*

Pyrrosia gardneri spores are of the *P. christii* type, characterized by a perispore that is much thinner in an oval area ('hatch') over the laesura. The perispore contains spherical bodies, while large verrucae are also present in some species. The exospore is rather thick, it lacks channels in the distal portion, and shows a dark tangential band. Only its smooth surface matches the description of the *Blechnum spicant* spore type.

The spores of *P. polydactyla* are of the *P. subfurfuracea* type. This spore type is characterized by a perispore containing many spherical bodies, which are sometimes forming ridges. The slight depressions often found on the otherwise smooth exospore, in which the spherical bodies contained in the perispore fit neatly, must be caused by these spherical bodies during or even after perispore formation. This indicates that in that last stage of spore wall formation the exospore material has not yet completely hardened, so that one may conclude that the formation of the exospore is not yet quite finished when perispore formation has already started. The outermost fairly thick, less electron dense perispore part is probably a TEM fixation artifact: on SEM the contours of the spherical bodies are clearly visible on the perispore surface, whereas on TEM the perispore surface is smooth and probably swollen during fixation. The smooth, not very thick, homogeneous exospore may well be of the *Blechnum spicant* type.

Pyrrosia princeps has given its name to the *P. princeps* spore type, which is characterized by a thin perispore that adheres closely to the contours of the exospore. The exospore surface may be smooth, but is markedly colliculate in some species. The thin and smooth exospore is of the *Blechnum spicant* type. The succession of smooth and verrucate surfaces as observed with TEM in *P. princeps* is not unlike the series described for *Drynaria sparsisora* (Van Uffelen, 1990). As the ontogenetic series shows some markedly verrucate surfaces, the species of *Pyrrosia* with a distinctly colliculate mature exospore surface could well show a development similar to that found in *P. princeps*. How the distinctly colliculate exospore of, e.g., *P. schimperiana* (Van Uffelen & Hennipman, 1985, Pl. I-5–8), which has a *P. princeps* type of spore, fits into Hennipman's system, is unclear.

The *P. rupestris* spore type, named after *P. rupestris*, is characterized by a bisculptate perispore with a basic colliculate pattern overlaid by more or less widely spaced large verrucae of varying shape. The thin, smooth or slightly colliculate exospore again tallies with a *Blechnum spicant* type of exospore.

Subfamily Drynarioideae

Of *Drynaria sparsisora* both spore development and mature spores have been studied with SEM and TEM (Van Uffelen, 1990).

Of the 557 character states recognized by Roos (1986) in his revision of the Drynarioideae, 21 relate to spores. In his chosen cladogram, where the two genera currently recognized in this subfamily, *Drynaria* and *Aglaomorpha*, are separated from each other on the basal node, spore characters show many parallelisms and reversals.

In the genus *Aglaomorpha* most of the 14 species have a smooth and inconspicuous perispore, except for two species (*A. meyeniana* and *A. cornucopia*), which have a thicker, verrucate perispore. Most species have no spines or baculae on the perispore, but for the two species with the thicker perispore, plus a third one (*A. coronans*). Spherical bodies are present in most species, except for *A. coronans* and *A. meyeniana*. The exospore is smooth in nine species, but globular in the three species already mentioned, plus in *A. parkinsoni*, *A. latipinna*, and *A. speciosa*.

In the genus *Drynaria* most of the 16 species have a thin, verrucate perispore with spines and/or baculae, but in four species the perispore is smooth and inconspicuous (*D. delavayi*, *D. sinica*, *D. pleuridioides* and *D. volkensii*, of which the last two lack spines and baculae). Spherical bodies are only present on spores of *D. volkensii*. The exospore is smooth in seven species of *Drynaria* (*D. mollis*, *D. rigidula*, *D. involuta*, *D. descensa*, *D. bonii*, *D. sparsisora*, *D. quercifolia*), globular in six species (*D. fortunei*, *D. propinqua*, *D. parishii*, *D. wildenowii*, *D. laurentii*, *D. volkensii*), and verrucate in three species (*D. delavayi*, *D. sinica*, *D.pleuridioides*), all of whom have a smooth and inconspicuous perispore.

This enumeration shows that the exceptions to the general situation in a drynarioid genus – in *Aglaomorpha* to a smooth exospore covered with a smooth and inconspicuous perispore without any spines or baculae, but with spherical bodies, in *Drynaria* to a smooth or globular exospore, covered with a thin, verrucate perispore with baculae or spines, and without any spherical bodies – are present in changing combinations, but in only a limited number of species. In *Aglaomorpha*, deviations from the usual perispore are found in *A. meyeniana*, *A. cornucopia*, and *A. coronans*, deviations from the usual, smooth exospore in these three species plus *A. parkinsoni*, *A. latipinna*, and *A. speciosa*. In *Drynaria* the perispore deviates in *D. delavayi*, *D. sinica*, *D. pleuridioides*, and *D. volkensii*, and the exospore in *D. delavayi*, *D. sinica*, and *D. pleuridioides*. Roos (1986) recognizes three spore types: the *quercifolia* type, which accommodates most of the drynarioid species and never has a verrucate exospore, whereas the perispore is variable, the *meyeniana* type, which is confined to *A. meyeniana*, and based on its unique perispore, and the *pleuridioides* type, which is characterized by a verrucate exospore, and accommodates *D. delavayi*, *D. sinica*, and *D. pleuridioides*. The use for these spore types in phylogenetic analysis is not evident, as the components of the circumscriptions already figure as separate character states in the data matrix. In the chosen cladogram (Roos, 1986) the only two species showing 'deviant characters', which may be interpreted as apomorphies, and ending up in the same clade are *D. delavayi* and *D. sinica*. In most instances of spore characters deviating from the usual situation in a genus, the species involved do not form a monophyletic group. Therefore, spore characters evidently have limited use in distinguishing the two drynarioid genera from each other, but are of little use in tracing relationships within each of the genera.

Subfamily Polypodioideae

Tribe Selligueinae

The specimen I studied of *Arthromeris lehmannii* has few perisporal spines, possibly caused by the fact that the spores studied were collected almost a hundred years ago. Tryon & Lugardon (1991) state that the spines may be eroded in older spores. They show both SEM and TEM micrographs of this species (l.c., p. 355): the exospore is 1.25 μm thick with few channels, the perispore is even thicker than the exospore, containing hollows.

According to Hennipman (1990), spores of this genus have a *Blechnum spicant* type of exospore, and an *Arthromeris* type of perispore (type Bc), of which the latter is confined to this genus. Hovenkamp (pers. comm.), who is preparing a revision of the genus *Selliguea* (incl. *Crypsinus*), thinks that the genus *Arthromeris* is separated from *Selliguea* by a number of apomorphies.

Hennipman circumscribes his perispore type Bb (1990, fig. 2.5.d) – perispore relatively thick, verrucate, with baculae or spines – as being confined to *Selliguea, Crypsinus,* and allies. However, the perispore of *Crypsinus simplicissimus* as studied with TEM, with its solid, c. 0.5 μm thick base, and spines which are continuous with the basal layer (Plate II-8) looks very much like TEM of the perispore of *Drynaria sparsisora* (Van Uffelen, 1990, Pl. XI-6). Moreover, SEM of the surface of *Arthromeris* spores (e.g., of *A. wallichiana,* see Hennipman, 1990, fig. 2.5.f; various species in Tryon & Lugardon, 1991, p. 355) looks very much like *Aglaomorpha meyeniana* (Hennipman, 1990, fig. 2.5.h). These similarities suggest a closer relationship between Drynarioideae and Selligueinae than is usually postulated. Treatment of the genera *Arthromeris* and *Selliguea* near the end of the chapter on Polypodiaceae in Tryon & Lugardon (1992), quite far apart from the drynarioid ferns, probably reflects their ideas on a distant relationship between the two groups. In Tryon (1985) the echinate spores of *Drynaria* and *Selliguea* are interpreted as a case of convergence by functional adaptation to spore transport by ants. However, Ching (1933) did regard the genus *Arthromeris* (subfam. Polypodioideae, tribe Selligueinae) as more closely related to *Drynaria* (subfam. Drynarioideae) than to *Polypodium* (subfam. Polypodioideae, tribe Polypodiinae). The rather thick exospore as found near the end of exospore formation, as opposed to the rather thin exospore in maturity (that is, when the perispore is also present), may be explained in two ways: either by consolidation of the exospore material during maturation, or by stretching of the exospore in a last fit of expansion.

In *Crypsinus simplicissimus,* as in *Drynaria sparsisora* (Van Uffelen, 1990) and species of *Belvisia* and *Microgramma* (Van Uffelen, 1992), blobs are involved in perispore formation.

Tribe Lepisorinae

A revision of the genus *Belvisia* has been published (Hovenkamp & Franken, 1993). SEM of mature spores of *Belvisia abbreviata* (as *Lemmaphyllum abbreviatum*) and *B. novoguineensis* hav been published in Van Uffelen (1992), as have data on mature spores and sporogenesis of *B. mucronata* (SEM and TEM) and *B. platyrhynchos* (SEM only).

There has been some confusion about the status of the genera *Lepisorus* and *Pleopeltis,* as *Lepisorus* has been included in *Pleopeltis* by Copeland (1947) and Pichi Sermolli (1977). In the present paper *Lepisorus* is treated as a separate, mainly Old World genus of about 40 species or less, related to the genera *Belvisia, Drymotae-*

nium, Lemmaphyllum, and *Paragramma.* These genera are placed together in the tribe Lepisorinae, as is supported by the spores, which all have a *Belvisia* type of exospore and an inconspicuous perispore.

In 1971, Mitui published an often overlooked account of sporoderm development in *Lepisorus thunbergianus.* He found a series of surface patterns similar to the series I described for *Belvisia mucronata* and *B. platyrhynchos* (Van Uffelen, 1992). However, as the freeze fracturing technique I applied was not available at that time, his micrographs are more difficult to interpret. He concludes that the different spore surfaces in the nine species of which he studied mature spores are all based on the same pattern of muri forming a reticulum, and that the muri are better developed in species with a higher ploidy level. According to Mitui's data and to the micrographs published in Tryon & Lugardon (1991), spores of the paleotropical genus of *Lepisorus* all have *Belvisia*-type spores. In Tryon & Lugardon (1991, p. 316) some doubt is expressed whether the spore surface ornamentation in *Lepisorus* is determined by the exospore surface, but the TEM micrographs of *L. nudus* and *L. ussuriensis,* published on p. 317 (l.c.), clearly show that the ornamented exospore surface is covered and followed by a much thinner perispore layer.

Tribe Microsorinae

The exospore surface as observed in *Dictymia brownii* is rather like that found in some species of *Belvisia,* e.g., *B. platyrhynchos* (see Van Uffelen, 1992). The perispore, which follows but softens the contours of the exospore ornamentation, is rather thick. Although the exospore surface suggests a *Belvisia* type of exospore in *Dictymia brownii,* the fairly thick perispore does not comply with Hennipman's statement (1990) that a *Belvisia*-type exospore always goes with a very thin (type A) perispore. Tryon & Lugardon (1991, p. 321) show TEM pictures of the perispore of another species of *Dictymia, D. mackeeii,* consisting of several thin layers. They also indicate relationship of *Dictymia* with the lepisoroid genera *Lemmaphyllum, Drymotaenium,* and *Belvisia.*

One of the species of *Lecanopteris, L. mirabilis,* has been assigned its own unique type of perispore by Hennipman (1990: "a dense mass of intertwisted filaments", see his fig. 2.7.g: SEM). In *L. darnaedii* (Hennipman, 1990, fig. 2.5.a) as well as in *L. celebica,* the flaky mass over the laesura may keep the spores together in pairs or tetrads. This is an example of synaptospory as defined by Kramer (1977), and as treated by Walker (1985) and Van Uffelen (1985b). Tryon (1985) interprets any form of synaptospory in the genus *Lecanopteris* as an adaptation to dispersal by ants, but Walker (1985) points out that the main function of synaptospory may be the maintenance of heterozygosity by the dispersal of several spores together, which may lead to several prothallia growing together, although spores of the same tetrad will not yield much recombination of genetic material.

Bosman (1991) treated the microsoroid ferns taxonomically and applied cladistic analysis, including species of *Microsorum, Leptochilus, Neocheiropteris,* and *Phymatosorus.* She concludes that with the data and methods available no acceptable hypothesis can be postulated. As of many species she included in her analysis the spores have not been studied with electron microscopy, it is impossible to check which spore characters are present in the groups resulting from this analysis.

In the two species of *Microsorum* studied here, *M. linguiforme* (for SEM, see Bosman, 1991, p. 39) and *M. punctatum* (see Tryon & Lugardon, 1990: SEM on p. 327, TEM on p. 329), the spores are smooth or almost smooth, with an inconspicuous perispore. Apparently both species have a *Blechnum spicant* type of exospore.

Of the five species of *Neocheiropteris* studied here, three have almost smooth, slightly verrucate spores, probably with a *Blechnum spicant* type of exospore, and a very thin perispore: *N. ensata* (for SEM see Tryon & Lugardon, 1991, p. 330), *N. normalis*, and *N. palmatopedata* (for SEM see Tryon & Lugardon, 1991, p. 330).

The spores of the two other species of *Neocheiropteris* observed here, *N. ovatus* and *Neocheiropteris* spec., have a verrucate/rugate exospore surface, rather like lepisoroid ferns, and probably have a *Belvisia* type of exospore. *Neocheiropteris* spec. has been transferred to this genus by Bosman (1991). It is based on *Polypodium pappei* Kuhn, and cited (as *Microsorum pappei*) by Hennipman (1990) as having a *Belvisia* type of exospore.

Spore wall development in *Phymatosorus commutatus* shows a number of quite distinctly verrucate surface patterns, which result in a smooth mature exospore surface. Similarities found with SEM after freeze fracturing between patterns in this species and in *Drynaria sparsisora* (Van Uffelen, 1990) are obvious: Plate IV-5 can be matched with Pl. V-7 & 8 (l.c.), Plate IV-6 with Pl. VIII-1 & 2 (l.c.), Plate IV-7 with Pl. VIII-4 (l.c.).

Spores in which the mature exospore surface shows impressions of elements contained in or even set upon the perispore surface indicate again that at the time of perispore formation, the exospore material has not yet completely 'hardened': it is still possible for perispore elements to leave an impression on the exospore surface (Plate IV-8).

Hennipman depicts a SEM micrograph of this species (1990: fig. 2.1.e), mentioning in the legend that it has a *Blechnum spicant* type of exospore. This concurs with my own observations of a rather thin, smooth exospore that results from a series of surface patterns as found in *Drynaria sparsisora*.

Spores of *Phymatosorus diversifolius*, with their conspicuously verrucate exospore surface, look like spores with a *Polypodium vulgare* type of exospore, e.g., *Pecluma singeri*, *Polypodium australe*, *P. fraxinifolium*, and *P. levigatum*. However, Hennipman (1990, fig. 2.3.g) states in the legend of a SEM micrograph of '*Microsorum* spec.', of the same specimen I studied as *Phymatosorus diversifolius* (Constable P8264), that it has a *Belvisia* type of exospore.

Spores of *Phymatosorus longissimus* have been depicted by Hennipman (1990, SEM as fig. 2.4.f, TEM as fig. 2.4.g) and Tryon & Lugardon (1991, p. 332). TEM shows a c. 2 µm thick, homogeneous exospore without any channels, and a very thin, echinate perispore with spherical bodies. It is hard to assign spores of this species to an exospore type as defined by Hennipman (1990): the rather smooth exospore surface suggests a *Blechnum spicant* type of exospore, but the exospore is rather thicker than the 1 µm indicated by Hennipman (l.c.).

SEM micrographs of *Phymatosorus scolopendria* have been published by Tryon & Lugardon (1991, p. 332). While the specimen I observed has rather smooth spores with small holes and only the slightest trace of colliculate verrucae, the spores depicted by Tryon & Lugardon (l.c.) have a more pronouncedly rugate/verrucate exospore surface, reminiscent of lepisoroid spores. Therefore, a *Belvisia* type of exospore seems the most likely type for this species.

Of the genus *Phymatosorus* Hennipman (1990) only cites *P. commutatus* as having a *Blechnum spicant* type of exospore, and an indistinct perispore. He found (pers. comm.) a *Belvisia* type of exospore in several other species of this genus (*P. cromwellii, P. geminatus, P. papuanus, P. scolopendria, P. subgeminatus*) and indeed the spore surface found in several species of *Phymatosorus* (see Tryon & Lugardon, 1991, p. 332) suggests that this type of exospore occurs in the genus.

Of the four species of *Phymatosorus* studied here, one or two (*P. commutatus,* possibly also *P. longissimus*) appear to have a *Blechnum spicant* type of exospore, one (*P. diversifolius*) a *Polypodium vulgare* type of exospore, and one (*P. scolopendria*) a *Belvisia* type of exospore. The surprising amount of variation encountered in *Phymatosorus* indicates the occurrence of parallel developments.

Tribe Polypodiinae

Of *Campyloneurum angustifolium* SEM micrographs have been published by Hennipman (1990, fig. 2.1.f) and Tryon & Lugardon (1991, p. 334). Hennipman assigns spores of this species to the *Blechnum spicant* type because of its fairly thin, colliculate exospore, and its very thin (type A) perispore: the spore surface is therefore determined by the exospore surface.

Hensen (1990) used *Campyloneurum* (as *Campyloneuron*) as an outgroup for rooting his cladogram of the 23 species of the *Polypodium loriceum*-complex. He supposed the genus to be sufficiently closely related to the species he studied to be of use in indicating plesiomorphies and apomorphies in the *Polypodium loriceum*-complex – but distantly enough to avoid the danger of using as an outgroup the group causing the complex under study to be paraphyletic. He describes the spores as being almost smooth to colliculate, with an inconspicuous perispore.

The genus *Campyloneurum* is supposed to be related to *Polypodium* by many authors, and the spore characters do not contradict this assumption.

Of *Microgramma ciliata,* both SEM and TEM micrographs have been published in Van Uffelen (1992). In the same publication, SEM micrographs have been published of mature spores of *M. heterophylla, M. lycopodioides,* and *M. persicariifolia.*

Small spines on the perispore, which covers a verrucate exospore surface, are also found in *Polypodium amorphum* (see Tryon & Lugardon, 1991, p. 347).

Baayen & Hennipman (1987) suggested that *Pleopeltis percussa* be placed in the genus *Microgramma,* but here it is treated as belonging in *Pleopeltis*. Note also the outer spore surface of *M. megalophylla,* which is reported by Hennipman (1990) to be similar to the *Belvisia* type, and of which Tryon & Lugardon (1991, p. 337) state that the surface and the exceptionally large size of the spores may reflect a higher ploidy level of the collection, and that the surface supports relationship with *Pleopeltis*. Hennipman et al. (1990, p. 224) interpret this similarity as to spore surface as a parallel development, but as they also report a hybrid between *Microgramma (Polypodium) lycopodioides* and *Polypodium plesiosorum* (as *Microgramma* × *moraviana* Gómez, p. 206), *M. megalophylla* might also be of hybrid origin. They use the existence of *M.* × *moraviana* as an argument to deny the *Microgramma*-group generic status.

A spore of *Niphidium crassifolium* is depicted on a SEM micrograph in Tryon & Lugardon (1991, p. 340). They suppose that the large spores (c. 82 µm long) of the specimen they examined indicate a higher ploidy level. The spores of *N. crassifolium* that I studied were c. 58–59 µm long, more in agreement with the other species of *Niphidium* that Tryon & Lugardon depicted, which are supposed to be of a lower ploidy level and which are c. 54 and 58 µm long. A close relationship with the genus *Campyloneurum* is postulated, based on the simplicity of the spores.

The numerous small depressions found on the exospore surface, as in *Lecanopteris darnaedii*, may be caused by the presence of small channels. However, this is not obvious on the TEM published by Hennipman (1990, fig. 2.4.b), where a section of the laesura shows a uniform, almost smooth exospore, probably of the *Blechnum spicant* type, a thin perispore, and numerous globular bodies, which are up to c. 1 µm ø.

The genus *Pecluma* has been described by Price in 1983 as separate from *Polypodium*, moving 28 species from this genus to *Pecluma*. It is based on Evans' (1969) *Polypodium pectinatum-plumula*-group. Its habit is very similar to *Ctenopteris taxifolia* (Grammitidaceae, see Hennipman et al., 1990), and the species I studied was indeed labeled as such when I examined its spores. Not all authors recognize the genus as separate from *Polypodium*, e.g., Tryon & Lugardon (1991, p. 347): "the prominently verrucate spores support treatment of the group in *Polypodium*." They depict a SEM micrograph of one species of *Pecluma, P. curvans*, under the name of *Polypodium curvens*. It has a verrucate exospore, the verrucae quite large, up to 6 µm ø.

The spores of *Pecluma singeri* have a *Polypodium vulgare* type of exospore, which is common in the subfamily of Polypodiinae, and also occurs in other subfamilies of Polypodiaceae. Study of sporogenesis with SEM shows a succession of verrucate patterns, which is similar to the series exhibited by another species with a *Polypodium vulgare* type exospore, *Microgramma ciliata* (Van Uffelen, 1992).

Therefore, the recognition of the genus *Pecluma* as separate from *Polypodium* is supported nor contradicted by spore characters.

Pleopeltis is here regarded as a genus comprising about 10 neotropical species, and closely related to the genus *Polypodium*, sometimes even included in *Polypodium* (Hennipman et al., 1990).

Copeland (1947) and Pichi Sermolli (1977) supposed this genus to comprise the species now currently placed in *Lepisorus*. *Pleopeltis* s. str. is reported as having a *Blechnum spicant* type of exospore (Hennipman, 1990), which supports the removal of *Lepisorus*, with a *Belvisia* type of exospore, from *Pleopeltis*.

Baayen & Hennipman (1987) suggested the move of *Pleopeltis percussa* to the genus *Microgramma* because of its frond indument. As *P. percussa* has a *Blechnum* *spicant* type exospore, whereas all species of *Microgramma* I studied have a *Polypodium vulgare* type, this move is not supported by spore characters. Moreover, the only exception I know of in the genus *Microgramma, M. megalophylla,* has a *Belvisia*-like spore surface (Hennipman, 1990; depicted in Tryon & Lugardon, 1991, p. 338).

The mature spores of *Pleopeltis lanceolata* as studied here are rather like those of *Campyloneurum angustifolium.*

Of *Pleopeltis percussa* the stage in outer exospore depicted on Plate V-7 closely resembles that depicted in Van Uffelen (1990, Pl. VIII-5) of a late stage in outer exospore formation of *Drynaria sparsisora,* which has a *Blechnum spicant* type of exospore, and none of the stages in exospore development of *Microgramma* or *Belvisia* (Van Uffelen, 1992). This supports the notion that both *P. lanceolata* and *P. percussa* have a *Blechnum spicant* type of exospore. Mature spores of several species of *Pleopeltis* have been depicted in Tryon & Lugardon (1991). Their surfaces, colliculate with very low, rounded verrucae, closely resemble each other, so that all these species of *Pleopeltis* may have the same type of exospore.

The circumscription of the genus *Polypodium* is not yet satisfactory. In Hennipman et al. (1990) it comprises about 200 species belonging to four different groups: the *Microgramma*-group, the *Polypodium*-group, the *Pleopeltis*-group, and the *Goniophlebium*-group. In other publications by collaborators of the Polypodiaceae-project a more strict definition is used, and the groups mentioned above are treated as separate genera, so that the genus *Polypodium* then comprises about 150 species. The fact that some species may be of hybrid origin may render reconstruction of the phylogeny of the group difficult or even impossible, as "a cladogram summarizes exclusively the divergent speciation" (Hensen, 1990).

Lloyd (1981) studied spore surfaces in *Polypodium* and related genera with the SEM. He recognized four perispore types in the genus, ranging from inconspicuous to thick and completely obliterating the exospore surface. Comparison of my own observations, combined with SEM and TEM pictures published, e.g., in Lloyd (1981), Hensen (1990), Rödl-Linder (1990), and Tryon & Lugardon (1991) indicate that most of the variation found in spore characters in the genera *Microgramma, Pleopeltis,* and *Goniophlebium* may also be found in the genus *Polypodium* s. str.

Hensen (1990) studied the so-called *Polypodium loriceum*-complex, consisting of 23 Neotropical species of *Polypodium* with goniophleboid venation and clathrate rhizome scales. The spores are quite variable, the mature exospore surface varying from smooth to coarsely verrucate, the perispore from inconspicuous to thickened and cristate. Of the 19 characters applied to construct a cladogram, eventullay 15 are used, three of which are spore characters, each with two to four character states. Spore colour (yellow vs. brown) turns out to be an important character, the perispore is of less importance, and the exospore surface even less so. Species ending up next to each other (i.e., together forming a monophyletic group) usually have similar spores.

However, definition of character states may be difficult: Hensen studied spores of two specimens of *Polypodium fraxinifolium,* of which the exospore surface of one is finely verrucate, of the other coarsely verrucate. In the description of the species, the exospore surface is said to be finely to coarsely verrucate, yet in the data matrix used for cladogram construction, the exospore surface is taken as finely verrucate.

Hensen (1990) concludes the general part of his publication with the description of the probable ancestor of the *P. loriceum*-complex, that is, he lists all plesiomorphic character states. Its spores are supposed to have been yellow, with a colliculate exospore and an inconspicuous perispore.

Despite the variation in the *P. loriceum*-complex, both of the species belonging to this complex that I studied, viz. *P. fraxinifolium* and *P. levigatum,* have similar spores with a verrucate exospore surface and an inconspicuous perispore.

Polypodium australe obviously has a *P. vulgare* type of exospore: a thick exospore with rather large verrucae, and channels around the laesura only. The perispore is inconspicuous, with some spherical bodies included in the thin basal layer. Lugardon (1974) observed the spores of *P. serratum* Christ (= *P. australe* Fée) with TEM and describes its exospore as 'blechnoïde', while by the circumscription of exospore types of Hennipman (1990), this species has a *P. vulgare* type of exospore, and not a '*Blechnum spicant* type'.

Polypodium fraxinifolium also has a *P. vulgare* type of exospore, and an inconspicuous (type A) perispore (Hennipman, 1990). The verrucate spore surfaces found during sporogenesis do not contradict a series of patterns similar to that found in *Microgramma ciliata,* which also has the same type of exospore. The dark tangential band found in some mature spores apparently is not confined to *Belvisia*-type exospores. They can be interpreted as differences in condensation of the exospore material, and may be a sign of immaturity of the spores.

Of *Polypodium hirsutissimum* both SEM and TEM micrographs have been published by Hennipman (1990, fig. 2.7.b, d, e). He describes its complex perispore as a unique type in Polypodiaceae, the *P. hirsutissimum* type, with a network of hollow, papillate projections and scattered with globular bodies. The slightly colliculate exospore is probably of the *Blechnum spicant* type.

SEM micrographs of the spores of *Polypodium levigatum* (as *P. glaucophyllum*) have already been published by Lloyd (1981, fig. 23) and by Hennipman (1990, fig. 2.2.g). It has a *P. vulgare* type of exospore.

After a thorough investigation of goniophlebioid ferns, Rödl-Linder (1990) concludes that *Goniophlebium* as she recognizes it is a monophyletic group of 23 simple-veined species, confined to the (sub)tropics of the Old World. They have smooth or colliculate spores and an inconspicuous perispore, or one that bears locally protruding ridges. Within *Goniophlebium,* the groups she recognizes are homogeneous as to exospore surface ornamentation: species of the *G. percussum*-group all have a smooth exospore, spores of the *G. subauriculatum-, G. argutum-, G. formosanum-,* and *G. hendersonii*-group have a colliculate exospore, whereas a distinctly verrucate exospore is confined to the species retained in *Polypodium.* Perispore ornamentation is more variable within groups, the most striking differences occurring in the *G. subauriculatum*-group, in which two species have an inconspicuous, thin perispore. The rest of the perispore variation within groups (ridges varying from low to high to locally protruding, equatorial excrescences absent or present) may be due to the ease with which parallelisms may develop in this group, or to the narrow circumscription of perispore types by Rödl-Linder (1990, p. 306).

She distinguishes five perispore types, based on the presence and morphology of the ridges. All species studied here (*G. korthalsii, G. percussum,* and *G. persicifolium*) belong to the same group, the monophyletic *G. percussum*-group, and all have spores with a smooth exospore and the same perispore type, the *G. percussum*-type, which features a perispore with high ridges that form equatorial excrescences.

The spores of *Goniophlebium korthalsii* have the longest equatorial appendages found in the genus. They have been depicted in Hennipman (1990, fig. 2.6.a).

As in *Pleopeltis percussa,* the few stages of outer exospore formation that were observed in *Goniophlebium percussum* most closely resemble those observed in *Drynaria sparsisora* (Van Uffelen, 1990, Pl. VIII-5). SEMs of mature spores of *Goniophlebium percussum* have already been published in Rödl-Linder (1990, p. 368), Hennipman (1990, fig. 2.6.c) and in Tryon & Lugardon (1991, p. 350).

Goniophlebium persicifolium has a less spectacular perispore than *G. korthalsii.* It has been depicted in Tryon & Lugardon (1991, p. 350). Both exospore morphology and spore wall formation indicate that spores of the genus *Goniophlebium,* which show only a limited amount of variation on the same theme, all have a *Blechnum spicant* type of exospore, and a perispore designed type Bd by Hennipman (1990) and circumscribed as winged or crestate. I prefer to use the term ridge in preference to fold (which implies a certain anatomy) or crest or wing (both implying a fairly high structure), and the term cristate (as in Van Uffelen & Hennipman, 1985) in preference to crestate.

Cristate perispores are found in species of a genus closely related to *Goniophlebium, Polypodium* (e.g., *P. dissimile* and *P. sessifolium,* see Hensen, 1990, fig. 42 & 59), and in the far more distantly related genus *Pyrrosia,* where species with a *P. nummulariifolia* type of spore have a cristate perispore, which in some species is indistinguishable from a *Goniophlebium* perispore.

According to Hennipman et al. (1990, p. 206), the existence of several hybrids "militates against recognition of *Goniophlebium, Phlebodium, Pleopeltis,* and *Microgramma* as genera distinct form *Polypodium* s. str." The occurrence of ridges in both *Goniophlebium* and *Polypodium* supports a close relationship between the genera, which is also supported by other characters. Whereas in the case of *Goniophlebium* and *Polypodium* the presence of perisporal ridges is most easily interpreted as a sign of relationship, in *Pyrrosia* it can only be interpreted as a parallel development, as the more distant relationship between the two genera is so firmly based on other characters.

CONCLUDING REMARKS

The use of spore types, as of any character, in reconstructing relationships leans heavily on their precise circumscription: if one type occurs in distantly related groups, it is tempting to look critically at these 'generalized' types and to split them up to make them unique to a possibly monophyletic group.

After studying more polypodiaceous spore material than Hennipman included in his 1990 study, it has become apparent that his spore types do not cover all variation found in the Polypodiaceae: not all spores I studied fit his rather narrow circumscriptions. For instance, tangential bands seem not to be confined to *Belvisia*-type spores, but to be more common (e.g., in *Pyrrosia gardneri* and *Polypodium fraxinifolium*), and a distinctly colliculate exospore as found in *Pyrrosia schimperiana* does not match Hennipman's description of the *Blechnum spicant* type of exospore.

Therefore, the exospore surface of *Blechnum spicant* type of spores should be described as "smooth to colliculate, distinctly colliculate in a few species." Furthermore, it should be stressed that tangential bands have been observed with TEM in all lepisoroid species, but may also occasionally be found in other polypodiaceous species of which the spores do not otherwise fit Hennipman's description of *Belvisia*-type spores.

Of the four exospore types in the family Polypodiaceae (Hennipman, 1990) one, the *Blechnum spicant* type, occurs in many other ferns outside this family (Lugardon, 1974). This makes it likely that the *Blechnum spicant* type is plesiomorphous, and that the other three types are derived from it. Except for the *Microsorum membranaceum* type, which is confined to this species, these apomorphous spore types occur in various groups of Polypodiaceae. Therefore, they must have originated several times, indicating many parallel developments in the phylogenetic tree of the family. However, the description of these spore types has yielded some apomorphies for polypodiaceous species, genera or groups of genera, which may be used to elucidate relationships within the family.

The results presented in this publication suggest that three of the exospore types found in mature spores as circumscribed by Hennipman (1990) may be linked with the series of surface patterns in developing exospores as described by Van Uffelen (1990, 1992). Spore wall development as described in *Drynaria sparsisora* results in a *Blechnum spicant* type of exospore, development as described in *Microgramma ciliata* in a *Polypodium vulgare* type of exospore, and development as described for two species of *Belvisia* results in a *Belvisia* type of exospore.

It is a practical solution to place together those species in which similar patterns occur during outer exospore formation. However, a large part of the likeness in pattern might be explained by 'non-genetically determined factors' (see Van Uffelen, 1991), that is, arising out of the universality of some processes in nature. This does not exclude the possibility that related organisms are more predisposed to one process (= series of patterns) than to another.

Of the seven perispore types Hennipman (1990) distinguishes, four are confined to one genus (type Bb to *Selliguea*, syn. = *Crypsinus*, the *Arthromeris* type) or even one species (the *Polypodium hirsutissum* type and the *Lecanopteris mirabilis* type). One is confined to two only distantly related genera (type Bd: *Goniophlebium* and *Pyrrosia*), and the remaining two perispore types must enclose the perispores of the remaining polypodiaceous ferns (type A: the indistinct perispore, type Ba: the relatively thin perispore). Although the description of these types serves to catch the greater part of the enormous variation existing in the polypodiaceous perispore, none of these perispore types elucidates relationships in the family, as the number of species fitting a certain type is either very limited or very large and occurring in distantly related groups within the Polypodiaceae.

ACKNOWLEDGEMENTS

Many of the TEM micrographs were made in the Laboratoire de Biologie végétale de l'Université P. Sabatier (Toulouse) with the kind help of Dr. B. Lugardon. With him, and with Dr. S. Blackmore of the Natural History Museum (London), I intensively discussed sporogenesis. My supervisors in the Netherlands, Prof. Dr. E. Hennipman and Prof. Dr. C. Kalkman have contributed to this series of publications on sporogenesis with many useful comments, as have Dr. G.M. Lokhorst, Head of the Cryptogams Department, and Dr. P. Hovenkamp.

I want to thank Dr. Trevor Walker from Newcastle University for the material of *Polypodium australe*. The staff of the botanic gardens in Leiden and Utrecht, who has been taking care of 'my' plants during all my years of study, are sincerely thanked. The help of Ms. Emma van Nieuwkoop in working up the manuscript for publication is gratefully acknowledged. The investigations were supported by the Foundation for Fundamental Biological Research (BION), which is subsidized by the Netherlands Organization for Scientific Research (NWO).

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LEGENDS OF THE PLATES

Plate I: Subfamily Platycerioideae — SEM and TEM of mature spores (e = exospore)

1: *Platycerium alcicorne*, lateral view of a spore with a peeling perispore; SEM, 1050 ×
2: *Pyrrosia princeps*, section of the laesura; TEM, 8000 ×
3: *P. polydactyla*, section of the spore wall, the perispore containing many spherical bodies; TEM, 5000 ×
4: *P. gardneri*, section of a mature spore; note tangential bands in the exospore, and the thick, verrucate perispore; TEM, 2050 ×
5: *P. angustata*, section of an exospore with a broken perispore; TEM, 4200 ×
6: *P. angustata*, detail of the structure of the perispore; note the repetitive arrangement of substructures; TEM, 30,000 ×
7: *P. rupestris*, perispore bisculptate; SEM, 850 ×
8: *P. rupestris*, section of the spore wall, showing the exospore and the thick, verrucate perispore; TEM, 4000 ×

Plate II: Tribe Selligueinae — SEM of mature spores; sporogenesis in *Crypsinus simplicissimus*

1: *Arthromeris lehmannii*, lateral view of a mature spore with a broken perispore; SEM, 1300 ×
2: *Crypsinus bakeri*, proximal/lateral view of a mature spore; SEM, 700 ×
3: *C. veitchii*, peeling perispore near the laesura, showing the slightly colliculate exospore surface; perispore distinctly colliculate; SEM, 2800 ×
4: *C. enervis*, lateral/proximal view of a mature spore; SEM, 800 ×
5: *C. simplicissimus*, lateral view of a mature spore; SEM, 750 ×
6: *C. simplicissimus*, blobs and lamellae involved in perispore formation; TEM, 20,000 ×
7: *C. simplicissimus*, detail of echinae on the mature perispore; SEM, 4000 ×
8: *C. simplicissimus*, section of a mature perispore, showing that the echinae are continuous with the basal layer; TEM, 10,000 ×

Plate III: Tribe Microsorinae — SEM of mature spores

1: *Dictymia brownii*, lateral view of a spore with peeling perispore, 950 ×
2: *Lecanopteris celebica*, lateral view, perispore with spherical bodies and flaky mass, 1100 ×
3: *L. darnaedii*, detail of 4, showing numerous small depressions, 2200 ×
4: *L. darnaedii*, lateral view of a spore after removal of most of the perispore, 950 ×
5: *L. celebica*, tetrad, 700 ×
6: *Neocheiropteris* spec. (= *Microsorum pappei*), proximal/lateral view, 1100 ×
7: *N. normalis*, lateral view, 800 ×
8: *N. ovatus*, lateral view, 1000 ×

Plate IV: Tribe Microsorinae — SEM and TEM of sporogenesis in *Phymatosorus commutatus* (e = exospore)

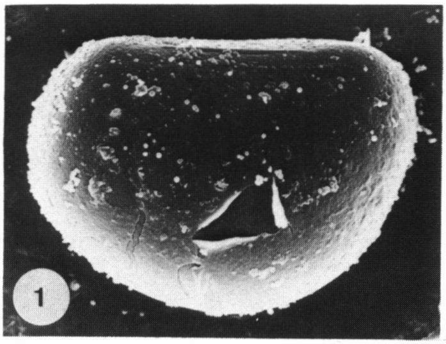
1: Beginning of outer exospore formation; section of a spore showing the laesural fold, and units of outer exospore material deposited on the smooth inner exospore layer; TEM, 30,000 ×
2: Outer exospore formation; section of a spore showing the laesural fold and prominent verrucae; TEM, 16,000 ×
3: Outer exospore formation; section of a spore showing the laesural fold, which is almost entirely covered with exospore material; note the low verrucae; TEM, 10,000 ×
4: Section of a mature, germinating spore; TEM, 980 ×
5: Beginning of outer exospore formation; proximal view; SEM, 1750 ×
6: Outer exospore formation; proximal view of two spores; SEM, 1300 ×
7: Outer exospore formation, proximal/lateral view, surface with low broad verrucae; SEM, 1500 ×
8: Lateral view of a mature spore; note the peeling perispore with many spherical bodies and echinae, and the exospore surface (82GR00146); SEM, 900 ×

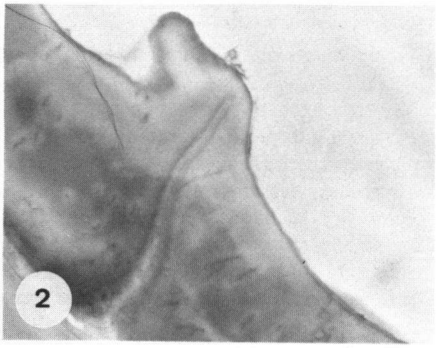
Plate V: Tribe Polypodiinae — mature spores and sporogenesis (1)

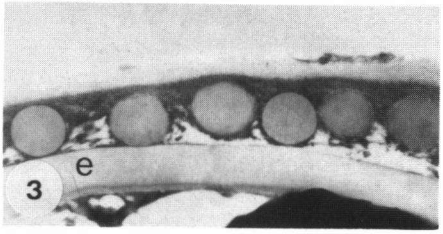
1: *Niphidium crassifolium*, lateral view of a mature spore, showing tiny depressions; SEM, 900 ×
2: *Pecluma singeri*, cross section of a developing spore, showing the laesura and many prominent verrucae on the spore surface; SEM, 2600 ×
3: *P. singeri*, developing spores with numerous spherical bodies on the surface; SEM, 650 ×
4: *P. singeri*, developing spores, showing spherical bodies in the process of merging with the spore surface, thus apparently forming verrucae; SEM, 4500 ×
5: *P. singeri*, lateral view of a mature spore, SEM, 1000 ×
6: *P. singeri*, cross section of a mature spore; verrucae around the laesura cut obliquely, therefore seeming extremely large; TEM, 2050 ×
7: *Pleopeltis percussa*, proximal view of a developing spore; SEM, 1400 ×
8: *P. lanceolata*, lateral view of a mature spore; SEM, 1050 ×

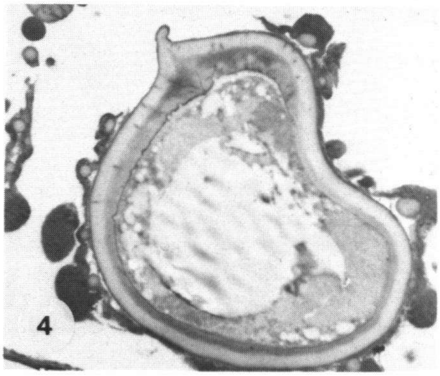
Plate VI: Tribe Polypodiinae — mature spores and sporogenesis (2)

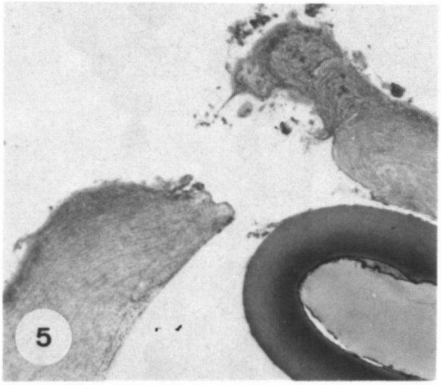
1: *Polypodium fraxinifolium*, proximal/end-on view of a developing spore; SEM, 1700 ×
2: *P. fraxinifolium*, cross section of developing spores, formation of outer exospore; TEM, 4000 ×
3: *P. fraxinifolium*, cross section of a spore where tapetal blobs are involved in perispore formation; TEM, 12.000 × (e = exospore)
4: *P. fraxinifolium*, cross section of a mature spore, 4000 ×
5: *P. hirsutissimum*, lateral view of a mature spore with a partly abraded perispore, showing the exospore surface and a cross section of the perispore; SEM, 1150 ×
6: *Goniophlebium percussum*, two developing spores; SEM, 1600 ×
7: *G. percussum*, lateral view of a developing spore; SEM, 1300 ×
8: *G. percussum*, lateral view of a mature spore with a torn perispore, showing the almost smooth exospore, and the fibrillar structure of the perispore; SEM, 2000 ×

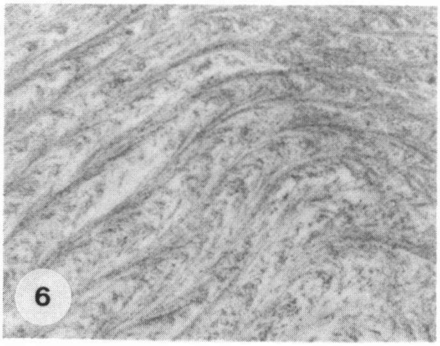


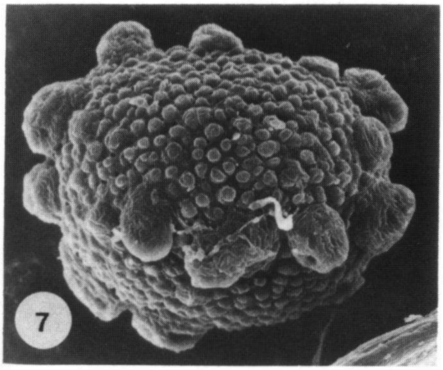


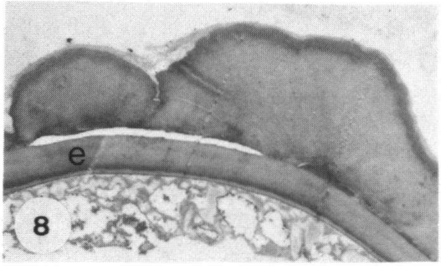












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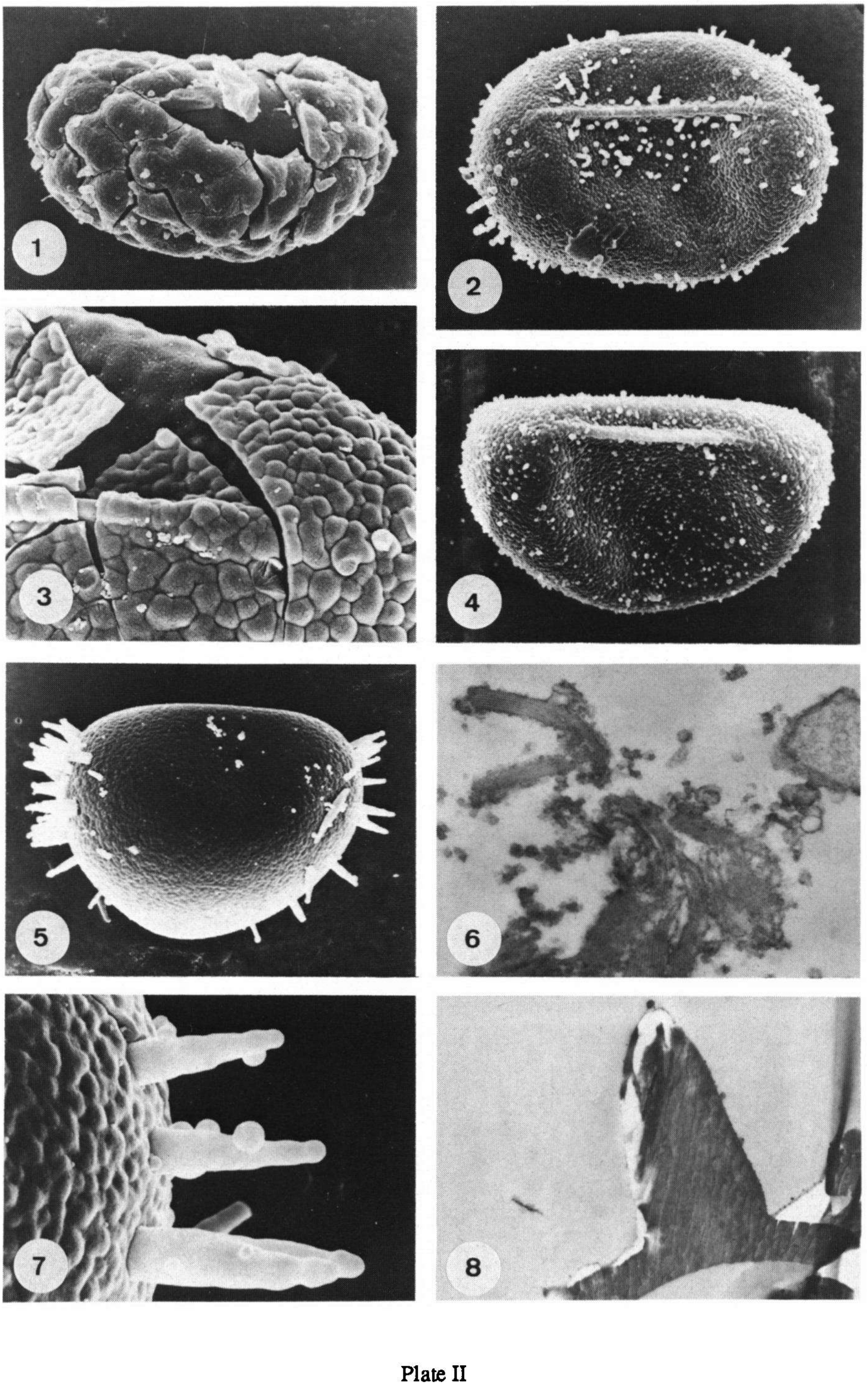

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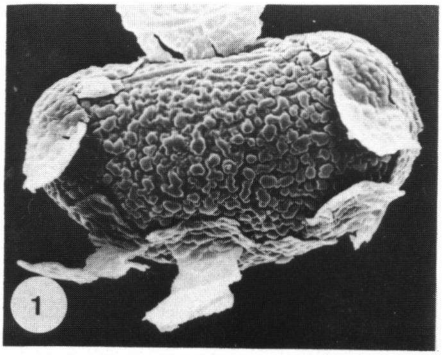
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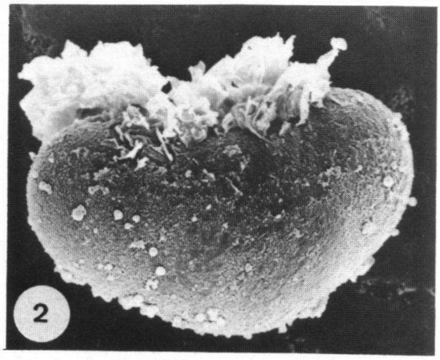
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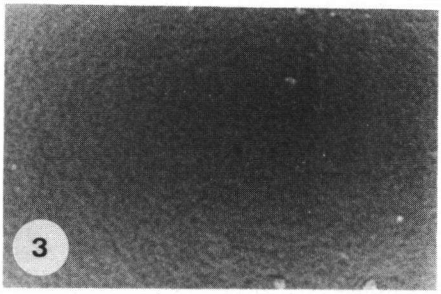
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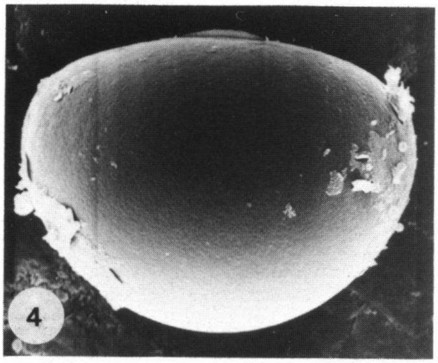
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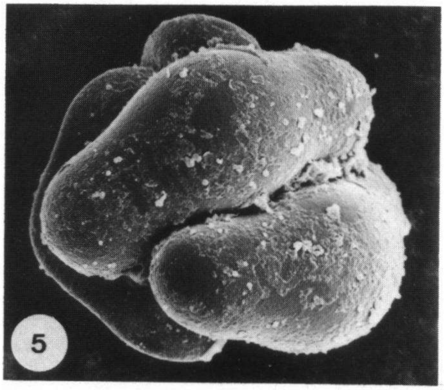
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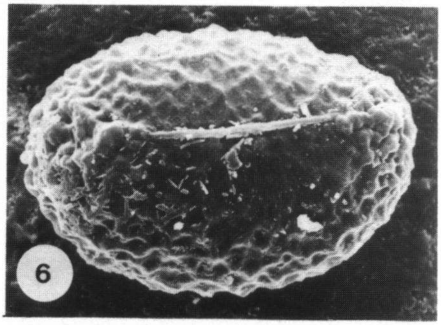
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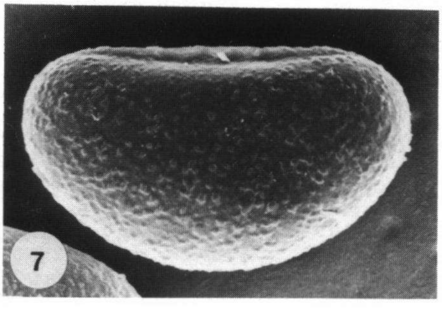
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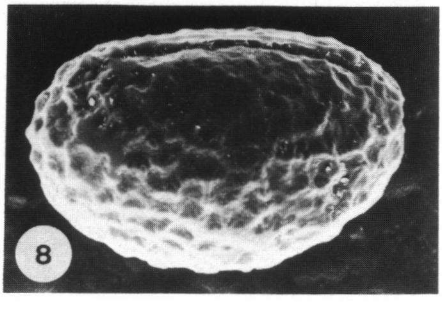
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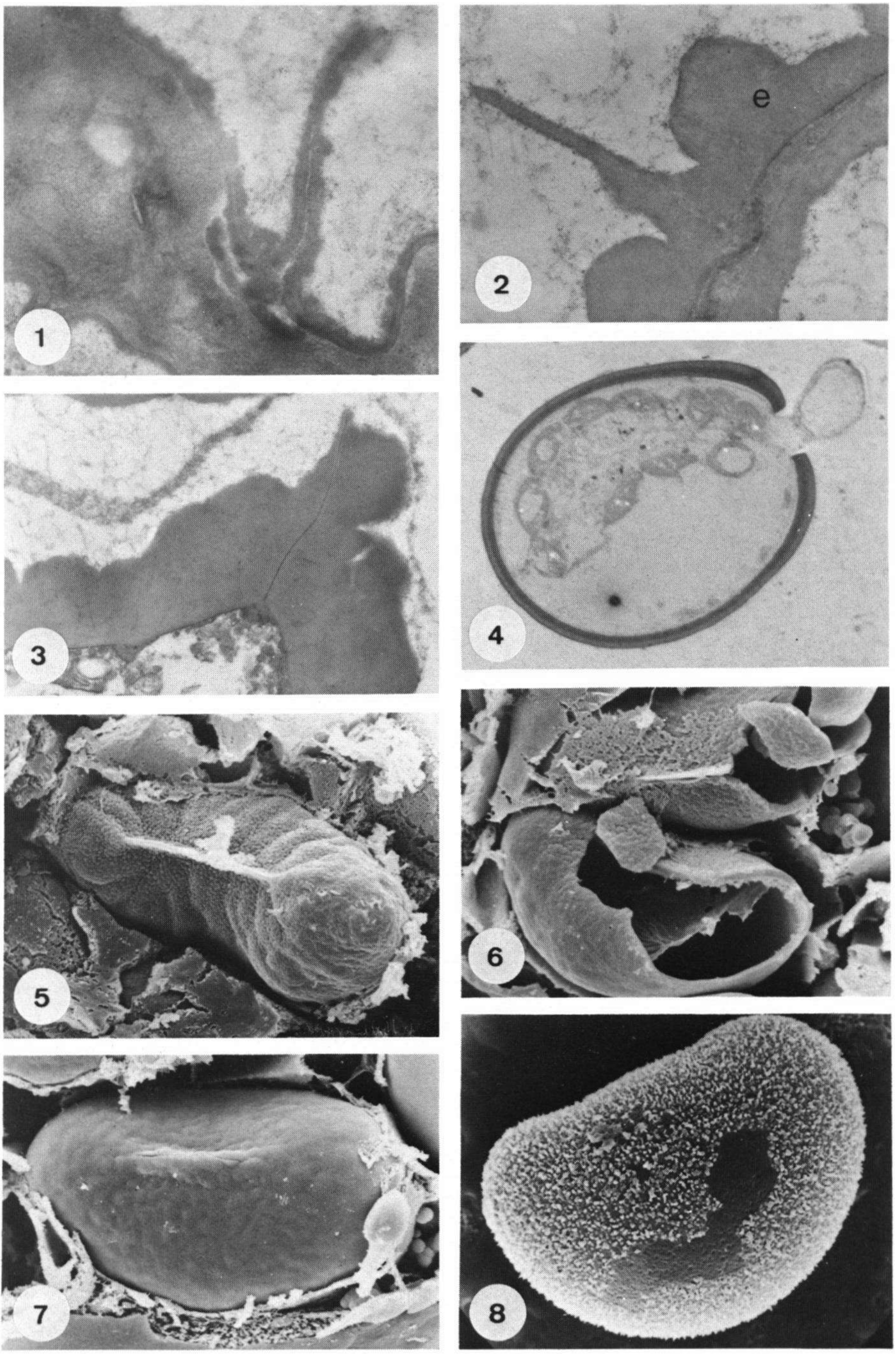

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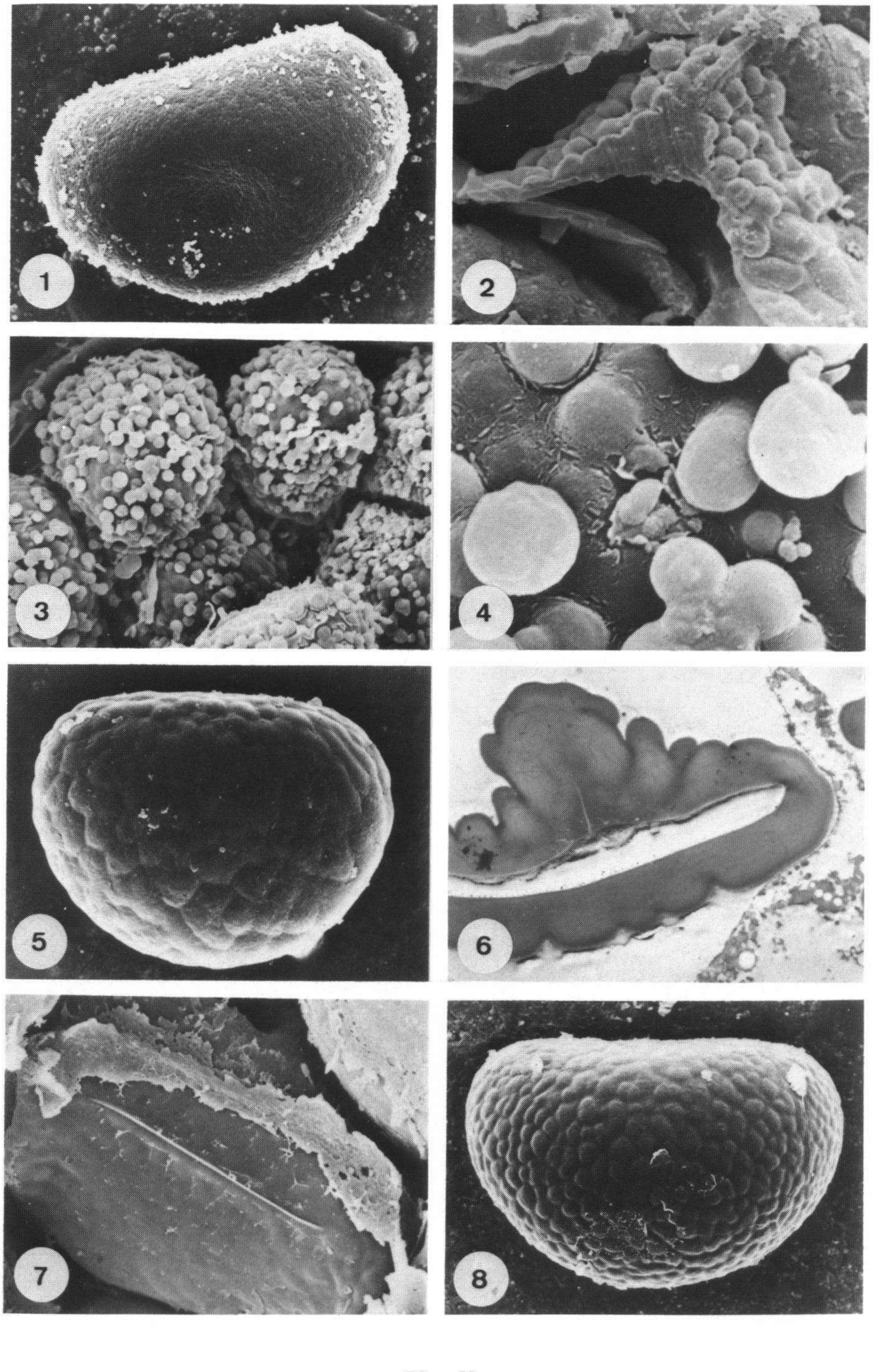

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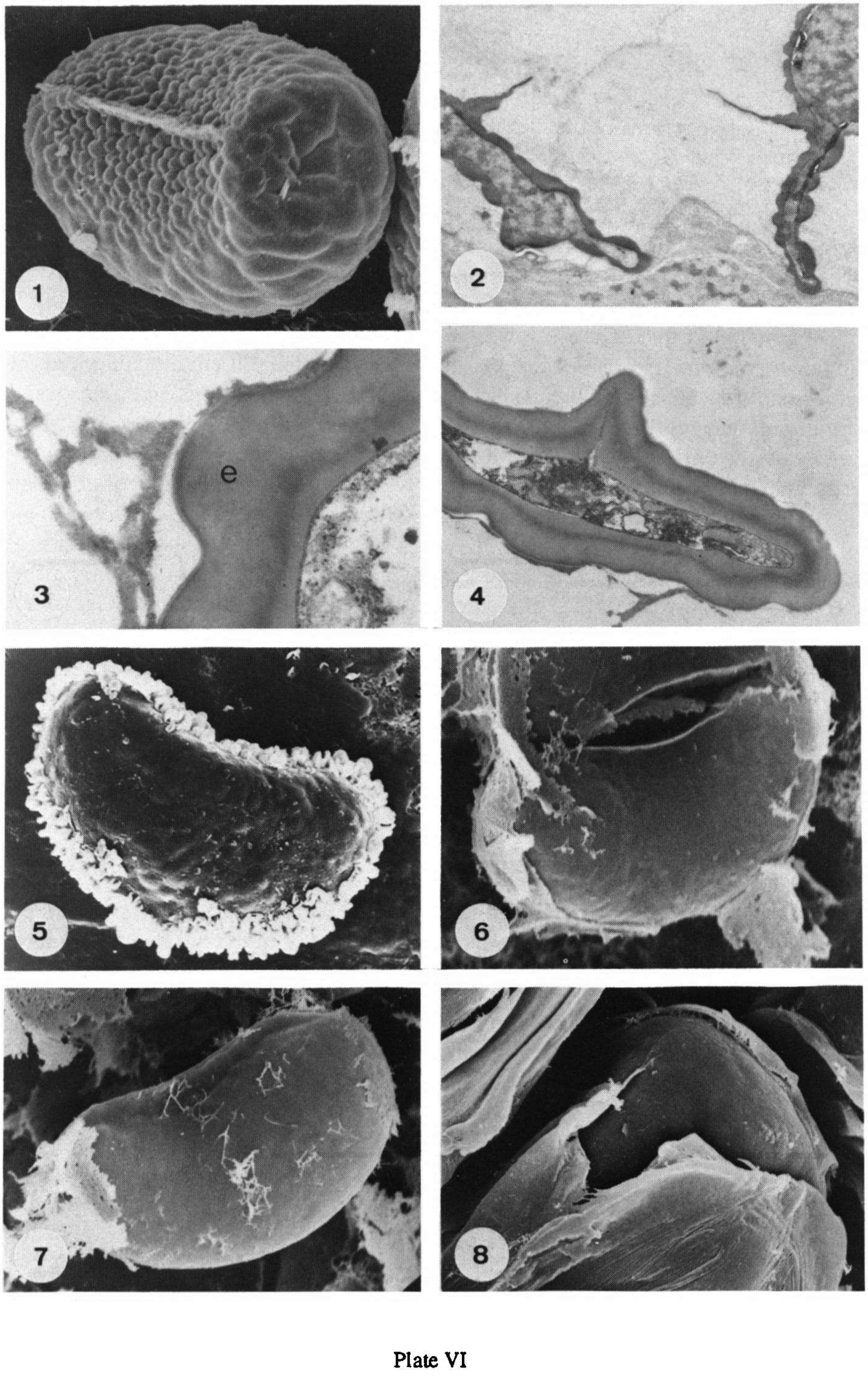

Plate VI