THE SPORES OF *PYRROSIA* MIRBEL (POLYPODIACEAE), A SEM STUDY

BY

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SOMMAIRE. — Les spores des 51 espèces actuellement reconnues dans le genre *Pyrrosia* (Filicinées isosporées) ont été étudiées au microscope électronique à balayage. Une périspore est présente dans toutes les espèces. La grande diversité de l'ornementation du sporoderme trouvée dans ce genre a été décrite. Nous avons distingué cinq types de spores qui sont fondés sur les caractères de la périspore.

Introduction.

Ferns of the genus *Pyrrosia* MIRBEL (Polypodiaceae) are characterized by the combination of stellate hairs with usually undivided, more or less xeromorphic fronds.

The distribution of *Pyrrosia* has its centre in tropical Asia. Species occur in tropical Africa, on the mainland of Asia in India, the Himalaya, Indochina and China, in Ceylon, Japan, Taiwan, Malaysia, Australia, New Zealand and Polynesia (COPELAND, 1947). Most of them are epiphytes.

The genus *Pyrrosia* as defined here includes species formerly attributed to *Drymoglossum* PRESL, thus following PRICE (1974), and *Saxiglossum* CHING, following TAGAWA and IWATSUKI (1975), and is closest related to the genus *Platycerium* DESVAUX (HENNIPMAN and ROOS, 1982). It should be noted that other authors, e.g. PICHI SERMOLLI (1977), keep these genera separate and indicate at the same time the isolated position of *Platycerium*. One of the most recent definitions of the family Polypodiaceae to which these genera belong is given by SEN and HENNIPMAN (1981).

This account of the morphology of the spores in the genus *Pyrrosia* occurs in association with the present monographic studies of this genus by HOVENKAMP (1986, in prep., see also HOVENKAMP, 1984) who identified all specimens studied.

Spores of *Pyrrosia* have already been studied by many authors, mainly with the aid of the light microscope (LM). A limited number of species is described and/or depicted in general works on fern spores (ERDTMAN and SORSA, 1971 ; KREMP and KAWASAKI, 1972), as well as in publications concerning fern spores found in a certain area (Anon., 1976 : China ; HARRIS, 1955 : New Zealand ; HUANG, 1981 : Taiwan ; MITUI, 1982 : Japan ; NAYAR and DEVI, 1964, DEVI, 1977 : India ; NAYAR, LATA and TIWARI, 1964 : West tropical Africa ; TARDIEU-BLOT, 1966 : Madagascar ; WELMAN, 1970 : South Africa). Spore characters are also included in certain floras (TINDALE, 1961 : South Eastern Australia ; NAYAR and CHANDRA, 1965 : India) and in local revisions of *Pyrrosia* in India (NAYAR, 1961, NAYAR and CHANDRA, 1967).

Scanning electron microscopy (SEM) on spores of *Pyrrosia* is limited to publications of LIEW (1976 b ; 6 species of *Pyrrosia* from Taiwan) and MITUI (1977 ; 2 species from Japan ; see also 1982). The latter will shortly publish a LM and SEM study of ca. 15 species of *Pyrrosia*.

Quite a lot of work has been published on spores of ferns and fern allies as studied with the aid of the transmission electron microscope (TEM) (HENNIPMAN, 1970, 1977, LUGARDON, 1971, 1972, 1974, 1975, 1979, 1981, TRYON and LUGARDON, 1978). So far no transmission electron micrographs of any *Pyrrosia* spores have been published, but TEM work on the spores of *Pyrrosia* and other Polypodiaceae is in progress (HENNIPMAN and SEN, in prep., 1986). Some *Pyrrosia* species are also included in the sporogenetic TEM studies by the first author (VAN UFFELEN, in prep.). The present study was performed by the first author as a MSc project. These last three studies on the spores of Polypodiaceae are part of the project on this family coordinated by the second author.

Material and methods.

In this survey all 51 species recognized in *Pyrrosia* by HOVENKAMP, and one *spec. dub.*, were studied. Most of the 124 specimens selected for study are located in the Rijksherbarium, Leiden (L) ; of some species fertile material on loan from other herbaria (A, BM, GH, K, M, P, U, US, WAG) was studied. The spores of some specimens cultivated in the botanical gardens of Leiden and Kew were also studied.

Sheets with fertile fronds on which many spores were visible under a dissecting microscope at a magnification of 10-80 × were selected for study. Although many workers prefer to study spores from closed sporangia in order to prevent contamination with other spores, we prefer to study spores from spontaneously opened sporangia as these are the

most likely to be full-grown. LUGARDON (1974) states that even this is not a sure way of obtaining full-grown spores as sporangia in dried material tend to crack and open even if not fully ripe. Spores were collected onto thin white paper.

In spite of procedures recommended by ADAMS and MORTON (1982), critical point drying of the spores when taken from a herbarium specimen was not necessary before study. Cylindrical aluminium specimen stubs were prepared with a glue solution made of double sided Scotch tape in aceton (2 cm in 10 ml). The stubs were then put upside down on the paper with a spore sample ; pressure was applied only if broken spores were wanted in order to study spore wall structure (e.g. plate III-3, 4, 8). If spores did not crack easily a large sample of them was embedded in ice and cut with a freezing microtome, equipped with a Gilette razor blade (plate VI-3). However, material cracked by the application of pressure usually supplies more information about the organization of spore wall layering than does sliced material.

Stubs with spores were coated with an extremely thin (0.05-0.1 μm) gold layer in a Polaron SEM coating unit (E5100, series II). Spores treated in this way remain suitable for examination under the SEM for at least one month. This is contrary to the statement of ADAMS and MORTON (1972) that both aluminium and gold coated specimens tend to deteriorate after about one week.

All micrographs in this survey were made with the scanning electron microscope (JEOL JSM-35) at the Rijksherbarium, Leiden, on Kodak Panatomic-x FXP film.

LIST OF SPECIES AND SPECIMENS STUDIED IN *Pyrrosia*.

Material located in the Rijksherbarium, Leiden, unless stated otherwise.

P. *abbreviata* (ZOLL. and MORITZI) HOVENKAMP. Sumatra : DE WILDE and DE WILDE-DUYFJES 12464, 13561, MEIJER 12189 ; Flores : SCHMUTZ 165, 3066.

P. *africana* (KUNZE) BALLARD. Republic of South Africa : DE JONCHEERE SAC254.

P. *albicans* (BLUME) CHING. Java : HOLSTVOOGD 332 ; Flores : SCHMUTZ F135.

P. *angustata* (SWARTZ) CHING. Borneo : MEIJER 2196.

P. *angustissima* (DIELS) TAGAWA and IWATSUKI. China : BODINIER 2117 (M), CAVALERIE 1883 (L and P).

P. *assimilis* (BAKER) CHING. China : TSANG 20896.

P. *asterosora* (BAKER) HOVENKAMP. BÜNNEMEIJER 5153, 9426.

P. *boothii* (HOOKER) CHING. Bhutan : LUDLOW et al. 18646 (BM).

P. ceylanica (GIESENH.) SLEDGE. Ceylon : FADEN and FADEN 76/300 (US), RAWSON 3056 (BM).

P. christii (GIESENH.) CHING. Borneo : ENDERT 3146, NOOTEBOOM 1227.

P. confluens (R. BR.) CHING var. *confluens*. Australia : COVENY 9400 ; New Caledonia : VIEILLARD 1990/91.

P. confluens var. *dielsii* (C. CHR.) HOVENKAMP. Australia : GOY 435 (BM).

P. costata (PRESL) TAGAWA and IWATSUKI. Thailand : TAGAWA *et al.* T7510 (L and US).

P. distichocarpa (METT.) SHING. Sumatra : LÖRZING 6078, cult. LEI 22871.

P. drakeana (FRANCH.) CHING. China : WANG 65171 (A).

P. eleagnifolia (BORY) HOVENKAMP. New Zealand : LAM 7023, cult. Kew 582-62 58101.

P. fallax (ALDERW.) PRICE. New Guinea : COODE *et al.* NGF 40420.

P. flocculosa (D. DON) CHING. Nepal : cult. Kew 606-67 60101 ; Thailand : HENNIPMAN 3352.

P. foveolata (ALSTON) MORTON var. *foveolata*. New Guinea : BRASS 5244, 31631, HIEPKO and SCHULTZE-MOTEL 1444.

P. foveolata var. *lauterbachii* (CHRIST) HOVENKAMP. New Guinea : BRASS 32606.

P. gardneri (METT.) SLEDGE. Ceylon : DAVIDSE 8253, KOSTERMANS 25512A, 27114, MACRAE 454.

P. hastata (HOUTT.) CHING. Japan : IWATSUKI 4556 ; Korea : TAQUET s.n., VII 1909 (GH).

P. heterophylla (L.) PRICE. Ceylon : LOBB s.n., 1860 (US).

P. kinabaluensis HOVENKAMP. Borneo : MEIJER 673.

P. laevis (BEDD.) CHING. India : MANN s.n., II 1888 (M), VIII 1889 ; Burma : TOPPIN 6330 (K).

P. lanceolata (L.) FARWELL. Thailand : HENNIPMAN 3344A, TAGAWA *et al.* T2260 ; Sumatra : IWATSUKI *et al.* S716, LÜTJEHARMS 4694, anon. (L. 908331-367) ; Timor : BLOEMBERGEN 3509 ; New Guinea : HENTY NGF 16680, MILLAR NGF 35287, VINK 12081 ; Zaire : DE JONCHEERE BC 066 ; Réunion : RAWSON 93?6 (BM), RICHARD 110 ; Fiji : SMITH 8110.

P. linearifolia (HOOKER) CHING. Taiwan : KAO K3843 ; Korea : TAQUET s.n., IX 1908.

P. lingua (THUNB.) FARWELL var. *lingua*. Japan : TAGAWA and IWATSUKI 716 ; Thailand : HENNIPMAN 3145 A.

P. lingua var. *heteracta* (KUHN) HOVENKAMP. Thailand : VAN BEUSEKOM and PHENGKLAI 2998.

P. longifolia (N. L. BURM.) MORTON. Celebes : EYMA 1592 ; Java : JACOBS 4787.

P. mannii (GIESENH.) CHING. Nepal : BANERJI 1534 (A).

P. niphoboloides (BAKER) PRICE. Madagascar : HUMBERT 5831 (K), HUMBLOT 310 (K).

P. novo-guineae (CHRIST) PRICE. New Guinea : BRASS 27921.

P. nummulariifolia (SWARTZ) CHING. Thailand : GEESINK and SANTISUK 5443 ; Celebes : cult. Kew 685-69 6337.

P. pannosa (KUHN) CHING. Ceylon : DAVIDSE and SUMITHRAARACHCHI 8080, SLEDGE 947 (K and U).

P. penangiana (HOOKER) HOLTTUM. Java : RACIBORSKI s.n., 1898.

P. petiolosa (CHRIST) CHING. China : CAVALERIE s.n., X 1910, DORSETT and DORSETT 3049, MEYER 958 (US).

P. piloselloides (L.) PRICE. Thailand : PHENGKLAI 1130.

P. platyphylla HOVENKAMP. Borneo : WOOD 2011 (K).

P. polydactyla (HANCE) CHING. Taiwan : cult. Kew 218-79 2104.

P. porosa (PRESL) HOVENKAMP. China : CAVALERIE s.n., XII 1908, HENRY 5486 (K), TSAI 53654 (A), YÜ 20861 (A) ; Hongkong : cult. LEI 366 ; India : BOR 46 (BM) ; Thailand : HENNIPMAN 3149.

P. princeps (METT.) MORTON. New Guinea : BRASS 8859, DAMASK 7, MILLAR NGF23312, cult. Kew 003-74 00071, 105-65 10505 ; Celebes : cult. LEI 20608.

P. rasamalae (RACIB.) SHING. Thailand : VAN BEUSEKOM and PHENGKLAI 840.

P. rhodesiana (C. CHR.) SCHELPE. Moçambique : PEDRO and PEDROGÃO 6466 (BM), TORRE 4577 (WAG) ; Rhodesia : WILD 2119 (K) ; Madagascar : BARON 3526 (P), COURS 4034 (P), POOL s.n., V 1876 (K).

P. rupestris (R. BR.) CHING. Australia : SCHODDE 3242.

P. samarensis (PRESL) CHING. Philippines : MADULID *et al.* 858, University of San Carlos 750.

P. schimperiana (KUHN) ALSTON var. *schimperiana*. Ethiopa : DE WILDE 5242 (WAG) ; Kenya : MAAS GEESTERANUS 6270 A ; Rhodesia : RICHARDS 17414 (K).

P. schimperiana var. *liebuschii* (HIERON.) HOVENKAMP. Tanzania : GLYNNE 244 (K), PETER 7979 (US).

P. serpens (G. FORSTER) CHING. Tahiti : VAN BALGOOY 1744.

P. sheareri (BAKER) CHING. China : FAN and LI 433 (GH), STEWARD *et al.* 422.

P. sphaerosticha (METT.) CHING. Philippines : CELESTINO 2547, JACOBS 7791 ; Celebes : POSTHUMUS 3436.

P. splendens (PRESL) CHING. Philippines : ELMER 13597.

P. stigmosa (SWARTZ) CHING. Thailand : VAN BEUSEKOM and SANTISUK 2783.

P. stolzii (ENGL.) SCHELPE. Malawi : CHAPMAN 86 (BM), PAWEK 3330 (K), STOLZ 891 ; Rhodesia : WHITE 2709 (BM).

P. subfurfuracea (HOOKER) CHING. China : CAVALERIE 1402, TSAI 53252 (A).

P. transmorrisonensis (HAYATA) CHING, *spec. dub.* Taiwan : TAGAWA 3728.

SPORE TERMINOLOGY AND MEASUREMENTS.

Spores.

Spores develop in tetrads, each tetrad arising from a single spore mother cell. The spore surface facing other spores during development in the tetrad is called the proximal surface, its centre the proximal pole. This surface usually bears the laesura, a fragile spot in the spore wall, which is supposed to play a part in germination (LUGARDON, 1972). In all polypodiaceae *s.s.* and in some other groups the laesura is a linear structure, therefore the spores are called monolete (as opposed to trilete and alete). Monolete spores have bilateral symmetry as seen in polar view (plate I-1, 3) and usually are roughly kidney shaped in lateral view (plate I-4). The part of the spore situated on the outside of the tetrad is called the distal surface, its centre the distal pole. The equator is the imaginary demarcation line between proximal and distal surfaces, the polar axis is the imaginary line connecting the two poles (CHEN and HUANG, 1974).

The shape of a bilateral monolete spore can be described as follows. The outline in lateral view may be concavo-convex (plate VI-2), the proximal pole being concave in outline, plano-convex (plate I-4), the proximal pole being flat in outline, or biconvex (plate I-2), the proximal pole being convex in outline (HARRIS, 1955). The outline in polar view (« amb ») may be ellipsoidal (ratio of the longest and the shortest axis, L/S, between 1.25 and 2, see plate I-1, 3), subellipsoidal (L/S > 2) or globose (L/S < 1.25, see plate V-1) [CHEN and HUANG, 1974].

Because of the doubtful homology between layers found in spore walls compared to those found in pollen walls, separate terms are used here that refer to the layers of the spore wall only. These terms were defined by LUGARDON (1971, 1972, 1974) who made a detailed study of the spores and spore development of many ferns and fern allies with the aid of the TEM. According to this author the spore wall in ferns may consist of at least three layers :

— the endospore, the innermost layer, which is continuous with the outer wall of the young gametophyte (plate II-6). It is not present until the moment of germination (LUGARDON, 1971) ;

— the exospore, usually the main layer in the spore wall (plate I-6, II-7), acetolysis-resistant, solid in homosporous ferns (LUGARDON, 1974), differentiated on the place of the laesura (plate VI-2, XI-3) [LUGARDON, 1972] ;

— the perispore, the outermost layer (plate I-8, VI-3, 7, VIII-6), formed towards the end of sporoderm formation out of material from outside the spore, sometimes acetolysis-proof, without any notable differentiation around the laesura (plate IX-8), sometimes partly or entirely detached from the spore (plate VII-3, VIII-6, X-4) [LUGARDON, 1974].

There has been much discussion about the presence of a perispore in all fern spores (DEVI, 1980). We consider the outermost layer of the spore wall of all *Pyrrosia* spores to be a perispore, a point that will be treated more extensively in the discussion.

Measurements.

Up to now most spore measurements have been made in LM-slides, in which the exospore outline is usually visible. These measurements hardly ever take the perispore into account (CHEN and HUANG, 1974), at least not its projections (HARRIS, 1955), although perispores may be taken for exospores when taking measurements (for instance in *Pyrrosia serpens* = *P. eleagnifolia* in HARRIS, 1955). In scanning electron micrographs of unacetolyzed spores the perispore usually is more or less intact, impeding measurement of the exospore outline.

The only measurements given are made of spores depicted on micrographs, thus obtaining data of only a small number of spores of each specimen. Moreover, the position of most of the spores in the micrographs seriously restricts the number of measurements possible (e.g. plate V-7).

As far as possible the length of the laesura (L1), the length of the spore (L), the largest width in lateral view (P) and the width in polar view (S), perispore included, (CHEN and HUANG, 1974) were measured in each specimen. All measurements were made in mm and transformed into μm, according to the magnification as indicated by a micron marker that is printed on the negative during exposure.

Description of sporoderm sculpture.

The descriptive terminology for sporoderm sculpture is quite comprehensive and rather inadequate at the same time. The main cause of this situation is the wealth of details of the spore wall surface that can be seen in scanning micrographs, whereas most of the descriptive terminology for pollen and spores is based on LM-observations (HARRIS, 1955, KREMP, 1965 ; CHEN and HUANG, 1974). Besides, not all authors give a clear definition or picture of the descriptive terms used. Some authors even desist from giving any description at all and « let the micrographs speak for themselves » (A. TRYON, pers. comm., see also TRYON and TRYON, 1982), others try to describe the spore walls all the same (LLOYD, 1981 ; LIEW, 1976 a, b, 1977).

The descriptive terms used in the present publication are given below, usually with an indication of their origin if a botanical source could be traced. Most terms originate in palynological literature, others come from other sources, e.g. a publication about seeds of the Cruciferae (MURLEY, 1951).

Another problem in assigning names to sculptural elements is the amount of knowledge about their structure that may be available. An example of this is the use of the terms saccate (« hollow looking elevations ») and verrucate (« projections... appear to be solid ») from HARRIS (1955), or the description of the small semi-spherical projections found in many *Pyrrosia* spores that are caused by the presence in the perispore of spherical bodies consisting of exospore material. We have tried to apply descriptive terms irrespective of such knowledge, in conformity with FAEGRI and IVERSEN (1964), who state that sculpture should be described without reference to internal construction.

Descriptive terms.

bisculptate (WAGNER, 1974) : with two different kinds of ornamentation covering all of the surface, of which one is superimposed on the other ; « there are actually two patterns, one upon the other » (plate IX-1).

colliculate (MURLEY, 1951) : with « rounded broad elevations, closely spaced, covering the surface » (plate I-5).

cristae (HARRIS, 1955) : « suture-like ridges, as if formed by portions of the outer wall uniting in a seam or crest, not less than 1 μm in height » (plate VII-1).

cristate : bearing cristae.

cristo-reticulate (HARRIS, 1955) : with « crests anastomosing to form a network » (plate VII-5).

dense patterns (HARRIS, 1955) : « when the space separating the projections is less than one-twentieth the equatorial diameter of the spore » (plate III-1).

echinulae (HARRIS, 1955) : « projections with tapering trunk and more or less sharp apex, their basis smaller than the vertical axis » (plate XI-8).

echinulate : bearing echinulae.

fingerprints (HARRIS, 1955) : « elevations or indentations, less than 1 μm wide, striate, not linear, but exhibiting parallellism » (plate IV-5).

foveolate (HARRIS, 1955) : « with cavities not less than 1 μm and up to 2 μm in diameter or, if larger, too widely separated to form a reticulum » (plate II-7).

granulae (HARRIS, 1955) : « more or less isodiametric projections, not less than 1 μm in diameter, not more than one twentieth the equatorial diameter of the spore if the latter is over 20 μm » (plate II-1).

granulate : with granulae.

peglike attachments (GASTONY and TRYON, 1976) : wrinkles on the perispore surface, radiating from granules ; « the spherical bodies appear to be attached to the perispore layer by peglike structures » (plate V-6).

projections (HARRIS, 1955) : « not less than 1 μm in height, less than twice as long as wide » in surface view (plate V-7).

ridges : a looser term for cristae and similar ornamentations like those in *P. transmorrisonensis* (plate III-1).

sparse patterns (HARRIS, 1955) : « the space separating the projections is in the main greater than one-tenth the equatorial diameter » (plate IV-1).

torus (THOMSON and PFLUG, 1953) : « the torus is a kind of swollen protrusion or invagination of exospore lamellae. This protrusion or invagination is restricted to a narrow or broad region which runs parallel to the Y-mark » (= laesura) (plate I-4).

verrucae (HARRIS, 1955) : « with broad projections, ... if more or less isodiametric, larger than granulate ; trunk not constricted » (plate IX-5).

verrucate : bearing verrucae.

warts : a looser term for verrucae, granulae, raised fingerprints or the components of a colliculate pattern.

wrinkle : long, elevated structure, about 1 μm wide.

Results.

SPORE WALL FEATURES FOUND IN *Pyrrosia*.

Broken spores (plate I-6, II-7, VI-3, 7, VIII-6) usually appear to be empty. This may be due to an accidental loss of spore contents when the spores were broken by the application of pressure, or cut with a freezing microtome (plate VI-3, 7, VIII-6). In other cases the spores may not have been fully ripe, with the few contents placed closely against the spore wall. Ripe spores contain few organelles, but are full of reserve materials. Prior to germination the cell is activated, the endospore is formed and the young gametophyte grows out of the spore (plate II-6). The wall of a ripe homosporous fern spore therefore consists of only two main layers : exospore and perispore, of which the perispore may be inconspicuously developed.

The exospore is the first part of the spore wall to be formed. In *Pyrrosia* it is solid and 0.7-2 μm thick. The inner surface appears to be smooth (plate VI-3) or very slightly colliculate (plate VIII-6) ; the outer surface may be smooth (plate VI-2, VII-3) or slightly (plate I-4, X-1) to markedly colliculate (plate I-7), with warts up to 5 μm ⌀ and 2 μm high. When the outer exospore surface is not colliculate, spherical bodies contained in the perispore (see under « perispore ») may have left circular impressions of up to 3 μm ⌀, rendering the exospore surface slightly foveolate (plate II-7, III-4, IV-4, V-5).

According to LUGARDON (1972) the exospore in homosporous ferns, represented by *Blechnum spicant* in his study (hence the term « blechnoïde »), consists of two layers. The inner layer (« exospore interne ») is very thin, only visible with the TEM. The outer layer (« exospore externe ») consists of a thin inner « strate fissurée » and a thick, solid, supple outer layer, comprising the main « body » of the exospore. This layer is usually traversed by many small channels, connecting the inner « strate fissurée » with the outer exospore surface. LUGARDON (1972) found most of the channels in *Blechnum spicant* to be situated around the laesura, but in other homosporous ferns they may occur all over the exospore surface. In *Pyrrosia* both conditions are found : in at least one species (plate I-5, 6, 8) small holes may occur all over the surface, especially between warts where the exospore is thinnest ; in other species (plate I-4, VII-4, 6, XI-7) they occur mainly or exclusively around the laesura. In one species (plate X-3) small holes have been found with small plugs in their centres. With the SEM we have never seen any channels in cross-sections.

In his definition of the exospore LUGARDON stresses the differentiation of this layer around the laesura. This feature is more striking as seen in cross-sections with the TEM than as seen from outside with the SEM. In *Pyrrosia* the laesura is a straight short ridge (plate I-2), sometimes medially grooved (plate VII-6) or situated on a variously distinct torus (plate I-4, 5). Occasionally, in both smooth and colliculate exospores spherical warts are merged into the laesural ridge (plate I-3, 7).

In some species small scales are found adhering to the exospore surface, especially near the impressions caused by spherical bodies present in the perispore (plate III-2, 3, V-5). LUGARDON (1974) mentions these scales under the heading of « écailles et lamelles profondes » as elements more or less distinct from the perispore but nevertheless belonging to this layer. According to him, they occur in ferns with rather thick perispores in order to allow some shifting of the rigid perispore with respect to the more elastic exospore, or even complete detachment of the perispore.

In *Pyrrosia* the perispore exhibits a surprising amount of variation, from extremely simple to astonishingly complex. The simplest perispore found in this genus comprises a thin layer, up to 0.2 μm thick, closely adhering to the outer surface of the exospore and only hardly visible with the SEM, e.g. where it peels off (plate I-1, 2, 8).

In many species of *Pyrrosia* and in some other groups of ferns spherical bodies are present in the perispore, their amount sometimes varying from sporangium to sporangium and from specimen to specimen (LUGARDON, 1981). Spherical bodies (« globules », LUGARDON, 1981) consist of exospore material and may be found free in the sporangium (« globules libres »)

or incorporated in the perispore (« globules captifs »). Free spherical bodies can accidentally be incorporated in the perispore, but captive spherical bodies can be structural elements that determine perispore morphology.

In *Pyrrosia* spherical bodies are found sandwiched in between two layers of perispore material (plate II-1, 2, 3, 4, 5). These layers may be so thin that the spherical bodies seem to lie between the exospore surface and the perispore (plate III-3), but thicker perispores containing spherical bodies are also found (plate III-8, IV-6). They may be very numerous, locally forming conspicuous ridges (plate III-1, 4). Spherical bodies in *Pyrrosia* are not always entirely spherical but may be flattened or irregular in outline (plate V-4, 7), sometimes lying so close together that they influence each other shape (plate II-5). Their size is usually between 1 and 2 μm ⌀, but warts caused by the presence of a spherical body may measure up to 10 μm ⌀. Sometimes they seem to be fastened to the perispore by what GASTONY and TRYON (1976) have called peglike attachments (plate III-5, IV-1, V-4, 6) ; actually these are radiating wrinkles in the part of the perispore that covers the spherical bodies.

Apart from and irrespective of any ornamentation caused by the exospore surface or by the presence of spherical bodies, the perispore surface may show several other specific kinds of ornamentation, which in part intergrade into one another, even in one spore (plate VIII-3) : wrinkles, fingerprint patterns, verrucae, echinulae and cristae.

Wrinkles may occur almost everywhere :
— radiating from spherical bodies (« peglike attachments », plate III-5) ;
— running parallel to each other over part of the surface (plate IV-3) ;
— forming a dense network (plate V-6) ;
— on top of warts (plate IX-2, 4, 6, 8) ;
— forming fingerprint patterns (plate IV-5), i.e. circles enclosing a number of parallel wrinkles, sometimes raised into wartlike structures (plate IV-7, VIII-1).

In some cases it may be difficult to distinguish between raised fingerprint patterns and large warts with a fingerprint on top. Nevertheless, this distinction appears to be convenient.

Warts may be small and touching each other, forming a colliculate pattern, usually 2-6 μm ⌀, sometimes up to 10 μm ⌀ (plate X-4, XI-1). This kind of perisporal wart may be difficult to distinguish from exosporal warts with a thin perispore adhering to them (plate I-5, 7). The colliculate perisporal warts may consists of several (up to 4) thin layers (plate X-4, XI-1) that are connected to each other in between the warts. However, the same kind of warts is found in solid perispores (plate XI-8). This illustrates the problem of relating similarities in outer surface ornamentation

to essential structural differences, a problem that is generally overlooked. However, perispores may be regarded as being composed of either many tightly packed layers, or of fewer thin layers with later deposition of perispore material in between. This problem is impossible to solve without a detailed sporogenetic study using the TEM.

Much larger warts, up to ca. 15 μm ⌀ and high, are also found, distributed more solitary than the smaller ones (plate VI, VIII, IX, X, and XI). These large verrucae are probably nearly always solid (plate VI-3, 7, VIII-6), but may be hollow (plate VIII-8). They occur either as the only ornamentation on a spore (plate VIII-7), or together with :
— granules caused by the presence of spherical bodies in the perispore (plate V and VI) ;
— cristae (plate VIII) ;
— colliculate smaller warts (plate IX, X, and XI).

In two species echinulae occur, together with colliculate warts (plate XI-6, 8). The echinulae are straight to slightly curved above the middle with a wrinkled surface sometimes bearing fingerprint patterns, up to 10 μm ⌀ and up to 15 μm high.

In two species with a cristate perispore, the cristae run the length of the spore. They measure up to 10 μm in height and are found as the only kind of ornamentation (plate VII-1). Large anastomosing cristae of 5-8 μm wide and up to 8-15 μm high are found in some other species (plate VII-5, 7, VIII-1, 2, 3, 4, 5), on their own (plate VII-5) or associated with usually raised fingerprints (plate VII-7). Verrucae and cristae occurring together on the same spore give the impression that cristae can break up into verrucae and that verrucae can fuse to form cristae (plate VIII-3). The cristae are solid and so do not consist of folds in the perispore. However, the perispore appears to be especially fragile along the cristae (plate VII-5, 8), which are in some cases situated exactly over the laesura (plate VII-4), allowing the thick perispore to open and to be shed easily.

In most of the species in *Pyrrosia* the perispore is continuous, without any differentiation over the laesura (plate IX-8), although in some species the laesura shows through the perispore as a slight ridge (plate I, II-3, IV-2). In one group of species (plate V and VI) the area around the laesura is strikingly different from the rest of the perispore surface. In these species a kind of oval hatch is present over the laesura, sometimes with a granular deposit (plate V-6, VI-4), where the perispore is thinner or even seemingly absent (plate V-1). This hatch lacks the ornamentation as found on the rest of the perispore surface and is sometimes shifted with respect to the laesura in the direction of its length axis (plate V-3). The structure of the hatch is clearly illustrated in plate V-5 showing only the hatch remaining connected to the exospore after abrasion of the rest of the perispore.

DESCRIPTION OF *Pyrrosia* SPORES.

Spores in the genus *Pyrrosia* are anisopolar, bilateral, monolete, slightly bi- to slightly concavo-convex in lateral view, and ellipsoidal in polar view. They are relatively large : most spores measure between 60 and 80 μm long and between 40 and 60 μm in height, perispore included.

The exospore is usually smooth, sometimes slightly to distinctly verrucate-colliculate, 0.7-2.0 μm thick ; if the perispore contains any spherical bodies the exospore surface can be foveolate because of the imprints these bodies apparently leave on the exospore. The laesura is short, 0.2-0.6 of the longest axis and usually most prominent on the exospore surface.

A perispore is present in all species. It may be extremely thin and fit tightly around the exospore, contain spherical bodies or be variously sculptured with wrinkles, cristae, verrucae, echinulae or a combination of different sculptural elements.

SPORE TYPES AND THEIR DESCRIPTION.

In the genus *Pyrrosia* five spore types are distinguished using morphological characters. Spores in this genus seldom are characteristic on the species level. Only *P. schimperiana* (plate I-5, 6, 7, 8), *P. gardneri* (plate VI-4, 5, 6, 7) and one specimen of *P. abbreviata* (DE WILDE and DE WILDE-DUYFJES 13561, plate VIII-6, 7, 8) have spores that are more or less unique within the genus. Therefore we refrain from giving descriptions of the spores of each species and merely indicate in the spore type descriptions which characteristics are not common to all species with a certain type of spores.

Each spore type is named after a fairly common species of which the spore structure is regarded as representative for the type. As these types are based on spore characters only, care has been taken not to name any spore type after a species that already has given its name to a group of species recognized by HOVENKAMP in his monograph of the genus.

1. **Pyrrosia princeps-type** (plate I) :

P. africana (KUNZE) BALLARD
P. costata (PRESL) TAGAWA and IWATSUKI
P. platyphylla HOVENKAMP
P. princeps (METT.) MORTON
P. schimperiana (KUHN) ALSTON
P. splendens (PRESL) CHING
P. stigmosa (SWARTZ) CHING

Outline in lateral view very slightly biconvex (*P. princeps*, BRASS 8859, plate I-2) to slightly concavo-convex, usually plano-convex ; ellipsoidal in polar view.

Laesura a short, straight ridge, running 0.4 (0.3-0.5) of the length of the spore, ca. 15-30 μm long, in *P. africana* (plate I-4) and *P. schimperiana* (plate I-5) sometimes situated on a broad torus that runs the length of the spore and has the same ornamentation as the rest of the sporoderm surface. The laesural ridge proper usually has no ornamentation, but may have the same ornamentation as the rest of the exospore (*P. schimperiana*, GLYNNE 244, plate I-7) or may consist of two rows of partly interlocking spherical structures (*P. platyphylla*, WOOD 2011, plate I-3).

Exospore surface smooth (*P. costata, P. platyphylla, P. princeps, P. splendens*, and *P. stigmosa*) to colliculate (*P. africana* and *P. schimperiana* ; sometimes very slightly so in *P. costata* and *P. splendens*), distinctly colliculate in *P. schimperiana* (plate I-5, 7) with warts up to 5 μm ⌀ and 2 μm high. Exospore approximately 1 μm thick, in ornamented exospores thicker at the warts. In *P. africana* (plate I-4) and *P. schimperiana* (plate I-6, 8) small holes may be visible between the warts, in *P. africana* mainly near the laesura.

Perispore thin, tightly adhering to the exospore surface, sometimes cracking and peeling off, up to 0.2 μm across.

L × P × S : 58(54-64) × 39(35-42) × 38(33-42) μm.

2. Pyrrosia subfurfuracea-type (plate II, III and IV) :

P. assimilis (BAKER) CHING
P. boothii (HOOKER) CHING
P. drakeana (FRANCH.) CHING
P. flocculosa (D. DON) CHING
P. hastata (HOUTT.) CHING
P. linearifolia (HOOKER) CHING
P. mannii (GIESENH.) CHING
P. pannosa (KUHN) CHING
P. penangiana (HOOKER) HOLTTUM

PLATE 1. — *Pyrrosia princeps*-type.

Scale bar is 10 μm unless stated otherwise.
1. — *P. princeps* (DAMASK 7), proximal view.
2. — *P. princeps* (BRASS 8859), lateral view.
3. — *P. platyphylla* (WOOD 2011), proximal view.
4. — *P. africana* (DE JONCHEERE SAC 254), lateral view.
5. — *P. schimperiana* var. *schimperiana* (RICHARDS 17414), general view.
6. — *P. schimperiana* var. *schimperiana* (DE WILDE 5242), detail of a broken exospore ; scale bar is 1 μm.
7. — *P. schimperiana* var. *liebuschii* (GLYNNE 244), lateral view.
8. — *P. schimperiana* var. *liebuschii* (GLYNNE 244), detail of the exospore surface and a broken perispore.
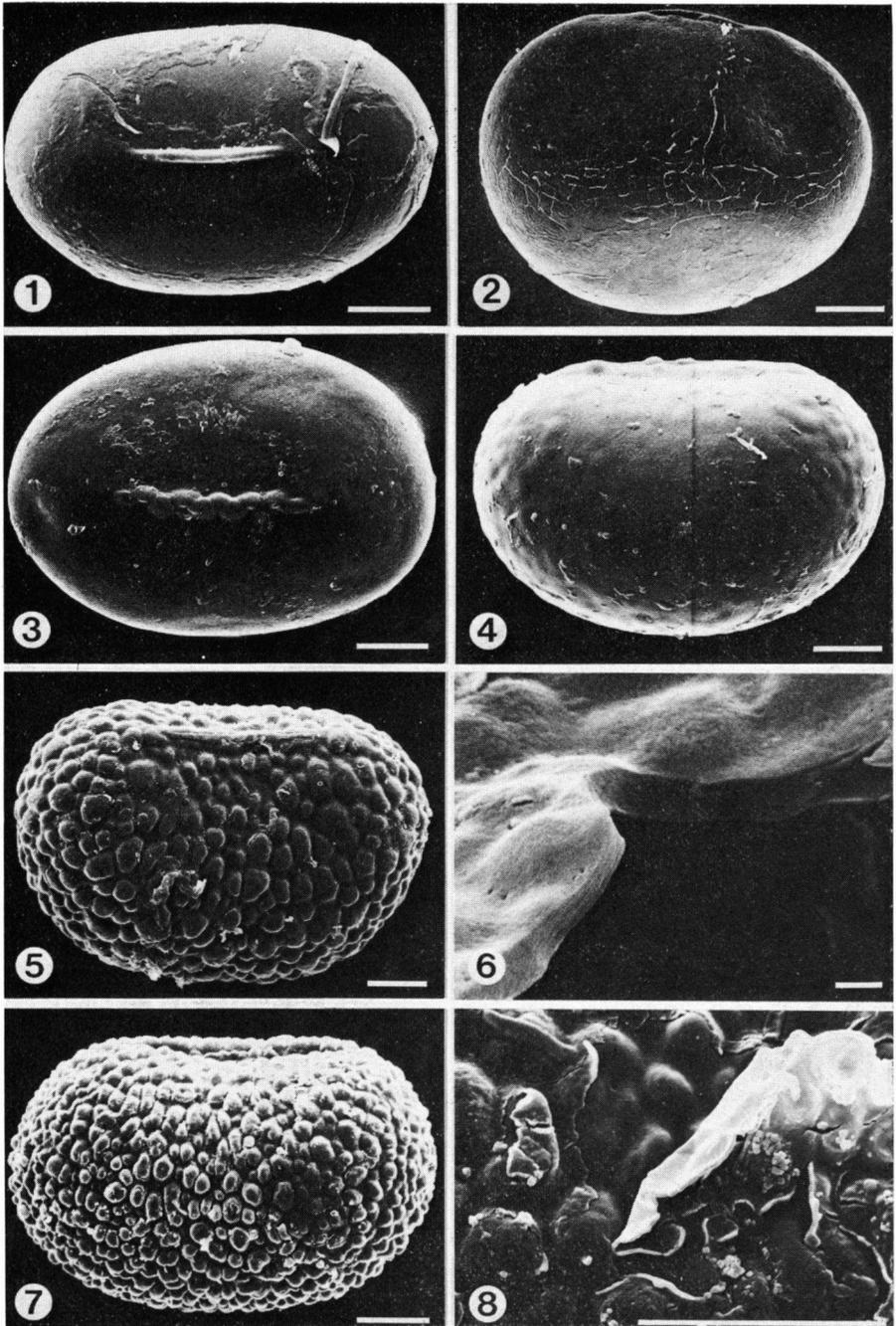
PLATE I.

P. polydactyla (HANCE) CHING
P. porosa (PRESL) HOVENKAMP
P. rhodesiana (C. CHR.) SCHELPE
P. sheareri (BAKER) CHING
P. stolzii (ENGL.) SCHELPE
P. subfurfuracea (HOOKER) CHING
P. transmorrisonensis (HAYATA) CHING

Outline in lateral view usually plano-convex, sometimes slightly biconvex or concavo-convex ; ellipsoidal in polar view.

Laesura a slight ridge on the sporoderm surface (plate II-3), running 0.4 (0.2-0.5) of the length of the spore, 28 (17-42) μm long, most prominent on the exosphere surface (plate III-2).

PLATE II. — *Pyrrosia subfurfuracea*-type.

Scale bar is 10 μm unless stated otherwise.
1. — *P. sheareri* (FAN and LI 433), lateral view.
2. — *P. sheareri* (FAN and LI 433), detail of the inner perispore surface ; scale bar is 1 μm.
3. — *P. subfurfuracea* (TSAI 53252), general view.
4. — *P. subfurfuracea* (TSAI 53252), detail of a broken perispore ; scale bar is 1 μm.
5. — *P. mannii* (BANERJI 1534), detail of a broken perispore ; scale bar is 1 μm.
6. — *P. hastata* (TAQUET s.n., VII 1909), germinating spore.
7. — *P. subfurfuracea* (TSAI 53252), broken exosphere.

PLATE III. — *Pyrrosia subfurfuracea*-type.

Scale bar is 10 μm unless stated otherwise.
1. — *P. transmorrisonensis* (TAGAWA 3728), general view.
2. — *P. transmorrisonensis* (TAGAWA 3728), lateral view of the exosphere.
3. — *P. polydactyla* (cult. Kew 218-79 2104), exosphere surface and broken perispore.
4. — *P. boothii* (LUDLOW et al. 18646), perispore partly gone.
5. — *P. flocculosa* (HENNIPMAN 3352), general view.
6. — *P. porosa* (TSAI 53654), general view.
7. — *P. linearifolia* (KAO K 3843), general view.
8. — *P. linearifolia* (KAO K 3843), detail of the exosphere and broken perispore ; scale bar is 1 μm.

PLATE IV. — *Pyrrosia subfurfuracea*-type.

Scale bar is 10 μm unless stated otherwise.
1. — *P. assimilis* (TSANG 20896), lateral view.
2. — *P. rhodesiana* (WILD 2119), lateral view.
3. — *P. rhodesiana* (BARON 3526), general view.
4. — *P. rhodesiana* (POOL s.n., V 1876), detail of the exosphere and broken perispore ; scale bar is 1 μm.
5. — *P. stolzii* (STOLZ 891), lateral view.
6. — *P. stolzii* (STOLZ 891), detail of a broken perispore ; scale bar is 1 μm.
7. — *P. stolzii* (WHITE 2709), general view.
8. — *P. stolzii* (STOLZ 891), detail of a broken perispore ; scale bar is 1 μm.
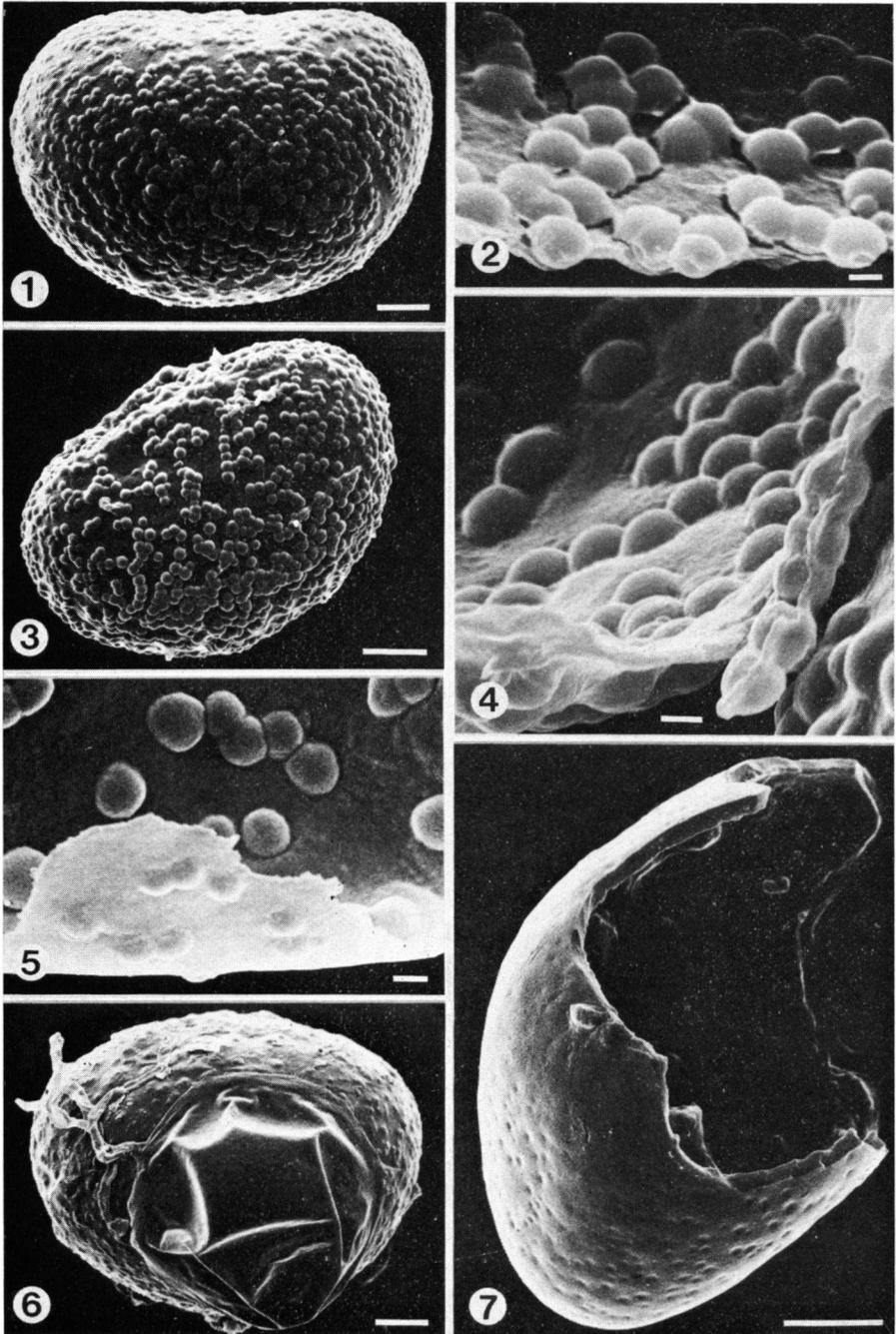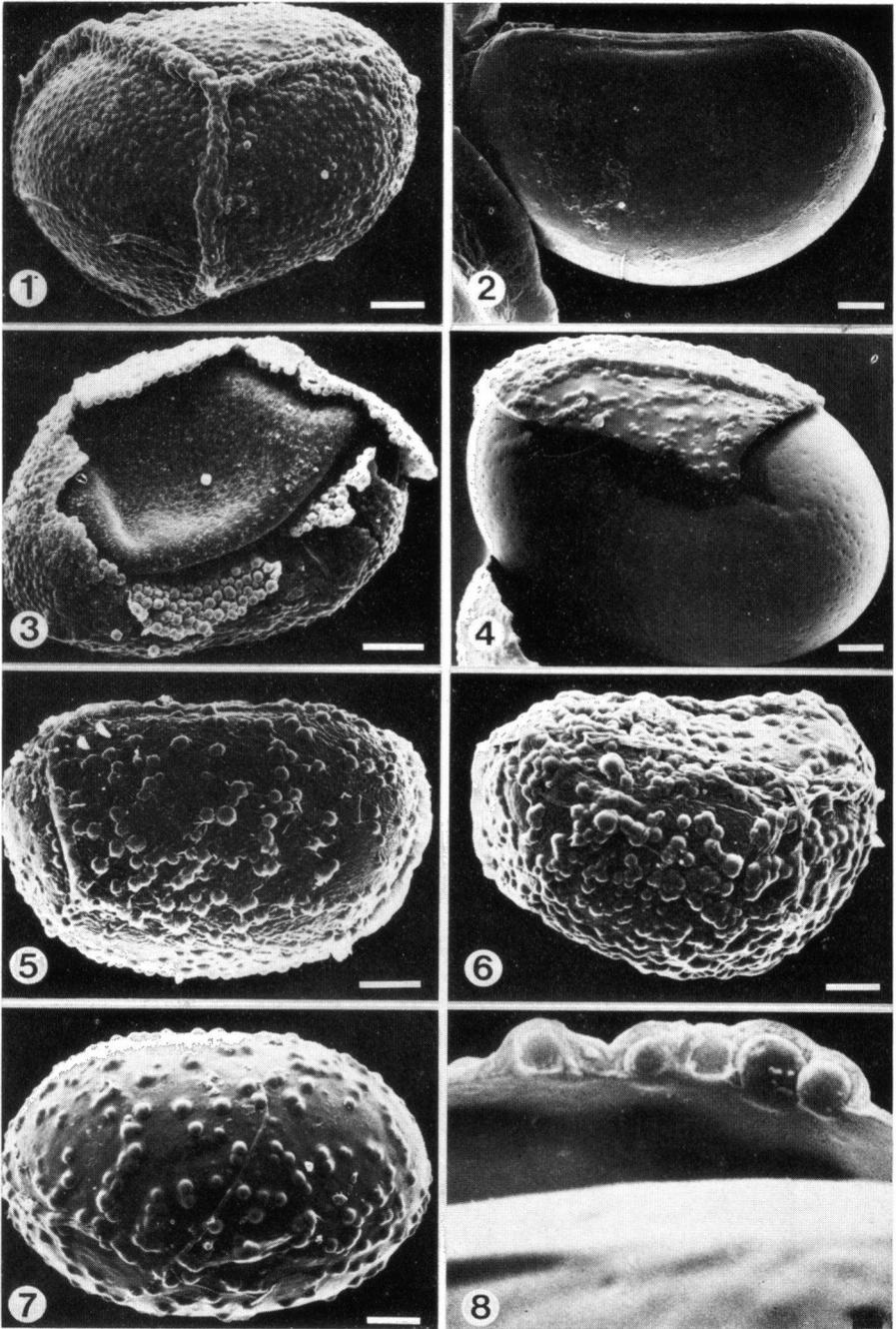
PLATE II.

PLATE III.
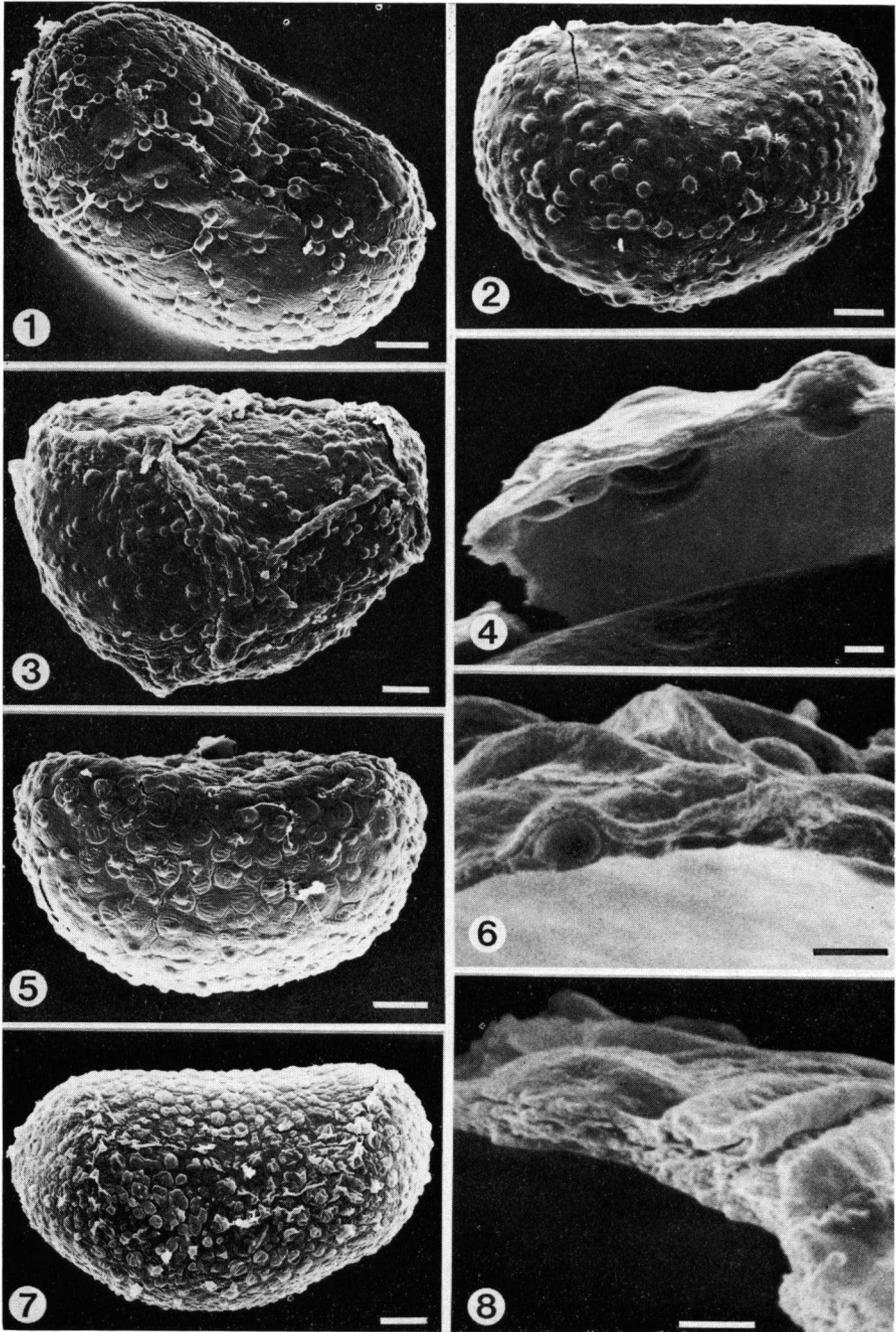
PLATE IV.

Exospore essentially smooth or sometimes very slightly colliculate *(P. assimilis, P. porosa, P. stolzii)*, usually foveolate because of the imprints of spherical bodies present in the perispore (plate II-7, all species except *P. hastata* and *P. polydactyla*), depressions 1-1.5 μm, up to 3 μm ∅ ; surface sometimes bearing thin scales *(P. hastata, P. polydactyla, P. porosa, P. transmorrisonensis)*, especially around the depressions (plate III-2, 3).

Perispore containing spherical bodies, usually causing both surfaces to be granulate (plate II-4, 5), the granules round but more irregular in shape if lying very closely together (plate II-3, 5), about 2 μm ∅, rarely up to 6 μm ∅ ; granules densely set in *P. boothii, P. drakeana, P. hastata, P. polydactyla, P. sheareri, P. subfurfuracea,* and *P. transmorrisonensis,* sometimes aggregating into long distinct ridges *(P. boothii* and *P. transmorrisonensis,* plate III-1) or entirely covering the spore surface *(P. polydactyla,* plate III-3) ; granules more sparse in *P. assimilis, P. flocculosa, P. linearifolia, P. mannii, P. pannosa, P. penangiana, P. porosa, P. rhodesiana,* and *P. stolzii.* Apart from these granules the perispore is usually smooth and thin, 0.15-0.40 μm across, in *P. linearifolia, P. porosa,* and *P. stolzii* sometimes thicker, up to 1 μm across (plate III-8, IV-8). The outside surface sometimes bears wrinkles and peglike attachments *(P. assimilis, P. flocculosa, P. porosa, P. rhodesiana, P. stolzii,* plate IV-3). In *P. rhodesiana* and *P. stolzii* fingerprint patterns occur irrespective of the distribution of the granules (plate IV-5) ; in *P. stolzii* they are sometimes raised into slight warts (plate IV-7).

L × P × S : 78 (46-104) × 58 (51-68) × 47 (35-58) μm.

3. Pyrrosia christii-type (plate V and VI) :

P. angustissima (Diels) Tagawa and Iwatsuki
P. christii (Giesenh.) Ching
P. gardneri (Mett.) Sledge
P. laevis (Bedd.) Ching
P. lingua (Thunb.) Farwell
P. petiolosa (Christ) Ching

Plate V. — *Pyrrosia christii*-type.

Scale bar is 10 μm.
1. — *P. angustissima* (Bodinier 2117), proximal view.
2. — *P. laevis* (Toppin 6330), lateral view.
3. — *P. laevis* (Toppin 6330), general view.
4. — *P. petiolosa* (Meyer 958), lateral view.
5. — *P. laevis* (Toppin 6330), detail of rest perispore over laesura.
6. — *P. lingua* var. *heteracta* (Van Beusekom and Phengklai 2998), proximal view
7. — *P. lingua* var. *lingua* (Hennipman 3145 A), general view.
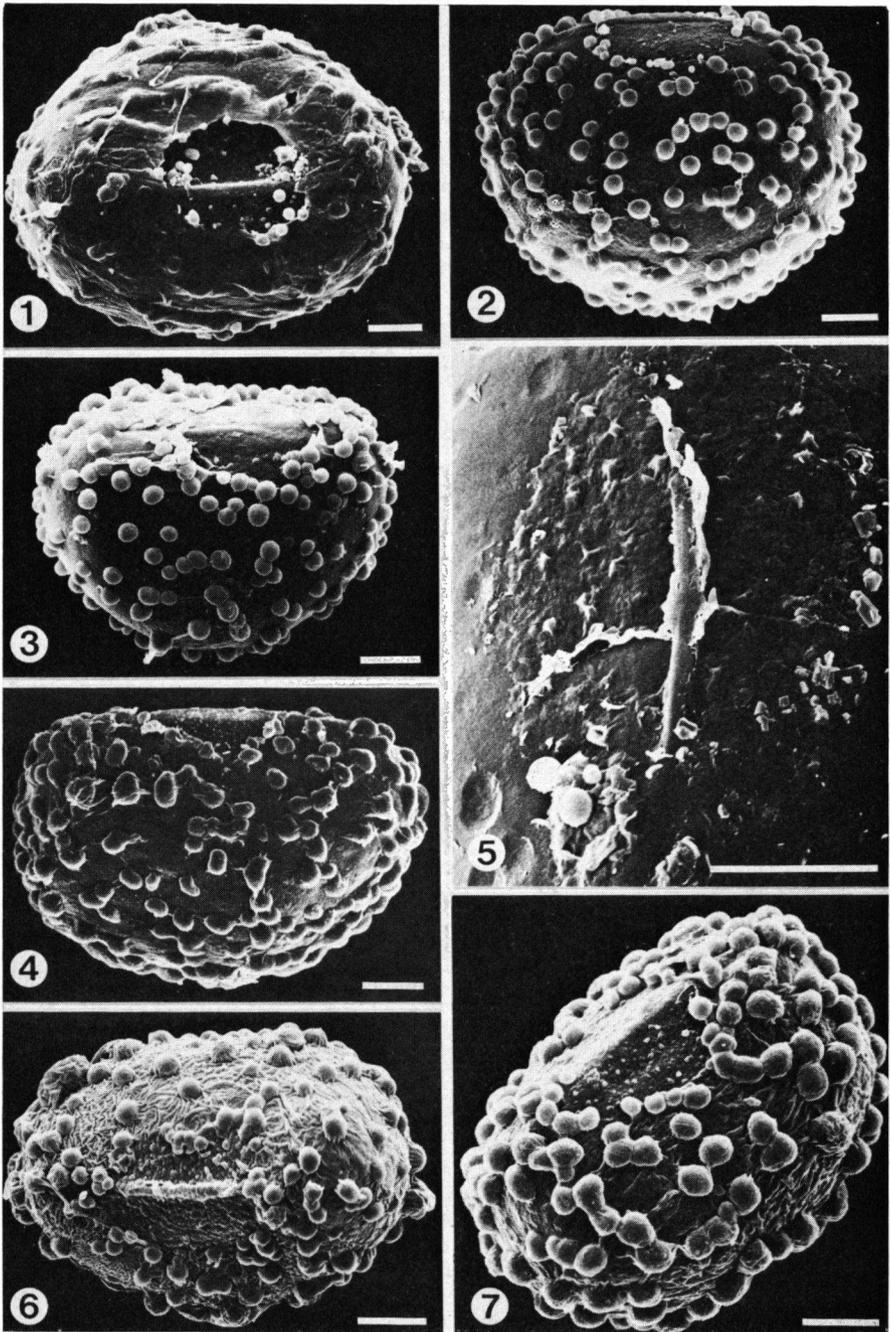
PLATE V.

Outline in lateral view slightly biconvex (plate V-2) to distinctly concavo-convex (plate VI-2), usually plano-convex ; in polar view usually ellipsoidal, except for some spores of *P. angustissima* (plate V-1).

Laesura usually a distinct ridge, running 0.3 (0.2-0.4) of the spore length, 21 (15-28) μm long, always clearly visible because of the lack of conspicuous perispore ornamentation on the proximal side of the spore.

Exospore essentially smooth (plate VI-2) but usually sparsely and slightly foveolate (plate V-5) by imprints of the spherical bodies contained in the perispore, the depressions 1-3 μm ∅, bearing some thin scales around the edges ; exospore 1.0-1.6 μm thick (plate VI-3, 7), sometimes with small holes of approximately 0.5 μm ∅ near the laesura *(P. angustissima, P. christii, P. laevis, P. petiolosa)*.

Perispore containing spherical bodies, causing both surfaces to be granulate, granules on the outer surface far more distinct than on the inner, 1.5-7 μm ∅, usually round but sometimes irregular in shape, especially in *P. lingua* and *P. petiolosa* (plate V-4, 6, 7) ; perispore in three species also verrucate *(P. christii, P. gardneri, P. lingua)*, verrucae large, round, wrinkled, 4-10 μm ∅ and up to 9 μm high (plate VI-1, 3, 6), usually mainly situated on the distal side, sometimes (especially in *P. gardneri*, plate VI-6) covering almost all of the perispore surface ; fingerprint patterns are often found on top of the verrucae *(P. gardneri*, plate VI-6) and verrucae occasionally fuse into ca. 3 μm wide ridges *(P. gardneri*, KOSTERMANS 27114, plate VI-5) ; outer perispore surface slightly to distinctly wrinkled, with peglike attachments over the granules. In some cases it is difficult to distinguish large granules from small verrucae (plate VI-6). Perispore lacking the ornamentation characteristic of the rest of the surface on the proximal side around the laesura, where it is provided with a hatch : here the perispore seems to be lacking or gone (plate V-1), or consists of a rather thick crust *(P. gardneri* and *P. lingua*, plate VI-4) or a thin layer with very small granules, often less than 1 μm ∅ (found in all species, plate V-7) ; in all

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PLATE VI. — *Pyrrosia christii*-type.

Scale bar is 10 μm unless stated otherwise.
1. — *P. christii* (NOOTEBOOM 1227), general view.
2. — *P. christii* (ENDERT 3146), lateral view of the exospore, perispore broken.
3. — *P. christii* (NOOTEBOOM 1227), broken spore.
4. — *P. gardneri* (MACRAE 454), proximal view.
5. — *P. gardneri* (KOSTERMANS 27114), lateral view.
6. — *P. gardneri* (MACRAE 454), two spores.
7. — *P. gardneri* (KOSTERMANS 27114), detail of a broken exospore and perispore ; scale bar is 1 μm.
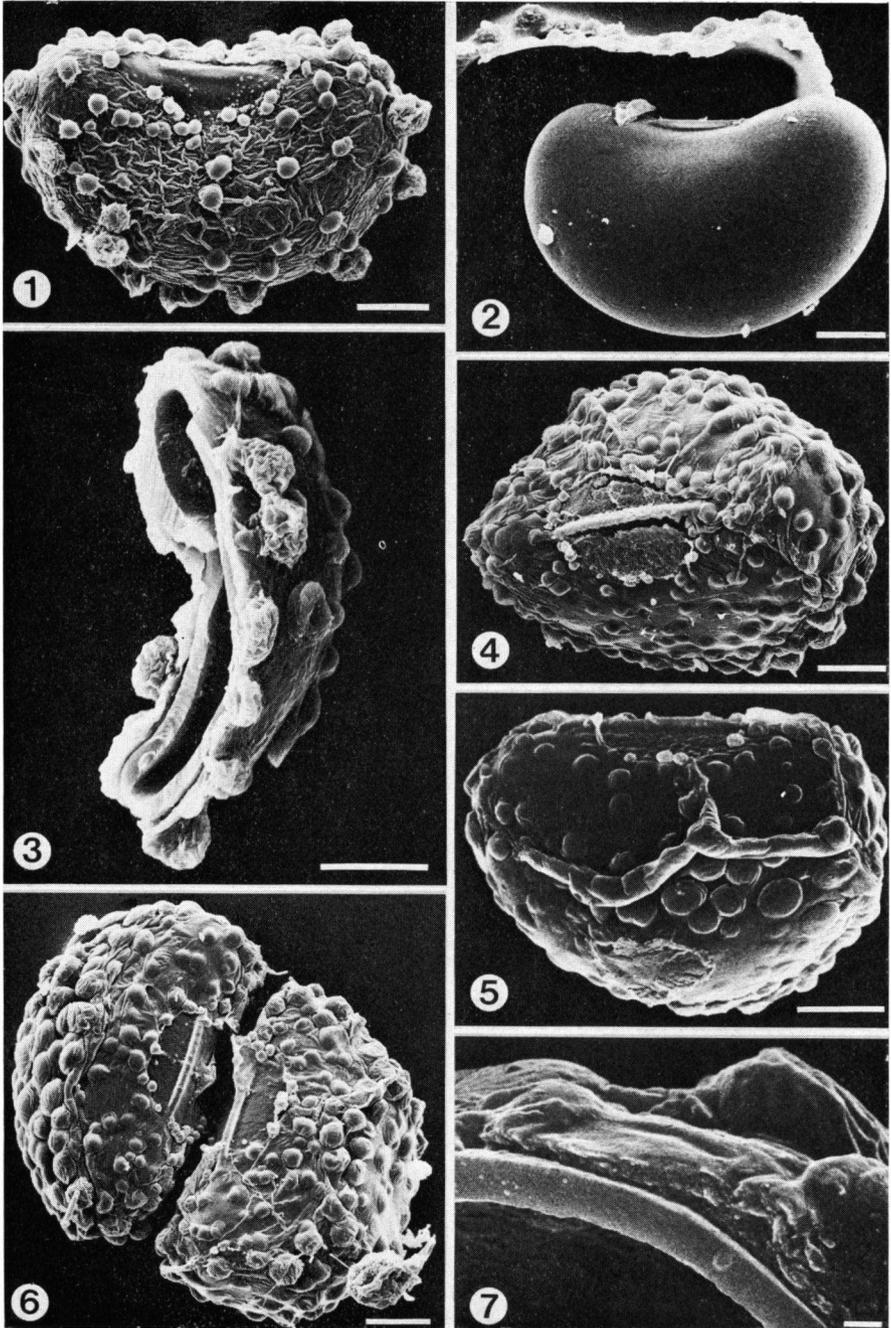
PLATE VI.

species two or all three of these situations have been found ; in spores that seem to be devoid of any perispore over the laesura this hatch is sometimes found to have shifted with respect to the laesural ridge, parallel to the longest spore axis (plate V-3).

L × P × S : 65 (56-81) × 49 (40-62) × 50 (39-68) μm.

4. Pyrrosia nummulariifolia-type (plate VII and VIII)

P. abbreviata (ZOLL. and MORITZI) HOVENKAMP

P. albicans (BLUME) CHING

P. angustata (SWARTZ) CHING

P. asterosora (BAKER) HOVENKAMP

P. distichocarpa (METT.) SHING

P. kinabaluensis HOVENKAMP

P. novo-guineae (CHRIST) PRICE

P. nummulariifolia (SWARTZ) CHING

P. rasamalae (RACIB.) SHING

P. samarensis (PRESL) CHING

P. sphaerosticha (METT.) CHING

PLATE VII. — *Pyrrosia nummulariifolia*-type.

Scale bar is 10 μm unless stated otherwise.

1. — *P. angustata* (MEIJER 2196), general view.
2. — *P. samarensis* (Univ. San Carlos 750), three spores hanging together.
3. — *P. samarensis* (Univ. San Carlos 750), detail of the exospore surface and broken perispore ; scale bar is 1 μm.
4. — *P. samarensis* (Univ. San Carlos 750), detail of a perispore broken over the laesura ; scale bar is 1 μm.
5. — *P. nummulariifolia* (cult. Kew 685-69 6337), general view.
6. — *P. asterosora* (BÜNNEMEIJER 5153), detail of the laesura on the exospore surface ; scale bar is 1 μm.
7. — *P. asterosora* (BÜNNEMEIJER 5153), general view.
8. — *P. asterosora* (BÜNNEMEIJER 5153), detail of a broken perispore ; scale bar is 1 μm.

PLATE VIII. — *Pyrrosia nummulariifolia*-type.

Scale bar is 10 μm.

1. — *P. albicans* (SCHMUTZ F 135), general view.
2. — *P. rasamalae* (VAN BEUSEKOM and PHENGKLAI 840), two spores hanging together.
3. — *P. sphaerosticha* (JACOBS 7791), general view.
4. — *P. novo-guineae* (BRASS 27921), general view.
5. — *P. abbreviata* (DE WILDE and DE WILDE-DUYFJES 12464), general view.
6. — *P. abbreviata* (DE WILDE and DE WILDE-DUYFJES 13561), detail of a broken spore.
7. — *P. abbreviata* (DE WILDE and DE WILDE-DUYFJES 13561), several spores.
8. — *P. abbreviata* (DE WILDE and DE WILDE-DUYFJES 13561), detail of a broken perispore.
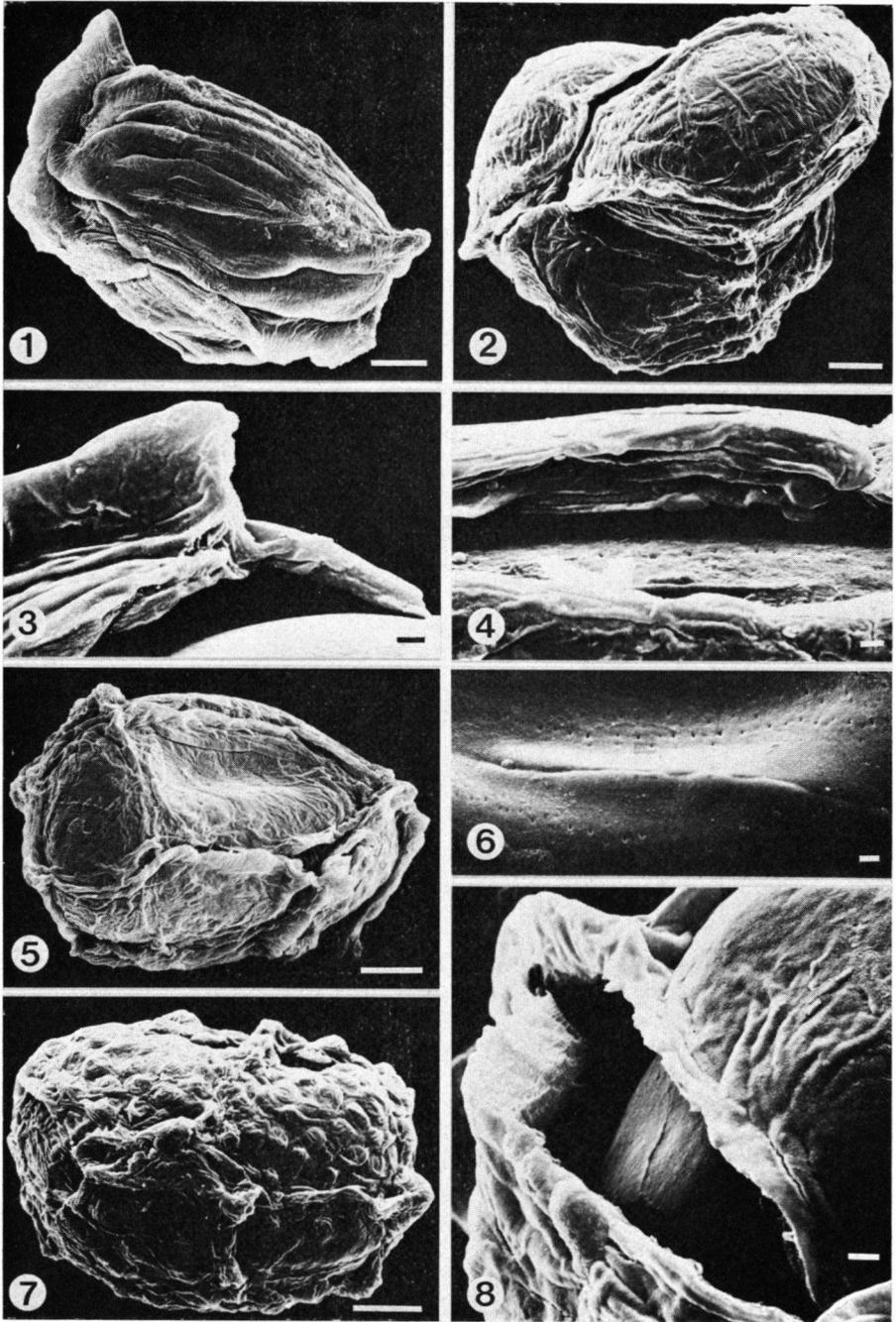
PLATE VII.
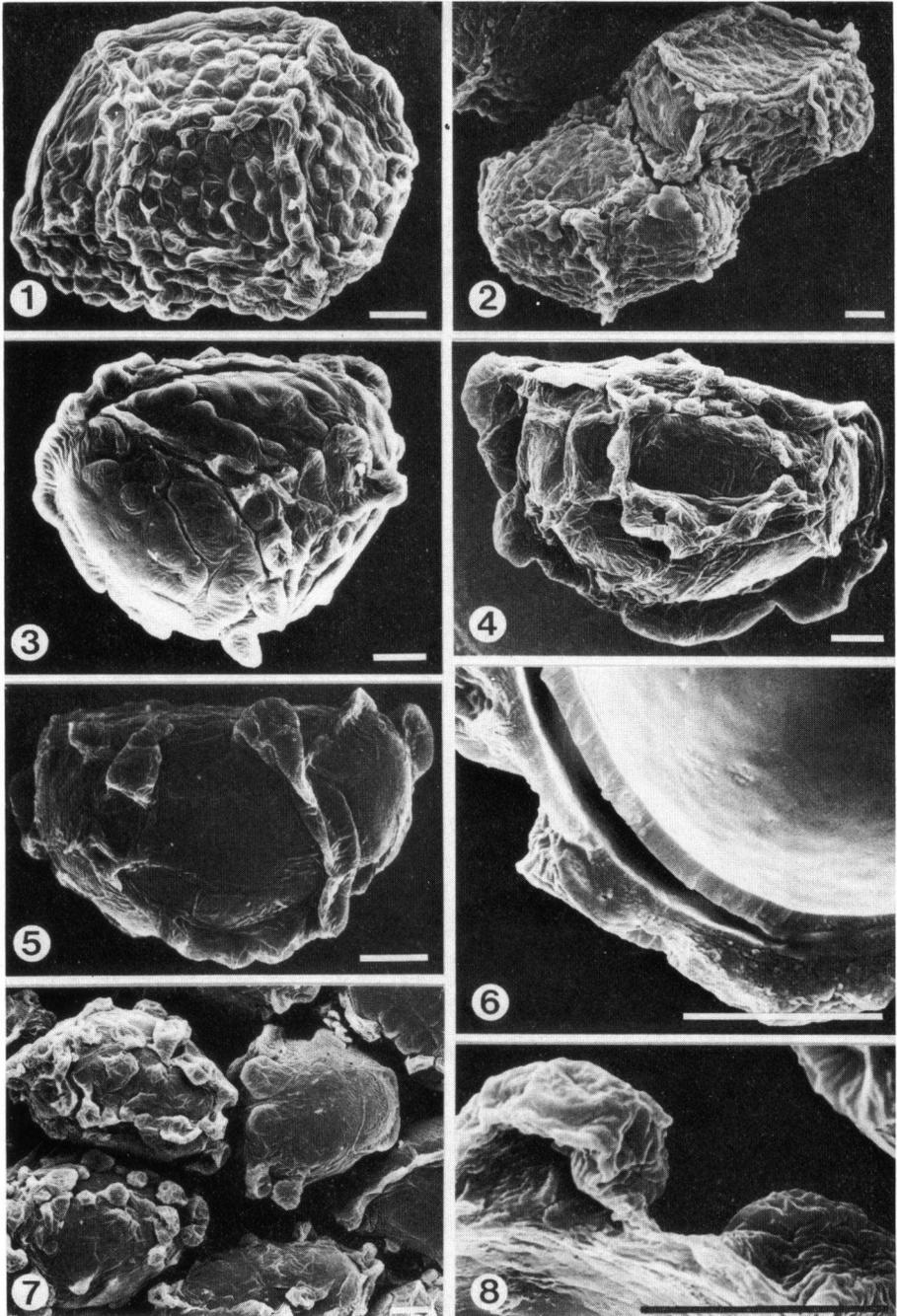
PLATE VIII.

Outline in lateral view about plano-convex to concavo-convex ; ellipsoidal in polar view.

Laesura a short straight ridge running ca 0.25 of the length of the exospore, invisible on the perispore surface.

Exospore 1.3-1.5 μm thick, inner surface slightly colliculate (*P. abbreviata*, plate VIII-6), outside surface smooth, in some species (*P. asterosora, P. distichocarpa, P. samarensis, P. sphaerosticha*, plate VII-4, 6) with small holes of up to 0.5 μm ∅ near the leasura.

Perispore at least 1 μm thick, solid (plate VII-3, 4 ; VIII-6), inner surface smooth to slightly wrinkled, outer surface either smooth with some parallel wrinkles (*P. abbreviata* p.p., *P. angustata, P. novo-guineae, P. samarensis*, plate VII-1, 2) or with fingerprint patterns, the fingerprints up to 4-10 μm long (*P. abbreviata* p.p., *P. albicans, P. asterosora, P. distichocarpa, P. kinabaluensis, P. nummulariifolia, P. rasamalae, P. sphaerosticha*), the fingerprints frequently elevated and up to 2 μm high (*P. albicans, P. asterosora, P. distichocarpa, P. nummulariifolia, P. rasamalae*, plate VII-7, VIII-1, 2) ; perispore also bearing either large cristae mainly running the length of the spore and up to 10 μm high (*P. angustata, P. samarensis*, plate VII-1, 2), or cristo-reticulate, bearing anastomosing cristae of 5-8 μm wide and up to 8-15 μm high (*P. abbreviata* p.p., *P. albicans, P. asterosora, P. distichocarpa, P. kinabaluensis, P. novo-guineae, P. nummulariifolia, P. rasamalae, P. samarensis* p.p., *P. sphaerosticha*, plate VII-5, 7), in some species tending to break up into series of verrucae, in one specimen even bearing verrucae only, some of which seem to be hollow (*P. abbreviata*, DE WILDE and DE WILDE-DUYFJES 13561, plate VIII-8), these up to 10 μm ∅ and high ; perispore breaking easily along the solid cristae (plate VII-5, 8).

L × P : 73 (64-83) × 50 (44-61) μm.

5. Pyrrosia rupestris-type (plate IX, X and XI) :

P. ceylanica (GIESENH.) SLEDGE
P. confluens (R. BR.) CHING
P. eleagnifolia (BORY) HOVENKAMP
P. fallax (ALDERW.) PRICE
P. foveolata (ALSTON) MORTON
P. heterophylla (L.) PRICE
P. lanceolata (L.) FARWELL
P. longifolia (N. L. BURM.) MORTON
P. niphoboloides (BAKER) PRICE
P. piloselloides (L.) PRICE
P. rupestris (R. BR.) CHING
P. serpens (G. FORSTER) CHING

Outline in lateral view slightly biconvex (plate IX-1) to concavo-convex ; ellipsoidal in polar view.

Laesura sometimes visible as a slight ridge over which the perispore pattern is continuous (plate IX-8), running 0.4 of the spore length, more distinct on the exospore surface (plate XI-3).

Exospore smooth to slightly colliculate (plate X-1), the warts ca. 2-5 μm ∅, sometimes with small holes of 0.1-0.2 μm ∅ around the laesura (*P. ceylanica, P. lanceolata, P. piloselloides*, plate XI-1, 7) or elsewhere on its surface *(P. foveolata)*, in *P. foveolata* some holes with small plugs in their centres (plate X-3) ; exospore thickness unknown.

Perispore at least 0.3-0.9 μm thick, rarely containing a few spherical bodies, usually consisting of several layers (*P. ceylanica, P. confluens, P. fallax, P. foveolata, P. lanceolata, P. longifolia, P. niphoboloides*, plate

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PLATE IX. — *Pyrrosia rupestris*-type.

Scale bar is 10 um.
1. — *P. confluens* var. *dielsii* (GOY 435), general view.
2. — *P. rupestris* (SCHODDE 3242), general view.
3. — *P. serpens* (Van BALGOOY 1744), general view.
4. — *P. eleagnifolia* (LAM 7023), general view.
5. — *P. lanceolata* (BLOEMBERGEN 3509), general view.
6. — *P. lanceolata* (SMITH 8110), general view.
7. — *P. lanceolata* (HENNIPMAN 3344 A), general view.
8. — *P. lanceolata* (LÜTJEHARMS 4694), broken perispore.

PLATE X. — *Pyrrosia rupestris*-type.

Scale bar is 10 μm unless stated otherwise.
1. — *P. lanceolata* (VINK 12081), lateral view of the exospore, broken perispore.
2. — *P. foveolata* var. *foveolata* (HIEPKO and SCHULTZE-MOTEL 1444), general view.
3. — *P. foveolata* var. *foveolata* (BRASS 5244), detail of the exospore surface ; scale bar is 1 μm.
4. — *P. foveolata* var. *lauterbachii* (BRASS 32606), broken perispore.
5. — *P. ceylanica* (FADEN and FADEN 76/300), general view.
6. — *P. ceylanica* (FADEN and FADEN 76/300), general view.

PLATE XI. — *Pyrrosia rupestris*-type.

Scale bar is 10 μm unless stated otherwise.
1. — *P. ceylanica* (FADEN and FADEN 76/300), detail of the exospore surface and broken perispore ; scale bar is 1 μm.
2. — *P. niphoboloides* (HUMBERT 5831), three spores hanging together.
3. — *P. niphoboloides* (HUMBLOT 310), general view of the exospore.
4. — *P. niphoboloides* (HUMBLOT 310), detail of a broken perispore.
5. — *P. heterophylla* (LOBB s.n., 1860), general view.
6. — *P. piloselloides* (PHENGKLAI 1130), general view.
7. — *P. piloselloides* (PHENGKLAI 1130), detail of the exospore surface.
8. — *P. piloselloides* (PHENGKLAI 1130), detail of a broken perispore ; scale bar is 1 μm.
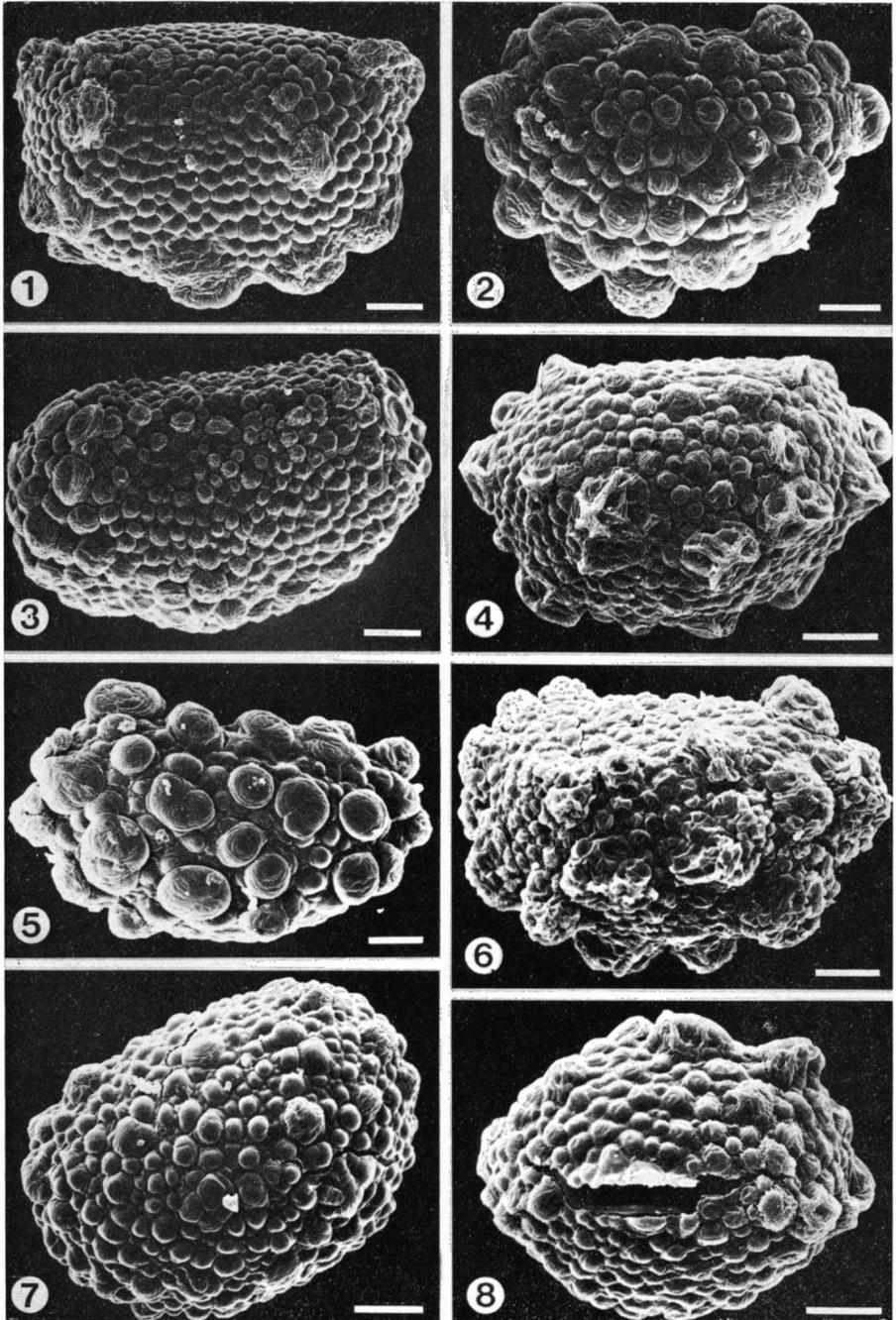
PLATE IX
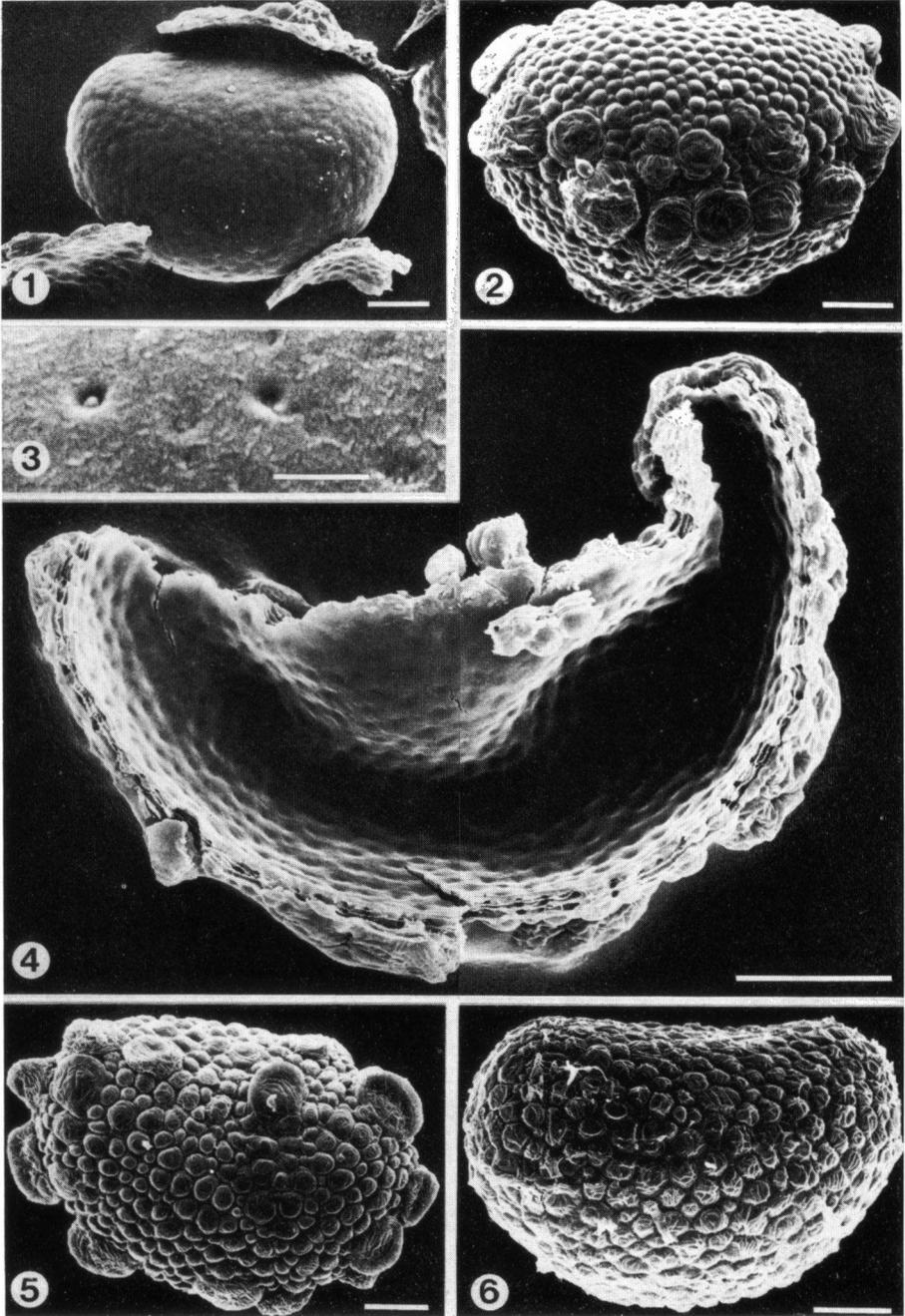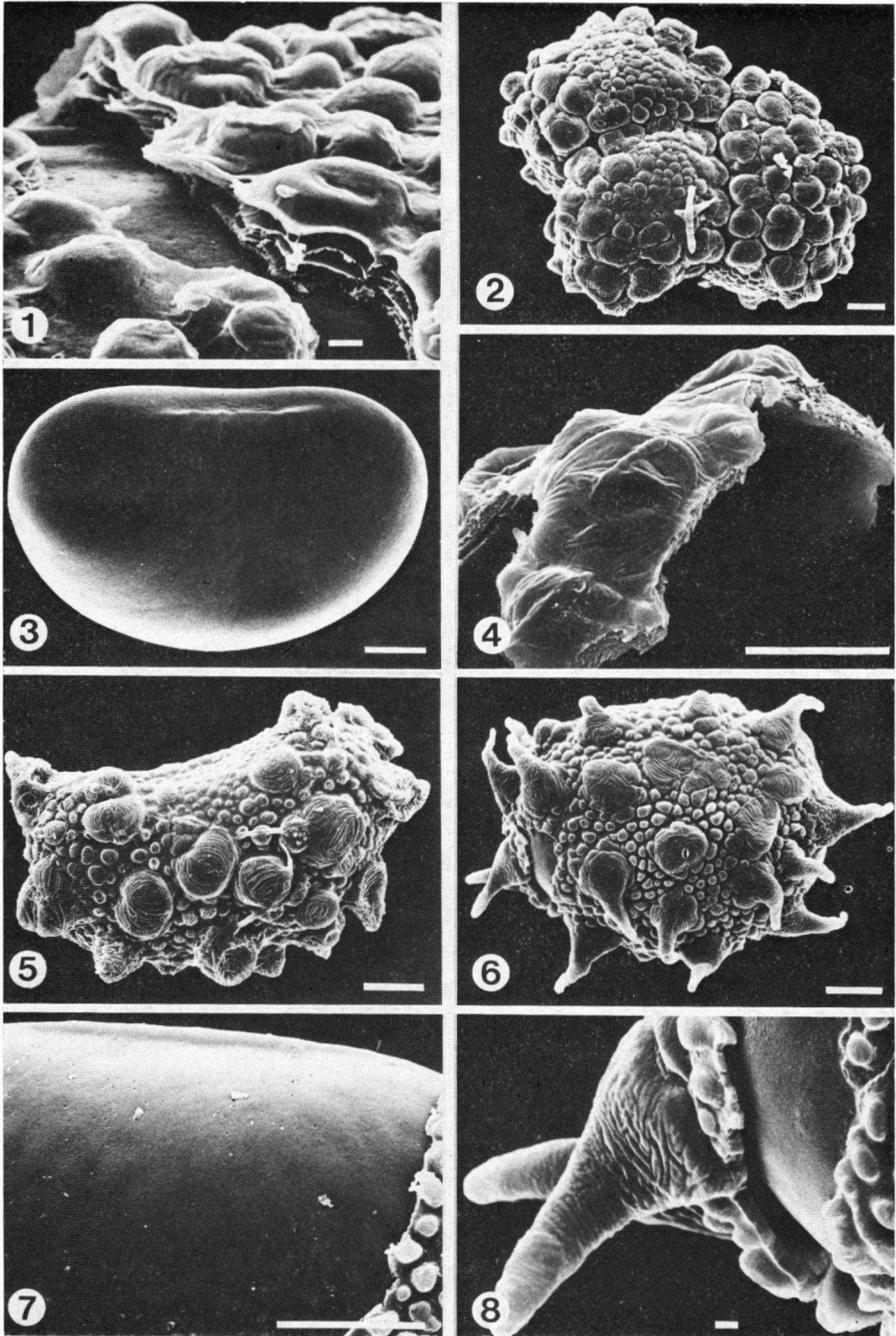
PLATE X.

PLATE XI.

X-4, XI-1), solid in *P. piloselloides* (plate XI-8), the inner surface foveolate (plate X-4) or smooth (plate XI-4), irrespective of exospore ornamentation, outer surface bisculptate : basic pattern colliculate, warts round to oval or angular, (1-) 2-6 (-10) μm ⌀ and up to 1.5 μm apart, smooth or wrinkled, sometimes with a fingerprint pattern, with superimposed on these large flattened (plate IX-5), rounded or conical (especially in *P. heterophylla*, plate XI-5), wrinkled verrucae of up to 15(-20) μm ⌀ and 3-15 μm high, or echinulae (*P. piloselloides*, *P. heterophylla* p.p.*, plate XI-6, 8) that are wrinkled, tapering, sometimes bent, their base ca. 10 μm ⌀, up to 18 μm high. In some species it is sometimes difficult to see any difference between the warts of the basic colliculate pattern and the larger solitary verrucae (*P. ceylanica*, *P. lanceolata*, *P. longifolia*, *P. serpens*, plate IX-3, 7, X-6).

L × P : 70 (54-78) × 50 (38-63) μm.

Discussion.

THE SPORE WALL IN *Pyrrosia*.

Up to now we have tacitly assumed that the outer layer in all *Pyrrosia* spores is a true perispore because LUGARDON (1974) states that probably all species of homosporous ferns do have one. The outer layer of *Pyrrosia* spores fits LUGARDON's concept of perispore on two points :

— it is rather easily separated from the underlying layer, that is, the exospore (LUGARDON, 1974),

— in many species this outer layer contains spherical bodies, LUGAR-DON's « globules captifs » (1981) ; they are found in all *P. subfurfuracea*-type and *P. christii*-type spores (20 species) and occasionally in *P. rupestris*-type spores ; in spores without any spherical bodies the outer layer has the same structure and/or ornamentation (fingerprints, verrucae) as the peri-spores that contain spherical bodies, therefore this outer layer also is a true perispore.

Considering these points it is obvious that the outer layer of all spores in *Pyrrosia* is indeed a perispore despite the surprising amount of variation observed. One spore type in *Pyrrosia*, the *P. christii*-type, has a unique feature not found in any other homosporous leptosporangiate fern : the hatch over the laesura in the perispore. This is of special interest as LUGARDON is not clear on the subject of the possible differentiation of the perispore over the laesura :

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* based on an observation of a LM-slide of *P. heterophylla* BEDDOME 15 (K).

— « la périspore est toujours continue au-dessus de l'aperture de l'exospore. Elle ne présente souvent aucune modification notable dans cette zone... Dans le cas des périspores épaisses, on peut néanmoins observer parfois des modifications plus ou moins marquées et de nature diverse au-dessus ou à proximité du bourrelet apertural (... couches amincies... écailles ou lamelles abondantes... une crête) » [LUGARDON, 1974, p. 220] ;

— « la périspore se caractérise essentiellement par l'absence de différenciation nette au niveau de l'aperture... » (LUGARDON, 1975, p. 157).

Little has been written about the possible function of the perispore. DEVI (1980) suggests that it acts as one more protective coat around the spore contents and that highly sculptured perispores may serve to retain moisture and to adhere to the substrate « to enhance healthy germination » (*op. cit.* p. 170). These last two functions may of course be performed by a sculptured exospore covered with a thin, tightly adhering perispore as well as by a sculptured perispore. However, in *Pyrrosia* this situation is encountered only in *P. africana* and *P. schimperiana*.

The exospore and perispore are composed of different materials (LUGARDON, 1971) and seem to behave differently under stress : the exospore reacts flexibly whereas the perispore breaks more easily. The solid, thick, elastic exospore suggests a mainly protective function, whereas the often layered, sculptured, rigid and probably lighter perispore suggests not so much a protective function as some function connected with dispersal, moisture retention (A. F. TRYON, pers. comm.), or adherence to the substrate.

KRAMER (1977) postulates a correlation between sporoderm sculpture and dispersal ecology. He suggests that most epiphytic taxa have more or less smooth spores that will not easily cohere, assuring individual dispersal to probably widely apart substrates ; he suggests that terrestrial groups have spores with a more elaborately sculptured sporoderm that will cohere more easily and spread not very far from the rather stable environment where the sporophyte grows. KRAMER proposes the term synaptospory for this phenomenon, suggesting that cohesion of spores during dispersal will enhance cross-fertilization. His hypothesis does not seem to hold for the spores of *Pyrrosia*, a mainly epiphytic genus with sometimes very elaborately sculptured perispores. Of course, the hypothesis is based on the assumption that the degree of cohesion between spores or between spores and substrate is correlated with sporoderm sculpture. While mounting spores for SEM they were never seen cohering in groups, not even the abundantly sculptured *P. rupestris*-type spores. The only times we found any spores hanging together (*P. samarensis*, plate VII-2 ; *P. rasamalae*, plate VIII-2 ; *P. niphoboloides*, plate XI-2) the perispores fitted so exactly into each other that they must have been formed in this position, much like the perispores of some species of *Bolbitis* (HENNIPMAN, 1977),

and must have stayed together after sporogenesis. Apparently there is little chance in *Pyrrosia* that spores from different tetrads get and stay together during dispersal. This subject is elaborated upon in a publication by the first author (1985, in press).

At germination the spore wall must be a formidable barrier to information about the outside world coming to the spore contents, and to the gametophyte coming out of the spore (plate II-6). LUGARDON suggested (pers. comm.) that the small channels found in the exospore are the means of communication between the inside and the outside of the spore. Information about moisture and mineral content of the substrate may pass through these channels and trigger off germination. As they are most often found around the laesura, they may even play a role in opening it up at germination. Once the circumstances are suitable for germination and the laesura opens, the exospore will pose no more barrier to the gametophyte, but before the gametophyte can grow out of the spore, it must get rid of the rigid, often thick perispore.

In *Pyrrosia* there are many features that may serve this purpose :
— the thin scales found in *P. subfurfuracea*- and in *P. christii*-type spores may enable the perispore to shift with respect to the exospore and come off more easily (plate III-3) ;
— the hatch as found in *P. christii*-type spores (plate V and VI) may be a way of allowing the gametophyte to come out of the spore by enabling part of the perispore to detach from the rest of the spore wall : the apparent lack of the perispore layer around the laesura as encountered in some *P. christii*-type spores may well be the first stage of germination ;
— *P. nummulariifolia*-type spores have by far the toughest perispores, but they open rather easily along the solid cristae, much like a zip-fastener (plate VII-5, 8). These cracks along the cristae often lie over the laesura (plate VII-4).

P. princeps-type spores (plate I) do not need any special features to get rid of the perispore because it is so very thin. In *P. subfurfuracea*-type spores (plate II, III and IV) the perispore is very fragile and comes off easily, or may be very thin and easily penetrated by the gametophyte (plate II-6). Spores of the *P. rupestris*-type (plate IX, X, XI) do not seem to have any special feature to allow the gametophyte to get out of the spore, and are probably fragile enough to break easily on germination.

SPORE TYPES AND TAXONOMY.

As already mentioned in the introduction, the genus *Pyrrosia* in the present sense contains some species formerly placed in *Saxiglossum* CHING, a monotypic genus, and *Drymoglossum* PRESL.

P. angustissima used to be known as *Saxiglossum angustissimum*. The spores of this species belong to the *P. christii*-type and this is used as an argument for inclusion of this species in *Pyrrosia*.

P. fallax, *P. heterophylla*, *P. niphoboloides*, *P. novo-guineae*, and *P. piloselloides* used to form a separate genus, *Drymoglossum* PRESL. The spores of *P. novo-guineae* fit very well in the *P. nummulariifolia*-type, taking up a more or less intermediate position between *P. angustata* and *P. samarensis* on the one hand and the remaining species with this spore type on the other. The spores of *P. fallax*, *P. heterophylla*, *P. niphoboloides*, and *P. piloselloides* are of the *P. rupestris*-type, although those of *P. piloselloides* and part of *P. heterophylla* are different from all the rest of this type in bearing echinulae instead of verrucae. Generally the spores of the former *Drymoglossum* species fit very well in the variation as shown by the spores in the genus *Pyrrosia*.

Perispore ornamentation usually is not characteristic on the species level, although such a wide variation in perispore sculpture is not found in any other genus of Polypodiaceae (HENNIPMAN and SEN, 1986, in prep.). *P. christii*-type, *P. nummulariifolia*-type and *P. rupestris*-type spores have never been found outside the genus *Pyrrosia*. Spores with very thin perispores like those of the *P. princeps*-type or with thin perispores containing spherical bodies are found in many other groups (e.g. *Polypodium* and related genera, LLOYD, 1981 ; *Platycerium*, HENNIPMAN and ROOS, 1982). For instance, most species in the closely related genus *Platycerium* have thin perispores containing spherical bodies, rather like *P. subfurfuracea*-type spores in *Pyrrosia*.

At first types were distinguished for convenience only, independently of results of the taxonomic treatment by HOVENKAMP (1986, in prep.) except for his species circumscriptions, and even then it was often difficult to fit each spore into a certain type.

In this respect, *P. princeps*-type spores, characterized by a very thin perispore that adheres tightly to the exospore surface, pose no problems.

P. subfurfuracea-type spores, characterized by a rather thin perispore containing spherical bodies, form a more heterogeneous group because of the slightly deviating spores of *P. rhodesiana* and *P. stolzii*, with thicker perispores and fingerprints that may even be raised. However, as *P. madagascariensis*, with true *P. subfurfuracea*-type spores, is regarded by HOVENKAMP as a synonym of *P. rhodesiana*, this species and *P. stolzii* were added to the group with *P. subfurfuracea*-type spores and the type description was extended accordingly.

P. christii-type spores are all well characterized by the hatch in the perispore over the laesura. As to other features, the presence of large

solitary verrucae in only half of the species is not very satisfactory. However, this would be no reason to split up this spore type because the occurrence of the verrucae is also rather variable within the species.

P. nummulariifolia-type spores, characterized by cristae and/or verrucae, form a heterogeneous group. Transitions between cristae and verrucae are often found, notably in *P. abbreviata*, of which one specimen had no cristae at all. Another reason for treating these spores as one type is the erratic way in which fingerprint patterns may occur. They are found in almost every spore type (all except the *P. princeps*-type) and seem to originate where the perispore is rather thick, possibly under mechanical pressure (plate XI-6).

P. rupestris-type spores, characterized by a bisculptate perispore that is colliculate and also bears verrucae or echinulae, are treated as one group despite the fact that the difference between the basic colliculate pattern and the larger solitary verrucae is not always very obvious. It is rather difficult to assess the importance of the difference in structure of the peri-spores of this type : in most of the species the perispore consists of several layers, but in at least one species *(P. piloselloides)* it appears to be solid. It might be justified to treat this species as having a separate spore type, also considering that the spores have echinulae instead of verrucae, but for the fact that one part of *P. heterophylla* has echinulae and another verrucae, so that a subdivision of the *P. rupestris*-type would result in one species having two types of spores.

HOVENKAMP (1986, in prep.) distinguishes ten tentative groups in the genus, leaving out eight species of uncertain affinity (table I). These groups are distinguished on the basis of rhizome structure and scales, frond shape, indument, venation, stomata, and spores. Although spores have been considered to some extent in characterizing the groups it seems useful to compare the spore types with HOVENKAMP's groups as these are mainly based on other characters. In most cases the spore types correspond to one or more of the groups, but there are some discrepancies that should be discussed here.

The *P. princeps*-type corresponds to two of HOVENKAMP's groups, the *P. africana*-group and the *P. costata*-group. It is possible to divide the *P. princeps*-type into two subtypes that coincide with these groups : *P. africana* and *P. schimperiana* with more or less colliculate exospores, and *P. costata*, *P. platyphylla*, *P. princeps*, *P. splendens*, and *P. stigmosa* with smooth exospores. As *P. africana*-spores can be almost smooth and spores of species in the *P. costata*-group can be very slightly colliculate it seems wiser not to base a subdivision of the spore type on this character alone.

TABLE I.

Species studied in *Pyrrosia*.

	1	2	3	4	5
P. abbreviata	4	VIII-5, 6, 7, 8	5	67	5
P. africana	1	I-4	1	59	1
P. albicans	4	VIII-1	2	71	6
P. angustata	4	VII-1	1	67	7
P. angustissima	3	V-1	2	81	—
P. assimilis	2	IV-1	1	84	3
P. asterosora	4	VII-6, 7, 8	2	64	6
P. boothii	2	III-4	1	104	4
P. ceylanica	5	X-5, 6 ; XI-1	2	66	9
P. christii	3	VI-1, 2, 3	2	65	5
P. confluens	5	IX-1	3	74	8
P. costata	1	—	1	54	2
P. distichocarpa	4	—	2	67	6
P. drakeana	2	—	1	69	4
P. eleagnifolia	5	IX-4	2	70	8
P. fallax	5	—	1	70	9
P. flocculosa	2	III-5	2	73	4
P. foveolata	5	X-2, 3, 4	4	72	—
P. gardneri	3	VI-4, 5, 6, 7	4	56	—
P. hastata	2	II-6	2	84	4
P. heterophylla	5	XI-5	1	68	10
P. kinabaluensis	4	—	1	77	6
P. laevis	3	V-2, 3, 5	3	62	—
P. lanceolata	5	IX-5, 6, 7, 8 ; X-1	13	66	9
P. linearifolia	2	III-7, 8	2	78	3
P. lingua	3	V-6, 7	3	63	5
P. longifolia	5	—	2	54	9
P. mannii	2	II-5	1	73	—
P. niphoboloides	5	XI-2, 3, 4	2	74	10
P. novo-guineae	4	VIII-4	1	83	7
P. nummulariifolia	4	VII-5	2	71	6
P. pannosa	2	—	2	46	—
P. penangiana	2	—	1	76	—
P. petiolosa	3	V-4	3	67	5
P. piloselloides	5	XI-6, 7, 8	1	74	10
P. platyphylla	1	I-3	1	59	2
P. polydactyla	2	III-3	1	75	4
P. porosa	2	III-6	7	68	3
P. princeps	1	I-1, 2	6	58	2
P. rasamalae	4	VIII-2	1	74	6
P. rhodesiana	2	IV-2, 3, 4	6	85	3
P. rupestris	5	IX-2	1	71	8
P. samarensis	4	VII-2, 3, 4	2	73	7
P. schimperiana	1	I-5, 6, 7, 8	5	64	1
P. serpens	5	IX-3	1	78	8
P. sheareri	2	II-1, 2	2	77	4
P. sphaerosticha	4	VIII-3	3	81	5
P. splendens	1	—	1	56	2
P. stigmosa	1	—	1	57	2
P. stolzii	2	IV-5, 6, 7, 8	4	87	3
P. subfurfuracea	2	II-3, 4, 7	2	74	4
P. transmorrisonensis	2	III-1, 2	1	88	—

Legend : 1 : spore type. — 2 : plate number. — 3 : number of specimens examined. — 4 : spore length in μm. — 5 : group according to HOVENKAMP.

The *P. subfurfuracea*-type corresponds to two of HOVENKAMP's groups, the *P. porosa*-group and the *P. sheareri*-group, and is found in three of HOVENKAMP's species incertae sedis, i.e. *P. mannii, P. pannosa,* and *P. penangiana,* and in *P. transmorrisonensis,* which is a dubious species in HOVENKAMP's treatment of the genus. The *P. sheareri*-group contains mainly species with densely granulate perispores *(P. boothii, P. drakeana, P. hastata, P. polydactyla, P. sheareri, P. subfurfuracea)* and one species with a more sparsely granulate perispore *(P. flocculosa).* It does not include another species with a very densely granulate perispore, *P. transmorrisonensis.* The *P. porosa*-group contains only species with a more sparsely granulate perispore (*P. assimilis, P. linearifolia, P. porosa, P. rhodesiana,* and *P. stolzii*). This kind of perispore is also found in three species incertae sedis, i.e. *P. mannii, P. pannosa,* and *P. penangiana.* Subdivision of the *P. subfurfuracea*-type into two or more subtypes does not seem feasible. Characters other than density of the granules (presence of peglike attachments, fingerprints, ridges, thickness of the perispore) do not support a subdivision based on this density.

The *P. christii*-type only partially corresponds to HOVENKAMP's *P. lingua*-group containing *P. christii, P. lingua,* and *P. petiolosa* with this spore type and *P. abbreviata* and *P. sphaerosticha* with *P. nummulariifolia*-type spores. The *P. christii*-type is also found in *P. angustissima, P. gardneri,* and *P. laevis,* species incertae sedis. Neither *P. christii, P. lingua,* and *P. petiolosa* on the one hand nor *P. angustissima, P. gardneri,* and *P. laevis* on the other have any spore characteristic exclusively in common. The data of the spores obviously do not support HOVENKAMP's *P. lingua*-group and the exclusion of *P. angustissima, P. gardneri,* and *P. laevis* from this (and every other) group.

The *P. nummulariifolia*-type corresponds to part of HOVENKAMP's *P. lingua*-group as mentioned above and to two other groups : the *P. albicans*-group and the *P. angustata*-group. The *P. angustata*-group contains *P. angustata, P. novo-guineae,* and *P. samarensis,* three species without fingerprints and with cristae running parallel to each other *(P. angustata, samarensis),* or anastomosing without much tendency to break up into verrucae *(P. novo-guineae).* The *P. albicans*-group contains six species (*P. albicans, P. asterosora, P. distichocarpa, P. kinabaluensis, P. nummulariifolia,* and *P. rasamalae*) with anastomosing cristae tending to break up into verrucae, and with fingerprints. Considering spore morphology only, *P. abbreviata* and *P. sphaerosticha* (*P. lingua*-group) clearly belong with these last six species. A subdivision of the *P. nummulariifolia*-type would make some sense, but not without including *P. abbreviata* and *P. sphaerosticha* in the *P. albicans*-group.

The *P. rupestris*-type corresponds to three of HOVENKAMP's groups, the *P. confluens-, P. lanceolata-* and *P. piloselloides*-group, and takes along

one of his species incertae sedis, *P. foveolata*. The *P. confluens*-group consists of *P. confluens*, *P. eleagnifolia*, *P. rupestris*, and *P. serpens*, species without any exclusive spore characteristic in common. The same applies to the members of the *P. lanceolata*-group, viz. *P. ceylanica*, *P. fallax*, *P. lanceolata*, and *P. longifolia*, and to the members of the *P. piloselloides*-group, viz. *P. heterophylla*, *P. niphoboloides*, and *P. piloselloides*. The spores of the species incertae sedis *P. foveolata* very well fit the *P. rupestris*-type. Subdivision of this type along the lines mentioned above would not serve any purpose.

SPORES AND PHYLOGENY.

About the significance of fern spores in phylogeny little has been written. WAGNER (1974) gives a list of spore characters with 26 pairs of primitive and derivative character states. Of these character states 17 can be assigned to *Pyrrosia* spores. According to WAGNER's list, spores of *Pyrrosia* are primitive as they are homosporous, with a non-ridged, sometimes unisculptate exospore (« exine ») without equator elaboration, perispore (« perine ») sometimes cristate, colour tan to yellow ; they are intermediate in size and exospore thickness, and derivative in being with less than 256 spores per sporangium, and in being bilateral, variable, with smooth or coarsely sculptured exospore, usually ridged laesura, perispore present, sometimes smooth or tuberculate. Following WAGNER's criteria, *Pyrrosia*-spores seems to have rather derivative character states, but not extremely so if compared with other fern spores.

WAGNER's series of character states is here regarded as an illustration of the spores as a promising field for supplying characters of phylogenetic significance. However, one has to be careful in drawing any conclusions from it, because WAGNER is rather vague about the concept of perispore. The importance of using perispore characters on the family, generic and species level is stressed by HENNIPMAN (1970), LUGARDON (1974), and LLOYD (1981).

A few authors have published about phylogeny in *Pyrrosia*. NAYAR and CHANDRA (1967) studied 13 species of *Pyrrosia* from India and wrote extensively about their phylogeny, including spore characters in their study. They state *P. subfurfuracea*-type spores *(P. mannii, P. subfurfuracea)* to be the most primitive and postulate five more or less separate lines of evolution to account for the variation found in the spores and other characters of the remaining 11 species. The names NAYAR and CHANDRA use cannot easily be matched with HOVENKAMP's treatment of the genus.

This may cause some confusion e.g. in *P. stigmosa* of which their description of the spores does not agree with the present observations. Concerning affinities between genera, they state that *Pyrrosia* is more closely related to *Platycerium* and *Drymoglossum* than to any other genus.

LIEW (1976 b) also mentions the close relationship between *Pyrrosia*, *Platycerium*, and *Drymoglossum*. He studies six species of *Pyrrosia* from Taiwan and proposes an evolutionary sequence for the spores of the six species concerned, stating that *P. lingua* with its « large and simple verrucae » is the most primitive, that there is a tendency towards « verrucae diminution and an increase in the density of distribution » *(P. linearifolia →* *P. porosa → P. sheareri)* « with the ultimate formation of smaller verrucae densely and compactly distributed on the sporoderm surfaces » *(P. polydactyla)* ; secondary enlargement of the verrucae should result in a sporoderm like that of *P. lanceolata*.

Recently, RAVENSBERG and HENNIPMAN (1986, in prep.) studied SEM micrographs of those *Pyrrosia* species formerly placed in the genera *Drymoglossum* and *Saxiglossum* and of some species in *Pyrrosia s.s.* They distinguish two spore types in *Drymoglossum*, one corresponding to the *P. rupestris*-type *(P. fallax, P. heterophylla, P. niphoboloides, P. piloselloides)* and the other corresponding to the *P. nummulariifolia*-type *(P. novo-guineae)*. In this publication they present a phylogenetic system for the six species formerly placed in *Drymoglossum* or *Saxiglossum*, also using spore characters. They regard the bisculptate *P. rupestris*-type spores as an apomorphic character state within the genus *Pyrrosia s.l.*

We think the *P. princeps*-type and *P. subfurfuracea*-type spores to represent the plesiomorphic condition as they are found in groups outside *Pyrrosia* (e.g. *Platycerium*, HENNIPMAN and ROOS, 1982 ; *Microsorium*, HENNIPMAN and SEN, 1986, in prep.) and as their perispores have the simplest structure. Although spores similar to those of the *P. nummulariifolia*-type are also found in the polypodiaceous genus *Goniophlebium* in Asia (HENNIPMAN and SEN, 1986, in prep.), spores of the *P. christii*-type, the *P. nummulariifolia*-type and the *P. rupestris*-type are thought to represent apomorphic conditions within *Pyrrosia*. However, relationships between the species with spores of these types are difficult to assess using sporoderm features only.

In conclusion, the complex perispore as found in some of these spore types shows a surface ornamentation that is unequalled in the ferns. Also the diversity in perispore ornamentation within the genus *Pyrrosia* is unique as compared to other genera in the leptosporangiate ferns.

Summary.

The spores of all 51 currently recognized species in the homosporous fern genus *Pyrrosia* have been studied with the aid of the scanning electron microscope (SEM). In all species a perispore has been found. The wide diversity in sporoderm sculpture as encountered in this genus has been described and five spore types have been recognized, mainly based on perispore characters.

Acknowledgements.

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