

Spore morphology in *Pottia starckeana* (Hedw.) C. Müll. (Pottiaceae, Musci) and its closest species

by

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With 11 plates

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Abstract: Light, scanning, and transmission electron microscopy surveys of spore morphology and ultra-structure are given in order to provide some insight into the problematic taxonomy of the *Pottia starckeana* aggregate, including *P. starckeana* (Hedw.) C. Müll., *P. davalliana* (Sm.) C. Jens., *P. commutata* Limpr., and *P. mutica* Vent.

Shared characteristics are noted, particularly in the fundamental wall structure, and two major spore types are described on the basis of their distinct shape, size, and sculptural pattern. Spores of type A, mainly with wavy outline and lacking marked perinous projections, correlate well with *P. starckeana*. Spores of type B, with regular outline, increased size, and more ornamented perine, characterize both *P. commutata* and *P. davalliana*. Much intergrading of spore morphology is noticeable, suggesting that localized introgressive hybridization may have taken place within the Mediterranean area involving these three species. No distinctive spore feature is considered useful for the taxonomic recognition of *P. mutica*. Furthermore, correlation is hardly ever found between spore type A and peristome structure. Resemblances between some spores of type A and certain spores from *Encalypta* (Encalyptaceae, Musci) seem to provide additional evidence for phylogenetic relationships between Pottiaceae and Encalyptaceae. Possibly adaptive characters of the sporoderm are discussed in relation to ecological and evolutionary considerations.

Introduction

With increasing regularity during the past few years, contributions on taxonomic bryology have been aimed at describing spore morphology so as to resolve possible relationships. Success has been primarily dependent upon the presence of suitable spore features for taxonomic exploitation, although the depth of study has, of

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course, played some part. Some excellent surveys which have been helpful in substantially improving our knowledge of certain groups are those on Encalyptaceae (Vitt & Hamilton 1974, Járαι-Komlódi & Orban 1975, Horton 1982a, 1983, Magill & Horton 1982), *Bruchia* (McClymont 1955, Rushing 1985), *Asterella* (Frey et al. 1991), or even the pleurocarpous *Plagiothecium* (Ireland 1987), with small spores. Attention has also been directed to bryophyte sporogenesis and ultrastructure, with emphasis on those processes that deal with wall development (e.g. McClymont & Larson 1964, Horner et al. 1966, Mueller 1974, Denizot 1976, Sorsa 1976, Olesen & Mogensen 1978, Neidhart 1979, Steinkamp & Doyle 1984, Brown & Lemmon 1980, 1981, 1984, 1985, 1986, 1990, Brown et al. 1982, 1986, Carrión et al. 1990). This is perhaps one of the most promising areas for the phylogenetic research at higher levels. The literature reports detailed information of several selected taxa, but comparative reviews are still scarce, mainly because little persistent work has been done apart from that by Brown and Lemmon's team.

Given their remarkable ornamentations, variability, and often large size, spores of the Pottiaceae have been repeatedly considered in floras (e.g. Dixon 1924, Augier 1966, Nyholm 1975, Scott et al. 1976, Smith 1978, Catcheside 1980, Frahm & Frey 1987, Crum & Anderson 1981), taxonomic reports (e.g. Saito 1975, Stone 1976, 1979, 1980, 1989, Derrick 1978, Matteri 1982, Guerra & Ros 1988, Guerra et al. 1990, 1991), and in a spore atlas (Boros & Járαι-Komlódi 1975). Several more specific surveys, including scanning and/or transmission electron microscopy, are those by Chamberlain (1968), Lewinsky (1974), Saito & Hirohama (1974), Rejment-Grochowska (1978), Castaldo-Cobianchi et al. (1982), Changoiwala & Chatterjee (1988), Herrnstadt & Heyn (1988), many of which have been discussed elsewhere (Carrión et al. 1990).

The present study concentrates on the spore morphology of *Pottia starckeana* (Hedw.) C. Müll. and its closest allies. The "*Pottia starckeana* aggregate" as defined here includes the stegocarpous species displaying a short, obtuse, conical operculum, and lacking a differentiated annulus, and includes all taxa considered by Chamberlain (1978) under *P. starckeana*, together with *P. commutata* Limpr., i.e., the European "Conostegiae" *sensu* Warnstorf (1916). Hence, we have excluded both the cleistocarpous species and those having a rostrate to well-beaked operculum. The study has been conducted in the western Mediterranean area, mainly on Spanish collections. Its main purpose is to provide some basis for the taxonomic treatment of such a traditionally problematic group. It is presented in this paper in the context of morphological, phylogenetic, and ecological discussion. Since it is part of a monographic study in progress on the genus *Pottia* (Reichenb.) Fürnr., little mention will be made here to characters which do not relate to spores.

Materials and methods

Spores were obtained from mature sporophytes of dried herbarium specimens, which are listed below. The samples were divided in three parts for light microscopy (LM), scanning electron microscopy (SEM), and transmission electron microscopy (TEM). For LM the spores were shaken in distilled water, mounted in a glycerol jelly, examined, measured and photographed with a Leitz Laborlux K microscope with an apochromatic $\times 100$ objective and compensating $\times 12.5$ eye-pieces. Because of its effect on a number of

taxonomically critical features, acetolysis was not performed. Spores to be used for SEM were critical point dried in a Balzer Union CPD using 100% acetone and CO₂ as transition fluid. Afterwards, the specimens were sputter coated (ca. 250 Å thickness) with gold and viewed with a Jeol JSM T300 at an accelerating voltage of 15 to 25 Kv. For TEM analysis of sporoderm architecture, the material was fixed in 3% glutaraldehyde for 2 hours, rinsed several times in 0.1 M Na-cacodilate buffer, and post-fixed in 2% OsO₄. After dehydration to 100% ethanol, it was infiltrated in Spurr's mixture and subsequently polymerized. Ultrathin sections were prepared using a diamond knife on a Reichert Jung Ultramicrotome, post-stained with uranyl acetate and lead citrate, and examined in Zeiss EM 10C and Zeiss EM 109 Turbo TEM instruments, operated at 80 Kv.

Selected specimens studied

ESPAÑA. — Albacete: Montealegre del Castillo, XH4595, Ros, 13.4.1991 (Bryoth. MUB 4251). Sierra del Relumbar, Casa de la Cueva, WH2771, Heras y Ros, 9.3.1986 (Bryoth. MUB 2549). Alicante: carretera Elche-Guardamar, YHO428, suelo arenoso, Ros et al., 6.2.1988 (Bryoth. MUB 4255). Laguna del Hondo, XH9129, Guerra y Ros, 6.2.1988 (Bryoth. MUB 2482). Entre Vall d'Ebo e Pego, YH49, Sérgio et al., 10.2.1983 (BCB 11861). Sierra del Maigmo, Ros, Guerra y Moya, 4.1991 (Bryoth. MUB 4247). Almería: Cabo de Gata, Playa de los Genoveses, Ros y García-Zamora, 9.2.1990 (Bryoth. MUB 4249). Cabo de Gata, base del Repetidor, Ros y García-Zamora, 9.2.1990 (Bryoth. MUB 4254). Gerona: carretera de Roses a Cadaqués, 2 km al N de Roses, Cap de Creus, 31TEG1481, Casas et al., 3.1.1984 (BCB 466). Granada: saladar entre Cúllar y Baza, WG3054, Ros y Guerra, 1.2.1990 (Bryoth. MUB 4261). Cúllar, Cortijo de Don Andrés, Guerra y Ros, 4.3.1988 (Bryoth. MUB 4262). Málaga: base de la Sierra del Torcal de Antequera, margas del Keuper, Guerra, 23.12.1988 (Bryoth. MUB 4252). Murcia: Cenajo del Agua Cernida, WH 8629, Ros, 16.3.1985 (Bryoth. MUB 4245). Herreña, XH2404, Ros, 6.2.1983 (Bryoth. MUB 4248). Jumilla, Salinas de la Rosa, YH5555, Ros, 3.3.1985 (Bryoth. MUB 4250). Cartagena, Los Belones, Rambla de la Carrasquilla, XG9465, Ros, 14.2.1987 (Bryoth. MUB 4253). Mazarrón, XG4561, Ros, 19.2.1984 (Bryoth. MUB 4258). Fuente de Meca, XG4361, Ros, 10.3.1984 (Bryoth. MUB 4259). Sierra de Carrascos, XG5190, Alvaro y Alvarez, 1.1989 (Bryoth. MUB 4260). Bullas, Ros, 6.2.1983 (Bryoth. MUB 2920). Mazarrón, Fuente de Meca, Ros, 10.3.1984 (Bryoth. MUB 3251). Bullas, El Carrascalejo, XH1313, Aboal y Ros, 8.2.1980 (Bryoth. MUB 655). Valencia: Carretera de Serra a Porta Coeli, 30SYJ1893, Pucho, 4.1988 (Bryoth. MUB 3570). FRANCIA. — Bouche du Rhône: 7.8 km après Raphèle vers Mas-Thibert, Hébrard, 15.2.1983 (Bryoth. MUB 1155). PORTUGAL. — Beira Litoral: Pombal, Eireiras, Sérgio et al., 13.12.1984 (Bryoth. MUB 4263).

Results

The spores examined range from 16 to 40 μm in their maximum lateral axis. Under LM they appear to be atreme, notwithstanding their customary heteropolarity. Lateral outline is elliptical or subcircular to strongly irregular, often biconvex or nearly plano-convex. Amb circular or subcircular to convexly angular, sometimes unevenly semi-lobate.

The structure of the sporoderm (Plates IX-XI) is that of most mosses, the main elements of which are known from work by McClymont & Larson (1964). The innermost layer or intine is homogeneous as seen in the TEM, thicker in the proximal (1-4 μm) than distal face (0.1-0.8 μm). It has a fibrillar appearance and medium to high electron-density. Frequently, the intine shows inner stratification at the proximal pole. The exine is non-stratified, and is thinner in the proximal (0-0.4 μm) than distal pole (0.2-0.6 μm), although sometimes its thickness becomes difficult to measure accurately as it displays an undulate or wrinkled outline, particularly at the boundary with the outer layer. The perine appears basally as a thin (mostly below 0.5 μm in thickness), more or less continuous, very electron-dense layer. It is uneven on its

outer surface, which has irregular depositions or flecks forming perforate to rugulate patterns as seen in the SEM. In addition, this layer may develop large, irregular processes (up to 4 μm) forming a more ornate pattern. Thus, the perine provides the topmost ornamentation even though the exine can make some contribution to the basis of the sculptured elements. Besides wall projections, both light and electron microscopy reveal small- to medium-sized granules, hardly integrated into the spore structure and randomly scattered over the basal surface or at the peaks of the projections. This sporophytic, granular material, like the ornamented perine, is highly electron dense in thin section.

The polarity of the spores under study is mainly an internal, structural phenomenon reflected in unequal thickening of the intine and exine on the proximal and distal faces. Although, as we shall see later, certain spores can display surface differences between the two faces, these were rarely observed in the size or density of the processes, which is of note in that the proximal face of many moss is seemingly less ornate than elsewhere (Brown & Lemmon 1990). Both the basal perine and the exine may be extremely thin or nearly absent in the centre of the proximal face. Thus, the proximal intinic thickening appears to be a marker of an apertural area.

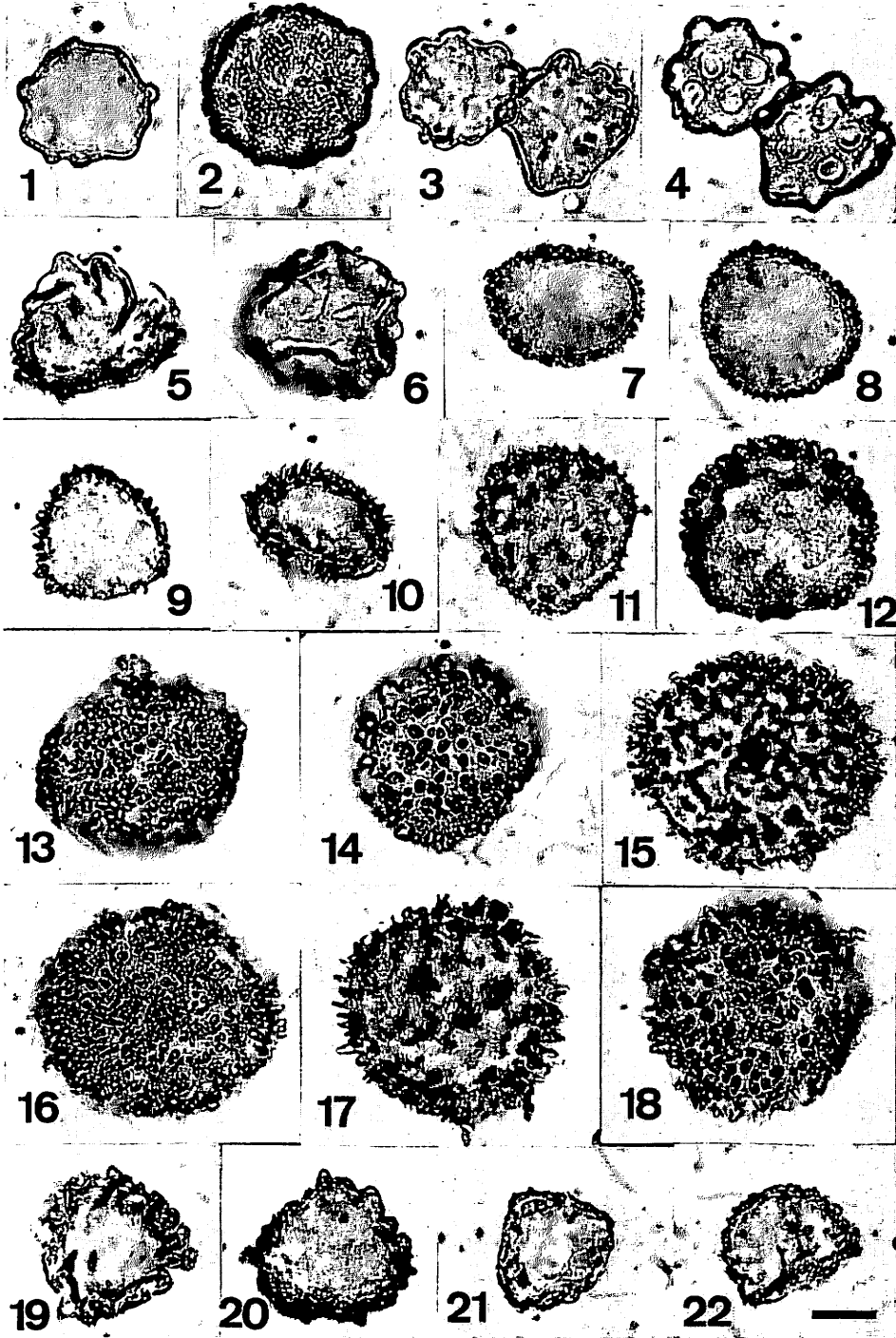
The spores of *P. starckeana* agg. share a number of characteristics, particularly in their fundamental wall structure. However, they are variable in shape, size, sporoderm thickness, and sculpturing. The following categories can be recognized:

Type A

Plates I-IV, IX

Spores ranging in size from 16 to 30 μm , but mostly between 18 and 25 μm . Distal sporoderm mostly thinner than 0.8 μm , excluding perine. Typically wavy in outline, sometimes spheroidal to slightly bilateral but, in either case, showing some areas with protuberances, which are either isodiametric, 2-5 μm across, or ridge-like and vermiform. Frequently, isodiametric protuberances appear on the distal surface, whereas radial plicae are directed towards the proximal pole. Structurally, there is no special contribution of the perine to the more marked protrusions; the enlargement involves the sporoderm as a whole. Even so, minor protuberances may exhibit localized thickening in some layer, or be the result of occasional constriction involving mainly perine and exine. The irregular perine surface produces a primarily dotted LM pattern. Under SEM it appears as nearly psilate, granulate, perforate or microreticulate. Oc-

Plate I (Figs. 1-22). Light micrographs of *Pottia starckeana* agg. spores showing variability in shape, size, and ornamentation. Figs. 1-6, spores of type A. Figs. 7-11, spores type B associated to well-developed peristome. Figs. 12-18, spores of type B associated with rudimentary or absent peristome. Figs. 19-22, intermediate forms. Figs. 1, 3, 5, and 19-22 show more or less wavy outlines, with further small processes in Figs. 19-22. Figs. 2, 4, and 6 show surface views with dotted pattern and isodiametric (Fig. 4) or vermiform (Fig. 6) protuberances. Figs. 7-10 are optical sections displaying regular outline and relatively short, mainly spine-like processes. Figs. 12-18 show larger spores with more prominent ornamentation. Figs. 12, 15, and 17, optical sections. Figs. 13, 14, 16, and 18, surface views. Scale 10 μm .



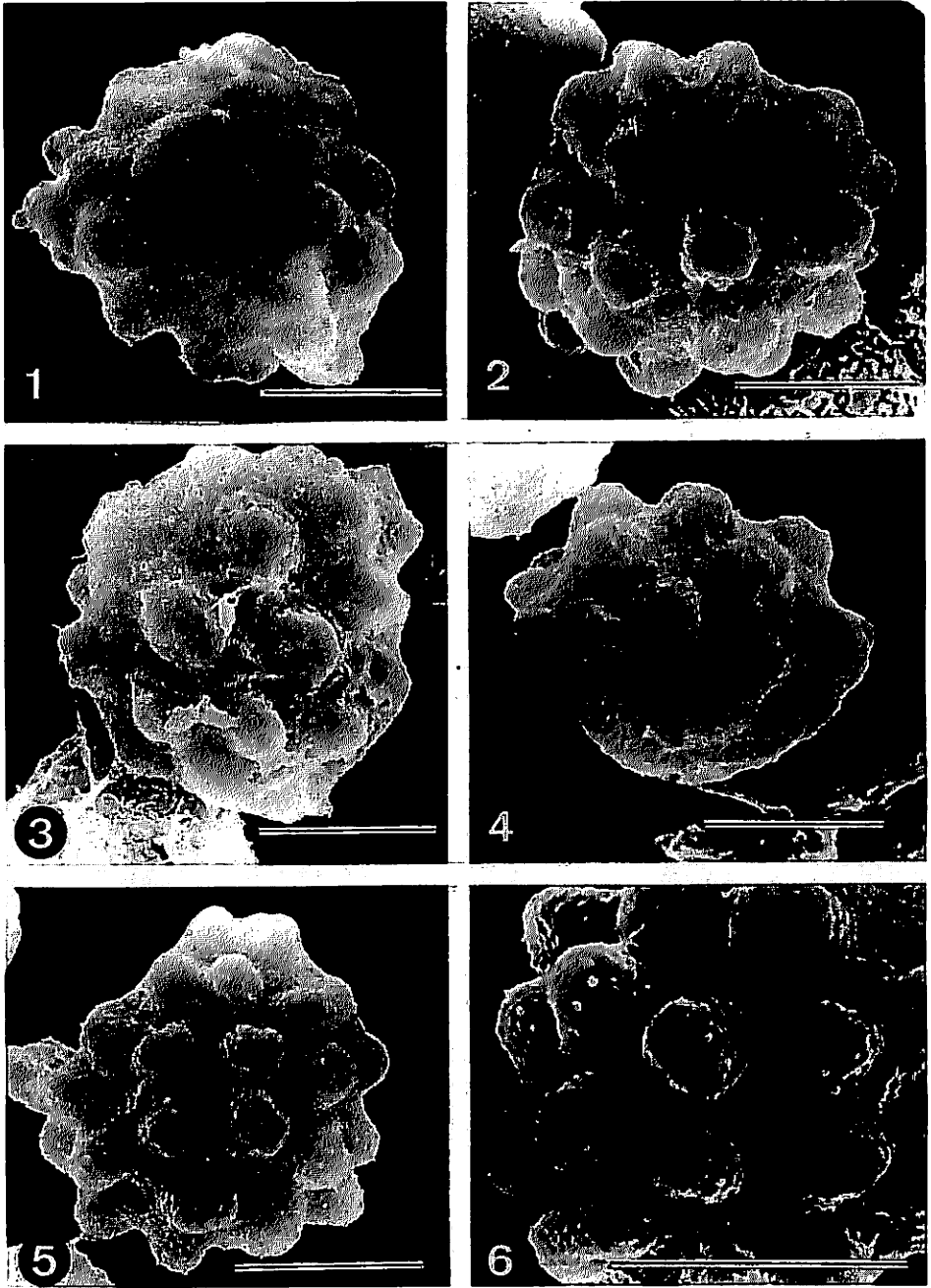


Plate II (Figs. 1-6). Scanning electron micrographs of *Pottia starckeana* agg. spores of type A showing isodiametric protuberances as well as nearly psilate (Fig. 1) to clearly perforate or microreticulate (Fig. 6) surface pathways. In lateral view (Fig. 4), note protuberances over distal face (above). Scale 10 μm .

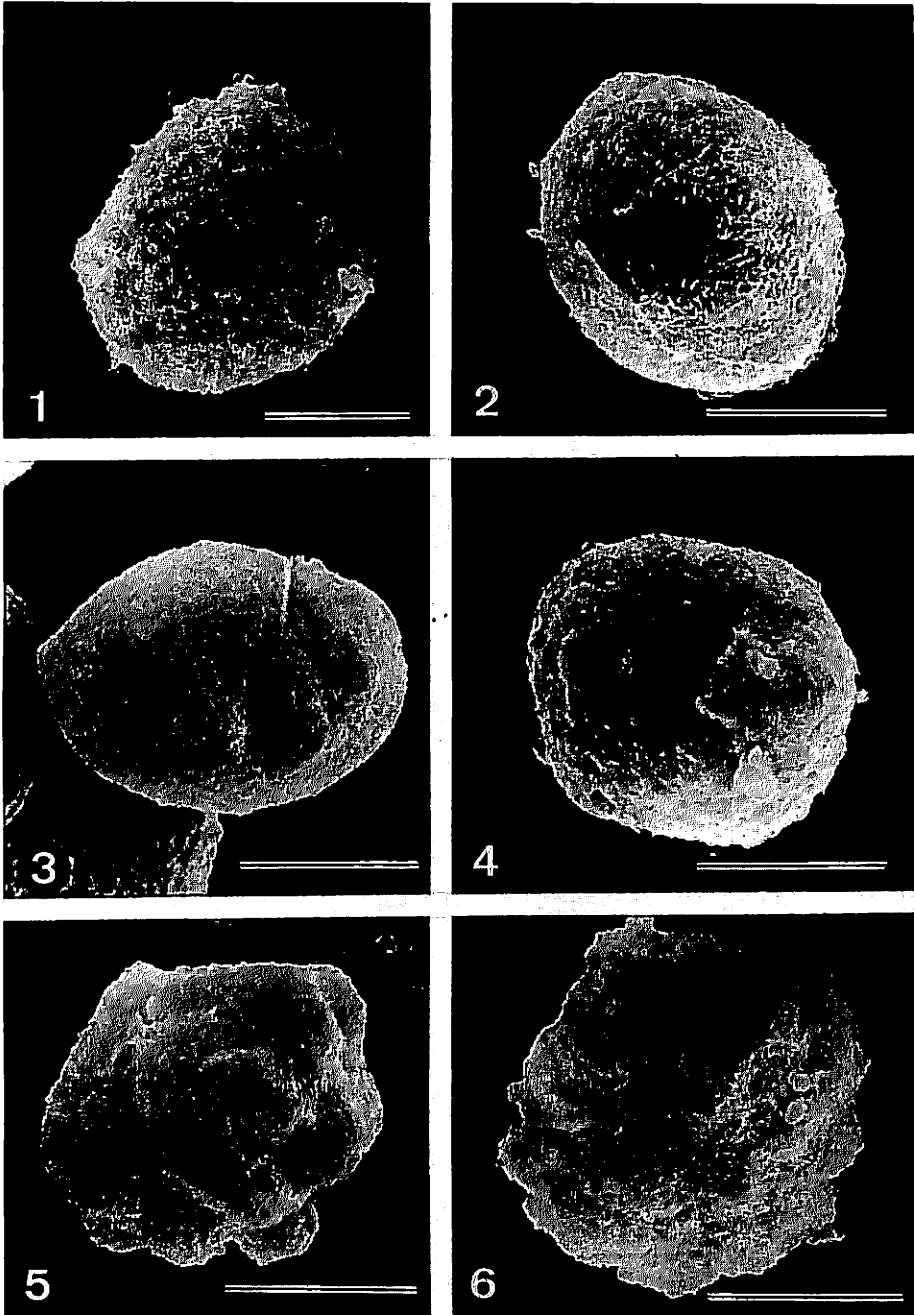


Plate III (Figs. 1-6). Scanning electron micrographs of *Pottia starckeana* agg. spores of type A. Shape is nearly regular in Figs. 1 and 2. See little marked (Figs. 3, 4) and ridge-like to vermiform (Figs. 5, 6) protuberances. Scale 10 μm .

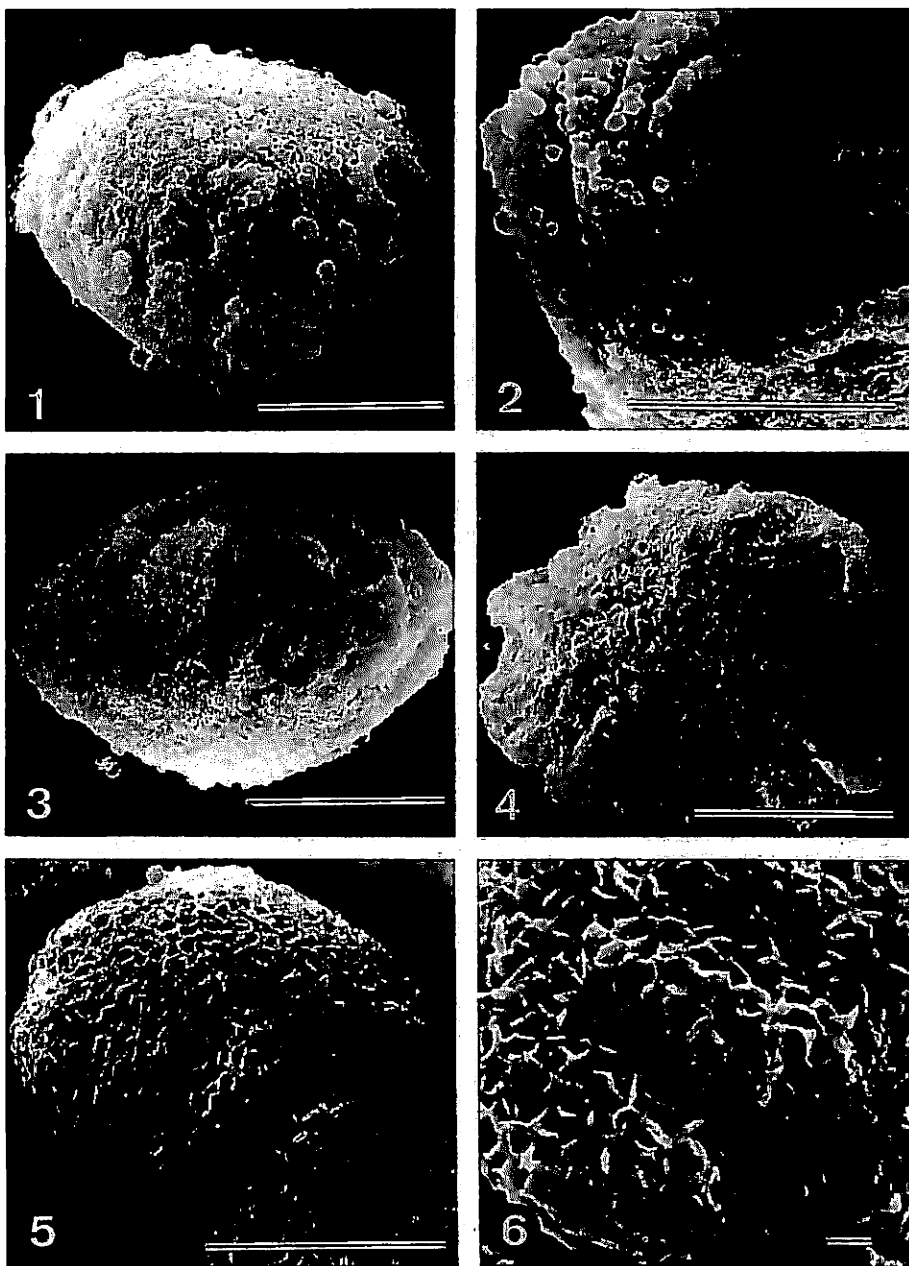


Plate IV (Figs. 1-6). Scanning electron micrographs of *Pottia starckeana* agg. spores of type A showing perforate (Figs. 1, 2) and rugulate (Figs. 3-6) sculpture. Globular perinous material is seen in Figs. 1, 2, and 4. Fig. 6 is an enlarged view of rod-like depositions producing rugulate pattern. Radial plicae converge towards the proximal face in Figs. 2 and 4. Scale 10 μm , except Fig. 6, 1 μm .

casional, further interlaced, rod-like depositions (ca. 0.5-1.1 μm long) produce a rugulate SEM pathway above the underlying perforate pattern. This spore type is associated with a well-developed, rudimentary or absent peristome.

Type B

Plates I, V-VII, X

Spores ranging in size from 19 to 40 μm , but mostly between 25 and 35 μm ; spheroidal to bilateral in shape, often biconvex or plano-convex. Distal sporoderm frequently thicker than 1 μm excluding perine. The basal sculpture is like that of type A, but these spores have extra ornamentation. The surface is conspicuously spinose, with variously-shaped processes (ca. up to 4 μm long), which are occasionally branched or confluent, curved echinae being the most frequent. Structurally, these processes are mainly perinic although exine may form the basis if the bordering sporoderm is constricted. Precise terminology is difficult, as the sculpturing is rather variable. This spore type is associated with a well-developed, rudimentary or absent peristome, although it is noticeable that peristomes with well-developed teeth correlate with smaller (predominantly below 25 μm), less spinose spores.

Intermediate forms

Plates I, VIII, XI

In many cases it becomes impossible to fit spores into either of the former types. Spores of type A generally lacks prominent processes, and sporoderm protrusions are absent from type B, but much intergradation is seen, where wavy or irregular optical sections are associated with more or less scattered processes. In these cases, the wall architecture shows intermediate thickening and increased complexity, sporoderm expansions and constrictions of various sizes being associated with very irregularly thickened perine. These spore types are associated with a well-developed, rudimentary or absent peristome, no correlation being discernible between the peristome development and the spore morphology.

It is of note that although all the samples analyzed display a certain amount of variation, it is limited within individuals as well as sporophytes, and allows the recognition of a major morph as type A, type B, or of intermediate status.

Discussion

The taxonomic dilemma

Ever since it was realized that a group might be segregated from the stegocarpous *Pottia* by following its distinctly shaped operculum, there has been much controversy in arranging the species involved from a taxonomic point of view. The major reason for such a lack of agreement has been striking phenotypic plasticity, even extending to the most critical characters. These have been primarily related to spore morphology and peristome involution, with minor consideration being given to vegetative structures (Husnot 1884-1890, Warnstorf 1916, Dismier 1924, Mönkemeyer

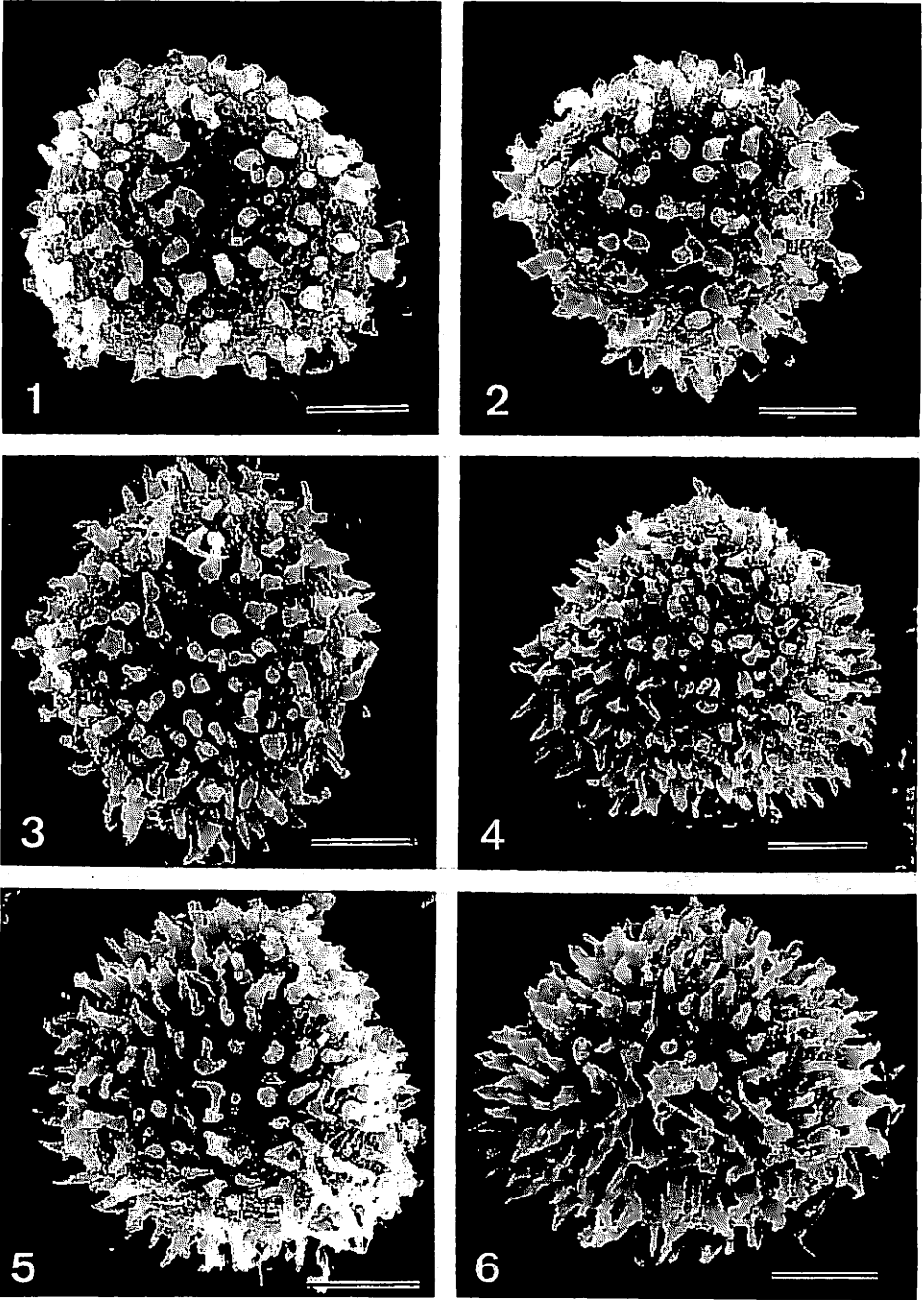
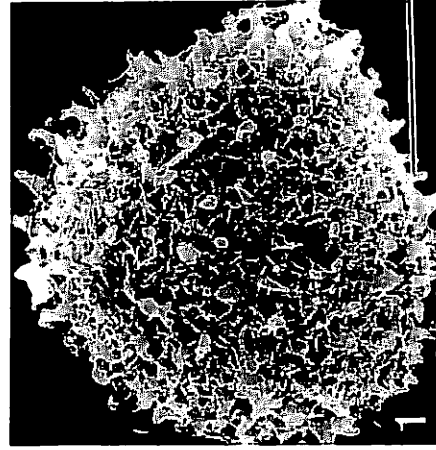
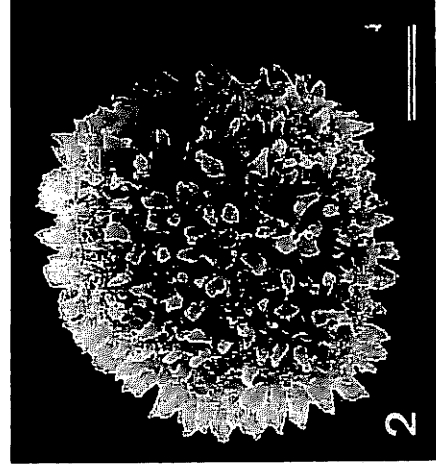


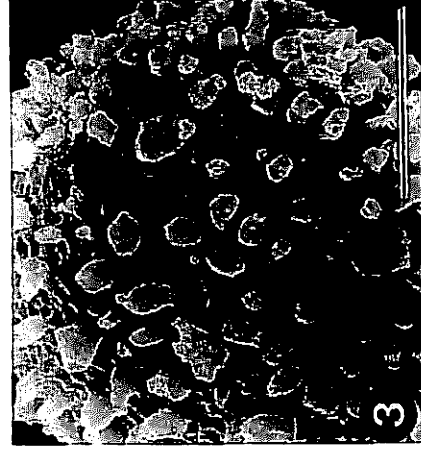
Plate V (Figs. 1-6). Scanning electron micrographs of *Pottia starckeana* agg. spores of type B extracted from capsules with rudimentary to absent peristome teeth. Spores are heavily ornamented in addition to perforate basal surface. Scale 10 μm .



1



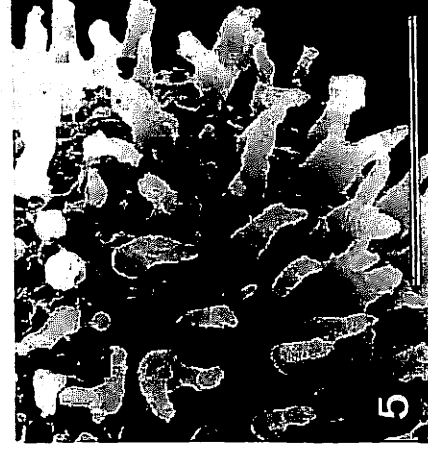
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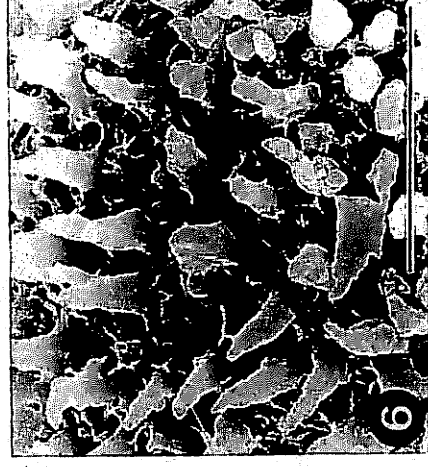
3



4



5



6

Plate VI (Figs. 1-6). Scanning electron micrographs of *Pottia starckeana* agg. spores of type B associated with rudimentary to absent peristomes. As in type A, rod-like depositions can be abundant between the processes (Fig. 1). Basal perforations and variably shaped projections are shown in the remaining figures. Scale 10 μm .

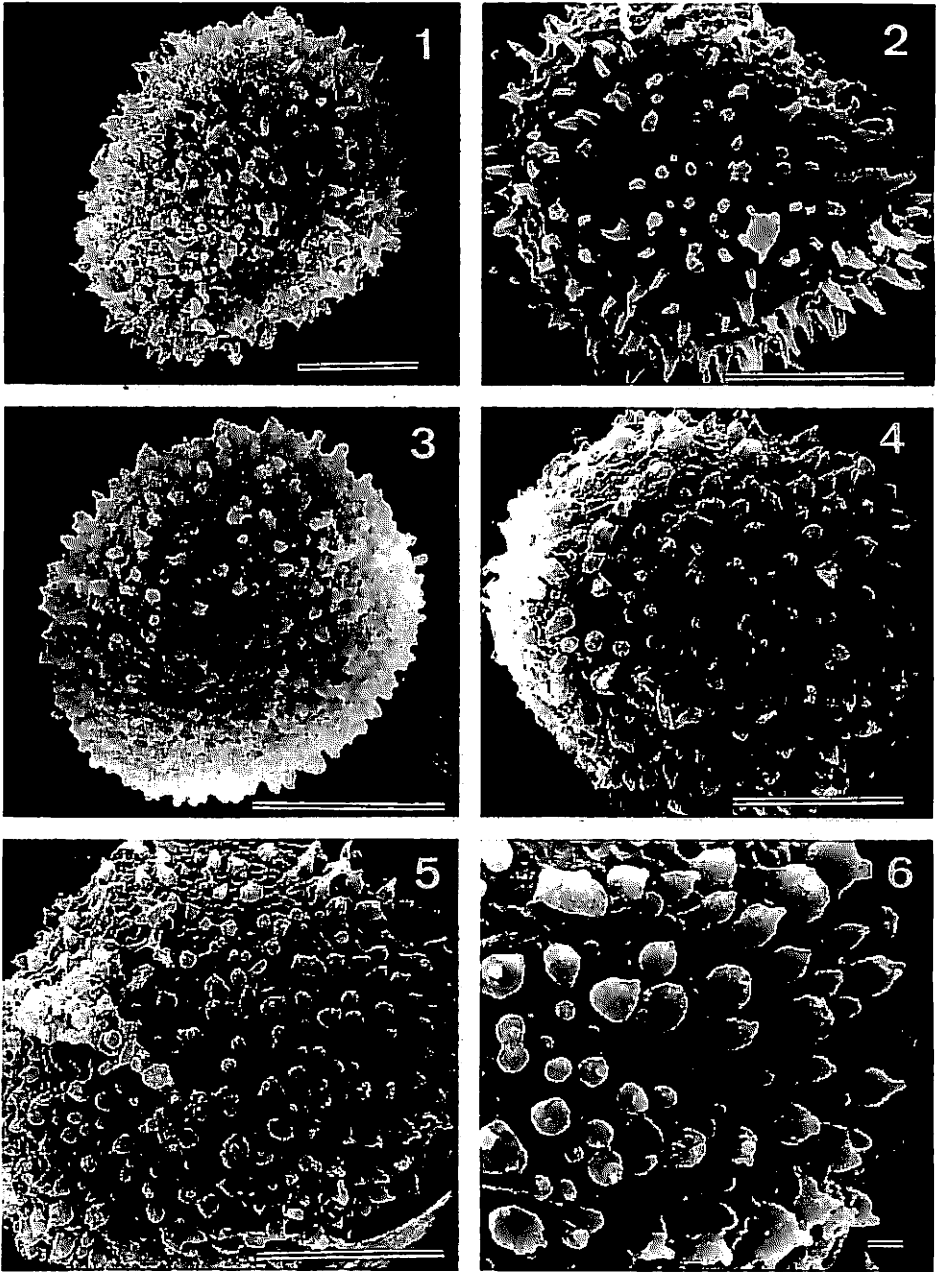


Plate VII (Figs. 1-6). Scanning electron micrographs of *Pottia starckeana* aggr. spores of type B extracted from capsules with well-developed peristome teeth. Processes are mostly spine-like, except in Fig. 3, where they are blunt. Note that they are mainly shorter than in Plates V and VI, except for Fig. 2. Scale 10 μm , except Fig. 6, 1 μm .

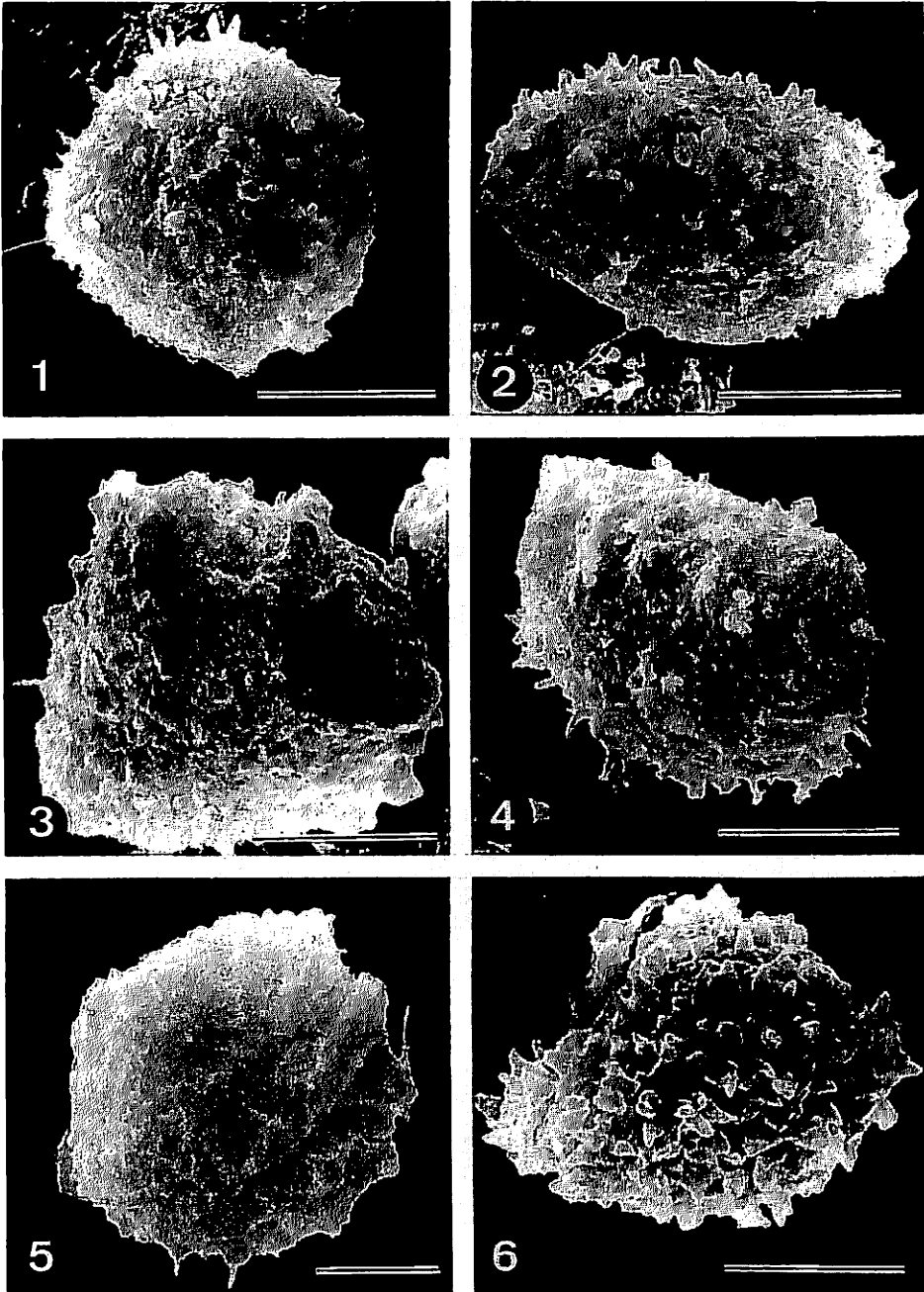


Plate VIII (Figs. 1-6). Scanning electron micrographs of *Pottia starckeana* aggl. spores with ornamentation intermediate between types A and B. Additionally to irregular protuberances, perinic processes can be observed that are scanty (Figs. 3, 5), frequent (Figs. 1, 2, 4) or relatively abundant (Fig. 6). Scale 10 μm .

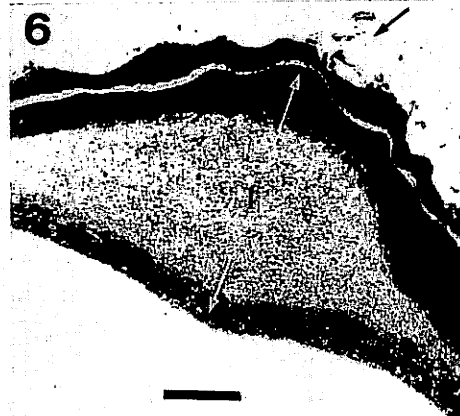
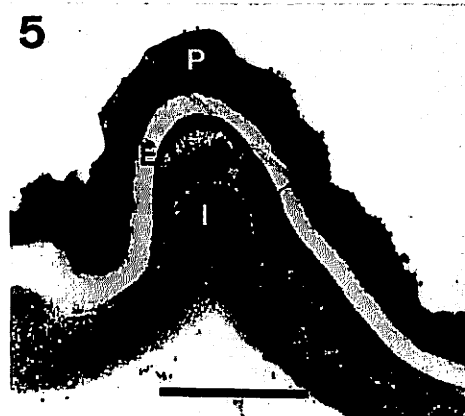
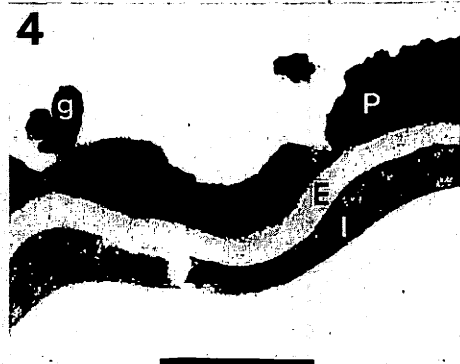
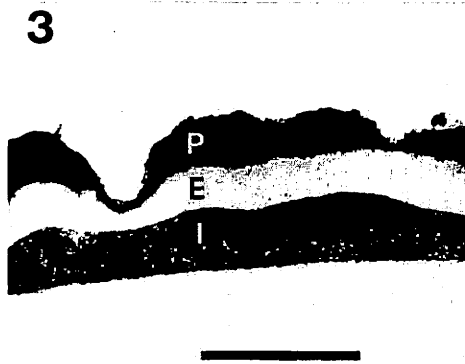
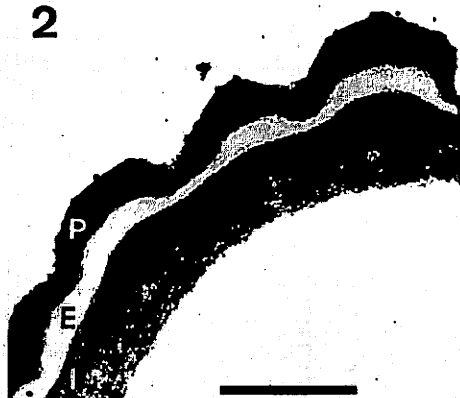
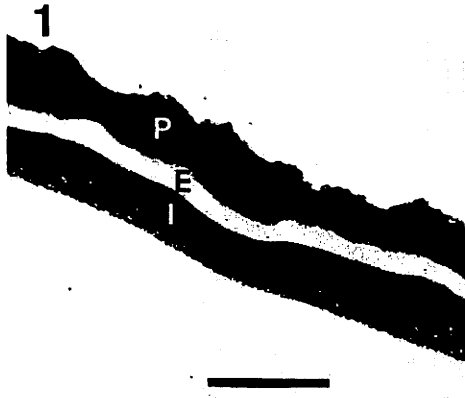
1927, Casares-Gil 1932, Demaret & Castagne 1959, Augier 1966, Nyholm 1975, Chamberlain 1978, Pierrot 1982). The fact is that, unfortunately, we are little better informed on the taxonomy of the group today than we were when Limpricht published his "Die Laubmoose Deutschlands, Österreichs und der Schweiz" in 1890.

P. starckeana (Hedw.) C. Müll. was traditionally associated with spores resembling type A, and with peristomes with well-developed teeth. In *P. commutata* spores of type B occur and are thus correlated with a peristome which may allegedly be well-developed or nearly rudimentary. Some difference of opinion is also to be noted for spore size and surface ornamentation. *P. davalliana* (Sm.) C. Jens. (*P. minutula* Fürnr.) appear from the source literature to be a better defined taxon. The tendency appears to have been to describe it as having (a) the spore surface covered by long, mainly spiny processes, and (b) the capsules without a peristome or with only a rudimentary one. Consequently, spore morphology also fits into the type B described herein. Complications arise in characterizing *P. mutica* Vent. Its peristome has been almost invariably described as rudimentary, but spore descriptions are rather confusing: spores covered by broad spines (Husnot 1884-1890); with small pustules and papillae (Warnstorff 1916); with small, rounded or conic papillae (Dismier 1924); with small protuberances (Casares-Gil 1932); with small papillae over verrucae (Chamberlain 1968); or densely papillose (Nyholm 1975). The concept is thus quite vague. Perhaps this is why the species has so often been reported to be closely related to various others of the remaining taxa in the group.

Not surprisingly, such diversity in the morphological relationships has given rise to considerable nomenclatural confusion. Currently, one of the most frequently used taxonomic treatments is that by Chamberlain (1978) -chiefly based upon unpublished Ph. D. studies at Oxford University 1968. In it, *P. starckeana* is considered in a broad sense comprising three subspecies: ssp. *minutula* (peristome absent, spores with echinae and regular outline), ssp. *starckeana* (peristome absent to well developed, spores with smooth to warty outline and lacking projections), and ssp. *conica* (peristome absent or rudimentary, spores with regular shape and variable processes). He distinguished the spores of *P. commutata* from those of *P. starckeana* ssp. *minutula* by their statistically smaller size (about 28-32 μm and 31-40 μm respectively) and less strong ornamentation. *P. starckeana* ssp. *conica* would appear to serve as the ragbag for those collections which lack, not only well-developed peristomes but also well-defined spores.

Judging from the material studied here the most versatile key to date in identifying the species of the group in question is that by Chamberlain (1978). Classification

Plate IX (Figs. 1-6). Transmission electron microscopy of *Pottia starckeana* agg. spores of type A showing wall ultrastructure. The thickness relationships are rather variable between intine (I), exine (E), and perine (P). Relative thickness can remain constant (Fig. 1). Perine and exine can coincidentally narrow in regular (Fig. 2) or uneven fashion (Fig. 3). The major sporoderm undulations (which cause marked protuberances in surface LM and SEM views) involve the three layers (Figs. 4, 5). Intine can be particularly thickened under some protrusions (Fig. 5) but constant thickening associated with inner stratification is seen only in the proximal pole (Fig. 6). Sporophytic material is incorporated as globules (Fig. 4, g) or lamellar and rod-like, minor depositions (Fig. 6, black arrow). Scale 1 μm .

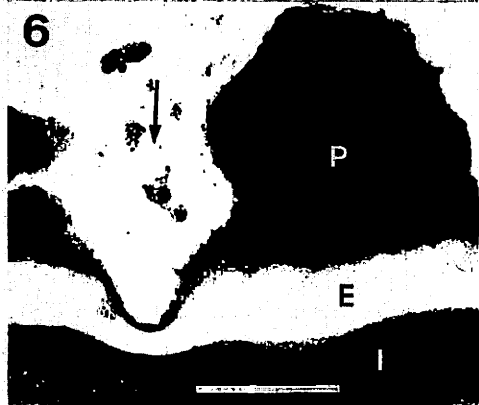
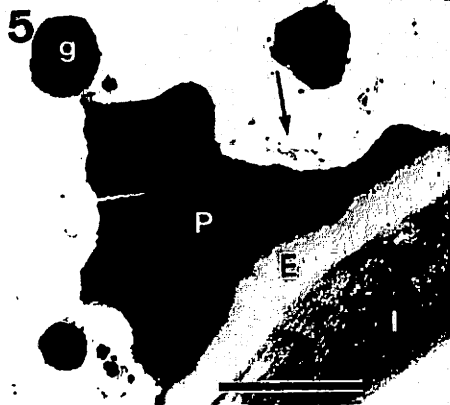
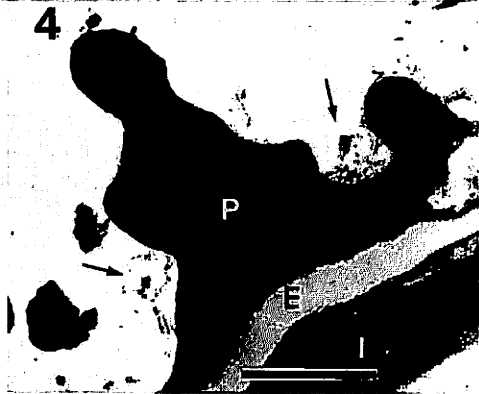
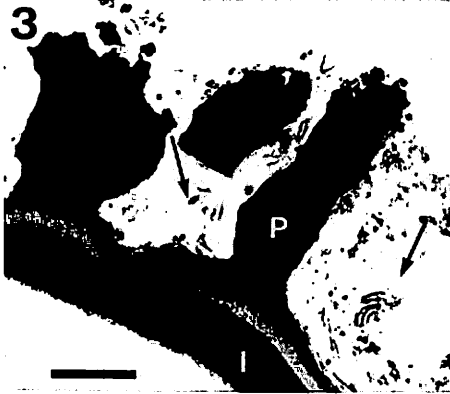
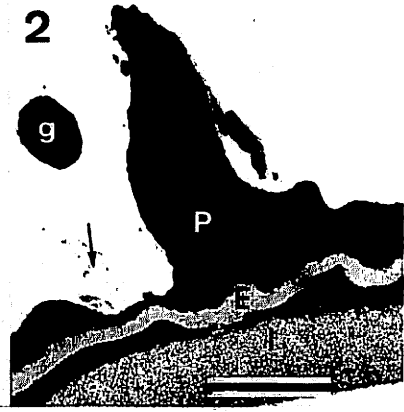
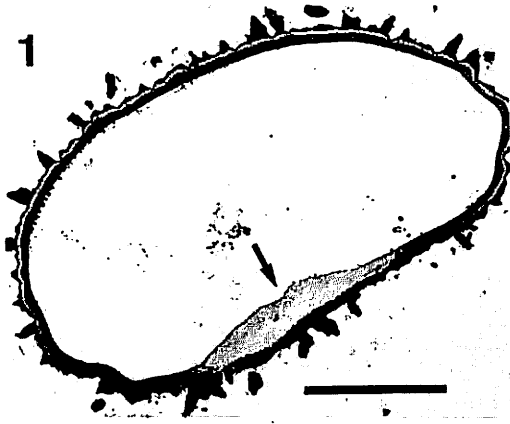


of diversity in peristome types is, without doubt, a major development. Nevertheless, the key does not, in our opinion, allow for unequivocal discrimination within the group. We were unable to place a number of specimens satisfactorily in that taxonomic scheme, particularly those in which the spores had a wavy outline as well as marked projections, either with a well or poorly developed peristome. It is to be remembered that any spore-peristome correlation is possible within the group. Whether this is partially the reflection of greater morphological variation among the Mediterranean populations than elsewhere in Eurasia is a matter of conjecture since too few biogeographical documentations are available. Nevertheless, a number of examples from other areas support the view that this is a problem which requires further research (e.g. Chamberlain 1968, Nyholm 1975).

This taxonomic difficulty becomes greater if one insists that conventional rank must be given to every individual collected. Such a view tends to ignore such factors as polyploidy, hybridity or environmental conditions, which may have affected structural continuity in the characters studied.

There are a few examples of intraspecific polyploidy and aneuploidy in the Pottiaceae (Newton 1968, Smith & Newton 1968). Given their predominantly autoicous condition, the species under consideration could be primarily inbreeders. However it seems likely that the existence of abundant intermediate spores may be the result of a certain degree of outbreeding and interpopulational gene flow. Hybrid complexes are relatively frequent, not only in ferns (Wagner 1954, Barrington et al. 1987) but also in mosses (Wyatt et al. 1987). Introgressive hybridization therefore represents a plausible hypothesis to explain variation within the *P. starckeana* agg., especially when considering the frequency with which the species grow in close proximity, sometimes even in the same cushion. Chamberlain (1968) reported British plants displaying a number of morphological features transitional between *P. starckeana* and *P. davalliana*, postulating that localized hybridization might have led to the formation of a hybrid swarm. Conversely, he found *P. commutata* to be stable and clearly defined by blunt processes over the spore surface. We agree that intergradation must be habitual between *P. starckeana* and *P. davalliana* because sporophytes with rudimentary or absent peristome may contain spores of intermediate type. Nevertheless, we have reservations about the Chamberlain's (1968) views with respect to *P. commutata*. Firstly, because well-developed peristomes, those typical of the species, are sometimes associated with intermediate spores, we suggest that gene flow must also have occurred between *P. commutata* and *P. starckeana*. Secondly, we think that spore descriptions by that author do not reflect the whole sculptural vari-

Plate X (Figs. 1-6). Transmission electron micrographs of *Pottia starckeana* agg. spores of type B showing wall ultrastructure. Variation in the relative thickness of the intine (I), exine (E), and perine (P) is also seen, but the main differences with respect to ultrathin sections in Plate IX deals with the presence of variably shaped perinic projections. Fig. 1 is a whole spore section showing the characteristic intine thickening in the proximal face (arrow). Exine may form the basis of the processes when narrower at their extremity (Fig. 6). Globular (g) and smaller, irregular depositions (arrow) are seen in Figs. 2-6, the last being responsible for rugula, granula, and small perforations in surface view. Scale 1 μm , except Fig. 1, 10 μm .



ation seen in our collections. Certainly, processes are often smaller than those from the supposed *P. davalliana*, but they are mostly rather spiny, not typically blunt. It seems probable, therefore, that Chamberlain was unable to observe the intrinsic variation of *P. commutata*, since his study was mainly restricted to British populations of a species whose distribution is reputedly centered in the Mediterranean area.

The hypothesis of genetic introgression between the three species should not be considered to exclude other possibilities. Other researchers viewing the available data might form different opinions. Thus, for instance, a cladistic approach would attempt to determine the limits of morphological variation for each species before considering any taxonomically intermediate condition. In this connection, it should be noted that we have deliberately excluded *P. mutica* from this discussion of gene exchange. This is not to deny existence of *P. mutica*, but rather the usefulness of spore morphology for its recognition. A taxonomic treatment based only on spore morphology would be unrealistic, and will therefore not be attempted. In summary, however, we suggest (1) that spores of type A may define *P. starckeana* s. str., independently from the development of the peristome teeth; (2) that spores of type B may characterize both *P. commutata* and *P. davalliana*, the sporoderm processes being generally higher in the latter; (3) that intermediate spore types might indicate localized introgressive hybridization involving the three taxa; and (4) that spore morphology is unable to characterize *P. mutica* accurately.

Phylogenetic, evolutionary and ecological remarks

Results from this paper raise further points of interest. In particular, spores included in type A (Plate II) bear a close resemblance to certain spores from Encalyptaceae that are characterized by warty outlines, isodiametric protuberances on the distal face as well as ridge-like protuberances converging towards the proximal pole (Horton 1983). This might provide additional evidence for the close relationship between the Pottiaceae and Encalyptaceae, since such a spore type has, to the best of our knowledge, been hardly found elsewhere in bryophytes. Even a similar perforate pattern (Plate II, Fig. 6), which is extremely rare in mosses, can be seen in *Encalypta* (Horton 1983), although this is a less suitable feature for phylogenetic studies. Other spore similarities are concerned with wall layering, the highest sculptural elements being nearly or totally perinous in both families (McClymont & Larson 1964). However, there are closer relationships implied by vegetative characters, and these relate especially to *Tortula*, *Desmatodon* and *Encalypta* (Horton 1983). Moreover, the perennial habit of the Encalyptaceae could be considered to be more primitive.

Considering that the Pottiaceae and Encalyptaceae probably shared a common origin, the evolutionary mechanisms which may have operated in giving rise to the spore similarities is a complicated problem. Since the spore characters involved are better defined in the Encalyptaceae, derivation of the Pottiaceae would imply some kind of asynchronous development in an evolutionary context. Morphological convergence is also conceivable, but means of examining the possibility are not yet to hand. Moss spores exhibit a comparatively small spectrum of sculptural patterns, repeated in phylogenetically remote taxa. This was precisely the problem pointed out by Saito & Hi-

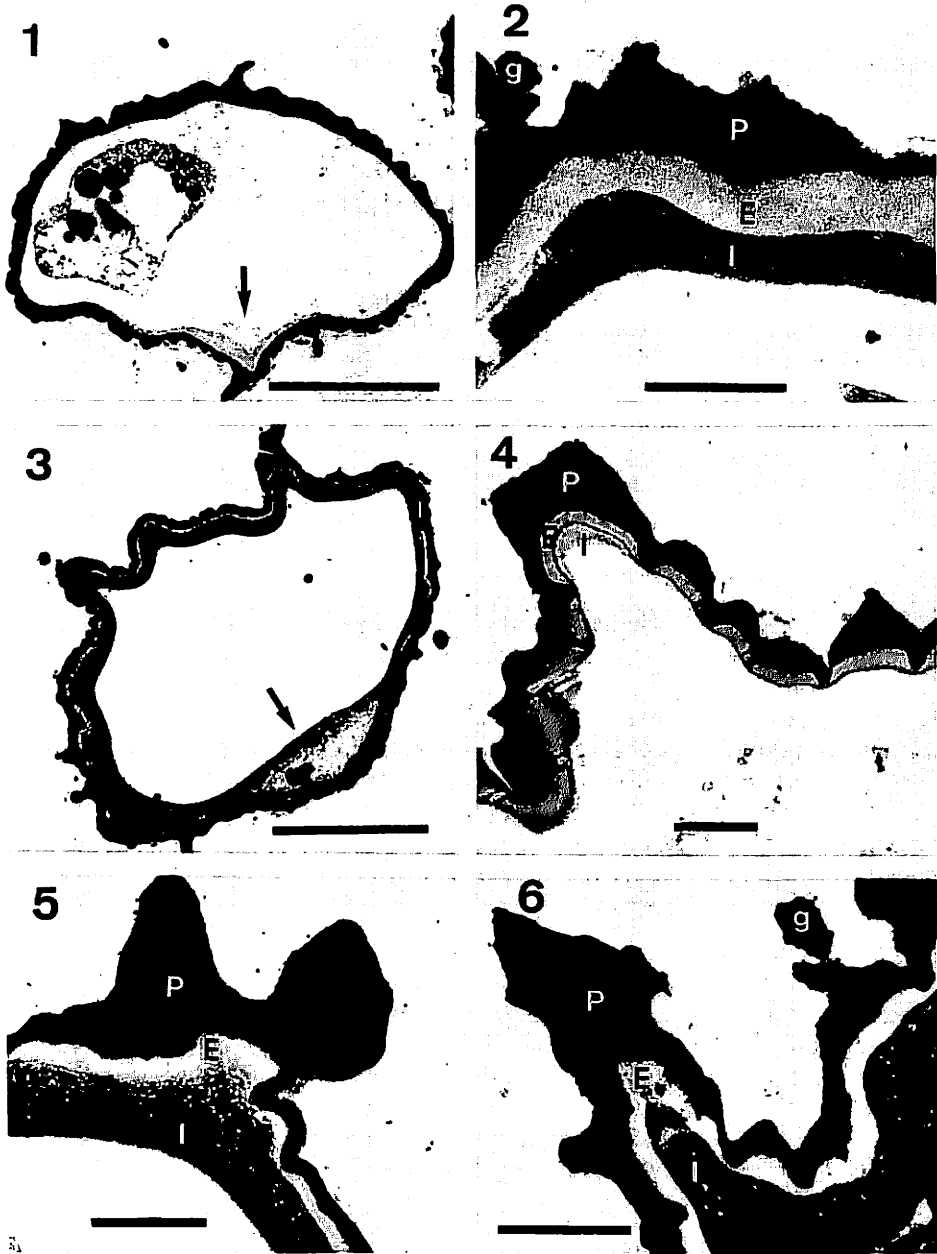


Plate XI (Figs. 1-6). Transmission electron micrographs of *Pottia starckeana* agg. intermediate spores showing wall ultrastructure. Figs 1 and 3 are whole spore sections showing lateral outlines with intine thickening (arrows), slight (Fig. 1) or marked protuberances (Fig. 3), as well as scattered processes. Intine (I) and exine (E) display nearly constant thickness (Fig. 2) or much irregularity in their course over the spore (Figs. 4, 6). Perine (P) forms large projections in Figs. 5 and 6, besides being associated in Fig. 6 with extraordinarily irregular sporoderm outline. Scale $1 \mu\text{m}$, except Figs. 1 and 3, $10 \mu\text{m}$.

rohama (1974) with regard to the use of spores in the Pottiaceae for taxonomic purposes. In fact, spores similar to type B of *Pottia* can be found in *Weissia*, *Pterygoneurum*, *Acaulon*, and *Phascum* (Boros & Járαι-Komlódi 1975, Stone 1989, Carrión et al. 1990).

In an evolutionary perspective, an increase in wall thickness appears to have been a line of specialization in Musci (Heckman 1970, Mogensen 1983), often associated with increasing size involving the perine (Horton 1982b). In ferns, it has been suggested that elaborated perispores may be considered to be derived (Tryon 1990). Thus, spores of type B, with increased sporoderm thickness and size as well as better-developed perine, might represent the apomorphic condition whereas the poorly ornamented spore of type A would represent the plesiomorphic status. Such a supposition deserves to be examined further by extrapolation to the phylogenetic relationships between *Pottia* and the closest, wholly cleistocarpous genus *Phascum*, wherein marked sporoderm variability also occurs. Paradoxically, within the Pottiaceae, the character state of wavy spores is restricted to *P. starckeana* agg., whereas spores that are heavily ornamented and with a regular outline are of widespread occurrence and hence could be taken to represent the ancestral form. There are similar complications in attempting to relate that evolutionary tendency to the supposed line deriving from *Tortula-Desmatodon* (Frey & Kürschner 1988).

Another interesting hypothesis was put forward by Kramer (1977), who suggested synaptospory as a mechanism capable of increasing the possibility of intergametophytic fertilization and, therefore, of survival as well. With regard to ferns, Kramer (1977) suggested that opportunity for synaptospory is higher if spore surfaces are strongly sculptured. In any case, synaptospory would be ineffective in promoting gene-flow if self-fertilization had occurred provided that all the spores produced by a sporophyte derived from self-fertilization would be genetically identical. Whatever the genecological connotations in the Pottiaceae, it must be remembered that a tendency for spores to cohere is yet to be demonstrated in mosses, even for the most intricately ornamented perines.

It is generally believed that the spore characteristics of many mosses growing on open soils have some correlation with their life strategies. Hence, following During (1979), the relatively large size of the spores of *Pottia* would tend to reduce their dispersal but, as a counterweight, their thick sporoderm could increase resistance to drought. This represents only a part of the definition of "annual or short-lived shuttle strategies" (During 1979), of which a predominance of sexual reproduction is a major feature. Longton (1988) raised very stimulating points concerning these strategies in bryophytes from arid environments.

Underlying the above considerations is the assumption that spore morphology has an adaptive significance, that is to say, that there is some interrelationship between different ecological or physiological conditions and sporoderm definition. Leaving out the possible existence of non-adaptive features, the fact is that, theoretically, this supposition is not unreasonable in many bryophytes whose spores directly affect survival of the plant. In a general context, bryophytes have been relegated to subordinate ecological states, frequently experiencing little competition, but in intrinsically

stressful conditions. Accordingly, selection would have operated by favouring the stress-tolerant phenotypes rather than the highly competitive ones. This might be particularly important for the dry terrestrial communities where the short-lived species of *P. starckeana* agg. grow, and whose environments must be chiefly controlled by abiotically-induced stress. Certainly, much more experimental and descriptive effort together with geologic documentation are needed to resolve these topics positively. We remain very much in ignorance of the origin and evolution of bryophytes.

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