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A new point of view on the taxonomy of *Pottia starckeana* agg. (*Musci, Pottiaceae*)

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Abstract: A new taxonomic treatment is proposed for the *Pottia starckeana* species complex. The peristome development is not considered to be a useful feature to separate the taxa. On the basis of spore morphology only two species are accepted: *P. starckeana*, with spores wavy in outline, and *P. davalliana*, with variously-shaped and developed processes on the spores. *Pottia starckeana* var. *brachyoda* is reduced to synonymy with *P. starckeana; P. conica* and *P. commutata* are treated as synonyms of *P. davalliana*. The species *P. mutica, P. affinis, P. salina, P. microphylla, P. texana,* and *P. arizonica* (included var. *mucronulata*) are considered taxa of doubtful affinity, as they have spore features intermediate between the two spore types established for the group. The identity of *P. appertii* and *P. recurvifolia* has not been elucidated because the type material has been destroyed.

In Europe there are four species traditionally grouped with *P. starckeana* (Hedw.) C. Müll. and placed by Warnstorf (1916) in the "Conostegiae". These are *P. commutata* Limpr., *P. conica* (Schwaegr.) Fürnr. ex Par., *P. davalliana* (Sm.) C. Jens. and *P. mutica* Vent. Additionally there are a number of infraspecific taxa.

This paper arose as the result of problems found when many samples from southeast Spain and North Africa, belonging to this group, could not be identified. In many cases the spore morphology did not fit that described for known taxa in the literature. Spore morphology was different and did not correlate with any peristome type of described taxa. We also frequently found small and dense turfs of mosses made up of the main members of this group, together with other not identifiable specimens, hitherto, there has been much controversy in arranging the species involved from a taxonomic point of view. Further, inexactitudes found in the consulted literature, made the identification of the species more difficult. It was common to find words such as pustule, wart, papille, spine, etc. whose shape and development are imprecise. In many cases the same word has been used to describe different sporodermic processes and consequently it is impossible to know exactly which type of ornamentation is meant. Sometimes a less scientific sentence such as "surface similar to a sack of potatoes" or "surface as a raspberry or a mulberry" is much clearer and more accurate.

The major difficulty in order to place taxonomically a number of species was in those cases 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. 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.

History

The only world monograph dealing with the genus *Pottia* is that of Warnstorf (1916). His "*Pottia* Studien" is a vast and useful work in which the author examined and described all the known taxa in the genus *Pottia*. He tried to categorize the variation observed taxonomically and consequently he described some new species in the "*Conostegiae*" and accepted a large number of varieties and forms besides those previously described (Warnstorf 1915).

Chamberlain's (1968) Ph.D. dissertation was on the taxonomy of *Pottia starckeana* agg. As a result of this research he published a short note proposing new nomenclatural combinations (Chamberlain 1969) but most of his conclusions appeared in Smith (1978). Other papers dealing with the taxonomic problems of this group have been published (Corbiére & Pitard 1909, Dismier 1924, Morquer 1924, Williams 1961, Demaret 1964, Eckel 1987). Zander (1993) in his recent and revolutionary work on the taxonomy of the *Pottiaceae*, discusses this subject, but he does not accept the genus *Pottia* (Ehrh. ex Reichenb.) Ehrh. ex Fürnr. and includes the *Pottia starckeana* agg. in the genus *Microbryum* Schimp. Carrion & al. (1993) made a study of spore morphology and revealed that only two spore types could be recognized. They suggested that possibly the great variability in the spore morphology of the number of intermediate forms could be due to a high degree of introgressive hybridization.

The taxonomic problems in this species complex have also been mentioned by other authors in more extensive works such as Casares-Gil (1932: 264), Nyholm (1975: 95) and Pierrot (1982). The great confusion in the taxonomy of this group is due on the one hand to the homogeneity of gametophyte characters and on the other hand to the great variability of sporophytic characters, which have been considered traditionally more important for taxonomy, especially peristome development and spore morphology. On the contrary, Zander (1993) considered that gametophytic characters are the most important in the taxonomy of the *Pottiaceae*. He emphasized the colour responses of leaf laminal walls to 2% KOH solution.

The size and papillosity of the upper cells of the leaves have been used to differentiate *P. davalliana* from *P. mutica* (Augier 1966), leaf morphology to separate *P. starckeana* from *P. commutata* (Mönkemeyer 1927) and the nerve ending in or below the apex to differentiate *P. mutica* from other species (Warnstorf 1916, Brotherus 1924, Casares-Gil 1932, Augier 1966) and *P. conica* from *P. davallia-*

Table 1. Possible combinations of peristome type and spore morphology in the main taxa of the group according to the opinion of the more important bryological works

Peristome	Spores wavy in outline	Spores papillose	Spores echinate
completely developed	*P. starckeana*	*P. commutata*	*P. commutata*
incompletely developed	*P. s.* var. *brachyodus* *P. minutula* var. *brachyoda* *P. mutica* *P. conica*	*P. commutata* *P. mutica* *P. conica*	*P. commutata* *P. davalliana*
absent	*P. s.* var. *brachyodus* *P. s.* var. *leiostoma* *P. minutula* var. *brachyoda* *P. conica*	*P. mutica* *P. conica*	*P. davalliana* *P. s.* subsp. *minutula* *P. mutica* *P. conica*

na (Casares-Gil 1932, Demaret & Castagne 1959) but we have not found any of these characters to be useful.

The same can be said for sporophyte features such as the shape of the capsule when empty, which has been used to separate *P. davalliana* from the rest of the taxa (Demaret & Castagne 1959, Chamberlain 1978), papillosity of the calyptra and the shape of the lid to differentiate *P. starckeana* from *P. commutata* (Mönkemeyer 1927).

The various combinations of peristome type and spore morphology used by different authors in defining the various taxa are shown in Table 1. The delimitation of the taxa is clearly very confused, varying from author to author. Corbiére & Pitard (1909) and Dismier (1924) demonstrated such variation but did not comment on how the species overlap.

Pottia starckeana s. str. is one of the more clearly defined taxa. The type material has a completely developed peristome and spores wavy in outline. This combination of features has been nearly and unambiguously attributed to *P. starckeana* subsp. *starckeana* var. *starckeana*. When the peristome is incomplete the name *P. starckeana* var. *brachyodus* is usually applied (Casares-Gil 1932, Wareham 1939). Husnot (1884–1890) proposed another combination, *P. minutula* var. *brachyoda*, but he considered that in this case the peristome can also be absent. Chamberlain (1978) agreed with Husnot but related the taxon to *P. starckeana* (*P. starckeana* subsp. *starckeana* var. *brachyodus*). Dismier (1924) used the combination proposed by Corbiére & Pitard (1909), *P. starckeana* var. *leiostoma*, when there is no peristome. In general it seems to be accepted that the spores with a wavy outline are characteristic of *P. starckeana*, regardless of the development of the peristome, which has been used only to differentiate the varieties.

In the holotype of *Pottia mutica* (determined by Venturi) we found that the peristome is reduced to a basal membrane and the spores, although wavy in outline, also have many round or spinous apical processes. Many and disputed opinions have been given about *P. mutica*. The spore morphology has been defined as being any of those possible within the group. There is unanimity about the lack of a completely developed peristome, but an enormous confusion and misunderstanding concerning spore morphology has existed since the beginning of the present century (Husnot 1884–1890, Limpricht 1890, Corbiére & Pitard 1909, Warnstorf 1916, Mönkemeyer 1927, Casares-Gil 1932, Augier 1966, Nyholm 1975, Pierrot 1982, Frahm & Frey 1987, Herrnstadt & al. 1991).

Pottia conica presents a similar combination of taxonomic characters. It has been combined in different taxonomic statuses with *P. starckeana* (Chamberlain 1969), *P. minutula* (Bruch & al. 1836–1851) and *P. davalliana* (Podpera 1954). The view of the last author is shared by Düll (1992). It has also been synonymized with *P. minutula* (Limpricht 1890), with *P. minutula* var. *brachyoda* (Husnot 1884–1890) and with *P. davalliana* (Corley & al. 1981). Examination of the holotype shows that there is a peristome and that the spores haves irregularly papillose processes. Nevertheless, there also exist great contradictions between different bryologists about observed spore morphology and peristome development (Husnot 1884–1890, Warnstorf 1916, Demaret & Castagne 1959, Demaret 1964, Chamberlain 1978).

Next to *Pottia starckeana, P. davalliana* is the best defined taxon of the complex. It is almost unanimously considered as lacking a peristome and to have echinate spores. We agree to a major extent with the European checklist of Corley & al. (1981) in the placement of varieties with papillose spores under *P. davalliana*. Casares-Gil (1932) stated that it can have a reduced peristome with only a basal membrane. Another feature often considered very important in distinguishing this species is the truncate capsule when empty. Although this can be seen in the type of Smith (in LINN), it cannot be considered a diagnostic feature because it is not constant.

Pottia commutata was abundantly and precisely described by Limpricht (1890) in the protologue. From this it is clear that the species shows great variability in peristome and spores (Limpricht 1890, Brotherus 1924, Morquer 1924, Mönkemeyer 1927, Augier 1966, Nyholm 1975, Chamberlain 1978, Pierrot 1982). Spore size has sometimes been used to distinguish this species from *P. davalliana*, the latter being said to have bigger spores. Thus, Pierrot (1982) stated that the spores of *P. davalliana* are up to 40 µm and of *P. commutata* 20–24 (–35) µm. According to Chamberlain (1978) the spores of *P. commutata* can be bigger, (23.5–)28–32(–37) µm. If the different spore sizes attributed to *P. davalliana* are analysed, 20–27 µm (Husnot 1884–1890), 24–40 µm (Demaret & Castagne 1959), 25–36 µm (Warnstorf 1916), 28–38 µm (Limpricht 1890), it can be concluded that a new study is needed.

Material and methods

Numerous herbarium specimens and fresh material collected by the authors have been studied. Also, type material of all the European taxa belonging to the *P. starckeana* agg. and the American species *P. texana* and *P. arizonica* has been studied. Samples from the Iberian Peninsula located in Spanish herbaria (BCB, BCC, GDAC, MA, MUB, VAB, VIT,

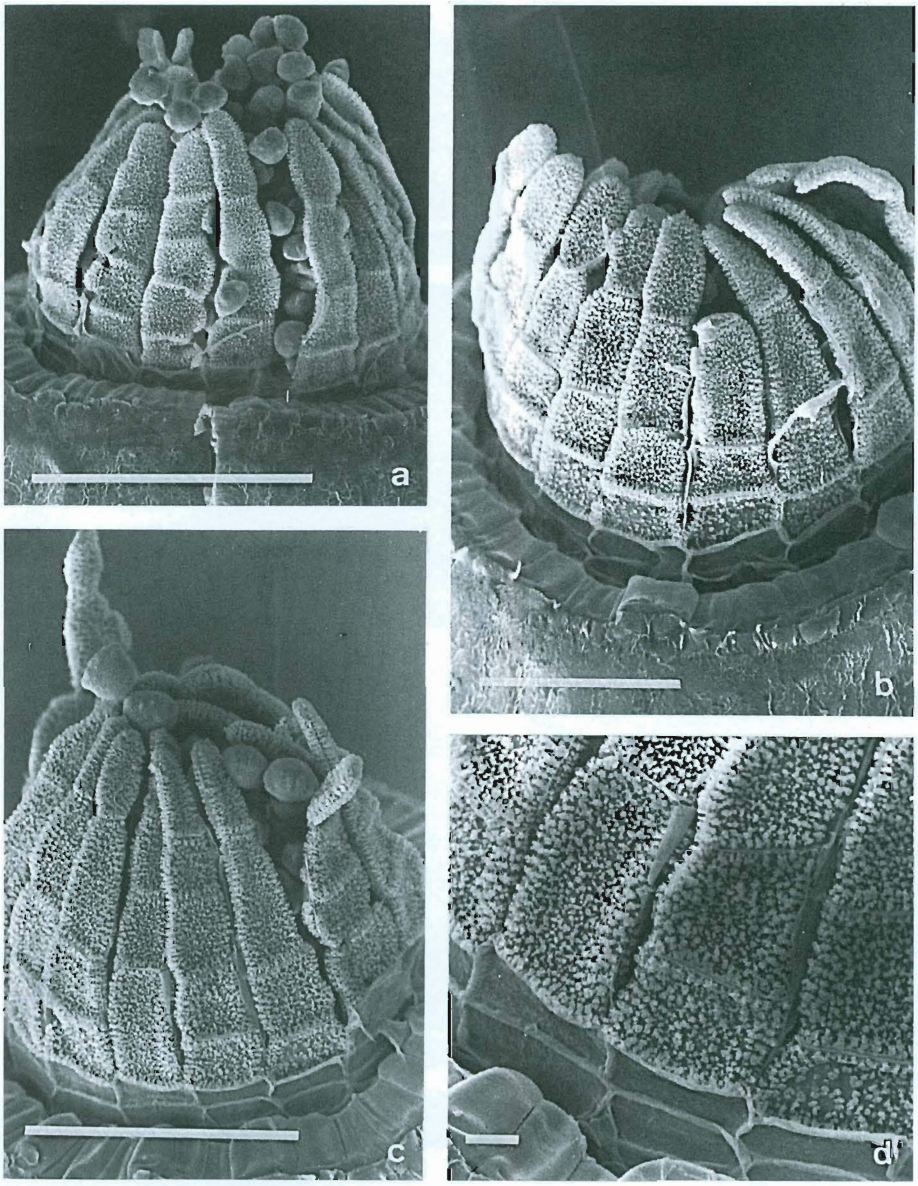

Fig. 1. *Pottia starckeana* agg. Well developed peristomes. Bars: *a–c* 100 µm, *d* 10 µm

Herb. R. Oliva) and from American and European herbaria (B, BM, BP, G, LINN, NY) have been studied.

From each sample, the characters traditionally used to distinguish the taxa, peristome development and spore morphology, were analysed. Additionally, the characters under the previous heading, sometimes regarded as being of taxonomic importance, were also studied. Techniques involved measurement, camera lucida drawings, photographs and SEM (using the same method as Carrion & al. 1993).

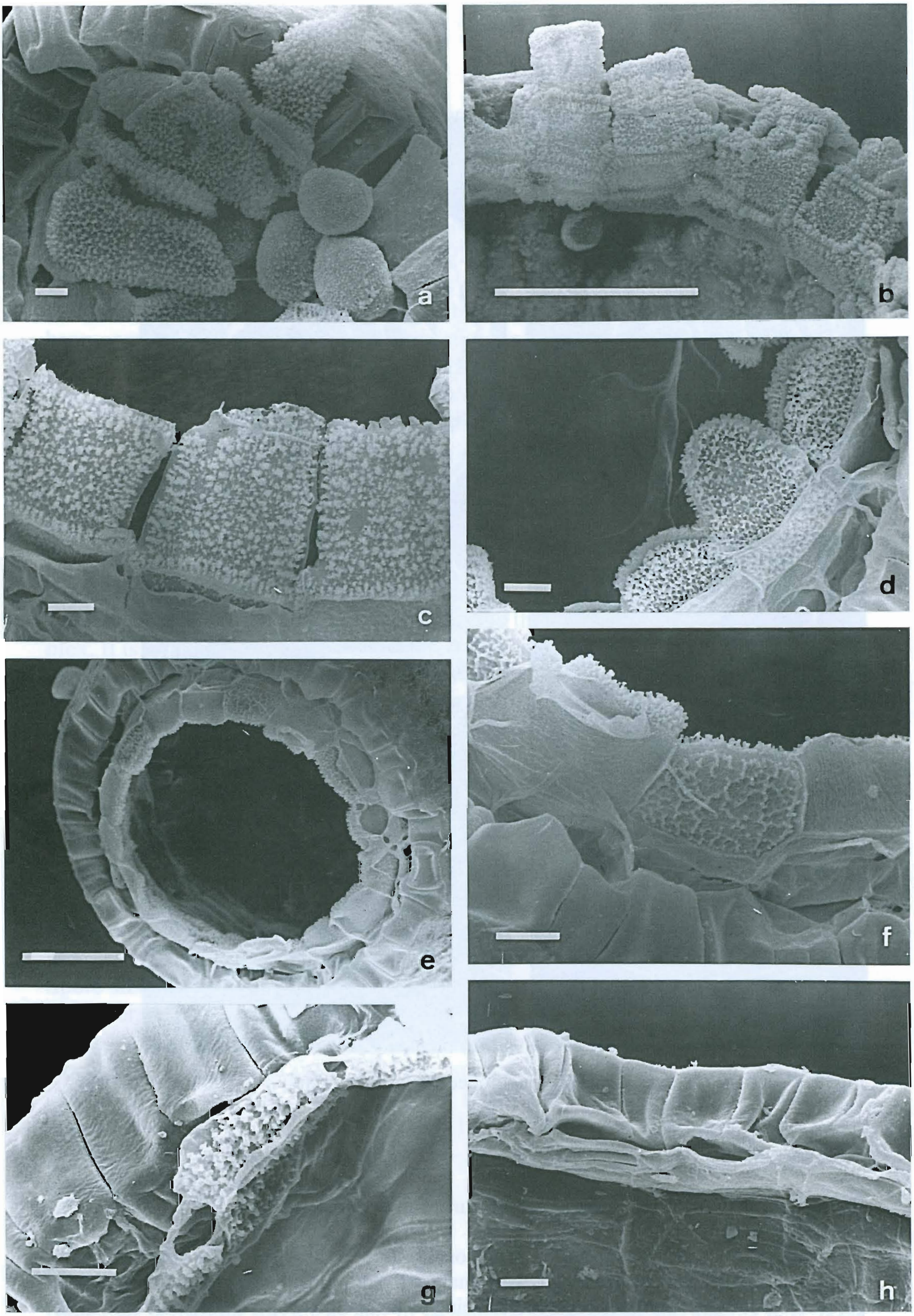

Fig. 2. *Pottia starckeana* agg. *a–f* Imperfect peristomes. (*b, c, e, f* truncate apex teeth; *d* round apex teeth); *g* very reduced peristome, without basal membrane; *h* apparently absent peristome, with traces of basal membrane. Bars: *a, c, d, f–h* 10 µm, *b* 100 µm, *e* 50 µm

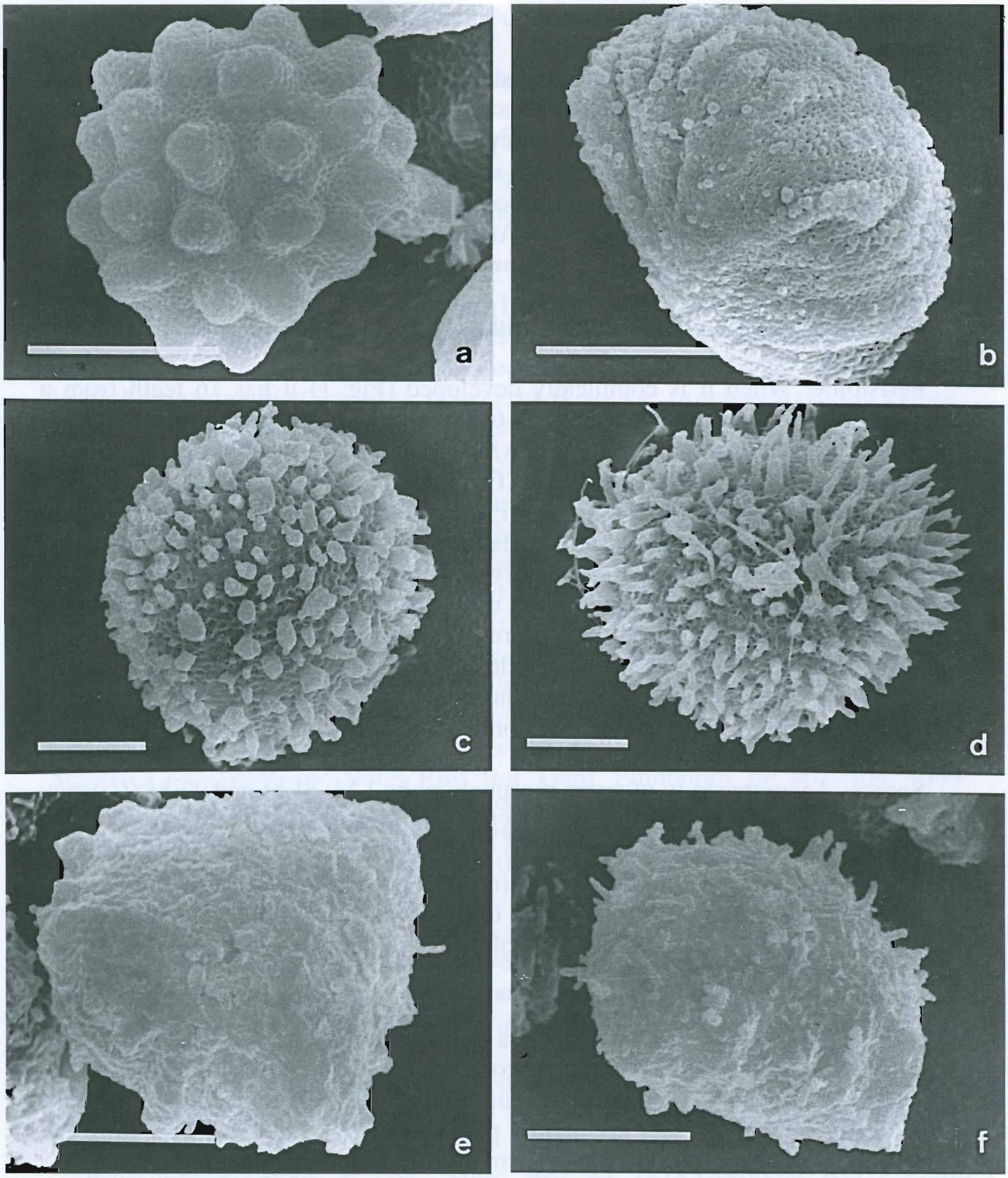

Fig. 3. *Pottia starckeana* agg. *a, b* Spores wavy in outline (*a* with isodiametric protuberances, *b* with ridge-like protuberances); *c, d* spores with large perinic processes; *e, f* spores with intermediate ornamentation: irregular protuberances and perinic processes. Bars: 10 µm

Results

Important morphological characters. As previously mentioned, gametophyte characters are not useful for separation of the taxa because they are very uniform. Sporophyte characters on the contrary are much more variable. However, only one of them is useful for separating the taxa. Their taxonomic value can be commented on as follows:

Seta: yellowish, orange or reddish, usually sinistrorsely spirally twisted, rarely dextrorsely, when dry, 1–3 mm long. Taxonomic value: none.

Capsule: ovoid, almost globose or cylindrical, usually constricted at mouth. Sometimes turbinate when empty, when so, associated with absent or rudimentary peristome and spores with echinate processes. The capsule size is very variable, 0.5–1 mm long and 0.35–0.6 mm wide. At the base there is a row of phaneroporous stomata. The capsule mouth has 1–3 rows of thickened cells. Taxonomic value: none.

Lid: conic and blunt, sometimes with a more pronounced beak. Taxonomic value: none.

Peristome: When it is completely developed (Fig. 1) it has 16 teeth from a smooth basal membrane. They have 3–6 densely papillose joints, up to 200 µm long and little narrowed at the apex, which is blunt or rounded. Very often an incomplete peristome with short teeth (Fig. 2 a–f) is present, one or more joints are absent and the apex can be rounded (Fig. 2 d) or truncate (Fig. 2 b, c), in which case they seem to be broken. Sometimes there is no basal membrane, just some teeth, usually referred to as a rudimentary peristome (Fig. 2 g). The precise nature of the peristome may be misinterpreted using the light microscope as sometimes traces of the basal membrane do not protrude beyond the mouth of the capsule (Fig. 2 h) leading to the erroneous conclusion that the peristome is absent. It can only be seen when the internal face of the capsule is observed. We have found no correlation between the type of peristome and any other sporophyte character. Taxonomic value: none.

Spores: Accurate study of spore morphology by LM, SEM and TEM (Carrion & al. 1993) shows that only two spore types can be recognized.

Spores "*starckeana* type" (Fig. 3 a, b), typically wavy in outline, showing some areas with isodiametric, ridge-like or vermiform protuberances. Structurally there is no special contribution of the perine to more marked protusions, the enlargement involves the sporoderm as a whole. The perine surface is nearly psilate, granulate, perforate or microreticulate.

Spores "*davalliana-commutata* type" (Fig. 3 c, d), with basal sculpture like that of *starckeana* type, but having extra ornamentation: the surface is conspicuously spinose, with variously-shaped processes (up to ca. 4 µm long), which are occasionally branched or confluent, curved echinae being the most frequent. Structurally, these processes are mainly perinical though the exine may form the basis if the bordering sporoderm is constricted. Taxonomic value: high.

There is a high frequency of spores that do not fit with either of the described spore types and they must be considered as intermediate forms (Fig. 3 e, f).

Taxonomic conclusions. On the basis of our present knowledge of the complex we think that only two taxa should be considered at species level, *P. starckeana* and *P. davalliana*.

Key of the species

A. Spores wavy in outline with mostly isodiametric exinic protuberances regularly distributed, sometimes ridge-like or vermiform, lacking conspicuous perinic processes .... *P. starckeana*

A'. Spores without or only with some isodiametric exinic protuberances, abundant processes often present..........B

B. Surface of spores covered with variously shaped processes..........*P. davalliana*

B'. Surface of spores with both protuberances and processes or sometimes almost or completely smooth (probably hybrids) ....*P. starckeana* agg.

Pottia starckeana (HEDW.) C. MÜLL. Syn. **1**: 547, 1849.

Type: Lutoso loco ad Gross-Tschirnau prope Lissanr Poloniae, 1795. (Neotype: G!).

Basionym: *Weissia starckeana* HEDW. Spec. Musc. **65**, 1801.

Synonyms: *Anacalypta starckeana* (HEDW.) FÜRNR., Flora **12(2)** Erg.: 25, 26, 1829. *A. starckeana* var. *brachyodus* B.S.G., Bryol. Eur. **2**: 47, 125 β, 1843 (Neotype: BM!); *Pottia starckeana* var. *brachyoda* (B.S.G.) C. MÜLL, Syn. **1**: 547, 1849; *Pottia minutula* (SCHWAEGR.) FÜRNR. ex HAMP. var. *brachyoda* (B.S.G.) HUSN., Musc. Gall. **78**, 1884. *Pottia starckeana* var. *leiostoma* CORB. in CORB. & PITARD, Bull. Soc. Bot. France **56**: 224, 1909 (Type not seen).

Pottia davalliana (SM.) C. JENS., Damm. Moss **2**: 342, 1923.

Type: Discovered in Switzerland by Mr DAVALL (Holotype: LINN!).

Basionym: *Gymnostomum davallianum* SM. in DRAKE, Ann. Bot. **1**: 577, 1805.

Synonyms: *Gymnostomum rufescens* SCHULTZ, Prodr. Fl. Starg, p. 278, 1806 (Type not seen); *Pottia rufescens* (SCHULTZ) FÜRNR. ex WARNST., Krypt. Fl. Brandenburg **2**: 209, 1904. *Gymnostomum minutulum* SCHWAEGR., Spec. Musc. Suppl. **1(1)**: 25, 1811 (Holotype: G!); *Pottia minutula* (SCHWAEGR.) FÜRNR. ex HAMPE, Flora **20**: 287, 1837; *Pottia starckeana* var. *minutula* (SCHWAEGR.) CORB., Mém. Soc. Sci. Nat. Cherbourg **26**: 239, 1889; *Pottia starckeana* subsp. *minutula* (SCHLEICH. ex SCHWAEGR.) CHAMBERLAIN, Notes Roy. Bot. Gard. Edinburgh **29**: 403–404, 1969. *Gymnostomum conicum* SCHLEICH. ex SCHWAEGR., Spec. Musc. Suppl. **1(1)**: 26, 1811 (Holotype: G!); *Pottia conica* (SCHWAEGR.) FÜRNR. ex PAR., Ind. Bryol., p. 1021, 1898; *Pottia rufescens* var. *conica* (SCHWAEGR.) WARNST., Hedwigia **58**: 137, 1916; *Pottia davalliana* var. *conica* (SCHWAEGR.) PODP., Consp., p. 225, 1954; *Pottia starckeana* subsp. *conica* (SCHLEICH. ex SCHWAEGR.) CHAMBERLAIN, Notes Roy. Bot. Gard. Edinburgh **29**: 403–404, 1969. *Pottia algiriensis* WARNST., Hedwigia **57**: 83, 1915 (Type not seen). *Pottia commutata* LIMPR., Laubm. Deutschl. **1**: 537, 1890, syn. nov. (Holotype: BP!); *Pottia davalliana* subsp. *commutata* (LIMPR.) PODP. Consp., p. 226, 1954.

Taxa of doubtful affinity. Included here are the taxa that in our opinion present a mixed combination of sporal characters between *P. starckeana* and *P. davalliana*.

Weissia affinis HOOK. & TAYL., Musc. Brit. **44**, 1818 (Neotype: BM!); *Pottia starckeana* var. *affinis* (HOOK. & TAYL.) BRAITHW., Brit. Moss Fl., p. 201, 1884; *Pottia affinis* (HOOK. & TAYL.) HERRNSTADT & HEYN, Bryologist **94**: 168–178, 1991, syn. nov.

Pottia mutica VENT. in DE NOT., Atti. Univ. Genova **1**: 592, 1869 (Holotype: BM!); *Pottia minutula* var. *mutica* HUSN., Musc. Gall. **78**, 1884.

Pottia salina WARNST., Hedwigia **57**: 83, 1915 (Holotype: B!).

Pottia microphylla WARNST., Hedwigia **58**: 141, 1916 (Holotype: B!).

Pottia texana WAREH. in GROUT, Moss Fl. N. Amer. **1**: 201, 1939 (Holotype: NY!).

Pottiana arizonica Wareh. in Grouth, Moss Fl. N. Amer. **1**: 202, 1939 (Paratype: NY!).

Pottia arizonica var. *mucronulata* Wareh. in Grout, Moss Fl. N. Amer. **1**: 203, 1939 (Paratype: NY!).

Discussion

One of the more important conclusions of this paper is that the nature of the peristome cannot be considered a diagnostic character to differentiate the taxa in the *P. starckeana* agg. and that the only really useful character of taxonomic value is spore morphology. If we analyse the value that traditionally has been given to the peristome in this group of species, it can be seen that it has not been extended in the same way to all the taxa. In *P. starckeana* there is general agreement that the spore is wavy in outline, regardless of peristome development. However, significance is placed on the nature of the peristome in defining *P. commutata* and *P. davalliana*. In both species spore ornamentation is very similar (with processes at least echinate in both and sometimes blunt or rounded in *P. commutata*). They have been distinguished on the basis of the absence of peristome in *P. davalliana* and the presence of a rudimentary or well developed peristome in *P. commutata*. If account is taken of the many instances when a peristome is apparently lacking but a basal membrane not exceeding the mouth of the capsule is present, the separation of the two taxa is not tenable.

Pottia conica has usually been accepted as a valid taxon, as a variety, subspecies or species. Nevertheless, from our observations, spore morphology cannot be considered different from that of *P. davalliana* or *P. commutata* because the only reputed differences from the last two species is the development of the perinic processes. If *P. commutata* and *P. davalliana* cannot be separated and *P. conica* has a similar relationship to them, this leads us to think that the three taxa are only a single species, in which peristome development can be as variable as in *P. starckeana*.

P. mutica is of doubtful affinity. The spores are similar to those of *P. starckeana*, but the spore type does not fit with either of the above described spore types in this paper. Consequently it seems more accurate to consider it as an intermediate form, with mixed spore characteristics of *P. starckeana* and *P. davalliana* rather than a synonym of *P. starckeana*. The same can be said of *P. salina, P. microphylla, P. texana,* and *P. arizonica*. Although in this work we have mainly studied the taxa of the *P. starckeana* agg. present in Europe, the cases of *P. texana* and *P. arizonica* were very interesting for us because from the descriptions and pictures of both species they looked like intermediate forms. Both American species have been treated taxonomically in different ways by different authors. Thus, *P. texana* has been synonymized with *P. starckeana* subsp. *conica* by Chamberlain (1969), an opinion accepted by Eckel (1987), but Anderson & al. (1990) have synonymized it with *P. starckeana*. On the other hand *P. arizonica* (including var. *mucronulata*) is considered by Chamberlain (1968) to be a synonym of *P. mutica* (although there has been no formal synonymization) but Anderson & al. (1990) found it to be a good species. In our opinion, after studying the types of both taxa, they are intermediate forms, like *P. mutica*. Although the spore morphology is different in the three species, none of them fits into the spore type defined herein. With the exception of *P. arizonica*, the taxa considered in this paper to be of doubtful affinity are included by CHAMBERLAIN (1969) as synonyms of *P. starckeana* subsp. *conica*, although to us, *P. conica* is not an intermediate form but possesses a "*davalliana-commutata* type" spore morphology.

The origin of the taxonomic problems of this complex of species has been dealt with elsewhere (CARRION & al. 1993). In that previous account, there was postulated that the existence of abundant intermediate spores could be the result of a certain degree of outbreeding or interpopulational gene flow. In any case, given the predominantly autoicous condition, the species under consideration should be primarily inbreeders. Introgressive hybridization 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 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. In any case, the discussion will remain speculative without more research including cytological observations of chromosome numbers. The available data for *P. davalliana* (n = 30, n = 27 + m, n = 28, n = 26) and *P. starckeana* (n = 26) (FRITSCH 1982, 1991) were allegedly obtained from samples taxonomically well defined. Our observations after many years identifying Mediterranean material lead us to conclude that all the described variation can be seen in a single cushion but, of course, further investigation on individuals is needed. Perhaps, in vitro culture studies, which are being developed in our laboratory, can highlight the problem if we are able to get a statistically representative number of hybrid sporophytes.

On the other hand, it must not be forgotten that in arid-semiarid climates and disturbed environments such as pastures, roadsides, cultivated fields, etc. where these *Pottiaceae* commonly grow, the potentiality for hybridization increases (ANDERSON 1980). Consequently, it seems inappropriate to try to name each form that is found in the field rather than consider them simply to be members of the *P. starckeana* agg.

We extend our appreciation to the curators of the herbaria that have lent material, and to Dr L. ELLIS (The Natural History Museum of London), who has studied the type of *Gymnostomum davallianum* located at LINN. The constructive suggestions of Dr A. J. E. SMITH (Bangor) on a previous version of the manuscript are gratefully acknowledged. This work has been carried out with financial support of the Spanish DGICYT (Project PB 93-1141) and the Regional Government of Murcia (Project PIB 93/08).

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