

A revision of the moss genus *Crossidium* (Pottiaceae) with the description of the new genus *Microcrossidium*

M. J. CANO, J. GUERRA, and R. M. ROS

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Abstract: A world revision of the genus *Crossidium* JUR. recognizes 11 species, which are described and discussed in the context of important taxonomic characters. An identification key is provided. *C. asirensis* FREY & KÜRSCHNER is reduced to synonymy with *C. davidai* CATCHESIDE, and the geographical range of *C. laevipilum* THER. & TRAB. is extended to Europe. Phylogenetic trends are interpreted on the basis of two main evolutionary lines associated with the presence or absence of hyaline hair-points on the leaves. A twelfth species is transferred to *Microcrossidium* GUERRA & CANO, gen. nov., as *M. apiculatum* (MAGILL) GUERRA & CANO, comb. nova, because of differences in stem anatomy, peristome configuration, and spore morphology.

The first revision of the genus *Crossidium* JUR. was carried out by DELGADILLO (1975), who recognized eight taxa: *C. rosei* WILLIAMS, *C. seriatum* CRUM & STEERE, *C. aberrans* HOLZ. & BARTR., *C. geheebii* (BROTH.) BROTH., *C. squamiferum* (VIV.) JUR. var. *squamiferum*, *C. squamiferum* var. *pottioideum* (DE NOT.) MOENK., *C. crassinerve* (DE NOT.) JUR. var. *crassinerve*, and *C. crassinerve* var. *laevipilum* (THER. & TRAB.) DELGADILLO. Further species (*C. davidai* CATCHESIDE, *C. spiralifolium* MAGILL, *C. laxefilamentosum* FREY & KÜRSCHNER, *C. apiculatum* MAGILL, and *C. asirensis* FREY & KÜRSCHNER) have since been described, bringing the total to 14 taxa (13 species and one variety). Additionally some taxonomically significant characters have been added (i.e., FREY & KÜRSCHNER 1991) and the taxonomic concept of some species has been considerably enlarged. In view of these developments, a new revision appeared to be necessary.

BRUCH & al. (1842) published the name *Chloronotae* for a section of the genus *Barbula* which is now recognized as *Crossidium*. VENTURI (1868) used *Barbula* sect. *Chloronotae* as the basionym of the genus *Chloronotus*. However, the Cambridge Botanical Congress rejected the name in favour of *Crossidium* (cf. GROUT 1930), which had been published by JURATZKA (1882).

In the present paper, the genus *Crossidium*, occurring mainly in arid and semi-arid areas, is revised taxonomically on a world basis. Data about the taxonomic status of *Crossidium* and its relationships with such genera as *Aloina* (C. MÜLL) KINDB., *Aloinella* CARD., *Pseudocrossidium* WILLIAMS have been given elsewhere

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by WILLIAMS (1915), DELGADILLO (1973 a, b), ZANDER (1979), and CHURCHILL (1990).

Material and methods

This revision is based mainly on herbarium material. More than 600 specimens of the species recognized in *Crossidium* were studied. The specimens, including type material are located in B, BCB, BCC, BM, CAME, DUKE, FH, FCO, FI, FLAS, G, H, K, LISU, MA, MACB, MO, MUB, NY, PC, RO, US, VAB, VIT, Herb. CATCHESIDE (South Australia), Herb. FREY (Berlin), Herb. GIACOMINI (Camerino), Herb. HÉBRARD (Marseille), Herb. HERAS (Vitoria), Herb. MARTÍNEZ ABAIGAR (Logroño), Herb. MUÑOZ (Oviedo), and Herb. OLIVA (Córdoba).

All the samples were studied by taking into account all the characters referred to in the following section. Measurements, plans, and drawings involved the use of a camera lucida attached to a light microscope. For SEM observations of leaves, peristomes, and spores, the material was critical-point dried, gold-sputtered with a 200–300 Å-thick layer, and analysed in a Jeol JSM-T 300 under 10–15 KV.

For each taxon, with the exception of *C. squamiferum*, the type is included. In those cases where the list of synonyms is long, we refer to the work of DELGADILLO (1975), noting only the basionyms and new synonymy before descriptions. For widespread species, we have followed the nomenclature of WIJK & al. (1959). The symbol (!) indicates that samples of this area have been studied.

Major characters

The morphological features of *Crossidium* were discussed by DELGADILLO (1973 a, b, 1975). The following details emphasize the particular characters examined during the present revision and those to which we attach special taxonomic significance.

Gametophyte. Leaf outline. This is relatively variable but represents a relevant character for some taxa (e.g., *C. crassinerve* group). Ranging from lingulate to ovate-lanceolate, ovate or oblong, the leaves are usually concave in their upper part. The apex varies from apiculate (e.g., *C. spiralifolium*) to rounded (*C. laevipilum*, *C. seriatum*), and is sometimes obtuse (*C. crassinerve*).

Costa. It is always excurrent, forming either a hyaline hair or a short (*C. davidai* and *C. spiralifolium*) or a long mucro (*C. rosei*). Some species show both hyaline and mucronate types (*C. laevipilum*). The hyaline hair is mostly smooth, rarely denticulate. Its length is usually 0.1–1 mm but reaches 3 mm in *C. squamiferum*. Anatomically, it is composed of 2–5(–6) guide cells arranged in a single layer as well as 2–8 layers of abaxial stereids. The number of stereids can be of diagnostic value as it usually remains constant within a given species. In addition, hydroids are intercalated between the stereids and guide cells.

Supracostal filaments. These are one of the most critical features. They are made up of quadrate, rectangular or subglobose, thin-walled cells with lateral projections. The number of cells varies from 1–2 (*C. aberrans*, *C. seriatum*) to 10–12 (e.g., *C. squamiferum*, *C. crassinerve*). Filaments may be simple or abundantly branched (*C. deserti*). Both shape and papillosity of the terminal cell represent decisive taxonomic characters. The two alternatives are: (a) a cylindrical or conical cell, which is either smooth or has 2–4(–5) papillae per cell (e.g., *C. squamiferum*, *C. crassinerve*, *C. laxefilamentosum*) and (b) a subspherical cell with 3–6(–8) papillae per cell (e.g., *C. aberrans*, *C. geheebii*, *C. asirensis*).

Laminal papillosity. Papillae occur in the upper half or upper third of the leaves. They are particularly noticeable in *C. seriatum* and *C. rosei*. The first shows 4–6(–8) single or bifurcate papillae per cell. The second possesses 4–6 papillae per cell. In *C. davidai*, the character is variable the cells usually bearing 1–4(–5) simple, or often bifurcate papillae but rarely they may be smooth. *C. geheebii* is characterized by smooth cells or by cells with inconspicuous papillae. *C. aberrans* exhibits a single central papilla, although occasionally there are two, which may be simple or bifurcate. *C. deserti* often displays a single papilla. In *C. crassinerve* the foliar pattern is mostly smooth but one can sometimes see small papillae projecting along the apical margin. In *C. spiralifolium*, the cells are typically smooth. Despite minor intraspecific variation, this character is of great taxonomic use.

Sexuality. Most species are dioicous or autoicous (cladautoicous, gonioautoicous) but some are invariably autoicous, as *C. squamiferum* (gonioautoicous) and *C. seriatum* (cladautoicous). *C. rosei* is heteroicous.

Sporophyte. This is not yet known in *C. deserti* and *C. laxefilamentosum*, and in other species such as *C. laevipilum* it has been scarcely studied because of the difficulty of finding suitable samples.

Seta. Usually reddish, its length is 4–19 mm. *C. aberrans* and *C. squamiferum* show longer pedicels, and the shortest one is that of *C. laevipilum*.

Capsule size and shape. This is narrowly ovoid to cylindrical, erect to somewhat inclined or curved. Size is variable in the genus, with smaller capsules occurring in *C. laevipilum*. The operculum is variable, being conical or rostrate, with an erect or slightly inclined beak, and is without taxonomic value.

Peristome. Its 32 filiform, articulate, papillose teeth, arise from a basal membrane and are mostly spirally twisted. In *C. rosei*, teeth fail to develop, so that the peristome is reduced to the basal membrane alone. Two major types of basal membranes occur: (a) those with a reticulum made up of clear, rectangular or sometimes quadrate depressions, which are delimited by marked, abundantly papillose ridges (e.g., *C. rosei*, *C. squamiferum*) (Figs. 1 g, h; 9 e, f); and (b) those with a reticulum in which depressions are lacking or hardly visible (e.g., *C. davidai*, *C. spiralifolium*, *C. seriatum*) (Figs. 2 g, h; 3 e, f; 4 e; 6 f). The first type is not frequent within *Crossidium*. It may well represent a primitive form, perhaps related to the basal membranes in *Tortula* HEDW. and *Tortella* (LINDB.) LIMPR. Even so, it should be remembered that this peristome type is found in *C. squamiferum*, which is allegedly a rather specialized taxon.

The second type is much more frequent, and is associated with peristome teeth which vary in both length and direction; they range from short and erect to long and spirally twisted, as in *C. aberrans* and *C. seriatum*. In either case, some intrapopulational variation in length occurs, and the character must therefore be treated cautiously.

Spores. They are mainly spheroidal, 9–32 μm in diameter, with the larger occurring in *C. rosei*. Sculpturing is relatively variable, but is recurrently granulate-vermiculate on surfaces with complete perinic deposition (Fig. 4 f, Fig. 5 f), and this characteristic of the mature spores is distinctive in relation to close genera.

Taxonomic conclusions

On the basis of present knowledge of the complex we considered that 12 taxa, all at specific level, can be recognized. For one we erect a new genus but the 11 which we refer to *Crossidium* can be identified by the following key.

Key of the species

1. Leaves without hyaline hair-point 2
1. Leaves with hyaline hair-point 5
2. Lamina cells smooth 3
2. Lamina cells papillose 4
3. Leaves oblong-lanceolate, the apex acute. Supracostal filaments up to 6 cells high 3. *C. spiralifolium*
3. Leaves ovate to oblong-ovate, the apex rounded and cucullate. Supracostal filaments up to 10 cells high 9. *C. laevipilum*
4. Peristome teeth present, twisted; basal membrane 50–60 µm high. Costa ex-current in a short mucro 2. *C. davidai*
4. Peristome without teeth; basal membrane 100–120 µm high. Costa usually ex-current in a large apiculus 1. *C. rosei*
5. Upper cells of lamina conspicuously papillose, with 1–8 simple or bifurcate papillae 6
5. Upper cells of lamina smooth or with 1–2 inconspicuous papillae 9
6. Upper cells of lamina with 4–6(–8) papillae. Terminal cell of filament generally subspherical 4. *C. seriatum*
6. Upper cells of lamina with 1–2(–3) papillae. Terminal cell of filament subspherical or not 7
7. Supracostal filaments 1–2(–3) cells high 5. *C. aberrans*
7. Supracostal filaments 4–5(–6) cells high 8
8. Leaves widely lingulate-spathulate; costa 38–44 µm wide in mid-leaf 7. *C. deserti*
8. Leaves oblong-ovate; costa 57–65 µm in midleaf 6. *C. geheebii*
9. Supracostal filaments 1–2(–3) cells high 5. *C. aberrans*
9. Supracostal filaments 3–12 cells high 10
10. Upper and median cells of lamina thick-walled, the lumens nearly obliterated toward leaf margin. Terminal cell of filament conical with 1–5 high papillae 11. *C. squamiferum*
10. Upper and median cells of lamina not thick-walled, the lumens not obliterated. Terminal cell of filament variable 11
11. Terminal cell of filament subglobose with 8–9 papillae 6. *C. geheebii*
11. Terminal cell of filament cylindrical or conical, rarely subglobose, with 0–4 papillae 12
12. Leaves lingulate-spathulate, the nerve 38–44 µm wide in mid-leaf 7. *C. deserti*
12. Leaves without these characters 13
13. Terminal cell of filament generally smooth 10. *C. laxefilamentosum*
13. Terminal cell of filament with 2–4(–6) papillae, very rarely smooth 14

14. Leaves usually with a short mucro, the apex strongly cucullate. Peristome teeth straight, 200–300 μm 9. *C. laevipilum*
14. Leaves usually with a long hyaline hair-point, the apex not cucullate. Peristome teeth twisted, 450–812 μm 8. *C. crassinerve*

Taxonomy

***Crossidium* JUR., Laubmoosfl. Oesterr. Ungarn: 127. 1882. nom. cons. Type species: *Crossidium squamiferum* (VIV.) JUR.**

Plants small, caespitose, growing in dense, often gregarious turfs. Stems erect, generally branched, in cross-section differentiated into a central strand of small cells with thin walls and a cortex of large cells; rhizoids branched, brown to reddish. Leaves lingulate, ovate-lanceolate or ovate to oblong, erect or erecto-patent when moist, twisted to slightly imbricate when dry; apex piliferous or mucronate, rounded, obtuse, emarginate or cucullate, usually concave above; margin revolute, recurved or plane, generally entire. Upper and median leaf-cells hexagonal, quadrate to rectangular, with walls variously thickened, papillose or smooth; basal cells rectangular to quadrate, with thin walls, smooth. Costa excurrent in a mucro or hyaline hair-point; in cross-section, with a group of thin-walled cells between the stereids and, generally in one row, 2–6 guide cells; photosynthetic supracostal filaments branched or not, 1–12 cells high; cells of filament, rectangular or quadrate to subspherical, with thin walls, the terminal cell cylindrical, conical or subspherical, often with thin walls, but sometimes thickened, mostly papillose. Dioicous, autoicous (cladautoicous, gonautoicous) or heteroicous. Perigonium bud-like with perigonal leaves short and broad. Perichaetial leaves little differentiated, generally wider and longer than stem leaves. Sporophyte with reddish seta often twisted to the left below and to the right above; capsule erect to slightly curved or inclined, cylindrical to elongate-ovoid or oblong; annulus of about 1–3 rows of small cells; operculum conical to rostrate, with beak erect or inclined; stomata few at the base of the capsule; peristome of 32 filiform, articulated and papillose teeth, mostly twisted spirally, sometimes straight when short; basal membrane projecting above capsule mouth; calyptra cucullate. Spores small, 9–32 μm in diameter, generally spherical, granulate under LM and granulate-vermiculate under SEM.

1. *Crossidium rosei* WILLIAMS, Bull. Torrey Bot. Club 42: 395. 1915. (Fig. 1 a–h). Type: Peru, vicinity of Lima, Rose, 18774 (Holotype: NY!).

Stems up to 2–2.5 mm high. Leaves ovate-oblong to oblong-lanceolate, 0.9–1.7 mm long, 0.4–0.6 mm wide; apex obtuse, subcucullate, margin plane to recurved. Costa 49–73 μm wide in middle of leaf, excurrent in a short to long mucro; cross-section showing 6–8 stereid layers; filaments 2–4(–5) cells high, the terminal cell subspherical, 15–28 μm long with 4–6 papillae. Upper leaf cells quadrate to rectangular, 11–23 μm long, with 2–6 simple or bifurcate papillae; median cells quadrate to rectangular, 13–28 μm long, smooth or papillose; basal cells rectangular, 15–20 μm long. Seta 5.5–7.5 long; capsule oblong, 0.8–1.2 mm; peristome without teeth, the basal membrane, approximately 100–120 μm high, with pronounced, rectangular, or sometimes quadrate foveae; operculum conical 0.4–0.5 mm long. Spores 24–32 μm in diameter.

Distribution. Peru and possibly Canada (McINTOSH 1989).

Illustrations. WILLIAMS (1915), DELGADILLO (1975: 272).

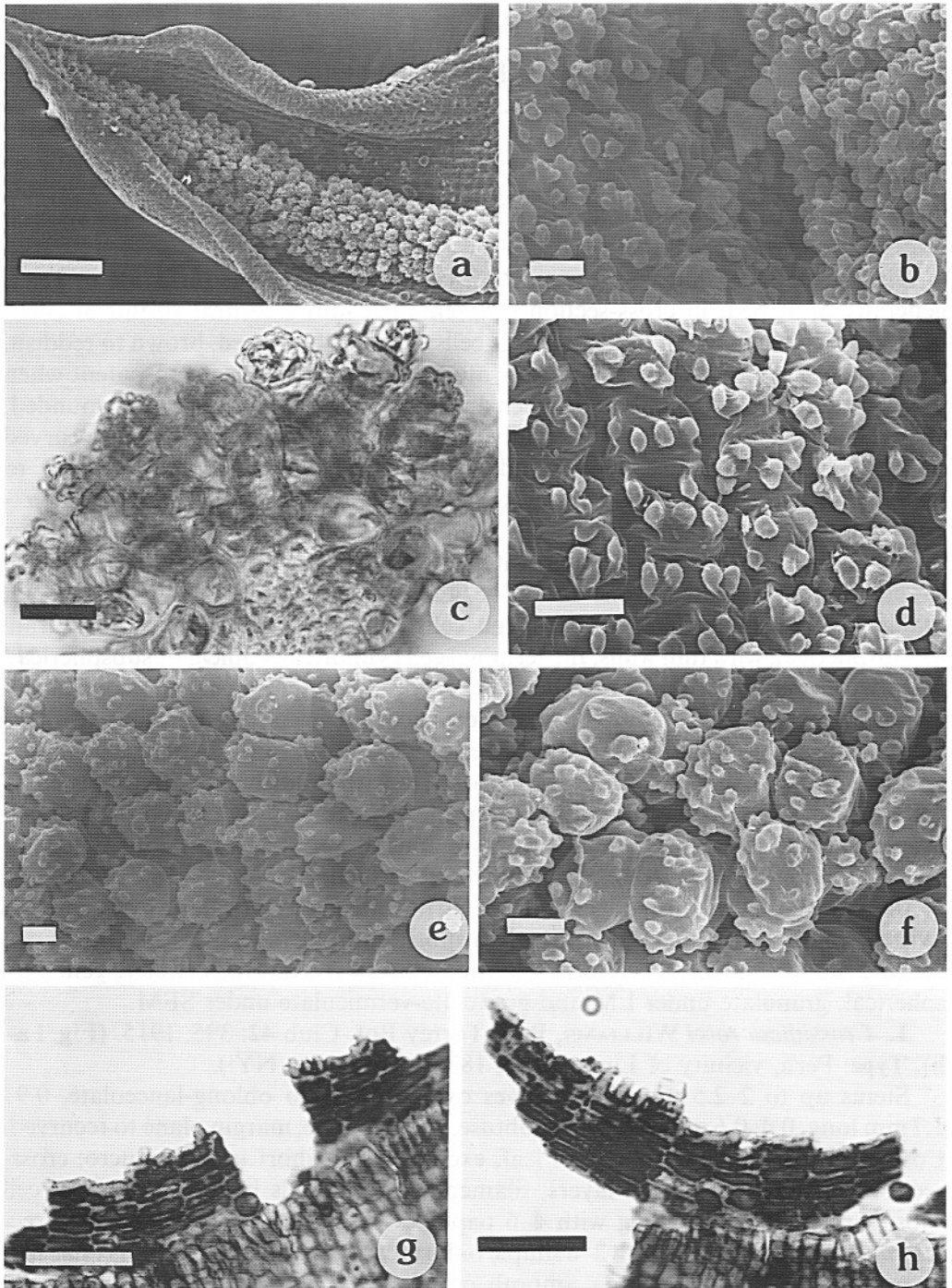


Fig. 1. *Crossidium rosei* (from Valcárcel 100 in FLAS). *a* Adaxial surface of leaf. *b* Lamina cells and supracostal filaments. *c* Cross section of leaf. *d* Lamina cells. *e*, *f* Supracostal filaments. *g*, *h* Basal membrane of peristome. Bars: *a*, *g*, *h*: 100 µm; *b*, *d*, *e*, *f*: 10 µm; *c*: 25 µm

Observations. A sterile sample, forming part of the material on which the MCINTOSH (1989) record was based, was the only Canadian material we were able to study. According to our own observations of papillosity and leaf outline, the sample may be closer to *C. davidai* than *C. rosei*. However, resolution of this problem would require access to a complete set of characters, including those of the peristome.

2. *Crossidium davidai* CATCHESIDE, Mosses of South Australia: 152. 1980 (Fig. 2 a–h). **Type:** South Australia, Gairdner division, 95 km south of Woomera by Port Augusta Road, on soil in scrub, D. E. A. CATCHESIDE, Sept. 1971 (Holotype: Herb. D. G. CATCHESIDE!). **Synonym:** *Crossidium asirensense* FREY & KÜRSCHNER, J. Bryol. 13: 25. 1984. **syn. nova.** **Type:** Saudi Arabia, Asir Mountains, near Biljursshi 20° 25' N, 41° 20' E, on soil, 1750 m, FREY & KÜRSCHNER, 23 November 1981, 81–572 (Holotype: B!).

Stems up to 2 mm high. Leaves ovate-oblong to oblong-spathulate, 0.8–2 mm long, 0.4–0.8 mm wide; apex obtuse to rounded, subcucullate; margin revolute to recurved. Costa 65–90 µm wide in middle of leaf, excurrent in a short mucro; cross-section showing 6–8 stereid layers; filaments 2–4(–5) cells high, the terminal cell generally subspherical, 14–25 µm long, with 4–8 simple or bifurcate papillae. Upper and median cells of leaf quadrate to rectangular, 10–20 µm long, with 1–4 simple or bifurcate papillae, sometimes smooth; basal cells rectangular, 18–50 µm long. Seta 5–9 mm long; capsule elongated-ovoid, 0.8–2 mm long, peristome teeth twisted, 300–365 µm long, basal membrane 50–60 µm high, operculum conical, 0.25–0.5 mm long. Spores 15–20(–22) µm in diameter.

Distribution. Southern Australia and Saudi Arabia.

Illustration. CATCHESIDE (1980: 152).

Observations. After studying several samples of *C. asirensense*, we concluded that it cannot be differentiated from *C. davidai*. Although the leaf as a whole showed less papillosity under LM in *C. asirensense*, SEM study demonstrated that the number of papillae per cell is similar in both taxa. In this context, it is also pertinent that papillosity is strongly dependent upon leaf development (MISHLER & LUNA 1991). Moreover, such variability is not unique to *C. davidai*, and occurs elsewhere, in *C. aberrans* (cf. PIERROT 1986).

3. *Crossidium spiralifolium* MAGILL, Flora of Southern Africa: 197. 1981 (Fig. 3 a–f). **Type:** Cape, Prieska poort, c. 14 km from Prieska on road to Vosburg, on soil, SMOOK & HARDING 705 (Isotype: MO!).

Stems up to 2 mm high. Leaves oblong-lanceolate, 1.2–1.6 mm long, 0.4–0.6 mm wide; apex acute; margin recurved. Costa 40–97 µm wide in middle of leaf, excurrent in a short mucro; cross-section showing 4–8 stereid layers; filaments 2–6 cells high, the terminal cells subglobose, 8–12 µm long, with 2–4 papillae. Upper and median cells of leaf quadrate to short-rectangular, 10–20 µm long, smooth; basal cells short-rectangular to rectangular, 13–42 µm long. Seta 11–15 mm long, capsule cylindrical, 1.2–1.5 mm long; peristome teeth twisted, 500–600 µm long; basal membrane 45–50 µm high; operculum long-conical, 0.6–0.9 mm long. Spores 15–20 µm in diameter.

Distribution. Southern Africa (MAGILL 1981).

Illustration. MAGILL (1981: 196).

Observations. Distinctive features of this species are the mucronate leaves and the absence of foliar papillae.

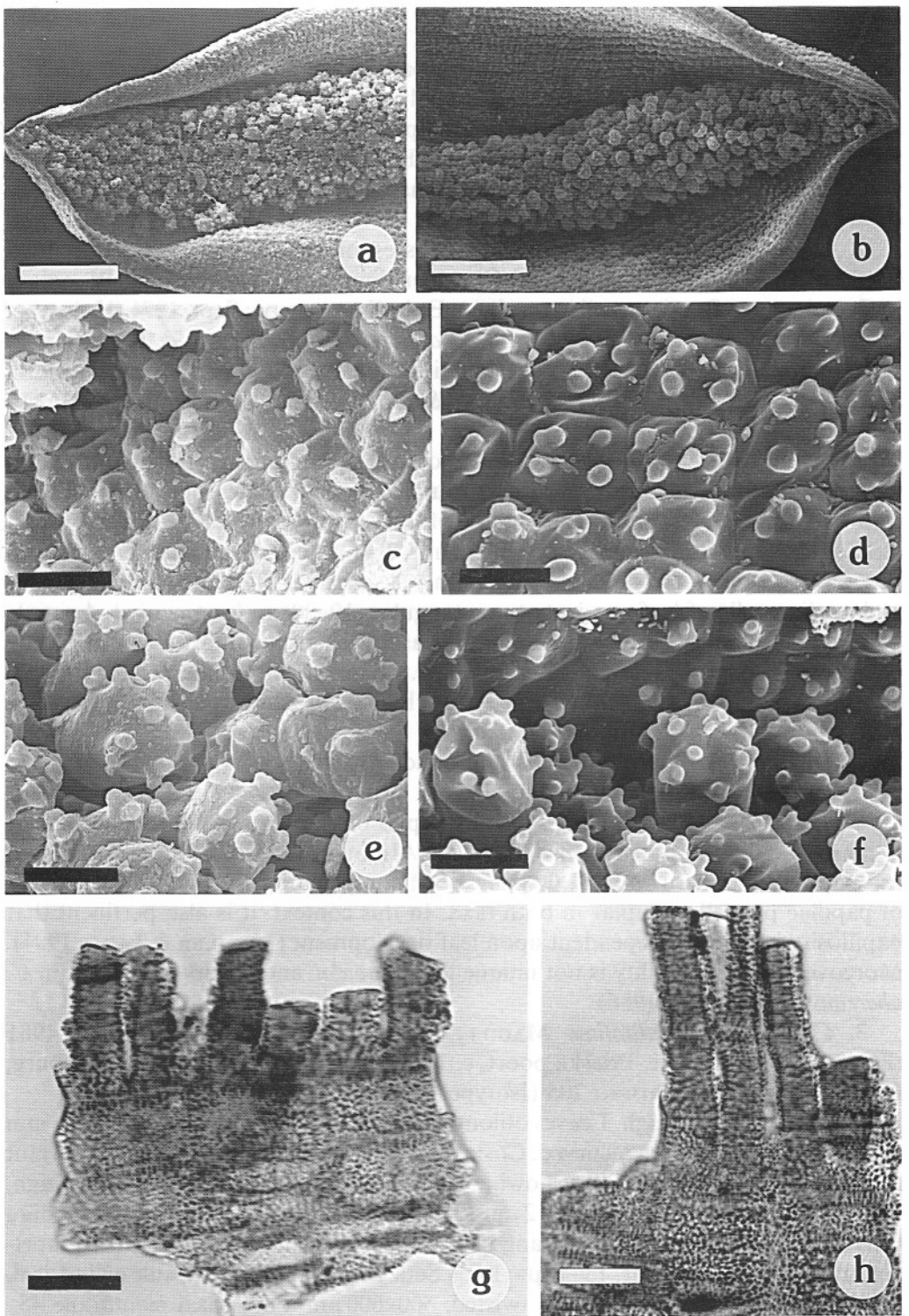


Fig. 2. *Crossidium davidai* (a, c, e, g from FREY & KÜRSCHNER 1-3545 in MUB) (b, d, f, h from type material in Herb. Catcheside). a, b Adaxial surfaces of leaves. c, d Lamina cells. e, f Supracostal filaments. g, h Peristome and basal membrane. Bars: a, b: 100 μm; c, d, e, f: 10 μm; g, h: 30 μm

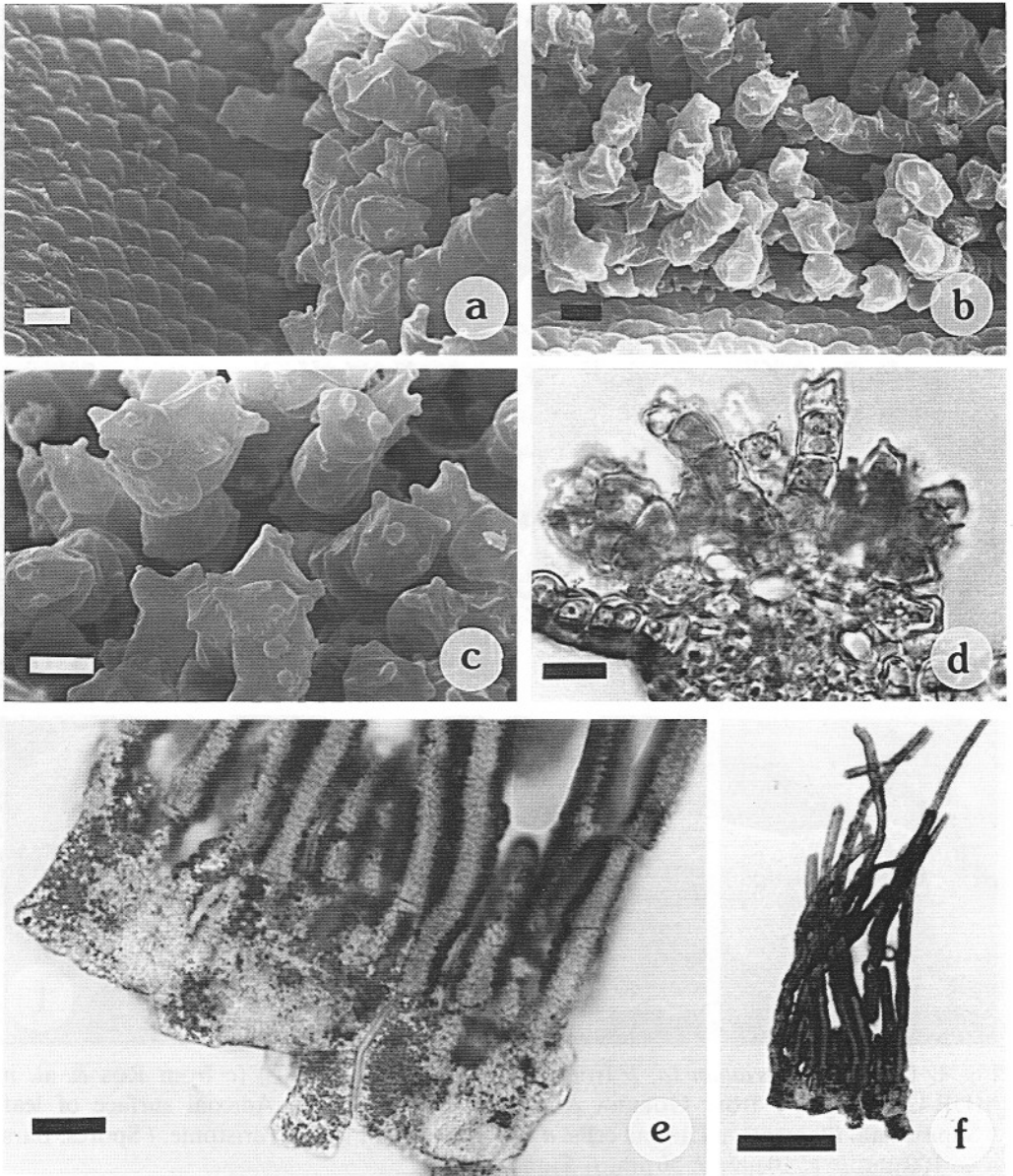


Fig. 3. *Crossidium spiralisfolium* (from type material in MO). *a* Adaxial surface to show supracostal filaments and lamina cells. *b*, *c* Supracostal filaments. *d* Cross section of leaf. *e*, *f* Peristomes. Bars: *a*, *b*, *c*: 10 μ m; *d*: 20 μ m; *e*: 30 μ m; *f*: 100 μ m

4. *Crossidium seriatum* CRUM & STEERE, Southw. Naturalist 3: 117. 1959 (Fig. 4 a–f). **Type:** Mexico, Baja California, Cedros Island, on silt, edge of arroyo, east side of north end, perhaps 6.4 km S, 300–600 m, STEERE 17533 c (Isotypes: DUKE!, NY!, US!).

Stems up to 2 mm high. Leaves ovate to oblong-ovate, sometimes lingulate, 0.4–0.9(–1.2) mm long, 0.3–0.6 mm wide; apex rounded; margin strongly revolute. Costa 37–65 μ m in middle of leaf, excurrent in hyaline hair-point 0.16–1 mm long; cross-

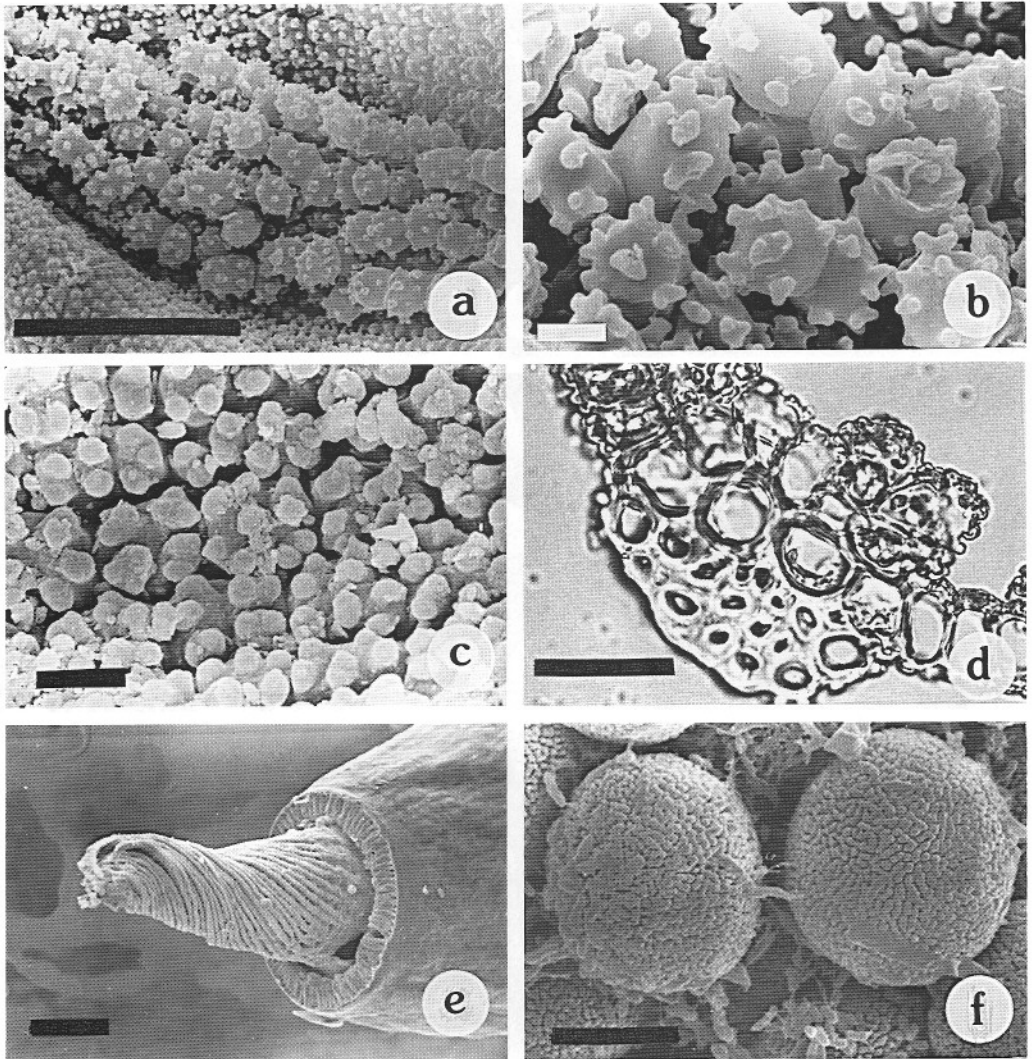


Fig. 4. *Crossidium seriatum* (a, b from type material in DUKE) (c from Ros & al. in MUB4265) (d, e, f from GUERRA & ROS in MUB4354). a Adaxial surface of leaf. b Supracostal filaments. c Lamina cells. d Cross section of leaf. e Peristome. f Spores. Bars: a, e: 100 μ m; b, c: 10 μ m; d: 50 μ m; f: 5 μ m

section showing 2–4 stereid layers; filaments 1–2(–3) cells high, the terminal cell generally subspherical, 13–22 μ m long, with 6–8 papillae. Upper leaf cells quadrate to rounded-hexagonal, 8–20 μ m long; median cells quadrate to rectangular, 9–22 μ m long; upper and median cells strongly papillose with 4–6(–8) simple or bifurcate papillae; basal cells rectangular, 14–50 μ m long. Seta 7–10 mm long; capsule cylindrical, 1.3–1.7 mm long; peristome teeth strongly twisted, 688–832 μ m long; operculum conical, 0.7–1 mm long. Spores 10.5–13 μ m in diameter.

Distribution. Northern and Central America (Mexico, United States), the most recent record being that by STARK & WHITTEMORE (1992), and Spain where the species is widespread (CANO 1992).

Illustrations. CRUM & STEERE (1959: 118), DELGADILLO (1975: 272), CANO & al. (1992: 281).

5. *Crossidium aberrans* HOLZ. & BARTR., *Bryologist* 27: 4. 1924 (Fig. 5 a–f).
Type: USA: Arizona, Pima Co., Sta Catalina Mts, BARTRAM 484 (Isotype: US!).

Stem up to 3 mm high. Leaves lingulate, sometimes ovate to ovate-lanceolate, 0.5–1.2 mm long, 0.3–0.6(–0.8) mm wide; apex obtuse or rounded, generally emarginate; margin recurved to revolute. Costa 35–75.5 μm wide in middle of leaf, excurrent in a hyaline hair-point 0.16–0.9 mm long; cross-section showing 2–5 stereid layers; filaments 1–2(–3) cells high, the terminal cell subglobose to quadrate-cylindrical, 16–24.5 μm long, with 3–4(–7) simple or bifurcate papillae. Upper cells of leaf rounded-hexagonal, sometimes quadrate, 10–20 μm long; median cells hex-

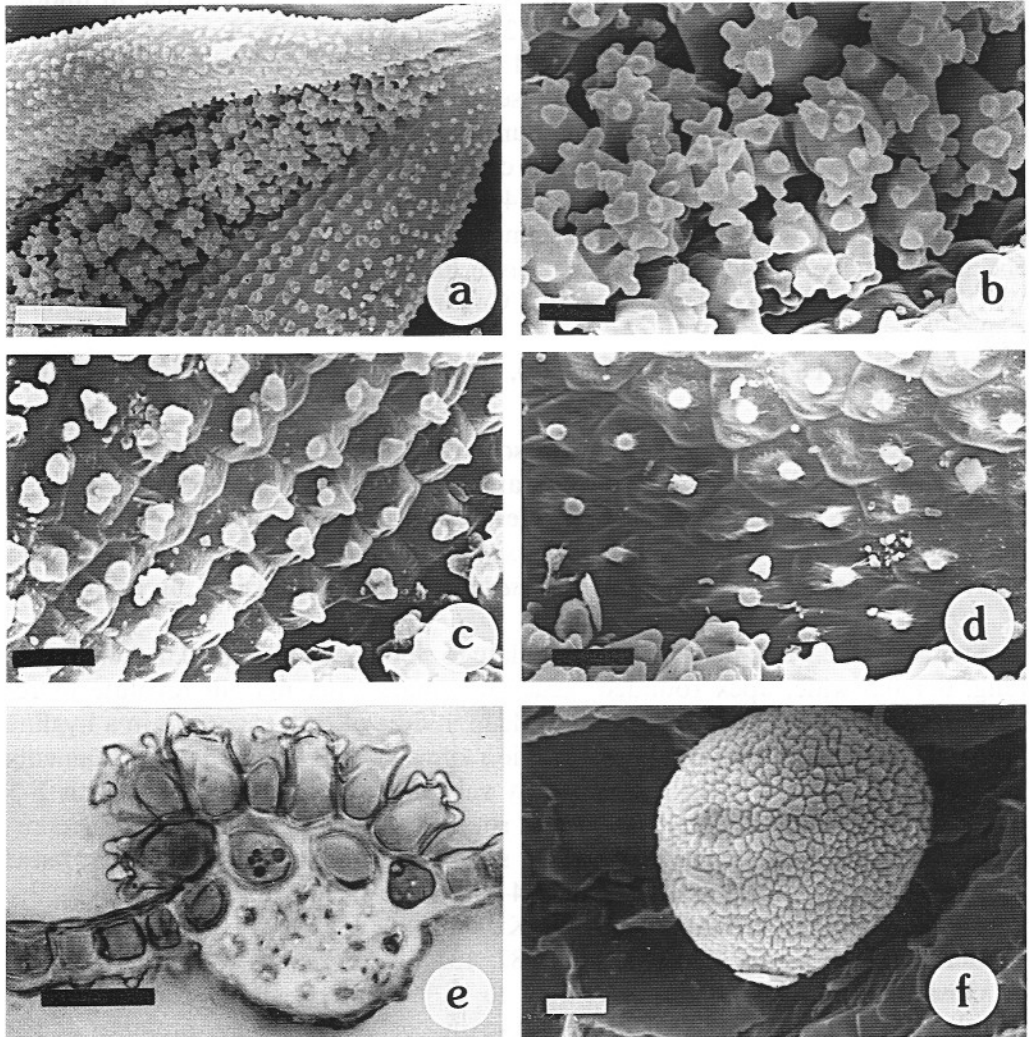


Fig. 5. *Crossidium aberrans* (from Ros & al. in MUB2399). *a* Adaxial surface of leaf. *b* Supracostal filaments. *c*, *d* Lamina cells. *e* Cross section of leaf. *f* Spore. Bars: *a*: 50 μm ; *b*–*d*: 10 μm ; *e*: 35 μm ; *f*: 1 μm

agonal-quadrate, 10–20 μm long; upper and median cells smooth or with 1–2 simple or bifurcate papillae; basal cells rectangular, 14–50 μm long. Perichaetial leaves oblong-ovate to spatulate. Seta 8–17 mm long; capsule elongated-ovoid to nearly cylindrical, 1.4–2.4 mm long; operculum conical, 0.8–1.2 mm. Spores 9–11 μm in diameter.

Distribution. Saudi Arabia, Algeria, Canada, Spain, United States, France, Jordan, and Mexico. The first report for Europe was by ROS & GUERRA (1986).

Illustrations. HOLZINGER & BARTRAM (1924: 7 and 9), DELGADILLO (1975: 272), ROS & GUERRA (1986: 72), FREY & KÜRSCHNER (1988: 125).

6. *Crossidium geheebii* (BROTH.) BROTH., Nat. Pfl. 1: 426. 1902 (Fig. 6 a–f). Type: New Zealand, ubi loco haud propius designato legit READER [Isotype (?) H!]. Basionym: *Tortula geheebii* BROTH., Oefv. Finsk. Vet. Soc. Foerh. 42: 98. 1900.

Stems up to 3 mm high. Leaves oblong to ovate, 0.7–1.5 mm long, 0.4–0.65 mm wide; apex obtuse to rounded; margin recurved. Costa 57–65 μm wide in middle of leaf, excurrent in hyaline hair-point 0.2–0.5 mm long, sometimes excurrent in a mucro; cross-section showing 3–4 stereid layers; filaments 4–5(–6) cells high; terminal cell 12–20 μm , generally subglobose, with 4–8 papillae. Upper cells of leaf quadrate, rectangular or more or less rounded, 10–20 μm long, smooth or with 1–3 small inconspicuous papillae; median cells quadrate to rectangular, 12–24 μm long; basal cells rectangular to quadrate, 14–50 μm long. Seta 5–10 mm long; capsule cylindrical to elongated-ovoid, 1.3–2.2 mm long; peristome teeth twisted, 315–660 μm long; operculum conical, 0.5–0.8 mm long. Spores 12–16 μm in diameter.

Distribution: New Zealand, Australia, Canary Islands (DIRKSE & al. 1993) and Egypt.

Illustrations: DELGADILLO (1975: 272), CATCHESIDE (1980: 151), FREY & KÜRSCHNER (1988: 125).

7. *Crossidium deserti* FREY & KÜRSCHNER, Nova Hedwigia 45: 132. 1987 (Fig. 7 a–d). Type: Saudi Arabia, Thumama, 70 km NNE of ar-Riyad (Arumah Plateau), 660 m, on soil between limestones, KÜRSCHNER, 23 October 1984, 1–3931 (84–500) (Holotype: B!). **Synonym:** *Crossidium desertorum* FREY & KÜRSCHNER, Nova Hedwigia 45: 132. 1987, non *C. desertorum* HOLZ. & BARTR., Bryologist 26: 72. 1923.

Stems up to 2.2 mm high. Leaves lingulate to slightly spatulate, 0.6–0.8(–1) mm long, 0.4–0.5 wide; apex rounded, generally emarginate, margin revolute to recurved. Costa very narrow, 38–44 μm wide in middle of leaf, excurrent in a hyaline hair-point 0.15–0.32 mm long; cross-section showing 2–3 stereid layers; filaments 3–6 cells high, the terminal cell generally subspherical, 14–24 μm long, with 2–5 papillae. Upper and median cells of leaf rounded-hexagonal, quadrate or rectangular, 10–16 μm long, smooth or with 1 simple and inconspicuous papilla; basal cells rectangular, sometimes quadrate, 14–40 μm long. Sporophyte unknown.

Distribution. Saudi Arabia (FREY & KÜRSCHNER 1987).

Illustration. FREY & KÜRSCHNER (1987: 133).

Observations. This species is related to *C. crassinerve*, but differs in (a) its lingulate-spatulate leaves, (b) its very narrow costa, and (c) the presence of supracostal filaments which are loosely arranged and markedly branched.

8. *Crossidium crassinerve* (DE NOT.) JUR., Laubmoosfl. Oesterr. Ungarn. 128. 1882 (Fig. 7 e–h). Type: Ad margines agrarum et in collibus ad vias circa Calarium

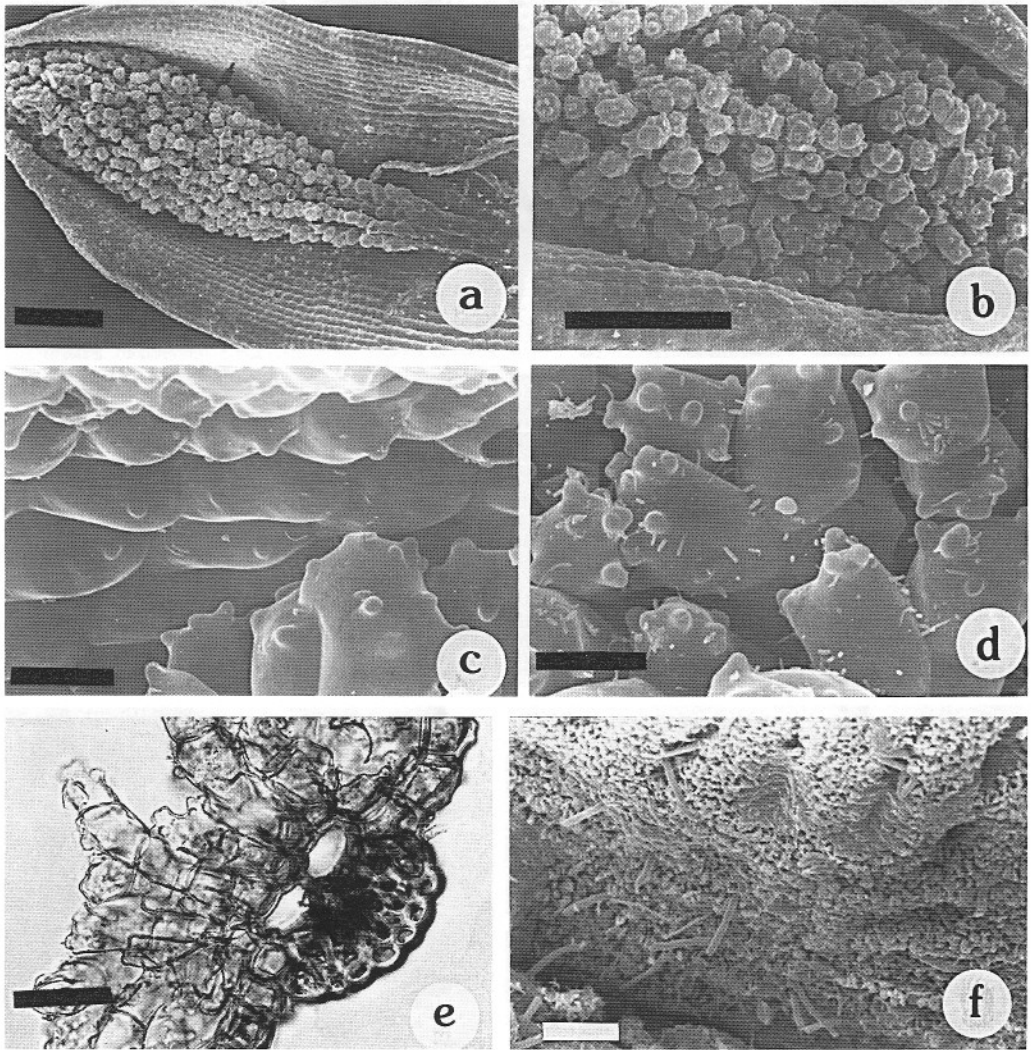


Fig. 6. *Crossidium geheebii* (from WEBER BRYO 50550 in B). *a, b* Adaxial surface of leaves. *c* Lamina cells and terminal cells of filaments. *d* Supracostal filaments. *e* Cross section of leaf. *f* Basal membrane of peristome. Bars: *a, b*: 100 μm ; *c, d, f*: 10 μm ; *e*: 35 μm

vulgo [Holotype (?): RO!]. **Basionym:** *Tortula crassinervia* DE NOT., Mem. R. Acc. Sc. Torino 40: 303. 1838.

Stems up to 3 mm high. Leaves ovate to oblong-ovate, (0.4)0.6–1.3 mm long, 0.3–0.5(–0.7) mm wide; apex generally obtuse; margin revolute to recurved. Costa 48.6–81(–100) μm wide in middle of leaf, excurrent in a hyaline hair-point 0.1–1(–1.5) mm long; cross-section showing 2–5 stereid layers; filaments 2–12 cells high, the terminal cell generally cylindrical, conical or rarely subspherical, 9–28 μm long, with 2–4 papillae, sometimes smooth. Upper cells of leaf quadrate, rectangular or rhomboid-oval, 8–20 μm long; median cells quadrate to rectangular, 8–22 μm long; basal cells rectangular, sometimes quadrate, 14–50 μm long. Seta 6–13 mm long; capsule elongated-ovoid, 0.9–2.2(–2.5) mm long; peristome teeth twisted, 450–

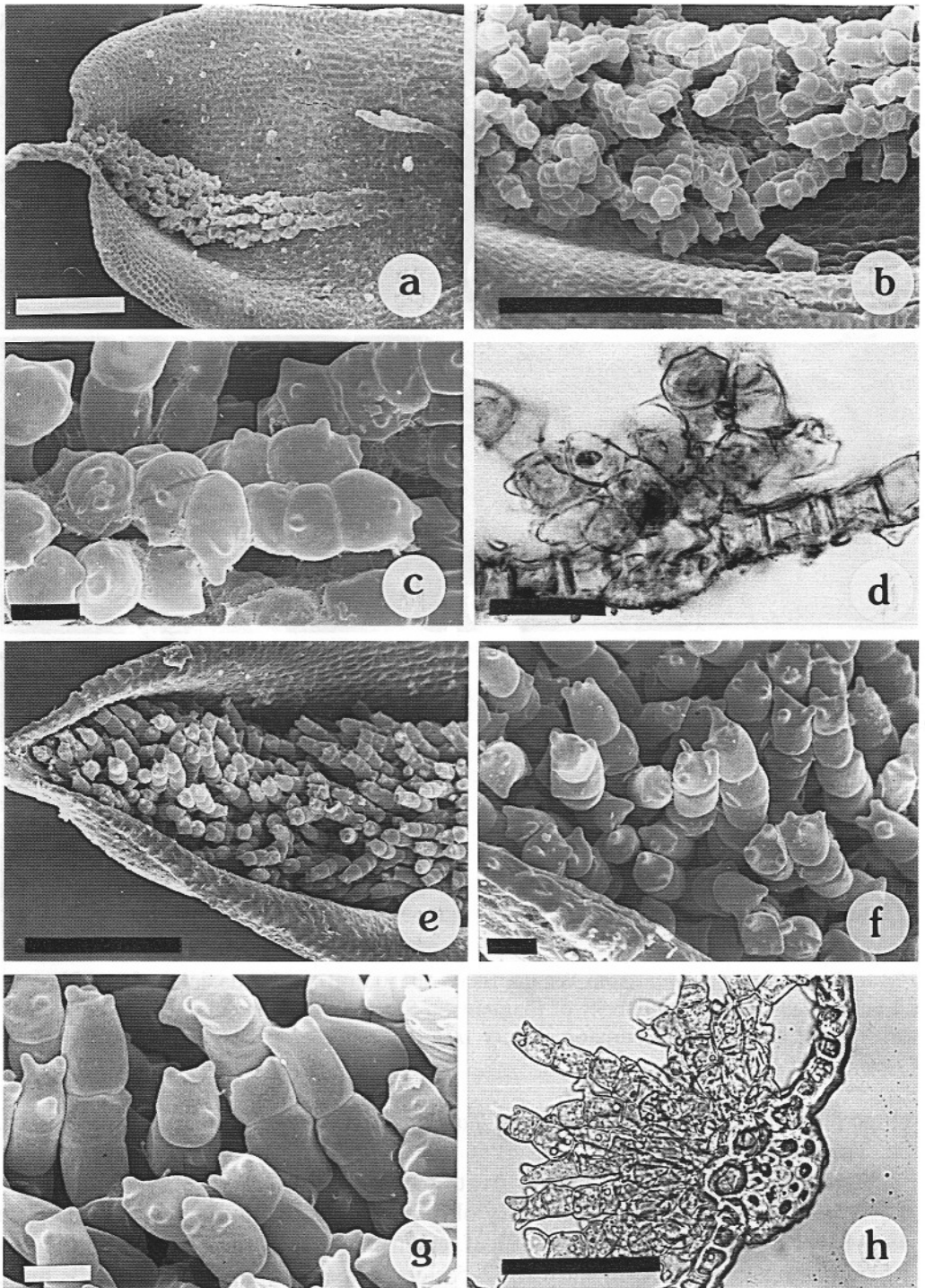


Fig. 7. *Crossidium deserti* (a–d from FREY 1-4558 in Herb. Frey) and *C. crassinerve* (e–h from GUERRA & ROS in MUB 3031). a, e Adaxial surfaces of leaves. b, c, f, g Supracostal filaments. d, h Cross sections of leaves. Bars: a, b, e, f: 100 μ m; c, g: 10 μ m; d: 40 μ m; h: 60 μ m

820 μm long; operculum conical or rostrate, 0.5–0.9(–0.95) mm long. Spores 9–16 μm in diameter.

Distribution. Europe (!), Africa 1 (!), America 1 (!), 2 (!), Asia 1, 2, 3 (!), 5 (!).

Illustrations. CRUM & ANDERSON (1981: 357), BRUCH & al. (1836–1851).

9. *Crossidium laevipilum* THER. & TRAB., Bull. Soc. Hist. Nat. Afr. Nord. **22:** 161. 1931 (Fig. 8 a–c). **Type:** Algeria, Sahara Septentrional, Ghardaia (Mزاب), sur la terre dans les fissures des rochers calcaires après les pluies, 18-2-1928, MAIRE, no 2463, p.p. (Holotype: PC!). **Synonym:** *Crossidium crassinerve* var. *laevipilum* (THER. & TRAB.) DELGADILLO, Bryologist **78:** 275–276. 1975.

Stems up to 3 mm high. Leaves ovate to oblong-ovate, 0.4–0.7 mm long, 0.3–0.7 mm wide; apex rounded and cucullate; margin revolute to recurved. Costa 30–

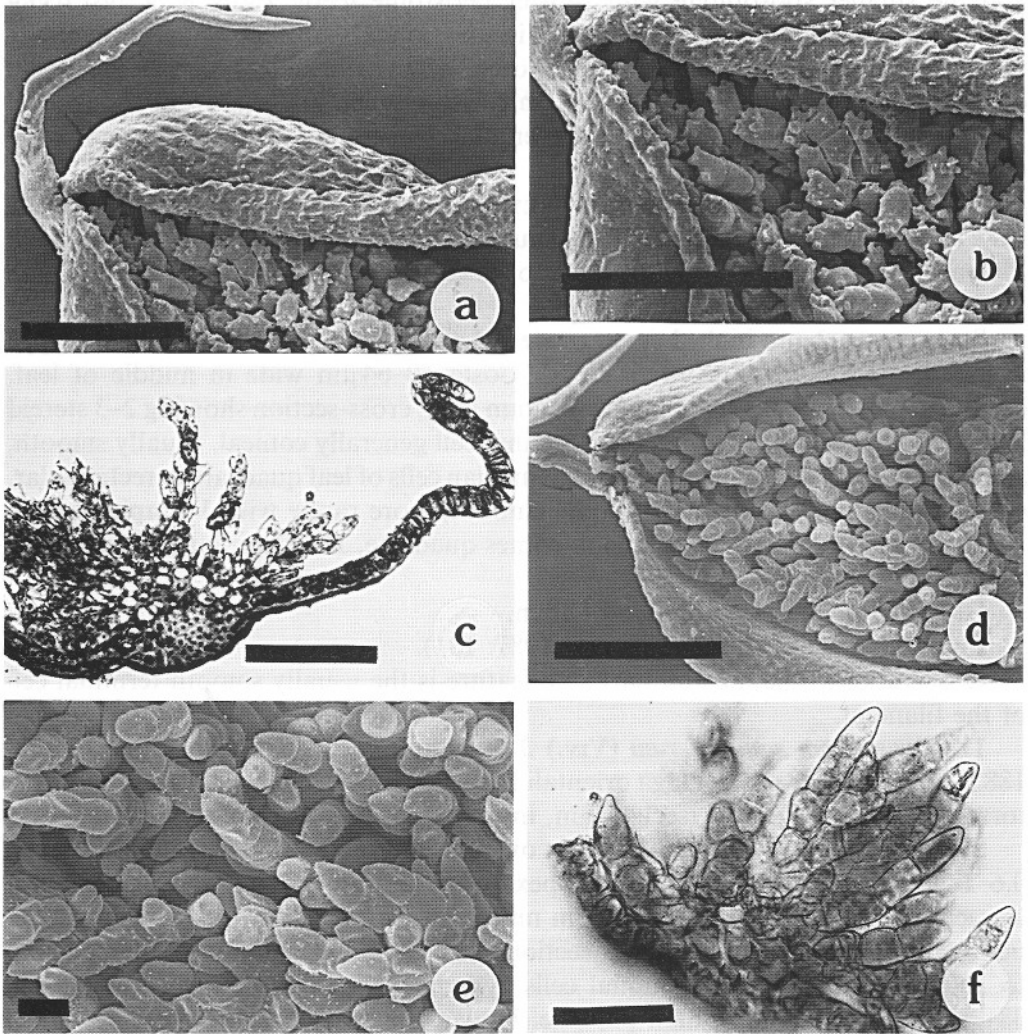


Fig. 8. *Crossidium laevipilum* (a–c from MARTÍNEZ-SÁNCHEZ in MUB4092) and *C. laxefilamentosum* (d–f from FREY 1-3936 in Herb. Frey). a, b, d Adaxial surfaces of leaves. c, f Cross section of leaves. e Supracostal filaments. Bars: a, b, d: 100 μm ; c: 80 μm ; e: 10 μm ; f: 50 μm

73 μm wide in middle of leaf; excurrent in a mucro or hyaline hair-point 0.1–0.8 mm long; cross-section showing 2–5 stereid layers; filaments 2–10 cells high, the terminal cell cylindrical, conical or subspherical, 14–24 μm long, with 2–6 papillae. Upper and median cells of leaf quadrate to rectangular, 10–22 μm long, smooth; basal cells short-rectangular or quadrate, 14–38 μm long. Seta 4–6 mm long; capsule oblong to elongated-ovoid, 0.8–1(–1.4) mm long; peristome teeth generally straight, 200–300(–500) μm long; operculum conical 0.5–0.7 mm long. Spores 8–13 μm in diameter.

Distribution. Northern Africa, Spain (new to Europe), Israel, and Jordan.

Illustrations. THERIOT (1931: 22), FREY & KÜRSCHNER (1991: 443).

Observations. It can be separated from *C. crassinerve* on account of its leaves imbricate when dry, the strongly cucullate leaf apex which is sometimes mucronate, and the smaller sporophyte with shorter peristome teeth. FREY & KÜRSCHNER (1991) suggested that the development of innovations also differs. Thus, innovations in *C. laevipilum* were described as basitonic, whereas in *C. crassinerve* they were considered to originate from rhizoids. In revising much material from the Iberian Peninsula and northern Africa, however, this feature has not been found to be constant.

10. *Crossidium laxefilamentosum* FREY & KÜRSCHNER, Nova Hedwigia 45: 130. 1987 (Fig. 8 d–f). Type: Saudi Arabia. Thumama, 70 km NNE of ar-Riyad (Arumah Plateau), 630 m, on soil between sandstones (Biyadh sandstones), FREY, 5 March 1985, 1–3932 (85–247 a) (Holotype: B!).

Stems up to 3 mm high. Leaves ovate 0.4–0.8 mm long, 0.3–0.5 mm wide; apex rounded; margin revolute to recurved. Costa 50–64 μm wide in middle of leaf, excurrent in a hyaline hair-point 0.2–0.4 mm long; cross-section showing 2–3 stereid layers, filaments 4–8 cells high, the terminal cell generally conical, usually smooth, sometimes with 1–2 papillae. Upper and median cells of leaf quadrate to rectangular, sometimes hexagonal, 10–18 μm long, smooth, more rarely with 1 simple papilla; basal cells generally rectangular, sometimes quadrate, 15–30 μm long. Sporophyte unknown.

Distribution. Saudi Arabia and Oman.

Illustration. FREY & KÜRSCHNER (1987: 131).

Observations. The most remarkable feature is the usually smooth terminal cell of the filament.

11. *Crossidium squamiferum* (VIV.) JUR., Laubmoosfl. Oesterr. Ungarn. 127. 1882 (Fig. 9 a–f). Type: In Plaga orientali Liguria. Legnaro nella di Levanto, prope torrentem Valle da Fonda, secus viam, in murorum fissuris (Holotype: not seen).

Stems up to 7(–9) mm high. Leaves ovate to oblong-ovate or ovate-lanceolate, 0.6–1.5 mm long, 0.5–0.95 mm wide; apex obtuse to rounded, serrulate; margin flat to recurved. Costa 58–125 μm wide in middle of leaf, excurrent in a hyaline hair-point 0.3–2.7(–3.2) mm long; cross-section showing 2–4 stereid layers; filaments up to 10(–11) cells high, the terminal cells cylindrical or conical, thick-walled, 16–38 μm long, with 1–3(–5) high papillae. Upper and median cells of leaf rhombic, rectangular or more or less round, 10–30 μm long, with very thick walls, the apical and marginal cells hyaline, nearly linear, with lumens nearly obliterated, forming a whitish marginal band; basal cells rectangular or quadrate, 10–63 μm long. Seta 4–19 mm long; capsule elongated-ovoid to cylindrical, 1–3 mm long; peristome teeth

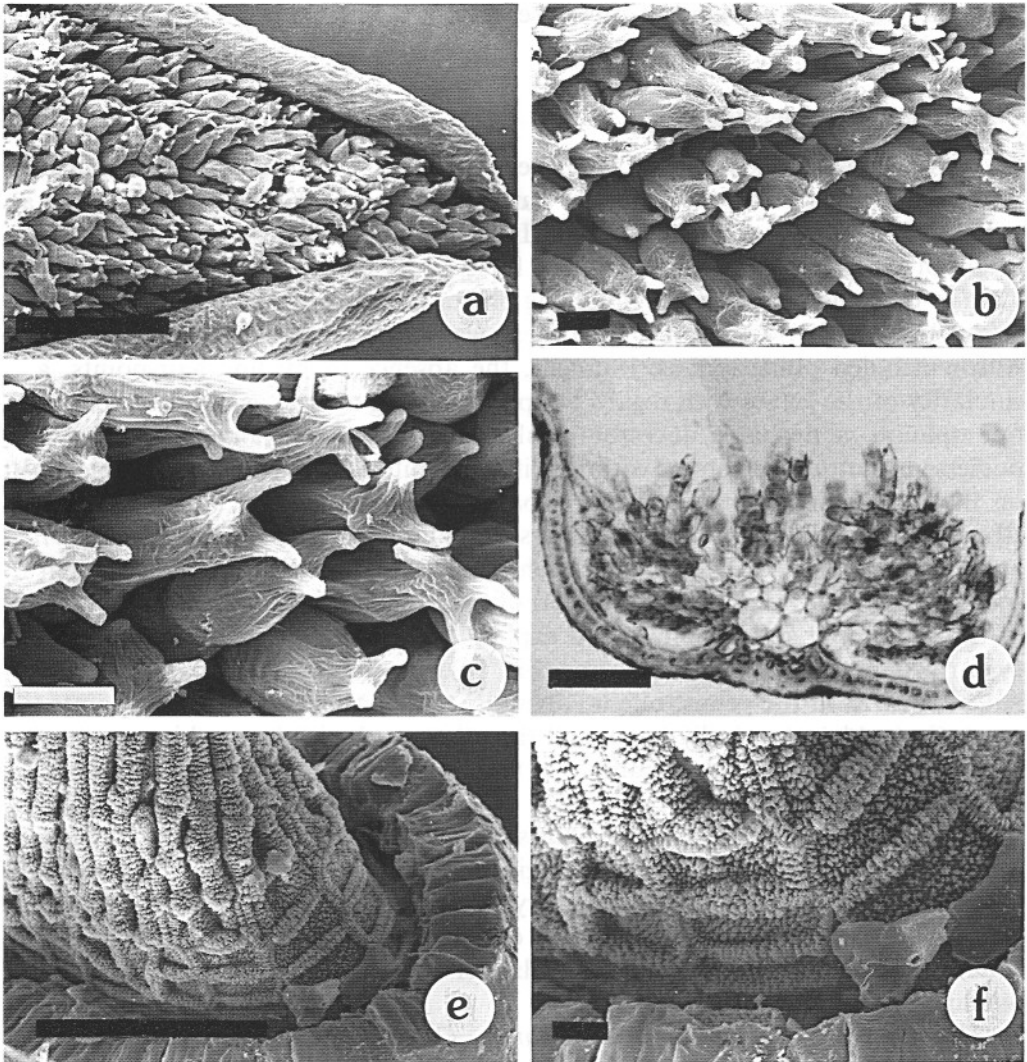


Fig. 9. *Crossidium squamiferum* (from ROS & MOYA in MUB 4438). *a* Adaxial surface of leaf. *b, c* Supracostal filaments. *d* Cross section of leaf. *e, f* Basal membrane of peristome. *a, e*: 100 μ m; *b, c, f*: 10 μ m; *d*: 90 μ m

long and strongly twisted, or short, irregular and generally straight, 160–1110 μ m long; basal membrane with pronounced rectangular, sometimes quadrate, foveae; operculum conical or rostrate, 0.54–1.55 mm long. Spores 11–20 μ m in diameter.

Distribution. America 1, Asia 1, 3 (!), 5 (!), Africa 1 (!), Europe (!).

Illustration. DEMARET & CASTAGNE (1959: 343).

Observations. The correlation between undifferentiated leaf margin and small sporophyte, which has been used to define the var. *pottioideum*, is not, in our opinion, constant. It would, therefore, appear inappropriate to maintain the variety, and this is in agreement with the view of DELGADILLO (1975). EL OQLAH & al. (1988) note that the var. *pottioideum* occurs in more arid, desert-like conditions

than the var. *squamiferum* but our observations do not support this habitat difference.

Phylogenetic considerations

Two phylogenetic schemes have so far been proposed for the genus *Crossidium* one by DELGADILLO (1975), the other by FREY & KÜRSCHNER (1984), and include all species which were known at the time. In addition, a plausible hypothesis for the origin of the genus *Crossidium* was put forward by CHEN (1941) who proposed a *Tortula*-type ancestry, perhaps involving plants which shared similarities with *Tortula atrovirens* (SM.) LINDB. The hypothesis was based on morphological characters which included pluripapillose leaf-cells, the absence of hyaline hair-points, and similarity of the leaves with regard to spiral twisting as well as costa structure. In our opinion, a probable ancestor would have lacked a hyaline hair-point and possessed a Pottioid peristome with 32 filiform papillose segments, equally thickened on the inner and outer layers, and a basal membrane with a marked reticulate structure. This combination of characters is common in numerous species of *Tortula* and *Tortella* (cf. VITT 1984). From such an ancestor, progressive development of specialized structures on the ventral part of the nerve and modification or reduction of the leaves and sporophytes could explain the origin of *Crossidium*. According to our proposed phylogenetic scheme (Fig. 10), two main evolutionary lines would have appeared in the genus: one involving species without hyaline hair-points (*C. rosei*, *C. davidai*, *C. spiralifolium*), and the other, ecologically-speaking, more successful, consisting of a larger number of taxa, the species that possess hyaline hair-points on their leaves.

The appearance of hyaline hair-points in *Crossidium* species could be considered to represent an important ecophysiological adaptation associated with successful colonization of dry soil in arid territory. Hair-points are involved in capture of water when leaves are contracted and curved during periods of drought (BELL 1982). It is accepted that this structure also serves as protection against mechanical damage by sunlight (SCOTT 1982).

The most primitive species (*C. seriatum*, *C. rosei*) possess a large number of papillae per leaf-cell, 4–6(–8), as in the hypothetical ancestor. Indeed, the papillosity of both, especially *C. rosei*, recalls the type found in present-day species of *Tortula*, although *C. rosei* has undergone considerable modification of the peristome, which is reduced to the basal membrane.

A subsequent modification common to both evolutionary lineages appears to have involved a reduction in the number of papillae per cell, an outcome particularly marked in the line giving rise to species with hyaline hair-points. Thus, *C. aberrans*, which is closely related to *C. seriatum* as regards leaf-form, differs from it in having only 1–2 papillae per cell. This reduction in leaf papillosity seems to have continued: *C. geheebii* has reduced leaf papillosity (1–3 papillae per cell) and papillosity is even less in *C. deserti*, vanishing almost entirely in the *C. crassinerve* group (*C. crassinerve*, *C. laevipilum*, *C. laxefilamentosum*). With respect to *C. rosei*, *C. davidai* seems to have undergone marked reduction in papillosity, while *C. spiralifolium* has completely smooth cells.

Increase in the number of cells per supracostal filament seems to be correlated with a fall in leaf papillosity in both evolutionary lines. In the lineage lacking

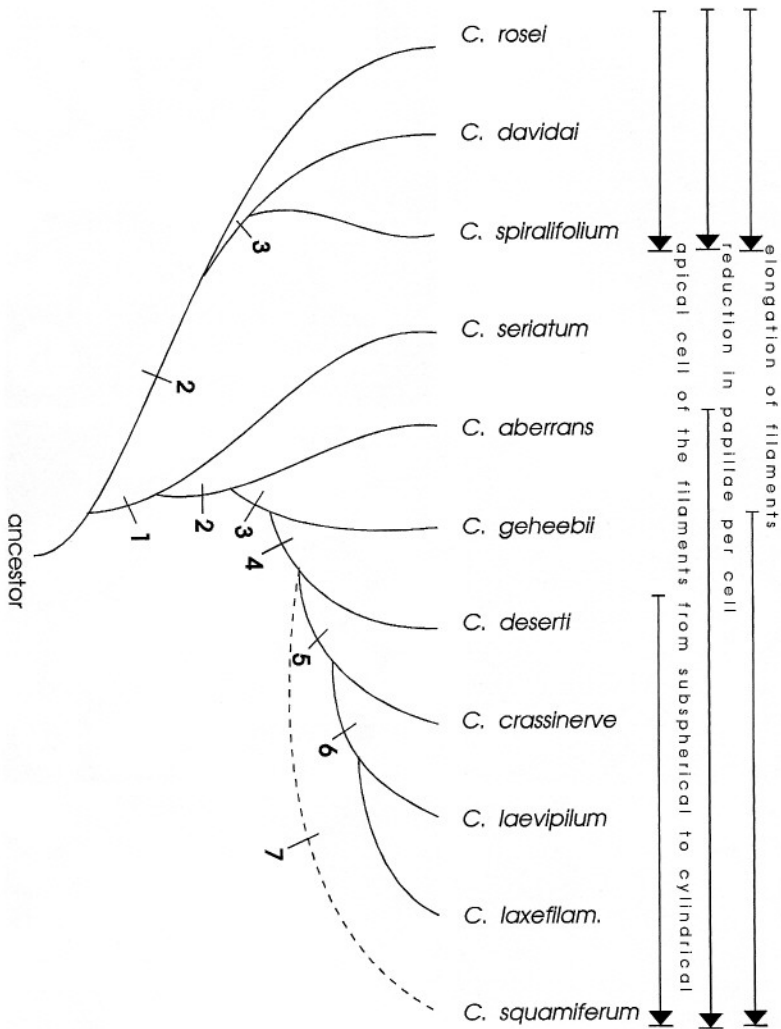


Fig. 10. Putative phylogenetic relationships among *Crossidium* species. 1 Appearance of hyaline hair-point. 2 Reduction in the number of papillae per cell. 3 Increase in the number of cells per supracostal filament (elongation of filaments). 4 Transformation of the apical cell of the filaments from subspherical to cylindrical. 5 Reduction in the number of papillae on the apical cell of filaments. 6 Appearance of cucullate leaf apex and reduction of peristome teeth. 7 Thickening of the leaf cell walls and filaments

hyaline hair-points, the shortest filaments are seen in *C. rosei* and the longest in *C. spiralifolium*. Progressive increase in filament length is likewise to be seen in the lineage with hyaline hair-points. Filaments with 1–2(–3) cells are characteristic in *C. aberrans* and *C. seriatum*, giving way to species with ever longer filaments: *C. deserti* (3–6 cells), *C. geheebii* (4–6 cells), *C. crassinerve* (2–12 cells).

In our opinion, an important clue hinting at the primitive nature of species lacking hyaline hair-points is the fact that in the three such species the apical cell of the filament has remained subspherical, notwithstanding both a clearly progressive reduction in the number of papillae per leaf cell and elongation of supra-

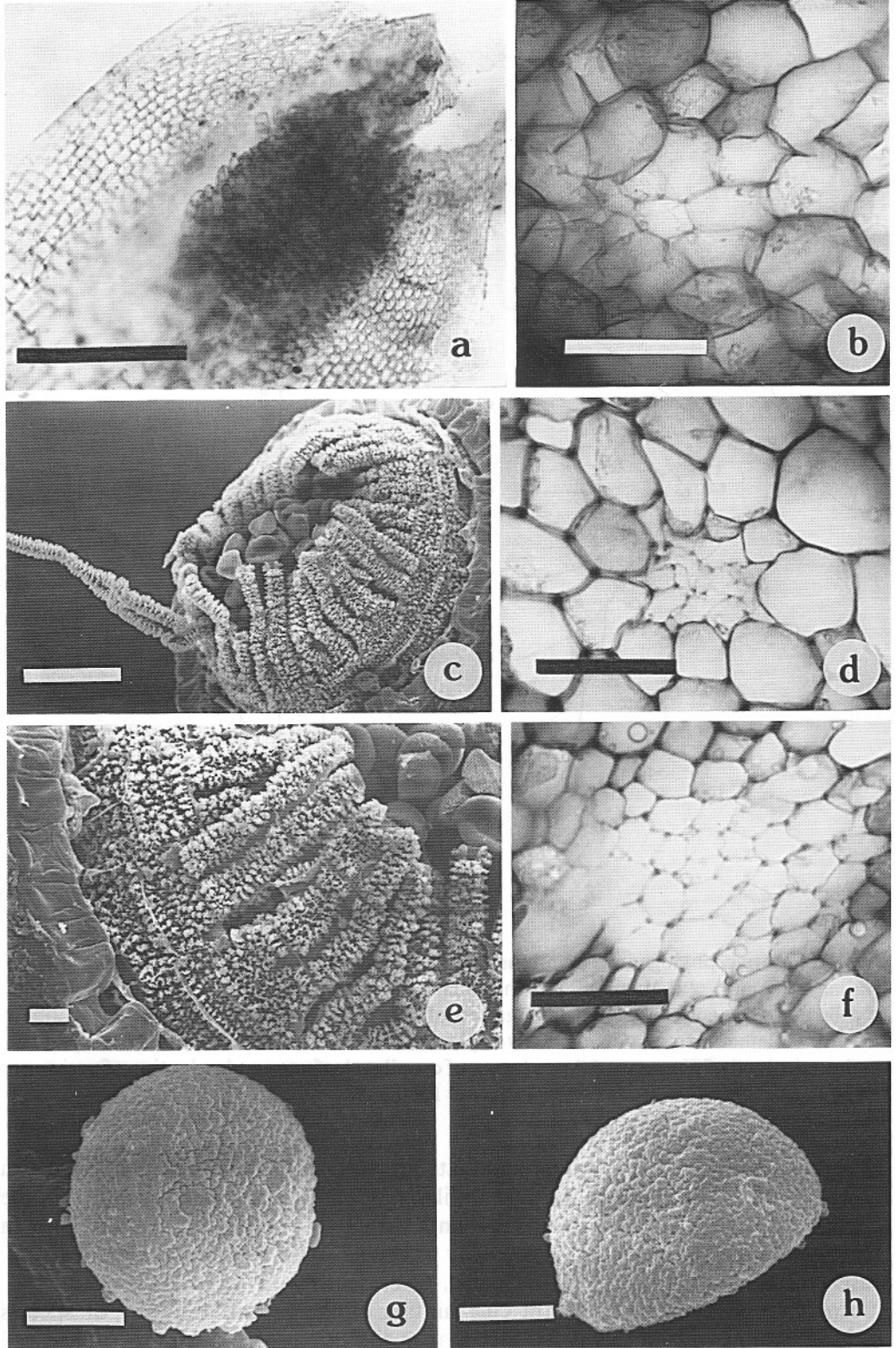


Fig. 11. *Microcrossidium apiculatum* (a–c, e, g, h from MAGILL & SCHELPE 3893 in MO). a Adaxial surface of leaf. b Cross section of stem, note absence of central strand. d, f Central strand in *Crossidium* and *Pottia*, respectively. c, e Peristomes. g, h Spores. Bars: a: 0.2 mm; b, d, f: 0.04 mm; c: 50 μ m; e: 10 μ m; g, h: 5 μ m

costal filaments. The filament apical cell however, tends to a more cylindrical shape from *C. deserti* toward *C. squamiferum*, together with reduced papillosity of the apical cell. Both the process of transformation of the apical cell from subspherical to cylindrical, and that of reduction in the number of papillae borne by it, seem to have culminated in *C. crassinerve*, *C. laevipilum*, *C. laxefilamentosum* and, above all, *C. squamiferum*. *C. squamiferum* retains what may well be a primitive character in its very developed and foveolate basal membrane of the peristome. However, thickening of the cell walls of the leaves and filaments, the cells of which are fully cylindrical, coupled with a complete absence of leaf papillosity, support the inference that it is the most evolved species.

***Microcrossidium* GUERRA & CANO, gen. nov.** (Fig. 10 a–c, e, g, h)

A genere *Crossidium* JUR. differt caulibus cylindro centrali carentibus, peristomate dentibus 16, duplicibus, erectis leniterque articulatis constanti atque parietibus sporarum caracteribus.

Type: *Crossidium apiculatum* MAGILL.

Following examination of a number of samples of *C. apiculatum* MAGILL (including the type) from South Africa, we have concluded that *C. apiculatum* shares with typical *Crossidium* only the presence of supracostal filaments. Firstly plants are bulbiform, to 1 mm, with appressed leaves, and they resemble any small *Pottia* (REICHENB.) FÜRN. Plants belonging to *Crossidium* are larger and the leaves tend to become spirally twisted when dry. Secondly, unlike *Crossidium* (Fig. 11 d), the stem of *C. apiculatum* lacks a central strand, and in this it also differs from *Pottia* (Fig. 11 f). Thirdly, peristome morphology clearly differs from that of *Crossidium*. In *C. apiculatum*, not only are the 16 incomplete teeth double, but their articulation is little marked and they remain erect when dry. Finally, the spore sculpturing of *C. apiculatum* is distinctive. Whereas that of *Crossidium* displays a vermiculate pattern formed by interconnecting perinic granulae, the spore surface of *C. apiculatum* is additionally ornamented by several layers of granulae, which give rise to an irregularly granulate pattern, and shows no tendency to a vermiculate pattern.

***Microcrossidium apiculatum* (MAGILL) GUERRA & CANO, comb. nova.** **Basionym:** *Crossidium apiculatum* MAGILL, Flora of Southern Africa: 195. 1981. **Type:** Cape, Knersvlakte, near Kobee, 6 km NE of Vanrhynsdorp, along road to Niewoudtville, MAGILL & SCHELPE 3877 (Isotype: MO!).

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