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Antipodal mosses: XV. Taxonomy and distribution of *Schistidium cupulare* (Bryopsida: Grimmiaceae)

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ABSTRACT: *Schistidium cupulare* (Müll. Hal.) Ochyra, an obscure and poorly known species originally described from Îles Kerguelen as *Grimmia cupularis* Müll. Hal. and subsequently reported from a single station in the Antarctic, is re-assessed taxonomically. It is considered to be a distinct species of sect. *Conferta*, closely related to *S. amblyophyllum* (Müll. Hal.) Ochyra *et* Hertel, from which it differs in its distal- and mid-leaf areolation of short, isodiametric, quadrate to shortly rectangular cells; stouter costa, 50–75 µm wide in the distal and median part, semi-terete to subrectangular in cross-section and prominently convex on the dorsal surface, (2–)3-stratose above, 3(–4)-stratose below; leaf margins regularly 2–3-stratose in 1–3 rows of cells forming fleshy, bulging limbidia; presence of a distinct central strand; and finely roughened to nearly smooth peristome teeth. *S. celatum* (Cardot) B.G. Bell from South Georgia and Tierra del Fuego is considered to be conspecific with *S. cupulare*. Some details of the type specimens of both species are illustrated. The geographical range of *S. cupulare* is evaluated and it is considered to be an amphiatlantic subantarctic species. A new record of the species from Livingston Island in the Antarctic is provided and a key to species of *Schistidium* in Antarctica is given.

Key words: Antarctica, Subantarctica, Tierra del Fuego, Bryophyta, Bryopsida, Grimmiaceae, *Schistidium*, taxonomy, distribution.

Introduction

At the turn of 1874 and 1875 Dr F.C. Naumann, a naturalist to the German Transit of Venus Expedition on the ship *Gazelle*, made a large collection of mosses on Îles Kerguelen. It was the first moss collection made on this remote subantarctic island since the famous British Antarctic Expedition of 1839–1843 on the ships *Terror* and *Erebus*. As a result of Naumann's collections during the *Gazelle* voyage, 80 species of mosses were described as new to science by Müller (1883, 1889). Among these, no less then 17 species were placed in the then all-encompasing genus *Grimmia* Hedw., although this author himself indicated their disposition in at least four sections of this genus which are now generally considered to be genera in their own right.

Four of these species were placed in sect. *Platystoma* Müll. Hal. which is an equivalent of the modern genus *Schistidium* Bruch *et* Schimp. and actually all these species have later been given names under this genus. These are mostly poorly known species and their unfamiliarity is strictly associated with generally very imperfect knowledge of the taxonomy of the genus *Schistidium* in the austral region. One of these species, *S. stylostegium* (Müll. Hal.) Zant. was considred conspecific with *S. amblyophyllum* (Müll. Hal.) Ochyra *et* Hertel (Ochyra and Hertel 1990). The remaining three species, namely *S. chrysoneurum* (Müll. Hal.) Ochyra, *S. serratomucronatum* (Müll. Hal.) Ochyra and *S. cupulare* (Müll. Hal.) B.G. Bell, have been merged by Bremer (1980), without any comment, with *S. apocarpum* along with many other exotic species of the genus, thus making the latter an exceedingly heterogeneous taxon which could hardly be defined and defended.

Schistidium cupulare was described as *Grimmia cupularis* from a single collection made on dry rocks in Foundery Branch and was characterized as being quite similar to small forms of *Schistidium apocarpum*, differing only in its wide-mouthed capsule. Since then, the species has only been rediscovered once on Îles Kerguelen, at Port Joanne d'Arc, and Thériot (1924) provided good illustrations of various details of the leaves and sporophytes but he did not discuss the affinities of the species. Finally, *S. cupulare* was recorded at a very distant locality on King George Island in the South Shetland Islands in the maritime Antarctic (Ochyra 1998). The Antarctic plants showed close correspondence to the Kerguelen type material and exhibited the close relationship to *S. amblyophyllum*.

During the course of the final work on the projected *Illustrated Moss Flora of Antarctica* (Ochyra *et al.* 1997, Lewis Smith *et al.* 1998) I have critically re-examined *Schistidium cupulare* for two reasons. Firstly, having examined a limited number of specimens, this species appeared to be so closely related to *S. amblyophyllum* that for a moment I considered them to be inseparable from one another. Accordingly, *S. cupulare* has been excluded from the list of species occurring in the Antarctic (Ochyra *et al.* 2003). Secondly, having considered some of the existing patterns in the distribution of austral mosses, the absence of *S. cupulare* from other subantarctic islands, especially from South Georgia, appeared to be quite strange. Therefore I paid special attention to taxa of *Schistidium* known from this island because many species of moss shows transatlantic disjunction occurring, on the one hand, in southern South America and South Georgia and, on the other, appearing on various islands in the Kerguelen Province in the southern Indian Ocean, for example *Schistidium falcatum* (Hook.f. *et* Wilson) B. Bremer, *Holodontium strictum* (Hook.f. *et* Wilson) Ochyra and *Bartramia patens* Brid. (Ochyra 1998). As a result of a revision of South Georgian species of *Schistidium* it has become evident that *S. celatum* (Cardot) B.G. Bell and *S. cupulare* are identical species and have to be considered conspecific, the latter having priority. In addition, examination of the larger number of specimens showed that *S. cupulare* and *S. amblyophyllum* are definitely different, though closely related species.

Description

Schistidium cupulare (Müll. Hal.) Ochyra

Fig. 1

Schistidium cupulare (Müll. Hal.) Ochyra, Fragm. Florist. Geobot. **43**: 105. 1998. — *Grimmia cupularis* Müll. Hal., Bot. Jahrb. Syst. **5**: 80. 1883. — TYPE CITATION: all species described as new by Müller (1883) are included in the section "I. Bryologia Kerguelensis"; later Müller (1889) wrote: "Ins. Kerguelen, Foundery branch, in rupibus siccis (11.1874) cum Andreaeis" [LECTOTYPE (*vide* Ochyra 1998: 169): "Ex Museo botanico Berolinensi. Grimmia cupularis C. Müll. n. sp. Kerguelenland. Foundery branch in rupib. siccis Nov. 1874 Dr. Naumann" – S-Dusén!; ISOTYPES: H-Broth!, PC-Card!, PC-Thér!).

Grimmia celata Cardot, Bull. Herb. Boissier Sér. 2, **6**: 22. 1906. — *Schistidium celatum* (Cardot) B.G. Bell, Brit. Antarct. Surv. Bull. **63**: 86. 1984. — TYPE CITATION: [South Georgia] Cumberland bay: connecting valley between S. and W. fiords [HOLOTYPE: "Svenska Sydpolarexpeditionen 1901–03. Ser. Nr 318 in parte. Grimmia celata Card. sp. nova Géorgie du Sud: baie Cumberland, vallée entre les fjords S. and O. D. 21./5 1902 Carl Skottsberg. Det. J. Cardot" – PC-Card!; ISOTYPES: S!, S-Roth/Möller!], *syn. nov.*

Plants small to medium-sized, forming short, rigid, compact cushions, not or somewhat lustrous, yellow- or olive-green above, brown to blackish-brown below, sometimes blackish throughout. *Stems* erect, 0.5–2.0 cm tall, copiously dichotomously branched, in transverse section rounded, consisting of 2–3 layers of small, brown, stereid or substereid cortical cells with strongly thickened walls and small lumina, rather sharply demarcated from 3–4 layers of large, hyaline to yellowish-hyaline medullary cells with moderately thickened walls, central strand present, usually large; *rhizoids* usually copious at the base of the stem, long, brown, branched, smooth; *axillary hairs* filiform, composed of 6–9 cells, hyaline throughout, composed of 2–4 short basal and elongate distal cells. *Leaves* densely set, closely imbricate and erect on drying, erecto-patent on wetting, not ranked, straight to somewhat curved, narrowly ovate-lanceolate to more widely ovate- to oblong-lanceolate, (0.9–)1.3–2.1(–2.4) mm long, 0.3–0.6 mm wide, non-decurrent, sharply keeled in the distal part, narrowly canaliculate in the proximal portion, gradually tapering to the acute or sometimes rounded and obtuse apex, epilose, or the uppermost leaves shortly piliferous, with a short, to 0.4 mm long, hyaline or yellowish-hyaline awn; *hair-point* short, to 0.4 mm, straight, flattened, bluntly denticulate, hyaline, yellowish-hyaline to yellowish-brownish, mostly non-decurrent; *margins* entire, recurved on both sides for varying distances, usually to 4/5–5/6 way up the leaf, plane or somewhat deflexed near the apex, 2(–3)-stratose in the distal portion forming 1–2(–3)-seriate fleshy, bulging limbidia, becoming unistratose with frequent bistratose patches in the proximal portion; *costa* ending in the apex or somewhat below, smooth, strong, 50–75 μm wide above, becoming thinner towards the base, distinctly convex on the dorsal surface, in transverse section semi-terete to subrectangular 2–3-stratose above, 3(–4)-stratose in the proximal portion; *laminal cells* unistratose throughout or with occasional bistratose streaks, patches or short striae below the apex, smooth, mostly

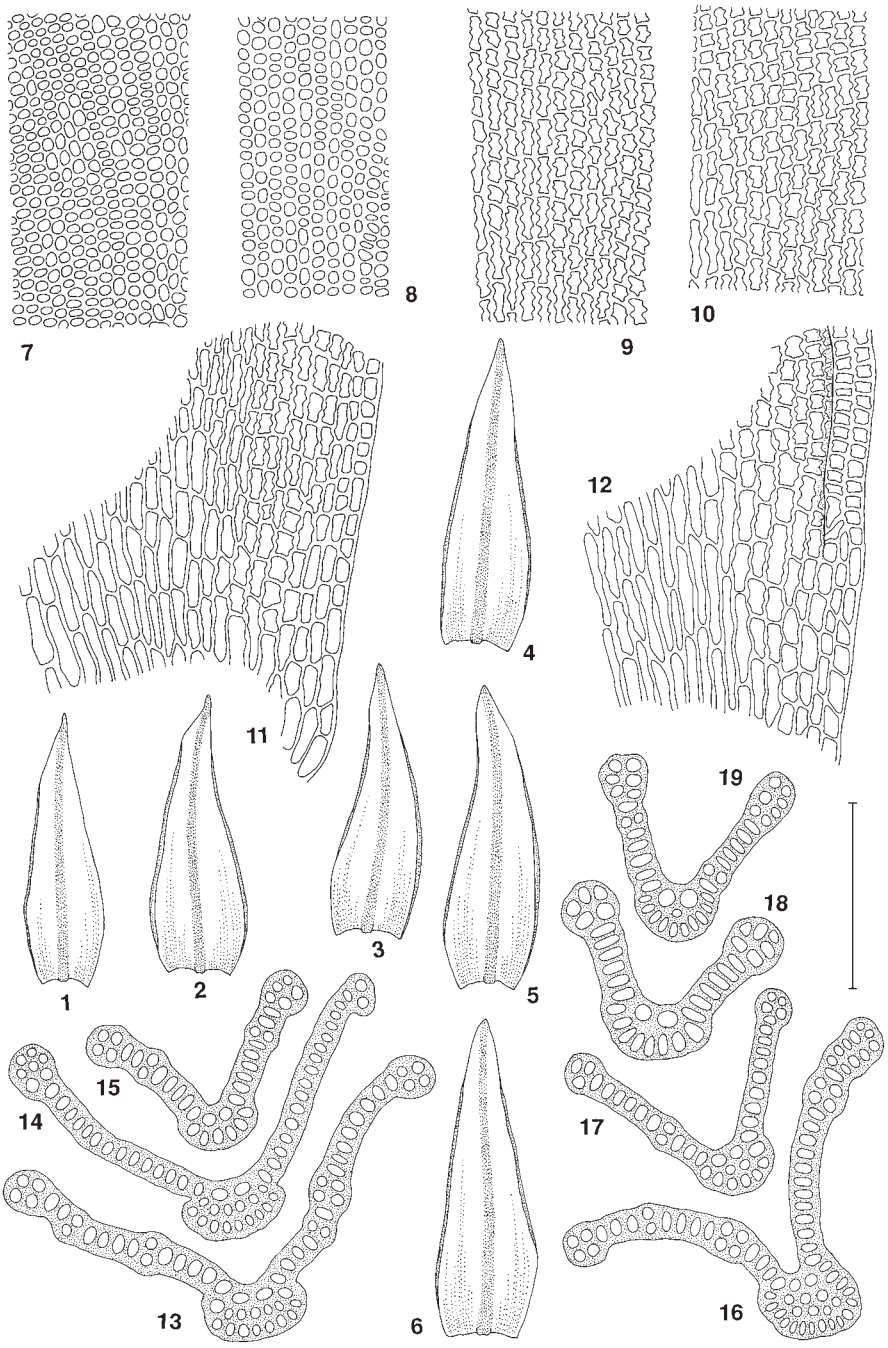

Fig. 1. *Schistidium cupulare* (Müll. Hal.) Ochyra. **1–6**. Leaves. **7–8**. Mid-leaf cells. **9–10**. Supra-basal leaf cells. **11–12**. Basal leaf cells. **13–19**. Transverse sections of leaves [1–3, 7, 9, 11, 13–15 from *Skottsberg 318 pp*., isotype of *Grimmia celata*; 4–6, 8, 10, 12, 16–19 from *Naumann s.n.*, XI.1874, lectotype of *G. cupularis*; both in S]. Scale bar: 1 mm (1–6) and 100 mm (7–19).

isodiametrical, irregularly quadrate to shortly oblong in the upper and median parts, sometimes oblate near the apex, 4–9(–12) µm long, 3–8(–12) µm wide, with straight or weakly sinuate, but not distinctly sinuose or nodulose walls, becoming long-rectangular, 20–40 µm long, 5–10(–13) µm wide, with weakly to strongly sinuose walls in the supra-basal area; *basal juxtacostal cells* long-rectangular to linear, 35–90 µm long, 5–10 µm wide, becoming shorter towards the margins, hyaline or yellowish-hyaline and usually sharply demarcated from intensively yellow supra-basal cells, with thick or often thin walls, making the basal areolation lax, and consistently straight walls throughout the base; *basal marginal cells* hyaline, subquadrate to oblong, translucent, straight-walled, with markedly thickened transverse walls, forming a more or less distinct, 1(2–3)-seriate marginal border composed of 10–25 cells. *Autoecious*. *Perichaetial leaves* very large, up to twice the size of vegetative leaves, erect, straight and rather stiff, concave, widely oblong- or ovate-lanceolate to ovate, 2.0–3.2 mm long, 0.8–1.2 mm wide, gradually acuminate to a short, acute or less often broadly obtuse cuspidate point, recurved on both side in the upper half, epilose or ending with a short, hyaline or yellowish-hyaline, smooth hair-point, to 0.3 mm long, with an areolation of irregular cells with strongly incrassate cells in the upper half, becoming rectangular and sinuose-walled in the median and lower parts and thinner- and straight-walled in the proximal part. *Seta* short, 0.25–0.4 mm long, pale yellowish-brownish, straight, thick; *capsule* profoundly immersed in the perichaetial leaves, ovoid to obloid, sometimes suburceolate, wide-mouthed, 0.7–1.0 mm long, 0.7–0.9 mm wide, pale yellowish to light brownish, smooth; *operculum* convex, rostellate, with a slanted or straight rostrum; *exothecial cells* irregular, mostly rounded or rounded-quadrate mixed with oblong, 18–40 µm long, 10–20(–25) µm wide, moderately thick-walled with distinct corner thickenings, becoming transversely rectangular, oblate to quadrate, orange-brownish in 5–7 layers at the mouth; *stomata* few, 3–5 per urn at the extreme base, bicellular, round-pored; *peristome teeth* straight and erect, 280–320 µm long, 110–130 µm wide at the base, yellow-orange to orange-brown, erect-spreading to recurved with age, lanceolate, narrowed to a rather broad obtuse apex, sometimes with uneven margins, entire or perforated, sometimes cleft at the apex, finely roughened to almost smooth. *Spores* globose, pale brownish, smooth to minutely papillose, 9–12 µm wide. *Calyptra* small, subcucullate, irregularly split at the base, covering only the rostrum.

Discussion

Cardot (1906) provided a brief diagnosis of the new species *Grimmia celata* which was based upon a single collection made in Cumberland Bay on Subantarctic South Georgia by C. Skottsberg during the Swedish South Polar Expedition of 1901–1903. The species was described as similar to *G. occulta* Müll. Hal.

from which it differed in the leaf areolation. The species was subsequently redescribed and illustrated by Cardot (1908) who additionally compared it with *G. abscondita*, a newly described species from Tierra del Fuego. The latter was different in the shape of the capsule and leaves and the almost entirely bistratose upper laminal cells. Subsequently, *G. celata* was only reported once by Cardot and Brotherus (1923) from Tierra del Fuego and since then it has long remained a poorly known and neglected species. Bell (1984) rediscovered *G. celata* at several additional stations on South Georgia, redescribed it and transferred to *Schistidium*. He maintained it as a distinct species, though closely related to *S. hyalinocuspidatum* (Müll. Hal.) B.G. Bell which, in turn, is conspecific with *S. amblyophyllum* (Ochyra 1998).

A comparison of the type material of *Schistidium cupulare* (Fig. 1.4–6, 8, 10, 12, 16–19) with the type and non-type collections of *S. celatum* from South Georgia and Tierra del Fuego (Fig. 1.1–3, 7, 9, 11, 13–15) showed the perfect correspondence of the shape, areolation and anatomical structure of the leaves in both species and therefore they must be considered conspecific.

Schistidium cupulare is primarily distinguished by its leaf areolation. The basal cells are elongate, moderately thick- to thin-walled and they have consistently straight, not sinuose walls, from the costa to the leaf margin. The basal marginal cells are hyaline, subquadrate to oblong, transparrent and have markedly thickened transverse walls. They form a more or less distinct, 1(–3)-seriate marginal border composed of 10–25 cells which warrant the placement of the species in sect. *Conferta*. The basal cells grade into short-rectangular supra-basal cells with distinctly sinuose walls. In contrast, the cells in the median and upper parts of the leaf are mostly isodiametrical, irregularly quadrate to shortly oblong, sometimes oblate near the apex and have straight or weakly sinuate, but not distinctly sinuose or nodulose walls. Additional diagnostic traits of *S. cupulare* are (*1*) the stronger costa which is semi-terete to subrectangular and strongly convex in the dorsal surface in cross-section, (2–)3-stratose distally and sometimes 4-stratose in the proximal part; (*2*) the regularly 2(–3)-stratose leaf margins in 1–3 rows of cells forming a bulging border; (*3*) the presence of a distinct central strand in the stem; and (*4*) the smooth to finely roughened peristome teeth.

Schistidium amblyophyllum is closely related to *S. cupulare* and both species are most safely distinguished by their leaf areolation. The leaf cells of *S. amblyophyllum* are elongate throughout the lamina and mostly distinctly sinuose-walled, whereas in *S. cupulare* the cells in the median and upper parts of the leaf are short, mostly isodiametric, irregularly quadrate to shortly oblong and are not sinuose-walled. The basal juxtacostal cells in *S. amblyophyllum* are yellow to yellowish-hyaline, rectangular to linear, forming prominent juxtacostal ‘windows’ separated from the margins by distinctly sinuose-walled cells. Conversely, the basal cells in *S. cupulare* are long-rectangular and straight-walled throughout the base, becoming shorter towards the margins and often they have thinner walls which

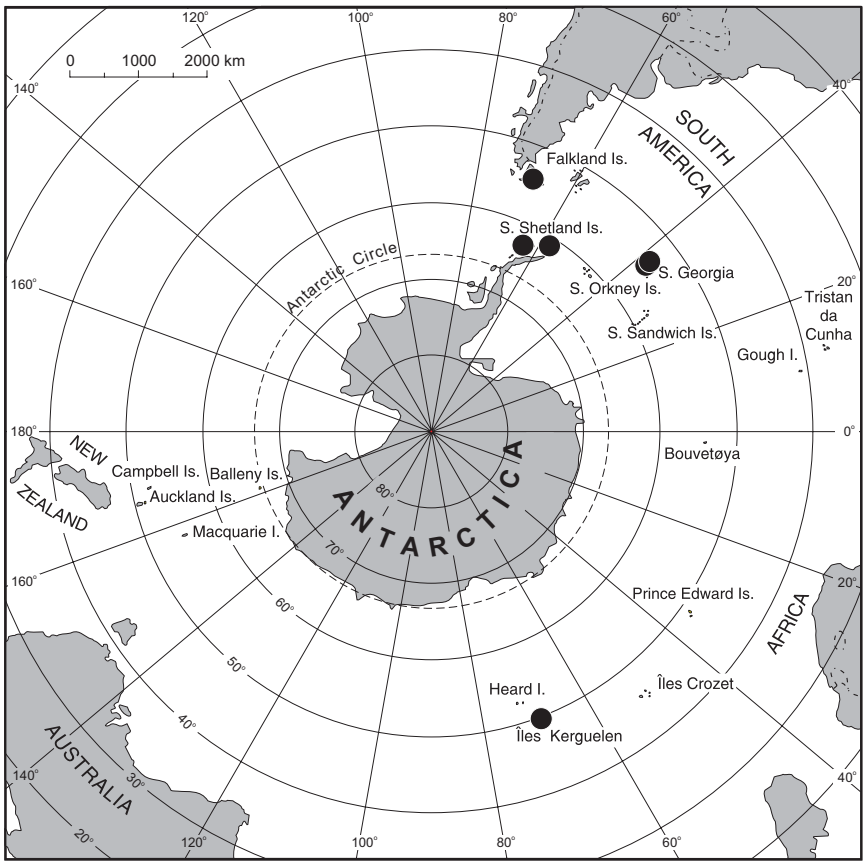

Fig. 2. Global distribution map for *Schistidium cupulare* (Müll. Hal.) Ochyra.

make the basal areolation lax. They are usually yellowish-hyaline and sharply set off from the supra-basal cells which are intensely yellow, long-rectangular and weakly to strongly sinuose-walled. In addition, the costa in *S. amblyophyllum* is weaker, 40–60 μm wide in the upper and median parts, subrectangular to semi-terete in transverse section, 2(–3)-stratose above, (2–)3-stratose in the lower part, with two somewhat larger ventral epidermal cells.

Conversely, in *Schistidium cupulare* the costa is stronger, 50–75 μm wide in the distal and median part, semi-terete to subrectangular, strongly convex in the dorsal surface, as seen in cross-section, (2–)3-stratose above, and 3(–4)-stratose below. The leaf margins are unistratose throughout or variously bistratose in one row of cells in *S. amblyophyllum*, whereas those in *S. cupulare* are usually regularly bi- or occasionally tristratose in 1–3 rows of cells forming fleshy, bulging limbidia. Moreover, *S. amblyophyllum* lacks a central duct and has warty papillose peristome teeth, whereas *S. cupulare* has a distinct and usually large central strand and its peristome teeth are smooth or only finely roughened.

Schistidium cupulare is a saxicolous species showing a relatively broad ecological amplitude. It grows on dry and exposed rock outcrops but it shows a preference for moist conditions and often thrives on vertical rock surface near melting streams, as well as on moist ashy soil. In the Antarctic it is associated with communities of the fruticose lichen and moss cushion subformation and often grows together with *Usnea antarctica*, *Bartramia patens*, *Hymenoloma antarcticum*, *Schistidium antarctici* and *Leptogium puberulum*.

The taxonomic conclusion on the conspecificity of *Schistidium cupulare* and *S. celatum* and extension of its geographical range to South Georgia provides a strong argument for considering *S. cupulare* as an amphiatlantic subantarctic species as was earlier suggested (Ochyra 1998). This distribution pattern comprises species occurring exclusively or nearly so within the South American, Atlantic and South Indian Ocean of Subantarctica, *i.e.* in practice on South Georgia, Bouvetøya and on the islands in the Kerguelen Province including Prince Edward Islands, Îles Crozet, Îles Kerguelen and Heard Island (Ochyra 1998). This type of distribution is exhibited by a small group of austral species, for example *Holodontium strictum* (Ochyra 1993), *Syntrichia saxicola* (Cardot) R.H. Zander (Ochyra 1997), *Hymenoloma grimmiaceum* (Müll. Hal.) Ochyra, *Schistidium falcatum*, *Notoligotrichum trichodon* (Hook. *et* Wilson) G.L. Sm. and *Syntrichia filaris* (Müll. Hal.) R.H. Zander which usually also extend to the northern maritime Antarctic (Ochyra 1998).

Schistidium cupulare is so far known from Îles Kerguelen and South Georgia, extending southwards to the northern maritime Antarctic where it is a very rare and occasional species. It is known only from King George and Livingston Islands in the South Shetlands, reaching its southernmost locality at lat. 62°41' S. It grows at low elevations between 35 and 60 m a.s.l. Additionally, *S. cupulare* is known from a single station on Isla Grande de Tierra del Fuego where it was collected at a higher elevation at Rio Olivia near Ushuaia (Cardot and Brotherus 1923).

Specimens examined. SOUTH AMERICA. **TIERRA DEL FUEGO**. Rio Olivia near Ushuaia, *Skottsberg 367* (PC, S).

SOUTH GEORGIA. ***Stromness Bay***: Hansen Point, alt. *ca* 30 m, *Greene 3392* (AAS, KRAM); west side of Olsen Valley, opposite Ruby Peak, alt. *ca* 35 m, *Greene 2959d* (BM). ***Cumberland Bay***: without closer locality data, *Skottsberg 318 p.p.* (PC, S – type of *Grimmia celata*); Moraine Fjord, *Bell 3295* (BM); south-east side of Moraine Fjord near Harker Glacier snout, alt. 0 m, *Bell 557* (AAS, KRAM); Sandebugten on the west shore of Barff Peninsula, alt. *ca* 3 m, *Greene 560a* (BM). ***Schlieper Bay***: at foot of Scree Gap, alt. 15–60 m, *Lewis Smith 2801*(AAS, KRAM). ***King Haakon Bay***: north side of the bay, opposite Vincint Islands, alt. 3–40 m, *Lewis Smith 2802* (BM); promontory at south side of Nuñez Peninsula, alt. 3–65 m, *Lewis Smith 2803* (AAS, KRAM). ***Allerdyce Range***: in south-east part without closer locality data, grid square 140 100, *Walton, Callaghan* and *Gunn* BAS Misc. *163* (BM).

ÎLES KERGUELEN. Port Jeanne d'Arc, *Peau 8* (PC); Foundery Branch, xi.1874, *Naumnann s.n.* (H, PC, S).

WEST ANTARCTICA. **SOUTH SHETLAND ISLANDS.** ***King George Island***: Admiralty Bay, Upłaz, alt. 40 m, *Ochyra 1536/80* (KRAM). ***Livingston Island***: Byers Peninsula, between Smellie Point and Chester Cove, 35–50 m, *Lewis Smith 3788* (AAS, KRAM).

The reinstatetment of *Schistidium cupulare* as a species in its own right increases the total number of species of the genus *Schistidium* now known to occur in the Antarctic. It consists of 13 species and this makes *Schistidium* the largest moss genus in this biome. They may be recognized by the following key.

1. Leaf margin plane or inflexed; leaves concave to canaliculate throughout, U-shaped in cross-section; costa often diffuse, elliptical to semi-elliptical in cross-section, scarcely prominent on the dorsal surface in the distal part (subg. *Canalicularia*) · · · · · · · · 2

1. Leaf margin recurved to revolute for varying lengths; leaves keeled, V-shaped in cross-section, at least in the distal portion; costa semi-terete to subrectangular in cross-section, mostly strongly convex and prominent on the dorsal surface (subg. *Apocarpa*) · 3

2. Leaves lanceolate, mostly falcato-secund; costa excurrent as a cuspidate point; peristome well-developed; spores 15–28 µm wide · · · · · · · · · · · · · · *S. falcatum*

2. Leaves ovate, ovate-lanceolate to lanceolate, straight or recurved, never secund; costa percurrent; peristome very rudimentary or absent; spores 9–11 µm · · · *S. lewis-smithii*

3. Spores large, 15–25 µm wide; leaf margins sometimes distantly denticulate to serrulate at the apex; plants of very moist to wet habitats; leaves broadly ovate to broadly ovate-lanceolate, subobtuse, always lacking hair-point; costa semi-terete, 4–5-stratose in cross-section (sect. *Rivularia*) · *S. rivulare*

3. Spores small, 7–13 µm wide; leaf margins always entire; plants of dry habitats; leaves ovate-lanceolate to lanceolate, often piliferous; costa semi-terete to subrectangular, 2–3-stratose in cross-section · 4

4. Lamina irregularly bistratose in the distal part of the leaf; leaf margin recurved on one or both sides for 3/4–4/5 of the leaf length; exothecial cells predominantly oblong to rectangular in central and lower parts of the urn (sect. *Atrofusca*) · · · · · · *S. praemorsum*

4. Lamina unistratose throughout, with occasional bistratose strands distally; leaf margin recurved to revolute to the apex; exothecial cells predominantly transversely elongate and isodiametrical in central and lower parts of the urn · · · · · · · · · · · · · 5

5. Basal marginal cells chlorophyllose, small, isodiametrical, not forming a distinct group or border; plants red to red-brown, sometimes with blackish, greyish or green-yellowish tones; reaction of the upper leaves with KOH red or orange; peristome teeth curved, entire (sect. *Apocarpiformia*) · *S. andinum*

5. Basal marginal cells hyaline, isodiametrical to elongate with thickened transverse walls, forming a rectangular group or a leaf border; plants olivaceous, often with yellowish tones; reaction of the upper leaves with KOH yellow; peristome teeth straight, often irregular and strongly perforated, sometimes reduced to rudimentary (sect. *Conferta*) · · · · · · · · · 6

6. Leaf margins revolute throughout; peristome teeth vestigial or absent · · · · *S. steerei*

6. Leaf margins narrowly recurved for varying lengths; peristome teeth well-developed to variously reduced · 7

7. Plants hoary; leaves with spinulose-denticulate hair-points, longer than 0.4 mm · · · · 8

7. Plants not hoary; leaves epilose or with smooth or denticulate hair-points, shorter than 0.4 mm · 9

8. Exothecial cells with strongly incrassate walls, 4–8 μm thick; upper laminal cells rectangular, with sinuose, strongly thickened walls; central strand absent · · · *S. urnulaceum*
8. Exothecial cells thin-walled, usually less than 1 μm thick; upper laminal cells isodiametric to oblong, with straight, moderately evenly thickened walls; central strand present · *S. halinae*

9. Peristome teeth reduced, mostly truncate in the middle; leaves usually arranged in distinct spiral rows · *S. antarctici*
9. Peristome teeth well-developed, occasionally eroded at the apex; leaves not spirally ranked· 10

10. Costa weak, to 40 μm wide, scarcely prominent on the dorsal surface, often nearly of the same thickness as the lamina · *S. leptoneurum*
10. Costa strong, 50 or more μm wide, prominently convex on the dorsal surface, much thicker than the laminal cells · 11

11. Capsules cupulate, 0.5–0.6 mm long; exothecial cells with incrassate walls; costa semiterete to elliptic, with undifferentiated ventral cells; leaves sharply keeled throughout, narrowly V-shaped, with blades of the lamina in transverse section forming a < 30° angle, usually parallel at the junction with the costa; furrow very narrow· · · · *S. deceptionense*
11. Capsules ovoid to obloid, 0.7–1.1 mm long; exothecial cells thin-walled; costa subrectangular to semi-terete, usually with 2 ventral cells somewhat larger than central and dorsal cells; leaves concave below, keeled in the distal portion, broadly V- or U-shaped, with blades of the lamina in transverse section forming a > 45° angle, divergent at base; furrow more open · 12

12. Upper laminal cells long-rectangular, with strongly sinuose-nodulose walls; basal cells never lax, merging into long-rectangular sinuose-walled cells extending along the margin nearly to the base; central strand absent · · · · · · · *S. amblyophyllum*
12. Upper laminal cells quadrate to shortly rectangular, with straight or weakly sinuate walls; basal cells often lax, straight-walled, merging into rectangular cells with sinuose walls not extending to the base along the margins; central strand present · *S. cupulare*

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