

A SYNOPTIC FLORA OF SOUTH GEORGIAN MOSSES: *TORTULA*

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ABSTRACT. Descriptions, taxonomic notes and habitat details are given for the eight South Georgian species of the genus *Tortula*. A key for identification is provided together with distribution data and full lists of specimens examined for each species are available. Two species, *T. anderssonii* Aongstr. and *T. geheebiaeopsis* (C. Muell.) Broth. are reported from the island for the first time and twelve species and two varieties are reduced to synonymy. *T. lingulaefolia* Card. et Broth. is reduced to synonymy with *T. arenae* (Besch.) Broth.; *Barbula leptosyntrichia* C. Muell. and *T. robusta* var. *laxa* Bartr. with *T. robusta* Hook. et Grev. var. *robusta*; *T. rivularis* Dus. with *T. fontana* (C. Muell.) Broth.; *T. excelsa* Card. and *T. robustula* Card. with *T. filaris* (C. Muell.) Broth.; and *T. fuscoviridis* Card. with *T. saxicola* Card. *T. grossiretis* Card. var. *grossiretis* and var. *atrata* Card., and *T. heteroneura* Card. are reduced to synonymy with *T. princeps* De Not. var. *princeps*. *T. fuegiana* (Mitt.) Mitt., *T. monoica* Card. and *T. pusilla* Aongstr. (*hom. illeg.*) are synonymized with *T. magellanica* Mont., which is treated as a variety of *T. princeps*, and the new combination *T. princeps* var. *magellanica* (Mont.) P. J. Lightowlers is made. *T. conferta* Bartr. is also treated as a variety of *T. princeps*, and the new combination *T. princeps* var. *conferta* (Bartr.) P. J. Lightowlers is made. Previous reports of the New Zealand species *T. serrata* Dix. from South Georgia are based on a misidentification.

INTRODUCTION

The genus *Tortula* forms a prominent part of the moss flora of South Georgia. There are eight species, two of which, *T. robusta* Hook. et Grev. and *T. geheebiaeopsis* (C. Muell.) Broth., are very common and are major constituents of the bryophyte vegetation. Both of the latter species are frequently found forming an understory to *Acaena* shrubs but they also occur in other habitats. The remaining six species, though local or rare, occupy niches ranging from dry rock faces and crevices to streamsides, flushes and bogs. Only one species of the genus has hair-pointed leaves and the majority have dentate or denticulate upper leaf margins, a character which appears to be unique to southern hemisphere taxa.

The arrangement of the text, descriptions of specimens and field records follows the format of earlier papers in this series (Greene, 1973; Bell, 1984). The collections studied are those indicated by Greene (1973) and Bell and Greene (1975), with an additional collection by G. Lawson made in 1974-76.

POTTIACEAE

Tortula Hedw. *nom. cons.*

On South Georgia the genus is characterized by its papillose leaves which do not have an adaxial stereid band in the nerve, and by the sporophyte which has a cylindrical, exerted capsule with a peristome of 32 teeth which are twisted into a helix and united to form a tube at the base.

Outside the family Pottiaceae, *Tortula* species are likely to be confused only with species of *Encalypta*. However, *Encalypta* leaves may be distinguished by their basal cells which have thickened and pigmented transverse walls whereas the basal cells of

Tortula leaves have walls which are uniformly thickened and hyaline or evenly coloured. Sporophytes, if present, differ in several respects between the two genera. *Encalypta* capsules are covered until they dehisce by a large conspicuous calyptra, but in *Tortula* the calyptra is small, inconspicuous and fugaceous. The peristome in *Encalypta* is variable but never twisted and fused into a tube as is invariably the case with *Tortula* species.

In the family Pottiaceae, *Tortula* may be confused with species of *Barbula*, *Bryoerythrophyllum*, *Didymodon*, and *Tortella*. However, the last three genera are rare on South Georgia, and only *Barbula* specimens are likely to be encountered frequently. These differ from *Tortula* in their leaves which are appressed and slightly twisted, but not curled, when dry, and in dried specimens by the colour which is green to black below and not green to yellowish-orange or brown like *Tortula* specimens. *Barbula*, *Bryoerythrophyllum*, *Didymodon* and *Tortella* can all be distinguished from *Tortula* by examination of leaf transverse sections. The leaves of these genera possess a band of stereid cells on the adaxial and abaxial surfaces of the nerve which are seen in cross-section as groups of thick-walled cells with small lumina. However, species of *Tortula* have only one stereid band on the adaxial side of the nerve. Species of *Pottia* or *Willia* and *Saraconeurum glaciale* (C. Muell.) Card. et Bryhn may also be mistaken for *Tortula*. *S. glaciale* was described by Greene and others (1970) and differs notably in its deciduous leaf apices. South Georgian and Antarctic *Pottia* species have been described by Matteri (1977a, b) and can be distinguished from *Tortula* species by their small size (their stems rarely reach 1 cm in height) and by the capsules which are obloid or ovoid and not cylindrical. They also lack the long spirally twisted peristome found in *Tortula*. The only South Georgian species of *Willia*, *W. austro-leucophaea* (Besch.) Broth., was described by Bell (1974) and is gametophytically similar to hair-pointed species of *Tortula*. The most reliable vegetative differences are the leaf shape, leaf margins and the morphology of the perichaetial leaves. *W. austro-leucophaea* has slightly pandurate leaves with plane margins but leaves of hair-pointed *Tortula* specimens are not pandurate and always have recurved or revolute margins unless the plants are very small. Perichaetial leaves of *Tortula* species are similar to the other leaves but in *W. austro-leucophaea* the perichaetia have extended hyaline tips on the laminae. Sporophytes, however, are the simplest means of distinguishing the genera since the capsules of *Willia* are immersed and aperistomate, and very different from the longly exserted, peristomate capsules found in *Tortula*.

Terminology in the key and descriptions follows that given by Smith (1978) and in some instances Stearn (1966). However, the use of the word 'bordered' may be a source of confusion and the following definition is adopted here. In many species of *Tortula* there is a tendency for the margin of the leaf to become differentiated. In freshly collected specimens this may be seen as a reddish colouration at the margin, or in herbarium material as more sparsely papillose or more thickly walled cells. In *T. robusta* the cells of the marginal row are often about one half the size of other leaf cells. However, this does not alter their quadrate shape. In these cases, although there is some differentiation, the leaf is not described as 'bordered' as this term is reserved for leaves which are edged with cells that are different in shape from the inner cells. In bordered leaves the marginal cells are usually rectangular, and the inner cells are quadrate, as in *T. arenae* (Besch.) Broth., for example, where the leaf margin is consistently well developed and forms a useful character for identifying the species (Fig. 3c).

In the taxonomic accounts specimens are described as 'authentic' if they are known to have been identified by the original author of the taxon in question. It is often unknown whether they are of type significance or not but, in cases where type material is not available, they are important in verifying the identity of taxa.

Key to species

The South Georgian taxa of *Tortula* are identified in the following key. Particular care should be taken in deciding whether the leaves of specimens are dentate or entire. In many cases this is obvious but in older leaves erosion of cell walls occurs near the leaf apex and may make dentate leaves appear entire or entire leaves appear dentate. In cases of doubt, young leaves taken from near the apex of a stem should be examined.

1. Leaves hair-pointed, apex abruptly producing a hyaline or reddish hair rarely reduced to an apiculus in some leaves of small plants, leaves oblong to ovate-lingulate 10
 Leaves not hair-pointed, nerve percurrent or if excurrent producing a short cusp or subula (up to 0.3 mm long), leaves lanceolate or lingulate to broadly oblong in shape 2
2. Leaves entire 3
 Leaves dentate or denticulate near apex 4
3. Leaves lanceolate or oblong-lanceolate, apex acuminate, nerve percurrent or excurrent. (Fig. 20b) *T. saxicola*
 Leaves oblong-lingulate to lingulate-spathulate with an obtuse to broadly acute apex, nerve excurrent in a mucro (Fig. 1b) *T. anderssonii*
4. Leaves broadly oblong-spathulate or oblong-pandurate (Fig. 7a), leaves erect to patent when moist *T. fontana*
 Leaves lingulate to lingulate-spathulate or lanceolate to oblong-lanceolate, (Figs. 1a, 3a, 5a, 9a, 16a), rarely oblong (Fig. 17e) but then not spathulate and leaves recurved when moist 5
5. Leaves with 2 to 9 rows of elongated cells extending up leaf margin to at least mid-leaf, leaves lingulate to lingulate-spathulate, (Fig. 3a), nerve percurrent (Fig. 3b) ... *T. arenae*
 Leaves without elongated cells at the leaf margin or with 1 to 2 rows not extending to mid-leaf, leaves lanceolate to oblong-lanceolate or oblong, (Figs. 5a, 9a, 16a, 17e), rarely oblong-lingulate to lingulate-spathulate (Fig. 1a) but then nerve excurrent in mucro (Fig. 1b) 6
6. Leaves oblong-lingulate to lingulate-spathulate with an obtuse to broadly acute apex (Fig. 1a), nerve excurrent in a short mucronate point (Fig. 1b) *T. anderssonii*
 Leaves lanceolate to oblong-lanceolate with an acute or acuminate apex (Figs. 5a, 9a, 16a), rarely oblong with an acute to broadly acute apex (Fig. 17e) but then nerve percurrent 7
7. Cells in upper leaf 7.5–12 μm wide, very densely papillose *T. geheebiaeopsis*
 Cells in upper leaf 9–23 μm wide, sparsely papillose 8
8. Nerve ending in a sharply defined group of rhomboidal cells at the leaf apex in most leaves (Fig. 5b). Leaves up to 4 mm long, cells in upper leaf 9–15 μm wide *T. filaris*
 Nerve ending in rhomboidal cells not forming a sharply defined group, (Fig. 16b). Leaves (3.2–) 4.4–8 mm long, upper leaf cells 11–21 μm wide 9
9. Leaves lanceolate to lingulate-lanceolate, 4.4–8 mm long, leaves erecto-patent to recurved when moist *T. robusta* var. *robusta*
 Leaves oblong to oblong-lanceolate, 3.2–4.8 mm long, leaves recurved when moist *T. robusta* var. *recurva*
10. Stems slender forming dense tufts, leaves small (less than 1.4 mm long excluding hair-point), hair-point short (less than 0.4 mm long), leaf margin plane *T. princeps* var. *conferta*
 Stems neither slender nor densely tufted. Leaves larger (over 1.4 mm long excluding hair-point), hair-points longer (over 0.4 mm), leaf margin recurved or revolute 11
11. Leaf apex cucullate to plane in profile, hair-points hyaline, plants small (stems 0.5–1.5 cm high), sporophyte common *T. princeps* var. *magellanica*
 Leaf apex plane or recurved in profile, hair-points hyaline or reddish, but if hyaline then plants moderately robust (stems over 1.5 cm high), sporophyte occasional in robust plants *T. princeps* var. *princeps*

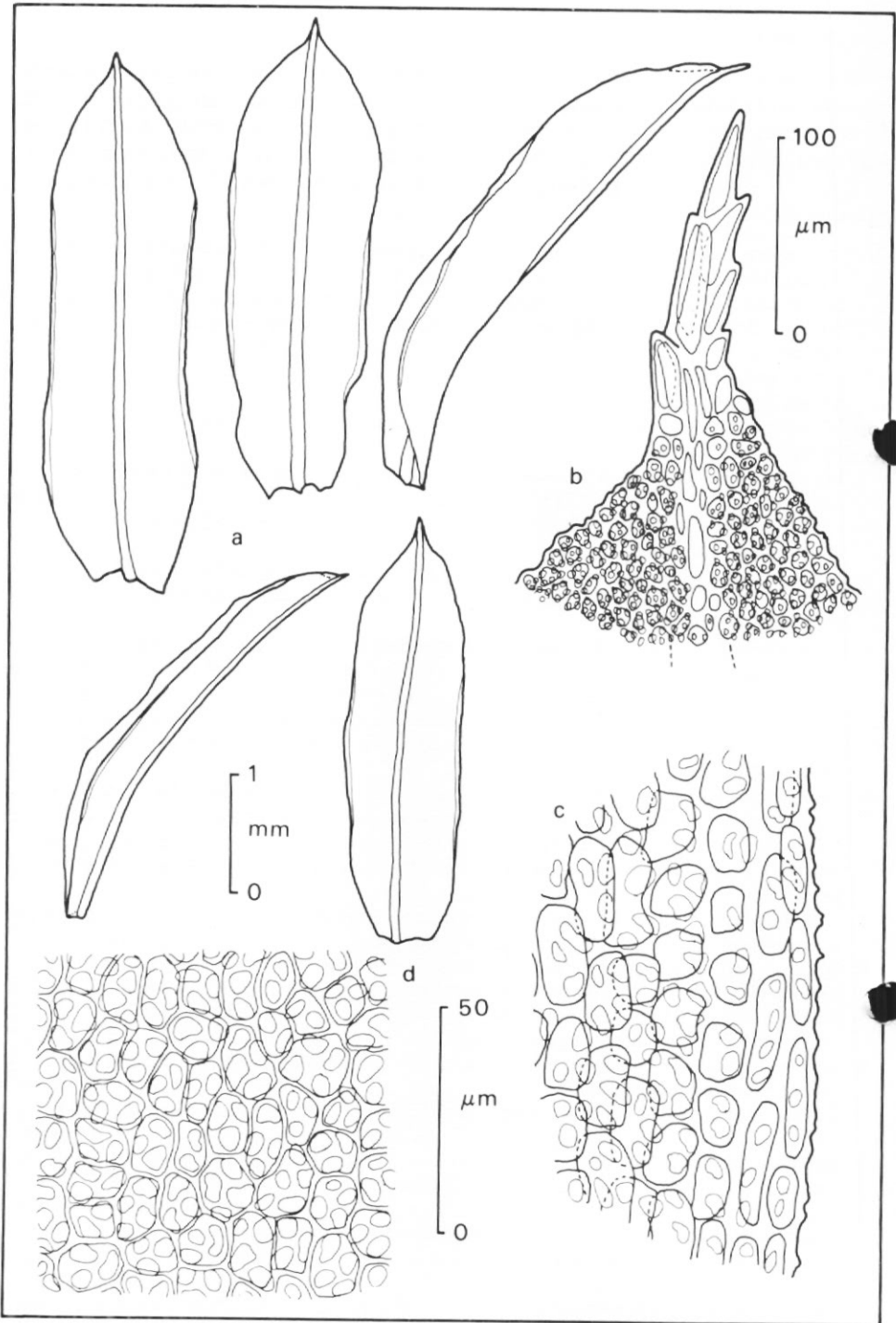


Fig. 1. *Tortula anderssonii*: a, leaves; b, leaf apex; c, cells of upper basal leaf margin; d, upper lamina cells. Scales: left hand for leaves; upper right-hand for leaf apex; lower for cells.

Tortula anderssonii Aongstr.

Stems erect, forming cushions 1.0–4.5 cm high, often branched, with or without a central strand. Leaves, 2.1–4.3 × 0.6–1.4 mm, when moist erecto-patent to patent, when dry appressed or incurled and slightly twisted; oblong-lingulate, often weakly pandurate or spatulate, apex obtuse or broadly acute, cuspidate. Leaves differentiated into a chlorophyllose papillose upper limb and a hyaline, smooth sheath, the latter sheathing the stem for a fifth to a third of the leaf length. Leaf margins weakly to strongly recurved or revolute below mid-leaf, plane above, entire or rarely denticulate or dentate, marginal 5–10 rows of cells often more thick-walled but not otherwise differentiated from inner lamina cells. Nerve excurrent in a crenate or denticulate reddish micro (95–250 μm long in most leaves), nerve sometimes becoming obscure or disappearing below leaf apex. Abaxial nerve surface smooth or papillose with simple verrucate papillae. Cells above 6–20 × 8–13.5 μm , irregularly quadrate, densely papillose with complex papillae. Basal cells 26–100 × 6–23 μm , shortly rectangular to longly rectangular, 2–7 times as long as wide, sometimes lax and inflated. Longly rectangular cells often continuing up leaf margin into limb. Rhizoids smooth, brown, sparsely produced on lower parts of stem. Antheridia not seen in South Georgian material. Perichaetial bracts similar to other leaves or broader at the base. Sporophyte unknown on South Georgia. (Fig. 1).

Habitat and distribution

A rare species of moist rock ledges and crevices. Alt. 30–300 m. (Fig. 2).

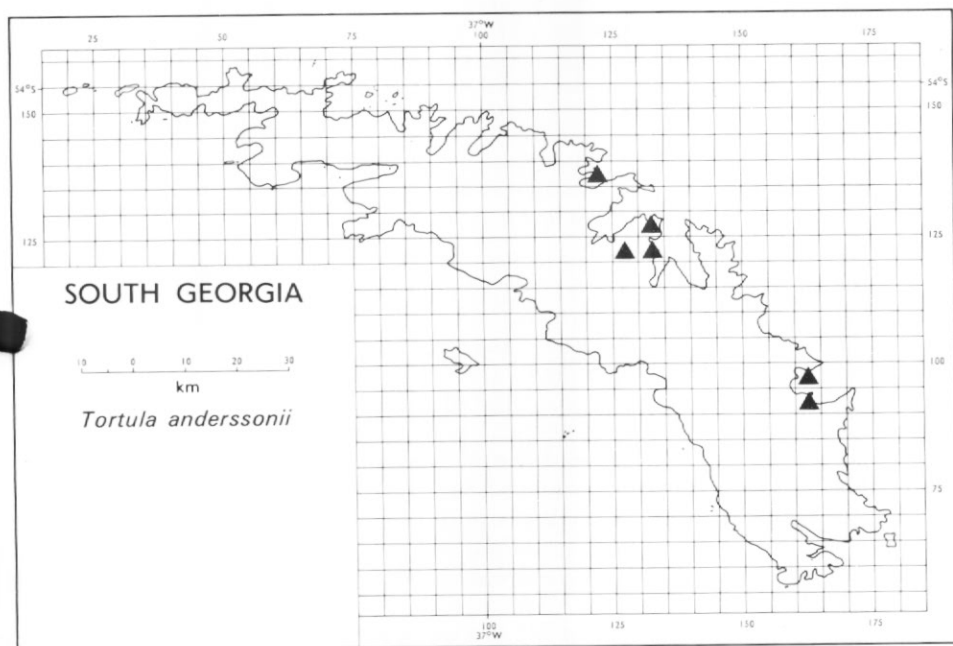


Fig. 2. The known distribution of *Tortula anderssonii* on South Georgia, by 5-km squares.

Notes

A distinctive plant unlikely to be mistaken for any other species because of its oblong-lingulate leaves with a nerve which is excurrent in a reddish mucro. *T. arenae* has leaves which are similar in shape but that species is readily distinguished in most instances by the presence of a pronounced border to the leaf and a percurrent nerve.

T. anderssonii from South Georgia usually has entire leaves but some specimens have a few small teeth near the leaf apex. This is remarkable as the leaves of the other South Georgian species are either always entire or always dentate. However, Sainsbury (1955) noted that New Zealand plants of this species (as *T. bealeyensis* R. Br. ter.) also occasionally have dentate leaves, and South American specimens have been observed by the present author to vary in the same way.

Taxonomy

T. anderssonii was first described by Ångström (1872) from Tierra del Fuego and is here reported from South Georgia for the first time. An isotype has been examined (Andersson s.n. NY., *Tortula* (*Syntrichia*) *Anderssonii* J. Ångst. Port Famine fret magell., N. J. Andersson) which differs from South Georgian specimens in some respects, notably it has slightly longer leaves (some with more acute apices) longer mucronate points on some leaves and basal cells which occasionally have thick porose walls. These differences may be the result of variation in climate and are minor in relation to the similarities in leaf shape, leaf apex areolation, cell size and papilla density. There is therefore little doubt that South Georgian material is best referred to the South American species.

The type specimen has both female and synoecious inflorescences but antheridia have not been found in South Georgian plants and thus it is not possible to determine their sexual state. However, Cardot (1908) remarked that South American specimens of this species may be either dioecious or synoecious.

Tortula arenae (Besch.) Broth.

Syn. *Barbula arenae* Besch.

Tortula lingulaefolia Card. et Broth.

Stems erect, forming cushions or turves, 0.4–3.0 cm high, sparingly branched, with or without a central strand. Leaves 1.9–3.7 (–4.6) × 0.5–1.1 mm, when moist erecto-patent to patent, when dry appressed and slightly curled; lingulate to lingulate-spathulate, apex acute to obtuse and apiculate. Leaves differentiated into chlorophyllose, papillose upper limb and a hyaline, smooth sheath, the latter sheathing the stem for a quarter to a third of the leaf length. Leaf margins plane or slightly recurved below mid-leaf, denticulate to coarsely dentate near apex, weakly to strongly bordered to mid-leaf or above. Nerve ending in apex in a group of smooth rhomboidal cells, often reddish in colour. Abaxial surface of nerve smooth or papillose with simple verrucate papillae. Cells above 7–20 × 9.5–17 μm, irregularly quadrate, sparsely papillose with complex papillae, 2–9 rows of marginal cells elongated, sometimes thick-walled, forming a conspicuous border to at least mid-leaf. Basal cells 33–87 × 13–23 μm, shortly to longly rectangular, 2–8 times as long as wide, smooth, hyaline, sometimes lax and inflated. Rhizoids smooth, brown, sparsely produced on lower parts of stem. Dioecious. Perichaetial bracts similar to the other leaves, perigonal bracts shorter and broader at the base. Sporophyte rare. Seta 5–15 mm, when dry dextrorse (externe visus) above, slightly sinistrorse at base. Capsule

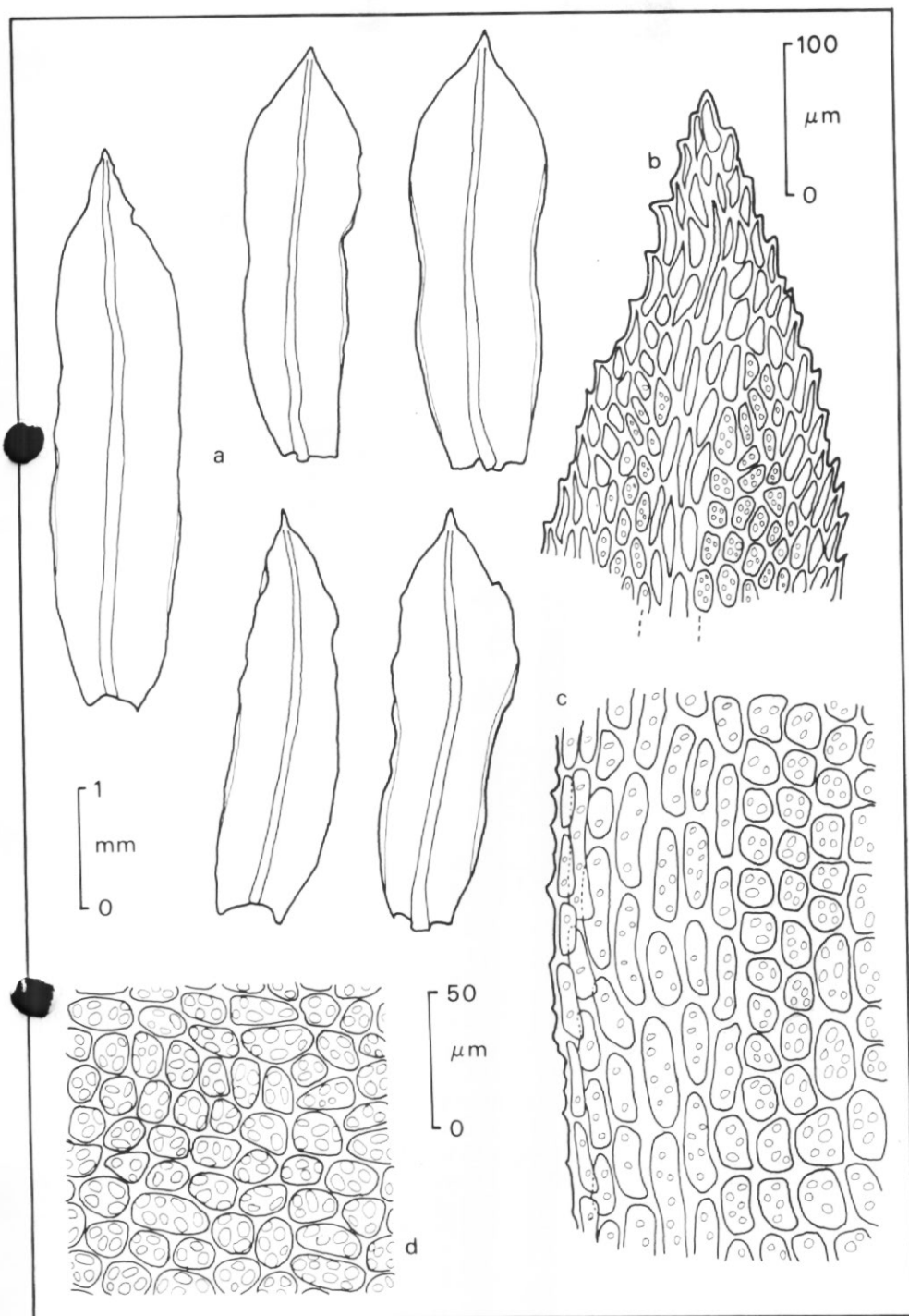


Fig. 3. *Tortula arenae*: a, leaves; b, leaf apex; c, marginal cells at mid-leaf; d, upper lamina cells. Scales: left-hand for leaves; upper right-hand for leaf apex; lower for cells.

2.0–3.0 × 0.2–0.6 mm, erect, cylindrical. Operculum longly subulate. Peristome teeth united for about three quarters of their length at the base forming a tube, twisted into a dextrorse helix. Spores 12–14 μm in diameter. (Fig. 3).

Habitat and distribution

An occasional plant of moist rock crevices and mud particularly near streams or waterfalls. However it has also been found on tussock grass bases. Alt. 3–300 m. (Fig. 4).

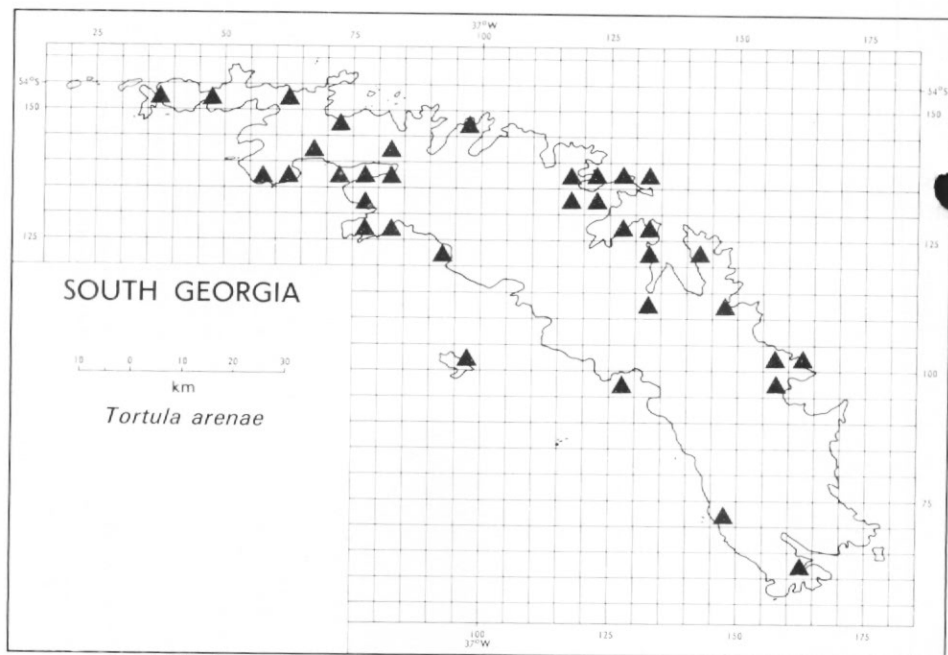


Fig. 4. The known distribution of *Tortula arenae* on South Georgia, by 5-km squares.

Notes

This species is distinctive because of its lingulate to lingulate-spathulate leaves which have a prominent border. The latter is variable, however, and is reduced to a few elongated marginal cells above the leaf sheath in the leaves of some specimens. The shape of the leaves together with the vestige of a border should distinguish it from all other species. Only *T. anderssonii* has leaves of a similar shape and size and in cases of doubt it may be separated by its excurrent nerve.

The sporophyte of *T. arenae* has peristome teeth which are united for about three-quarters of their length, forming a long tube. In other South Georgian species the proportion of the peristome which is fused is smaller and rarely exceeds one-half of the length of the teeth.

Taxonomy

The earliest name for this species appears to be *Barbula arenae* Besch., which was described by Beschereille (1885) from material collected in Tierra del Fuego. Type material has been located (Lectotype (nov.) Hariot 37, BM, *Barbula arenae* Besch.

Punta Arenas de Magellan. 7 Mai 83. Herb. Emil Bescherelle 1900) which agrees well with South Georgian specimens. *B. arenae* was transferred to the genus *Tortula* by Brotherus (1902).

South Georgian plants of this species have previously been referred to *T. lingulaefolia* Card. et Broth. (Cardot and Brotherus, 1923). Three type specimens have been examined (Lectotype (nov.), Skottsberg 22, PC, *Tortula lingulaefolia* Card. sp.nova, Georgia australis: Cumberland Bay, Moraine Fiord. Leg. C. Skottsberg 18.4.1909. Herb. J. Cardot. Expedition suecica 1907-09; Isotypes H!, two specimens). All are typical specimens of *T. arenae*, and *T. lingulaefolia* can thus be regarded as a synonym.

Tortula filaris (C. Muell.) Broth.

Syn. *Barbula filaris* C. Muell.

Tortula excelsa Card.

Tortula robustula Card.

Stems erect forming cushions or turves 0.8–5.2 cm high, sparingly branched, with central strand. Leaves 2.0–4.4 × 0.7–1.0 mm, when moist patent to spreading, when dry lightly curled and twisted, lanceolate to oblong-lanceolate, apex acute to slightly acuminate. Leaves differentiated into a chlorophyllose, papillose upper limb and a hyaline, smooth basal sheath, the latter sheathing the stem for a fifth to a third of the leaf length. Margin plane to weakly recurved at mid-leaf, dentate to obscurely denticulate near apex. Nerve ending in apex in a well defined group of rhomboidal cells, abaxial surface smooth or papillose with simple verrucate papillae. Cells above 6–20 × 9–15 μm, irregularly quadrate, marginal row sometimes slightly smaller, sparsely papillose with complex papillae. Basal cells 42–106 × 10–25 μm, rectangular to linear, 4 to 10 times as long as wide, smooth, hyaline, sometimes lax and inflated. Longly rectangular cells occasionally continuing up leaf margin into limb. Rhizoids smooth, brown, sparingly to abundantly produced on lower parts of stem. Dioecious. Perichaetial bracts similar to other leaves but longer, perigonal bracts shorter with a broader base. Sporophyte uncommon. Plants sometimes polysetous. Seta 10–15 mm long, when dry dextrorse (externe visus) in upper part, sinistrorse below. Capsule 1.9–2.5 × 0.3 × 0.6 mm, erect or slightly inclined, cylindrical. Operculum subulate. Peristome of 32 teeth united below for about half their length and twisted into a dextrorse helix. Spores 11.6–14.1 μm in diameter. (Fig. 5).

Habitat and distribution

An occasional species found in several habitats including moist rock crevices, streambanks, whalebones, concrete and in disturbed places such as amongst glacial detritus. The species has a wide altitudinal range but only specimens from below about 100 m have sporophytes. Alt. 2–575 m. (Fig. 6).

Notes

T. filaris is superficially similar to *T. geheebiaeopsis*, *T. robusta* and *T. saxicola* and confusion may arise with any of these species. *T. geheebiaeopsis* resembles *T. filaris* in leaf size and leaf shape but is easily distinguished by its small, very densely papillose lamina cells and strong nerve which is frequently slightly excurrent. *T. robusta* is generally a much larger plant and can be separated by its leaves which are over 4 mm long and frequently have cells over 15 μm wide. Also, *T. robusta* leaves typically have margins which are strongly dentate for much of the upper third of the leaf but, in

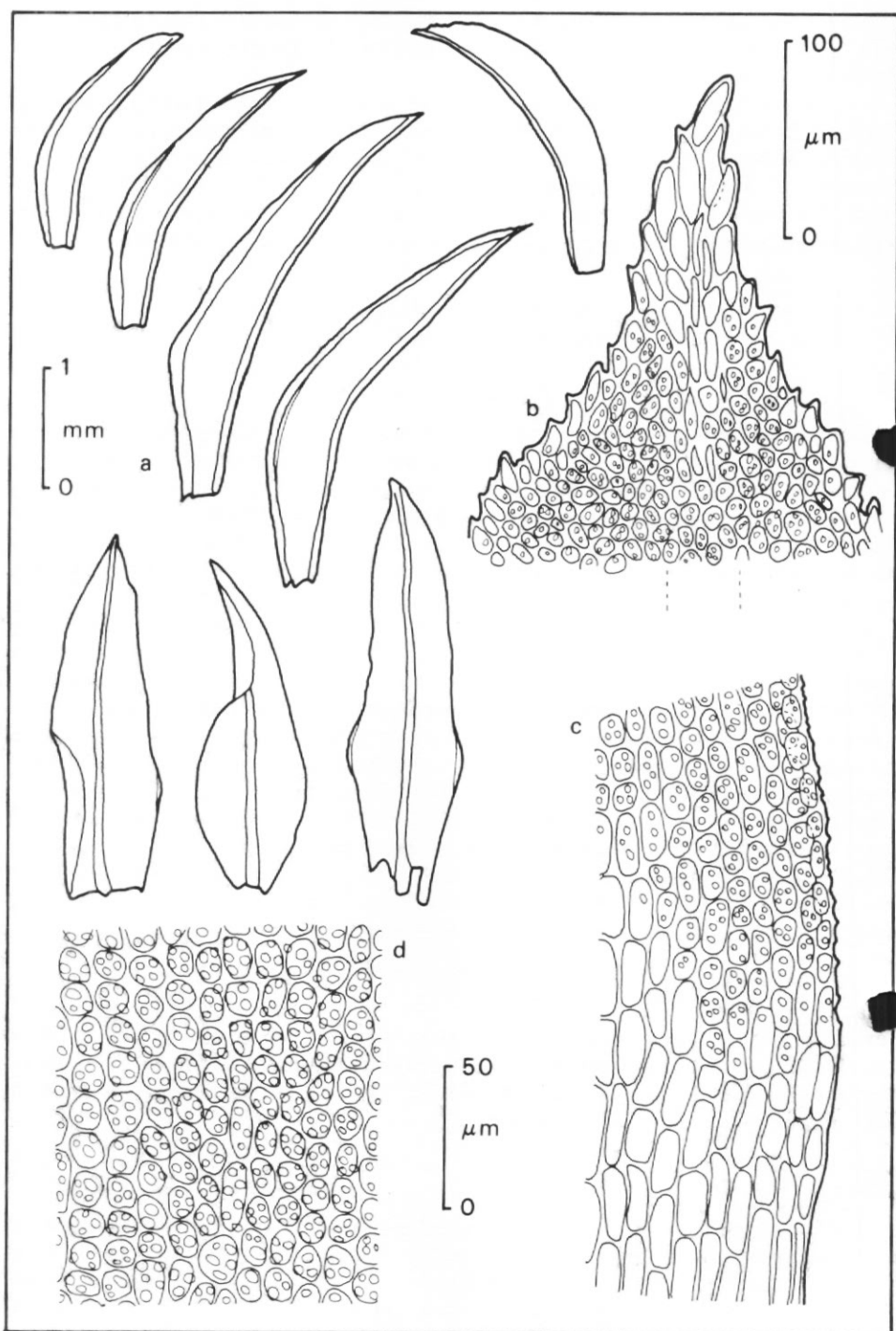


Fig. 5. *Tortulaflaris*: a, leaves; b, leaf apex; c, upper basal leaf margin; d, upper lamina cells. Scales: left-hand for leaves; upper right-hand for leaf apex and leaf margin; lower for cells.

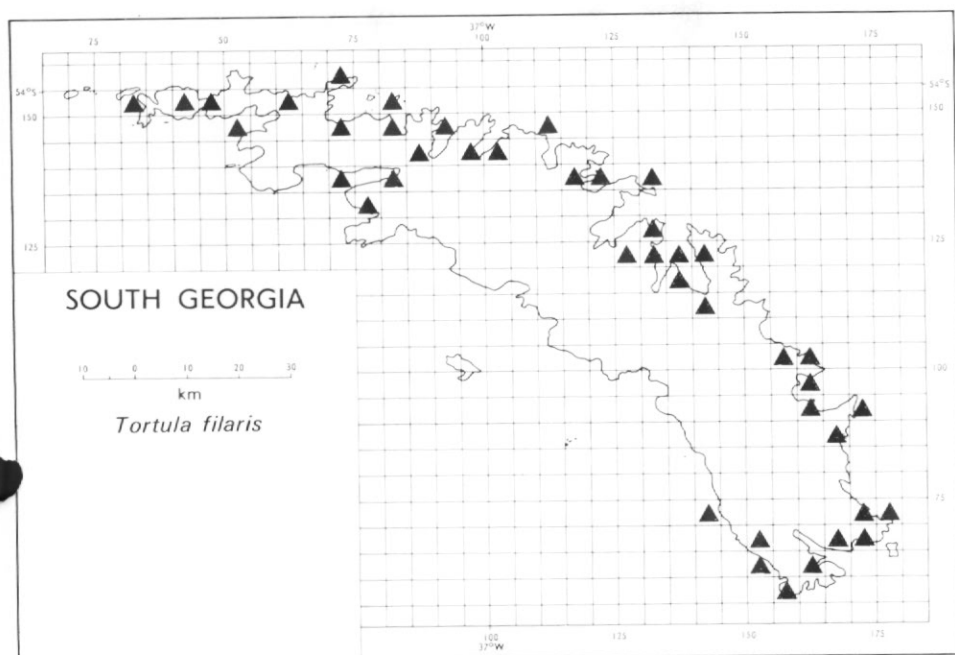


Fig. 6. The known distribution of *Tortula filaris* on South Georgia, by 5-km squares.

T. filaris the leaves are usually more sparsely dentate or denticulate and have a distinctive group of rhomboidal cells at the apex of most leaves. These cells are wider than nerve cells, are not papillose like the surrounding lamina cells and appear to form a more well defined group than the corresponding apical cells of *T. robusta*. This group of rhomboidal cells is only found in *T. filaris* and is a useful diagnostic character of the species. The differences between *T. filaris* and *T. saxicola* are considered under the notes for latter species.

Taxonomy

This species was first described by Müller (1980) as *Barbula filaris* C. Muell. from material collected on South Georgia in 1882–83 by Will. Type material has been examined (Lectotype (nov.), Will s.n., HBG, *Barbula* (*Syntrichia*) *filaris* C. Müll. n.sp. Austro-Georgia, oberes Whalerthal in Felsspalten. Leg. Will 20. III. 1883. Isotypes H! M!) which agrees well with other South Georgian specimens. However, the type description describes the species as synoecious and all fertile material examined in this study has been found to be dioecious. Unfortunately only female inflorescences have been seen in the type specimens but it is possible that Müller (1890) was mistaken. *B. filaris* was transferred to the genus *Tortula* by Brotherus (1902).

T. robustula Card., a species described from Tierra del Fuego and the Falkland Islands by Cardot (1905) is reduced to synonymy with *T. filaris*. Type material (Lectotype (nov.), Skottsberg 61, PC, *T. robustula* Card. sp.nova. Terre du Feu: Ushuaia. C. Skottsberg 3.10.1902. Herb. J. Cardot, Svenska Sydpolarexpeditionen 1901–03, Isotype S!; Syntype, Skottsberg 225, P.C. *T. robustula* Card. sp.nova. Iles Falkland: Port Louis C. Skottsberg, 6.8.1902. Herb. J. Cardot, Svenska Sydpolarexpeditionen 1901–03) is very similar to South Georgian *T. filaris*, although Cardot

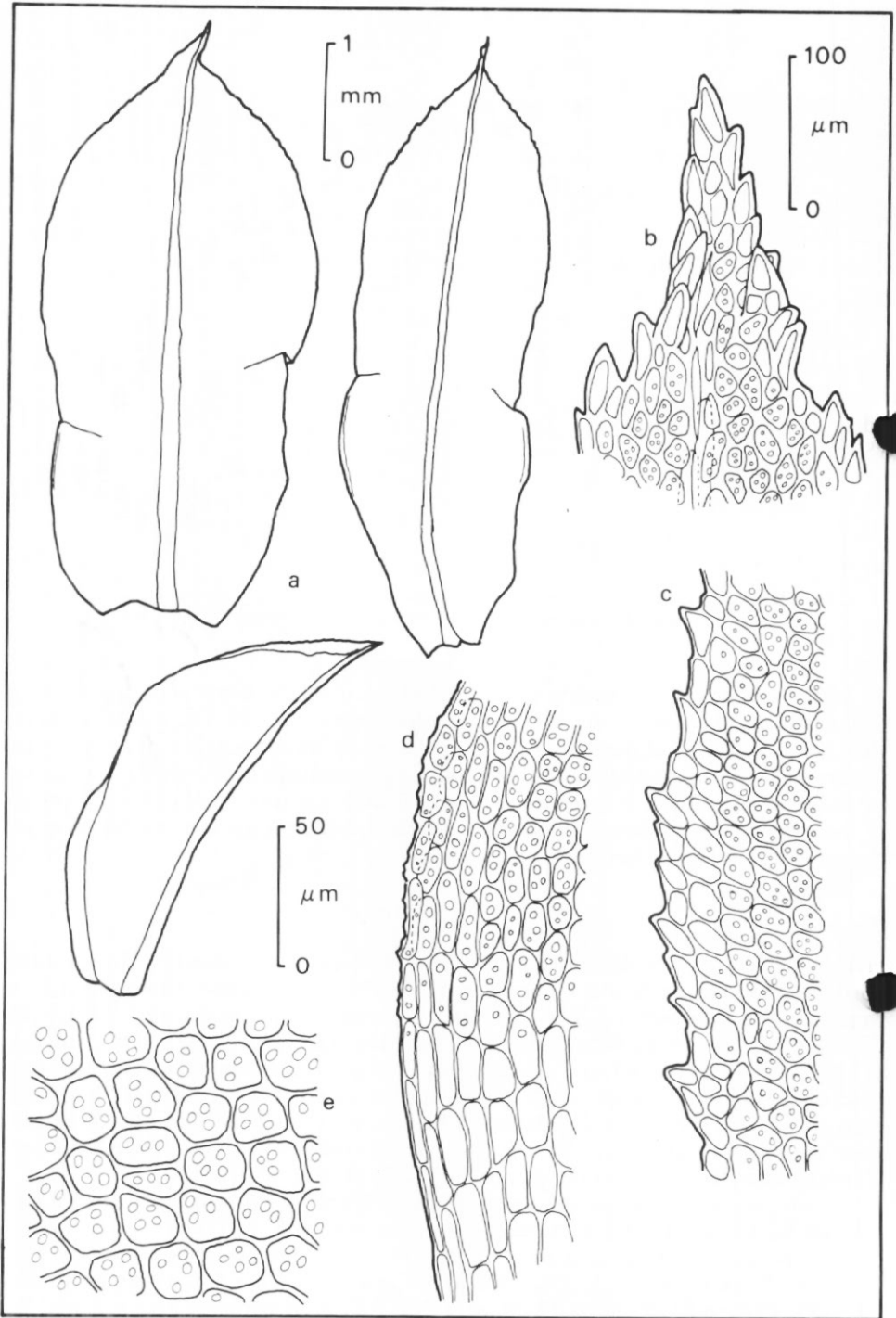


Fig. 7. *Tortula fontana*: a, leaves; b, leaf apex; c, upper leaf margin; d, upper basal leaf margin; e, upper lamina cells. Scales: upper left-hand for leaves; upper right hand for leaf apex and leaf margins, lower for cells.

(1908) noted that this species had more slender stems, leaves more equal in size throughout the stem, with more strongly papillose cells and less differentiation of cells at the leaf margin than *T. robusta*. However the range of variation observed in South Georgian material suggests that these differences are trivial. Cardot (1908) also described *T. robustula* as autoecious rather than dioecious like *T. filaris*. One of the type specimens of *T. robustula* is fertile (Skottsberg 61), and on examination male and female inflorescences were found to be closely associated although not on the same plant, indicating that *T. robustula* is also dioecious. In any event it is considered unwise to separate the two species of *Tortula* by sexual state alone when they are otherwise identical.

In the type description of *T. excelsa* Card., Cardot (1906) remarked that this species was similar to *T. filaris* but could be distinguished by its larger size. Type material has been examined (Lectotype (nov.) Skottsberg 447, BM, *T. excelsa* Card. sp.nova, Ile Nelson, Shetland du Sud, Harmony Cove. C. Skottsberg 11.1.1902. Herb. J. Cardot. Svenska Sydpolarexpeditionen 1901-03, N.R. 447, Isotypes BM ex K! PC!) and was found to be robust but otherwise typical of *T. filaris*. This material is similar to South Georgian specimens in areolation, leaf shape, leaf size and cell size, and differs only in the height of the stems. A range of specimens from the Antarctic Peninsula has been examined and found to be similar in size to South Georgian plants. The tall stems of the type specimen of *T. excelsa* are thus probably a result of a particularly favourable habitat as there is no overall difference between Antarctic and South Georgian plants. *T. excelsa* is therefore considered to be synonymous with *T. filaris*.

Tortula fontana (C. Muell.) Broth

Syn. *Barbula fontana* C. Muell.

Tortula rivularis Dus.

Stems erect forming turves 2.0-10.5 cm high, sparingly branched, without a central strand. Leaves (2.9-) 3.9-5.8 × 1.3-2.3 mm, when moist erect to patent, when dry appressed, lightly curled and twisted; oblong to broadly oblong, usually pandurate or sub-spathulate, narrowing to an acute to obtuse apex. Leaves differentiated into a chlorophyllose, papillose upper limb and a hyaline smooth sheath, the latter sheathing the stem for a quarter to a third of the leaf length. Leaf margin plane or weakly recurved below mid-leaf, dentate to denticulate near apex. Nerve narrowing towards the leaf apex, percurrent, abaxial surface smooth or papillose with simple verrucate papillae. Cells above 13-39 × 13-23 μm, irregularly quadrate but becoming shortly rectangular towards the basal sheath, marginal 1-2 rows usually smaller, sparsely papillose with complex papillae. Basal cells 53-120 × 19-40 μm, shortly rectangular to rectangular, 1.5-5 (-7) times as long as wide, narrower toward the margins of the leaf sometimes forming a border, smooth, hyaline, sometimes lax and inflated. Longly rectangular cells often continuing up leaf margin into limb. Rhizoids smooth, brown, sparingly to abundantly produced on lower parts of stem. Sterile, gametangia and sporophytes unknown on South Georgia. (Fig. 7).

Habitat and distribution

A rare plant of flushes, bogs and wet rocks. Alt. 2-120 m. (Fig. 8).

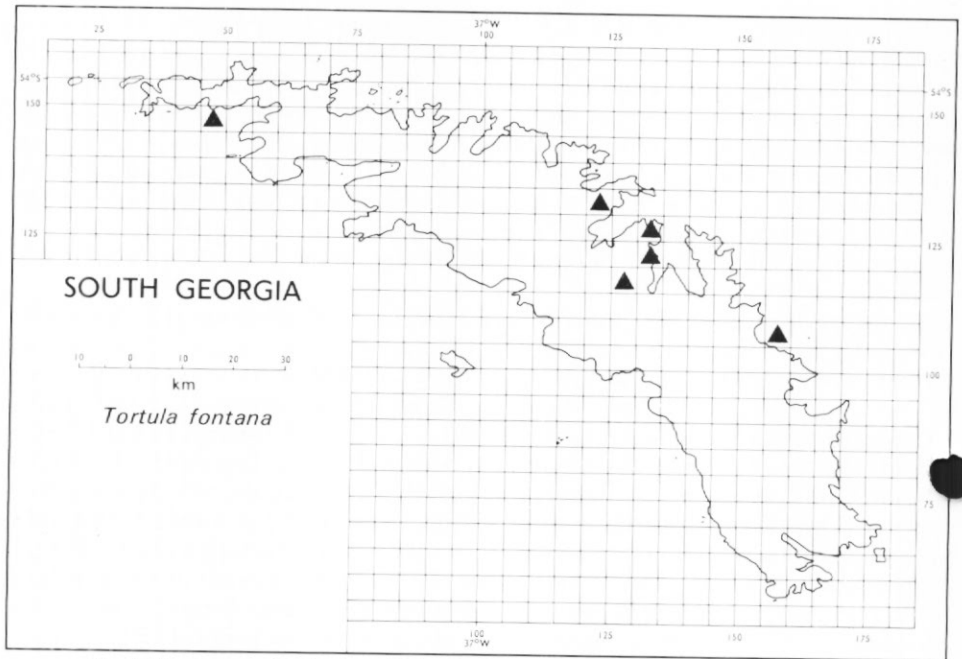


Fig. 8. The known distribution of *Tortula fontana* on South Georgia, by 5-km squares.

Notes

A very distinctive plant unlikely to be confused with any other species except *T. robusta* var. *recurva*, which is similar in size, leaf shape and areolation. This variety differs in two respects: first the leaves are oblong and never pandurate or spatulate; and second the leaves are recurved when moist. Leaf shape in *T. fontana* is variable, particularly in the width of the upper part, but all leaves show some narrowing in the lower half which produces the pandurate or spatulate shape. The leaves are erect to spreading when moist and their tips are not reflexed as is the case with *T. robusta* var. *recurva*.

Taxonomy

This species was first described by Müller (1890) as *Barbula fontana* C. Muell. from material collected on South Georgia by Will in 1882–83. An original specimen survives in Munich (Will s.n., M, *Syntrichia fontana* C. Müll. n.sp., Quelle auf dem Hochplateau, Süd-Georgien, Leg. Will 14/VII.83). The label information of this specimen does not agree exactly with the protologue given by Müller (1890), but this is the only surviving original collection of this species according to Greene (1973) and it is therefore designated the lectotype. The specimen agrees well with other South Georgian material examined during this study and there is no doubt about the identity of this species. *B. fontana* was transferred to the genus *Tortula* by Brotherus (1902).

Type material of *T. rivularis* Dus. has also been examined (Syntype, Dusén s.n., BM, *Tortula rivularis* Dus., Lago Viedma in paludosis, P. Dusén, Febr. a 1905. Plantae Patagonicae e territorio Sta Cruz reportatae). This specimen falls within the range of variation shown by *T. fontana* on South Georgia and from the type description (Dusén, 1906) there is no doubt that this is the same species. *T. rivularis*, as the later name, is therefore reduced to synonymy with *T. fontana*.

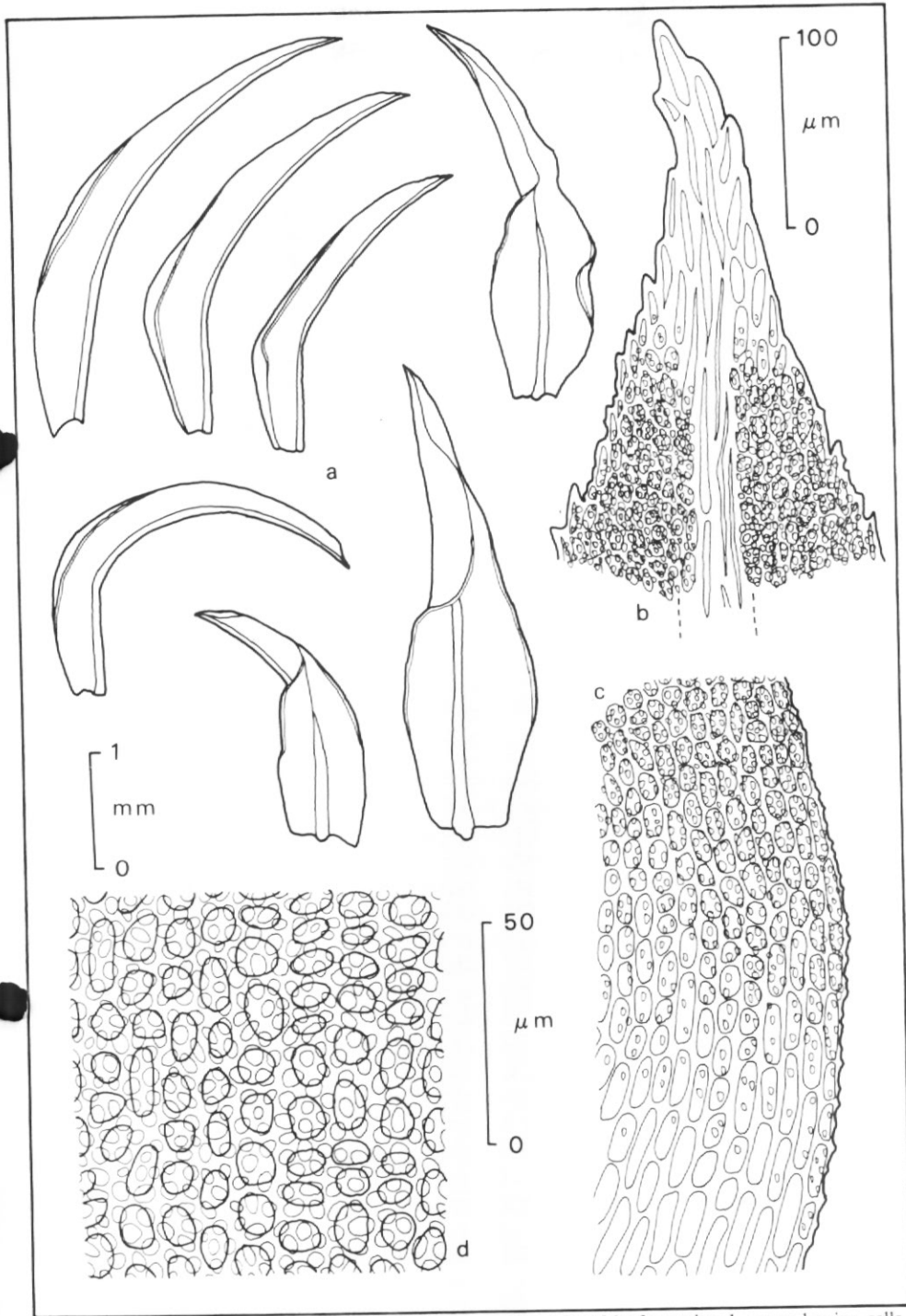


Fig. 9. *Tortula geheebiaeopsis*: a, leaves; b, leaf apex; c, upper basal leaf margin; d, upper lamina cells. Scales: left-hand for leaves, upper right-hand for leaf apex; lower for cells.

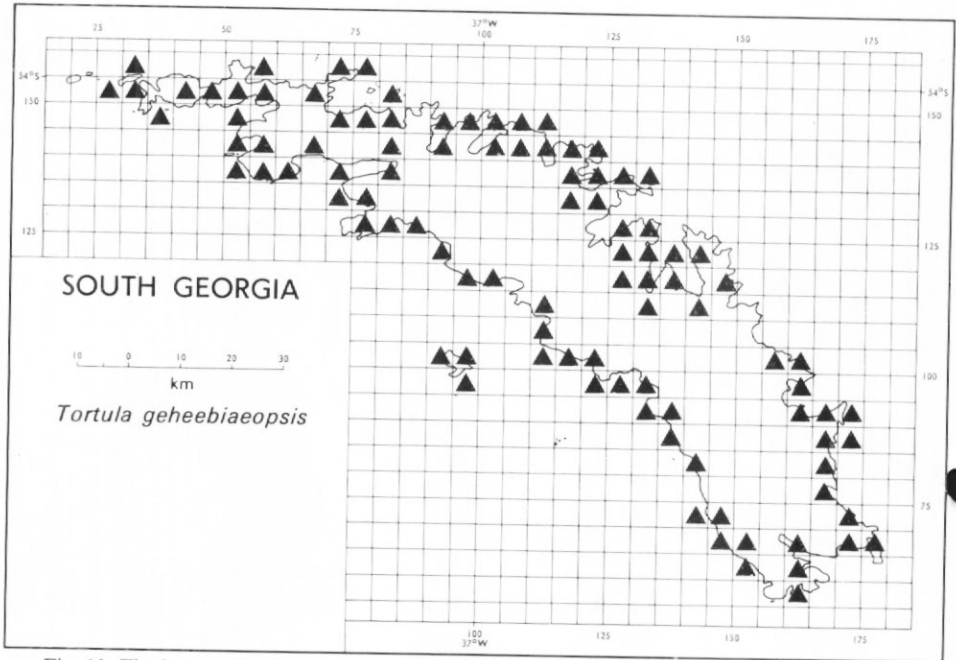


Fig. 10. The known distribution of *Tortula geheebiaeopsis* on South Georgia, by 5-km squares.

Tortula geheebiaeopsis (C. Muell.) Broth.

Syn. *Barbula geheebiaeopsis* C. Muell.

Stems erect forming cushions or turves 1.5–6.0 cm high, sparingly branched, with or without a central strand. Leaves 2.8–4.0 (–5.0) × 0.7–1.1 mm, when moist patent to recurved, when dry lightly curled and twisted. Leaf shape lanceolate, narrowing to a finely acute apex. Leaves differentiated into a chlorophyllose, papillose upper limb and a hyaline, smooth sheath, the latter sheathing the stem for a quarter to a third of the leaf length. Margin recurved for about two-thirds of the leaf length, denticulate near apex. Nerve strong, ending in apex or excurrent in a short thick point (*c.* 60 μm), abaxial surface smooth or papillose with simple verrucate papillae. Cells above 6.5–19 × 7.5–12 μm, irregularly quadrate to shortly rectangular below, usually thick-walled, very densely papillose with complex papillae. Basal cells 40–107 × 5–20 μm, rectangular to linear, 3 to 11 times long as wide, sometimes porose, often narrower towards the leaf margin forming a weakly differentiated border, smooth, hyaline, sometimes lax and inflated. A few longly rectangular cells often continuing up leaf margin into limb. Rhizoids smooth, brown, very sparsely produced on lower parts of stem or absent. Dioecious. Perchactial bracts similar to other leaves or longer with an extended sheathing basal region. Perigonial bracts shorter with broader bases. Sporophyte uncommon, plants sometimes polysetous. Seta 7–14 mm, when dry dextrorse (*externe visus*) in upper part, sinistrorse below. Capsule 1.2–2.5 × 0.25–0.7 mm erect or slightly inclined, cylindrical. Operculum subulate. Peristome of 32 teeth united below for about one third of their length forming a tube and twisted in a dextrorse helix. Spores 12–13.5 μm in diameter. (Fig. 9).

Habitat and distribution

A common species found in a range of habitats including screes, under *Acaena*, rock crevices and ledges, *Festuca* grassland and flushes. Alt. 2–450 m. (Fig. 10).

Notes

T. geheebiaeopsis is a distinctive species which can readily be distinguished from *T. robusta*, *T. filaris* and *T. saxicola*, which have similar leaf shapes. The most useful diagnostic character of *T. geheebiaeopsis* is the density of papillae on the lamina cells, which are more densely packed than those of any other South Georgian species. The papillae appear as closely packed projections when focusing up and down on the leaf surface with a microscope. In such species as *T. robusta*, *T. filaris*, *T. princeps* and *T. fontana* the papillae are found only above the lumen of each cell and consist of three or four round or 'C'-shaped projections which, in comparison with all other species, are sparsely arranged. *T. anderssonii* and *T. saxicola* have smaller papillae which are more densely packed, but it is still possible to distinguish from which cells they originate. In *T. geheebiaeopsis*, however, the papillae are very densely packed across the whole leaf surface and there are no spaces between the papillae of different cells.

A further character which helps to distinguish *T. geheebiaeopsis* is the small size of the lamina cells which is emphasized by a tendency for the cell walls to thicken in most specimens, making the cell lumina particularly small. However, some small *T. robusta* specimens also have small, thick-walled cells so this character must be used with caution. *T. geheebiaeopsis* has a strong thick nerve which is frequently slightly excurrent at the apex, an additional feature which aids in differentiation from similar species.

T. robusta var. *robusta* and *T. filaris* which have leaf shapes similar to *T. geheebiaeopsis* both have larger and less densely papillose lamina cells. In *T. robusta* most cells are between 12 and 20 μm wide, in *T. filaris* between 10 and 15 μm wide, and in *T. geheebiaeopsis* between 8 and 10 μm wide. *T. robusta* has larger leaves, which are always over 4 mm long but those of *T. filaris* are similar in size and shape to those of *T. geheebiaeopsis*. There is a slight difference, however, as the leaves of *T. filaris* are more oblong-lanceolate, wider in upper leaf and more shortly pointed at the apex than *T. geheebiaeopsis* leaves. Differences between *T. geheebiaeopsis* and *T. saxicola* are discussed under the latter species.

Taxonomy

This species was described by Müller (1883) as *Barbula geheebiaeopsis* C. Muell. and transferred to the genus *Tortula* by Brotherus (1902). An authentic specimen of *B. geheebiaeopsis* has been traced in Helsinki (Naumann s.n., H, *Barb. geheebiaeopsis* C.M., Kerguelen Leg. Naumann.) which may be a portion of the type specimen extracted by Brotherus. No further original material has been found and it is likely that it was destroyed in Berlin during the 1939–45 war (Greene, 1973). The identity of this species thus rests on the sparse Helsinki specimen which is here designated lectotype. Fortunately, agreement with South Georgian material is good and there is no doubt that the name can be applied.

This is the first report of this species from South Georgia. Material from the island was previously referred to a New Zealand species, *T. serrata* Dix., by Cox (1961) and Greene (1964, 1968, 1973). According to Cox (1961) this decision was based primarily on the similar cell sizes and papilla density of the plants. The type specimen of *T.*

serrata has been examined (Lectotype (nov.), Gray 46, BM, *T. serrata* Dixon sp.nov., Wairarapa, N.Z., Coll. W. Gray 1909, Type, Herb. H. N. Dixon) and is identical to South Georgian plants in these respects. However, it differs in leaf size and leaf serration having leaves about 5.4 mm long which are strongly spinose dentate in the upper part. South Georgian specimens have leaves which rarely exceed 4 mm in length and are only denticulate near the apex. *T. serrata* thus appears quite distinct from the South Georgian species and cannot be considered synonymous.

Dixon (1930) transferred *Barbula geheebiaeopsis* to *Leptodontium* after examination of a specimen from Iles Crozet determined by Kaalaas. A specimen of the same collection has been traced (Ring and Raknes 246, BM, *T. geheebiaeopsis* (C. Müll.) Broth. det. Kaal., Possession Island: Crozetgruppen: Doctors Bay, Januar 1908. Leg. Ring and Raknes. Ex herb. Univ. Osloensis) and is clearly *Leptodontium microruncinatum* Dus. Dixon's combination was thus based on a misidentified specimen and should be discounted.

Tortula princeps De Not.

Syn. *Barbula antarctica* Hamp.

Tortula antarctica (Hamp.) Wils.

Tortula grossiretis Card. var. *grossiretis*

Tortula grossiretis var. *atrata* Card.

Tortula heteroneura Card.

Stems erect, forming cushions or turves 0.2–5.0 cm high, sparingly branched, with or without a central strand. Leaves 0.5–3.5 (excluding hair-point) \times 0.3–1.3 mm, when moist erecto-patent to recurved, when dry appressed and slightly curled, broadly oblong to lingulate or ovate-lingulate, rarely very weakly pandurate or ovate. Leaves differentiated into papillose, chlorophyllose limb and smooth hyaline sheath, the latter sheathing the stem for a third to one half of the leaf length. Leaf margins entire, plane, recurved or revolute at mid-leaf for up to two-thirds of the leaf length. Leaf apex rounded to obtuse, abruptly producing a hair-point, rarely reduced to an apiculus or absent. Leaf apex cucullate to recurved. Nerve reaching leaf apex or becoming obscure or disappearing in upper leaf, abaxial surface smooth or sometimes verrucate or obscurely dentate towards the apex, without papillae or having simple verrucate papillae on longly rectangular cells, and complex papillae on quadrate cells. Hair-point 0.1–1.6 mm long, very rarely absent, smooth to denticulate, hyaline or reddish. Cells above 8–25 \times 9–20 μ m, irregularly quadrate, papillose with complex papillae. Quadrate cells spreading down margin of upper basal region of leaf. Basal cells 40–135 \times 13–33 μ m, rectangular to linear, 3–10 times as long as wide, smooth, hyaline, sometimes lax and inflated. Rhizoids smooth, brown, sparsely produced on lower stem and on abaxial surface of nerve at leaf base. Autoecious, paroecious or dioecious. Perichaetial bracts similar to other leaves but broader at base. Perigonial bracts variable, often shorter and broader than other leaves. Sporophyte occasional. Plants sometimes polysetous. Seta 5–14 mm, when dry dextrorse (externe visus) above, often slightly sinistrorse at extreme base. Capsule 1.9–2.4 \times 0.35–0.8 mm, erect, cylindrical. Operculum subulate. Peristome of 32 teeth united below for about half their length forming a tube and twisted into a dextrorse helix. Spores 11–15 μ m in diameter.

var. *princeps*.

Stems 0.6–5.0 cm high, robust. Leaves 1.2–3.5 (excluding hair-point) \times 0.6–1.3 mm, when moist patent to recurved, oblong to lingulate. Leaf margins almost plane to

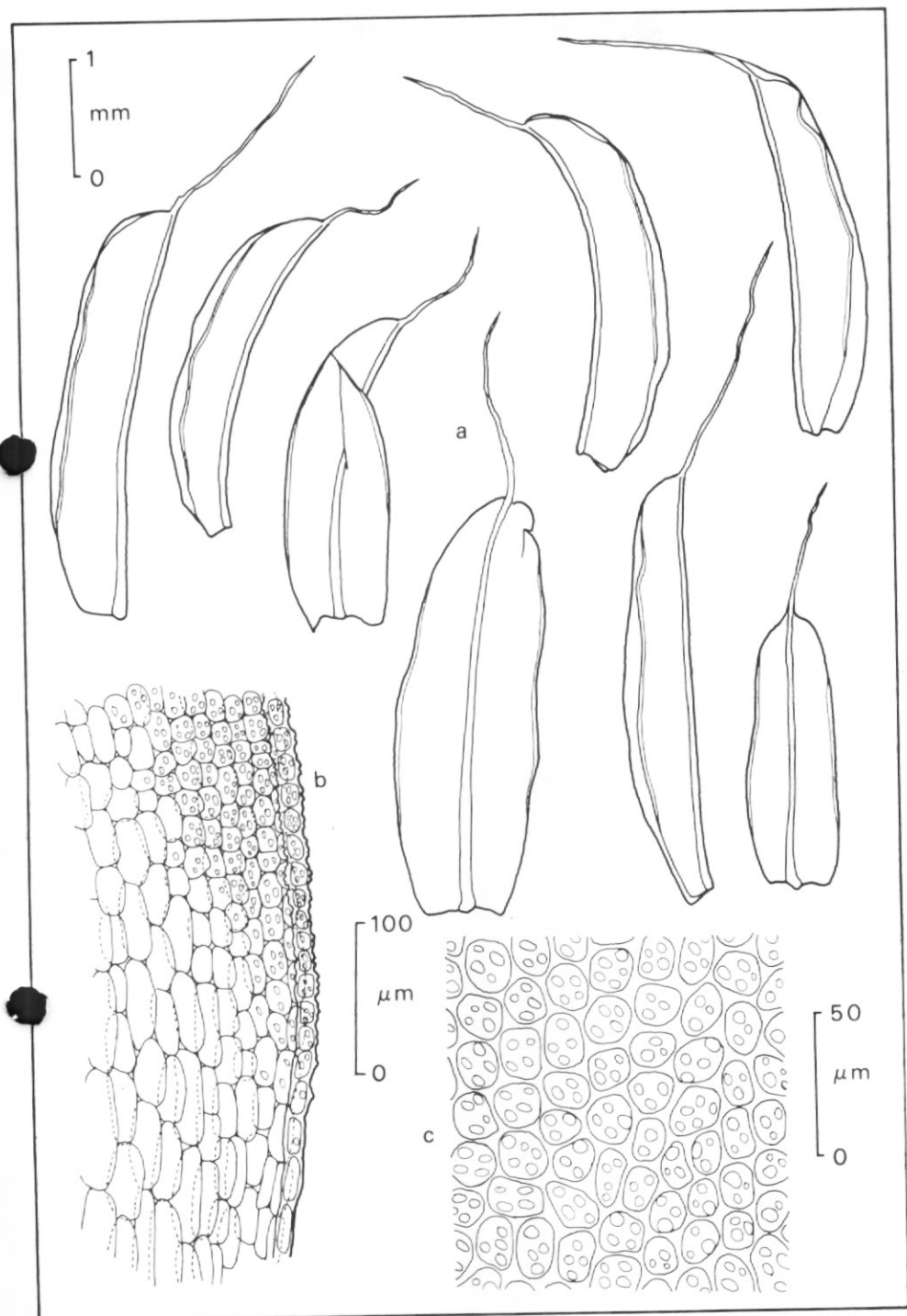


Fig. 11. *Tortula princeps* var. *princeps*: a, leaves; b, upper basal leaf margin; c, upper lamina cells. Scales: upper left-hand for leaves; lower centre for leaf margin; lower right-hand for cells.

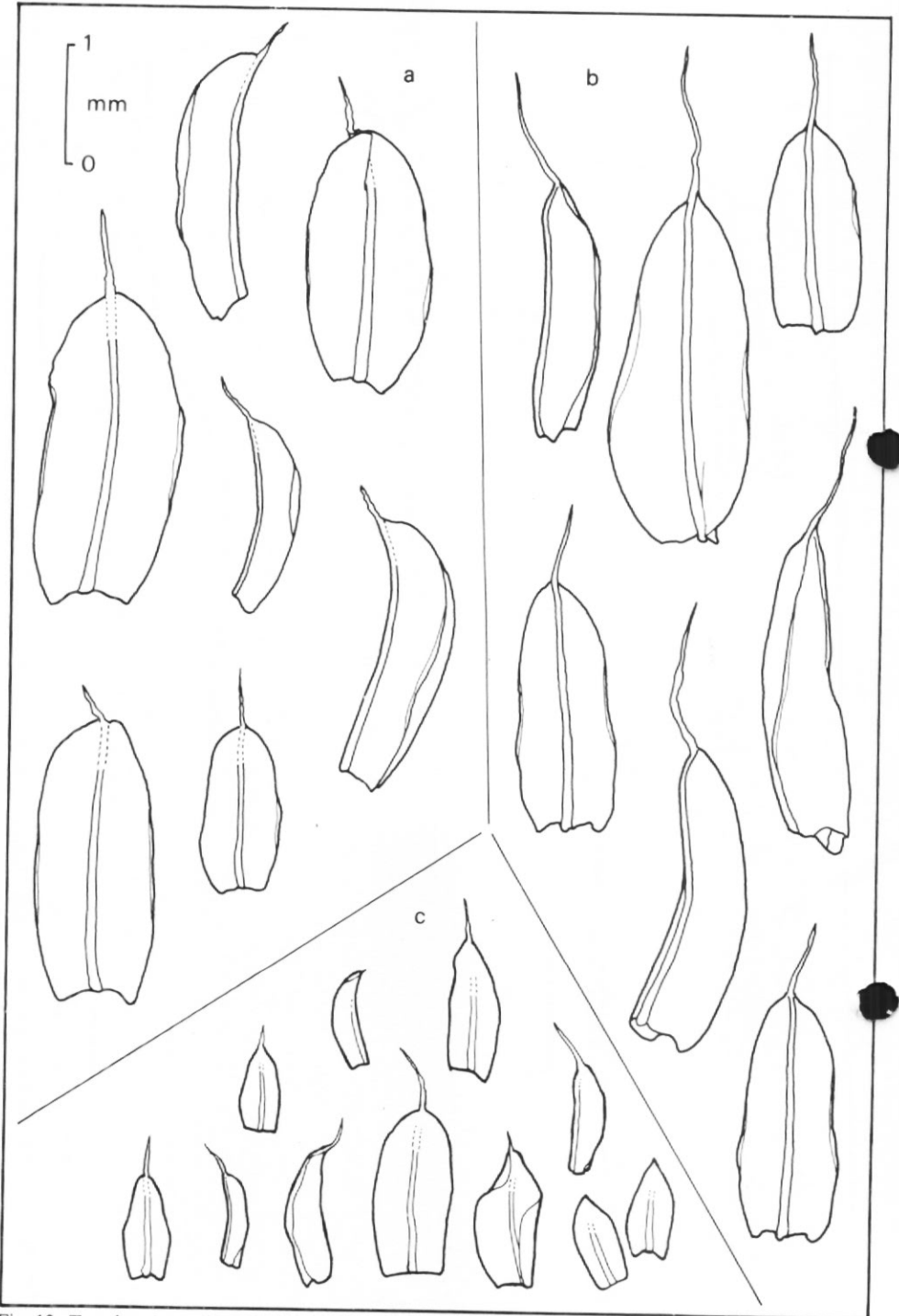


Fig. 12. *Tortula princeps* leaves: a, small forms of var. *princeps* with red hair-points; b, var. *magellanica*; c, var. *conferta*. Scale: upper left-hand for all leaves.

recurved or revolute for up to two-thirds of the leaf length. Leaf apex plane or recurved. Nerve continuous to leaf apex, or indistinct above. Hair-point 0.2–1.6 mm long, rarely reduced to an apiculus, crenate to denticulate, hyaline or reddish. Autoecious or dioecious. Sporophyte occasional. (Figs. 11 and 12a).

var. *conferta* (Bartr.) P. J. Lightowlers *comb. et stat.nov.* Basionym: *Tortula conferta* Bartr., *Bryologist* 60, 140, 1957.

Stems 0.2–1.5 cm high, slender. Leaves 0.5–1.4 (excluding hair-point) × 0.3–0.75 mm, when moist erecto-patent to spreading, broadly oblong to ovate or lingulate. Leaf margins plane, rarely weakly recurved at mid-leaf. Leaf apex cucullate, plane or recurved. Nerve becoming indistinct or ceasing entirely in upper leaf. Hair-point 0.1–0.4 mm long, smooth to crenate, hyaline or reddish, sometimes reduced to an apiculus or absent. Sterile. Sporophyte unknown. (Fig. 12c.)

var. *magellanica* (Mont.) P. J. Lightowlers *comb. et stat.nov.* Basionym: *Tortula magellanica* Mont., *In Gay, C. Historia fisica y politica de Chile. Vol. 7. Botanica.* Gay, Paris, pp. 145–6. 1850.

Syn. *Syntrichia fuegiana* Mitt.

Tortula fuegiana (Mitt.) Mitt.

Tortula magellanica Mont.

Tortula monoica Card.

Tortula pusilla Aongstr. *hom. illeg.*

Stems 0.5–1.5 cm high. Leaves (1.0–) 1.4–2.9 (excluding hair-point) × 0.5–1.0 mm, when moist erecto-patent to patent, oblong to ovate-lingulate. Leaf margins recurved for about a third to a half of the leaf length. Leaf apex cucullate, rarely plane in profile. Nerve continuous to leaf apex. Hair-point 0.3–1.0 mm long, smooth to crenate, hyaline. Autoecious or paroecious. Sporophyte common. (Fig. 12b.)

Habitat and distribution

An occasional species found in a range of habitats such as among coastal rocks, on peaty banks, on gravel or rocks by streams, on whale bones and in environments influenced by man such as on waste ground and on walls. There is little evidence at present to suggest that the varieties of *T. princeps* have different habitat preferences, but var. *conferta* appears to be commonest on dry rocks and walls. Further field observations are required to assess whether the varieties have any ecological significance. Most specimens have been collected from altitudes below ten metres but it is unlikely that this is due to climatic influences as the species is also found at higher latitudes in the Antarctic Peninsula. Sea spray may be an important habitat factor for this species in providing a high pH when most rocks and soils are base-poor. This may be particularly important in this case as *T. princeps* has been shown to have a high salt tolerance (Moore and Scott, 1979). Alt. 1–200 m. (Figs. 13, 14 and 15).

Notes

T. princeps is the only hair pointed species of *Tortula* on South Georgia and is therefore readily identified. However, confusion with *Willia austroleucophaea* may occur and differences between these plants are outlined in the notes on the identification of the genus *Tortula* at the beginning of this paper.

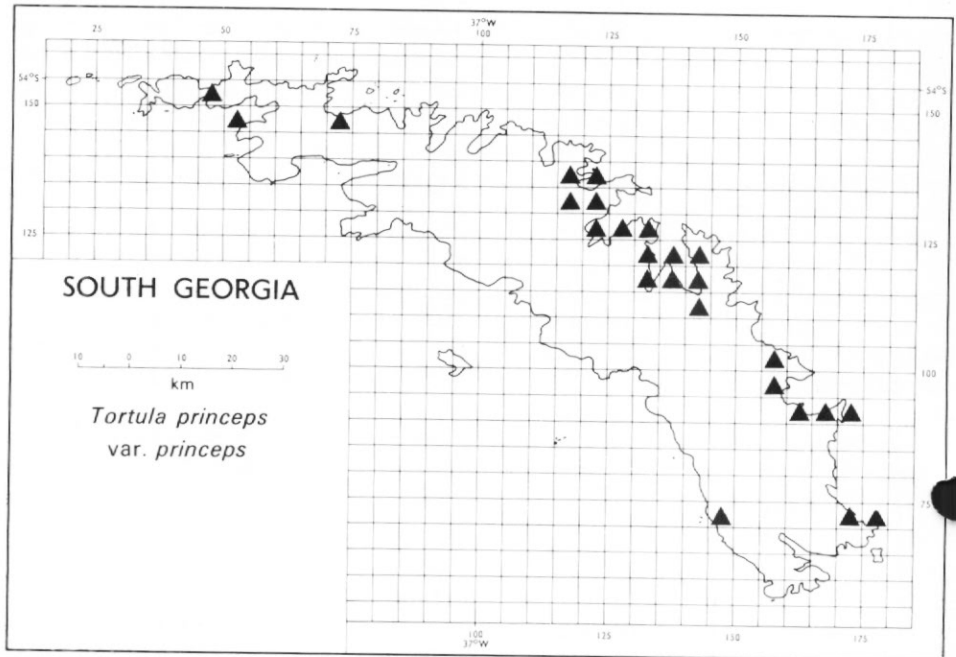


Fig. 13. The known distribution of *Tortula princeps* var. *princeps* on South Georgia, by 5-km squares.

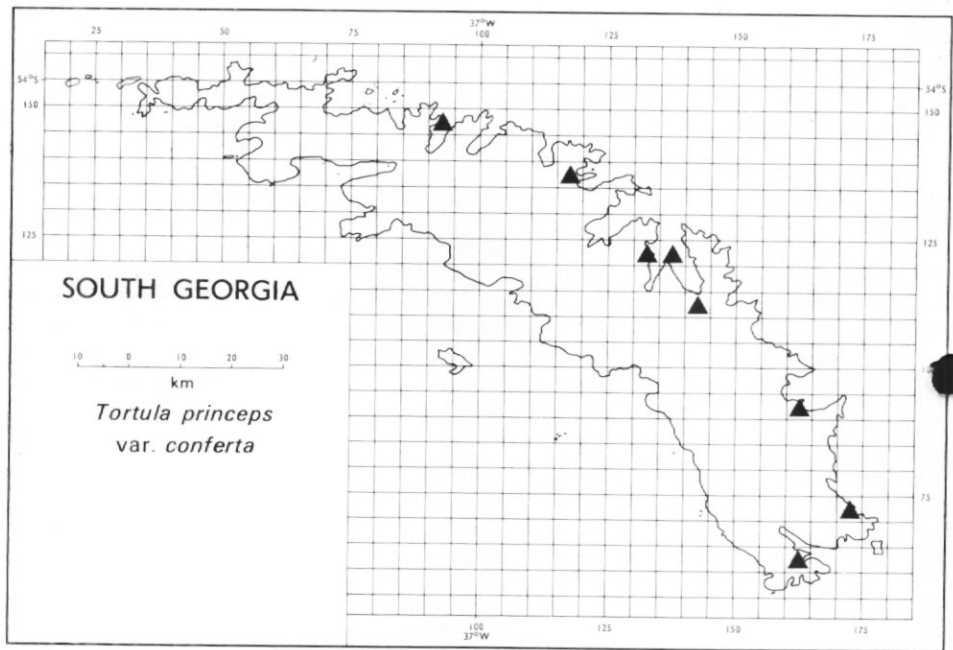


Fig. 14. The known distribution of *Tortula princeps* var. *conferta* on South Georgia, by 5-km squares.

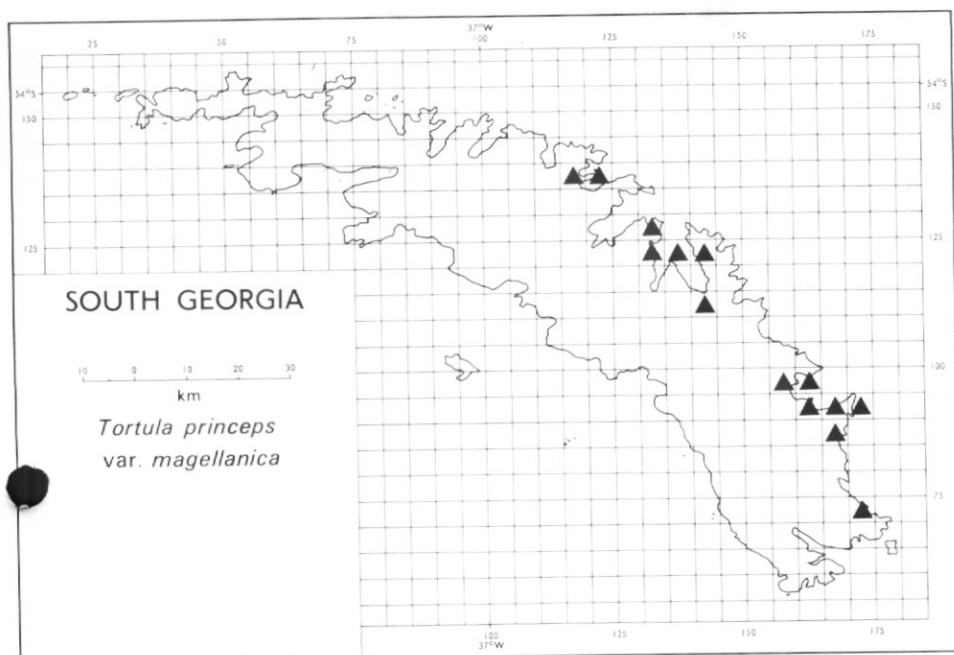


Fig. 15. The known distribution of *Tortula princeps* var. *magellanica* on South Georgia, by 5-km squares.

T. princeps is a variable polymorphic species and identification to variety may be difficult. The classification proposed here is based on both traditional and statistical investigations (Lightowers, 1983), which recognised four infra-specific taxa. Two of these groups correspond with var. *conferta* and var. *magellanica* while the other two are included within var. *princeps*. As presently defined, the var. *princeps* includes a group of plants with red hair-points and recurved leaves which are, on average, slightly smaller than other var. *princeps* specimens. Although these plants come from a group which is as coherent and distinct as the other varieties, it is not recognized here because growth experiments (Lightowers, 1983) have suggested that typical var. *princeps* or var. *magellanica* plants may adopt the red hair-pointed phenotype under certain environmental conditions and, unlike the other varieties of *T. princeps* recognized here, the red hair-pointed plants have not been previously described as a discrete taxon.

The present infra-specific classification of *T. princeps* is provisional and further information from growth experiments and field observations is needed before variation within the species can be fully understood. It is unlikely that the group of red hair-pointed plants, the var. *magellanica* and the var. *princeps* are simply habitat forms since they are often found together in the same tuft with no apparent intergradation. However, intermediates which are difficult to place in any variety also occur.

T. princeps var. *conferta* is rare on South Georgia and variation in this taxon can only be investigated fully by the examination of material from the Antarctic botanical zone where it is more abundant. Antarctic specimens show wide variation in size and morphology and show a tendency to intergrade with both var. *magellanica* and with red hair-pointed plants.

*Taxonomy**T. princeps* var. *princeps*

The earliest name applicable to this species appears to be *T. princeps* De Not. which was described from Sardinia (De Notaris, 1838). The first report of the species from the austral-Antarctic area was made by Wilson (in Hooker, 1847) who reported it as *T. muelleri* Hook. f. et Wils., an illegitimate name for *T. princeps*. The original material collected by J. D. Hooker on the Falkland Islands has been traced and examined (Hooker s.n., BM ex K, *Tortula mülleri* Br. + Sch., Falkland Islands Antarct. Exp. 1839-43, J.D.H.). It is similar to South Georgian material but differs in two respects: first in its larger size, which is perhaps due to the more favourable climate in the Falkland Islands; and second it is synoecious and not dioecious or autoecious like South Georgian specimens. Synoecy in European plants has been regarded as a key character of the species by Dixon (1924), Smith (1978) and Kramer (1980). However, according to Dixon (1923) New Zealand plants are synoecious or autoecious and Sainsbury (1955) notes that some are dioecious. Steere (1939) also describes North American *T. princeps* as synoecious or autoecious. Therefore, outside Europe the species seems to be variable in its sexual state and it would be unwise to distinguish between South Georgian and Falkland Islands material solely on this character. In addition, South Georgian plants are often sterile and antheridia are rare, so that any classification using this character would be impractical. The South Georgian material is therefore regarded as conspecific with Hooker's Falkland Islands specimens.

Hampe disagreed with Wilson's decision (in Hooker, 1847) to refer Falkland Islands material to the northern hemisphere *T. muelleri* (= *T. princeps*) and described Hooker's material as a new species, *Barbula antarctica* Hamp. (in Müller, 1849). The type specimen has been found (Lectotype (nov.), Hooker s.n., BM, *Barbula antarctica* Hamp. n.sp., Falkland Islands, Antarct. Exp. 1839-43, J.D.H., Herb. Hampe 1881.) and it is identical to other plants referred to *T. muelleri* by Wilson. No differences between *T. princeps* and *B. antarctica* are given by Hampe in the type description (Müller, 1849) but the following diagnosis appears on the type specimen: 'Differt a B. Mülleri statura graciliori, foliosum forma apice retusa et textura teniore magis conspicua foliosiore.' These differences are not consistent in a range of South American and Fuegian specimens examined by the author and do not justify a separate species.

Hooker's Falkland Island material has been compared with an isotype of *T. princeps* (De Notaris s.n., E, *T. princeps* D. Nts, in montibus Sardinia australis D. Nts). The two plants agree in leaf shape and stance, in the recurvature of the leaf margin, in sexual state and in the type of papillae on the abaxial nerve surface, and there seems no reason at present to question Wilson's decision to refer Falkland Island specimens to *T. princeps*. *B. antarctica* is therefore considered a synonym of *T. princeps*, as is the combination *T. antarctica* (Hamp.) Wils. which was made by Wilson (in Hooker, 1860). However, *T. princeps* as presently understood, is a variable, cosmopolitan species which is in need of monographic revision to clarify the relationships between European, North American and southern hemisphere populations.

South Georgian *T. princeps* material has previously been referred to *T. grossiretis* Card., a species described from the island by Cardot (1905). *T. grossiretis* var. *atrata* Card. was also described in the same publication. Type specimens of both taxa have been traced and examined (Lectotype (nov.), Skottsberg 299, S, *Tortula grossiretis* Card. sp.nova, South Georgia, Cumberland Bay, Pot Harbour. D. 15/5/1902. Det. J. Cardot, Carl Skottsberg Svenska Sydpolarexpeditionen 1901-03 N.R. 299; (Lectotype (nov.), Skottsberg 300, S, *Tortula grossiretis* var. *atrata* Card. var. nova, Géorgie

du Sud: Cumberland Bay. Leg. Skottsberg 1902. No. 300). The *T. grossiretis* specimen is a typical specimen of *T. princeps* var. *princeps* and the *T. grossiretis* var. *atrata* specimen differs only in very minor respects. According to Cardot (1906, 1908) the variety is based on the darker green colour of its leaves, its large size, its fastigiate branching and leaves with more rounded apices. The range of material available during this study indicates that these differences are trivial, these characters showing continuous variation between wide extremes. Both *T. grossiretis* and the var. *atrata* are therefore considered to be synonyms of *T. princeps* var. *princeps*.

Cardot (1911) described another hair-pointed species of *Tortula*, *T. heteroneura* Card., from the Antarctic Peninsula. Type material has been examined (Lectotype (nov.), Gain 211, PC, *Tortula heteroneura* Card. sp.nova, Ile Petermann, sur la terre humide entre les rochers. Leg. Gain 5.1.1909. No. 211., Isotypes BM ex K!, H!) and as the type description suggests, these plants are similar to *T. princeps*. They differ, however, in the nerve structure in the upper leaf, which becomes less distinct and disappears below the leaf apex. Plants with this type of nerve have been found on South Georgia and they intergrade with typical specimens of *T. princeps*. Examination of Antarctic material confirms this, as all specimens with abnormal nerve structure also have some normal leaves. No taxonomic significance can be attached to variation in this character and *T. heteroneura* is therefore treated as a synonym of *T. princeps*.

var. *conferta*

T. princeps var. *conferta* was first described by Bartram (1957) as *T. conferta* Bartr. from material collected on the Antarctic Peninsula. Type specimens have been examined (Lectotype (nov.), Siple 335.12, FH, *Tortula conferta* Bartr. sp.nov. det. E. B. Bartram, Lysted Island, Melchior Archipelago, P. A. Siple collector, 1 March 1941, United States Antarctic Service Expedition of 1940-41 No. 335.12; Syntype, Siple 345.1, FH, *Tortula conferta* Bartr. and *Pohlia cruda* var. *imbricata* det. E. B. Bartram, Lambda Island, NE landing, Melchior Archipelago, P. A. Siple collector, 3 March 1941, United States Antarctic Service Expedition of 1940-41 No. 345.1) as has other material from the Antarctic Peninsula, the South Shetland Islands and the South Orkney Islands in the British Antarctic Survey Herbarium (AAS). The small number of South Georgian specimens available fall well within the wide variation shown by this taxon in its more southerly localities. All of its distinguishing characters such as its small leaf size, reduced nerve structure and plane leaf margins show intergradation with the var. *magellanica* and with red hair-pointed forms of the var. *princeps*. The ecology of the var. *conferta* and its behaviour in growth experiments have not yet been studied, but its small stature and simplified structure suggest it is a depauperate form of *T. princeps*. However, *T. princeps* var. *conferta* is abundant in Antarctic latitudes and it is retained as a variety until its variation and ecology are better understood.

var. *magellanica*

T. princeps var. *magellanica* was first described by Montagne (1850) as *T. magellanica* Mont. An authentic specimen has been located (Lectotype (nov.), s.n., PC, *Tortula magellanica* Montag., Voy. Pole Sud) but the packet contains plants referable to both var. *magellanica* and var. *princeps*. The type description indicates that the plants have smooth hair-points and sporophytes which clearly separates the plants in the packet, since the var. *princeps* plants have strongly denticulate hair-points and are sterile. Montagne (1850) also remarks that the taxon has 'una cerda lisa... la cual no es la prolongacion derecha de la nerviosidad, pero en su nacimiento forma con la punta de la hoja una encorvadura con el seno obtuso por bajo', thus describing the cucullate profile of the leaf. South Georgian specimens agree in all respects with

the *T. magellanica* material and they are therefore referred to this taxon. *T. magellanica* is here reduced to a variety of *T. princeps* because of its intergradation with hyaline hair-pointed forms of the var. *princeps* and var. *conferta*.

Müller (1885) and Cardot (1908) noted *T. magellanica* but neither seem to have examined material closely. The synonymy of other taxa with more widely used names has thus not been considered. South Georgian plants of *T. princeps* var. *magellanica* have previously been referred to *T. monoica* Card. (Cardot 1906, 1908, Cardot and Brotherus 1923, Dixon 1934). This species was described by Cardot (1905) from the Falkland Islands and the type material has been examined (Lectotype (nov.), Skottsberg 223, PC, *Tortula monoica* Card. sp.nova. Falkland Islands, Port Louis. D.25/7 1902 Greenpatch in rupibus marit., Det. J. Cardot, Herb. J. Cardot, Carl Skottsberg, Svenska Sydpolarexpeditionen 1901-03 N.R. 223, Isotype H!) This specimen has a few weathered sporophytes and has mainly oblong rather than oblong-lingulate leaves, but it is well within the range of the variation shown by this taxon on South Georgia. *T. monoica* is therefore considered a synonym of *T. princeps* var. *magellanica*.

Wijk and others (1969) cited *T. monoica* as a synonym of the New Zealand species *T. tenella* Broth. Type material of this species has been examined (Isotype, Petrie 822, BM, *Tortula tenella* Broth., Otago New Zealand. Coll. D. Petrie Det. Brotherus Herb. H. N. Dixon, Ref. No. 822) and found to differ from the South Georgian taxon in general habit and leaf shape. *T. tenella* is more densely tufted, the leaves are slightly pandurate, the nerve is stronger, the hair-point smoother and the leaf lacks the cucullate apex of South Georgian material. Wijk and others (1969) base their decision on a remark by Dixon (1923) which was probably not intended as a formal reduction to synonymy. *T. tenella* is therefore maintained as a distinct species. A report of *T. tenella* from King George Island, South Shetland Islands, by Pizarro and Sáiz (1977), appears to be based on this false synonymy and refers to *T. monoica*. Two type specimens of *Syntrichia fuegiana* Mitt., a species described by Mitten (1859), have been located and examined (Lectotype (nov.), Lechler 1088, NY, Capo negra fret. Magellan, Type, Herbarium of William Mitten 1906, Isotype BM ex K!; Syntype, Hooker s.n., NY, *Barbula*, Sandhills, Uranie Bay, Falkland Islands, J. D. Hooker, Berbarium of William Mitten 1906). Both undoubtedly belong to *T. princeps* var. *magellanica* and *S. fuegiana* should therefore be considered a synonym. The South American specimen (Lechler 1088) is more robust than South Georgian material but this is to be expected for climatic reasons. The Falkland Island specimen is smaller than the other type specimen and within the size range of South Georgian plants. Mitten (1860) described *S. fuegiana* as dioecious, but both type specimens are clearly autoecious. He transferred *S. fuegiana* to *Tortula* (Mitten, 1869) and *T. fuegiana* (Mitt.) Mitt. therefore should also be listed among the synonyms of *T. princeps* var. *magellanica*.

T. pusilla Aongstr. *hom. illeg.* (*non T. pusilla* Mitt.) was described by Ångström (1872) from Tierra del Fuego. Authentic material has been examined (Lectotype (nov.), Andersson s.n., S, *Tortula* (*Syntrichia*) *pusilla* J. Ån., Port Famine fret. Magell., N. J. Andersson) and found to belong to *T. princeps* var. *magellanica*. Thus *T. pusilla* Aongstr. should be regarded as a synonym of this taxon.

Tortula robusta Hook. et Grev.Syn. *Barbula anacamptophylla* C. Muell.*Barbula leptosyntrichia* C. Muell.*Barbula runcinata* C. Muell.*Tortula anacamptophylla* (C. Muell.) Broth.*Tortula leptosyntrichia* (C. Muell.) Broth.*Tortula robusta* var. *laxa* Bartr.*Tortula robusta* var. *runcinata* (C. Muell.) Broth.*Tortula runcinata* (C. Muell.) Broth.

Stems erect, forming turves 2.0–8.0 cm high, sparingly branched, without central strand. Leaves (3.2–) 4.4–8.0 × 0.9–2.0 mm, when moist erecto-patent to recurved, when dry slightly curled and twisted, lanceolate to oblong, narrowing to an acuminate, acute or obtuse apex. Leaves differentiated into a chlorophyllose, papillose upper limb and a hyaline, smooth basal sheath, the latter sheathing the stem for a quarter to a third of the leaf length. Leaf margin recurved from base to mid-leaf or above, rarely plane, denticulate to coarsely dentate in upper third. Nerve percurrent, abaxial surface smooth or papillose with simple verrucate papillae. Cells above 8–36 × (9–) 11–21 (–24) μm , irregularly quadrate but becoming shortly rectangular to rectangular towards the basal sheath, marginal row often smaller, papillose with complex papillae. Basal cells 47–160 × 10–40 μm , rectangular to longly rectangular or linear, 2–12 times as long as wide, sometimes porose, narrower towards the leaf margins, sometimes forming a border, smooth, hyaline, sometimes lax and inflated. Longly rectangular cells often continuing up leaf margin into limb. Rhizoids smooth, brown, sparingly produced on older parts of stem. Dioecious. Perichaetical bracts similar to other leaves or longer. Perigonial bracts shorter than other leaves with broader basal region. Sporophyte occasional. Seta 13–27 mm, when dry dextrorse (externe visus) in upper part, sinistrorse below. Capsule 2.2–3.9 × 0.45–0.7 mm, erect or slightly inclined, cylindrical. Operculum subulate. Peristome of 32 teeth united below for about one third of their length and twisted into a dextrorse helix. Spores 9.5–13.5 μm in diameter.

var. *robusta*

Leaves 4.4–8.0 × 0.9–2.0 mm, erecto-patent to spreading or rarely recurved when moist, lanceolate to lingulate-lanceolate tapering to an acute or acuminate apex. Leaves rarely having a border of elongated cells extending for up to two-thirds of the leaf length. Sporophyte occasional. (Figs. 16 and 17a, c, d.)

var. *recurva* P. J. Lightowlers

Leaves 3.2–4.8 × 1.0–1.8 mm, recurved when moist, oblong-lanceolate to oblong, narrowing to an acute or obtuse apex. Sporophyte unknown. (Fig. 17b, e.)

Habitat and distribution

T. robusta var. *robusta* is a very common plant which is widely distributed at lower altitudes. Habitats include scree, forming an understory to *Acaena* shrubs, *Rostkovia* bogs, tussock grass, or *Deschampsia* meadows, particularly where moist. Alt. 0–370 m. In contrast the var. *recurva* is rare and found in rocky habitats at higher altitudes. However it has been collected in bogs associated with *T. fontana*. Alt. 90–425 m. (Figs. 18 and 19.)

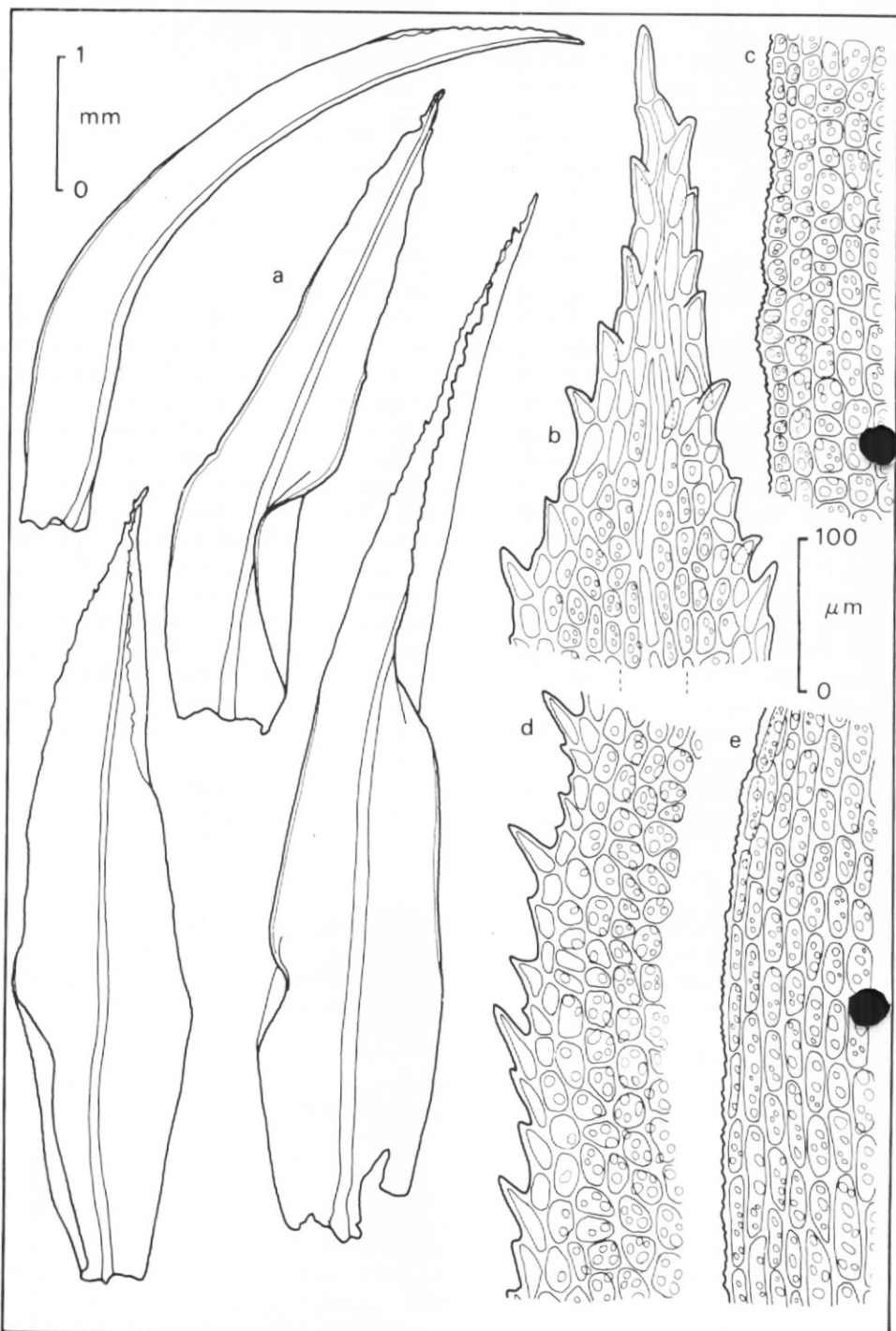


Fig. 16. *Tortula robusta* var. *robusta*: a, leaves; b, leaf apex; c, marginal cells at mid-leaf; d, upper leaf margin; e, upper basal leaf margin. Scales: upper left-hand for leaves; right-hand for leaf apex and leaf margins.

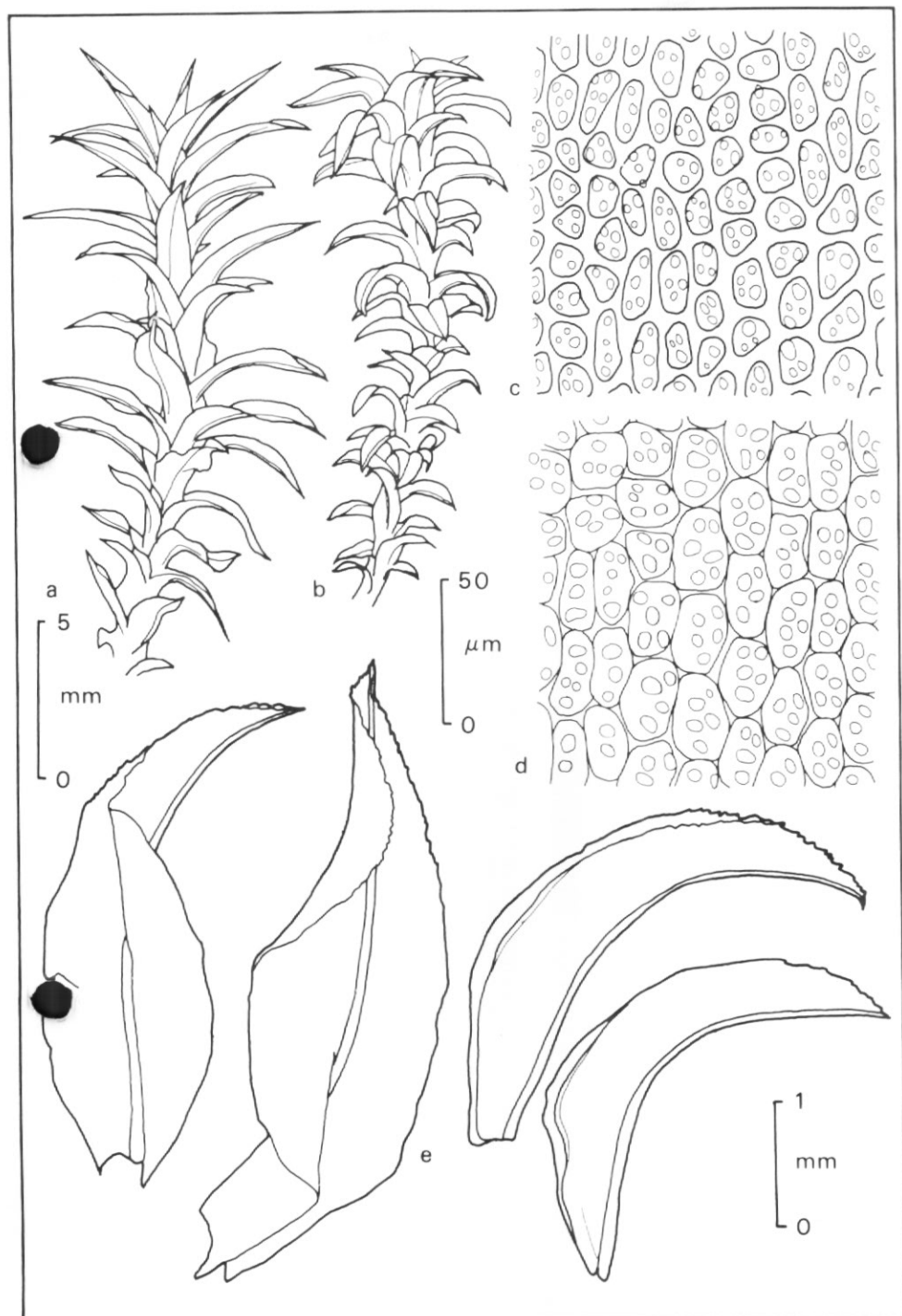


Fig. 17. *Tortula robusta*: a, var. *robusta* shoot; b, var. *recurva* shoot; c and d, var. *robusta* upper lamina cells; e, var. *recurva* leaves. Scales: left-hand for shoots; centre for cells; lower right-hand for leaves.

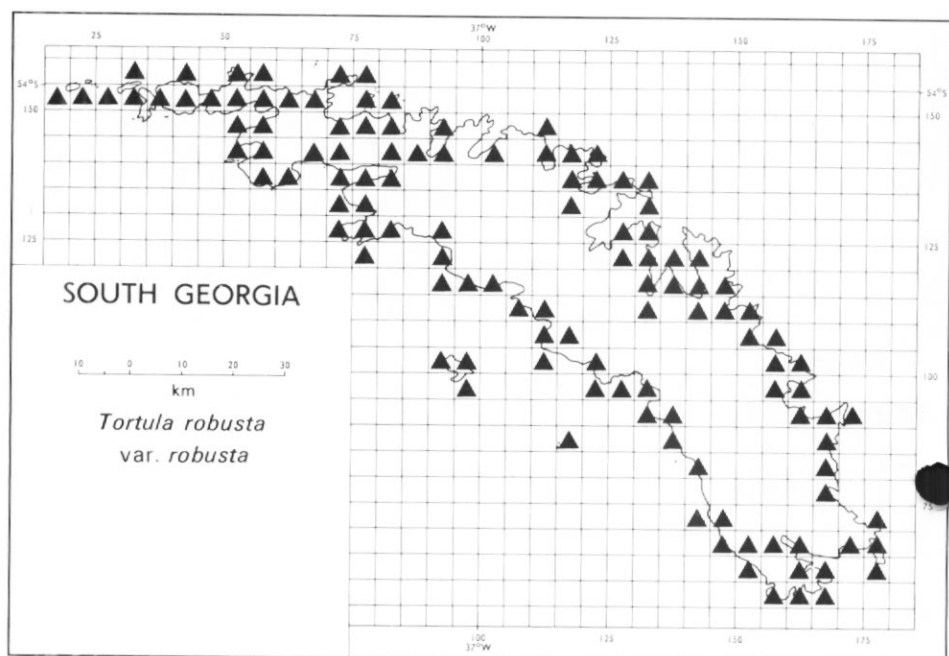


Fig. 18. The known distribution of *Tortula robusta* var. *robusta* on South Georgia, by 5-km squares.

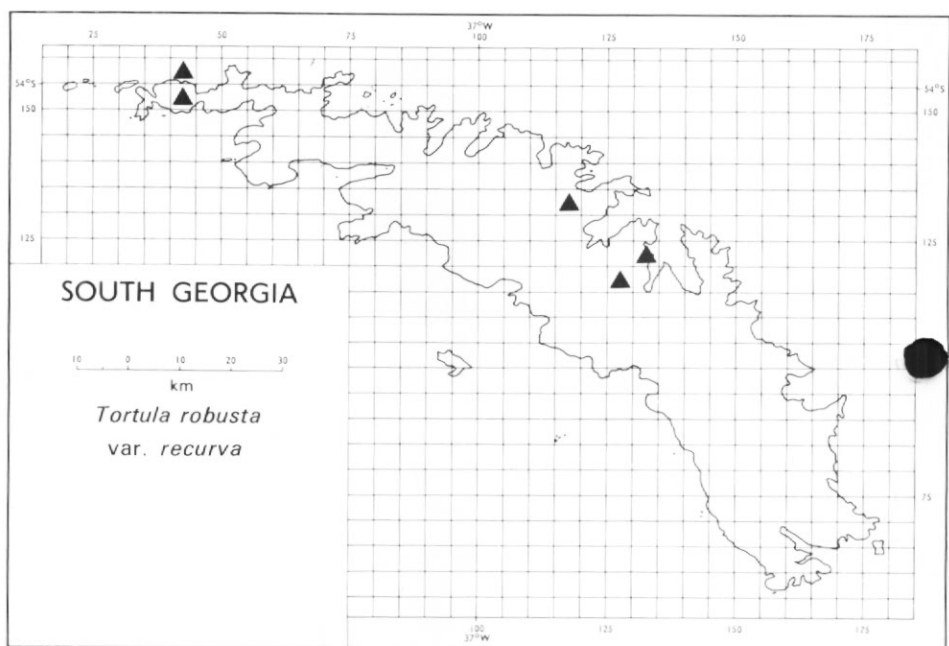


Fig. 19. The known distribution of *Tortula robusta* var. *recurva* on South Georgia, by 5-km squares.

Notes

T. robusta var. *robusta* shows a wide range of variation in many characters, notably leaf size and cell size. Average leaf length in specimens may vary between about 4.5 and 7.5 mm and average cell width between 12 and 22 μm . Specimens with large stems and leaves are distinctive and are unlikely to be confused with other species. However, small forms may resemble *T. filaris* or, if the leaves have thick cell walls, *T. geheebiaeopsis*. Ways of distinguishing these taxa and *T. saxicola*, which has a similar leaf shape, are described in the notes for those species.

The var. *recurva* is characterised by its rather short, oblong leaves which are recurved when moist. The appearance of the stems should identify the variety in most instances, however broad leaved forms of var. *robusta* occur in which the leaves are not recurved and are too long to be included in var. *recurva*. Specimens of var. *robusta* with recurved leaves are also found which differ from var. *recurva* in leaf size and shape.

T. robusta var. *recurva* is similar to *T. fontana* in size, leaf shape and areolation and confusion may occur between these taxa. Distinguishing characters are considered in the notes for *T. fontana*.

Taxonomy

Tortula robusta was described by Hooker and Greville (1824) from a specimen, the collecting details of which are unknown. Hooker and Greville (1824) record merely that the specimen was obtained from a 'Mr. Dickson', probably James Dickson (1738–1822), the British horticulturalist and hepaticologist. Dickson is known to have exchanged specimens with Archibald Menzies (Long, 1979) and it is likely that the type specimen of *T. robusta* was collected by him on Staten Island, Tierra del Fuego, during his expedition of 1787 (Godley, 1965). Indeed, several specimens from this source are mentioned by Hooker and Greville (1824). Type material has been examined (Lectotype (nov.), s.n., BM ex K, *Tortula robusta* sp. novo, Herb. Hookerianum 1867) which, although fragmentary, is very similar to South Georgian material. Three species described by Müller (1890) from South Georgia fall within the morphological limits of *T. robusta*. These are *Barbula runcinata* C. Muell., *B. lepto-syntrichia* C. Muell. and *B. anacamptophylla* C. Muell. All are transferred to the genus *Tortula* by Brotherus (1902).

Two syntypes of *B. runcinata* survive in Munich (Will 39, M, *Barbula* (*Syntrichia*) *runcinata* C. Müller c. fr., Fündort: Oberhalb des magnetischen Observatoriums, Süd-Georgien, 1883, Will; Lectotype (nov.), Will 39, M, *Barbula* (*Syntrichia*) *runcinata* C. Müller n.sp., Fündort: Landzuge in S.-Rand des Hochplateaus, sehr Häufig, an den Hängen in Wasserrinnen u. sonstigen sehr feuchten Stellen, Süd-Georgien, 10/II 83, Will). Both are large specimens of *T. robusta* var. *robusta* with lanceolate leaves and strongly recurved leaf margins, *B. runcinata* is therefore regarded as a synonym. There appears to be no justification for retaining the taxon as a variety, which was suggested by Brotherus (Cardot and Brotherus 1923), and *T. robusta* var. *runcinata* (C. Muell.) Broth, is also reduced to synonymy.

Three authentic specimens of *B. lepto-syntrichia* have been found in Brotherus' herbarium in Helsinki (H). These are labelled '*Barbula* (or *Tortula*) *lepto-syntrichia* C.M. Süd Georgien. Leg. Will' and one specimen is marked '*fo. robusta*'. All three are *T. robusta* var. *robusta* and hardly differ from the type specimens of *B. runcinata*. However, the leaves are only slightly denticulate and are often worn at the apex, which may have led Müller (1890) to describe them as entire. *B. lepto-syntrichia* is therefore reduced to synonymy with *T. robusta* var. *robusta*.

Unfortunately type or authentic material of *B. anacamptophylla* has not been located either in this study or by Greene (1973). Cardot (1906), however, examined Will's material and noted that *B. anacamptophylla* was merely a slender form of *B. lepto-syntrichia*, and that, contrary to Müller's (1890) comments, there was little difference between the areolation of the species. Cardot (1906) reduced *B. anacamptophylla* to synonymy with *T. lepto-syntrichia*, and since the latter species is here treated as synonymous with *T. robusta*, *B. anacamptophylla* is also regarded as a synonym of that species.

Bartram (1946) described *T. robusta* var. *laxa* Bartr. from specimens collected by Roivainen in Tierra del Fuego. The type specimen has been examined (Lectotype (nov.), Roivainen 1895, FH, *Tortula robusta* var. *laxa* Bartr. n.var., Fuegia Media. Estancia Cameron, Puesto medio, in serato humido. 1928-12. XII, Leg. H. Roivainen, Det. E. B. Bartram, Bryophyta Fuegiana No. 1895). As the type description suggests, the leaves are large with lax cells up to 20 μm wide. Such specimens have been found to be one extreme of a wide range of variation that is continuous and there is no justification for retaining this variety. *T. robusta* var. *laxa* is thus reduced to synonymy with the var. *robusta*.

T. robusta var. *recurva* was recently described (Lightowlers, 1984) after growth experiments showed that it remained distinct from other South Georgian taxa when grown in constant conditions. Details of these growth experiments are provided elsewhere (Lightowlers, 1983).

Tortula saxicola Card.

Syn. *Tortula fuscoviridis* Card.

Stems erect forming cushions 0.9-4.0 cm high, sparingly branched, with or without a central strand. Leaves 1.6-4.5 \times 0.3-0.9 (-1.0) mm, when moist erecto-patent to spreading, when dry incurled and slightly twisted. Leaf shape lanceolate to oblong-lanceolate, tapering to a finely acuminate apex. Leaves differentiated into a chlorophyllose, papillose upper limb and a hyaline, smooth sheath, the latter sheathing the stem for a quarter to a third of the leaf length. Leaf margin entire, weakly recurved to revolute for up to two thirds of the leaf from base. Nerve percurrent or excurrent as a fine hyaline, reddish or yellow-brown subula, c. 0.1-0.3 mm long, rarely becoming obscure above and disappearing before reaching leaf apex. Abaxial surface of nerve smooth or papillose with simple verrucate papillae. Cells above 6-14 \times 8-12 (-13.5) μm , irregularly quadrate, densely papillose with complex papillae. Quadrate cells spreading down margin of upper basal region of leaf. Basal cells 40-120 \times 8-20 μm , rectangular to linear, 3 to 10 times as long as wide, sometimes lax and inflated. Rhizoids smooth, brown, sparsely produced on lower parts of stem. Antheridia not seen. Perichaetial bracts similar to the other leaves or broader at base. Sporophyte unknown on South Georgia. (Fig. 20.)

Habitat and distribution

A rare to occasional species limited to rock faces, crevices and ledges. Alt. 2-300 m. (Fig. 21).

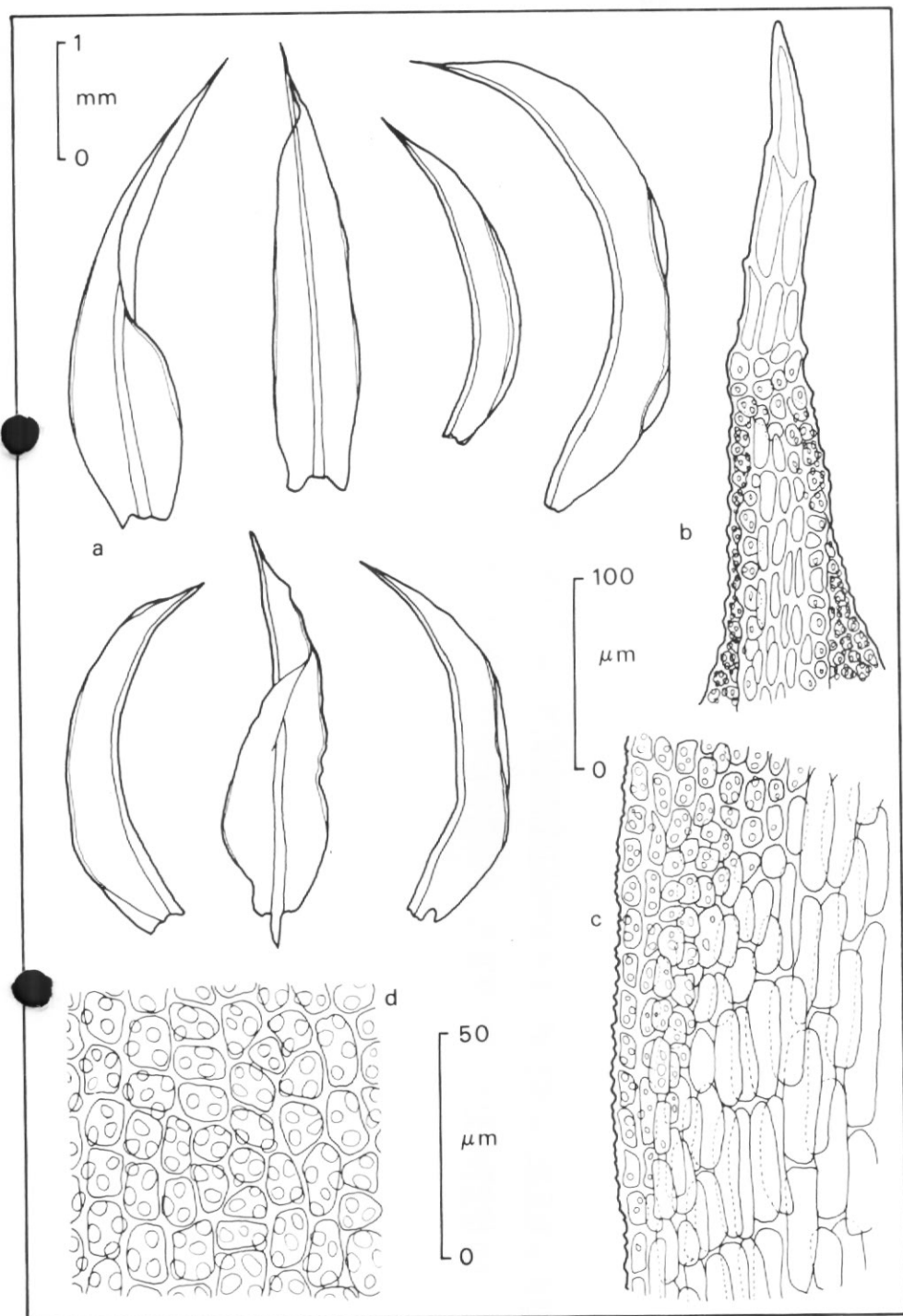


Fig. 20. *Tortula saxicola*: a, leaves; b, leaf apex; c, upper basal leaf margin; d, upper lamina cells. Scales: upper left-hand for leaves; centre for leaf apex and leaf margin; lower for cells.

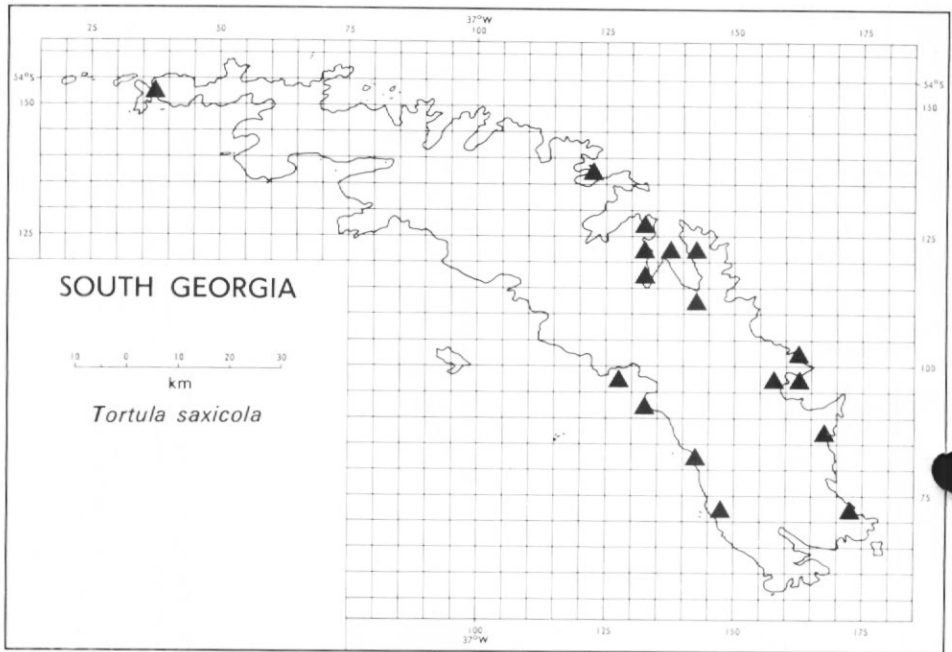


Fig. 21. The known distribution of *Tortula saxicola* on South Georgia, by 5-km squares.

Notes

Although similar to *T. filaris*, *T. geheebiaeopsis* and *T. robusta* var. *robusta* in leaf shape, *T. saxicola* is probably not closely related to these species. It differs not only in the fine, acuminate leaf apex with its characteristic areolation, but also in its entire leaves and the cell arrangement at the leaf base. The quadrate cells at the margin of the leaf limb spread down the basal leaf margin towards the leaf base in this species, but in the other non-hair-pointed species the basal marginal cells are elongated like the inner basal cells, and, in many cases, long rectangular cells spread up the leaf margin into the leaf limb. The basal cells also never become narrower toward the leaf margin in *T. saxicola*, forming a border, as sometimes occurs in *T. geheebiaeopsis*, *T. fontana* or *T. robusta* leaves. On the basis of these differences *T. saxicola* appears similar to *T. princeps* rather than to other non-hair-pointed South Georgian *Tortula* species.

The lamina cells of *T. saxicola* are rather small and densely papillose which may be used to separate this species from *T. princeps*, *T. filaris* and *T. robusta* in the absence of undamaged leaf apices. The cells of *T. geheebiaeopsis* leaves are slightly smaller, more thick walled and more densely papillose and are thus not likely to be confused with those of *T. saxicola*.

A species of *Barbula*, *B. cf. pycnophylla* Card., is likely to be mistaken for *T. saxicola* and will key out as the latter in the key to *Tortula* taxa provided. It can be distinguished from *T. saxicola* by the leaves which, when dry, are appressed and slightly twisted but not curled as in *T. saxicola*. Herbarium specimens are also green above and black below, not orange-brown like *T. saxicola*, and the cells on the adaxial surface of the nerve at mid-leaf are longly rectangular or linear and smooth, not quadrate and papillose as in all species of *Tortula*.

Taxonomy

Cardot (1905) first described this species from material collected in Tierra del Fuego, an isotype of which has been located and examined (Skottsberg 62, S. *Tortula saxicola* Card. sp.nova, Tierra del Fuego, Ushuaia, ad saxa., 6/10/1902, Det. J. Cardot, Carl Skottsberg, Svenska Sydpolarexpeditionen 1901-03 N.R. 62). This agrees with South Georgian specimens in all important characters, particularly leaf shape, cell size, areolation at the leaf apex, lack of teeth on the upper leaf margin and the density of papillae on the leaves. There is no doubt that South Georgian material can be referred to this species.

Cardot (1906) also described a similar species, *T. fuscoviridis* Card., from South Georgian material. Type material has been examined (Lectotype (nov.), Skottsberg 298, PC, *Tortula fuscoviridis* Card. sp.nova, South Georgia, Royal Bay, Mount Krokisius usque 500 m. s.m., det. J. Cardot, Carl Skottsberg, Svenska Sydpolarexpeditionen 1901-03 N.R. 298, Isotype S!) which is typical of South Georgian *T. saxicola* specimens. *T. fuscoviridis* thus appears to be a synonym of *T. saxicola*, however Cardot (1906, 1908) noted that *T. fuscoviridis* had more slender stems, less acuminate leaves and larger, more papillose, chlorophyllose cells than *T. saxicola*. These differences are within the limits of variation observed in South Georgian specimens and the two species are therefore considered to be synonymous.

ACKNOWLEDGEMENTS

I am grateful to the staff of the following herbaria for the loan of specimens: Botanical Museum, Helsinki; Botanische Staatssammlung, München; British Museum (Natural History), London; Farlow Herbarium, Harvard University, Cambridge USA; Museum National d'Histoire Naturelle, Paris; Naturhistoriska Riksmuseet, Stockholm; New York Botanical Garden; Royal Botanic Garden, Edinburgh; Staatsinstitut für allgemeine Botanik, Hamburg.

My thanks go to B. G. Bell and Dr S. W. Greene for the supervision of the Ph.D. study of which this work formed a part, to the former also for helpful advice on the manuscript and to the latter for the benefit of his experience of *Tortula* on South Georgia. Thanks are also due to Mrs A. Halcrow and Mr T. D. Murray for herbarium assistance.

Received 8 October 1984; accepted 27 December 1984

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APPENDIX

SPECIMENS EXAMINED

In previous papers in this series comprehensive specimen details have been given. Due to the large number of specimens examined in this revision only the number of specimens of each taxon is provided (Table I), together with details of the herbaria in which the specimens have been deposited. However, further information on all of the material examined may be obtained from the British Antarctic Survey bryophyte herbarium, which is housed at the Institute of Terrestrial Ecology, Bush Estate, Penicuik, Midlothian EH26 0QB, Scotland.

Table I. Number of specimens of each taxon examined together with the distribution of duplicates in cases where taxa have not been distributed to all the herbaria noted in the Appendix.

Taxon	No. of specimens examined	Distribution to herbaria
<i>Tortula anderssonii</i>	8	ALTA, BA, CHR, H, KRAM, MEL NIPR, PC, PRE, S.
<i>T. arenae</i>	41	
<i>T. filaris</i>	39	
<i>T. fontana</i>	11	
<i>T. geheebiaeopsis</i>	85	
<i>T. princeps</i> var. <i>princeps</i>	33	
<i>T. princeps</i> var. <i>conferta</i>	12	ALTA, BA, H, KRAM, MEL, NIPR, NY, PC, TNS.
<i>T. princeps</i> var. <i>magellanica</i>	29	
<i>T. robusta</i> var. <i>robusta</i>	140	
<i>T. robusta</i> var. <i>recurva</i>	6	ALTA, B, BA, CHR, H, LE, MEL, NY, O, TNS.
<i>T. saxicola</i>	28	

Apart from the historical specimens noted in the text, all of the specimens examined come from unidentified collections in the British Antarctic Survey herbarium (see Greene, 1973). After identification, this material has been distributed to herbaria as follows: major sets of specimens are held in AAS and BM; duplicate sets representing each taxon have been sent to all of the following herbaria: ALTA, B, BA, CHR, H, KRAM, LE, MEL, NIPR, NY, O, PC, PRE, S, TNS. If the material available was insufficient to allow this, duplicates have been distributed as shown in Table I. Herbarium abbreviations follow Holmgren and others (1981).