TAXONOMIC STUDIES IN ANTARCTIC BRYOPHYTES WITH PARTICULAR REFERENCE TO THE GENUS *Tortula*

by P.J. Lightowlers

Ph.D.

University of Edinburgh

1983

CONTENTS

ABSTRACT

The confused taxonomy of Antarctic bryophytes is placed in context with an account of the early collections and studies of the flora. The extreme Antarctic climate causes depauperation and modification of bryophytes which has resulted in taxonomic difficulties. These may be overcome by first studying the flora of the sub-Antarctic Island of South Georgia, which is similar but not subject to the same environmental stresses. A taxonomic revision of Tortula, an abundant moss genus on the Island, was carried out assisted by statistical techniques, growth experiments and scanning electron microscopy.

Twelve preliminary taxa were defined and further delimited by measurement and scoring. Data obtained are presented as histograms and scatter diagrams and results of a principal components analysis and cluster analyses are given.

Bryophyte cultivation techniques are described which allowed various Antarctic taxa to be maintained in Britain. An experimental method was developed which enabled species to be grown in controlled conditions provided by refrigerated cabinets. Comparisons of growth in these conditions were made and taxonomic conclusions drawn.

Scanning electron microscopy was used to investigate leaf, peristome, spore and rhizoid surfaces of South Georgian species.

Conclusions from the examination of herbarium specimens, statistics, cultivation and scanning electron microscopy are brought together in a taxonomic account of Tortula for South Georgia. Eight species and three varieties are recognised, and a key, descriptions and figures are given, together with notes on habitat, nomenclature and distribution.

The probable origin of the Antarctic flora is considered in relation to

the distribution of Tortula species in the southern hemisphere, and a comparison of species in north and south temperate zones suggests the genus may have arisen in austral regions. The value of statistics, growth experiments and scanning electron microscopy in taxonomic studies of little known floras is discussed.

ACKNOWLEDGEMENTS

This work was carried out at the Institute of Terrestrial Ecology, Bush Research Station and I acknowledge the facilities and financial assistance that have made this work possible. I would like to express my thanks to my supervisors Mr. B.G. Bell, Dr. S.W. Greene and Dr. R.F.O. Kemp for their support and guidance given during this study. I am also most grateful to Dr. A. Crossley for his expert help with the scanning electron microscope and with photography, and to Mr. R.I. Smith for his tireless assistance with statistics and computing. Growth experiments would not have been possible without the collections of Dr. R.I.L. Smith and Dr. D.W.H. Walton, who were also able to give me some benefit of their field experience of Antarctic plants, or without technical assistance from Mr. T.D. Murray. I would also like to thank Dr. M.E. Newton for her chromosome counts and access to her records of chromosome literature, Dr. A.E. Bailey-Watts and Dr. P.A. Mason for their help with light micro-photography and Dr. D.F. Chamberlain, Dr. G.C.S. Clarke, Mr. D. Long, Dr. C.C. Townsend and Dr. R.H. Zander for occasional advice. I am also indebted to the staff of the herbaria noted in Appendix 5, for specimens obtained on loan, particularly Dr. A. Eddy, Mr. L. Ellis and Dr. A.J. Harrington of the British Museum (Natural History) who enabled my visits to the cryptogamic herbarium and, in the case of Dr. Harrington, provided a telephone referencing service. The office staff at I.T.E. Bush deserve special mention for their patient typing of the manuscript as do the management, administration and the librarian, Ms. L.M. Scoular, for their cooperation. Finally my thanks go to my friends and colleagues who, in many cases unwittingly, contributed to the completion of this thesis.

Philip Lightowlers

Bush, October 1983.

Chapter 1 : INTRODUCTION

The vascular flora of Antarctica is very limited and the majority of the vegetation is composed of bryophytes and lichens. These have colonised a wide range of habitats and are of great ecological importance. In sub-Antarctic regions vascular plants are more frequent but cryptogams are still a very important part of the flora. On the sub-Antarctic Island of South Georgia for example, there are six times as many moss species as phanerogams.

The unique nature of Antarctic and sub-Antarctic terrestrial vegetation is being studied by ecologists who seek to understand the role that cryptogams play in the ecosystem. Mosses, the larger of the two bryophyte classes, are particularly important but the taxonomic framework needed for their identification is lacking. Although determinations of specimens can sometimes be made, they are based on descriptions which have resulted from insufficient observations, so the foundations of the taxonomy are fundamentally weak. Bryologists and phytogeographers unfamiliar with the region, have failed to realise this and have added to the confusion by citing inadequate nomenclature. Few have had the opportunity of working on Antarctic plants or visiting the area, with the result that the flora has become neglected and its ecological and phytogeographical significance has yet to be fully appreciated.

Botanical exploration relevant to the Antarctic bryophyte flora began with expeditions to southern South America, the flora of

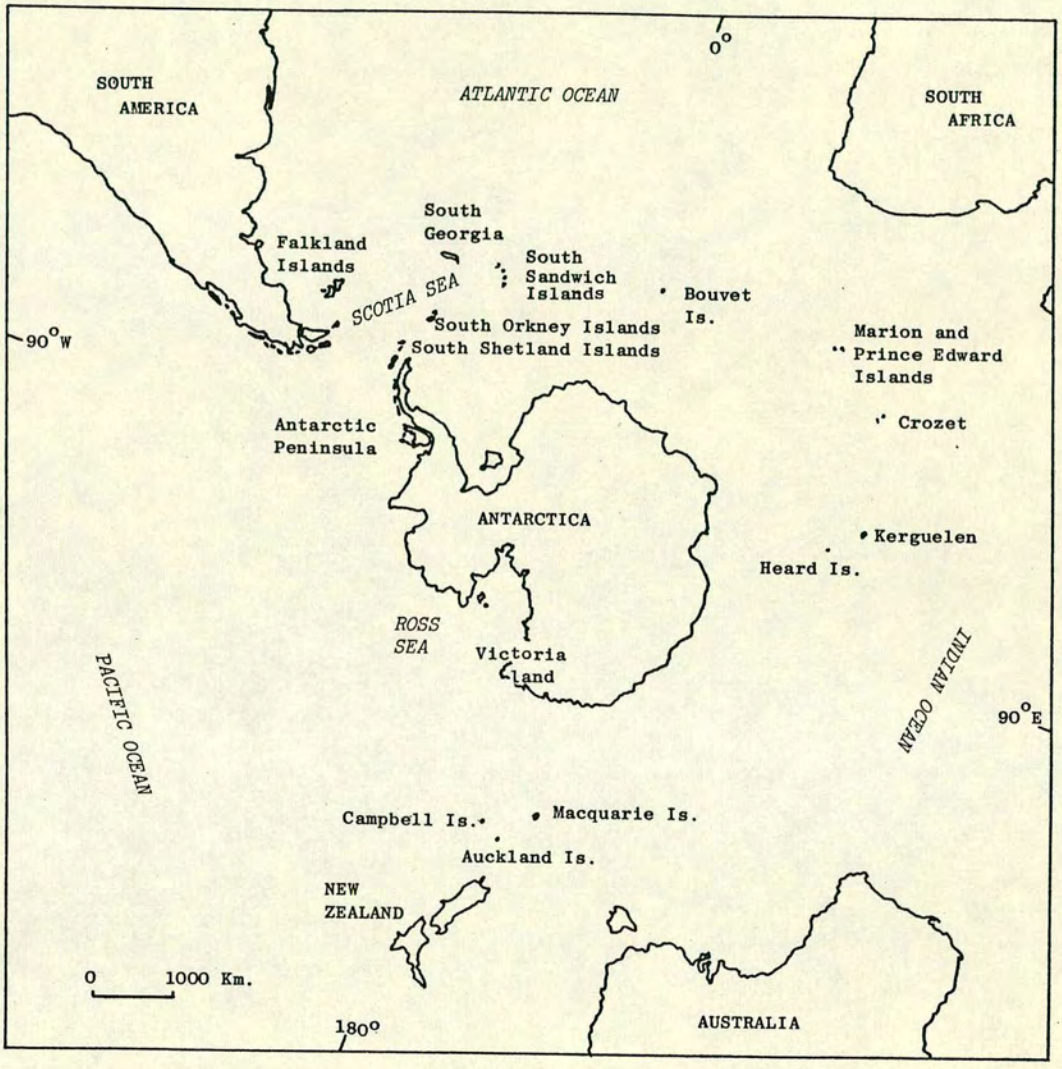


Figure 1. Map of the southern hemisphere showing Antarctica and the major Antarctic and sub-Antarctic islands.

which has strong links with that of the Antarctic Peninsula and the Islands of the Scotia Sea (Fig. 1). The first collection from Tierra del Fuego was made by G. Handisyd in 1690 but Middleton (1909) notes that it contains no bryophytes. A. Menzies appears to have been the first to collect these in 1787 from Staten Island (near Cape Horn). Unfortunately his specimens did not receive prompt attention.

Further south, the sub-Antarctic Island of South Georgia was discovered by Cook in 1775 during his voyage on the 'Resolution'. The purpose of his expedition was to find the legendary Southern Continent, and South Georgia was therefore a disappointment, being only 100 miles long and 20 miles wide. His first impressions were not favourable, and he wrote: "The inner parts of the country was not less savage and horrible: the Wild rocks raised their lofty summits till they were lost in the Clouds and the Vallies laid buried in everlasting Snow. Not a tree nor shrub was to be seen, no not even big enough to make a tooth pick" (Cook, 1777). His only observations on the flora were as follows: "Our botanists found here only three plants, the one is a coarse, strong bladed grass that grows in tufts, Wild Burnett, and a Plant like Moss which grows on the rocks". The identity of the "Plant like Moss" remains a mystery but the first two are clearly identifiable as Poa flabellata (Lam.) Hook. fil. and Acaena adscendens Vahl. respectively, indeed one specimen of the latter still survives (Greene, 1964b).

Like many other sub-Antarctic Islands, South Georgia was visited

only by passing whalers and sealers for many years after its discovery. Few plants were collected during this period and it was not until 1882-83 that a collection was made on South Georgia. This included both phanerogams and bryophytes and was the work of H. Will, botanist to the German International Polar Year Expedition.

Cook did not find Antarctica, despite several southward journeys during which the Antarctic Circle was crossed for the first time. It was established that if Antarctica did exist, it lay in the inhospitable icy waters of the extreme south. The Antarctic Continent was eventually discovered in 1820 when both Bransfield and Palmer independently sighted land south of the South Shetland Islands, which is now recognised as the northernmost tip of the Antarctic Peninsula.

The earliest surviving collection of Antarctic plants appears to be that of James Eights, naturalist to a United States expedition which visited the South Shetland Islands in 1829-30. Steere (1965) reports that specimens of three moss species survive in the U.S. National Herbarium. Godley (1965) however notes that Bellinghausen collected plants during his visit to the same Islands in 1821 but it is not known whether these have been preserved. Webster also visited the South Shetlands one year before Eights; Hooker (1847) mentions Webster's name in connection with one lichen (Usnea melaxantha Ach.) and an alga (Scyothallia jacquintotii Mont.). It is not clear if Hooker made these determinations from descriptions alone, or whether specimens were available, but it seems likely that they did exist.

The early Antarctic expeditions suffered from the lack of trained naturalists and as a result their botanical value is small. J.D. Hooker however, naturalist and assistant surgeon on the 'Erebus', had sufficient expertise to make full use of his Antarctic voyage. H.M. Discovery Ships 'Erebus' and 'Terror' circumnavigated the Antarctic, calling at Kerguelen, Victoria land, Australia, New Zealand and Tierra del Fuego. Hooker made important moss collections on the Falkland Islands, Hermite Island (in Fuegia) and notably on Cockburn Island near the Antarctic Peninsula, where 5 mosses, 6 lichens and 7 algae were found. On his return, a government grant enabled him to compare the specimens of many collectors, including Banks and Solander, Menzies, Eights and others, and produce a comprehensive work on the Antarctic flora. 'Flora Antarctica', published in 1847, remains a landmark and principal work on the botany of the region.

As the nineteenth century progressed, collections from the Fuegian-Antarctic region become more numerous. Some of the most important are listed in Table 1. Although incomplete, the table shows that many collections have been made over a period of nearly 150 years. This form of exploration led to a fragmentary literature on the flora. Reports are scattered in obscure journals, with the result that most were prepared with insufficient knowledge of earlier works. Bryologists who failed to find descriptions of their specimens in the literature were eager to describe them as new, so numerous synonyms appeared. For example, in Index Muscorum (Wijk et al, 1969) there are 108 species and varieties of Tortula listed from southern South

Table 1. Some early collections of mosses made in the austral American - Antarctic area.

Date	Collector(s)	Places visited	Mosses published by:	Notes
1787	A. Menzies	Staten Island	W. J. Hooker (1818) J. D. Hooker (1847)	See Godley (1965)
c. 1825-30	J. Gillies	Argentina	Greville (1830)	Noted by Turrill (1920)
1827-8	E. Pöppig	Chile	Müller (1843, 1849, 1851)	Noted by Turrill (1920)
1827-31	C. J. Bertero	Chile (Juan Fernandez, Tahiti)	Müller (1849, 1851)	Looser (1933-6) gives an account of Bertero's collections.
1829-30	J. Eights	South Shetland Islands	-	See Steere (1965) and Calman (1937)
1831-36	C. R. Darwin	Magellan Straits, Falkland Islands, Chile	Mitten (1869)	
1837-40	Jacquintot, Hombron and Le Guillou	Port Famine, Magellan Straits, South Orkney Islands, Terre Adelie, Auckland Islands	Montagne (1845, 1850)	Voyage of the 'Astrolabe' and 'Zelee' under d'Urville
1838-42	Unknown	Isla Hoste, Cape Horn South Shetland Islands	Sullivant (1859)	United States Exploring Expedition under C. Wilkes

Table 1 (cont'd)

Date	Collector(s)	Places visited	Mosses published by:	Notes
1839-43	J.D. Hooker	Falkland Islands, Hermite Island, Cockburn Island, Kerguelen, (Auckland and Campbell Islands)	Wilson and Hooker in J. D. Hooker (1847	Voyage of the 'Erebus' and 'Terror'
c. 1850	W. Lechler	Fuegia, Chile Falkland Islands	Mitten (1860)	Little information known except see Lechler (1857)
1852	N. J. Andersson	Port Famine	Ångström (1872)	Voyage of the 'Eugenie'
1870-1880	P.G. Lorentz	Argentina	Müller (1879, 1897)	see Turrill (1920)
1872-76	H. N. Moseley	Kerguelen	Mitten (1876)	'Challenger' Expedition
1874-5	A. E. Eaton	Kerguelen	Mitten (1879)	Transit of Venus Expedition
1874-6	F. Naumann	Fuegia, Kerguelen, (New Guinea, W. Africa, Australasia)	Müller (1883, 1889)	'Gazelle' Expedition
1876-79	P.A.L. Savatier	Magellan Straits, Fuegia	Bescherelle (1885) Bescherelle (1889)	Voyage of the 'Magicienne'
1881-2	C. Spegazzini	Fuegia, Staten Island, Ushuaia, Argentina	Müller (1885)	

Table 1 (cont'd)

Date	Collector(s)	Places visited	Mosses published by:	Notes
1882-83	Hahn, Hariot and Hyades	Fuegia, Cape Horn, Isla Hoste	Bescherelle (1885) Bescherelle (1889)	Voyage of the 'Romanche'
1882-83	H. Will E. Mosthaff	South Georgia	Müller (1890)	German International Polar Year Expedition
1889	E. G. Racovitza	Gerlache Straits, Tierra de Fuego	Cardot (1900, 1901)	Belgian Antarctic Expedition
1895-96	P. Dusen	Chile, Argentina	Dusen (1903b, 1905a, b, 1906, 1907)	Initially with O. Nordenskjold's Expedition to Patagonia but later joining a Chilean government expedition to the Andes. See Birger (1926) and Dusen (1903b).
1896-97	J. B. Hatcher	Fuegia and Patagonia, Punta Arenas, Ushuaia, Lapataia	Dusen (1903a, b, 1905a, b, 1906, 1907)	
1898-1900	C.E. Borchgrevink	Victoria Land, Antarctic Continent	Bryhn (1902)	British Antarctic Expendition, see Borchgrevink (1901)
1901-03	C.J.F. Skottsberg	Fuegia, South Georgia, Antarctic Peninsula	Cardot (1905, 1906, 1908)	Swedish South Polar Expedition see Sprague (1963-4)

Table 1 (cont'd)

Date	Collector(s)	Places visited	Mosses published by:	Notes
1901-04	R.N.R. Brown	Laurie Island, Gouch Island, Diego Alvarez, Ascension Islands	Cardot (1911a, 1912)	Scottish National Antarctic Expedition see Brown et al (1906)
1904-05	P. Dusen	Patagonia	Dusen (1907)	see Birger (1926)
1907-09	C.J.F. Skottsberg and T.G. Halle	Fuegia, including Falkland Islands, South Georgia (Juan Fernandez)	Cardot and Brotherus (1923)	Swedish Magellan Expedition see Sprague (1963-4)
1908-09	Gain	Antarctic Peninsula	Gardot (1911b)	Second French Antarctic Expedition under Dr. J. Charcot
1911-15	P.N. Costes	Chile	Theriot (1917)	
1928-9	H. Roivainen	Tierra del Fuego	Roivainen (1934) Bartram (1946)	Geographical Society of Finland Expedition, see Roivainen (1933)
1940-41	P. A. Siple and others	Antarctica: Weddell Coast, Melchior archipelago	Bartram (1957)	United States Antarctic Service Expedition

America and Antarctica alone. North America by contrast has only 35. This large number is not only due to the obscure and scattered literature, but also to the radical change in the species concept since the beginning of this century. Plants that would now be considered conspecific were divided because of apparently minor differences. Before the widespread acceptance of the theory of evolution, the species was considered to be uniform and immutable, each having been created by a divine being for its particular niche in the natural world. Important modern ideas including an understanding of populations, intra-specific variation, geographical and ecological races as well as the process of speciation, had not yet been put forward. It was not surprising that taxonomists interpreted the species rather narrowly. There was also no reason to believe that the same species might occur in widely separated areas. Unaware of theories of long distance dispersal or continental drift, it was a natural supposition that the plants of an isolated island such as South Georgia would be specifically distinct from those of neighbouring lands. Thus Müller (1890) when examining Will's collection of mosses from South Georgia, described 51 of the 52 species present as endemic and new to science.

Practical difficulties existed then as now. One in particular is the occurrence of modified or reduced forms due to the extremely severe climatic conditions. These forms have often been given specific status, although their morphology may be so abnormal that they have been placed in the wrong genus. The environment is also responsible for the failure of most species to produce

sporophytes, but these are not as essential as was once thought for the identification of species.

Many early specimens were small and inadequate but few taxonomists refrained from erecting new species when the material was poor. The basis of species described from a single specimen are doubtful since their range of variation is unknown. Type specimens which were ample at one time have sometimes been so divided amongst herbaria that only a single stem now remains. Other type specimens have been destroyed such as those of Müller, which perished in Berlin during the 1939-45 war. Even when original material is plentiful, type descriptions may be too short, leaving out vital information but explaining in great detail some character now considered trivial. Fortunately the standard of type descriptions has improved since 1883 when Müller described Bartramia polymorpha C. Muell. in one line: 'Quod ramulos dimorphos et folia dimorpha jam species distinctissima'.

False assumptions about the relative worth of characters and a reliance on ones of doubtful value are fundamental to much early confusion in bryophyte taxonomy. Cardot (1908), for example, divided species of Tortula into monoecious, dioecious and synoecious groups. His reasons for so doing may have been similar to those of Linnaeus in proposing the sexual system, ie. the belief that the sexual part of plants are conservative and do not vary. The results in Tortula were artificial and division of the genus based on sexual state has obscured the recognition of polygamous species and contributed to the excessive publication of synonyms.

The Antarctic flora did not receive the attention of many bryologists, and very few attempts were made to produce a manual listing the species and helping identification. The most recent of these is Cardot's 'La flore bryologique des Terres Magellaniques, de la Géorgie du Sud et de l'Antarctide' (1908) which must be considered as the starting point for further work on the flora. Cardot attempted to include all of the species described and to recognise synonymy. For example, he remarked on the inadequacy of Müller's (1890) approach to the South Georgian flora and considered 15 of Müller's 51 'endemics' to be synonyms. He also expressed the belief that many more so called endemics could be found in other parts of the region. 'La flore bryologique .....' is, however, little more than a check-list of species and their distribution, since diagrams and descriptions are limited to those species which Cardot himself described as new to science. No key is provided and the work is of little use for identification, so that bryophytes can only be named by those specialising in this region.

The scarcity of material has been a major obstacle in resolving the problems of austral South American - Antarctic bryophyte taxonomy. Today, however, large collections of Antarctic and South Georgian plants are available for study in the British Antarctic Survey Herbarium (AAS). Details of the principal collections are given in Table 2. These are mainly the work of British Antarctic Survey scientists such as Bell, Clarke, Greene, Longton and Smith but some material from international projects such as the Transecta Botanica de Patagonia Austral are

Table 2. Major Antarctic, South Georgian or other austral bryophyte collections in the British Antarctic Survey Herbarium, (AAS).

Collection	Date(s)	No. of bryophyte specs.	Localities
Adams, W.A.	1977	60	Isla Hoste (Tierra del Fuego)
Allison, J.S.	1970-71	90	South Shetland Is.
Barrow, C.J. Field record	1972-73	1,800	South Georgia
Baylis, J.P.	1976-77	70	South Shetland Is.
Bell, B.G.	1971-79	3,350	South Georgia, Iles Crozet.
Bell, B.G. Field record	1971-72	1,100	South Georgia
Bonner, W.N.	1950-61	150	South Georgia
Brading, C.G.	1959-61	20	Antarctic Peninsula
British Graham Land Expedition	1934-37	40	Antarctic Peninsula, South Shetland Is.
Cameron, A. and Kennett, P.	1961-62	40	South Georgia, South Orkney Is. Antarctic Peninsula, South Shetland Is.
Chuter, J.W.	1976-77	20	South Shetland Is.
Clarke, G.C.S. and Greene, S.W.	1967-68	700	South Georgia
Collinge, I.B. and Jennings, P. Field record	1973-4	20	Antarctic Peninsula
Collins, N.J. Field record	1970	200	South Georgia
Corner, R.W.M.	1963-65	350	Antarctic Peninsula
Cousins, M.J.	1965-66	20	Antarctic Peninsula
Cragg, J.	1955-57	20	South Georgia, South Orkney Is.
Davies, L.	1968-73	30	Iles Crozet
Discovery Investigations.	1927-37	20	South Orkney Is. South Shetland Is., South Georgia.
Edwards, J.A. Field record.	1970		South Georgia

Table 2 (cont'd)

Collection	Date(s)	No. of bryophyte specs.	Localities
Fenton, J.	1976	20	Antarctic Peninsula
Greene S. W.	1960-61	3,500	South Georgia
Gressitt, L. Lippert, G. and Llano, G.A.	1965-66	100	Antarctic Peninsula, South Shetland Is.
Holdgate, M.W.	1961-64	450	South Georgia, South Orkney Is. South Sandwich Is. Bouvet Is.
John, B.S. and Sudgen, D.E.	1966	20	South Shetland Is.
Kennett, P.	1963-64	30	Antarctic Peninsula.
Killingbeck, J.	1960-63	80	South Shetland Is., Antarctic Peninsula, Falkland Is.
Kuhnemann, O.	1944-59	250	Tierra del Fuego, South Orkney Is. South Shetland Is., Antarctic Peninsula.
Lamb, I.M.	1944-46	20	Antarctic Peninsula.
Lawson, G.	1974	90	South Georgia
Light, J.J. and Heywood, R.B.	1973-74	80	Antarctic Peninsula
Lindsay, D.C.	1965-66	180	South Shetland Is. South Orkney Is.
Longton, R.E.	1963-65	1,300	East Antarctica, Falkland Is., South Shetland Is., South Georgia, South Sandwich Is., South Orkney Is., Antarctic Peninsula.
McManmon, M.	1971	100	South Orkney Is.
Scott, A.	1972-75	100	Antarctic Peninsula
Sladen, W.J.L.	1947-55	50	South Georgia
Smith, J.	1956-58	150	South Georgia
Smith, R.I.L.	1964-81	1,600	South Georgia, Antarctic Peninsula, South Orkney Is., South Shetland Is., South Sandwich Is.

Table 2 (cont'd)

Collection	Date(s)	No. of bryophyte specs.	Localities
Smith, R.I.L. Field record	1969-70	1,000	South Georgia
Smith, R.I.L. Field record	1970-71	2,450	South Georgia
Taylor, B.J.	1959-63	220	South Orkney Is., South Shetland Is., Antarctic Peninsula.
Transecta botanica de Patagonia austral	1975-76	600	Patagonia
Walton, D.W.H. Callaghan, T.V. and Gunn, T. Field record	1973-74	1,300	South Georgia
Webb, R.	1971-72	200	South Orkney Is.
Wright, E.P. Field records	1970	150	South Georgia

also available. With this material it should be possible to solve some of the questions which have arisen through the inadequate circumscription of taxa.

A group of researchers on the taxonomy and biology of Antarctic bryophytes was established by the British Antarctic Survey in the early 1960s under Dr. S.W. Greene. Among the first taxonomic studies were those of Cox (1961) and Greene (1968). The first volume of an Antarctic moss flora was produced in 1970 (Greene et al) but work has recently been done on the South Georgian flora. The 'Synoptic flora of South Georgian mosses', a series published in the British Antarctic Survey Bulletin (Greene 1973, Bell 1973, 1974, Clarke 1973, Newton 1974, 1977a, 1979a, Matteri 1977) has so far covered 49 species. In the same journal, short papers have been published in the series 'Notes on Antarctic bryophytes'. In addition to this British initiative, valuable contributions have also been made by Vitt (1976, 1979), Zanten (1971), Horikawa and Ando (1961, 1963, 1967) and Kanda (1981) among others. Thus certain taxa are now adequately covered but several important groups have yet to be studied.

Progress in bryophyte taxonomy, in the Antarctic and elsewhere, has been made by traditional herbarium methods. Until recently these were the only techniques available but new ideas and technology can now provide the taxonomist with more data. New techniques include chemotaxonomy, cytology, scanning electron microscopy, cultivation experiments and biometrics, all of which have been used in angiosperm taxonomy but are only now beginning

to be applied to the bryophytes. Chemotaxonomy has been used by Krzakowa (1978) to show the existence of enzyme races in species of Conocephalum and Plagiochila, and enzyme differences between species of Pellia have also been found. Newton (1977b) has applied the Giemsa C- banding technique to the chromosomes of Pellia and detected cytological affinities between species. The scanning electron microscope has been used to examine the fine structure of surfaces, particularly the ornamentation of spores (Clarke 1979). Leaves, peristomes and rhizoids also have complex surfaces which may provide additional taxonomic characters (Duckett and Soni 1972a & b., Robinson 1971, Hirohama and Iwatsuki 1980). Lodge (1960b) cultivated species of Drepanocladus in various environments and made valuable taxonomic conclusions. Wigh (1975a) had similar success with species of Brachythecium. Cox (1961), Lodge (1960a), Newton (1979b) and Wigh (1975b) used biometric techniques to describe and differentiate between species. Yli-Rekola (1980) has compared multivariate statistical methods in analysing patterns of variation in Polytrichastrum alpinum (Hedw.) G.L. Sm. Bryophyte taxonomy is thus beginning to benefit from these new methods and in the Antarctic in particular, there are many problems which might now be resolved.

The production of a moss flora for the Antarctic mainland is bound to meet with difficulties because of the depauperation, modification, frost damage and sterility of specimens. The same species, however, can often be found growing luxuriantly and

abundantly on South Georgia where the climate is less severe. The floras of South Georgia and the Antarctic Continent have strong connections as their geographical positions might suggest (Fig. 1), although South Georgia has a larger number of species (Steere 1961 a, b). A manual to the flora of this Island could be produced without the problems found in the Antarctic. Furthermore, once understood on South Georgia, species may be recognised more easily further south where the harsh environment induces changes in morphology. The genus Pohlia in the Antarctic, for example, was revised by Greene et al (1970) and later from South Georgia by Clarke (1973). During re-examination of Antarctic material determined by Greene et al (1970), Lightowlers (1983, see Appendix 2) found overlooked specimens of P. inflexa (C. Muell.) Wijk et Marg., a species described from South Georgia and known from the Antarctic by a single specimen only. Misidentified specimens of Mielichhoferia austro-georgica. C. Muell. were also found and this is a species only recently reported from the Antarctic (Clarke and Lightowlers 1983, see appendix 3). The South Georgian moss flora also has an intrinsic phytogeographical interest, since relict species may have survived there during the severe austral glaciations which are no longer present in more northerly areas due to amelioration of the climate. Finally there are no problems of defining the geographical limits of an island, and if necessary, the flora can be studied without reference to the literature of other areas. For these reasons a South Georgian approach to the Antarctic moss flora was considered to be both practical and valuable, and most attention has been

given in this study to the extensive South Georgian collections in the British Antarctic Survey Herbarium (Table 2).

The genus Tortula, which contains 6-9 species on South Georgia, has caused some taxonomic confusion and has not been studied in detail. Ecologically the genus is very important on the Island, and one species, T. robusta Hook. et Grev., forms an association with Acaena spp. which constitutes an important pioneer formation (Greene 1964b). Although some work has been done on the taxonomy of this species (Cox 1961), the genus as a whole still requires a detailed taxonomic revision. Difficulties also exist in the separation of species such as T. robusta and the allied T. excelsa Card., and also between T. grossiretis Card. and T. monoica Card. (B.G. Bell and S.W. Greene, personal communication).

By concentrating on 2-3 species in the genus, it was intended to use both traditional and new taxonomic methods such as growth experiments, to study the variation in this group. A visit to South Georgia was originally planned and experiments and observations on plants in the field, together with the collection of living material for subsequent growth experiments, were expected to form an important part of this study. After the first year of work, when plans were well advanced, it was found that the visit could not proceed. Field work was therefore impossible and it was necessary to rely entirely on living material collected by others. This was often in poor condition on arrival in Britain and did not represent all taxa or forms recognised in the herbarium material. To make best use of the living specimens,

the scope of the study was widened to include the entire genus. The aims of this study thus became:-

1. To produce a taxonomic account of the genus Tortula on South Georgia by traditional herbarium methods. This included the establishment of a stable nomenclature for the taxa by investigating the literature and examining specimens from South Georgia, other sub-Antarctic Islands, the Antarctic continent and austral South America.

2. To conduct experiments in cultivation, chemotaxonomy, cytology, scanning electron microscopy and biometrics in order to expand the taxonomic basis of the genus as a whole.

Chapter 2 : TAXONOMY OF *Tortula*

2.1 History and modern concept.

Of the genera in the family Pottiaceae, *Tortula* is one of the largest and most morphologically diverse. It is comprised of about 200 species which are found in the temperate zones of both hemispheres. It was first described by Hedwig (1782) who distinguished it from the related genus *Barbula* by its monoecious sexual state and by the shape of the male flower. This division was highly artificial and many authors, including Hooker and Greville (1824) soon realised that these criteria separated plants which were similar in much more important respects. There was widespread agreement among bryologists at this time that the genera should be united, but they disagreed over which name the resulting genus should take. Bruch, Schimper and Gümbel (1842), Müller (1849), Schimper (1876) and Bescherelle (1885) used the name *Barbula*, but Hooker and Taylor (1818), Hooker and Greville (1824), De Notaris (1838) and Hooker (1847) preferred *Tortula*.

This disagreement was settled when Limpricht (1888) introduced a new character into the taxonomy of the Pottiaceae - the presence or absence of an adaxial stereid band in the nerve of the leaf. Species without this stereid band were placed in the sub-family Pottiaeae, which included *Tortula*, and those with the stereid band were placed in the Trichostomeae, which included *Barbula*. The two genera were thus redefined on the basis of this character, although Lindberg (1878, 1879) had

previously arrived at a similar conclusion without its benefit. Limpricht (1888) defined Tortula not only on the absence of an adaxial stereid band but also on the peristome of 32 twisted teeth and the lack of any secondary photosynthetic organs on the leaf.

The history of the genus was further complicated by the erection of the genus Syntrichia by Bridel (1800). It was defined as having the peristome teeth united at their bases to form a short tube. Some authors, eg. Schultz (1823) and Mitten (1860) placed all Tortula and Barbula species in Syntrichia, except those which do not have a peristome tube, which were assigned to a redefined Barbula. Syntrichia was only widely accepted, however, at the rank of section or subgenus, by such workers as Montagne (1838), Müller (1849), Mitten (1869) and Ångström (1872). Limpricht (1888) treated Syntrichia as a subgenus of the redefined genus Tortula. Brotherus (1924) followed this decision, but authors such as Chen (1942), Herzog (1954) and Podpéra (1954) have given Syntrichia full generic status. Steere (1939) remarked that since many species excluded from Syntrichia have a small but distinct peristome tube, the difference is not clear cut. He did not recognise Syntrichia as a genus, and most recent authors (Smith 1978, Kramer 1980, Crum and Anderson 1981) have concurred with this decision. Kramer (1980) does however uphold the concept of this genus but points out that the type species of Tortula, T. subulata Hedw. (Wijk et al, 1969) is also a Syntrichia. Syntrichia is thus a synonym and

must be abandoned at both generic and sectional levels, unless new type species are designated.

Tortula Hedw. was given nomen conservandum status at the International Botanical Congress of Stockholm in 1950 (Lanjouw 1950). If this had not been done, an angiosperm homonym, Tortula Roxburgh in Willdenow (1800), would have taken priority. Although Tortula Hedw. was first published in 1782 (Hedwig 1782) the starting date for moss nomenclature is 1st January 1801 (Article 13, I.C.B.N, (Stafleu 1972) and earlier descriptions of mosses are invalid.

The definition of Tortula has not changed since Limpricht's (1888) study. The peristome of 32 twisted teeth, the lack of both an adaxial stereid band in the nerve and secondary photosynthetic lamellae or filaments remain the important delimiting characters within the Pottiaceae. Thus defined, Tortula is the largest genus in the Pottiaceae, and Wijk et al (1969) list 290 species. Its morphological limits are very wide. A definition based on a single character is untenable, and some species do not show all of the three defining characters. Brotherus (1924) for example, noted aperistomate species and species with peristomes which are only slightly or not twisted at all. He noted even greater variation in the gametophyte. The nerve at the leaf apex may be percurrent to excurrent in a hyaline hair; the leaf margin may be toothed or entire, recurved or plane, and sometimes differentiated to form a border. The leaf shape may be spathulate or lanceolate

and several types of vegetative propagules are found such as caducous leaf tips and foliar or axillary gemmae. This variation in morphology together with the large number of species make Tortula a somewhat miscellaneous assemblage of many species not closely related to each other.

2.2 Classification within the genus.

The trend within the Pottiaceae, as within bryophytes as a whole, has been to recognise progressively smaller genera, the genus Barbula as defined by Dixon (1924) or Smith (1978) for example, has now been divided into Pseudocrossidium, Didymodon, Geheebia, Bryoerythrophyllum and Barbula (sensu stricto) by Corley et al (1981) and many other authors. The subdivision of Tortula into smaller, more clearly defined genera does not yet seem possible. The relationships between the species are not well understood and as a result treatments of the various sections of the genus are often incomplete and inconsistent. In their recent list of European mosses, Corley et al (1981) found that Tortula was the only genus in which they were unable to allocate all species to sections.

There are no modern treatments of the genus on a worldwide basis. The most recent is Brotherus (1924), who defined four sections within the genus (Table 3). This classification has been modified, sect. Hyophiladelphus (C. Muell.) Broth. is now included in Barbula (Wijk et al, 1969) and the distinction between Zygotrichia (Brid.) Mitt and Syntrichia (Brid.) Hartm. is not followed in later European treatments (Podpéra 1954,

Table 3. A history of classification of the genus Tortula. Equivalent taxa are linked by continuous lines, broken lines are used where the relationship is uncertain. Genera are given in capitals, all other taxa have sectional rank.

Brotherus (1924)	Podpéra (1954)	Corley et al (1981)	Index Muscorum Wijk et al (1969)
Tortula	Eutortula Moenkm.	Cuneifolia (B.S.G.) Spruce	Cuneifolia (B.S.G.) Spruce
			Caespitosae De Not.
			Piliferae De Not.
	Crassicostatae (Schimp.) Podp.	Crassinerves (Milde) Wijk et Marg.	Crassinerves (Milde) Wijk et Marg.
Zygotrichia (Brid.) Mitt.			
Syntrichia (Brid.) Hartm.	SYNTRICHIA Brid.	Tortula	Tortula
		Rurales De Not.	Rurales De Not.
			Bulbibarbula (C. Muell.) Wijk et Marg.
Hyophiladelphus (C. Muell.,) Broth. (= BARBULA sect. Hyophiladelphus)			
			Leptopogon Mitt.
			Neobarbula (Dus.) Card.

Corley et al 1981).

Since sections containing the type species of a genus automatically take the name of that genus (Article 22, I.C.B.N., Stafleu 1972), the choice of type species is crucial to the naming of sections. Brotherus (1924) and Podpéra (1954) considered T. muralis to be the type, but Index Muscorum (Wijk et al, 1969) and Corley et al (1981) chose T. subulata Hedw. Section Tortula sensu Brotherus (1924) is therefore different from that of Corley et al (1981). The latter is equivalent to the sections Zygotrichia and Syntrichia of Brotherus (1924), but excludes those species now placed in sect Rurales De Not. (Table 3).

Although the treatment of Corley et al (1981) is accepted in this study, it includes only European species. Index Muscorum (Wijk et al, 1969) lists three sections which originate from other regions. All appear to be little used. Sect. Bulbibarbula (C. Muell.) Wijk et Marg. is based on an African species, T. eubryum (C. Muell.) Wijk et Marg. According to the original description (Müller 1879) species of this section have bulb-like propagules. Sect. Leptopogon Mitt. was described by Mitten (1879) and contains three South American species, all of which are transferred by Wijk et al (1969) to other genera. This section must therefore be excluded from Tortula. Finally section Neobarbula (Dus.) Card. is based on a Falkland Islands species, T. densifolia (Hook. f. et Wils.) Hook. f. et Wils. Cardot (1908) intended this

section to contain species with a thick leaf margin, including the European species T. marginata (B.S.G.) Spruce. Brotherus (1924), Podpéra (1954) and Corley et al (1981) have however, placed this species in other sections. Thus the sections described from non-European material are few and in need of revision.

The problems of classification within a large and diverse genus such as Tortula are considerable and the lack of a recent complete treatment, the confusion over the affinities of species and the composition of sections show that this genus is not easily subdivided. Many obscure species, such as those to be considered in this study, need to be described and understood before the classification of the genus can be clarified.

2.3 South Georgian species

For the purpose of this study, specimens of Tortula were recognised by their papillose leaf cells, the form of the sporophyte and peristome and the absence of an adaxial stereid band in the nerve of the leaf. Specimens of Encalypta could be distinguished by their thick transverse-walled basal cells, Pottia by their size, leaf shape and capsules and Barbula (sensu lato)by the prominent adaxial stereid band. Two genera in the sub-family Pottieae endemic to austral-Antarctic regions could be mistaken for Tortula. Willia differs in its immersed, aperistomate capsule, more rigid texture and hyaline-tipped perichaetial leaves and

Sarconeurum has leaves with deciduous apices and a peristome of only 16 teeth (Matteri 1982).

Nine species and one variety of Tortula are reported from South Georgia in the literature (Table 4). These species may be conveniently placed in two distinct groups depending on the presence or absence of a hair-point at the leaf apex. Members of the hair-pointed group have entire, oblong to lingulate leaves with rounded or obtuse apices and a nerve excurrent in a hyaline, reddish or brownish hair-point. All sporophytes examined possess a tall peristome tube and therefore this group can be assigned to the section Rurales De Not. There is much variation in size in this group although leaf shape is fairly constant. The largest specimens appear to be referred to T. grossiretis Card. (Cardot 1906, 1908) smaller specimens to T. monoica Card. (Cardot 1905, 1908) and very small densely tufted plants have been referred to an Antarctic species, T. conferta Bartr. (S.W. Greene, personal communication).

The non-hair-pointed group are much less uniform in leaf shape. This varies from narrowly lanceolate to oblong-spathulate, the margin may be entire or coarsely serrate and the nerve may be percurrent or excurrent at the apex. When excurrent the leaf apex is never rounded, but obtuse or acute to acuminate and the nerve extends to form only a short cusp or mucro. There is variation in the type and pattern of papillae on the leaves, and some plants have a conspicuous leaf

Table 4. Check list of South Georgian Tortula species. References to the first report of each species is given in brackets.

T. filaris (C. Muell.) Broth. (Barbula, Müller 1890)

T. fontana (C. Muell.) Broth. (Barbula, Müller 1890)

T. fuscoviridis Card. (Cardot 1906)

T. grossiretis Card. (Cardot 1906)

T. lepto-syntrichia (C. Muell.) Broth. (Barbula, Müller 1890)

(syn. Barbula anacamptophylla C. Muell. fid. Cardot 1906)

T. lingulaefolia Card. et Broth. (Cardot and Brotherus 1923)

T. monoica Card. (Cardot 1906)

T. robusta Hook. et Grev.

(syn. T. rubra Mitt. fid. Cox 1961, Greene 1964a)

var. runcinata (C. Muell.) Broth. (Barbula runcinata, Müller 1890)

T. serrata Dix. (Cox 1961, Greene 1964a)

margin. The group without hair-points is apparently richer in species than that with hair-points, T. filaris (C. Muell.) Broth., T. fontana (C. Muell.) Broth., T. fuscoviridis Card., T. leptosyntrichia (C. Muell.) Broth., T. lingulaefolia Card. et Broth., T. robusta Hook. et. Grev. and T. serrata Dix. all belong to the former. All species have tall peristome tubes and can only at present be referred to the section Tortula, (sensu Corley et al 1981).

The only recent taxonomic work on South Georgian species is that of Cox (1961). A detailed study of the variation in T. robusta Hook. et Grev., a species without a hair-point, was attempted using biometric methods. Measurements of leaf length, leaf width and cell size showed that two species, T. rubra Mitt. and T. serrulata Hook. et Grev. (described from New Zealand and Tierra del Fuego respectively) could not be separated from T. robusta. Leaf length and width measurements of this species showed a tendency to cluster in two groups, suggesting the existence of ecotypes or even varieties. One distinct species was detected however, and identified as T. serrata Dix., previously known only from New Zealand. Four other species were discussed in some detail: T. subantarctica Sainsb. from Campbell Island which was considered to be a synonym of T. robusta; T. pseudorobusta Dus. and T. rivularis Dus., two South American species which both appeared to be distinct; and T. robustula Card. which was found to be similar to T. robusta but in need of further investigation.

A revision of the genus on South Georgia is required to classify the species listed in Table 4, some of which may need to be reduced to synonymy. None of these species has been described since the original type description was made and it is not clear where the morphological limits of each taxon should be drawn. Descriptions of each taxon are therefore needed, including diagrams and a comparison of major distinguishing characters in a dichotomous key.

It is likely that Table 4 is incomplete: B.G. Bell and S.W. Greene (personal communication) consider that the Antarctic T. excelsa Card. and T. conferta Bartr. also occur on the Island. Plants described from other areas including Kerguelen, New Zealand and South America may also be present. Material from these regions has been studied to provide the earliest available names for taxa and to find the geographical distribution of the species recognised. Robinson (1972) notes that the large number of South American species described has made it difficult to understand the Antarctic taxa. Indeed, it is not clear whether Antarctic species are present in South America or not. Index Muscorum (Wijk et al 1969) lists 95 species from South America, 33% of all listed Tortula species. Research into the genus in South America is thus time consuming, although there is a great need for the clarification it might achieve.

Chapter 3 : PRELIMINARY CLASSIFICATION OF *Tortula* SPECIMENS FROM SOUTH GEORGIA

3.1 Morphological and anatomical examination

3.1.1 Taxonomic characters

A list of potentially useful characters for discriminating between South Georgian taxa was assembled from several recent taxonomic revisions, i.e. Steere (1939), Sainsbury (1955), Saito (1973), Smith (1978) and Kramer (1980). Forty seven different characters were identified (Table 5) including differences in stem and leaf size, leaf anatomy, morphology, areolation etc. S. W. Greene and B. G. Bell (personal communication) considered the following characters important in the classification of South Georgian species : leaves cucullate or plane at the apex, nerve continuous to leaf apex or disappearing in upper leaf and the nature of the areolation of the leaf apex.

3.1.2 Methods

Initially each specimen, which often consisted of several tufts or cushions, was checked for homogeneity. A representative portion of a few larger stems was removed to make microscope slides of the leaves. The stems were soaked in water for about 12 hours then transferred to a microscope slide. The leaves were removed with fine forceps and all soil grains and debris separated from them. They were then surface dried and covered with a few drops of gum chloral mountant (Watson 1968). Bubbles formed at this stage were teased out and a glass cover slip placed over the leaves. The slide was labelled and the mountant

Table 5. Some key characters used in the classification of *Tortula* species, compiled from Steere (1939) (abbreviated as St), Sainsbury (1955) (Sn), Saito (1973) (S), Smith (1978) (Sm) and Kramer (1980) (K).

1. Stem height (Sm. S. Sn.).
2. Plant colour (Sn.).
3. Habitat (corticolous vs. saxicolous) (Sn. St.).
4. Sexual state (autoecious, dioecious, synoecious or polyoecious (Sm. S. St. K.).
5. Tuft density (St.).
6. Erect or procumbent habit (S.).
7. Stance of leaf on stem when moist (Sm. S. K.).
8. Leaves wavy or crisped when dry (Sm.).
9. Leaves distant or crowded (S.).
10. Central strand in stem cross-section present or absent (S.).
11. Presence or absence of gemmae including brood leaves, leaf gemmae, deciduous leaf apices and rhizoidal gemmae (St. Sn. S. Sm. K.).
12. Gemma shape (St.).
13. Position of gemmae on leaf (St. S.).
14. Leaf size (Sn. Sn. K.).
15. Leaf shape (Sm. St. Sn. K.).
16. Leaf unistratose or multistratose (K.).
17. Type of leaf apex (hair-pointed, not hair-pointed, nerve excurrent, percurrent or ending below leaf apex) (St. Sn. S. Sm. K.).
18. Smoothness or roughness of hair-point or excurrent nerve (St. Sm. K.).

Table 5 (cont'd)

19. Length of hair-point (St.).
20. Colour of hair-point (St. Sm. K.).
21. Leaf margin plane, recurved or revolute and extent of recurvature (St. Sn. Sm. K.).
22. Leaf margin entire, crenulate or toothed (Sn. S.).
23. Leaves bordered or not (St. Sn. Sm. K.).
24. Roughness of adaxial surface of nerve in upper leaf (Sn.).
25. Width of nerve (Sn.).
26. Degree of differentiation of stereid band (S.).
27. Number of rows of stereid cells in cross-section of nerve (Sm.).
28. Nerve in cross-section with or without hydroid cells (K.).
29. Nerve in cross-section with or without substereid cells (K.).
30. Leaf base extended or not (K.).
31. Basal cells of leaf differentiated from upper cells or not (S.).
32. Leaves fragile (or brittle) or not (St. K.).
33. Shape of perichaetial leaves (St.).
34. Upper leaf cells smooth or papillose (St. S. Sm.).
35. Cells papillose on lower surface of leaf only or on both surfaces (K.).
36. Density of lamina cell papillae (S. K.).
37. Shape of lamina cell papillae (K.).
38. Shape of paillae on adaxial nerve surface (K.).
39. Cells mammillose or not (K.).
40. Width of upper lamina cells (St. Sm. K.).
41. Length of basal cells (Sm.).
42. Basal cells yellowish or hyaline (St.).

Table 5 (cont'd)

43. Cells of leaf border bistratose and elongated or unistratose and quadrate (St.).

44. Thickness of upper marginal cell walls (S. K.).

45. Colour of cell walls (Sm.).

46. Capsule shape (St.).

47. Length of peristome tube (St. Sm.).

allowed to harden for a few days at room temperature.

This method of slide preparation is well established in the study of bryophytes (Sayre 1941, Anderson 1954, Bowers 1964). Nevertheless it was found to cause distortion of leaves and cells. Most leaves became severely distorted shortly after contact with the mountant, but regained their natural shape, at least partially, after several days. The degree of recovery varied between specimens and those with thin-walled, large-celled leaves remained most distorted. Anderson (1954) and Zander (1979) also had this problem in their studies of the genera Mnium and Tortella as well as Tortula.

The distortion resulting from mounting in gum chloral solution made cell size, leaf shape and areolation difficult to observe and measure in many preparations. Tests using two alternative water soluble mountants, Gelvatol and Gurr's water soluble medium, were made, both of which gave similar or inferior results. However, soaking specimens in a viscous solution such as glycerol, lactic acid or polyethylene glycol 400 (PEG 400) before mounting improved the quality of preparations. PEG 400 in a 50% aqueous solution gave the best results with most specimens, but some deterioration was noted after several months. This method was sufficiently reliable to be used as a routine mounting procedure (Lightowlers 1981, see Appendix 1). Specimens which were too susceptible to distortion to be mounted in this way were dissected in water and covered with a coverslip secured in place by two gummed paper strips. These

preparations dried out rapidly but could be re-hydrated within minutes by introducing a drop of water containing detergent to the edge of the coverslip.

Sections of stems and leaves, if required, were cut either by hand, using a sharp scalpel, or freezing microtome.

3.1.3 Hair-pointed and non-hair-pointed groups

A total of 404 Tortula specimens were examined, and it was immediately apparent that they could be placed in 2 groups, those with hair-points on the leaves and those without (Figs. 2, 3 and 32). The latter group was the larger, containing about 80% of the material (319 specimens), the remainder (85 specimens) being hair-pointed. These groups were found to be distinctive and each was considered separately in subsequent taxonomic and experimental work.

3.2 Provisional taxa : non-hair-pointed group

Differences in leaf shape, leaf margin and leaf apex between non-hair-pointed specimens enabled four distinct taxa to be delimited. Three of these were found to be homogeneous and could not be subdivided. These are described using terms defined in Smith's (1978) glossary, and illustrated by sketch diagrams of leaves in Fig. 2.

Taxon A : Leaves lingulate - spathulate, margin bordered and dentate at leaf apex.

Taxon B : Leaves lingulate, nerve excurrent in a short red

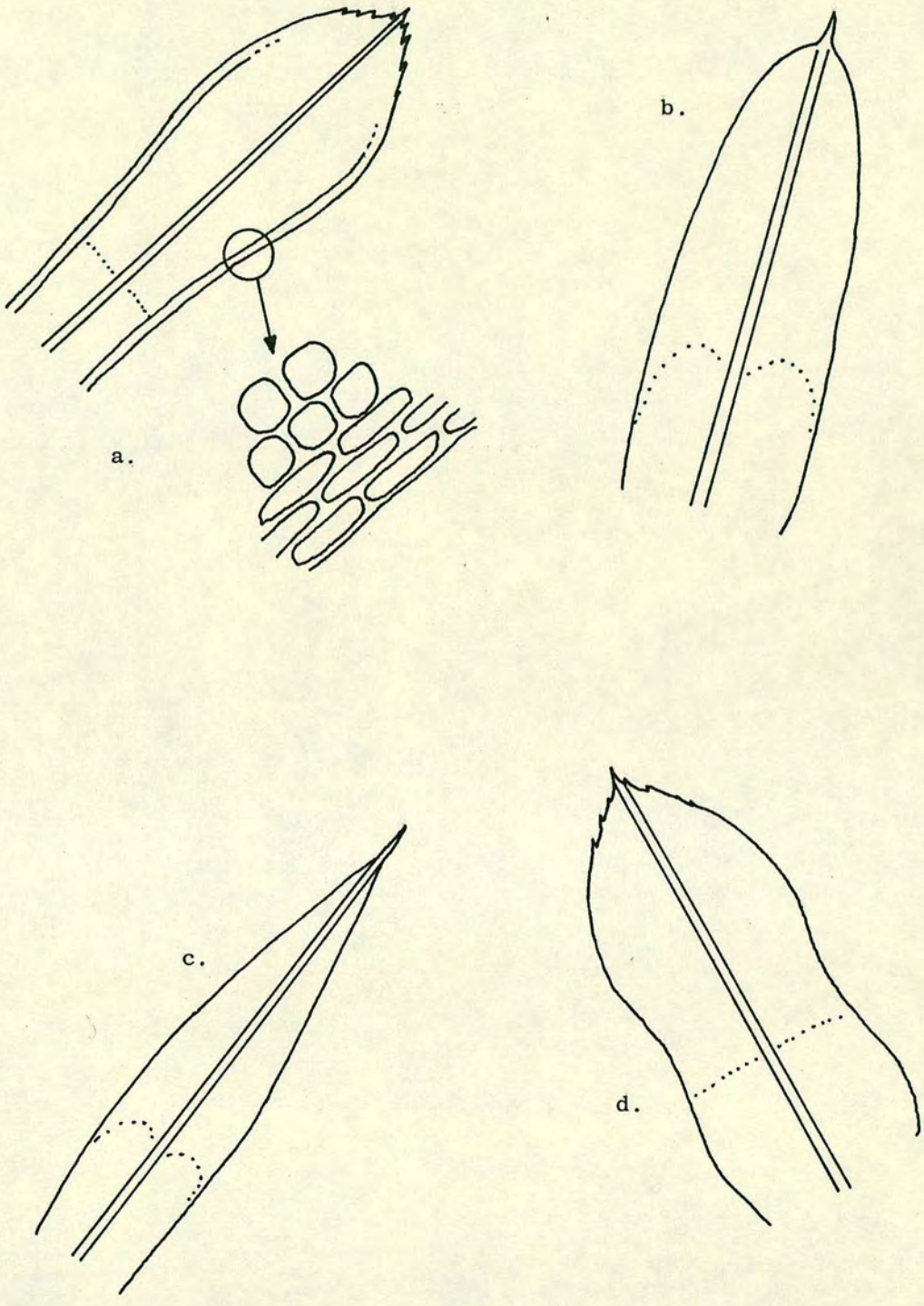


Figure 2. Sketch diagrams of leaves of provisional non-hair-pointed taxa

a). taxon A b). taxon B c). taxon C d). taxon D

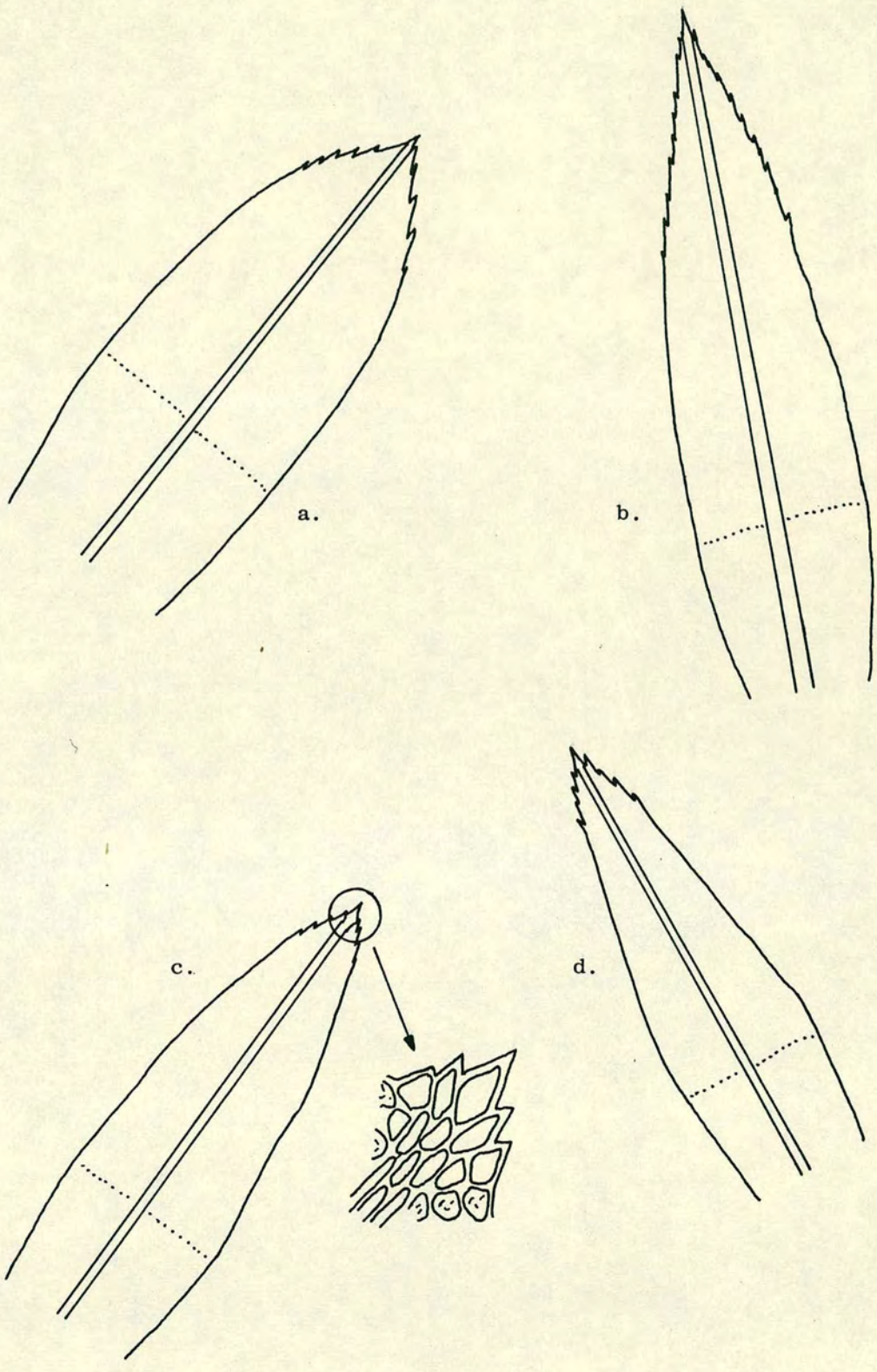


Figure 3. Sketch diagrams of leaves of provisional non-hair-pointed taxa

a). taxon E b). taxon F c). taxon G d). taxon H

cusp, margin not bordered, entire.

Taxon C : Leaves lanceolate, tapering to a fine point, margin not bordered, entire.

The remaining group included specimens with leaves which varied considerably in size and shape, but were all dentate with similar patterns of areolation and had unbordered leaves. Further separation of this group was made on stem/tuft height leaf shape, cell size, papilla density, areolation of the leaf apex and leaf stance, producing five further taxa (Figs. 2 and 3):

Taxon D : Robust plants with broadly oblong-pandurate leaves and large cells (c. 15 - 20 μ). Leaves patent.

Taxon E : Robust plants with broadly oblong but not pandurate leaves. Cells large (c. 15 - 20 μ). Leaves patent to spreading with recurved tips.

Taxon F : Robust plants with lanceolate or lingulate-lanceolate leaves. Cells large (c. 15 - 20 μ). Leaf stance variable.

Taxon G : Moderate sized plants with lanceolate to oblong-lanceolate leaves and medium sized cells (c. 10 - 15 μ) with a characteristic group of smooth, long rhomboidal cells at the leaf apex. Leaves patent.

Taxon H : Moderate sized plants with oblong-lanceolate to lanceolate shaped leaves and small cells (< 10 μ). Papillae very dense. Leaves patent.

The differences between these taxa were less marked than the differences between taxa A, B and C. Specimens which were intermediate between taxa sometimes occurred, for example, small plants of taxon F were similar to taxon G plants in size and leaf shape. Leaf size, leaf shape and lamina cell width were the most important distinguishing characters and it was determined that a quantitative assessment of these would help to define the taxa.

3.2.1 Measuring methods

Specimens of taxon F were the most abundant and showed a large amount of variation. Fifty specimens of this taxon were therefore taken at random and ten from each of the other taxa, D, G and H for measurement. Specimens of taxon E were scarce however, and only five were available for measurement.

Measurements were made using a compound microscope with an eyepiece graticule. Leaf width was measured at the widest point of the leaf and lamina cell width was measured midway between the leaf margin and the nerve at about two thirds of the way up the leaf from the base. Leaf width/length ratios were also calculated. Further details of measurements are given in Table 6.

Table 6. Measurements made on non-hair-pointed Tortula specimens.

	No. of measurements per specimen	Estimated Accuracy
Leaf length	5	± 0.1 mm
Leaf width	5	± 0.05 mm
Lamina cell width	10	± 1 μ

3.2.2 Results

The resulting data were plotted as histograms and scatter diagrams. Histograms were used to show the range of measurements obtained in each taxon and to assess whether the distribution of these values was normal or abnormal. Scatter diagrams were used to represent the measurements of each taxon relative to all others thus allowing variation between and within taxa to be assessed. Leaf length, leaf width, leaf width/length ratio and cell width histograms of taxa D, E, F, G and H are given in Figs. 4 - 23, and measurements of all taxa are compared in scatter diagrams (Figs. 24 - 27).

3.2.3 Discussion

(a) Histograms. Histograms present data so that the distribution of values can be compared with the ideal normal distribution expected in natural populations. More measurements of taxon F were made than the other taxa, and these histograms were therefore expected to approach a normal distribution most closely. However, histograms for this and other taxa showed large deviations from normal distribution. The leaf length histogram of taxon F (Fig. 12) for example, had two peaks at 6.2 and 6.4 mm. This could have been interpreted as evidence for a bimodal distribution of leaf length values, but reorganisation of the histogram size classes (ie. from 1 - 5, 6 - 10 etc., inclusive, to 0 - 4, 5 - 9 ..... etc.) produced a result closer to a normal distribution (Fig. 28). As a further check, another 50 taxon F

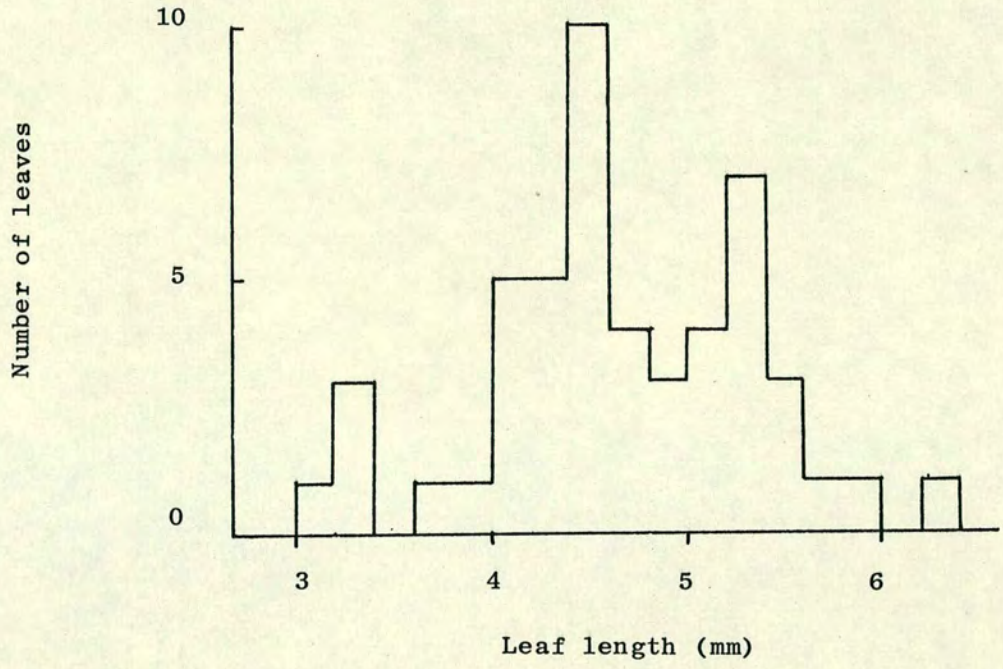


Figure 4. Taxon D: Histogram of leaf lengths of 50 leaves taken from 10 specimens.

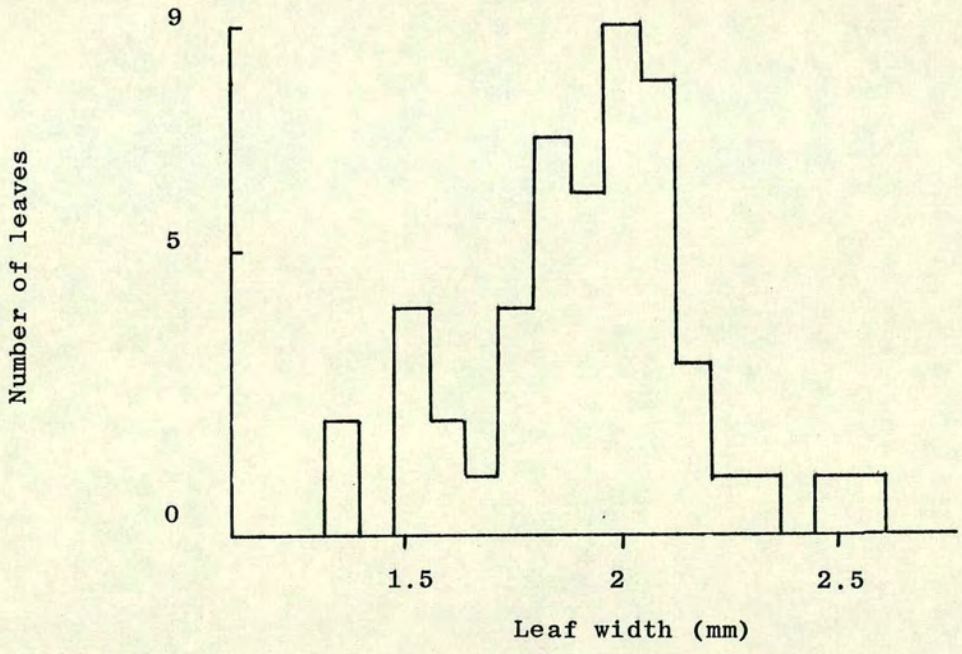


Figure 5. Taxon D: Histogram of leaf widths of 50 leaves taken from 10 specimens.

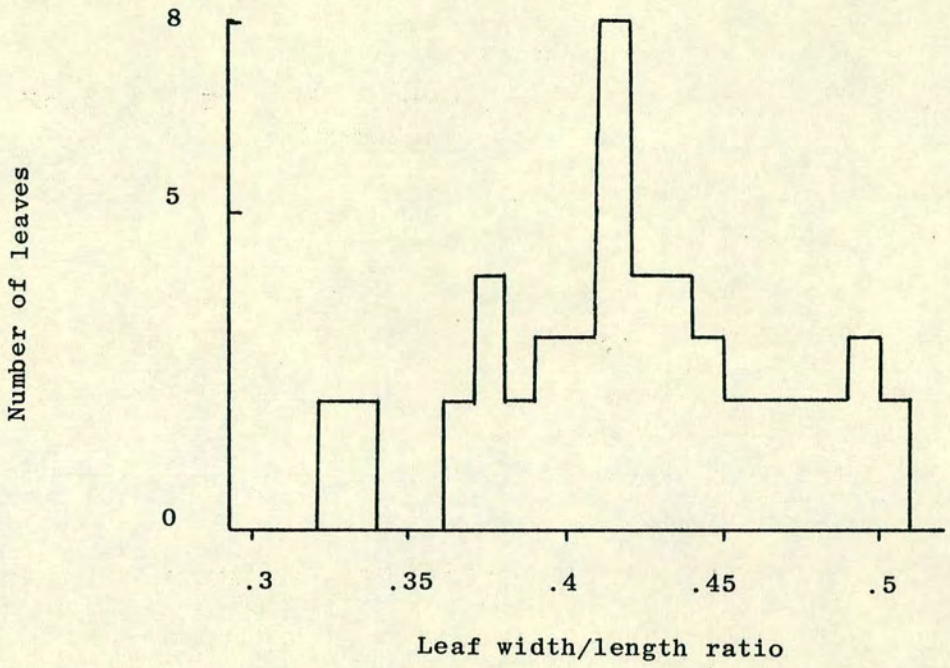


Figure 6. Taxon D: Histogram of leaf width/length ratio of 80 leaves taken from 10 specimens.

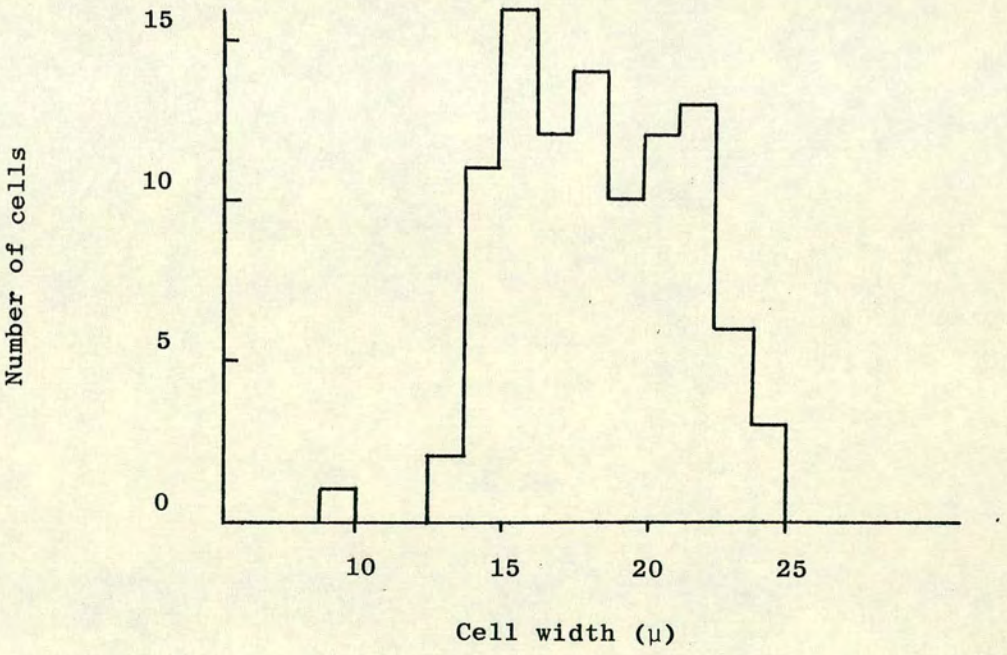


Figure 7. Taxon D: Histogram of cell widths of 100 cells taken from 10 specimens.

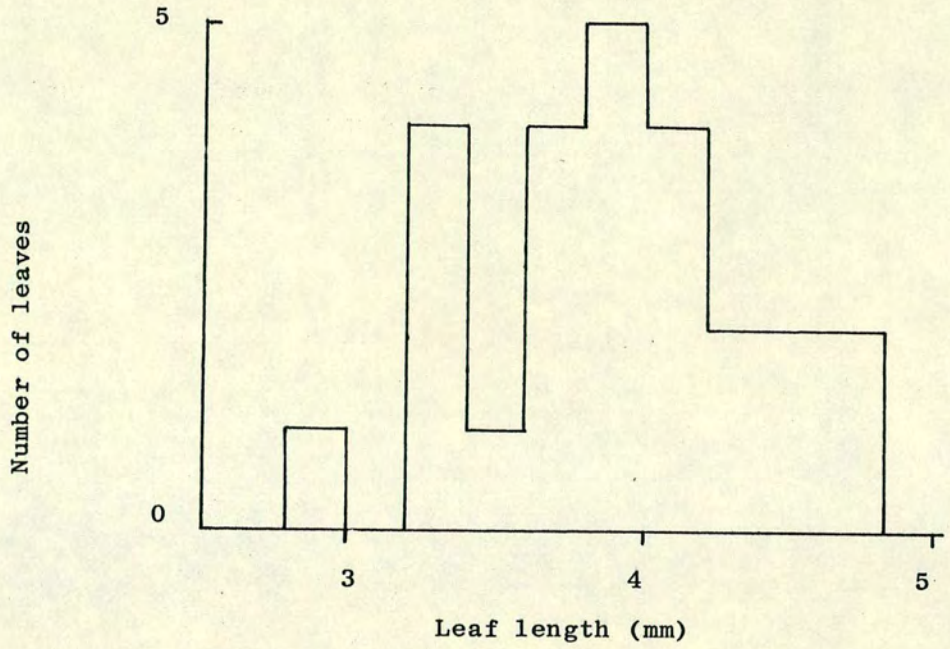


Figure 8. Taxon E: Histogram of leaf lengths of 25 leaves taken from 5 specimens.

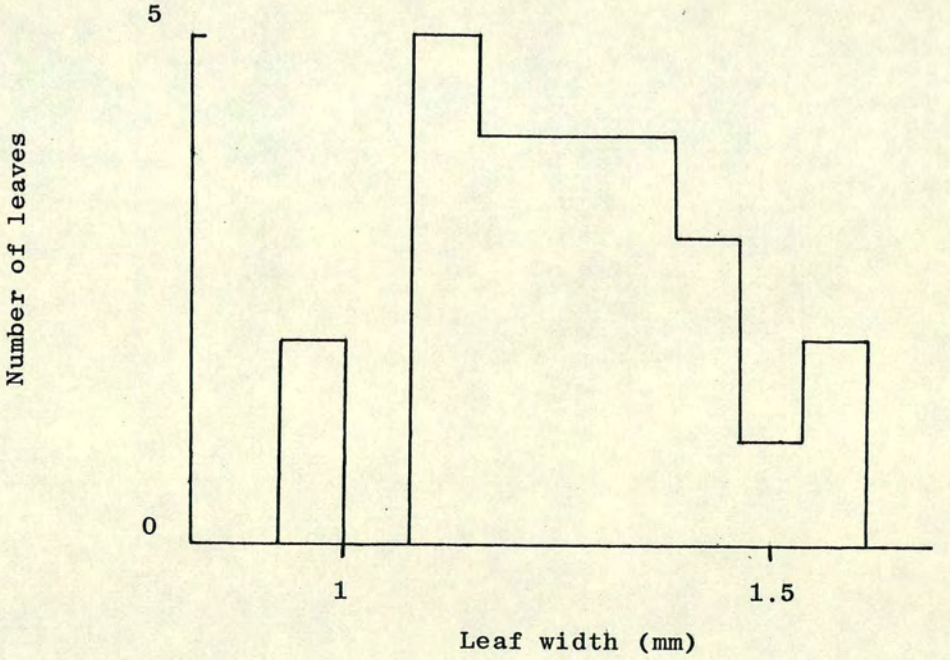


Figure 9. Taxon E: Histogram of leaf widths of 25 leaves taken from 5 specimens.

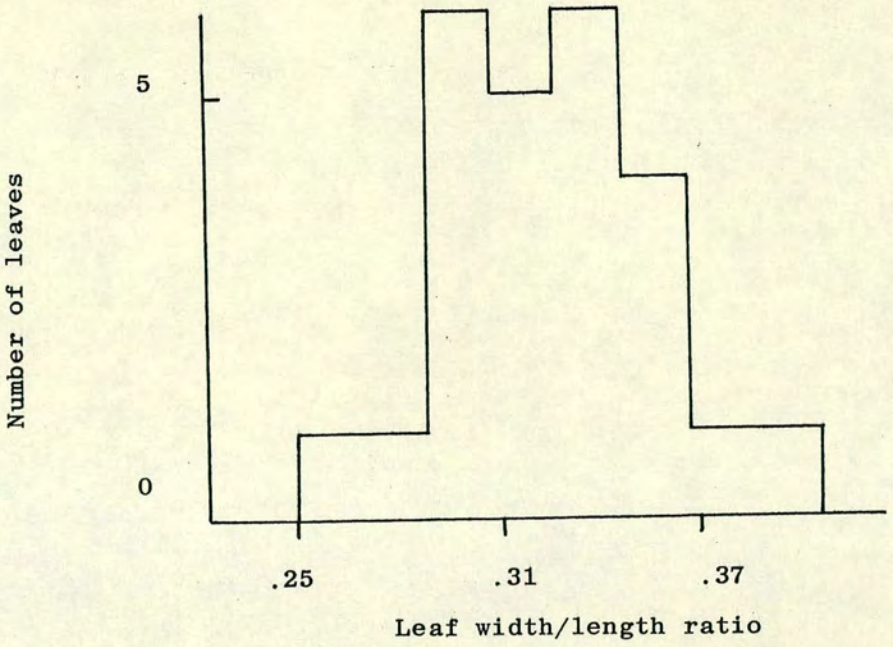


Figure 10. Taxon E: Histogram of leaf width/length ratios of 25 leaves taken from 5 specimens.

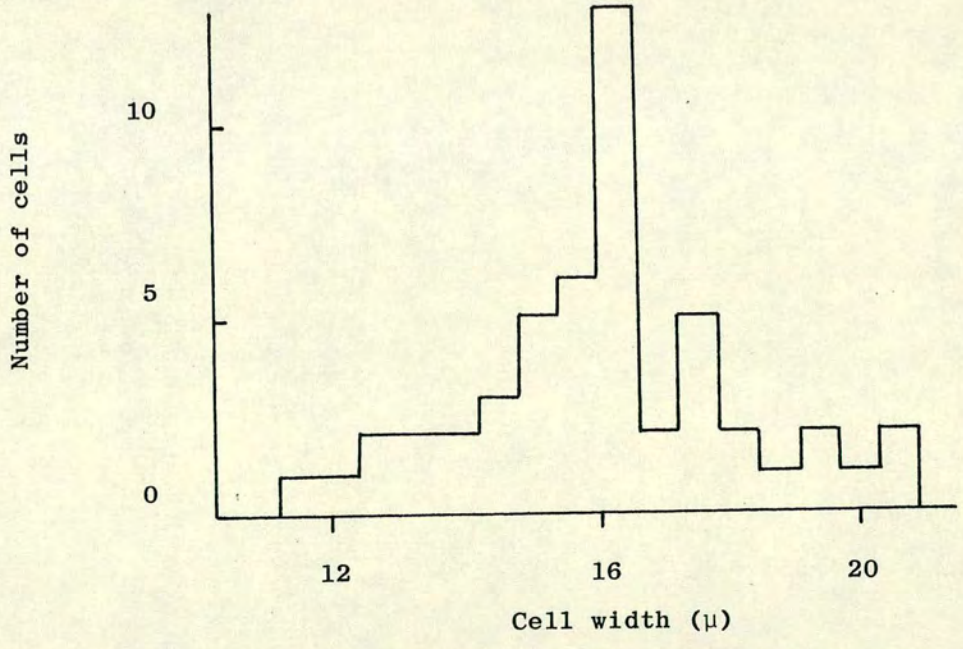


Figure 11. Taxon E: Histogram of cell widths of 50 cells taken from 5 specimens.

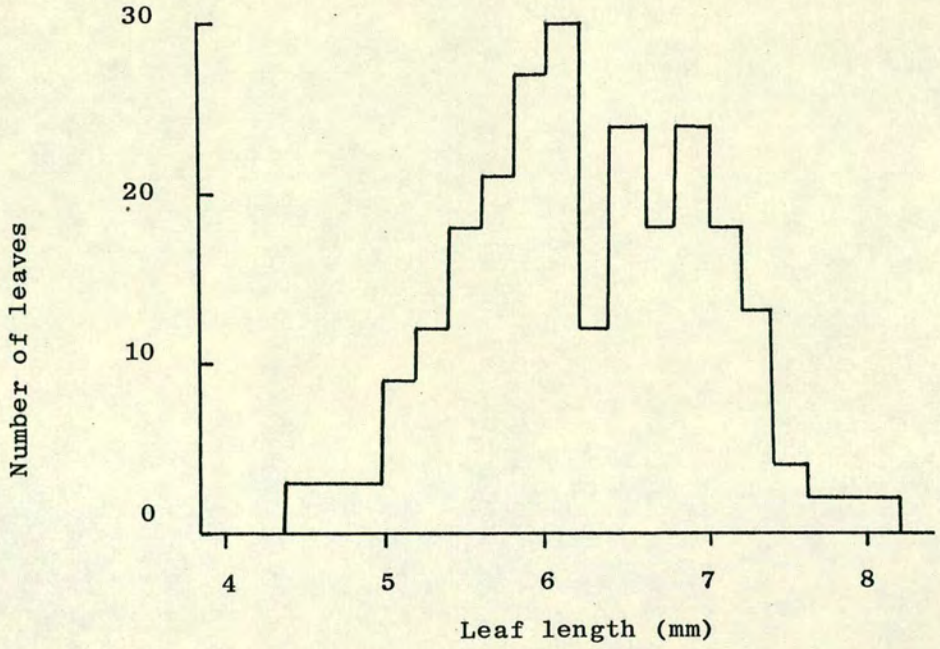


Figure 12. Taxon F: Histogram of leaf lengths of 245 leaves from 49 specimens.

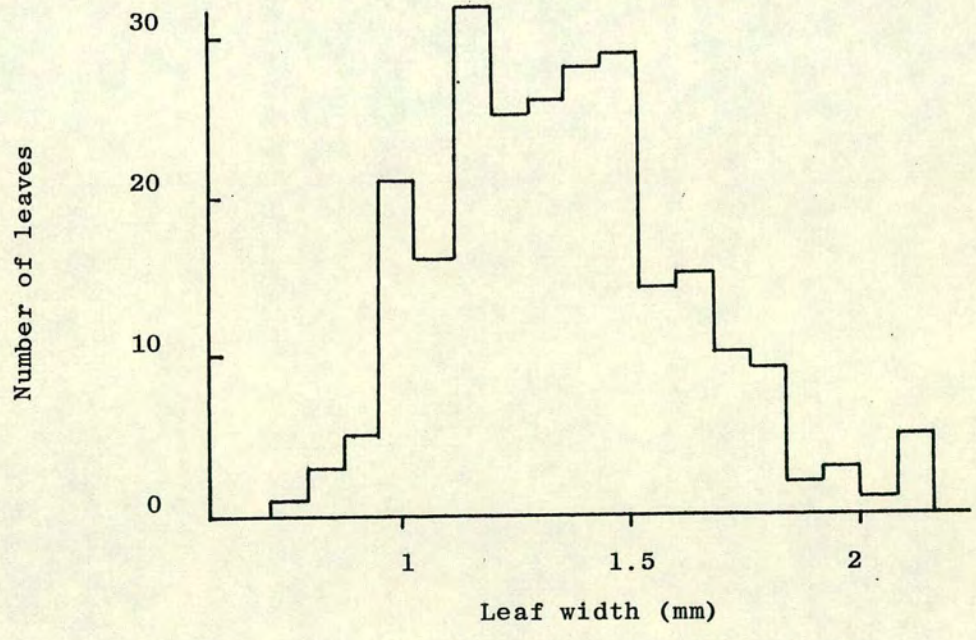


Figure 13. Taxon F: Histogram of leaf widths of 245 leaves from 49 specimens.

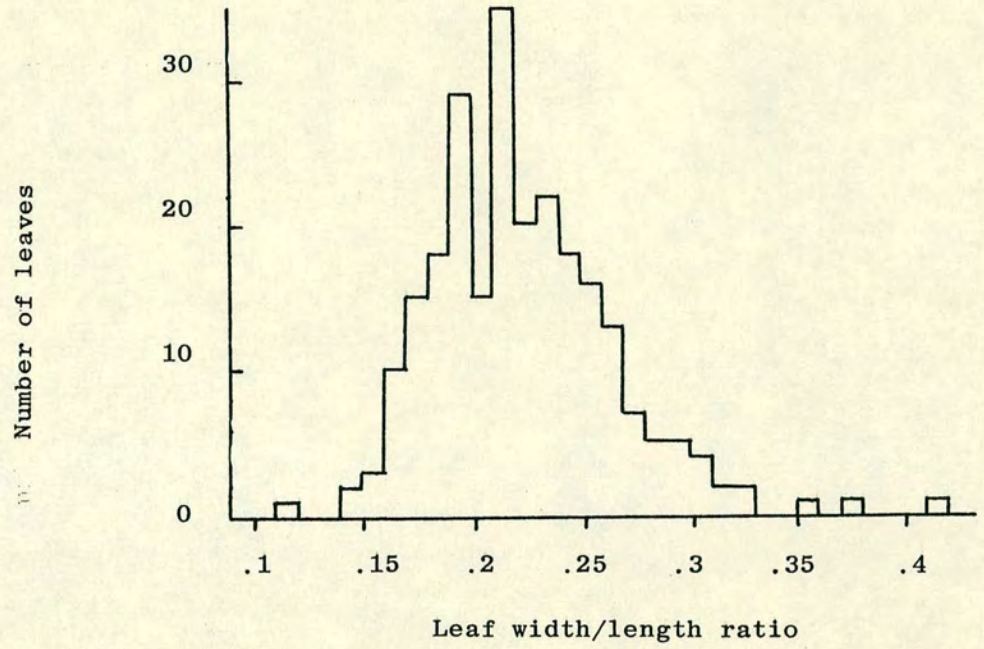


Figure 14. Taxon F: Histogram of leaf width/length ratios of 245 leaves taken from 49 specimens.

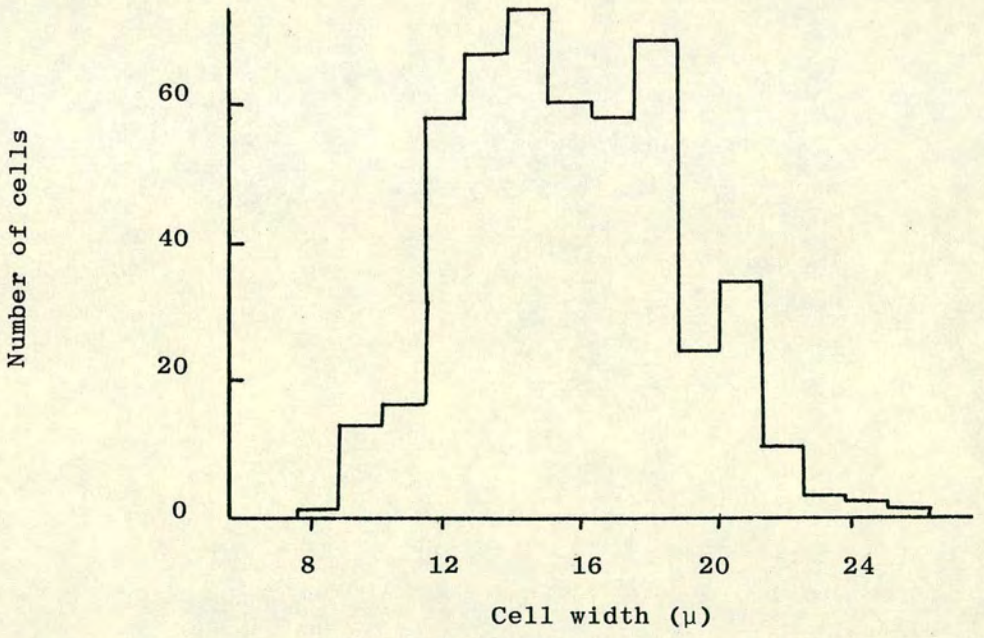


Figure 15. Taxon F: Histogram of cell widths of 490 cells taken from 49 specimens.

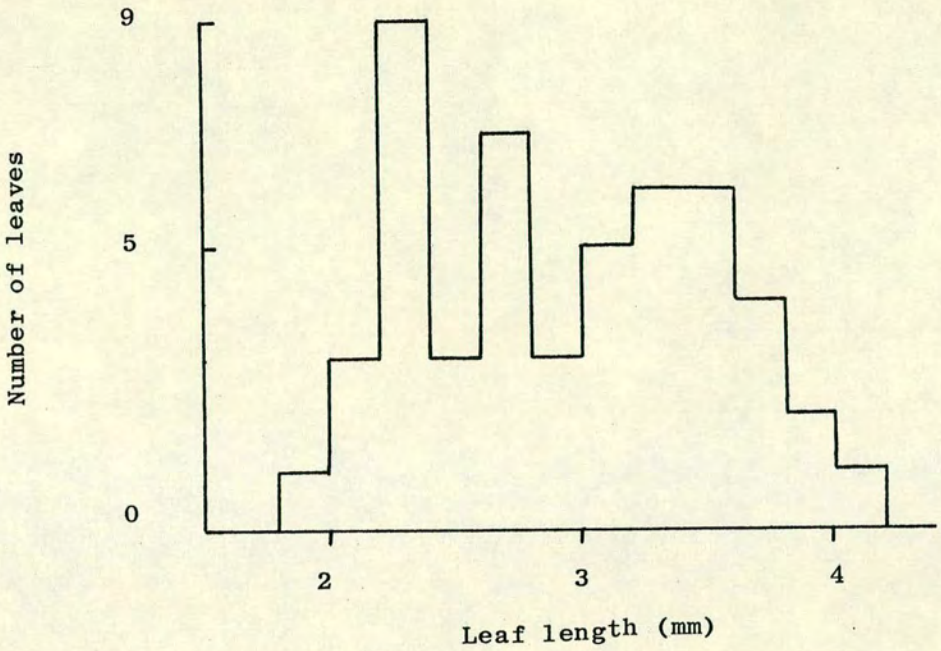


Figure 16. Taxon G: Histogram of leaf lengths of 50 leaves taken from 10 specimens.

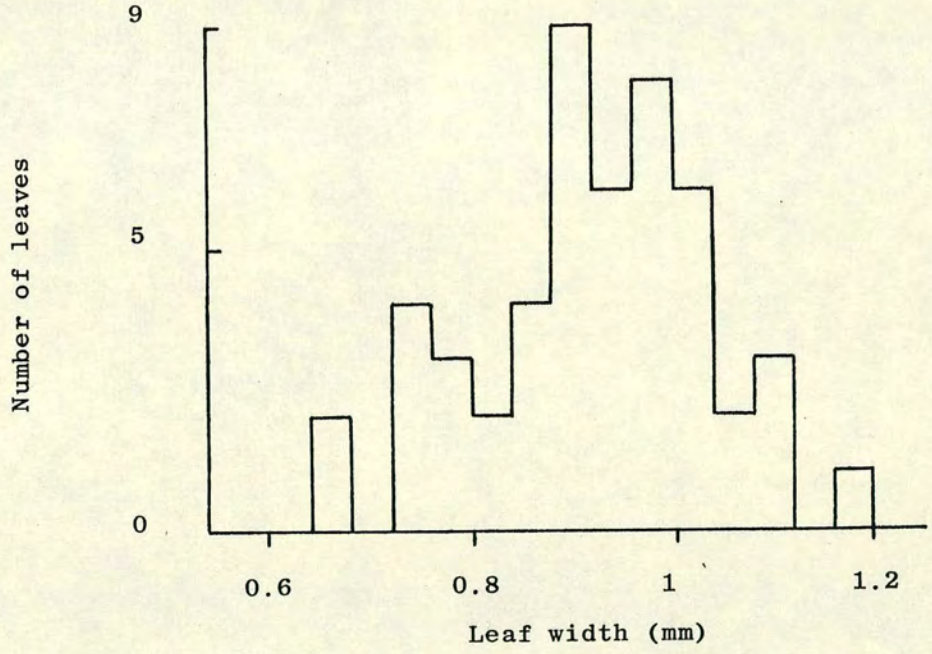


Figure 17. Taxon G: Histogram of leaf widths of 50 leaves taken from 10 specimens.

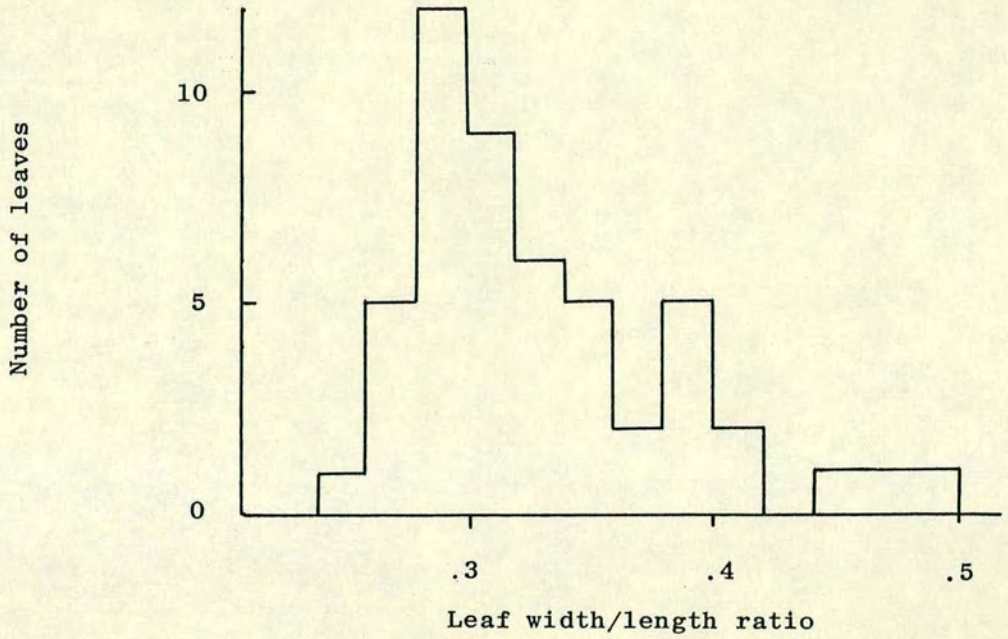


Figure 18. Taxon G: Histogram of leaf width/length ratios of 80 leaves taken from 10 specimens.

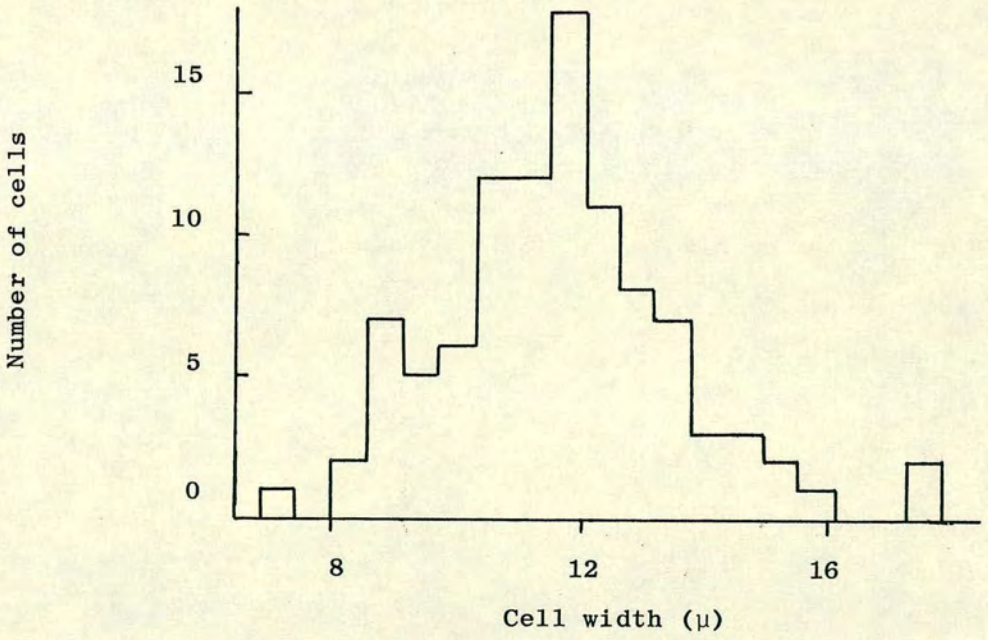


Figure 19. Taxon G: Histogram of cell widths of 100 cells taken from 10 specimens.

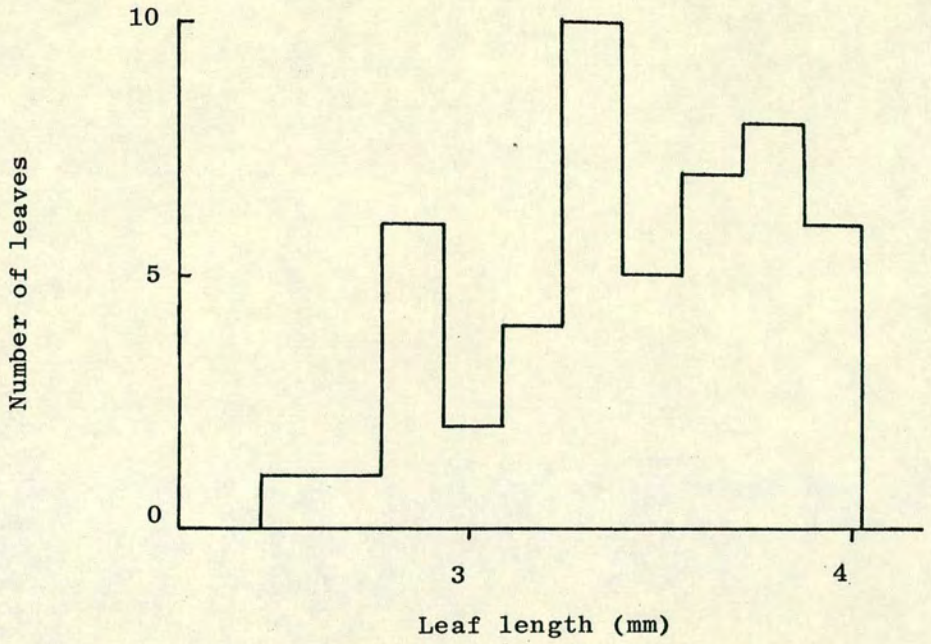


Figure 20. Taxon H: Histogram of leaf lengths of 50 leaves taken from 10 specimens.

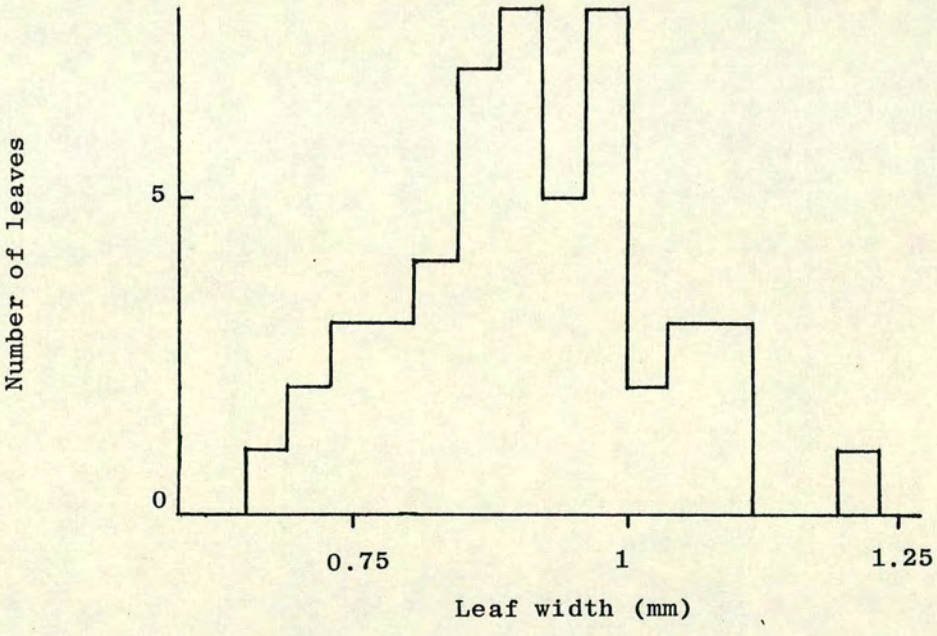


Figure 21. Taxon H: Histogram of leaf widths of 80 leaves taken from 10 specimens.

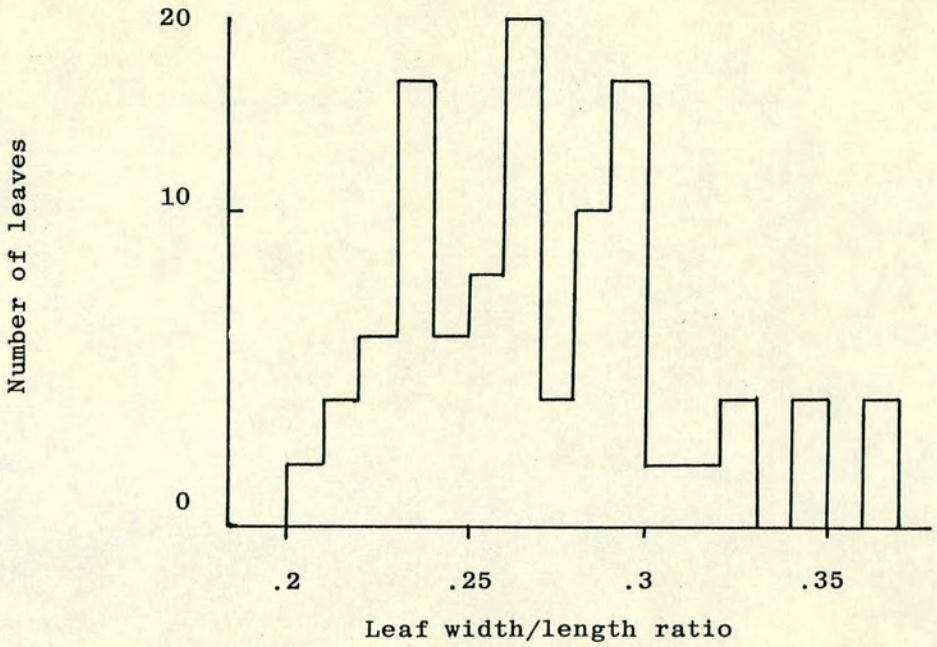


Figure 22. Taxon H: Histogram of leaf width/length ratios of 80 leaves taken from 10 specimens.

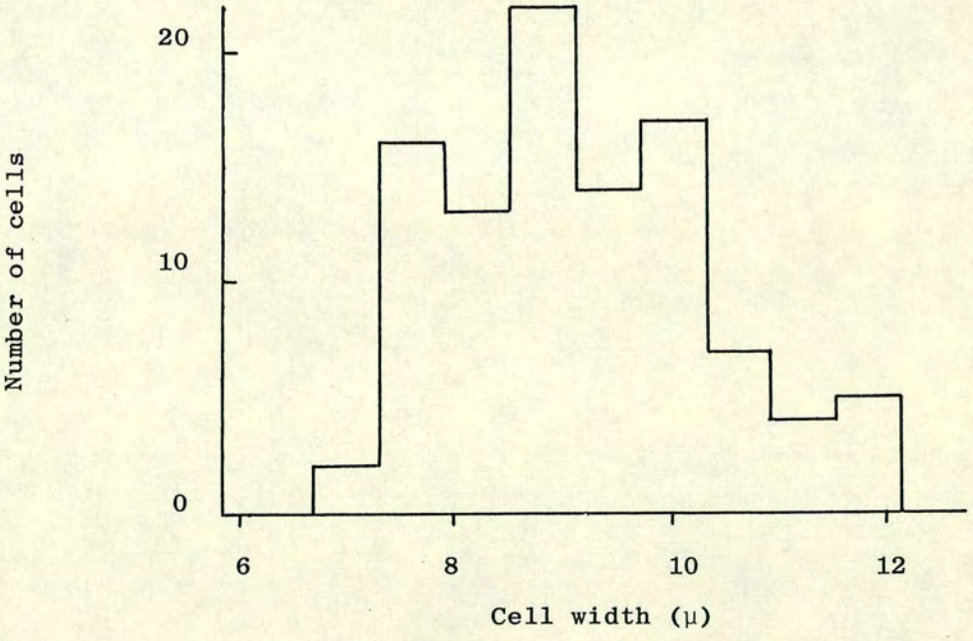


Figure 23. Taxon H: Histogram of cell widths of 100 cells taken from 10 specimens.

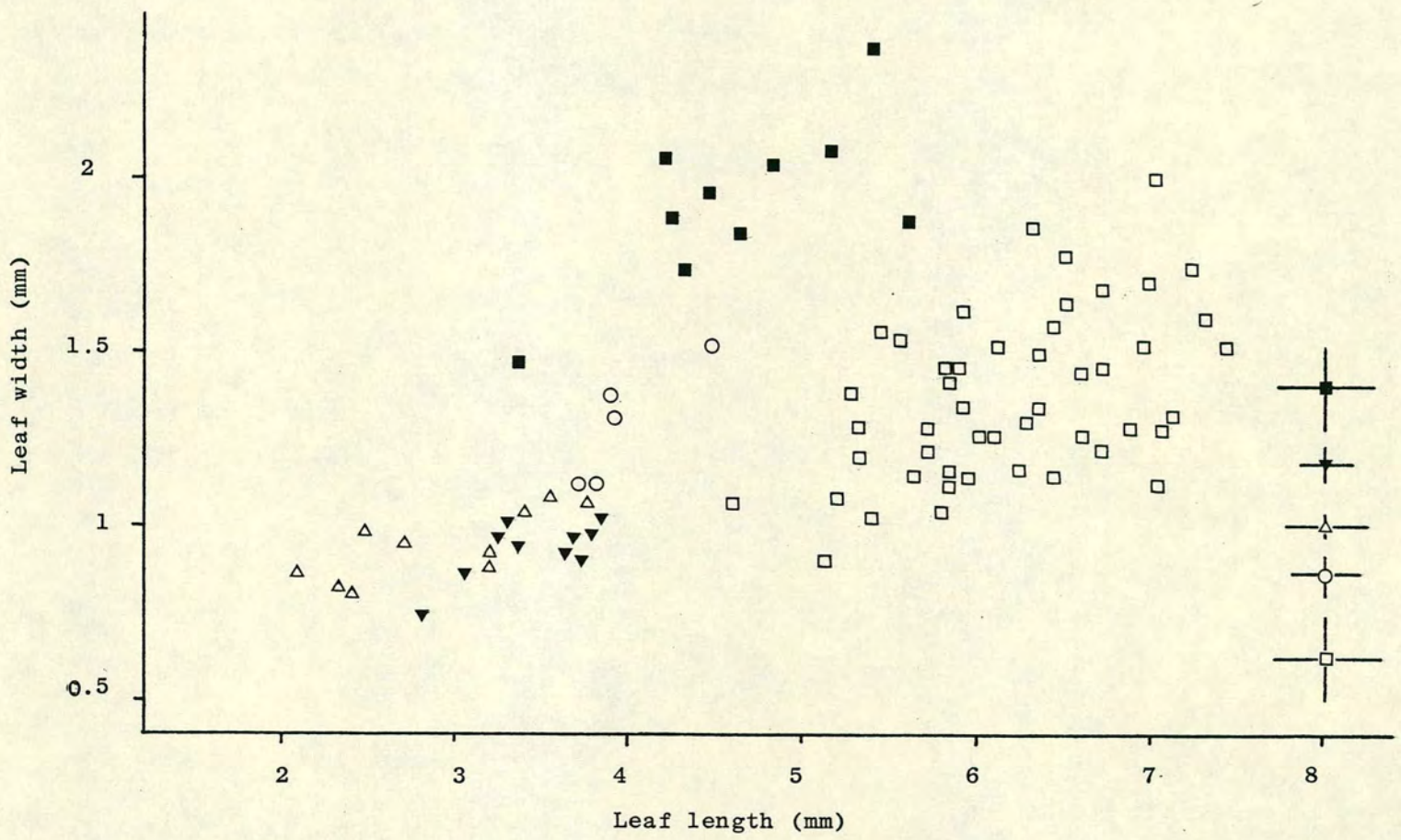


Figure 24. Scatter diagram showing leaf length and leaf width values of taxa D (■), E (○), F (□), G (△) and H (▼). Each point is the mean of five values, standard errors are plotted in the right hand margin.

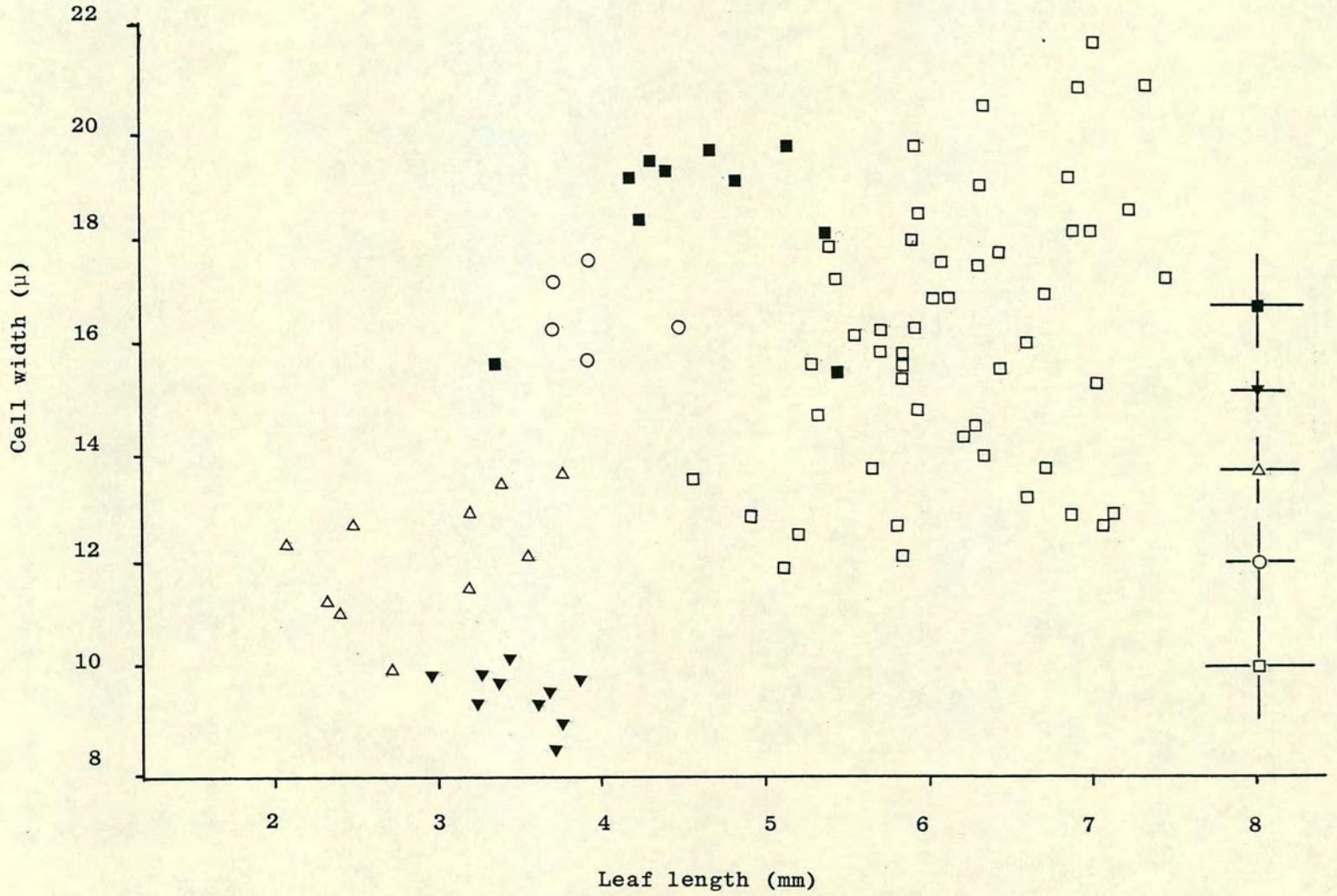


Figure 25. Scatter diagram showing leaf length and cell width values of taxa D (■), E (○), F (□), G (△) and H (▼). Each point is the mean of 5 leaf and 10 cell values, standard errors are given in the right hand margin.

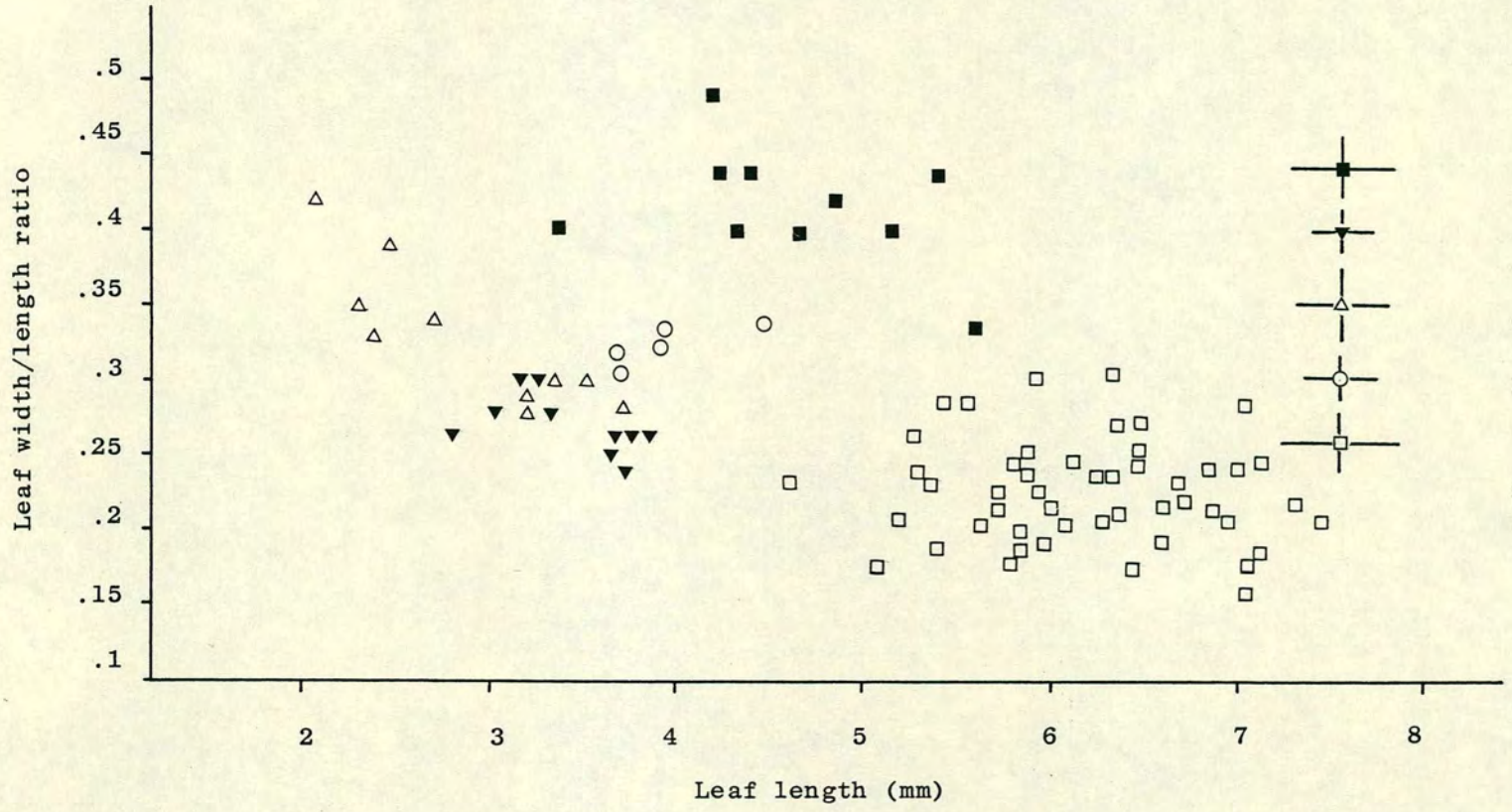


Figure 26. Scatter diagram showing leaf length and leaf width/length ratios of taxa D (■), E (○), F (□), G (△) and H (▼). Each point is the mean of 5 values, standard errors are given in the right hand margin.

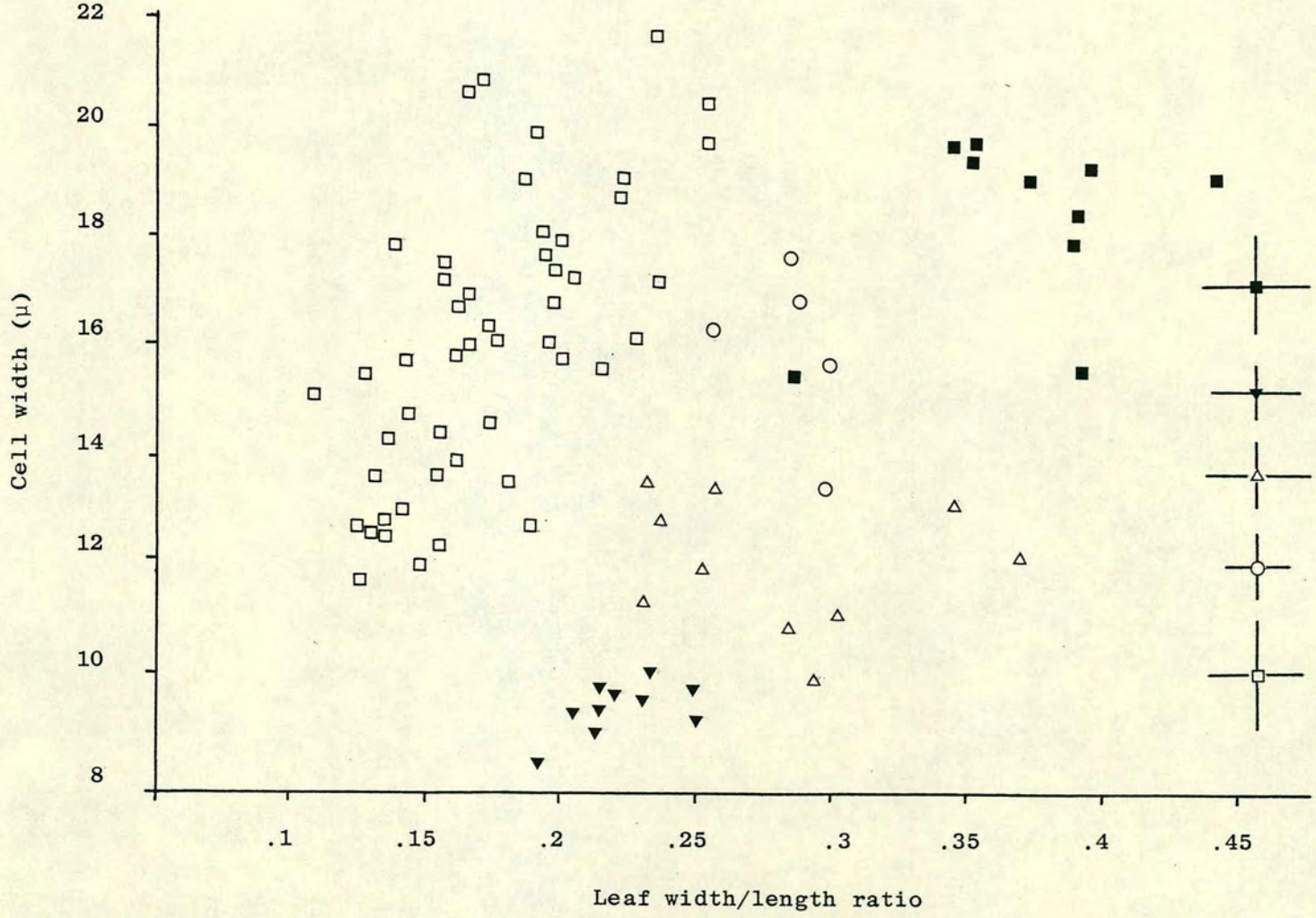


Figure 27. Scatter diagram showing leaf width to length ratios and cell width values of taxa D (■), E (○), F (□), G (△) and H (▼). Each point is the mean of 5 values, standard errors are given in the right hand margin.

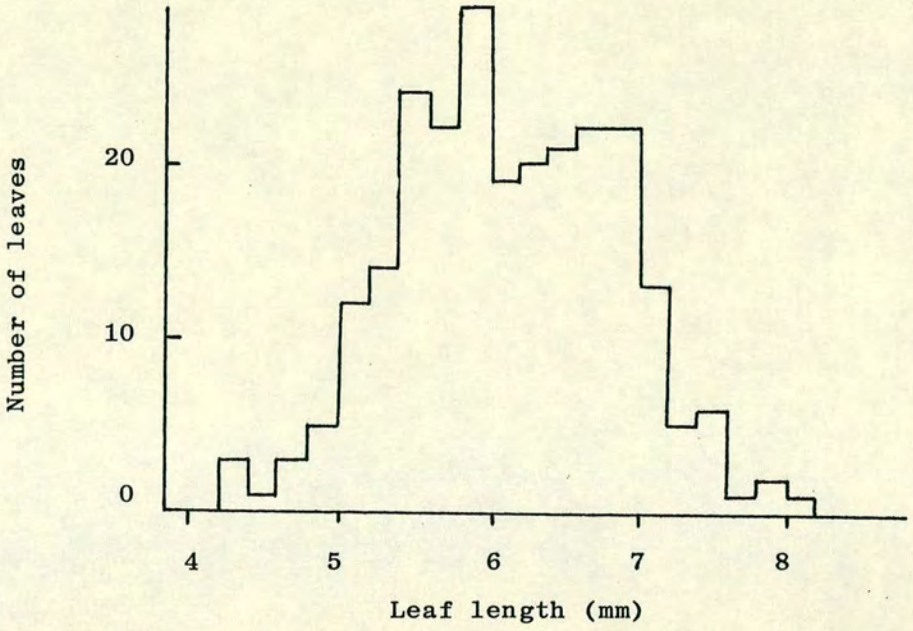


Figure 28. Taxon F: Histogram of leaf lengths from 49 specimens. Plotted from the same data as Fig. 12 but with re-defined size classes.

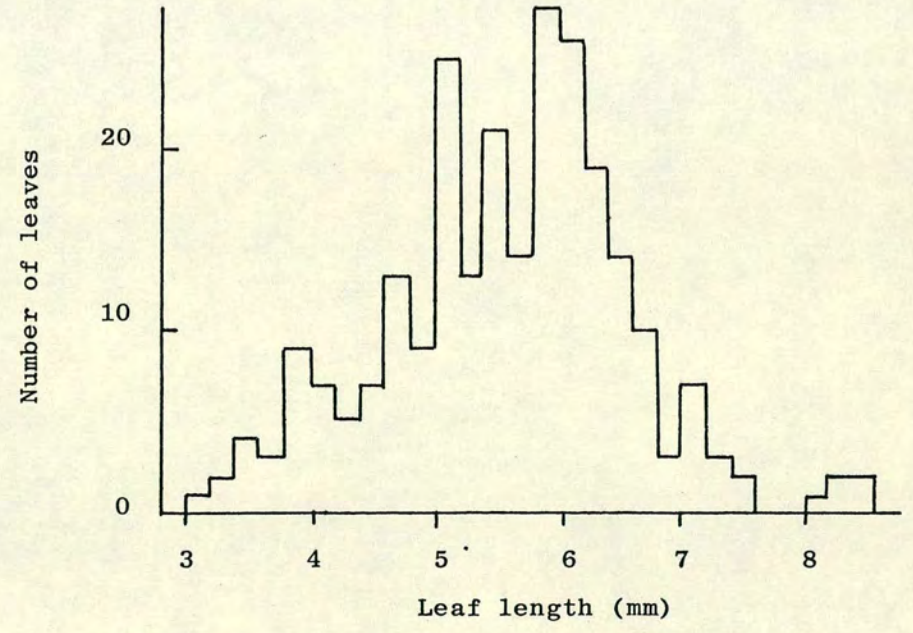


Figure 29. Taxon F: Histogram of leaf lengths of 250 leaves plotted from an additional 50 specimens, for comparison with Figs. 12 and 28.

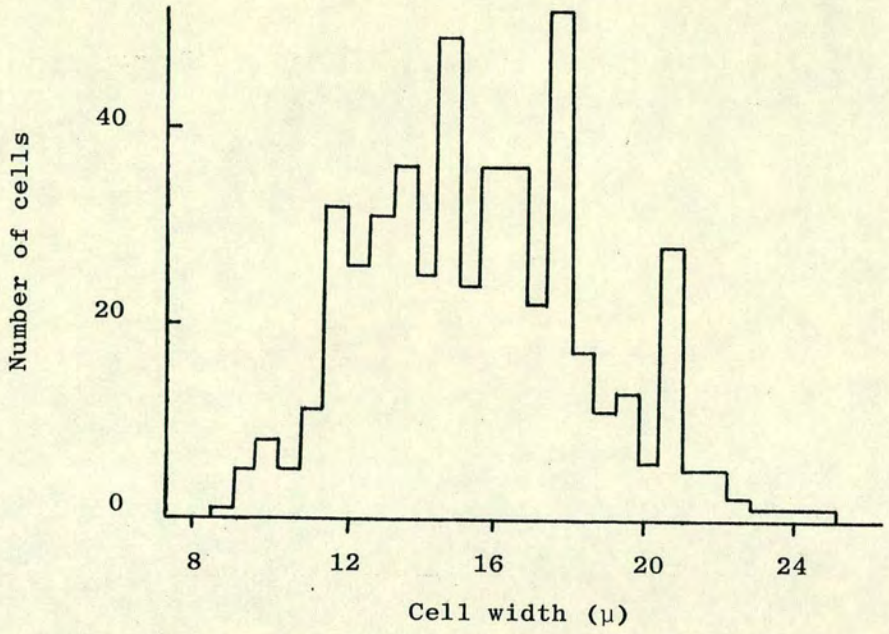


Figure 30. Taxon F: Histogram of cell widths of 490 cells taken from 49 specimens. Plotted from the same data as Fig. 15 but with reduced size classes.

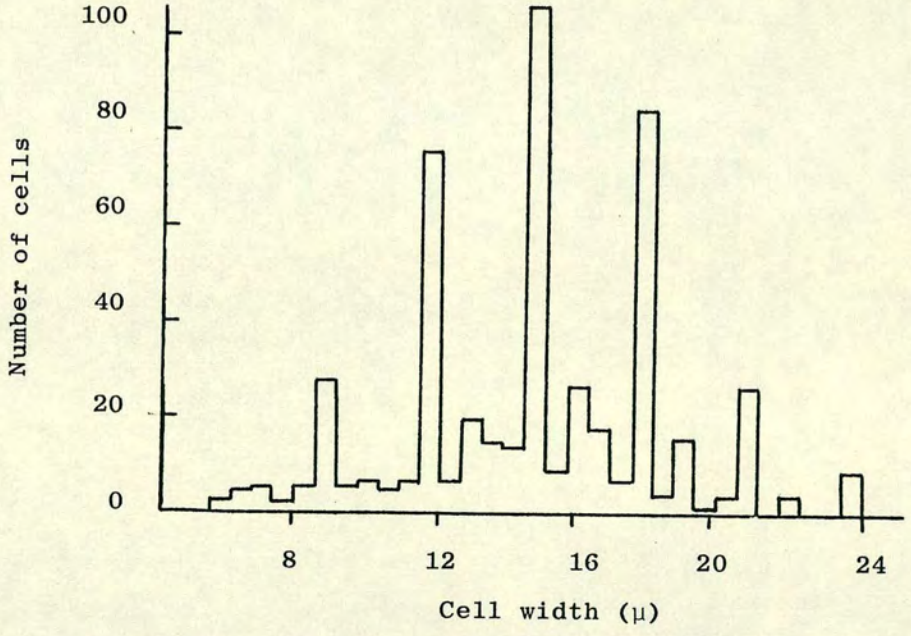


Figure 31. Taxon F: Histogram of cell widths of 500 cells taken from an additional 50 specimens, for comparison with figures 15 and 30.

specimens were taken at random and measured in the same way. Leaf length data were plotted (Fig. 29) and were found to show no evidence of a bimodal distribution. The two-peaks in the original leaf length histogram of taxon F thus appeared to be only a chance deviation. A chi-square 'goodness-of-fit' test (Snedecor and Cochran, 1967) was carried out on these data, which gave a probability value of 0.25. This was too high to reject the null hypothesis that the leaf lengths were normally distributed about a single mean. The distribution pattern in Fig. 12 was therefore not significantly abnormal and deviations as great or greater than these could be expected in the other histograms.

While deciding on a suitable scale for plotting the Taxon F cell width histogram (Fig. 15) irregularities were seen in these data. If plotted with smaller size classes (Fig. 30) peaks were visible at 12 μ, 15 μ, 18 μ and 24 μ. These corresponded to values of 20, 25, 30 and 40 units on the eye-piece graticule on which the measurements were taken. Regular maxima were more apparent in a set of measurements taken from a further 50 specimens of taxon F. (Fig. 31). These effects can be explained by rounding off errors similar in size to the estimated accuracy of the measurements given in Table 6.

(b) Scatter diagrams. The scatter diagrams show the size and nature of differences between taxa.

(i) Taxon D: This taxon had greater leaf length, leaf width

and cell width values than taxa H and G (Figs. 24 and 25). It also had a larger leaf width/length ratio than any other taxon (Figs. 26 and 27) although some overlap with taxa E and G occurred. Confusion with the latter was unlikely because of its narrower leaves, but was possible with taxon E which was similar in size.

(ii) Taxon E: Taxon E was intermediate between all other taxa in leaf length, leaf width and leaf width/length ratio (Figs. 24 and 26). Separation from other taxa could therefore be difficult except that the cell width values were high and only likely to be mistaken for those of taxa D and F (Figs. 25 and 27).

(iii) Taxon F. Plants of this taxon differed from taxa H and G in leaf length, leaf width and cell size (Figs. 24 and 25). The leaves of taxon F were generally over 4.5 mm long, which was only slightly longer than any measured in taxon E, so confusion could have occurred here. Taxon D however, was distinct from taxon F in its lower leaf width/length ratio (Fig. 26), ie. below 0.35.

(iv) Taxa G and H. Both taxa G and H differed from taxa E and F in leaf length, leaf width and cell width (Figs. 24 and 25). Leaves of taxa G and H were generally less than 4 mm long and 1.1 mm wide, with lamina cells below 14 μ wide. Leaf width and cell width also distinguished these taxa from taxon E, which had wider leaves and cells (Figs. 24 and 25). Taxon G and taxon H were similar in leaf dimensions but taxon G was distinguished by its wider cells (Fig. 25). These were over

10 μ wide and taxon H rarely had cells of this width. Leaf width/length ratios could also have been used to separate these taxa (Fig. 27).

3.2.4 Conclusions

The histograms gave a useful indication of the distribution of values in the data but often showed what appeared to be large deviations from normal distribution. These were found to be due to chance and were not statistically significant. Histograms were thus poor indicators of normal or non-normal distribution. The appearance of histograms was also affected by the choice of 'size-classes' and the size of these classes in relation to the accuracy of the measurements.

The scatter diagrams showed that the taxa formed distinct clusters, suggesting that each could be defined almost on leaf and cell measurements alone. When taxa were also characterised by other features, such as dense papillae in taxon H for example, this was useful confirmation that the taxa were valid.

(i) Taxon D. This taxon was distinct from all others except taxon E in its measurements, but was also distinguished by its pandurate-shaped leaves which were widest above mid-leaf.
(ii) Taxon E. This taxon was sometimes difficult to separate from taxon D or taxon F on the basis of its measurements. There were however leaf shape and leaf stance differences between the three taxa. The leaves of taxon D were pandurate,

widest above the middle and erecto-patent on the stem. In taxon E the leaves were broadly oblong, widest at mid-leaf and patent to spreading with recurved tips. In taxon F they were lingulate-lanceolate, widest below mid-leaf and had leaf stance varying between erecto-patent and spreading. Nevertheless, confusion between these taxa was possible in some instances. Taxon E appeared to form a link between taxa D and F, which were otherwise distinct.

(iii) Taxon F. Apart from possible confusion with taxon E discussed above, this taxon was distinct from all others in its measurements, despite a wide range of variation in leaf and cell size.

(iv) Taxon G. Taxon G was readily defined on the basis of its measurements but could also be separated, from small taxon F specimens for example, by a characteristic group of smooth, long-rhomboidal cells at the leaf apex.

(v) Taxon H. This taxon was distinct in its leaf and cell dimensions and was also characterised by its small, densely papillose cells.

All taxa could therefore be delimited except for taxon E in relation to taxa D and F. Unfortunately taxon E was rare (only 5 specimens were seen) so further measurements were not possible.

The ranges of leaf length, leaf width, leaf width/length ratio and cell width of the taxa are summarised in Table 7.

Table 7. Leaf length, leaf width, leaf width/length ratio and cell width ranges of plants belonging to taxa D, E, F, G and H.

Taxon	Leaf length (mm)	Leaf width (mm)	Leaf width/ length ratio	Cell width µ
D	Medium 8.5 - 5.5	Large 1.5 - 2.5	Large 0.35 - 0.5	Large 15 - 20
E	Medium 4.0 - 5.0	Medium 1.0 - 1.5	Medium 0.3 - 0.35	Medium to large 14 - 18
F	Large 4.0 - 7.5	Small to medium 0.75 - 2.0	Small to medium 0.15 - 0.3	Medium to large 14 - 22
G	Small 2.0 - 4.0	Small 0.75 - 1.25	Medium 0.25 - 0.4	Small to medium 10 - 14
H	Small 3.0 - 4.0	Small 0.75 - 1.25	Small to medium 0.25 - 0.3	Small 8 - 10

3.3 Provisional taxa : hair-pointed group

Four provisional taxa were defined using the following characters: stem height and leaf length, the shape (profile) of the leaf apex, the colour of the hair-point, the appearance of the nerve in upper leaf and the frequency of sporophyte production. The taxa are described using terminology defined in Smith's (1978) glossary and are illustrated in Fig. 32.

Taxon I : Stems and leaves medium to large sized, leaf profile recurved or plane, hair-point reddish, short, nerve becoming obscure before reaching leaf apex, sporophyte infrequent.

Taxon J : Stems and leaves medium to large sized, leaf profile plane, hair-point hyaline, long, nerve well defined to leaf apex, sporophyte occasional.

Taxon K : Stems and leaves small to medium sized, leaf profile cucullate, hair-point hyaline, nerve well defined to leaf apex, sporophyte frequent.

Taxon L : Plants too depauperate to be placed reliably in taxa I, J or K. Stems slender and leaves small, leaf apex plane or entire leaf concave; hair-point hyaline or reddish, short, nerve usually disappearing in upper leaf, sporophyte unknown.

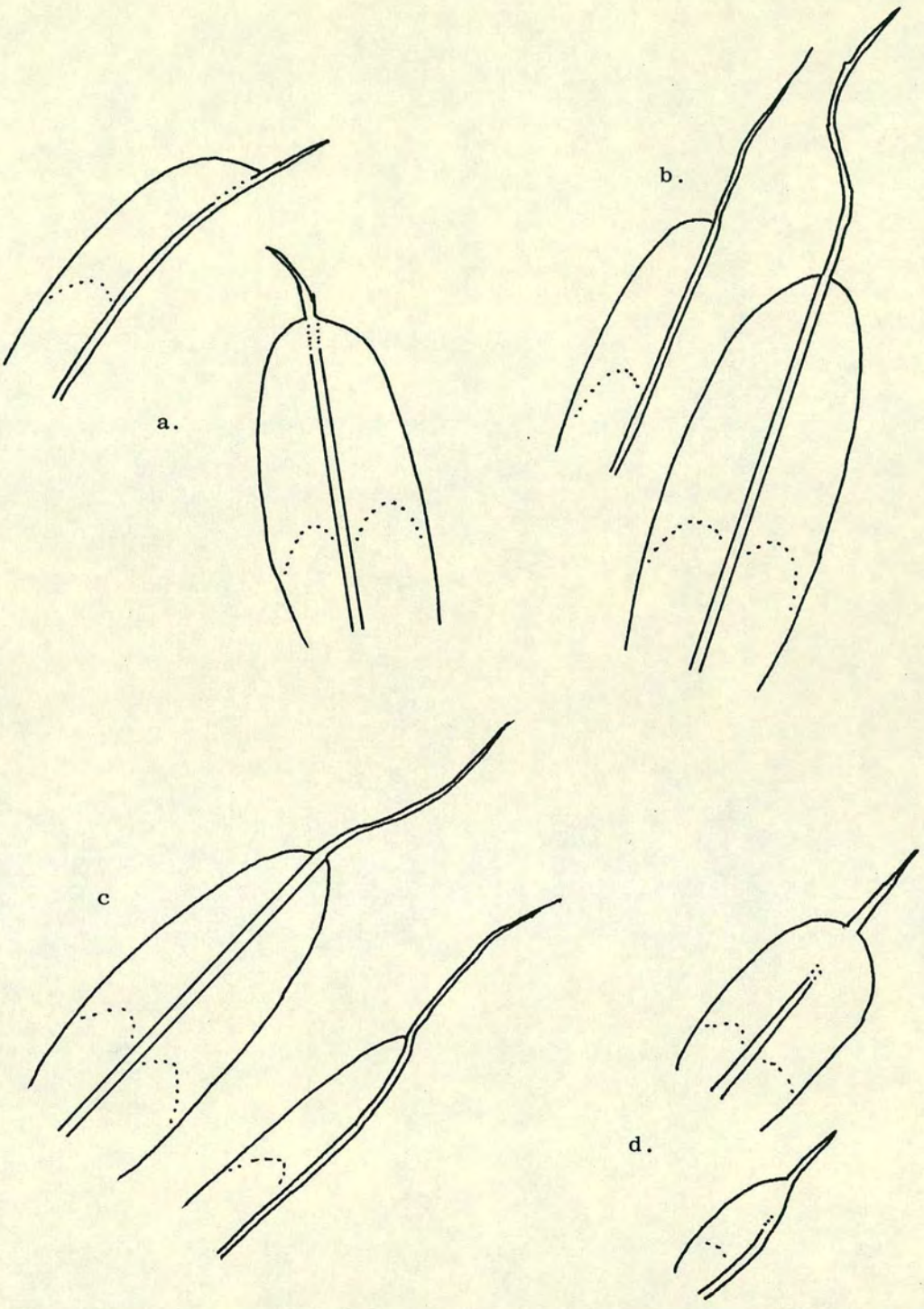


Figure 32. Sketch diagrams of leaves of provisional hair-pointed taxa

a). taxon I b). taxon J c). taxon K d). taxon L

Most plants were easily assigned to one or other of these taxa, however, intermediates between taxa I and J, and taxa K and L did occur. Some plants in taxon J were also very similar to some in taxon K, and others in taxon K approached taxon L.

3.3.1 Measuring and character scoring methods

Herbarium observations suggested that the hair-pointed taxa were not completely distinct from each other because specimens with intermediate character combinations occurred. In an attempt to confirm or reject this a quantitative assessment of the taxa was made.

Characters relevant to this assessment included those used for defining taxa, i.e. stem height, leaf length and leaf width, leaf profile type, hair point colour and length, nerve type and sporophyte frequency. The following also appeared to show some variation between taxa: the stance of the leaves on the stem, leaf shape, acuteness of the leaf apex, roughness of the hair-point and the proportion of the leaf margin which was recurved or revolute.

Stem height, leaf length, leaf width and hair-point length were measured by ruler or microscope eyepiece graticule. Upper lamina cell width, basal cell width and basal cell length, which have been used to distinguish British species (Smith 1978), were also measured since small but diagnostic differences between taxa could have been overlooked. Further details of these measurements are given in Table 8. Leaf profile type, nerve type, hair-point colour and the amount of recurvature

Table 8. Method, number and estimated accuracy of measurements made on hair-pointed *Tortula* specimens.

Measurement	Method	No. of measurements per specimen	Estimated accuracy
Approximate stem height	Ruler	1	± 1 mm
Leaf length	Microscope eyepiece graticule	5	± 20 μ
Leaf width (maximum)	"	5	± 20 μ
Hair-point length	"	5	± 20 μ
Lamina cell width	"	10	± 1 μ
Basal cell length	"	10	± 1 μ
Basal cell width	"	10	± 1 μ

of the leaf margin could not be measured but, as they varied continuously between two extremes, were scored in discrete numbered categories. The resulting data could be subjected to mathematical, graphical or statistical techniques in a similar way to the measurements. Scoring methods and the definition of the score classes are given in Table 9. The presence or absence of sporophytes was noted in each specimen. Stance of the leaves on the stem, leaf shape, acuteness of the leaf apex and roughness of the hair-point were not included in the study because no accurate and fast method of measuring them could be found.

In total, 7 different variables were measured and 4 scores were taken per specimen. In order to reduce the time spent making measurements the number of specimens was limited to 30. These were picked at random and one mature stem from each was removed. The height of this stem was measured and five mature leaves were dissected from it. The dimensions of each of these leaves were measured and the necessary scores recorded. For each leaf the width of 2 lamina cells and the width and length of 2 basal cells were also taken.

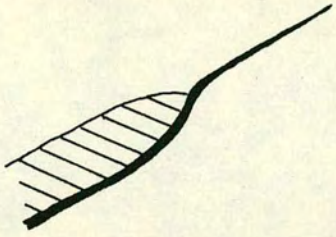
3.3.2 Results

Initial results suggested that stem height, leaf length and leaf profile were important characters. These were therefore measured and scored on a further 30 specimens. The data is presented in Figs 33 - 43. Histograms of measured data produced nothing of direct relevance to the discussion and are therefore given in Appendix 4.

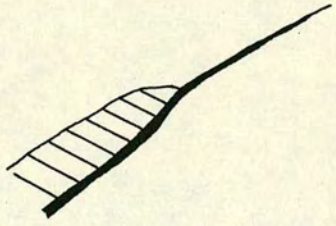
Table 9. Methods of scoring hair-pointed Tortula specimens. Each character was scored 5 times per specimen.

Character	Method of scoring
Leaf profile	Placed in 4 categories

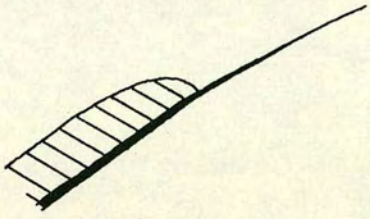
1. Leaf apex cucullate



2. Leaf apex sub-cucullate



3. Leaf apex plane



4. Leaf apex recurved

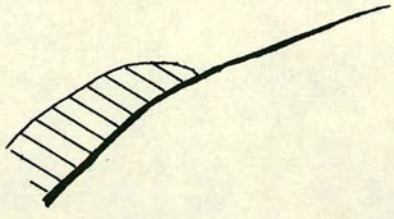
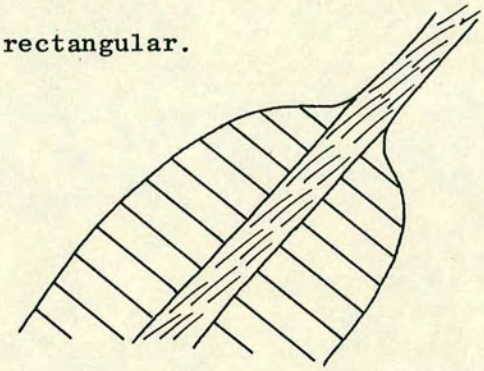


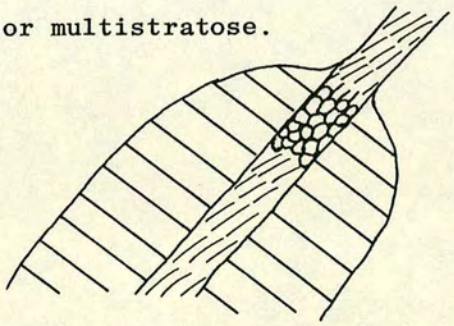
Table 9 (continued)

Character	Method of scoring
Nerve type	Placed in 3 categories

1. Nerve continuous to leaf apex. Cells of abaxial nerve surface long rectangular.



2. Nerve becoming obscure near leaf apex. Abaxial cells quadrate near apex. Shape of nerve retained, cells bistratose or multistratose.



3. Nerve not reaching leaf apex. Nerve merging into quadrate unistratose lamina cells.

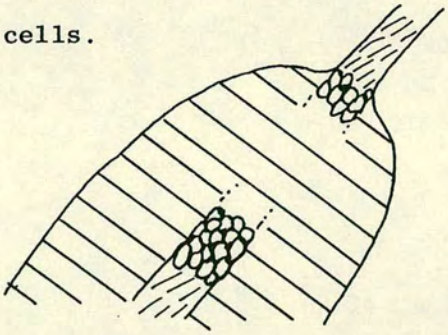


Table 9 (continued)

Character	Method of scoring
Colour of hair-point	Placed in 3 categories: 1. Hair-point coloured (reddish or yellow/brown) throughout, or hyaline only at extreme tip. 2. Hair coloured for about half its length from the base. 3. Hair hyaline throughout or coloured only at extreme base.
Recurvature of leaf margin	Measured on 1 side of leaf. Placed in 5 categories:- 1. Leaf margin not recurved. 2. Margin recurved < $\frac{1}{2}$ lamina. 3. Margin recurved > $\frac{1}{2}$ < 2/3 lamina. 4. Margin recurved > 2/3 < $\frac{3}{4}$ lamina. 5. Margin recurved > $\frac{3}{4}$ < 1 lamina.

3.3.3. Discussion

(a) Histograms of scored data are compared in Figs 33 - 36 which show the relative proportions of scores in each score-category for the taxa I, J, K and L. The plants were chosen at random and the number in each taxon differs, because of this the figures are more easily compared than simple histograms. Only two taxon L plants were scored for some characters and these data do not therefore show the full range of variation.

(i) Leaf profile. Taxon I had a high proportion of recurved leaves but plane and ~~notched~~ sub-cucullate leaves were also found (Fig. 33). In taxon J most leaves were plane, although some were recurved and others ~~notched~~ sub-cucullate. Taxon K had a high proportion of cucullate and ~~notched~~ sub-cucullate leaves, some plane leaves but no recurved leaves. Taxon L had leaves which were cucullate, ~~notched~~ sub-cucullate or plane.

(ii) Nerve type. Each of the four taxa had different types of nerve (Fig. 34). Most leaves in taxa J and K had nerves which were continuous to the leaf apex and taxon I had leaves in which the nerve structure became obscure. In taxon L the nerve usually stopped altogether below the leaf apex although both other nerve types were present.

(iii) Hair-point colour. Taxon J plants and most of those in taxon K had hyaline hair-points (Fig. 35). Taxon I specimens had red or reddish, intermediate hair-points and taxon D specimens had hyaline or intermediate hair-points.

Figure 33. Diagram showing the proportion of leaf profile scores in each category for taxa I, J, K and L. The method of scoring leaf profile is given in Table 9.

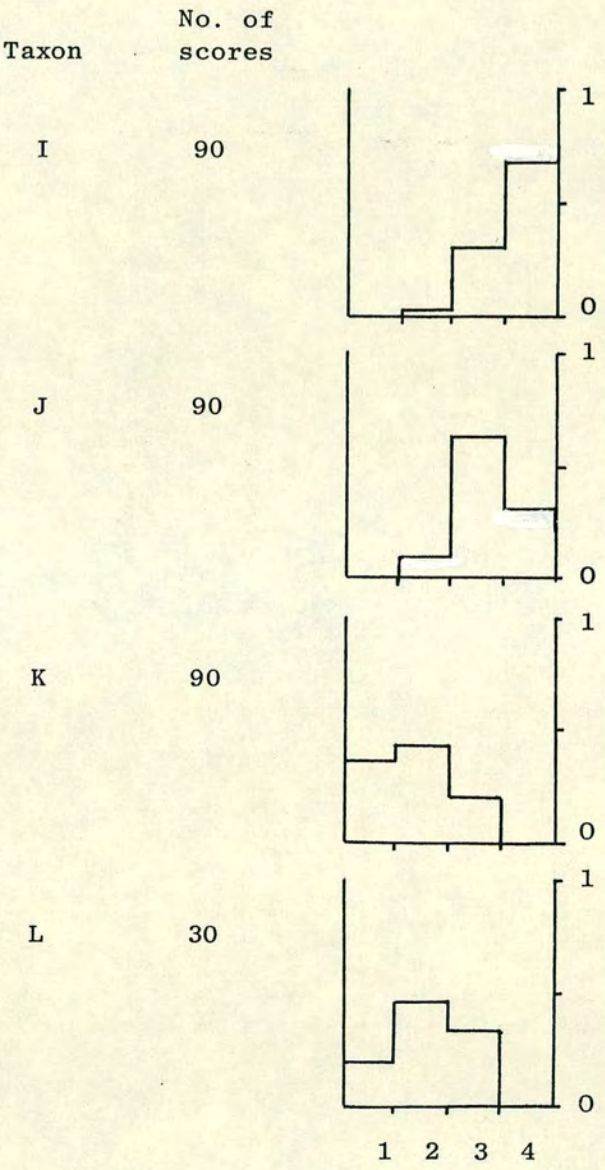


Figure 34. Diagram showing the proportion of nerve-type scores in each category for taxa I, J, K and L. The method of scoring nerve-type is given in Table 9.

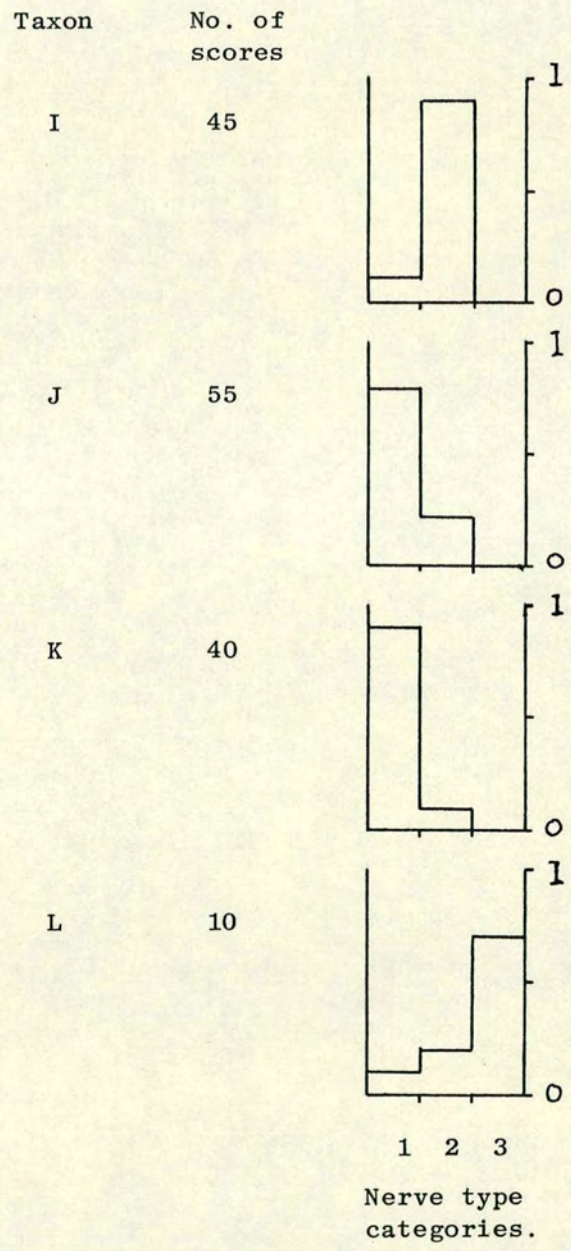
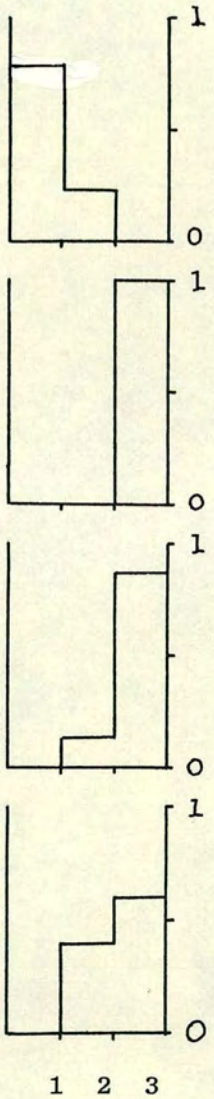


Figure 35. Diagram showing the proportion of hair-point colour scores in each category for taxa I, J, K and L. The method of scoring hair-point colour is given in Table 9.

Taxon	No. of scores
I	45
J	55
K	40
L	5



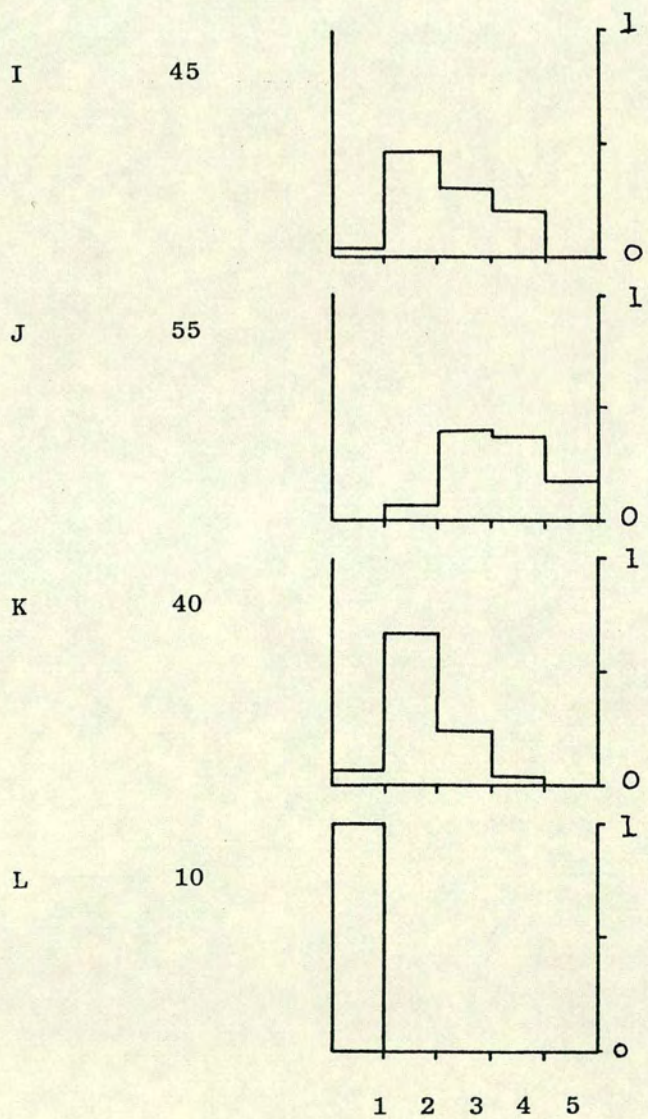
(iv) Leaf margin recurvature. The different ranges of leaf margin recurvature are shown in Fig. 36. Taxon J specimens had leaves with the longest recurved margins, taxa I and K had less of the leaf margin recurved and in taxon L the leaves were not recurved at all.

(v) Frequency of sporophyte production. Sporophytes were unknown in taxon L and rare in taxon I, (Fig. 37). In taxon J however about 30% of specimens had sporophytes, and in taxon K about 80%.

(b) Scatter diagrams

(i) Stem height and leaf size. The scatter diagram of stem height against leaf profile (Fig. 38) showed that the taxa overlapped in these characters particularly in stem height. A scatter diagram of leaf length against leaf profile (Fig. 39) gave a clearer separation. Scatter diagrams of other parameters showed less well defined clusters, or no evidence of grouping. In a scatter diagram of leaf length against leaf width (Fig. 40) for example, the points approximated to a straight line. This was expected since the leaf shapes of all taxa were similar. Taxon J plants however had the largest leaves, followed by taxa K, I and L. Hair-point length plotted against leaf length (Fig. 41) produced a similar result to the previous figure. The approximation to a straight line in this case was not so clear, suggesting that leaf length and hair-point length were less strongly correlated than leaf length and leaf width.

Figure 36. Diagram showing the proportion of leaf margin recurvature scores in each category for taxa I, J, K and L. The method of scoring leaf margin recurvature is given in Table 9.



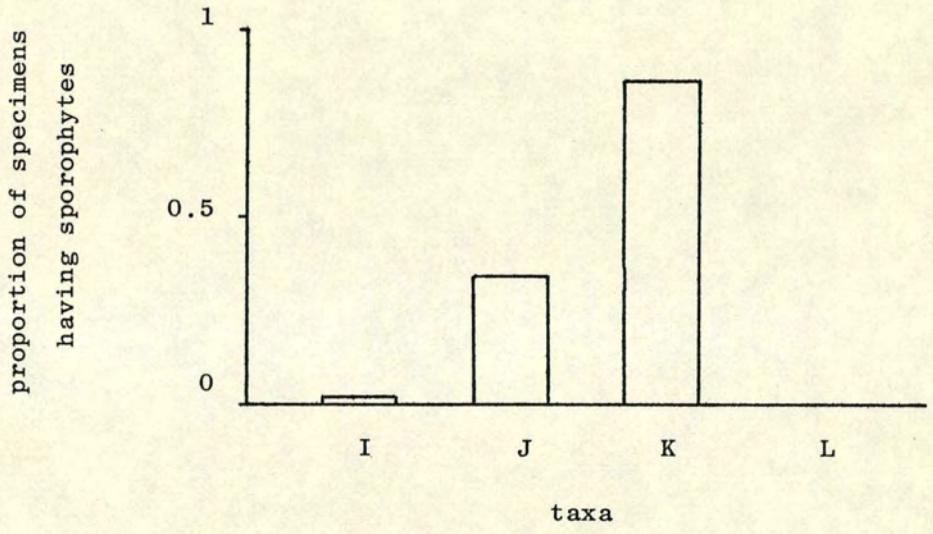


Figure 37. Diagram showing proportion of plants with sporophytes in each taxon I, J, K and L.

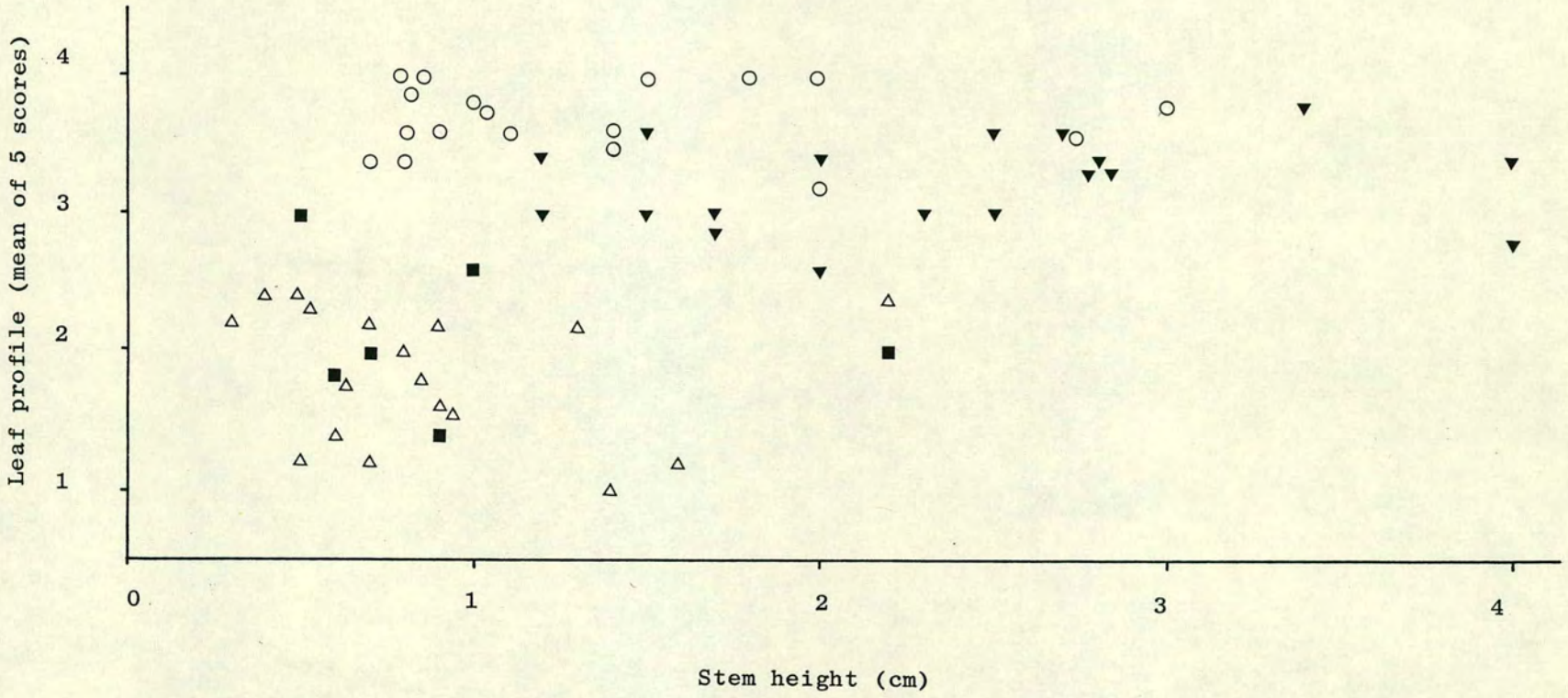


Figure 38. Scatter diagram of stem height against mean leaf profile score showing taxa I (○), J (▼), K (△) and L (■).

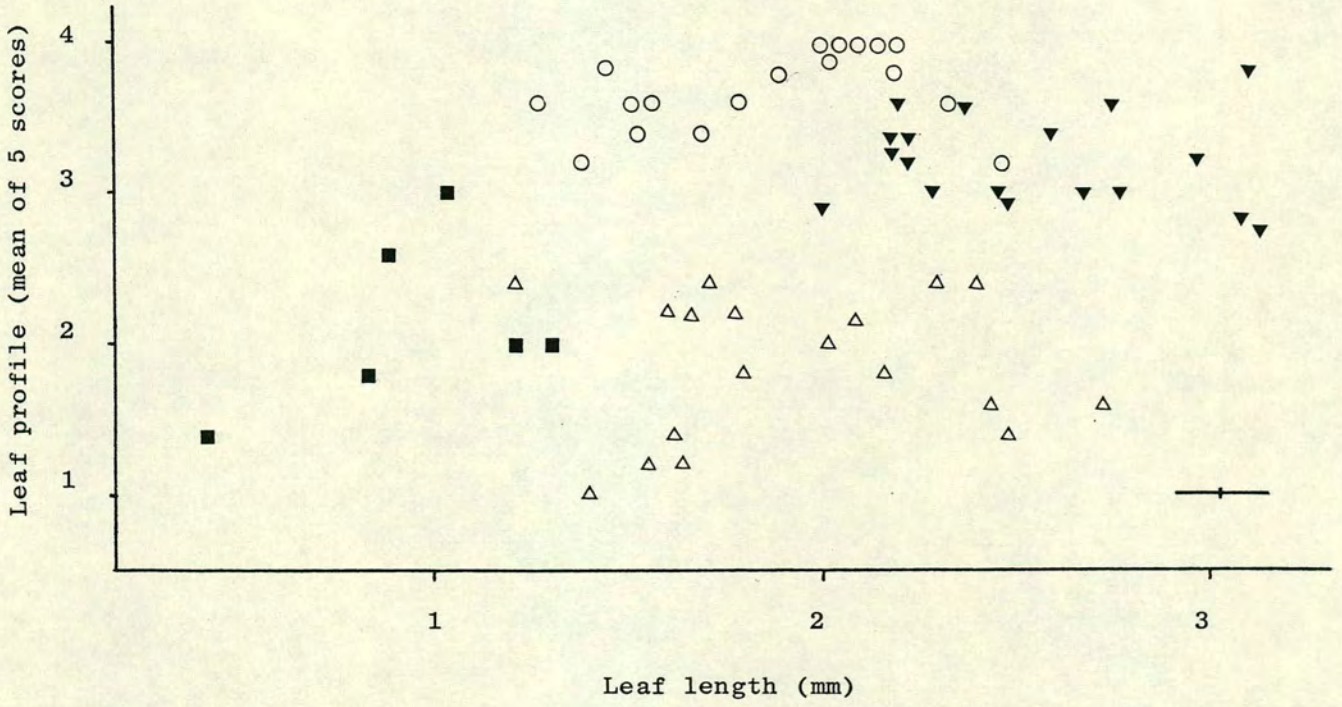


Figure 39. Scatter diagram of leaf length against mean leaf profile score showing groups I (○), J (▼), K (△) and L (■). Leaf length values are means of 5 measurements, the standard error of leaf length means is plotted in the right hand margin.

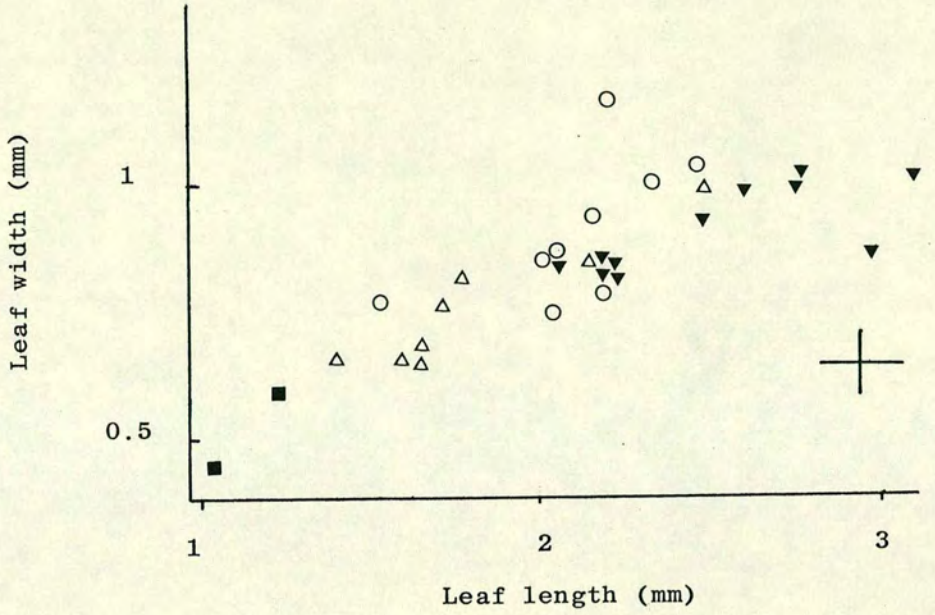


Figure 40. Scatter diagram of leaf length against leaf width showing the hair-pointed groups I (○), J (▼), K (△) and L (■). Each point is a mean of 5 leaf length and 5 leaf width values. Standard errors are plotted in the right hand margin.

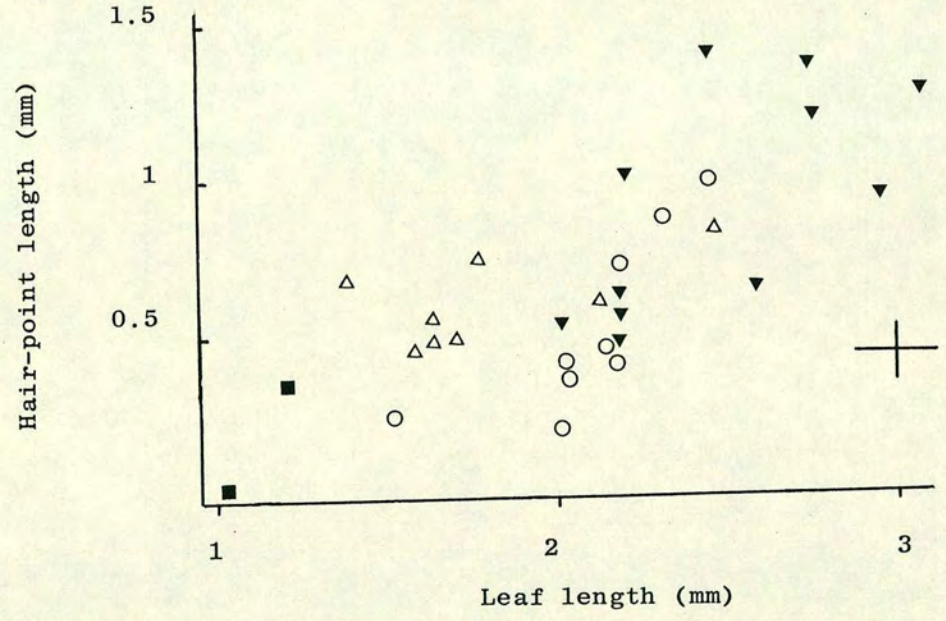


Figure 41 Scatter diagram of leaf length against hair-point length showing the hair-pointed groups I (○), J (▼), K (△) and L (■). Each point is a mean of 5 leaf length and 5 hair-point length values. Standard errors are plotted in the right hand margin.

(ii) Cell sizes. In a scatter diagram of leaf length against lamina cell width (Fig. 42) the four taxa appeared similar in cell size and all of the clustering was due to the leaf length data. Basal cell dimensions (Fig. 43) showed no clustering, except in taxon L where the basal cells were smallest.

3.3.4 Conclusions

(a) Scored characters. The scored characters, leaf profile, nerve type, hair-point colour and leaf margin recurvature were shown to vary between taxa. Some character states were diagnostic of certain taxa, red hair-points for example, were only found in taxon I, and only taxon L had leaves in which the nerve stopped below the apex. These character states although diagnostic for these taxa were of little use as key characters because they were not always present.

(b) Measured characters. Cell measurements were of little value for differentiating hair-pointed taxa. Leaf width and hair-point length measurements appeared to be strongly correlated with leaf length. Leaf length was a good character for identifying taxa and was more reliable than stem height.

(c) Distinctions between taxa. The best separation of taxa was achieved in the scatter diagram of leaf profile against leaf length (Fig. 39). Although clusters corresponding to each of the taxa were present, considerable overlap occurred between them. Scatter diagrams thus suggested that the taxa were not distinct. In order to test this conclusion

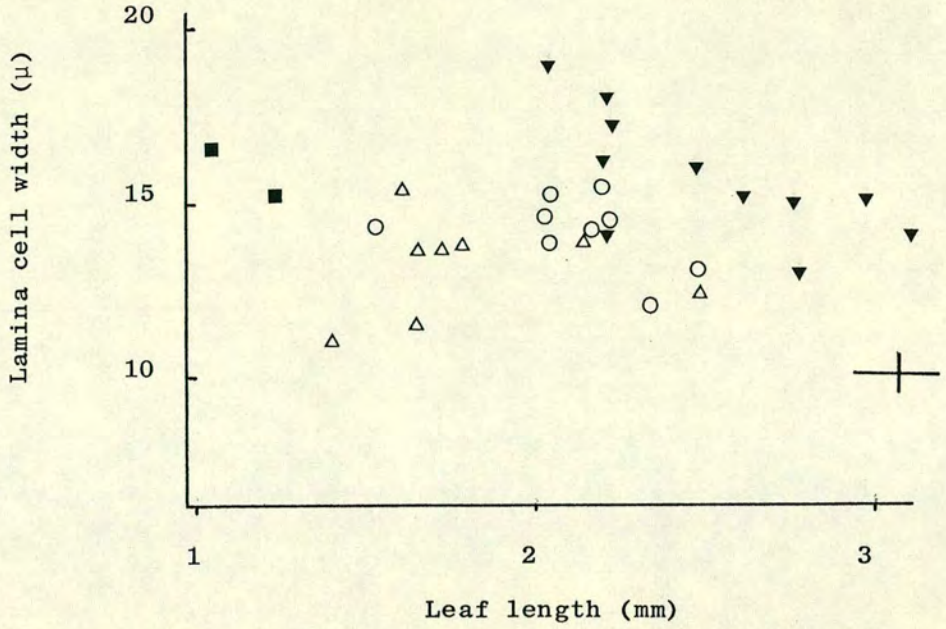


Figure 42 Scatter diagram of leaf length against lamina cell width showing hair-pointed taxa I (○), J (▼), K (△) and L (■). Each point is the mean of 5 leaf and 10 cell measurements. Standard errors are plotted in the right hand margin.

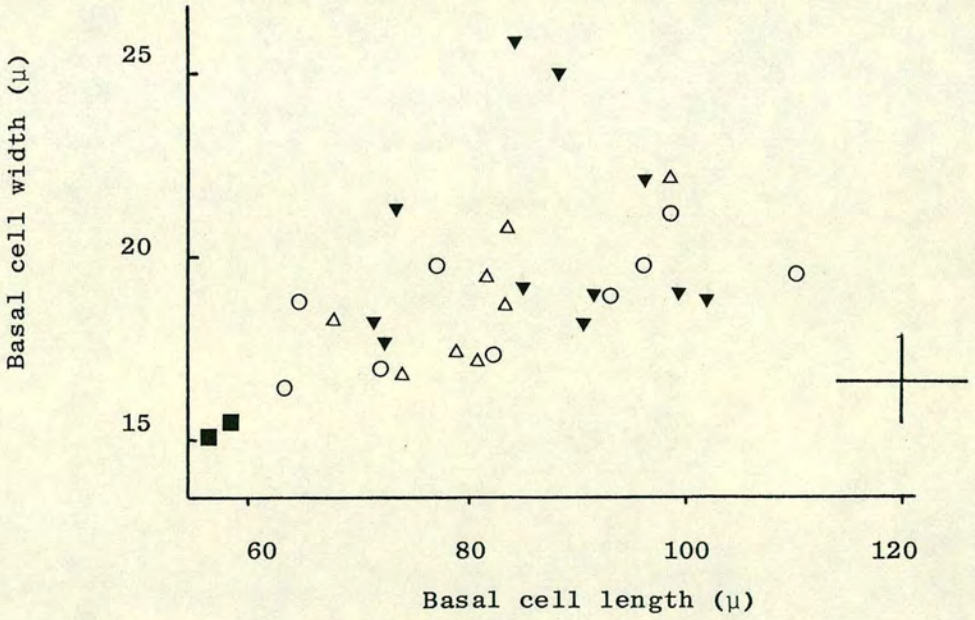


Figure 43. Scatter diagram of basal cell length against basal cell width showing hair-pointed taxa I (○), J (▼), K (△) and L (■). Each point is a mean of 10 length and 10 width values. Standard errors are plotted in the right hand margin.

multivariate analyses of the data were undertaken.

3.3.5 Multivariate analysis

Multivariate statistical analyses were used in an attempt to extract further information from the data and to test the conclusions from the scatter diagrams. The data consisted of measurements and scores of 10 variables made on 30 specimens. Collection of this data was described in section 3.3.1.

(a) Principal component analysis. A principal components analysis (Jeffers 1964, Blackith and Reyment, 1971) is a method of investigating inter-relationships within a set of variables by representing them as a smaller number of independent variates called principal components. The process may be best explained as a plot of all of the variables together in hypothetical multi-dimensional space, with each variable occupying one dimension. A line is drawn through the longest axis of the resulting scatter of points. This represents the axis along which there is most variation and is called the 1st component. Subsequent components are drawn at right angles to the 1st component so that each accounts for as much of the remaining variation as possible. The results are a series of vectors which are expressed in terms of the original variates. Each accounts for progressively less and less of the variation in the data and, unlike the original variables, the components are not correlated with one another.

If the analysis is successful, the larger components will express most of the variation in the data. The pattern of variation in many variables is thus simplified into variation between fewer independent components.

(i) Method. Only mean values of each variable for each specimen were considered in this analysis, to reduce computer time needed. It was also necessary to assume that each of these mean values was continuous.

Correlation coefficients were calculated between all specimen mean values to construct a correlation matrix (Table 10). This was used as the starting point for the principal components analysis.

(ii) Results. The first 3 principal components were found to account for 80% of the variation in the data. These components and their constituent coefficients are given in Table 11, and plotted on a three dimensional graph in Fig. 44.

(iii) Discussion. The largest constituents of component 1 were leaf length, leaf margin recurvature, leaf width and hair-point length, suggesting that this component was a general measure of leaf size. The second component consisted mainly of leaf profile, nerve type and hair-point colour ~~and lamina cell width~~, and may be regarded as an indication of differences at the leaf apex. The third component included basal cell width, lamina cell width and hair-point colour.

Table 10. Correlation matrix of hair-pointed specimen mean values.

Leaf profile	1									
Nerve type	2	0.39								
Hair-point colour	3	-0.41	-0.68							
Leaf margin recurvature	4	0.22	-0.34	0.30						
Leaf length	5	0.31	-0.39	0.28	0.68					
Hair-point length	6	-0.07	-0.62	0.41	0.48	0.68				
Leaf width	7	0.26	-0.26	0.08	0.52	0.76	0.55			
Lamina cell width	8	0.27	0.13	0.02	0.08	0.02	-0.10	0.01		
Basal cell length	9	0.16	-0.19	0.12	0.14	0.41	0.11	0.27	0.01	
Basal cell width	10	0.06	-0.20	0.23	0.23	0.25	0.09	0.22	0.20	0.26
		1	2	3	4	5	6	7	8	9	10

Table 11. First three principal components and their coefficients obtained from analysis of hair-pointed specimen data.

	Component 1	Component 2	Component 3
% Variance	42.5	23.0	14.4
Leaf profile	-0.08	-0.61	0.13
Nerve type	0.33	-0.43	0.09
Hair-point colour	-0.26	0.42	-0.36
Leaf margin	-0.41	-0.12	0.12
Leaf length	-0.45	-0.12	0.19
Hair point length	-0.39	0.18	0.24
Leaf width	-0.40	-0.19	0.24
Lamina cell width	-0.03	-0.35	-0.56
Basal cell length	-0.28	-0.18	-0.18
Basal cell width	-0.25	-0.14	-0.58

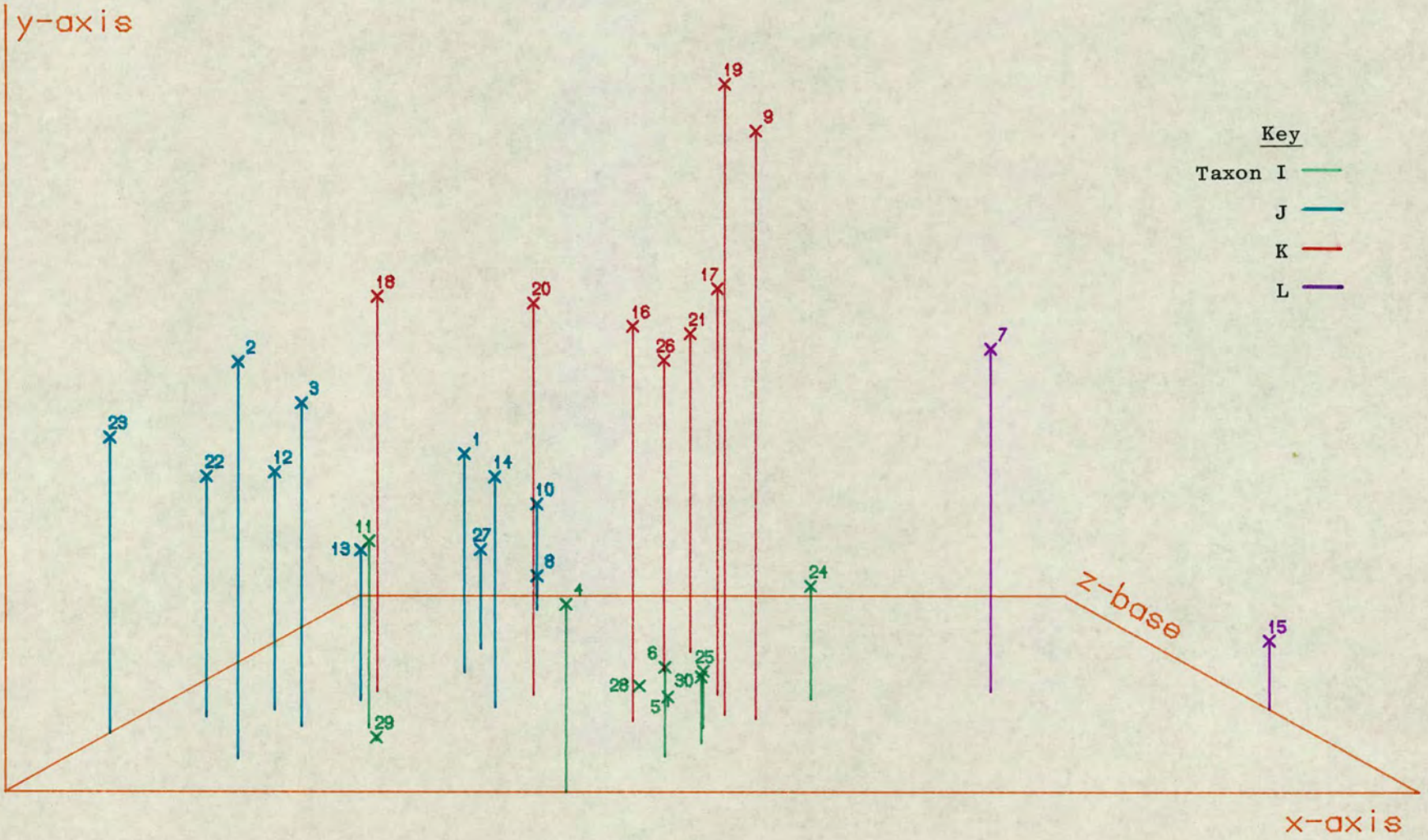


Figure 44. A three-dimensional scatter diagram showing the results of a principal components analysis on data from 30 hair-pointed Tortula specimens. Colours represent four provisional taxa. x - axis = 1st component, y - axis = 2nd component, z - base = 3rd component.

A three dimensional plot of the first three components showed some clustering of the taxa, but there was little evidence of large discontinuities between taxa I, J and K, and in particular between taxa I and J. Taxon L was too poorly represented in the analysis to allow any conclusion to be drawn, but both points did fall on the same side of the main grouping.

(b) Cluster analyses

The validity of the proposed taxa was tested using cluster analysis techniques (Mardia, Kent and Bibby 1979, Gordon 1981, Blackith and Reyment 1971). Cluster analyses are designed to find groups in the data, but as clusters can be defined in several ways, different results can be obtained. Several methods were therefore tried and compared.

(i) Methods. Similarity coefficients (Gower 1971) were used as a general measure of similarity between specimens. These were calculated between each pair of specimens for all variables and assembled into a matrix. This was used as a starting point for 5 different cluster analysis methods. These were 1) single linkage or nearest neighbour analysis (Cormack 1971, Mardia, Kent and Bibby 1979, Gordon 1981), 2) complete linkage or furthest neighbour analysis (Cormack 1971, Mardia, Kent and Bibby 1979), 3) centroid analysis (Sokal and Michener 1958, Gower 1967, Cormack 1971), 4) average linkage cluster analysis (Sokal and Michener, 1958), 5) median cluster analysis (Gower 1967).

(ii) Results. The results of the cluster analyses are given as dendrograms in Figs. 45-49.

(iii) Discussion. Single linkage cluster analysis placed all specimens in a single group at the 85% level of similarity (Fig. 45). This suggested that the groups were ill-defined, but single linkage methods are liable to merge groups if intermediates are present. This is because the similarity of any two groups is defined as the similarity of the nearest, most similar units of each group. There is little emphasis on internal cohesion of the groups which therefore tend to be straggling and amorphous.

Complete linkage analysis recognised 4 groups at the 80% level of similarity (Fig. 46) which corresponded with the proposed taxa. This method differs from single linkage analysis in that similarities of groups are defined on the maximum distance, or least similarity, between pairs of units in each group. More emphasis is placed on internal cohesion and clusters are not as likely to be grouped together.

Other methods of clustering, with properties intermediate between single linkage and complete linkage, gave similar results. Centroid analysis produced 4 groups at the 90% level of similarity but left the 2 taxon L specimens ungrouped. (Fig. 47). Two of the 4 groups corresponded with taxa I and K, and the remaining 2 were subdivisions of taxon J. Average linkage analysis recognised 3 groups and left the 2 taxon L specimens ungrouped at the 90% level of similarity (Fig. 48). The 3 groups corresponded with taxa I, J and K.

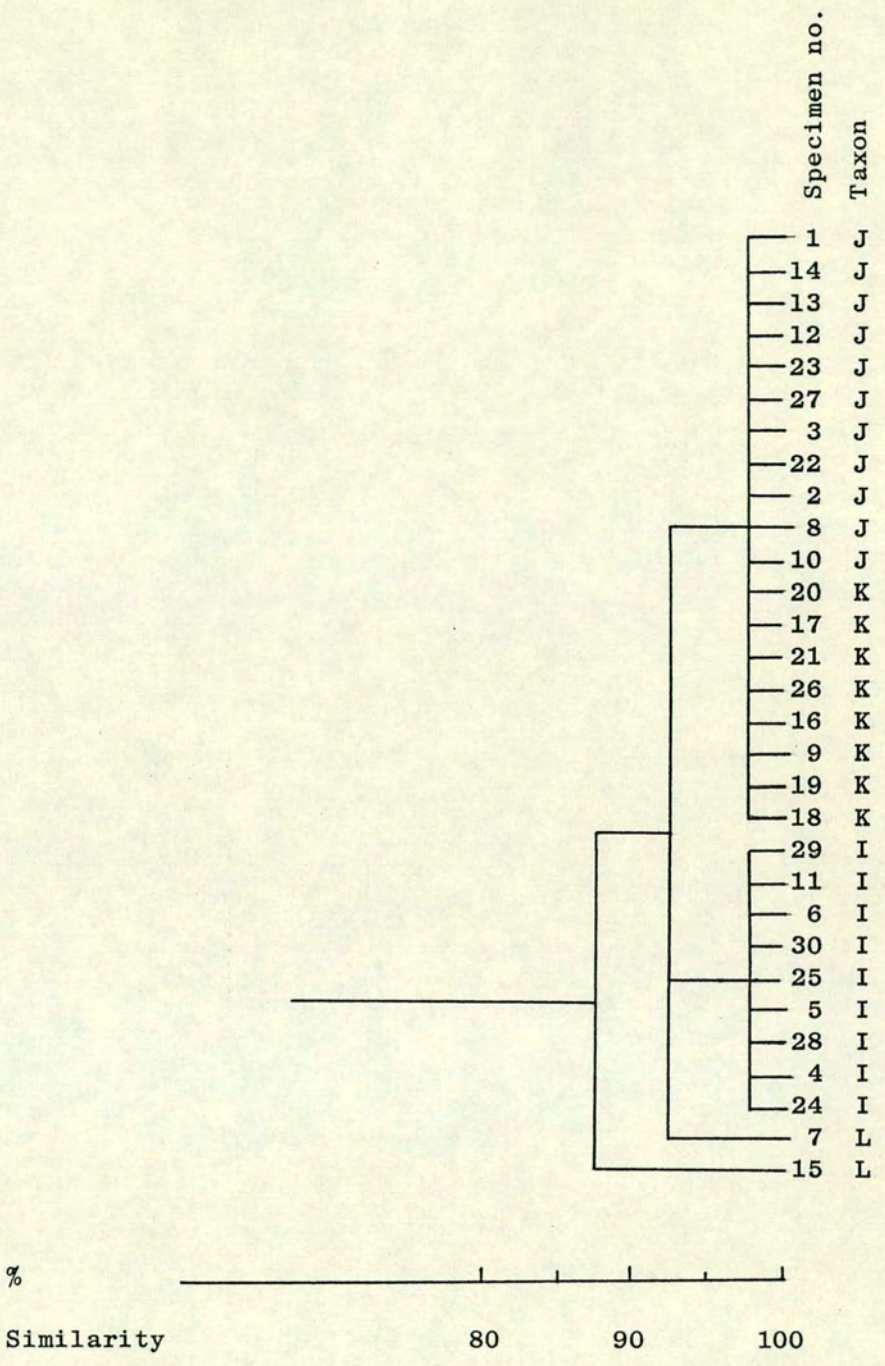


Figure 45. Dendrogram showing results of single linkage cluster analysis on 30 hair-pointed Tortula specimens.

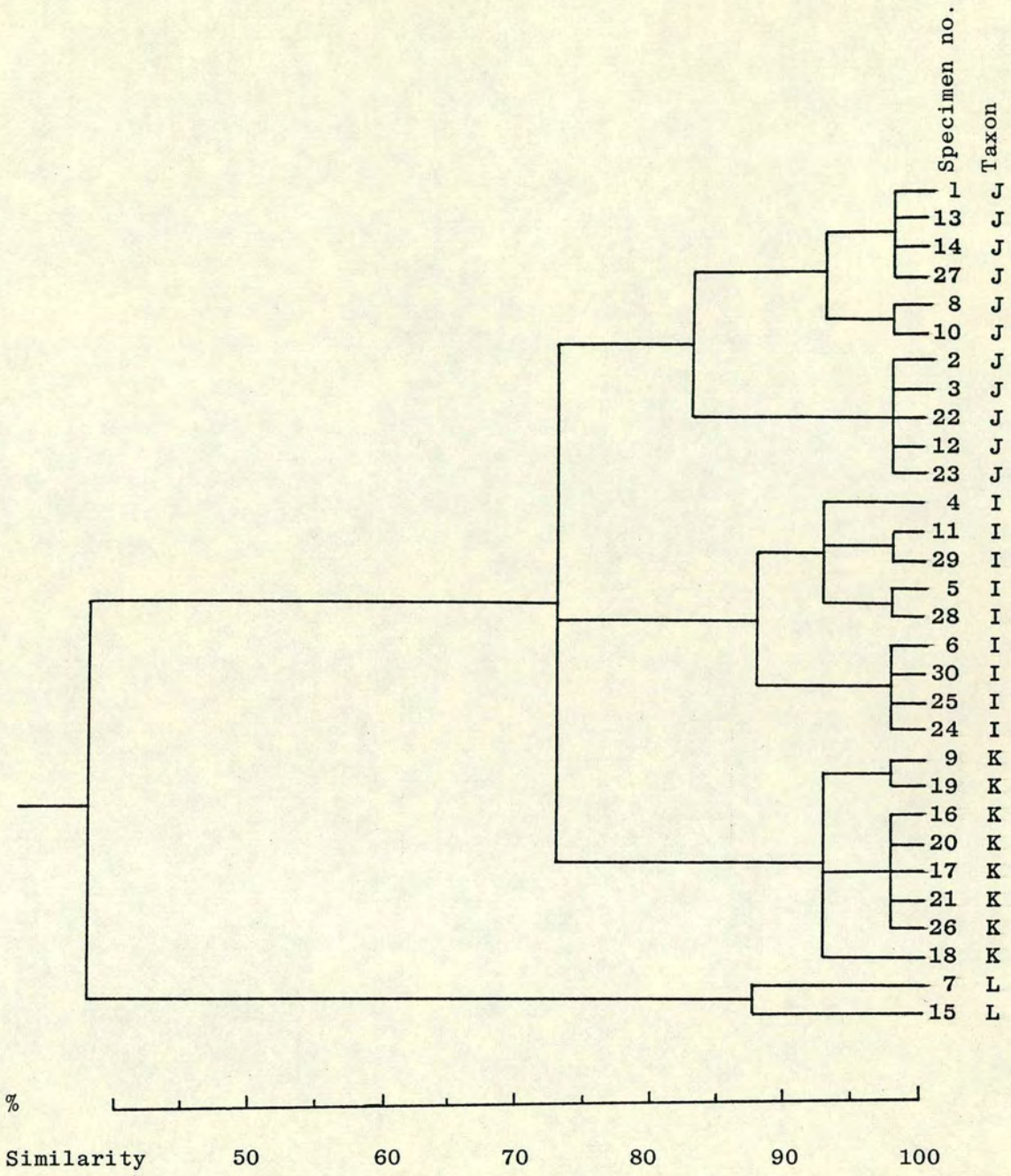


Figure 46. Dendrogram showing results of complete linkage cluster analysis on 30 hair-pointed Tortula specimens.

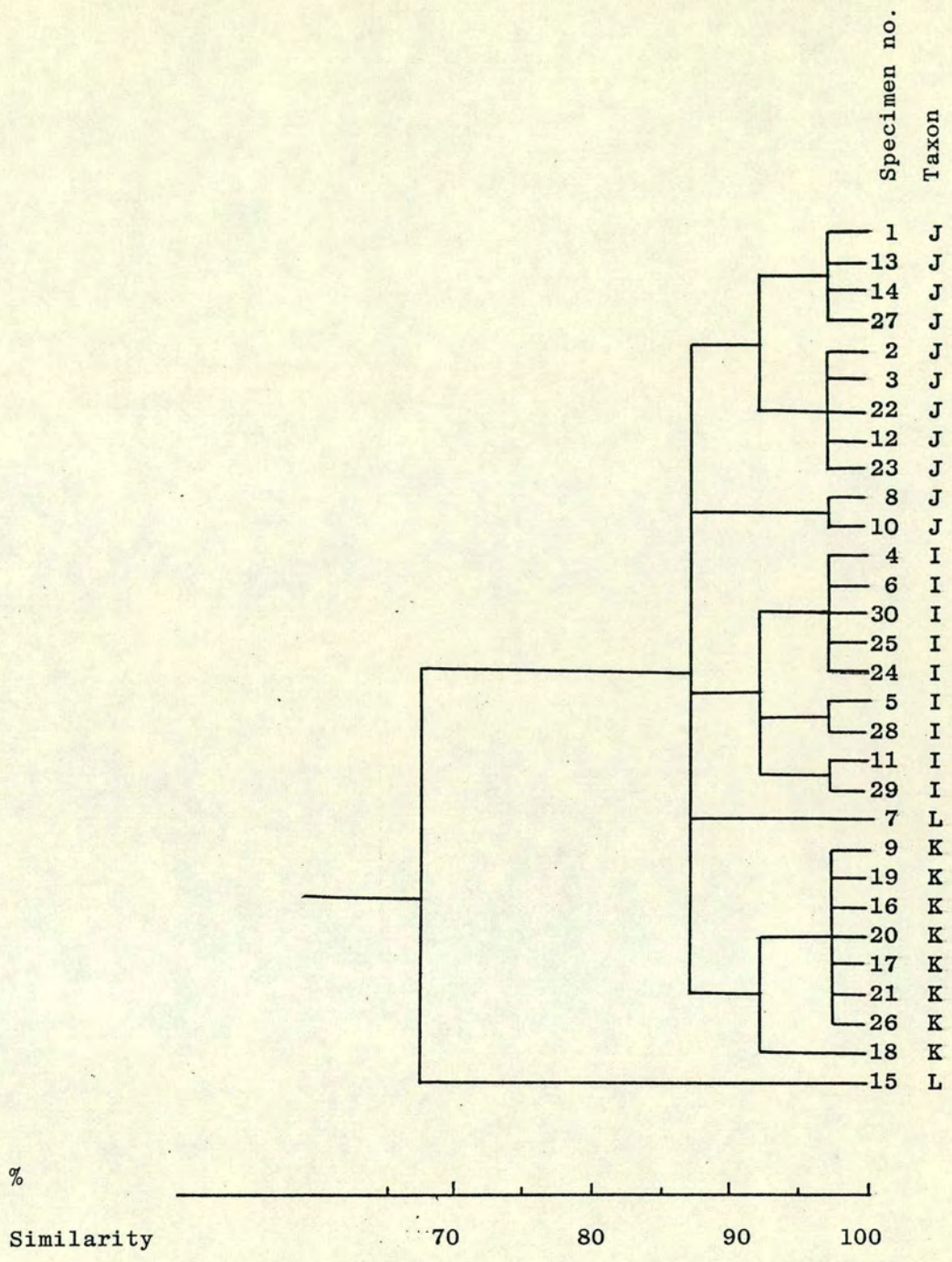


Figure 47. Dendrogram showing results of centroid cluster analysis on 30 hair-pointed Tortula specimens.

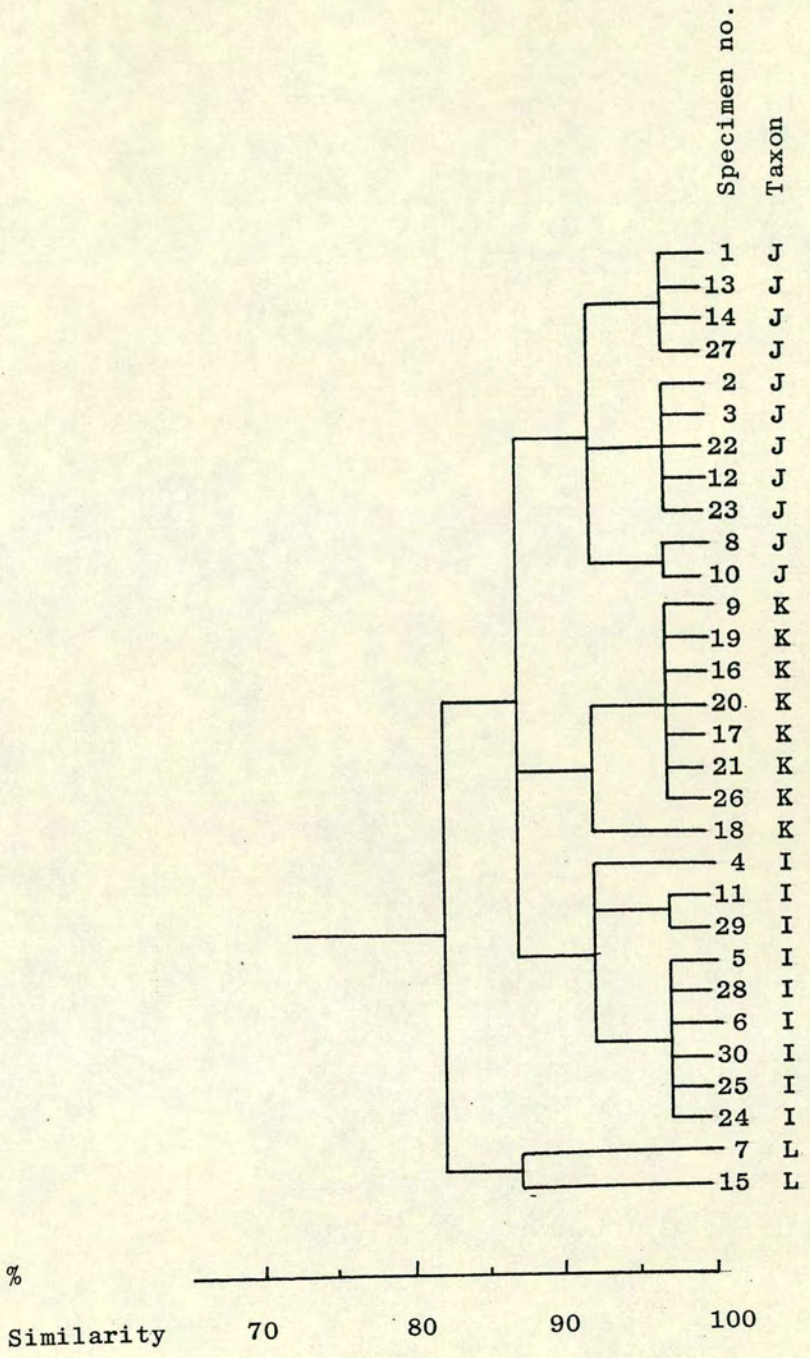


Figure 48. Dendrogram showing results of average linkage cluster analysis on 30 hair-pointed Tortula specimens.

Finally median cluster analysis found 4 groups and left 3 specimens ungrouped at the 95% level of similarity (Fig. 49). One of the groups was equivalent to taxon I, 2 were subdivisions of taxon J and the other contained all taxon K specimens except one. Both taxon L specimens were ungrouped at this level of similarity, but were grouped together at the lower level.

(c) Conclusions

The statistical analyses were successful in producing new representations of the data. Results of principal components analysis and single linkage cluster analysis emphasized the continuity present in the data, and the lack of distinct groups. The results of complete linkage, centroid, average linkage and median cluster analysis each gave some support to the recognition of the proposed taxa. Complete linkage and average linkage methods gave results which agreed most closely, and the commonest difference of the other methods was the failure to group the 2 taxon L specimens. This was not surprising as the number of specimens of this taxon in the analysis was so small. It is therefore not appropriate to draw conclusions about taxon L. However, the occurrence of intermediates between taxa I, J and K shows that they are not morphologically distinct and any taxonomic rank assigned to them should therefore be infra-specific.

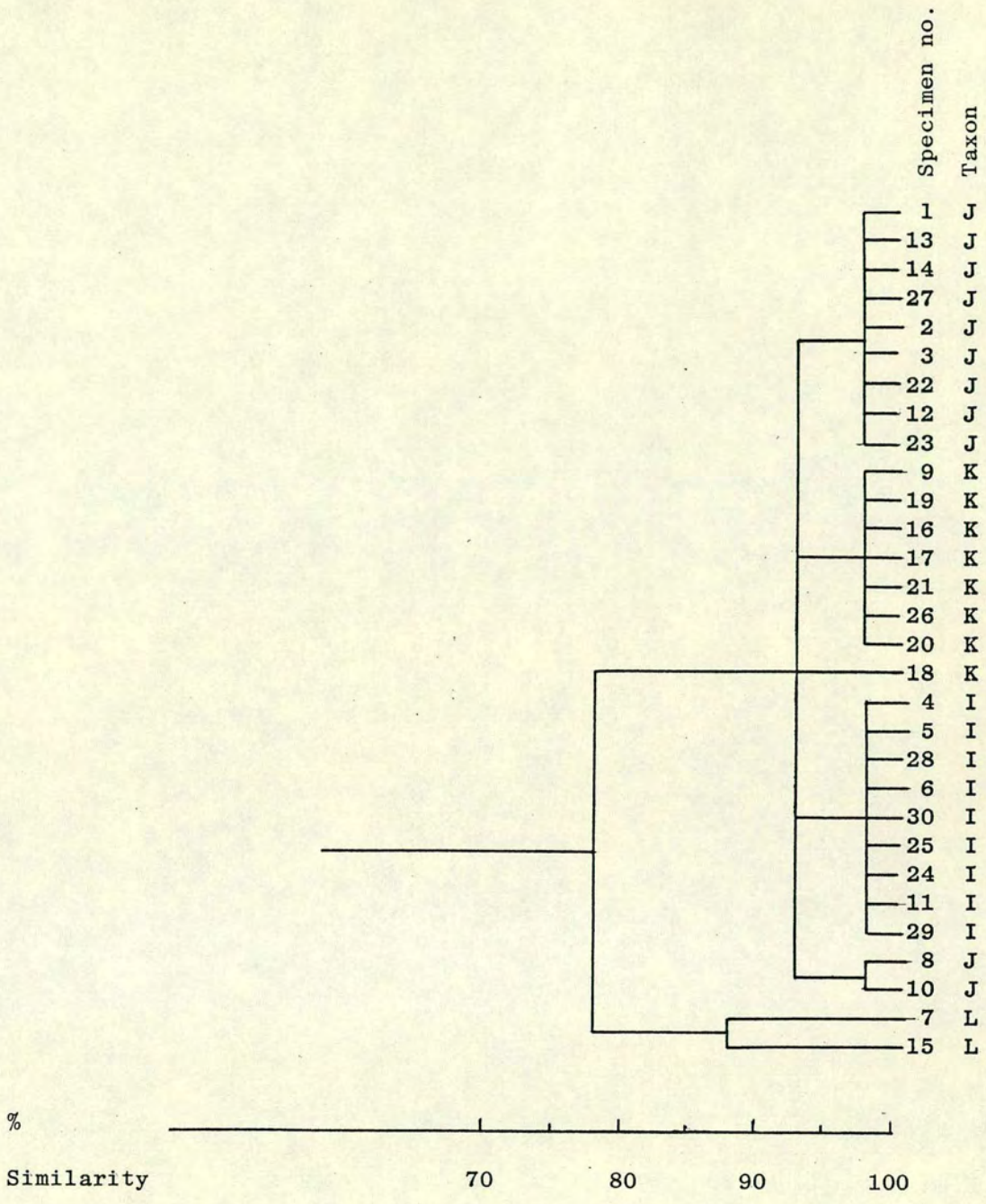


Figure 49. Dendrogram showing results of median cluster analysis on 30 hair-pointed Tortula specimens.

Chapter 4 : CULTIVATION

4.1 Introduction

Following herbarium study, uncertainties remained in the status of the non-hair-pointed taxon E and the hair-pointed taxa I, J, K and L. These taxa were investigated by a series of growth experiments.

The experimental cultivation of bryophytes for taxonomic purposes is a relatively new technique but similar studies on higher plants are numerous. Allen (1966) for example, lists some 320 publications in which about 70 British infraspecific taxa are reported to have been tested in cultivation. Understanding of vascular plant culture is such that cultivation is rarely troublesome. With bryophytes however this knowledge is lacking and the failure of many authors to give full details of their methods has not helped.

In bryophytes, as with angiosperms, different types of study can be attempted, from simple observation of transplants to more detailed biometric analyses of plants grown in artificially controlled environments. One important difference is that angiosperms may be cultivated from seeds, but bryophyte experiments have not been attempted using material produced from spores. Angiosperm systematists tend to favour seed-grown material since environmental influences are less likely to be transmitted to the plants. This may also be true for bryophytes grown from spores. The use of spores has been

discouraged by the difficulty of obtaining them and by problems of germination and subsequent development which can be very time consuming.

The difficulties of experimenting with bryophyte growth are greater for the systematist than for those working on other types of problem. Plants may be required to produce considerable new growth under a range of different conditions. This involves a different level of competence in cultivation than, for example, maintaining material in a viable condition, until a physiological experiment can proceed.

Basic work on bryophyte culture has been done by Richards (1947) and Fletcher (1978) who have grown many species in glasshouses or cold frames. Fletcher (1978) pointed out that the substrate pH and watering programme are particularly important factors. It is clear from both studies that the key to success in many species is the imitation of the plant's natural habitat. An understanding of the range of conditions tolerated is thus important, particularly as more specialised experiments can involve growing plants in more than one environment.

Useful taxonomic results were obtained by Crundwell (1956) using the simplest of cultivation techniques. Two taxonomic varieties of Tortula subulata Hedw. were grown together on an unspecified medium in a glasshouse. Unfortunately no further details of the growth conditions are given, but the two taxa remained distinct, adding further weight to their separate taxonomic status.

Another early example of growth work is much more detailed and quantitative. Lodge (1959, 1960a and b) grew two species of Drepanocladus under aquatic and terrestrial conditions, in media of different solute concentrations and in different light intensities. Samples were grown for about 2½ years in an unheated glasshouse and were given nutrient solution as required. He was able to show that there were differences in morphology due to the different environments and also that important taxonomic characters such as the type of angular cells, remained constant. Briggs (1965) cultivated four British species of Dicranum and showed that they remained distinct in cold frame conditions. Considerable infra-specific variation was noted however, some of which affected taxonomic characters such as leaf undulation.

Corley (1976) found that five species of Campylopus grown in a glasshouse on peat for 2-3 years remained distinct. Variation within each species was considerably reduced and all species had a tendency to show certain characters more strongly in culture than in natural conditions.

Many taxonomists have used more controlled environments for growth experiments. Crundwell and Nyholm (1964) grew gemmiparous Bryum species on a nutrient agar medium in constant but unspecified light and temperature conditions. Problems relating to the identification of gemmae were solved and the distinct nature of the species verified. A similar but more detailed study by Lewis and Smith (1977) on bulbiliferous Pohlia species produced results which necessitated changes in

the classification of British species. Bulbil morphology was confirmed as a valuable taxonomic character, although in some species the morphology of the bulbils varied a lot with age. The species also differed in the amount of environmental and genetically induced variation they showed for this character.

Hatcher (1967) and Steel (1978) succeeded in cultivating Lophocolea species on several agar media and in different light intensities. Hatcher (1967) grew clones of L. heterophylla (Schrad.) Dum. and concluded that although environmental factors accounted for a large part of the variation observed in the field, distinct genetic races could be identified. Steel (1978) found that the two morphologically similar species, L. bidentata (L.) Dum. and L. cuspidata (Nees) Limpr., remained distinct in several controlled environments differing in pH and light intensity. Cultivated plants of both species overlapped in all characters examined. For some characters however, this overlap was relatively small and these could still be used to separate the species.

Wigh (1975a) cultivated Brachythecium rutabulum (Hedw.) B.S.G. and B. rivulare B.S.G. under various conditions of temperature, light and humidity. He observed the constancy or variability of taxonomic characters in different environments, and recorded the effects of environment on the morphology of both species. The most reliable means of separating the species was also determined.

Most cultivation studies have used species whose taxonomy is

already relatively well known, usually from Europe or North America. Florschutz-de-Waard and Worrel Schets (1980) however have experimented with South American Campylopus species, using techniques described by Schelpe (1953). They showed that differences in costal anatomy between two of the species were environmental and not genetic in origin. In other species the costal anatomy was stable and probably genetically controlled.

Growth experiments with bryophytes have therefore been successful in their principal aim of investigating the effects of the environment on taxonomic characters. They range in complexity from those using uncontrolled environments such as a glasshouse to those using several sets of controlled conditions produced in growth cabinets. The methods of evaluation of the results also differ, with the simplest relying entirely on observation by the taxonomist. Such studies are qualitative and are not supported by measurements. In this respect their results are similar to those of a classical systematic investigation and indeed, may be incorporated with them (e.g. Crundwell and Nyholm 1964). At the other extreme data may be gathered on the plants before and after cultivation and analysed statistically. This involves more work but it produces quantitative results which can easily be compared or verified. It was determined to adopt the latter method for growth experiments on species of Tortula from South Georgia.

4.2 Source of living material

In September 1978, at the start of this study, some material

was already in cultivation, having been collected on South Georgia during the austral summer of 1976-77. This had been transported to Britain in cool storage under artificial lighting. The total transit time was about 15 weeks, during which the specimens were watered but received no other attention. They arrived in Britain during May 1977 and had thus been in cultivation for about 16 months in September 1978. Further collections of living material were made in 1978-79 and 1980-81. These were also transported in cool storage, and arrived in Britain in May 1979 and May 1981 respectively. Some specimens were in poor condition on arrival, especially if they had been waterlogged. These were green in appearance but lacked vigour and did not produce new growth for several months. These specimens eventually improved sufficiently to be used in growth experiments.

Living material from a collection made in 1971-72 was also available in frozen storage. On defrosting, this material appeared brown and dead but green buds were later produced in leaf axils. After about one year some specimens were in a sufficiently good condition to be used for experiments. Many specimens had apparently been frozen in a wet state, which is known to be more damaging to bryophytes than dry freezing (Collins and McManmon, personal communication). Although potentially useful, freezing was not used further as a method of storage for transport of material from South Georgia because of the long recovery period needed.

All material arriving in Britain, or removed from frozen

storage, was numbered and a sample was taken and dried for later comparison.

4.3 Culture methods

Material transported in cool storage or defrosted needed to be maintained and some specimens had to be returned to a healthy condition before growth experiments could begin. Facilities for maintaining stock were thus necessary. Details of the equipment and methods used are given below.

4.3.1 Cold frame and growth bench

Living material was maintained in a cold frame or on an air-conditioned growth bench.

The cold frames were provided with an automatic mist system which supplied water from May to October. During winter months the plants were watered by watering can, because the pipes of the automatic system had to be drained to prevent damage by frost. From May to October protection from summer sunshine was given by white emulsion paint applied to the glass frames.

The growth bench facilities are illustrated in Fig. 50. An air conditioning unit maintained temperatures between 0-15^{o}C. Natural light was provided by north facing windows along the length of the bench and this was supplemented with six 180W sodium lamps for twelve hours per day. Values of total usable photosynthetic light at plant level were about 150 $\mu E\ m^{-2}\ s^{-1}$ on an overcast day. An automatic watering system was fitted which consisted of four mist units each independently operated

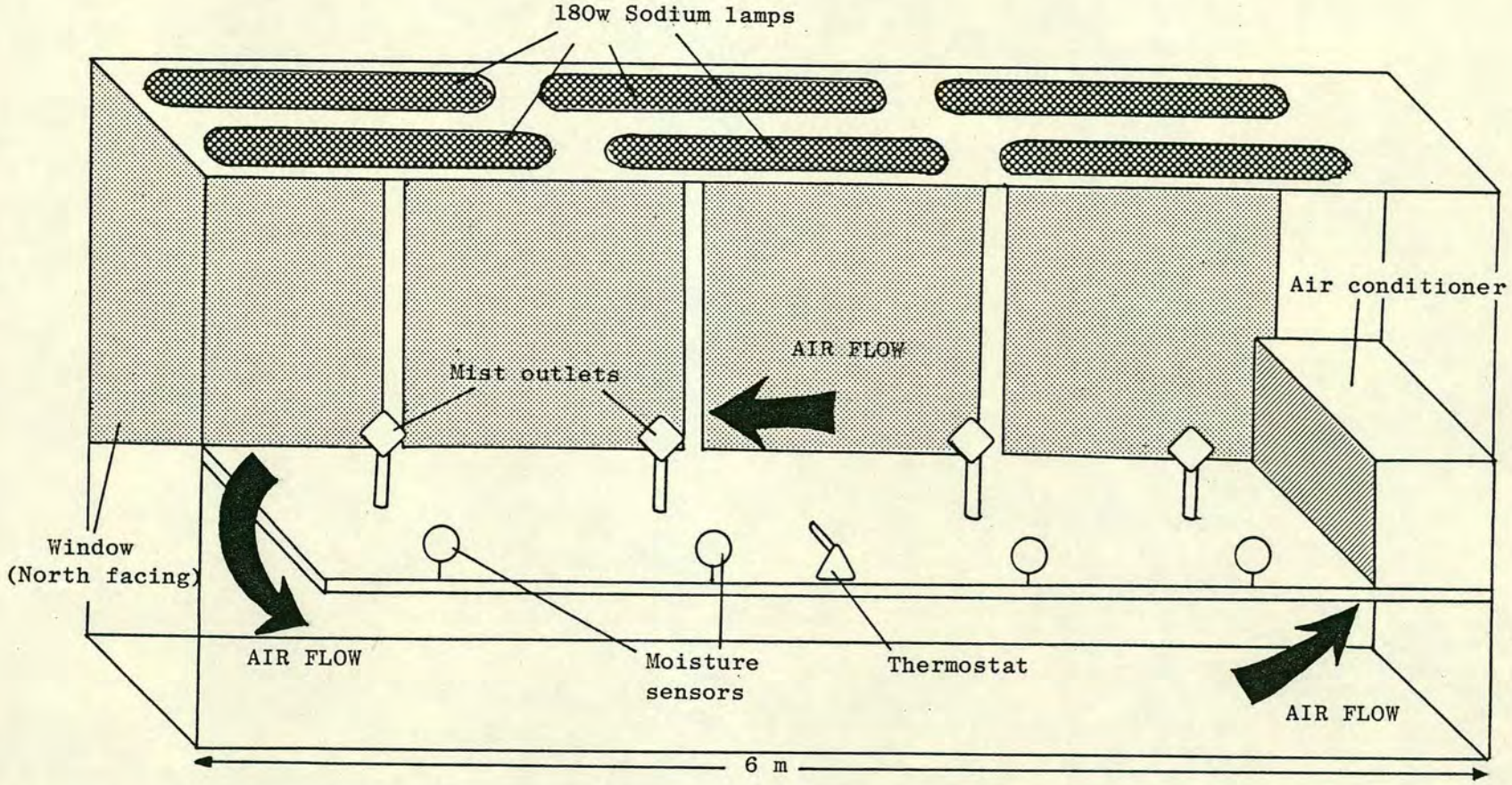


Figure 50. An air-conditioned growth bench used for growing bryophytes. The bench is enclosed in a polythene tunnel to maintain high humidity. Lighting and watering are controlled by time switches.

by mechanical balance switches or electronic moisture sensors. A time clock was also incorporated so that watering only occurred at predetermined periods during the day. The bench was surrounded in polythene sheet and air was recirculated under the bench to the air conditioner. This was designed to maintain a high humidity around the plants. Actual measurements of relative humidity made with a hair hygrometer gave values between 70-100%.

4.3.2 Pots and substrates

Plastic plant pots of various sizes were used. These were large enough to allow the plants to be situated below the rim of the pot, giving protection from drying air currents. Some specimens arrived with sufficient substrate to be put in pots using no additional compost. Those attached to lumps of peaty soil for example could simply be placed in pots filled with sufficient free draining crushed quartz gravel to obtain a suitable level in the pot. Usually a substrate was needed and sphagnum peat, crushed quartz and a 1:1 mixture of the two were tried initially since most South Georgian rocks and soils are acidic or base poor (Greene 1964b). These media worked well for genera such as Polytrichum, Drepanocladus, Pohlia and Dicranella but all three gave poor results with Tortula. Species varied in their reactions to these acidic substrates. One non-hair-pointed Tortula taxon survived relatively well on peat but hair-pointed specimens died within a few months.

Moore and Scott (1979) grew Australian T. princeps De Not. (a hair-pointed species) on beach sand, which is a relatively base rich medium. South Georgian Tortula species were found to grow well on this substrate and publications by R.I.L. Smith (1972, 1981) confirmed that Tortula species grow in base-rich habitats on South Georgia and in the Antarctic. These include base rich peat, on basic rock and amongst shell debris near the sea. All Tortula specimens in cultivation also grew well on enriched sedge peat and on loam.

4.3.3. Drainage, watering and humidity

In addition to pH, drainage properties of the substrate also affected the growth of Tortula specimens. The optimum drainage depended upon the watering regime. If watered only occasionally a poorly drained water retaining soil was advantageous, but plants became water logged if the watering was increased. Excess water appeared to be harmful to some Tortula species, particularly those with hair-points. Growth was slow and algae and fungi invaded the cultures. Dilks and Proctor (1979) showed that photosynthetic rate in some mosses of dry habitats, including a hair-pointed species of Tortula, declined at high water contents. It is possible that the poor growth rates observed were due to this effect.

Tortula specimens thrived on well drained substrates such as beach sand when well watered. Heavy watering could result in leaching however, and if continually wet, specimens appeared to loose their cushion or turf growth form and produced stems of many different heights. Care was taken therefore not to

water too heavily. Moderately well drained media such as sedge peat and beach sand mixtures were used and the watering adjusted as necessary.

Specimens were watered only from above with a fine spray of tap water. Watering from below by standing the pots in water was found to be deleterious. The upper parts of tall stems tended to dry out and the combination of wet substrate and dry air which resulted from this method of watering caused a whitish deposit to appear on the tips of the leaves. This was probably the result of the plants acting as wicks, drawing up water from the substrate which then evaporated, leaving dissolved substances on the most exposed parts of the leaf. Watering from above with a fine spray tended to wash away these encrustations and to increase the humidity around the plants. This seemed to be beneficial and good results were achieved by keeping the substrate moist and the humidity constantly high.

A humid environment could be maintained around specimens on the growth bench by frequent spraying from the misting system. Polythene collars held around the rims of pots with rubber bands were used to protect specimens from drying air currents. This was better than reducing the soil level in the pot because it allowed more light to reach the specimen.

In conditions where the humidity dropped at weekends in the summer months, plants grew less well than those in permanently moist atmospheres, even though only slight desiccation occurred. Similarly when the plants dried out every two or three days

little or no new growth was produced. During dry summer weather it was impractical to keep material moist in the cold frames because of high temperatures and high evaporation rates. Plants were therefore allowed to dry out and were remoistened in wet humid weather. These occasional dry spells seemed to have no harmful effects even when they lasted for 1 or 2 months. They may even have had beneficial effects such as discouraging less drought tolerant contaminents, especially algae and fungi, and helping to maintain a compact growth form. Prolonged desiccation however caused death of the lower leaves and stems so that only the stem apices recovered their green appearance on remoistening.

4.3.4. Nutrients

Plants survived on the same substrate throughout the period of study without the use of fertilizers or nutrient solutions. Repotting was rarely necessary and then only to give established colonies room to expand horizontally or vertically. Although otherwise healthy, older cultures often appeared yellowish. This was believed to be due to a nutrient deficiency since shoot tips of yellowish plants, when removed and placed on a fresh substrate, produced new growth of a normal bright green colour. Longton and Greene (1979) found that nutrient deficiency in Pleurozium schreberi (Brid.) Mitt. caused shoots to become yellow from the base upwards and eventually to die. The symptoms in this study were apparently not so severe, perhaps because of the mineral content of the tap water or a greater ability of Tortula plants to absorb minerals from

the substrate. Knop's solution was used at one tenth, one half and full strength on several yellowing cultures but no improvement in colour or vigour was noted. Experiments did show that the deficient factor could be obtained from the substrate since top dressing with mixtures of beach sand, sterilised loam and sedge peat, passed through a 1 mm^2 sieve, restored the colour to old cultures. This dressing was given in sufficient quantities to cover dead lower parts of stems and was applied when the plants were dry to prevent clogging the leaves with particles.

4.3.5 Propagation

New cultures were initiated by vegetative propagation from excised leaves, stem fragments or shoot tips. At first these were placed on sterilised filter paper moistened with nutrient solution. Regeneration occurred most rapidly from stem apices which produced new growth from the apical meristem. Stem fragments produced lateral buds with little proliferation of rhizoids (Figs 51 and 52). Leaf fragments however first developed rhizoid networks from the leaf base (Figs 53 and 54) and buds were then formed either at the leaf base (Fig. 55) or some distance away from the leaf on rhizoids (Fig. 56). Later experiments showed that regeneration was equally satisfactory on a sedge peat and beach sand compost. Care was taken to keep the developing stems permanently moist but no other special treatment was necessary.

No South Georgian or Antarctic specimens produced sporophytes in cultivation so that propagation by spores could not be

Figure 51 A stem fragment of a hair-pointed Tortula specimen regenerating by lateral buds on moist filter paper. Magnification x 24.

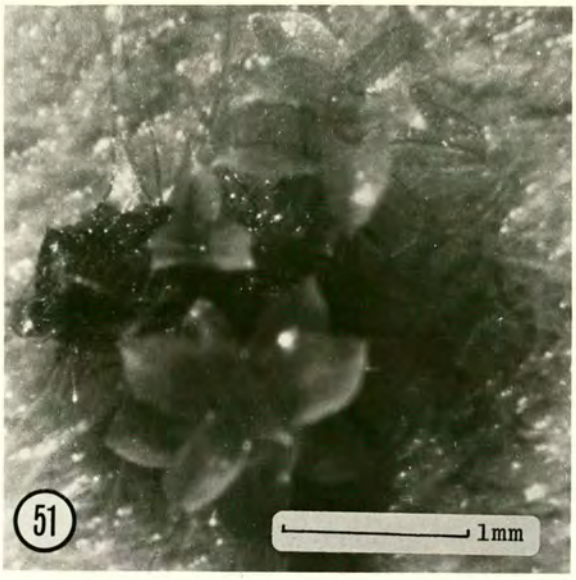
Figure 52 As above.

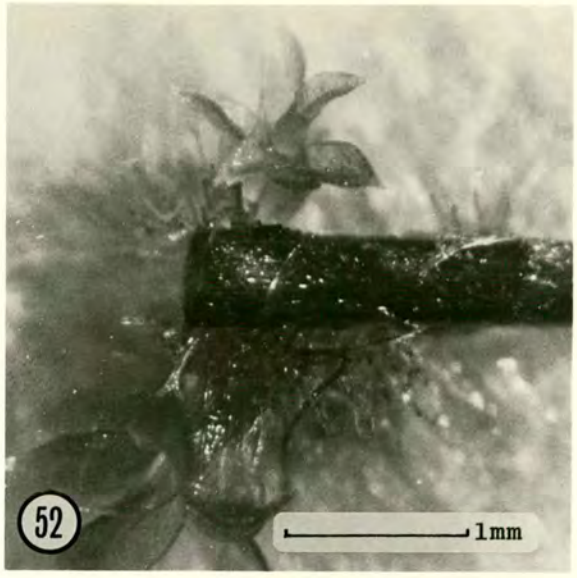
Figure 53 A leaf of a hair-pointed Tortula specimen regenerating on moist filter paper showing extensive production of rhizoids. Magnification x 24.

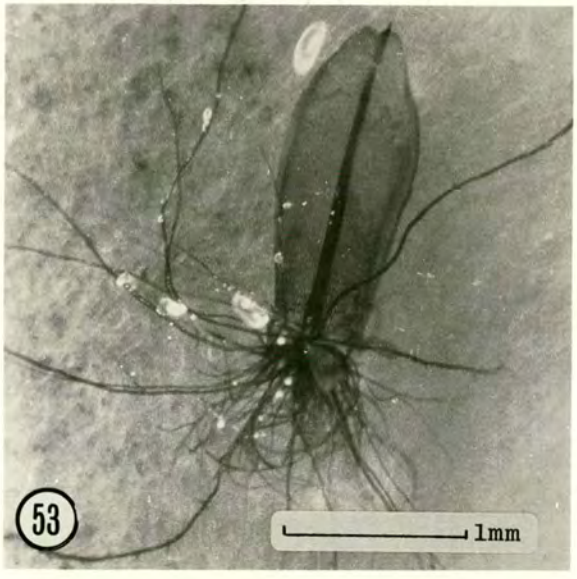
Figure 54 As above.

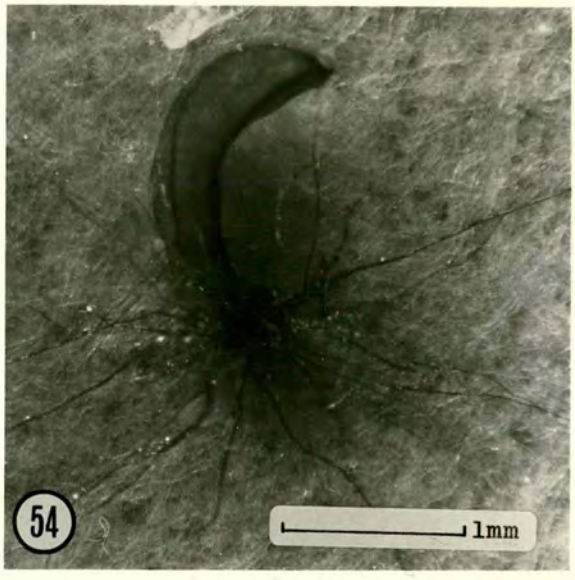
Figure 55 Two juvenile shoots and rhizoids produced at the base of a regenerating hair-pointed Tortula leaf on moist filter paper. Magnification x 50.

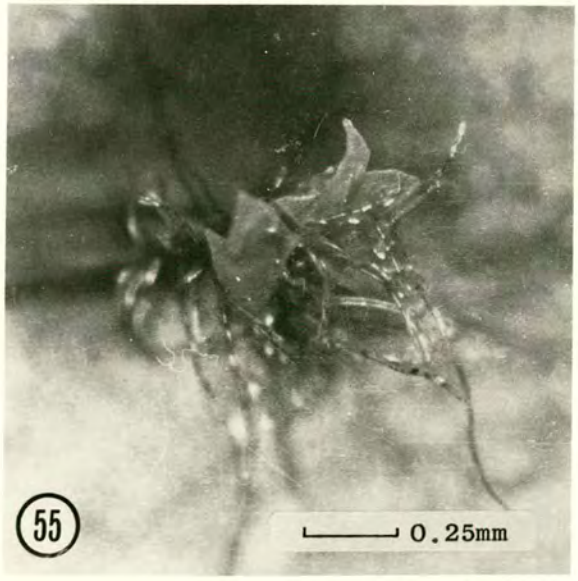
Figure 56 Juvenile shoots produced on rhizoids of a regenerating hair-pointed Tortula leaf on moist filter paper. Magnification x 24.

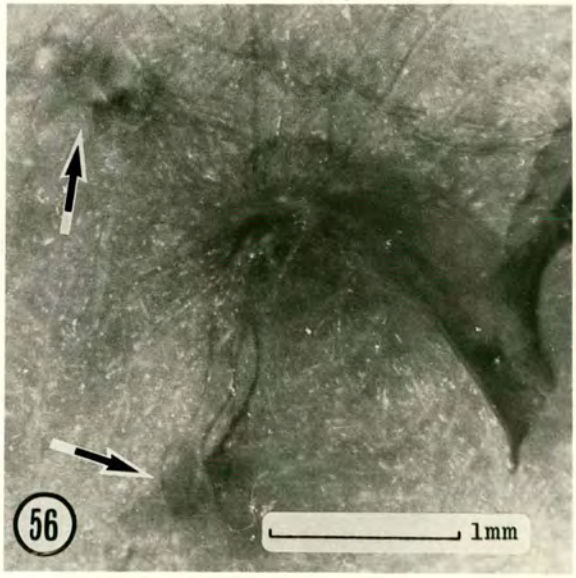

51
1mm


52
1mm


53
1mm


54
1mm


55
0.25mm


56
1mm

attempted.

4.3.6 Weeds and pests

Several weedy species of moss were often found in cultures. These included Funaria hygrometrica Hedw., Leptobryum pyriforme (Hedw.) Wils., Ceratodon purpureus (Hedw.) Brid., Pohlia spp. and Brachythecium spp. Weeding was carried out regularly using fine forceps and weeds were thus prevented from overgrowing cultures. Invasion by weed species had a harmful effect on new cultures initiated from stem fragments. In weed free conditions new shoots were produced from lateral buds and secondary shoots developed about 0.5 - 2 cm from the parent stem. These were probably produced from rhizoids like those seen in Fig. 56, and eventually covered much of the substrate surface. In cultures containing weeds these secondary shoots either did not develop or were restricted. This may have been due to an inhibitory effect similar to that observed by B.G. Bell and T.D. Murray (personal communication) between protonemata of different species growing together on agar in a petri-dish.

Animal pests were also troublesome, particularly crane fly larvae (Tipula spp.). These destroyed large areas of stems in late summer or early autumn. Attacks were successfully treated by drenching the substrate with commercial malathion liquid used at half the recommended strength (Liquid Malathion produced by Murphy's Chemical Ltd., used at 1 ml in 1 litre of water). This apparently had no harmful effects on the

plants. Some unidentified acarine mites were also found eating the growing points of hair-pointed Tortula shoots. These usually appeared soon after transport from South Georgia, and having been observed in herbarium specimens from the Island, probably originated from there. They were eradicated by treatment with the malathion solution applied in a spray.

4.4 Experimental techniques

4.4.1 Growth cabinets

Experiments were carried out under controlled conditions of temperature and lighting provided by controlled environment cabinets (Fig. 57). These were custom built perspex chambers 1.2 m long, 0.65 m wide and 0.6 m high. Each contained a 1/3 h.p. cooling system capable of producing temperatures as low as $5^{o}C$ controlled to within $\pm$ $1.5^{o}C$. Lighting was provided by 18 40W fluorescent tubes which gave usuable photosynthetic light values of between 50 - 130 $\mu E\ m^{-2}s^{-1}$. Lighting and refrigeration were controlled by time clocks which allowed a variable day/night regime with pre-set day and night temperatures. The floor of each cabinet was lined with capillary matting which was kept moist to maintain a high relative humidity. Air within the chamber was also kept circulating by a small electric fan.

4.4.2 Culture methods

Tortula specimens could be kept healthy and growing in growth

Figure 57. A controlled environment growth cabinet incorporating a refrigeration system and 18 40W fluorescent lamps.

cabinet conditions if placed inside a plastic propagating tray lined with wet gravel. This gave protection from currents of dry refrigerated air. Experimental cultures were established in 4 cm pots which were placed on a fine plastic grid overlying the wet gravel. This prevented water seeping into the pots from below and upsetting the watering regime of the experiment.

Beach sand or a 50% sand, 50% sedge peat mixture was used as a substrate. This was prepared by passing the materials through a 1 mm^2 sieve and then sterilising them in an autoclave for 30 minutes. Clean 4 cm pots were sterilised by soaking in strong hypochlorite solution and rinsed in sterile water. These were filled to about 1 cm below the rim with the sterile substrate.

Each culture was started with one or two 1 cm long shoots with the stem apices removed. These were washed in a jet of tap water and rinsed in sterile distilled water before planting to reduce the risk of contaminating the cultures. Plants were watered from above with sterile distilled water from a hand operated spray bottle. This was necessary about 3 times per week.

4.4.3 Results

The stems produced new shoots which were about 0.5 cm high after 6 months and continued to grow for at least 2 years. All new growth was axillary and could thus be distinguished from the original parent stem.

The sterilisation procedures used were moderately successful in preventing weeds from developing in the cultures. Control pots containing only sterile substrate were never infected, but pots containing Tortula fragments sometimes were. This contamination probably arose from spores or fragments on the parent stems. Unfortunately surface sterilisation techniques attempted were either too severe and killed the moss shoot, or else were ineffective in stopping infection.

Details of cultivation experiments are given in the following chapter.

Chapter 5 : COMPARISON OF GROWTH IN CONTROLLED CONDITIONS

Although herbarium studies had shown some Tortula taxa were taxonomically distinct, all of those represented in the collection of living material were grown in the controlled environments of growth cabinets. The new shoots produced were examined and compared with 'initial exsiccates' made when the material first arrived in Britain. Any differences in taxonomic characters were noted.

In the following account non-hair-pointed and hair-pointed groups are considered separately. In the non-hair-pointed group, results from taxa D, E and F were of particular interest as measurements of herbarium material had shown that they could be difficult to distinguish. In the hair-pointed group the status of all taxa was in need of investigation by growth experiments because statistical analysis suggested that they intergraded.

5.1 Method: non-hair-pointed group

Material of taxa C, D, E, F and G was grown in a single environment for 12 months. Two growth cabinets were used, both providing a constant day and night temperature of 10°C with a day length of 18 hours. Cultures were initiated in 4 cm pots using stems with apices removed. Full details of culture methods are given in the previous chapter (section 4.4). Information on specimens including the number of pots established is given in Table 12.

New shoots were produced and many reached 1 cm in height after 6 months. Several larger stems were removed from

Table 12 Non-hair-pointed specimens used in collateral cultivation experiment.

Specimen No.	Determination	Origin of Specimen	No. of pots established.
Control	-	-	24
TS9A	taxon E	Junction Valley South Georgia Leg R.I.L. Smith 1980/81	48
TS9B	taxon D	"	48
TS18B	taxon C	Horse Head, South Georgia Leg R.I.L. Smith 1980/81	48
CM159	taxon F	South Georgia Leg R.I.L. Smith 1976/77	48
TS4	taxon F	Burnet Cove South Georgia Leg R.I.L. Smith 1980/81	24
CM276	taxon G	South Georgia leg D. Walton 1978/79	48

each pot for examination after 6 months of cultivation and again after 1 year. These were compared with 'initial exsiccates' made when the material first arrived in Britain, and with herbarium material determined earlier in this study (Chapter 3).

An initial examination of the cultivated stems suggested that each taxon remained distinct in cultivation. Taxon C maintained its characteristic features such as the lack of teeth on the upper leaf margin and the pattern of areolation at the leaf apex. Differences in leaf size, leaf shape and cell width were also maintained between taxa D, E, F and G. Measurements of these characters were made to quantify the observed differences.

For each specimen 5 stems were taken at random from each of the three groups of plants to be compared, ie:

i) the 'initial exsiccate' made when the material first arrived in Britain.

ii) the growth after 6 months.

iii) the growth after 1 year.

On each stem the length and maximum width of 5 leaves were measured and the widths of 2 lamina cells in each leaf were also recorded.

5.2 Results: non-hair-pointed group

Measurements made on the experimental material of taxa D, E, F and G were compared with measurements of herbarium specimens

in scatter diagrams (Figs. 58 to 67). A comparison of data from all experimental specimens was also made after 6 month's growth and after 1 year's growth (Figs. 68 to 71). Overall mean data are given in Table 13.

Data from herbarium specimens and living material before and after cultivation have been compared for each taxon in Tables 14 to 18. Comparisons have also been made between different taxa grown in the same conditions.

5.3 Discussion: non-hair-pointed group

5.3.1. Taxon D. After 6 months in cultivation there was little difference between measurements of cultivated stems and the 'initial exsiccate' of taxon D (Table 14, Fig. 58). After 1 year, both leaf length and leaf width were reduced although leaf width/length ratios and cell width stayed the same (Table 14, Fig. 59).

The measurements of cultivated specimens suggested that confusion was only likely with taxon E (Figs. 68, 69, 70 and 71). Taxon D was characterised mainly by its high leaf width/length ratio but lower values were similar to those of taxon E. It was found, however, that taxa D and E could be separated after cultivation by their different leaf shape and leaf stance. Taxon D had pandurate, erecto-patent leaves and taxon E had oblong, patent leaves with recurved tips. Taxon D was therefore distinct in cultivation.

5.3.2. Taxon E. The leaf width of the 'initial exsiccate'

Table 13. Mean measurements of specimens of taxa D, E, F and G after arrival from South Georgia ('initial exsiccates') and after growth under controlled conditions for 6 months and 1 year. Leaf measurements are means of 25 values and cell measurements are means of 50 values.

	Taxon D (TS9B)			Taxon E (TS9A)			Taxon F (CM159)			Taxon F (TS4)			Taxon G (CM276)		
	Initial exsiccate	6 months growth	1 years growth	Initial exsiccate	6 months growth	1 years growth	Initial exsiccate	6 months growth	1 years growth	Initial exsiccate	6 months growth	1 years growth	Initial exsiccate	6 months growth	1 years growth
Leaf length (mm)	4.50	4.55	3.08	4.23	3.96	3.53	7.41	5.43	4.38	4.49	4.94	4.11	3.60	3.92	3.24
Leaf width (mm)	1.53	1.49	1.11	1.59	1.20	1.01	1.69	1.35	1.00	1.11	1.20	1.00	0.97	0.75	0.67
Cell width (μ)	18.18	17.66	17.54	16.03	16.08	15.70	18.46	17.05	16.31	14.10	15.86	15.43	12.86	12.02	12.15
Leaf width/ Length ratio	0.340	0.329	0.373	0.378	0.303	0.291	0.229	0.251	0.229	0.250	0.244	0.243	0.270	0.202	0.209

Table 14. Taxon D: Summary of comparisons between data gathered from herbarium specimens and living material (TS9B) before and after cultivation. Comparison is also made with data from different taxa grown in the same environment.

Comparisons between taxon D material from various sources	Character: Leaf length	Leaf width	Leaf width/ Length ratio	Cell width
Measurements of initial exsiccate relative to range of herbarium specimens	similar	at lower limit of range	at lower limit of range	similar
Measurements of 6 month old stems grown in experiment relative to initial exsiccate.	similar	similar	similar	similar
Measurements of 1 year old stems grown in experiment relative to initial exsiccate.	lower	lower	similar	similar
Comparison with material of other taxa grown in same experimental conditions				
6 months old stems	similar to taxa E & F	Larger than other taxa but close to taxa E & F	Larger than other taxa but close to taxon E	Similar to taxa E & F
1 year old stems	similar to taxa E, F & G	similar to taxa E & F	Larger than other taxa but close to taxon E.	Similar to taxa E & F.

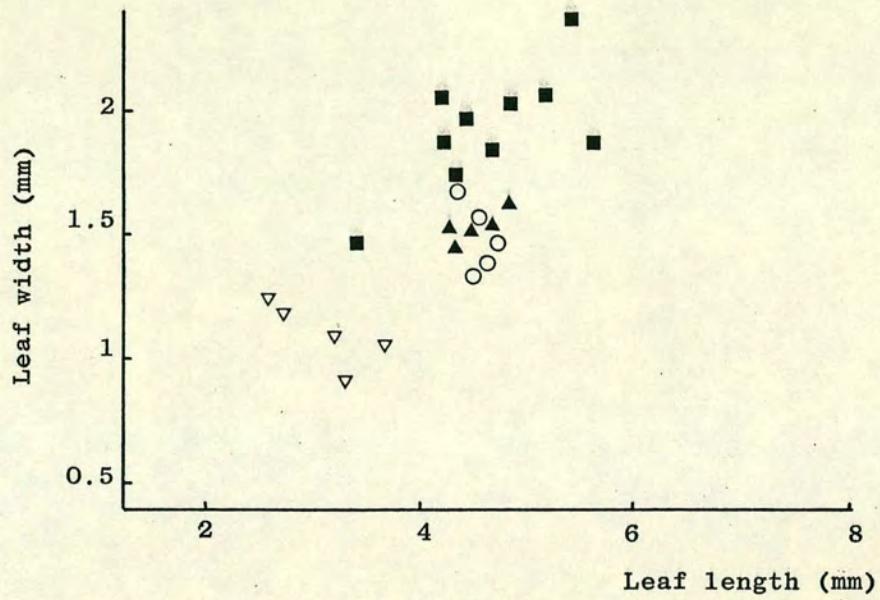


Figure 58. Scatter diagram of leaf length against leaf width showing herbarium specimens of taxon D (■), and living material of the same taxon (specimen TS9B) after arrival from South Georgia (▲) and after growth in controlled conditions for 6 months (○) and 1 year (▽). Each point represents mean stem values taken from 5 leaves.

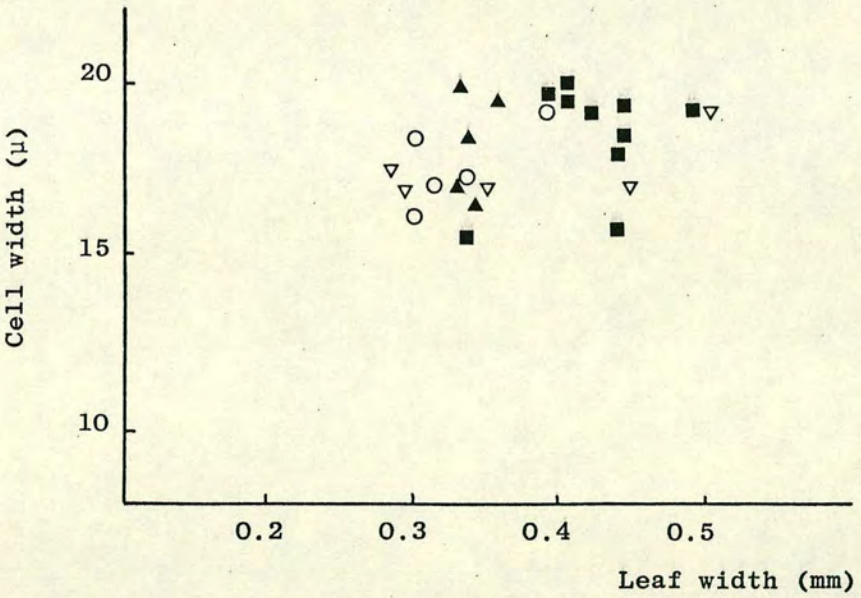


Figure 59. Scatter diagram of leaf width/length ratio against cell width showing herbarium specimens of taxon D (■), and living material of the same taxon (specimen TS9B) after arrival from South Georgia (▲) and after growth in controlled conditions for 6 months (○) and 1 year (▽). Each point represents mean stem values taken from 5 leaves.

of taxon E was greater than in the herbarium specimens, (Table 15, Fig. 60). During cultivation there was a progressive reduction in the width of leaves produced. Leaf length was also slightly reduced after 1 year in cultivation.

Taxon E measurements were similar to or intermediate between taxon D and F. Taxon D proved to be distinct in cultivation on the basis of leaf shape and leaf stance, but differences between taxon E and F appeared to be reduced. These two taxa are further considered in section 5.4.

5.3.3. Taxon F. The two cultivated specimens, numbered CM159 and TS4, represented the range of leaf and cell sizes found in herbarium specimens. The 'initial exsiccate' of CM159 had leaves and cells near the maximum size found in herbarium material (Table 16, Figs. 62 and 63) and the 'initial exsiccate' of TS4 had leaves and cells near the minimum size (Table 17, Figs. 64 and 65). After cultivation for 6 months and 1 year the leaf and cell sizes of both specimens were similar.

Leaf size in specimen CM159 was very variable. In the 'initial exsiccate' the leaves were approximately 8 mm long but after cultivation for 1 year they were only 4 mm long. Leaf width also varied in a similar way. These results suggest that much of the variation observed in herbarium material of this taxon was environmental in origin.

Specimens of taxon F after cultivation were only likely to

Table 15. Taxon E: Summary of comparisons between data gathered from herbarium specimens and living material (TS9A) before and after cultivation. Comparison is also made with data from different taxa grown in the same environment.

	Character			
Comparisons between taxon E material from various sources	Leaf length	Leaf width	Leaf width/ length ratio	Cell width
Measurements of initial exsiccate relative to range of herbarium specimens	similar	greater	greater	similar
Measurements of 6 month old stems grown in experiment relative to initial exsiccate	similar	lower	slightly lower	similar
Measurements of 1 year old stems grown in experiment relative to initial exsiccate	slightly lower	lower	slightly lower	similar
Comparison with material of other taxa grown in same experimental conditions				
6 months old stems	similar to taxa D & G	similar to taxa D & F	similar to taxa D & F	similar to taxa D & F
1 year old stems	similar to taxa D, F & G	similar to taxa D & F	similar to taxa D & F	similar to taxa D & F

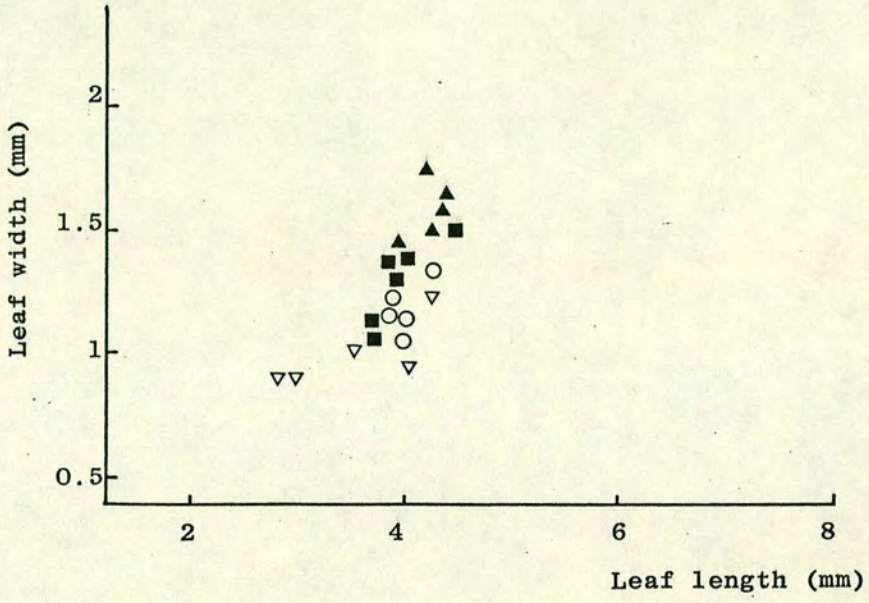


Figure 60 Scatter diagram of leaf length against leaf width showing herbarium specimens of taxon E (■), and living material of the same taxon (specimen TS9A) after arrival from South Georgia (▲) and after growth in controlled conditions for 6 months (○) and 1 year (▽). Each point represents mean stem values taken from 5 leaves.

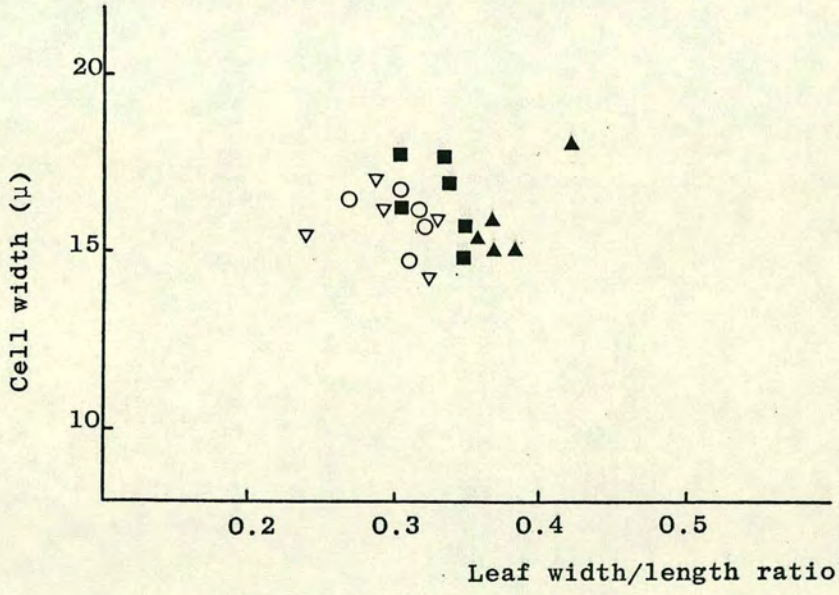


Figure 61 Scatter diagram of leaf width/length ratio against cell width showing herbarium specimens of taxon E (■), and living material of the same taxon (specimen TS9A) after arrival from South Georgia (▲) and after growth in controlled conditions for 6 months (○) and 1 year (▽). Each point represents mean stem values taken from 5 leaves.

Table 16. Taxon F: Summary of comparisons between data gathered from herbarium specimens and living material (CM159) before and after cultivation. Comparison is also made with data from different taxa grown in the same environment.

	Character			
Comparisons between taxon F material from various sources	Leaf length	Leaf width	Leaf width/ length ratio	Cell width
Measurements of initial exsiccate relative to range of herbarium specimens	at upper limit of range	in upper part of range	middle of range	in upper part of range
Measurements of 6 month old stems grown in experiment relative to initial exsiccate	lower	lower	similar	lower
Measurements of 1 year old stems grown in experiment relative to initial exsiccate	much lower	much lower	similar	lower
Comparison with material of other taxa grown in same experimental conditions.				
6 months old stems	larger than other taxa but close to taxon D.	similar to taxa D and E.	similar to taxa E and G.	similar to taxa D and E.
1 year old stems	larger than other taxa but close to taxa D and E.	similar to taxa D and E.	similar to taxa E and G.	similar to taxa D and E.

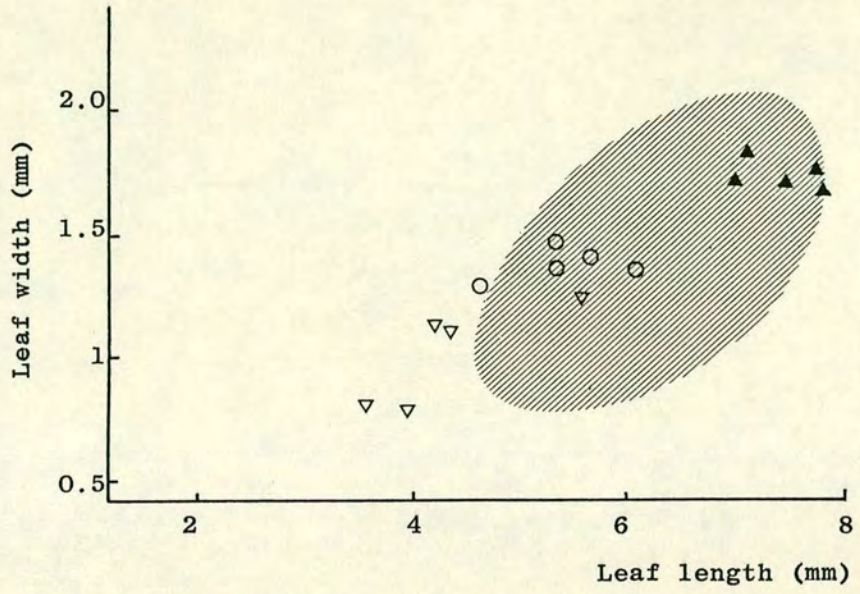


Figure 62. Scatter diagram of leaf length against leaf width showing the range of 50 herbarium specimens of taxon F ▨ and living material of the same taxon (specimen CM159) after arrival from South Georgia (▲) and after growth in controlled conditions for 6 months (○) and 1 year (▽). Each point represents mean stem values taken from 5 leaves.

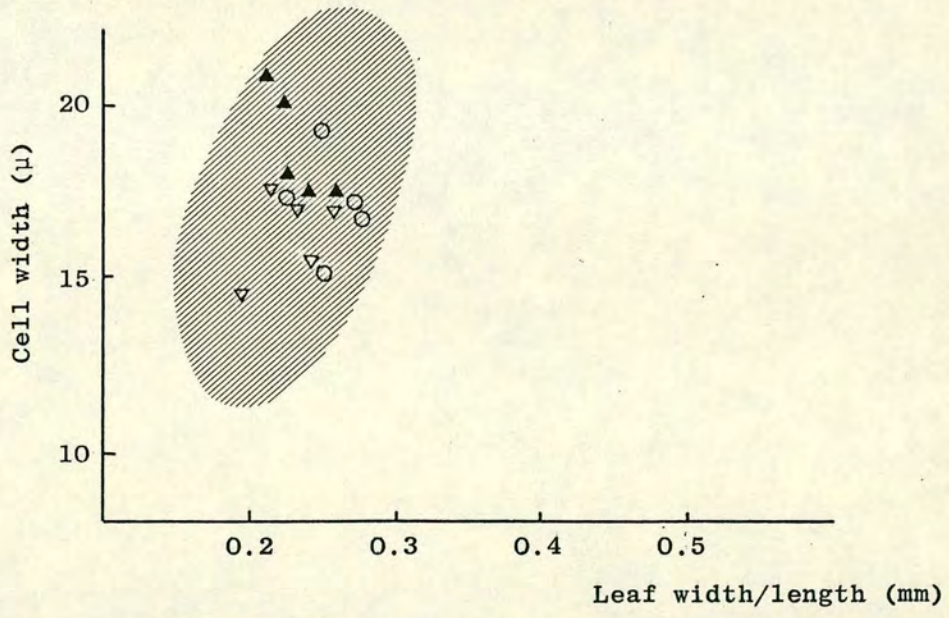


Figure 63. Scatter diagram of leaf width/length ratio against cell width showing the range of 50 herbarium specimens of taxon F ▨ and living material of the same taxon (specimen CM159) after arrival from South Georgia (▲) and after growth in controlled conditions for 6 months (○) and 1 year (▽). Each point represents mean stem values taken from 5 leaves.

Table 17. Taxon F: Summary of comparisons between data gathered from herbarium specimens and living material (TS4) before and after cultivation. Comparison is also made with data from different taxa grown in the same environment.

	Character			
Comparisons between taxon F material from various sources	Leaf length	Leaf width	Leaf width/ length ratio	Cell width
Measurements of initial exsiccate relative to range of herbarium specimens	at lower limit of range	in lower part of range	in upper part of range	at lower limit of range
Measurements of 6 month old stems grown in experiment relative to initial exsiccate	similar	similar	slightly lower	greater
Measurements of 1 year old stems grown in experiment relative to initial exsiccate	lower	lower	slightly lower	greater
Comparison with material of other taxa grown in same experimental conditions				
6 months old stems	similar to taxa D and E	similar to taxon E	similar to taxa E and G.	similar to taxa D and E.
1 year old stems	similar to taxa D, E and G.	similar to taxa D, E and G.	similar to taxa E and G.	similar to taxa D and E.

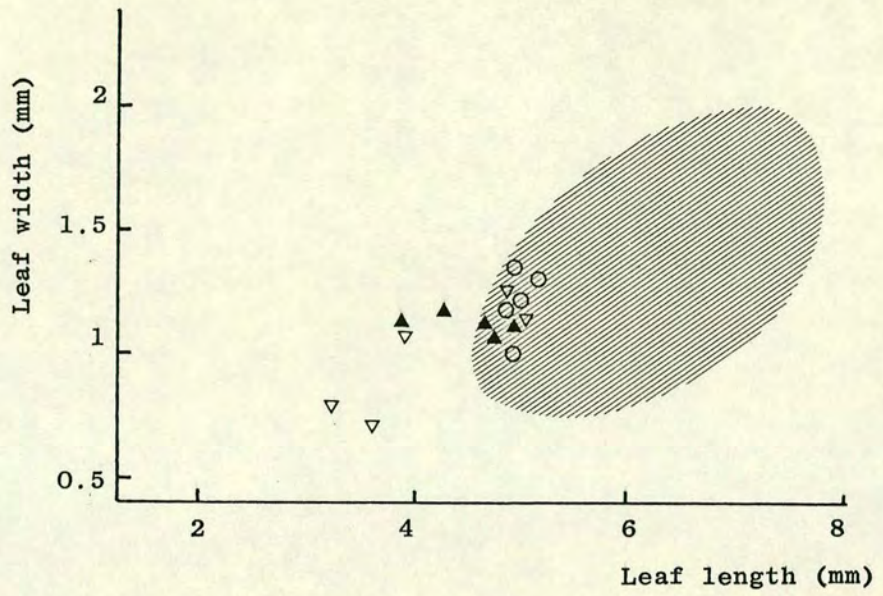


Figure 64. Scatter diagram of leaf length against leaf width showing the range of 50 herbarium specimens of taxon F ▨ and living material of the same taxon (specimen TS4) after arrival from South Georgia (▲) and after growth in controlled conditions for 6 months (○) and 1 year (▽). Each point represents mean stem values taken from 5 leaves.

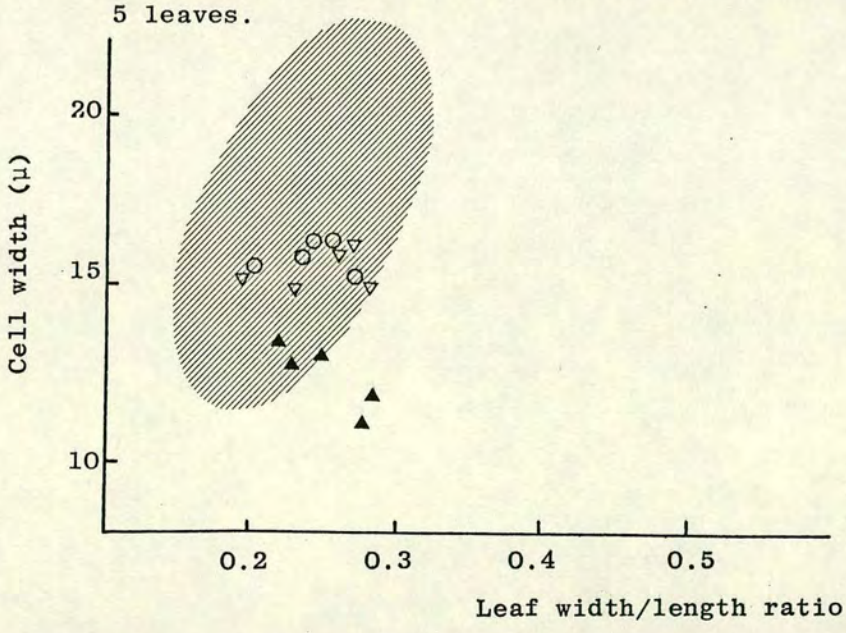


Figure 65. Scatter diagram of leaf width to length ratio against cell width showing the range of 50 herbarium specimens of taxon F ▨ and living material of the same taxon (specimen TS4) after arrival from South Georgia (▲) and after growth in controlled conditions for 6 months (○) and 1 year (▽). Each point represents mean stem values taken from 5 leaves.

be mistaken for taxon E. The differences between these taxa are further considered in section 5.4.

5.3.4. Taxon G. The 'initial exsiccate' of this taxon was similar to herbarium specimens in all measurements (Table 18, Figs. 66 and 67). After 6 months in cultivation however the width and width/length ratio of leaves produced was lower. There was no further change in leaf size after 1 year.

Taxon G was distinct in its small cell width before and after cultivation (Figs. 68, 69, 70 and 71). The characteristic areolation at the leaf apex was also retained by experimental plants.

5.3.5. General discussion. A progressive decline in size of leaves was found in all taxa during cultivation. In taxon F, specimen CM159 for example, the leaves were 8 mm long in the 'initial exsiccate' but after 6 months in cultivation they were about 6 mm long and after 1 year they were only 4 mm long (Fig. 62). This trend is probably due to a shortage of nutrients as the plants were not provided with minerals during the experiment and a gradual reduction in nutrient concentrations would be expected.

Specimens grown in the experiment had leaves which were pale and translucent with thin cell walls. They did not contain a brown pigment or have the thickened cell walls often seen in South Georgian herbarium material and in fresh specimens of British species collected in the field. Herbarium specimens

Table 18. Taxon G: Summary of comparisons between data gathered from herbarium specimens and living material (CM276) before and after cultivation. Comparison is also made with data from different taxa grown in the same environment.

	Character			
Comparisons between taxon G material from various sources	Leaf length	Leaf width	Leaf width/ length ratio	Cell width
Measurements of initial exsiccate relative to range of herbarium specimens	at upper limit of range	similar	at lower limit of range	similar
Measurements of 6 month old stems grown in experiment relative to initial exsiccate	similar	lower	lower	similar
Measurements of 1 year old stems grown in experiment relative to initial exsiccate	slightly lower	lower	lower	similar
Comparison with material of other taxa grown in same experimental conditions,				
6 months old stems	similar to taxon E	smaller than other taxa	similar to taxon F.	smaller than other taxa.
1 year old stems	similar to taxa D, E and F.	smaller than other taxa but close to taxon F.	similar to taxon F.	smaller than other taxa.

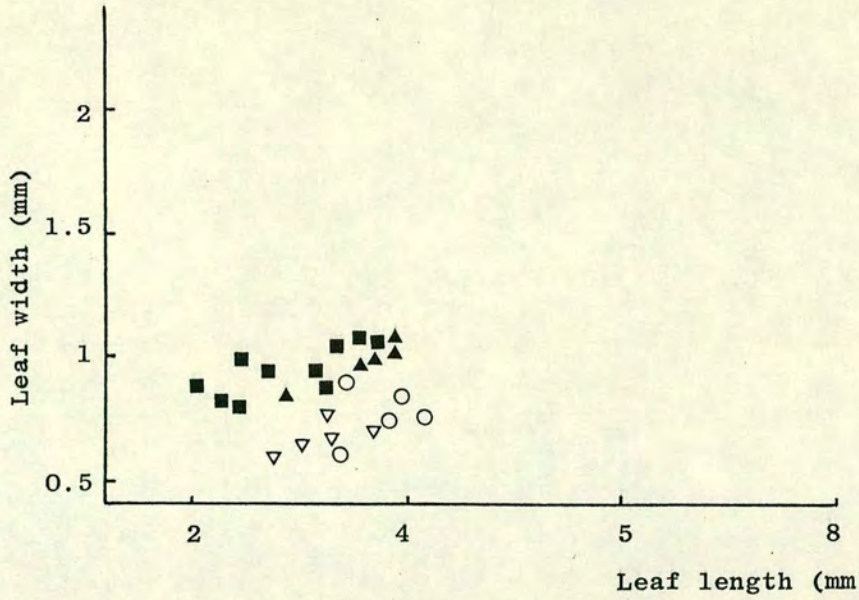


Figure 66. Scatter diagram of leaf length against leaf width showing herbarium specimens of taxon G (■), and living material of the same taxon (specimen CM276) after arrival from South Georgia (▲) and after growth in controlled conditions for 6 months (○) and 1 year (▽). Each point represents mean stem values taken from 5 leaves.

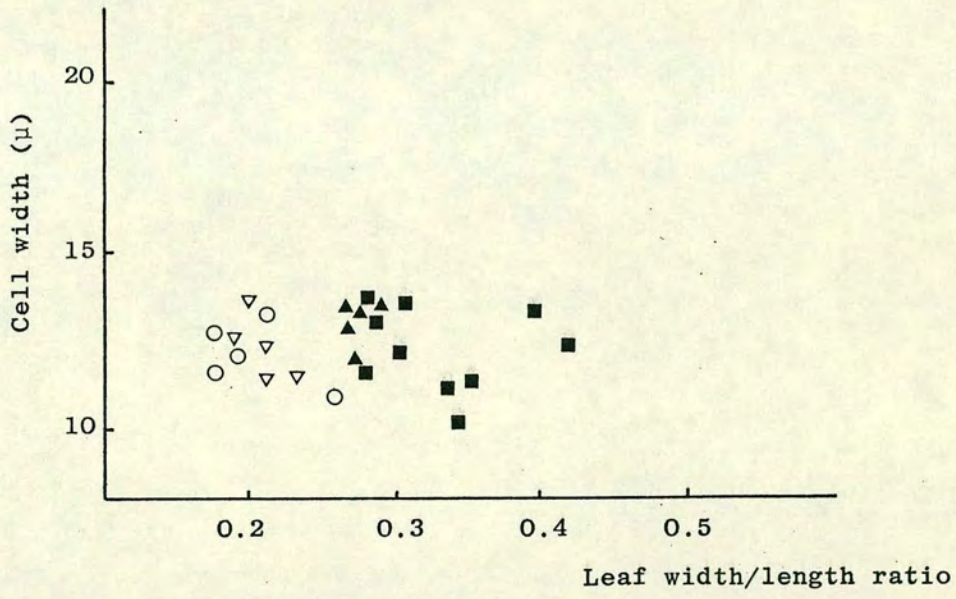


Figure 67. Scatter diagram of leaf width/length ratio against cell width showing herbarium specimens taxon G (■), and living material of the same taxon (specimen CM276) after arrival from South Georgia (▲) and after growth in controlled conditions for 6 months (○) and 1 year (▽). Each point represents mean stem values taken from 5 leaves.

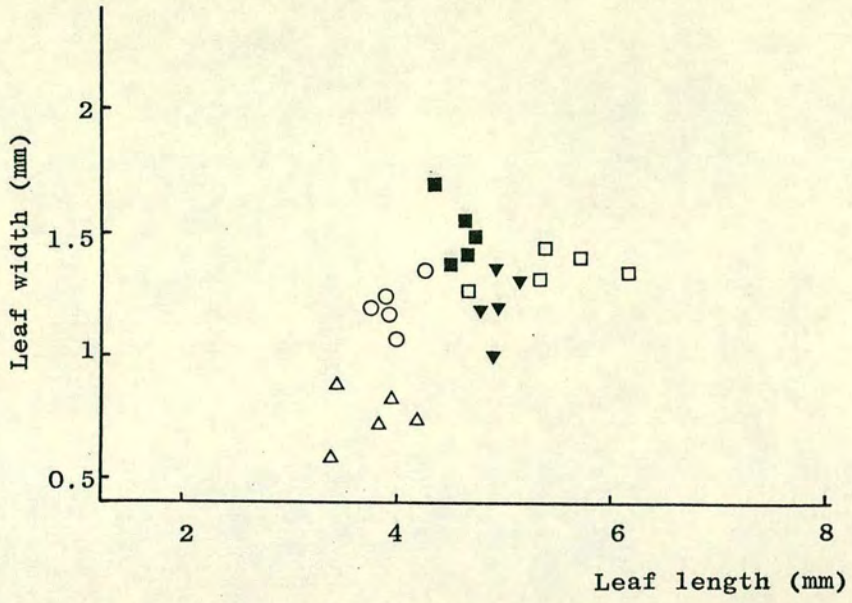


Figure 68. Scatter diagram of leaf length against leaf width for specimens grown in controlled conditions for 6 months. Key: Taxon D (■), Taxon E (○), Taxon F CM159 (□), TS4 (▼), Taxon G (△). Each point represents mean stem values taken from 5 leaves.

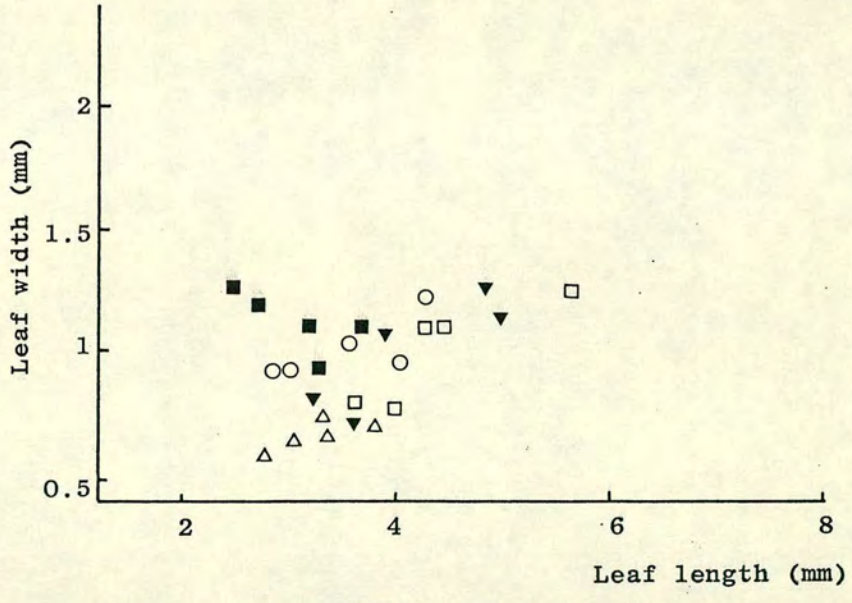


Figure 69. Scatter diagram of leaf length against leaf width for specimens grown in controlled conditions for 1 year. Key: Taxon D (■), Taxon E (○), Taxon F CM159 (□), TS4 (▼), Taxon G (△). Each point represents mean stem values taken from 5 leaves.

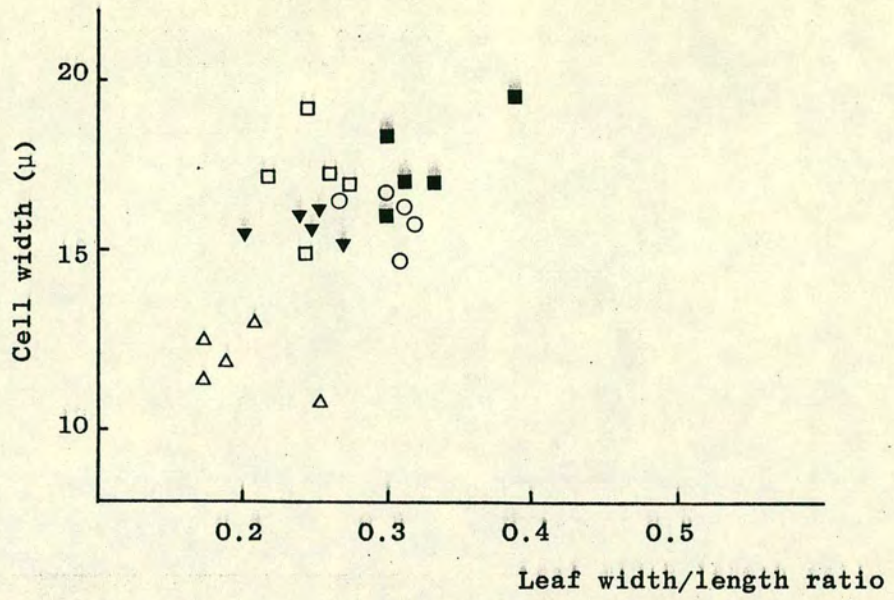


Figure 70. Scatter diagram of leaf width/length ratio against cell width for specimens grown in controlled conditions for 6 months. Key: Taxon D (■), Taxon E (○) Taxon F CM159 (□), TS4 (▼), Taxon G (△). Each point represents mean stem values taken from 5 leaves.

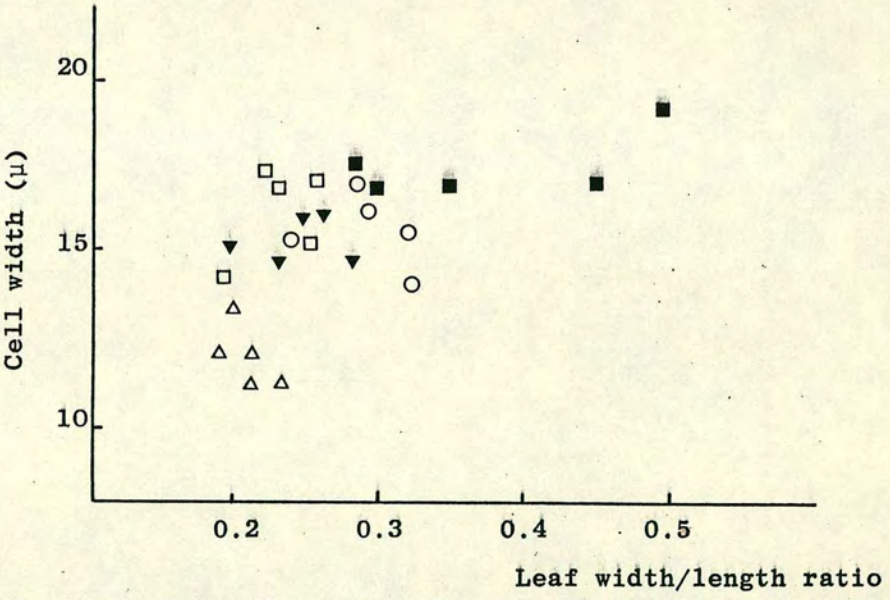


Figure 71. Scatter diagram of leaf width/length ratio against cell width for specimens grown in controlled conditions for 1 year. Key: Taxon D (■), Taxon E (○), Taxon F CM159 (□), TS4 (▲), Taxon G (△). Each point represents mean stem values taken from 5 leaves.

from very wet or permanently moist habitats were often similar to the plants from the experiment. Since the experimental material was kept permanently moist this suggested that the lack of desiccation was a cause of the differences in morphology.

Cultures of taxa E, F and G produced some stems with an unusual growth form which had not been observed in herbarium specimens. These stems differed in their erect, appressed leaves (Figs. 72, 73 and 74) but all other characters were normal. Leaves on the lower parts of the shoots usually showed typical leaf stance. As the stems came from the same fragments as normal stems this abnormality could not be genetic. The stems were robust and among the tallest in the cultures. White evaporation deposits were often found at the tips of the upper leaves suggesting that the abnormal leaf stance was a result of exposure to dry air.

5.4 Further discussion of taxa E and F.

Leaf shape and size were important characters for separating herbarium specimens of taxa E and F. During cultivation both characters changed considerably. 'Initial exsiccates' of taxon E and taxon F were compared with the ranges of measurements in herbarium specimens (Figs. 75 and 76). Three stems in the original sample of taxon E had wider leaves than found in herbarium material and 2 taxon F (TS4) stems had shorter leaves. In all other respects however the original samples agreed with the herbarium specimens.

Figure 72 One year old stems of taxon E (TS9A) produced in a controlled environment cabinet at 10°C, showing tall stems with an anomalous growth form. Magnification x 3.5.

Figure 73 One year old stems of taxon F (CM159) produced in a controlled environment cabinet at 10°C, showing tall stems with an anomalous growth form. Magnification x 3.5.

Figure 74 One year old stems of taxon F (TS4) produced in a controlled environment cabinet at 10°C, showing tall stems with an anomalous growth form. Magnification x 3.5.


72
5mm


73
5mm


74
5mm

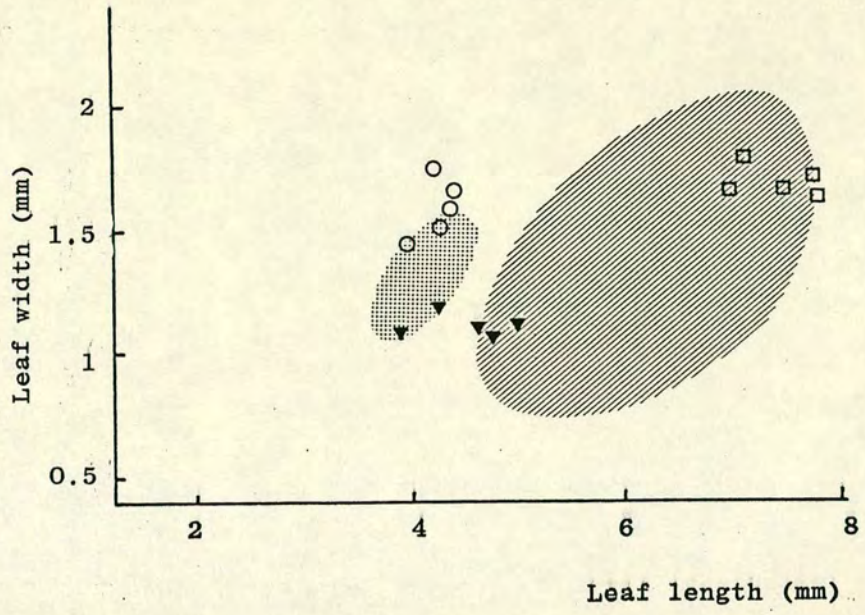


Figure 75 Diagram showing leaf length against leaf width of experimental plants of taxon E (○) and taxon F CM159 (□), TS4 (▼) after arrival from South Georgia. Ranges of taxon E ▒ and taxon F ▨ herbarium specimens are shown for comparison.

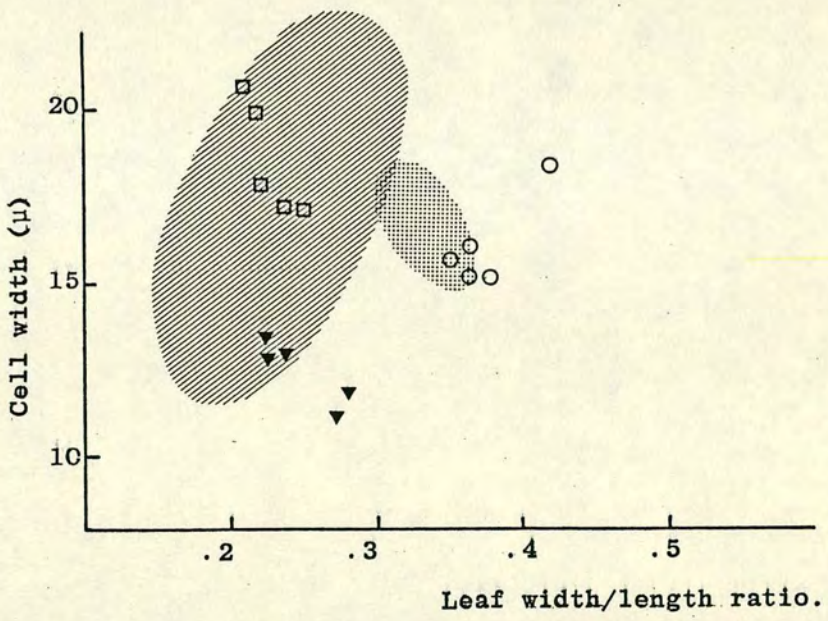


Figure 76 Diagram showing leaf width/length ratio against cell width of experimental plants of taxon E (○) and taxon F CM159 (□), TS4 (▼) after arrival from South Georgia. Ranges of taxon E ▒ and taxon F ▨ herbarium specimens are shown for comparison.

After 6 months in cultivation the measurements of both taxa were closer to those of the herbarium specimens than the 'initial exsiccates' (Figs. 77 and 78). The leaf width/length ratio of taxon E was much lower than in the 'initial exsiccate' but taxa E and F were still distinct.

After 1 year in cultivation the measurements of leaf length and leaf width were outside the range of herbarium material (Fig. 79). Leaf width/length ratio values of taxon F remained within the limits observed in herbarium material, but taxon E leaf width/length ratio values were smaller, and only slightly greater than taxon F values (Fig. 80).

Data from taxon E and taxon F differed only slightly after 1 year in cultivation. In practice however, stems picked at random from the experimental material could be classified correctly. This was due to differences in leaf shape, which were not reflected in the leaf width/length ratios and to differences in leaf stance.

Leaves of taxon E appeared to be wider in the upper part of the leaf than leaves of taxon F, both before and after cultivation. These differences were investigated by taking measurements of leaf length and leaf width at one third of the leaf length from the leaf apex, in cultivated and herbarium specimens. Twenty five leaves from 5 one year old cultivated stems of each taxon were measured and the results compared with 25 leaves taken from 5 herbarium specimens.

The results are given in Figs. 81, 82, 83 and 84. Differences

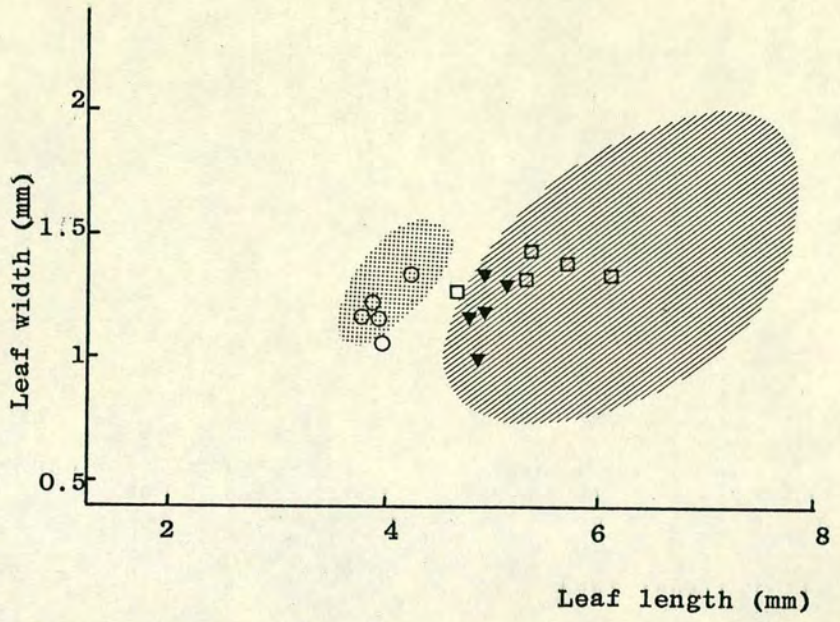


Figure 77. Diagram showing leaf length against leaf width of experimental plants of taxon E (○) and taxon F CM159 (□), TS4 (▼) after growth in experimental conditions for 6 months. Ranges of taxon E ▒ and taxon F ▒ herbarium specimens are shown for comparison.

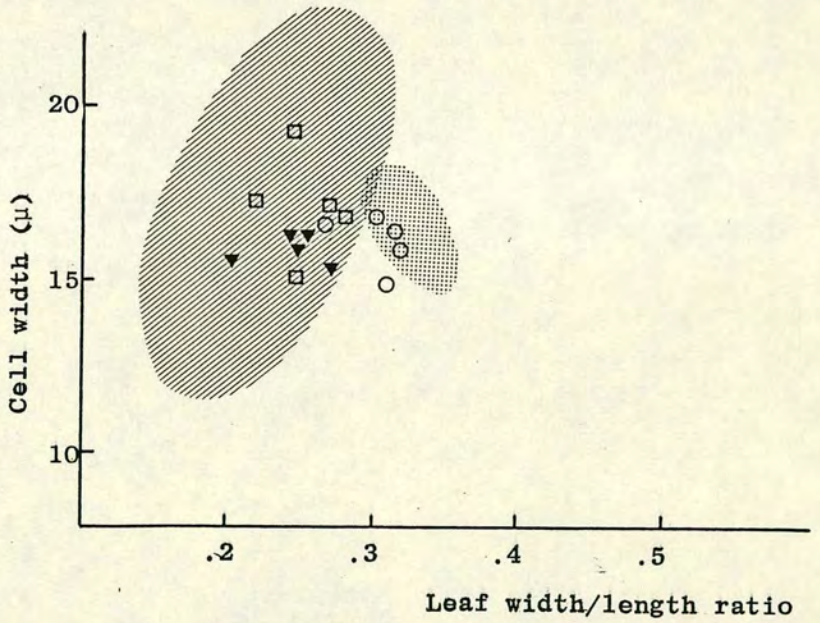


Figure 78 Diagram showing leaf width/length ratio against cell width of experimental plants of taxon E (○) and taxon F CM159 (□), TS4 (▼) after growth in experimental conditions for 6 months. Ranges of taxon E ▒ and taxon F ▒ herbarium specimens are shown for comparison.

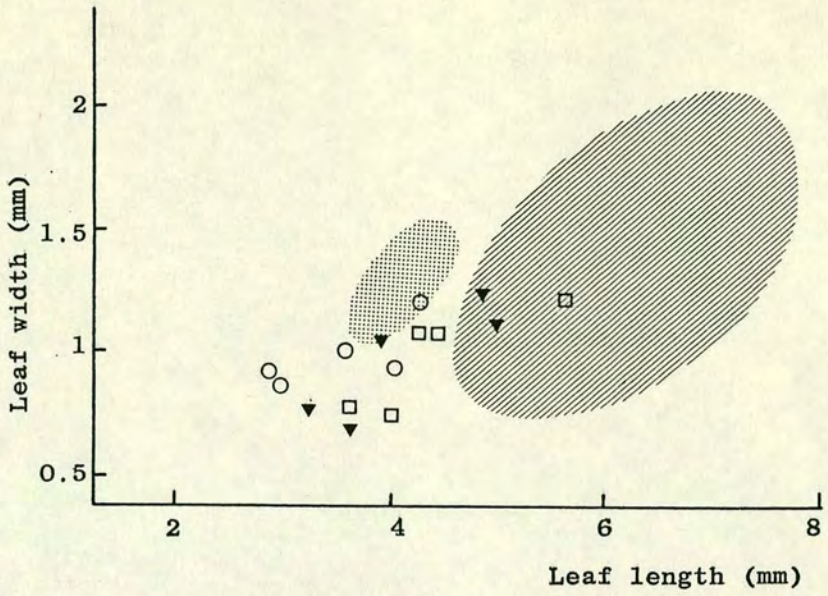


Figure 79. Diagram showing leaf length against leaf width of experimental plants of taxon E (○) and taxon F CM159 (□), TS4 (▼) after growth in experimental conditions for 1 year. Ranges of taxon E ▒ and taxon F ▒ herbarium specimens are shown for comparison.

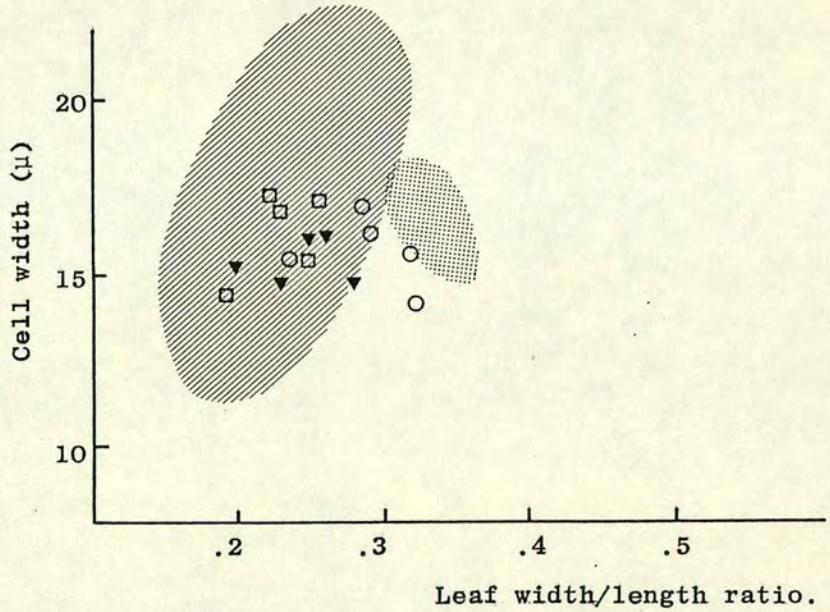


Figure 80. Diagram showing leaf width/length ratio against cell width of experimental plants of taxon E (○), and taxon F CM159 (□), TS4 (▼) after growth in experimental conditions for 1 year. Ranges of taxon E ▒ and taxon F ▒ herbarium specimens are shown for comparison.

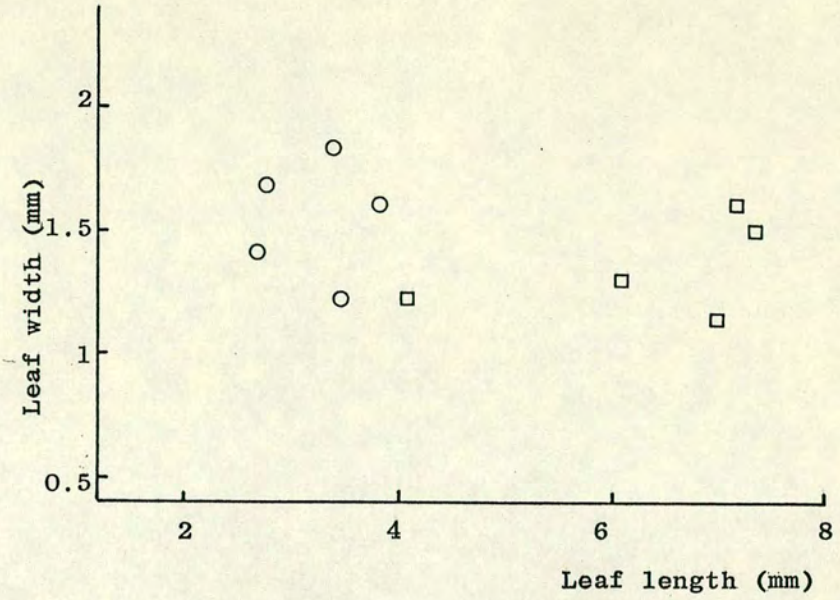


Figure 81 Scatter diagram showing leaf length against leaf width at one third of the leaf length from the apex in herbarium specimens of taxon E (○) and taxon F (CM159) (□).

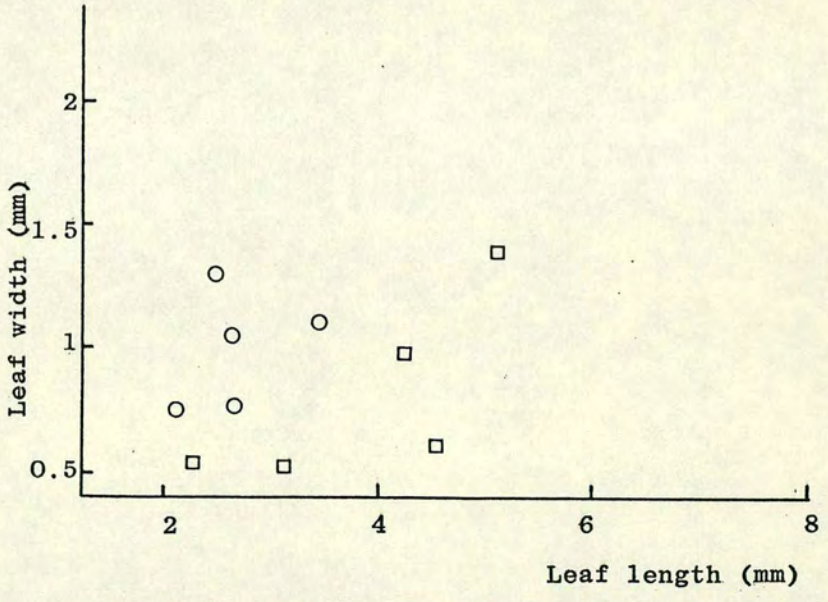


Figure 82 Scatter diagram showing leaf length against leaf width at one third of the leaf length from the apex in specimens grown in controlled conditions for 1 year. Key: taxon E (○), taxon F (CM159) (□).

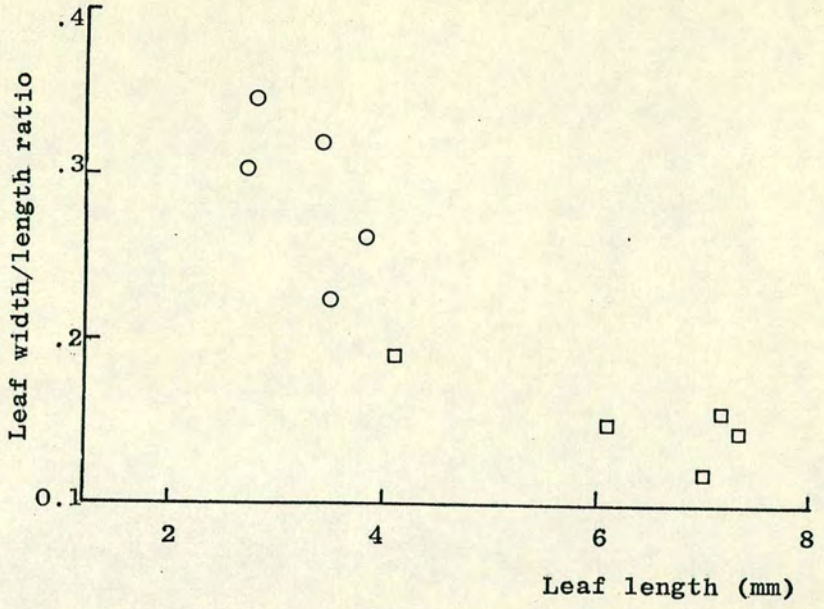


Figure 83 Scatter diagram showing leaf length against leaf width (at one third leaf length from the apex)/ length ratio in herbarium specimens of taxon E (○) and taxon F (CM159) (□).

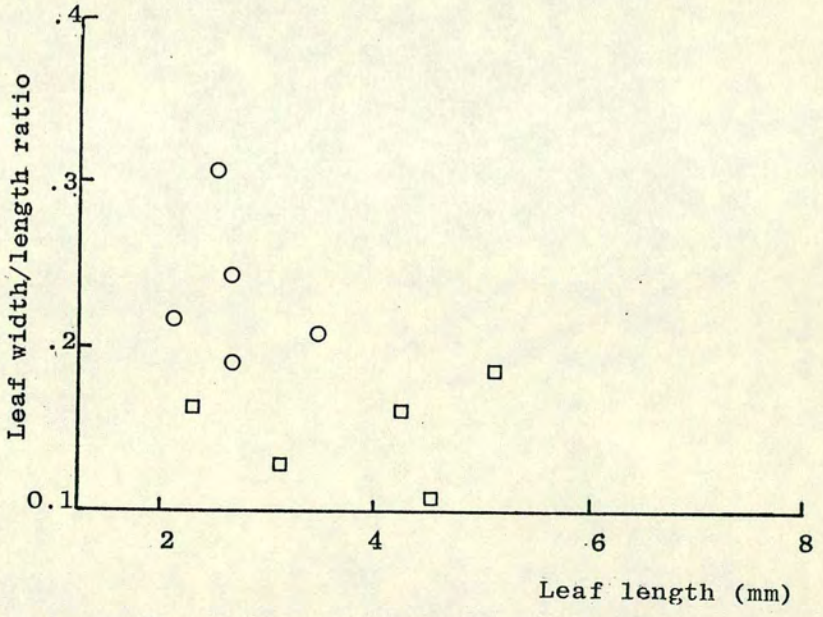


Figure 84 Scatter diagram showing leaf length against leaf width (at one third leaf length from the apex)/length ratio in specimens grown in controlled conditions for 1 year. Key: taxon E (○), taxon F (CM159) (□).

between the taxa were reduced during cultivation. The best separation was given by leaf width (at one third leaf length from apex)/leaf length ratio, which distinguished 1 year old cultivated plants more clearly than maximum leaf width/length ratio. The rather small differences observed, however, were surprising as the leaf shapes could easily be distinguished by eye.

Differences in leaf stance between the taxa remained constant in cultivation and could also be used to separate the taxa.

5.5 Conclusions: non-hair-pointed group

The non-hair-pointed taxa C, D, E, F and G remained distinct during cultivation. Taxa E and F became more alike and it is perhaps doubtful whether the remaining differences in leaf shape would be significant if a larger sample of specimens had been available for the study. Leaf stance, however, remained different and the taxa were easily distinguished by eye.

Taxonomic characters used for delimiting taxa were found to be stable in cultivation. These included the presence or absence of teeth on the upper leaf margin, the type of areolation at the leaf apex, leaf shape, lamina cell width and, in general the leaf sizes. Leaf length and leaf width were more variable in cultivation than leaf width/length ratio, leaf shape and lamina cell width.

5.6 Introduction: hair-pointed group

Observation and measurement of herbarium specimens of the hair-pointed taxa indicated that they were not distinct. Variation in this group was therefore investigated by a series of growth experiments.

Unfortunately, at an early stage in this study, the quantity of living hair-pointed material was not sufficient to allow an experiment similar to that conducted on the non-hair-pointed material. Only two hair-pointed specimens were available, and both had red hair-points and recurved leaves, characteristic of taxon I. However, 'initial exsiccates' of these specimens (i.e. stems removed from the material and dried on arrival) showed variation in taxonomic characters between the upper and lower parts of stems. The upper parts had characters of taxon I plants but the lower parts had the cucullate leaves and hyaline hair-points of taxon K. In the latter part of this study further material became available and this also showed similar changes in taxonomic characters following cultivation on the growth bench or in a cold frame. To investigate this a quantitative assessment of all living hair-pointed specimens and 'initial exsiccates' was undertaken.

5.7 Methods: hair-pointed group

Measurements and scores were made on all eight specimens in cultivation by the methods outlined in section 3.3.1. The 'initial exsiccate' of each of these specimens was also

scored and measured but leaves were selected from the lower parts of stems to avoid any growth produced in transit from South Georgia or after defrosting.

5.8 Results: hair-pointed group

Results of the quantitative assessment of 'initial exsiccates' and living material are given in Table 19. Material grown in growth bench or cold frame conditions differed from the lower parts of 'initial exsiccate' stems in the following ways:

i) Higher leaf profile score. Cucullate, notched or plane leaves (score 1, 2 or 3) were observed in the 'initial exsiccates' but only recurved leaves (score 4) were present in cultivated specimens.

ii) Higher nerve type score. The well developed nerve type with long cells on the abaxial surface (score 1) was found in the majority of leaves in the 'initial exsiccates'. In cultivated specimens most leaves had quadrate cells on the abaxial nerve surface (score 2).

iii) Lower hair-point colour score. The 'initial exsiccates' showed hyaline hair-points (score 3) but cultivated material had red or reddish hair-points (score 1 or 2).

iv) Greater leaf length. Specimens which had small leaves (below 2 mm in length) in the 'initial exsiccates'

Table 19. Mean scores and measurements of hair-pointed *Tortula* specimens growing on South Georgia compared with data from the same specimens after growth in growth bench or cold frame conditions.

Specimen No.	Period in cultivation	Place grown	Leaf profile	Nerve type	Hair-point colour	Leaf-margin recurvature	Leaf length (mm)	Hair-point length (mm)	Leaf width (mm)	Lamina cell width (μ)	Basal cell length (μ)	Basal cell width (μ)	Identification to taxon
CM48	5 yrs	South Georgia	2	1	3	1.4	1.07	0.31	0.53	14.58	49.7	17.55	K
		Growth bench	4	2	1	2	2.39	0.42	0.74	18.23	99.6	20.12	I
CM157	5 yrs	South Georgia	3	1	2.4	2	1.81	0.66	0.72	10.8	63.2	18.77	K
		Growth bench	4	2	1	1.8	2.84	0.39	1.00	14.04	106.9	15.26	I
CM294	3 yrs	South Georgia	1.8	1.2	2	2.4	1.77	0.19	0.79	13.64	82.1	22.28	K
		Growth bench	4	2	1.8	2.4	2.92	0.35	0.92	13.91	102.9	15.26	I
TM12	2½ yrs	South Georgia	3.2	1	3	4	2.67	0.88	0.86	14.58	72.2	16.88	J
		Growth bench	4	2	2	3	2.60	0.44	0.69	14.58	87.8	14.85	I
TS6	1 yr	South Georgia	4	1	3	4	1.86	0.10	0.76	15.39	85.2	20.93	J
		Cold frame	4	2	2	3	2.35	0.45	1.03	15.12	91.4	19.7	I
TS8	1 yr	South Georgia	1.8	1	2.8	2.4	2.79	1.27	0.97	16.2	77.9	18.63	K
		Growth bench	3.8	1	2.2	4	2.91	0.71	0.84	14.85	85.2	15.53	I
TS15	1 yr	South Georgia	3.8	2	2.6	3.4	2.17	0.37	0.99	16.34	73.2	19.71	J
		Growth bench	4	2	1.2	3.8	2.91	0.67	0.93	14.04	114.3	18.23	I
TS19	1 yr	South Georgia	3.2	1	3	4.6	3.43	1.01	1.04	14.04	112.7	22.28	J
		Growth bench	3.6	2	2	3.8	3.47	1.07	1.02	14.85	117.9	15.66	I

produced larger leaves in cultivation. Specimens which had large leaves in the 'initial exsiccate' continued to produce leaves of similar length.

5.9. Discussion and conclusions: hair-pointed group

After cultivation in growth bench or cold frame conditions all specimens had recurved leaves, nerves with quadrate cells on the abaxial surface near the leaf apex, reddish hair-points and, usually, longer leaves. The first three of these features are characteristic of taxon I, although 'initial exsiccates' show that all specimens originally had characters typical of taxa J or K.

Material grown on the growth bench or in a cold frame was not treated as uniformly as that in growth cabinets, but the results of an experiment conducted earlier in this study suggest that this is unlikely to have affected the results of the present investigation. The earlier experiment was carried out with two hair-pointed specimens to investigate the stability of characters in various controlled environments. The 'initial exsiccates' of these had upper leaves characteristic of taxon I and lower leaves characteristic of taxon K. Both were grown in two controlled environment cabinets at constant temperatures of 5 and 15^{o}C and the plants in each cabinet were given two different nutrient and watering treatments. After 6 months the stems were harvested, scored and measured as described in section 3.3.1. The results showed differences in stem height, hair-point length,

leaf length, leaf width, leaf margin recurvature and basal cell length between treatments, but none of these were taxonomically significant. All plants maintained the recurved leaves and red hair-points observed in the upper leaves of the 'initial exsiccates'.

The genotypes which produce phenotypes described as taxa J and K on South Georgia thus express taxon I phenotypes in the range of controlled conditions and the conditions prevailing on the growth bench or in cold frames. This suggests that the taxa I, J and K recognised in herbarium studies may be only different manifestations of the same genotype. In view of the confusion arising from changes occurring in transit, however, further growth studies are needed to elucidate these taxa.

Chapter 6: SCANNING ELECTRON MICROSCOPE STUDY OF SOUTH GEORGIAN *Tortula* TAXA

Scanning electron microscopy has been used by many bryologists in the detailed examination of spore surfaces (Clarke 1979). The spore surface has been shown to be taxonomically significant when light microscopy was unable to detect any variation. The scanning electron microscope (SEM) has also been used in the examination of the micro-ornamentation of the gametophyte. This was particularly important in this study as all *Tortula* species have papillose leaf surfaces but many do not produce spores on South Georgia. An SEM study of leaf surfaces was undertaken to find new characters of taxonomic importance, and to provide a better understanding of characters used at present.

6.1 Materials and methods

Herbarium specimens were hydrated in distilled water for 12 hrs. then dissected. Leaves and sporophytes were placed in a specimen holder (Crossley 1976) and passed through the following dehydration series:-

i) 25% ethanol, 75% water

ii) 50% ethanol, 50% water

iii) 75% ethanol, 25% water

iv) 100% ethanol

v) 100% ethanol

and then through a series of acetone and ethanol mixtures:-

vi) 25% acetone, 75% ethanol

vii) 50% acetone 50% ethanol

viii) 75% acetone 25% ethanol

ix) 100% acetone

x) 100% acetone

The material was allowed to equilibrate in each solution for at least 2 hrs. When the final stage was completed the material was critical-point dried to avoid the distortion which usually occurs on drying. Using a Polaron E 3000 critical-point drier, the material was flushed with liquid carbon dioxide under pressure at a temperature of approximately 15^{o}C for 1 hour to allow full impregnation of the tissue. After reflushing, the temperature was raised above the critical point of carbon dioxide (32^{o}C) to cause vapourisation. The gas was released leaving the material free of water. The material was removed from the specimen holder, placed on self-adhesive aluminium stubs and coated with 250 Ångstroms of gold at 1.5 kV in a Nanotech Semprep II splutter coater. The leaf specimens were then ready for examination using a Cambridge Stereoscan Mark IIA SEM at 20 kV with a final aperture setting of 200 µ.

Spores were critical-point dried inside unopened capsules which were opened on the stub before coating. The best results were obtained if the capsule wall was fixed to the stub surface with attached spores uppermost, since spores which came into direct contact with the adhesive tended to collapse. Preparations of air-dried and hydrated spores transfered into alcohol and then acetone before drying were unsatisfactory because they collapsed.

6.2 Lamina cell papillae: shape and variation

Scanning electron micrographs of lamina cell papillae of several Tortula species have been published including T. ruralis (Hedw.) Gaertn. et al. (Robinson 1971), T. ruralis var. hirsuta (Vent.) Par. (Casas de Puig and Molinas 1974), T. norvegica (Web. f.) Wahlenb. (Lewinsky 1974) and T. intermedia (Brid.) De Not. (Proctor 1979). Robinson (1971) remarked that many genera in the family Pottiaceae, such as Leptodontium, had similar papillae and micrographs of leaves of species in the genera Leptodontium (Zander 1972) Desmatodon (Magill et al 1974, Townsend and Whitehouse 1979) Encalypta (Proctor 1979), Pleurochaete and Anomodon (Dilks and Proctor 1979) all show papillae of approximately the same size and form as T. ruralis. Encalypta and Anomodon are not placed in the Pottiaceae so papillae of this type are not exclusive to this family.

Micrographs of South Georgian taxa were obtained for comparison with published micrographs and with light microscope observations.

Results. Scanning electron micrographs of leaf papillae of all South Georgian taxa are given in Figs. 85-101.

Discussion. In all taxa the papillae became less prominent and less complex towards the base of the leaf. A transition occurred in this region between the chlorophyllose, quadrate cells of the upper and middle parts of the leaf and the rectangular, hyaline cells of the leaf base. These basal

Figure 85 Upper lamina cell papillae of taxon A.

Magnification x 5,500.

Figure 86 Upper lamina cell papillae of taxon B.

Magnification x 2,400.

Figure 87 Upper lamina cell papillae of taxon B.

Magnification x 5,800.

Figure 88 Upper lamina cell papillae of taxon C.

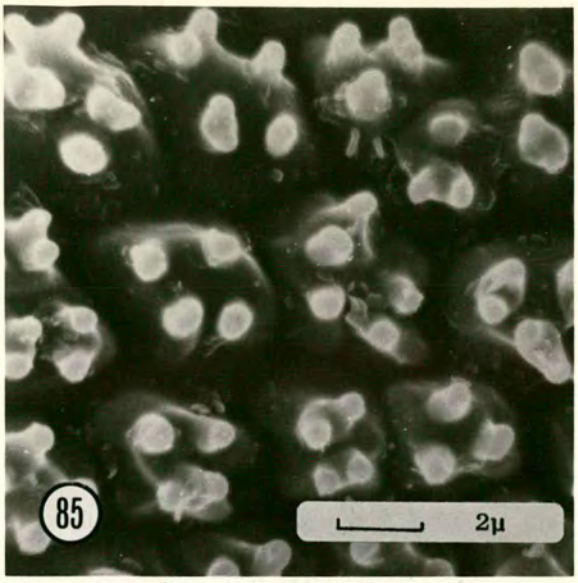
Magnification x 5,600.

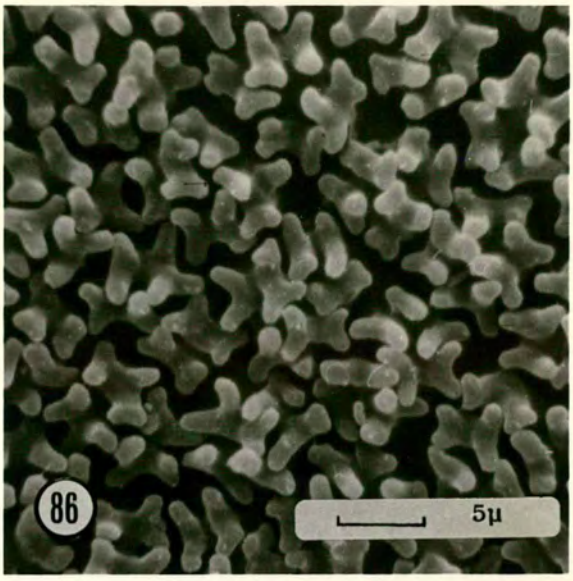
Figure 89 Upper lamina cell papillae of taxon D.

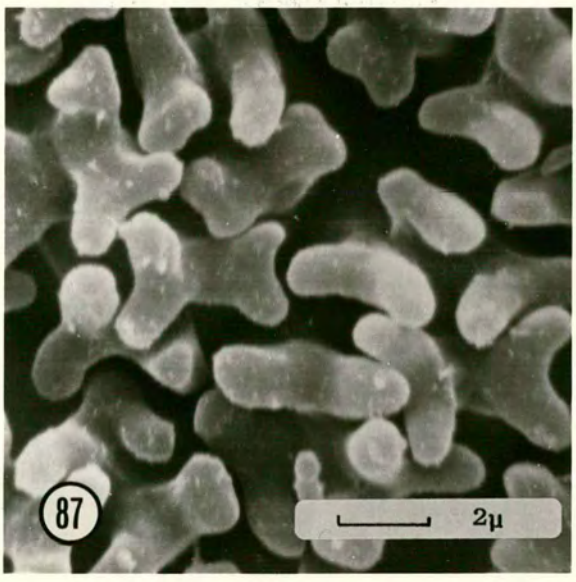
Magnification x 2,300.

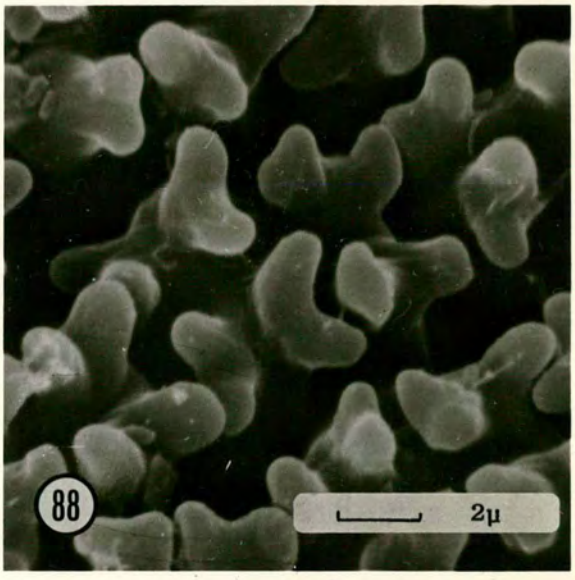
Figure 90 Upper lamina cell papillae of taxon E.

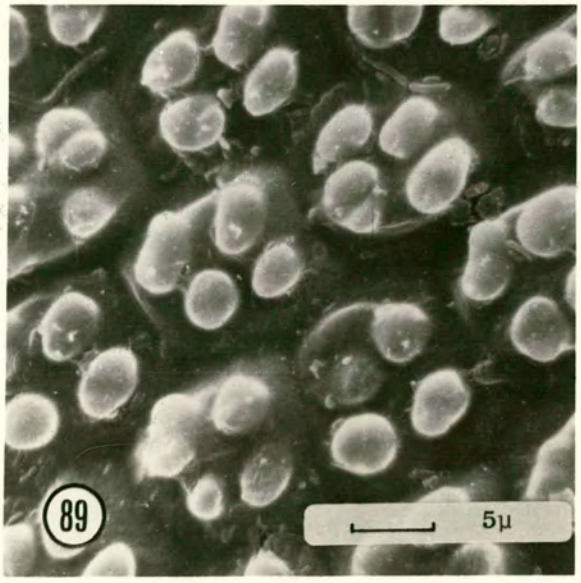
Magnification x 2,400.


85
2μ


86
5μ


87
2μ


88
2μ


89
5μ

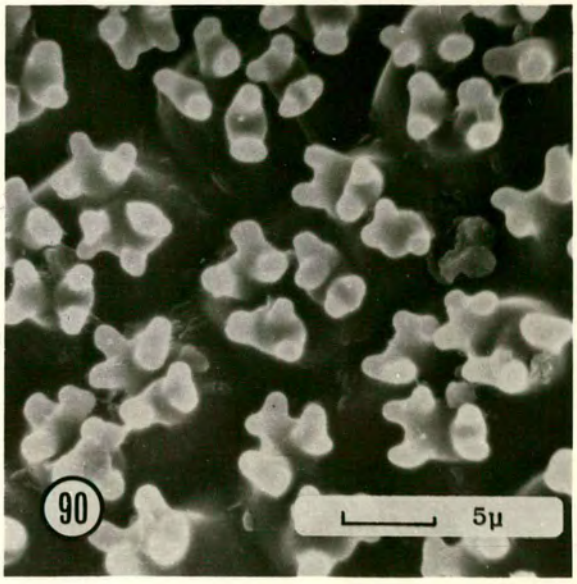

90
5μ

Figure 91 Upper lamina cell papillae of taxon F.
Magnification x 4,400.

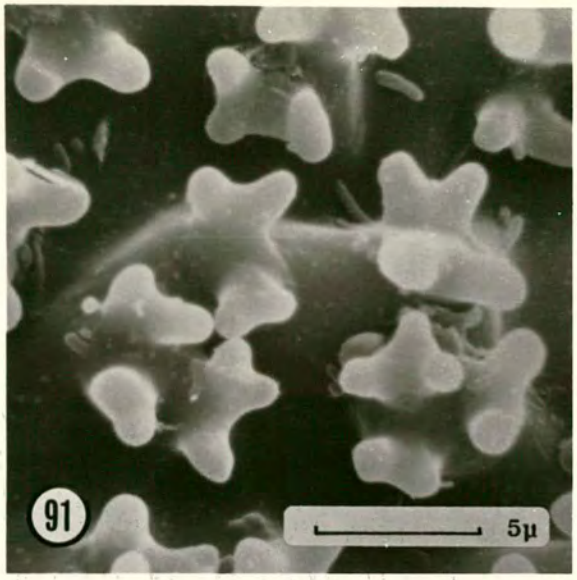
Figure 92 Upper lamina cell papillae of taxon G.
Magnification x 4,600.

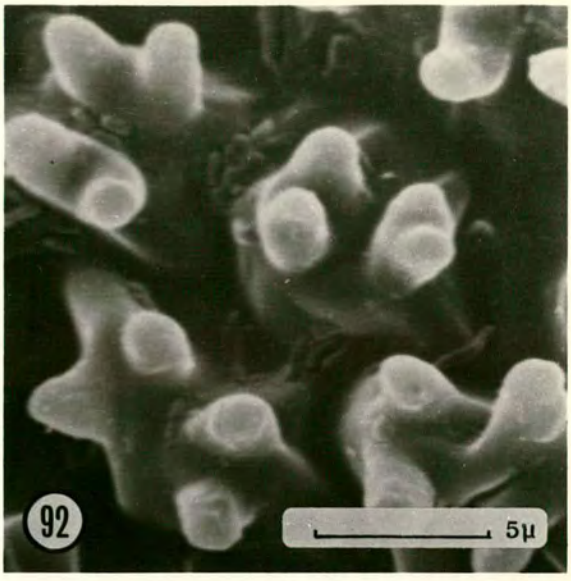
Figure 93 Upper lamina cell papillae of taxon H.
Magnification x 2,800.

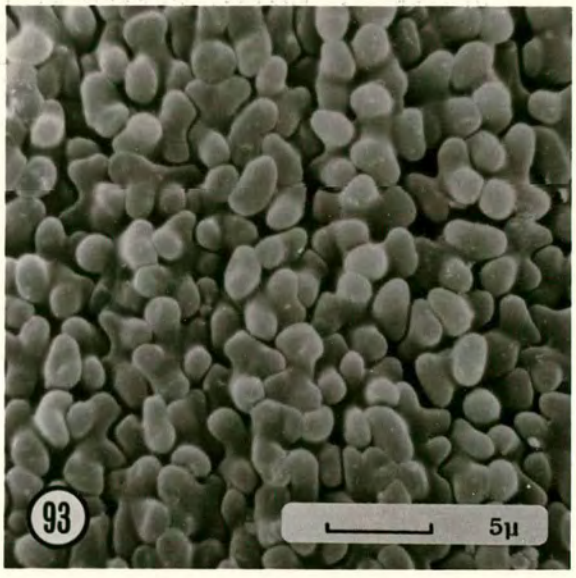
Figure 94 Upper lamina cell papillae of taxon H.
Magnification x 6,800.

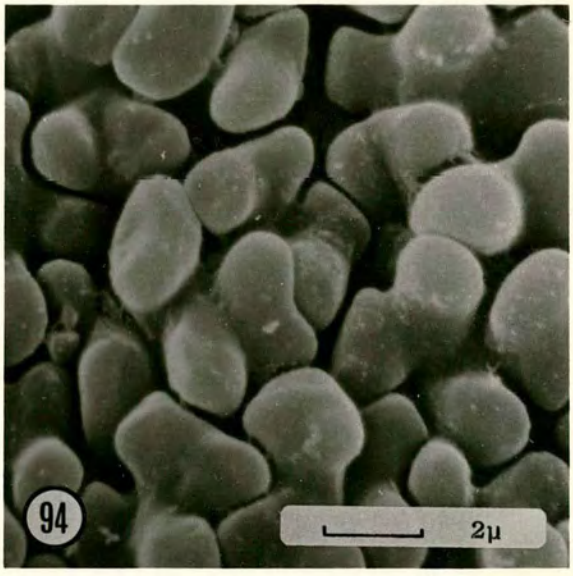
Figure 95 Upper lamina cell papillae of taxon I.
Magnification x 2,800.

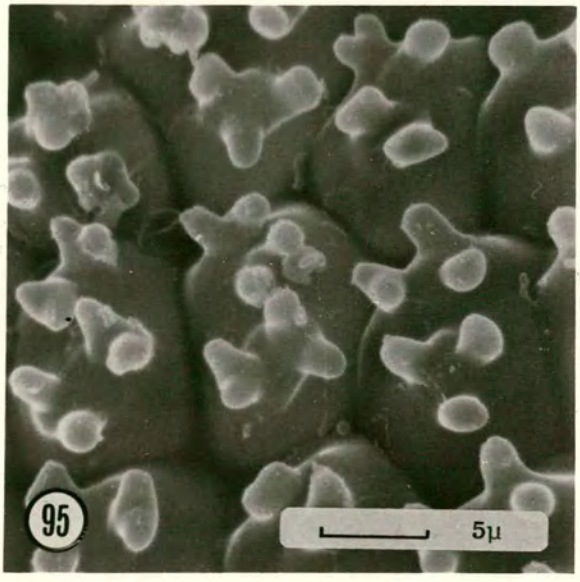
Figure 96 Upper lamina cell papillae of taxon I.
Magnification x 5,800.

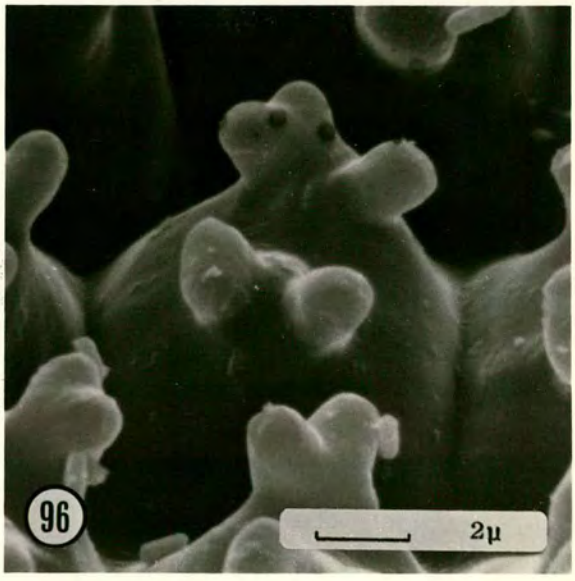

91
5µ


92
5µ


93
5µ


94
2µ


95
5µ


96
2µ

cells, were found to be smooth in all leaves (Figs. 102-104). The papillae on adaxial and abaxial surfaces of each leaf were identical.

Light microscope observations of papillae made on herbarium material suggested that some variation occurred between leaves of the same specimen and between specimens of the same species. This was confirmed by scanning electron microscopy and papillae observed in two taxon J specimens, for example, appeared slightly different (Figs. 97 and 98). In Fig. 97 the papilla processes appear longer than in Fig. 98.

Light microscopy also showed that some species had characteristic patterns of papillae. These could be classified into three types:

i) Very dense: dense papillae covered the entire surface of the upper lamina including the dividing walls between cells, (Fig. 105). This was observed in taxon H only and was an important diagnostic character.

ii) Dense: the papillae were seen only within the boundaries of cell walls but were densely packed, small and 'C'-shaped (Fig. 106). This was characteristic of taxa B and C.

iii) Sparse: the papillae were seen only within the boundaries of cell walls and were sparsely distributed and large 'C'-shaped (Fig. 107).

Figure 97 Upper lamina cell papillae of taxon J. Magnification x 2,550.

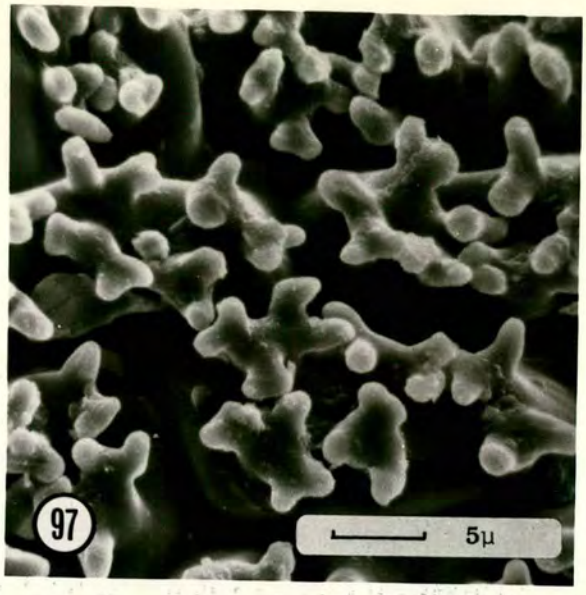
Figure 98 Upper lamina cell papillae of a young leaf of taxon J. Magnification x 5,600.

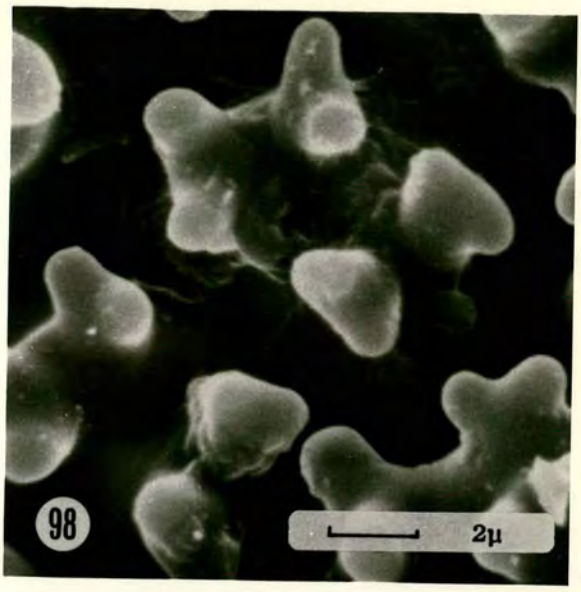
Figure 99 Upper lamina cell papillae of an old leaf of taxon J. Magnification x 6,200.

Figure 100 Upper lamina cell papillae of taxon K. Magnification x 2,600.

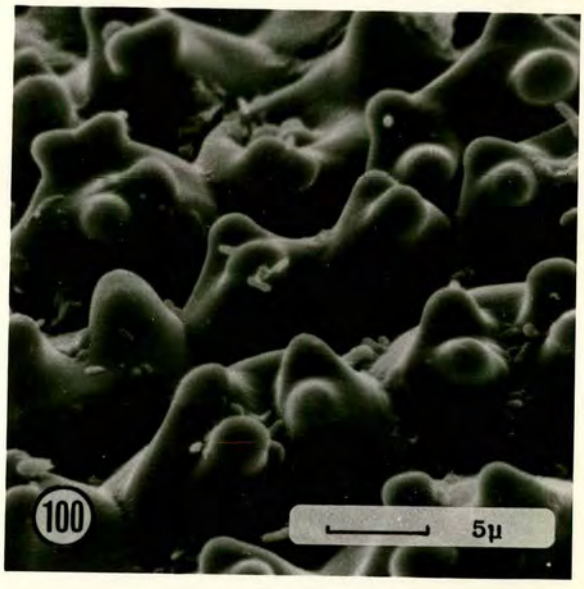
Figure 101 Upper lamina cell papillae of taxon L. Magnification x 2,200.

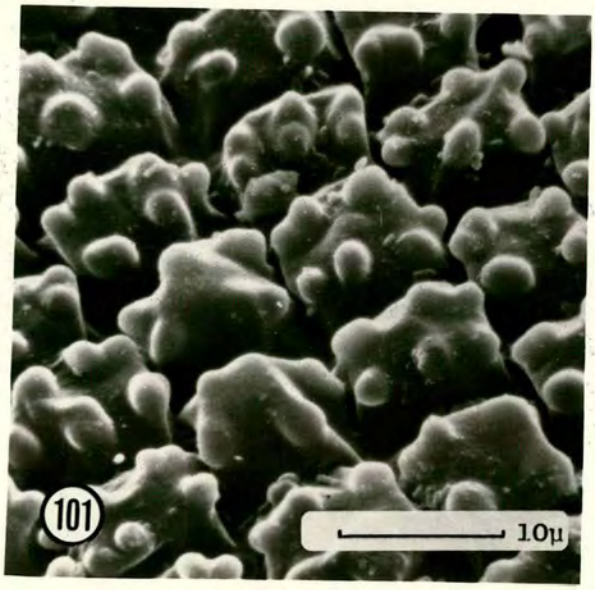
Figure 102 Transition between leaf base and upper lamina in taxon K. Magnification x 270.


97
5μ


98
2μ


99
2μ


100
5μ


101
10μ

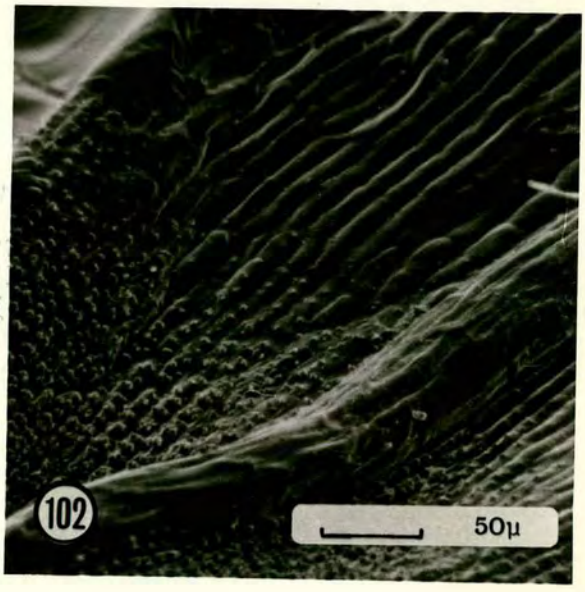
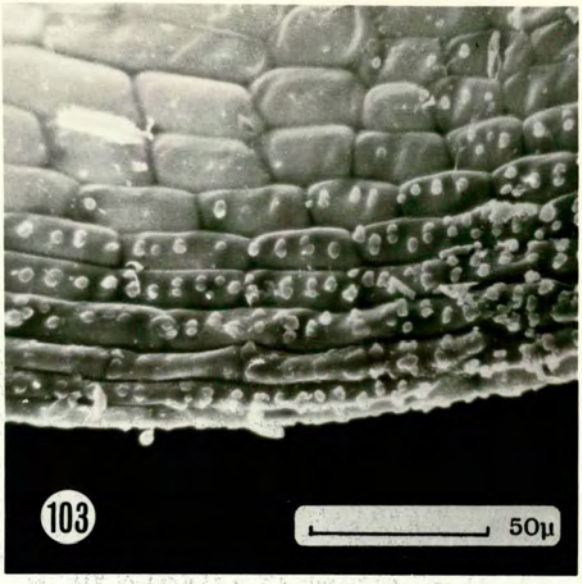

102
50μ

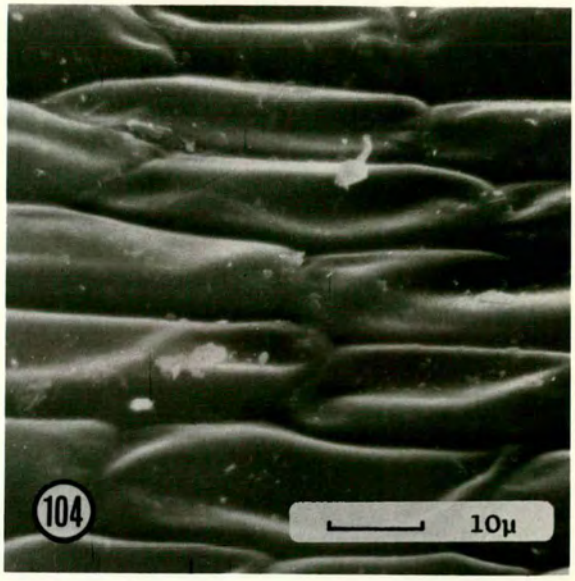
Figure 103 Transition zone between papillose upper lamina cells and smooth basal cells in taxon E. Magnification x 475.

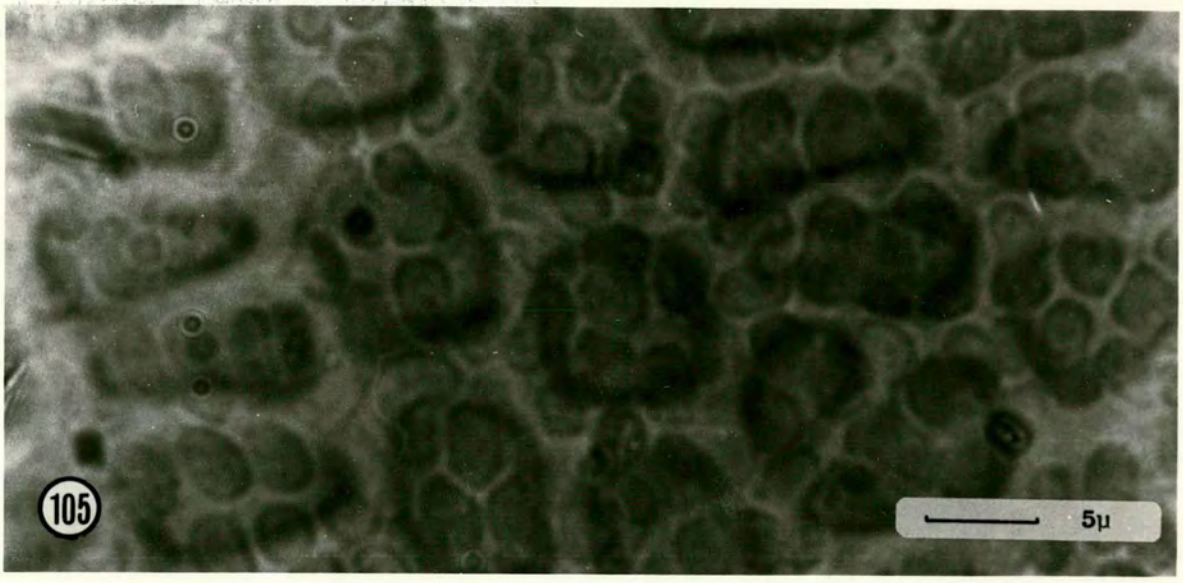
Figure 104 Smooth rectangular cells of leaf base in taxon D. Magnification x 1,200.

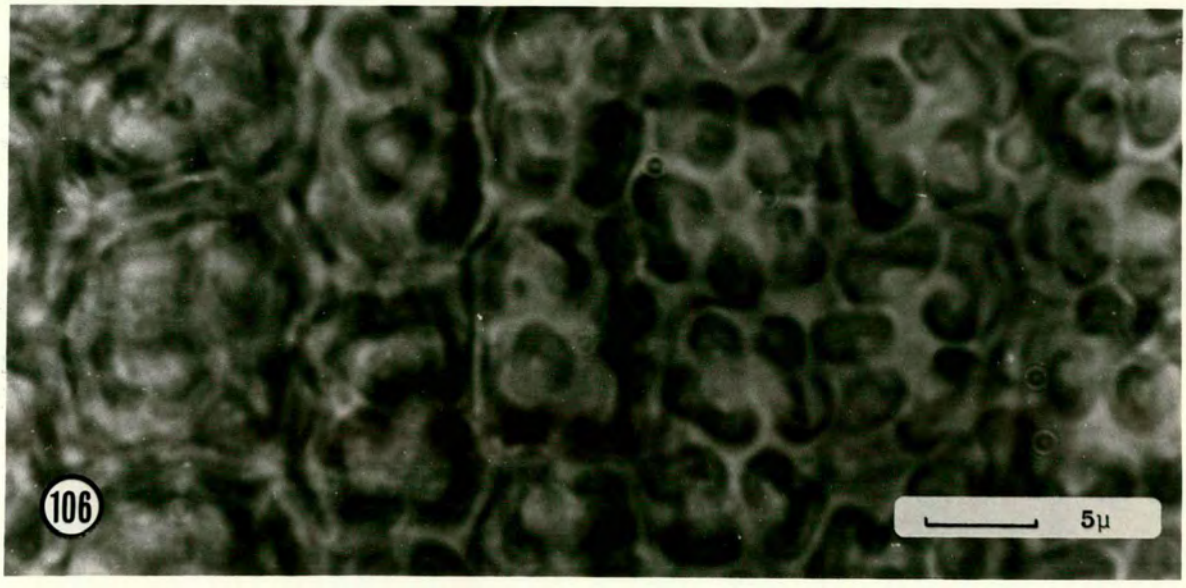
Figure 105 Light micrograph of upper lamina cells of taxon H showing very dense papillae. Magnification x 2,900.

Figure 106 Light micrograph of upper lamina cells of taxon B showing dense papillae. Magnification x 2,900.


103
50µ


104
10µ


105
5µ


106
5µ

This was characteristic of taxa A, D, E, F, G, I, J, K and L.

The scanning electron micrographs show, as Robinson (1971) and Lewinsky (1974) have remarked, that none of the lamina papillae are 'C' shaped. They are rounded (Fig. 89) to lobed (Fig. 98) or branched (Fig. 87) processes of the bulging, convex surfaces of the cells. The 'C' shaped appearance under the light microscope is perhaps produced by the refraction of light from the rounded surfaces of the papillae and this can be misleading.

Lamina papillae of Taxon H, which appear very dense under the light microscope, are also densely packed in scanning electron micrographs (Figs. 93 and 94). Nothing is visible below the papillae, and this agrees with the light microscope observations which show that the papillae cover the entire surface of the upper lamina. Micrographs of taxon B and taxon C papillae show a moderately dense arrangement (Figs. 86, 87 and 88) but the papillae of other taxa, such as taxa A, G and I, show well spaced simple papillae with few processes (Figs. 85, 92, 95 and 96).

As light microscopy suggests, the distinctive feature of the papillae of taxa B, C and H is their density. This is dependent not only on the number of papillae per cell and the cell size, but also on the degree of branching of the papillae. The three taxa have cells somewhat smaller than the other taxa, but the micrographs suggest that their papillae are also more branched. None of these papillae are as complex as those

illustrated by Casas de Puig and Molinas (1974) which are described as branched and raised on a long foot.

South Georgian Tortula taxa therefore have lamina cell papillae which differ in the density of processes on the cell surfaces. These differences are constant between taxa and are useful taxonomic characters.

6.3 Lamina cell papillae: internal structure

Method and Results. During the examination of the surfaces of critical-point dried leaves, fractures were observed which were useful for investigating the internal structure of papillae. Critical-point dried leaves of several taxa were therefore deliberately torn before SEM examination.

Scanning electron micrographs of leaf fractures are given in Figs. 108-11.

Discussion. The micrographs show that the papillae are hollow (Figs. 108 and 109) and this agrees with the results published by Proctor (1979). Figs. 110 and 111 also indicate that cytoplasmic protuberances reach into the papilla cavities. These do not appear to have been demonstrated previously but are consistent with Proctor's (1979, 1982) theory regarding the function of the papillae. They are believed to have a double function, firstly to form a series of channels (between papillae) which act as an external water conduction system, and secondly to act as sites of gas exchange between the cell and the atmosphere. The protuberance of cytoplasm into the papilla may enable the efficient movement of carbon dioxide

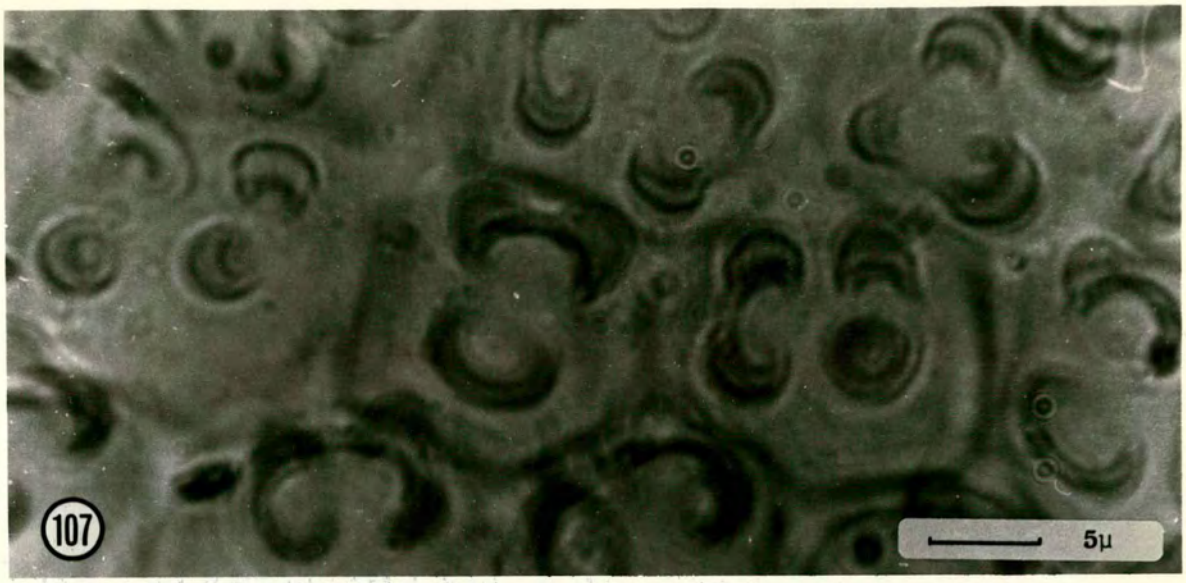
Figure 107 Light micrograph of upper lamina cells of taxon G showing sparse, 'C'-shaped papillae. Magnification x 2,900.

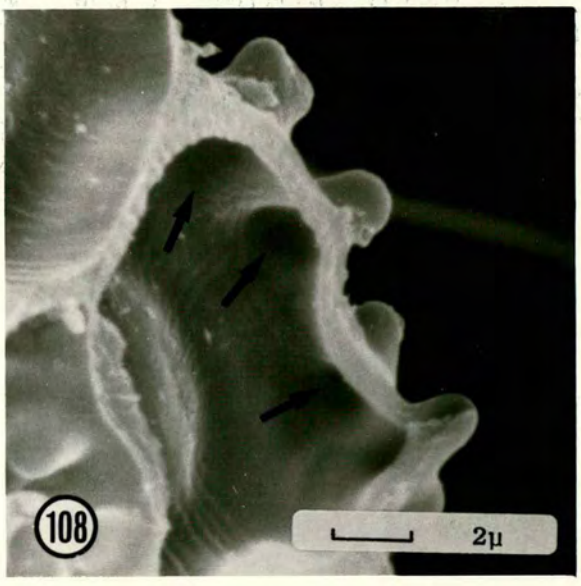
Figure 108 Torn leaf of taxon J showing hollow papillae. Magnification x 5,200.

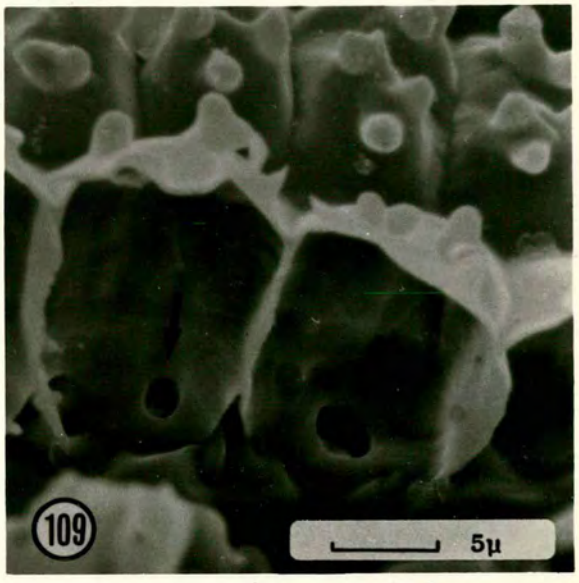
Figure 109 Torn leaf of taxon I showing hollow papillae. Magnification x 2,800.

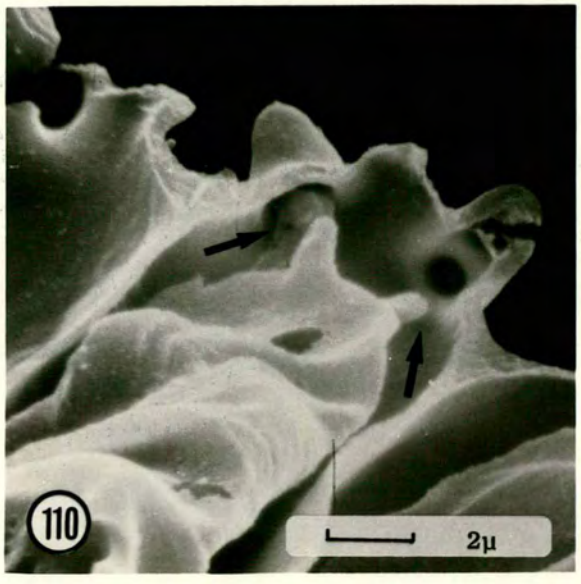
Figure 110 Torn leaf of taxon E showing hollow papillae and cytoplasmic protuberances. Magnification x 5,800.

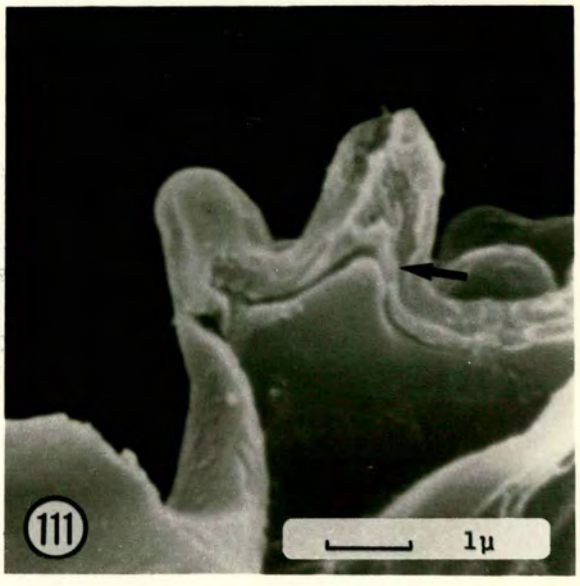
Figure 111 Torn leaf of taxon J showing cytoplasmic protuberance. Magnification x 11,000.


107
5µ


108
2µ


109
5µ


110
2µ


111
1µ

and oxygen into and out of the leaf cells.

The presence of cytoplasm inside the papillae may affect their refractive properties and hence their appearance under the light microscope. Papillae appear to be more prominent on young leaves than old, for example, and it has been suggested that this is due to the papillae being worn away as the leaves age (S.W. Greene, personal communication). Scanning electron micrographs of surfaces of both young and old leaves taken from the same specimen (Figs. 98 and 99) show that the papillae are similar in size and shape regardless of age. The old leaf is more soiled with dust and bacteria but there are no signs of abrasion. Differences in the appearance of the papillae may be due to the absence of cytoplasm in the papillae of dead cells in old leaves, and this may alter their refractive properties.

6.4 Nerve cell papillae

Nerve characters have been important in the classification of the Pottiaceae since Limpricht (1888) and Saito (1975) regarded the cells of the nerve surfaces as "useful criteria of genera, subgenera, sections and species". The 'roughness' or papilla type on the abaxial (dorsal) surface of the nerve has been used as a key character in Tortula by Dixon (1923), Sainsbury (1955) and Kramer (1980). An examination of South Georgian material by light microscopy indicated that there were differences in abaxial nerve papillae between taxa, and that variation occurred between different parts of the nerve surface. The character was difficult to see because of the

density of the nerve, but scanning electron micrographs could show nerve surfaces without difficulty. The SEM was therefore used to study nerve surfaces and particular attention was paid to taxa I and L as the structure of the nerve in the upper part of the leaf was an important distinguishing feature of these taxa.

Results. Scanning electron micrographs of adaxial (ventral) nerve surfaces are shown in Figs 112-115 and abaxial surfaces in Figs 116-128.

Discussion. The adaxial nerve surfaces of South Georgian taxa were all very similar. The cells were more or less quadrate, similar in size to the lamina cells with similar papillae (Figs 112 and 113). The nerve cells were occasionally elongated compared to adjacent lamina cells (Figs 114 and 115) but this did not appear to be taxonomically significant.

The abaxial nerve surface of taxon I in mid and lower leaf (Fig. 116) was similar to that of taxon J (Fig. 117) and all other taxa except L, in being composed of smooth or simply papillose long-rectangular stereid cells. In the upper part of the leaf, where light microscopy showed the nerve was obscure, the adaxial cells were shorter and more papillose. Immediately below the leaf apex the abaxial cells were typically quadrate with slightly lobed papillae (Fig. 118).

In taxon L a similar transition of cells was observed but the nerve was weaker and narrower than in taxon I and had no long-

Figure 112 Adaxial nerve surface of a leaf of taxon B. Magnification x 1,150.

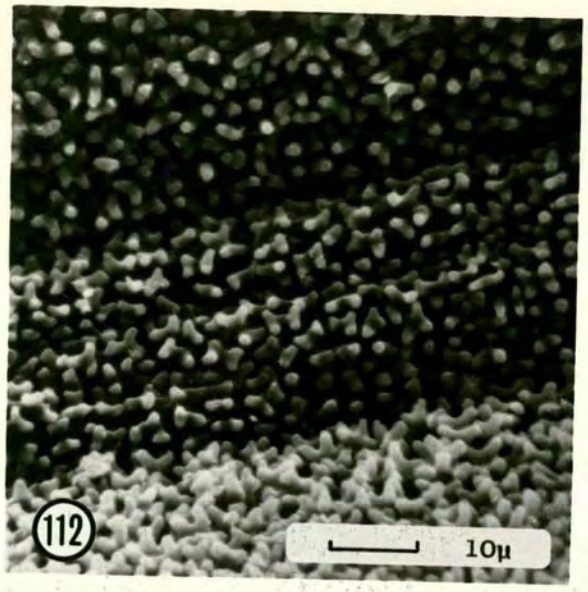
Figure 113 Adaxial nerve surface of a leaf of taxon C. Magnification x 1,100.

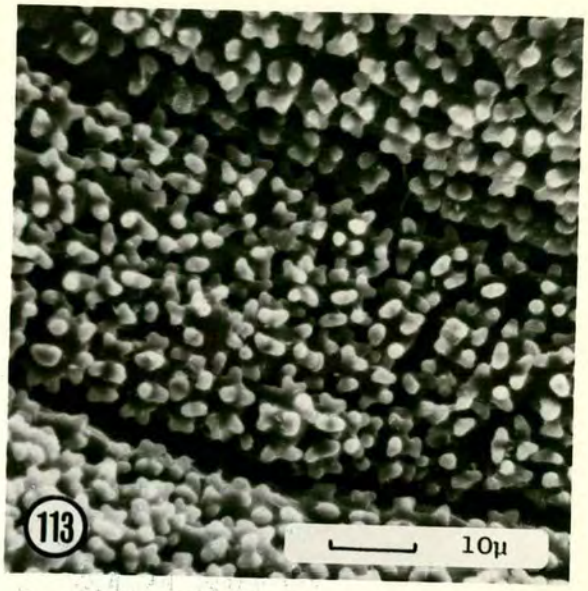
Figure 114 Adaxial nerve surface of a leaf of taxon K. Magnification x 650.

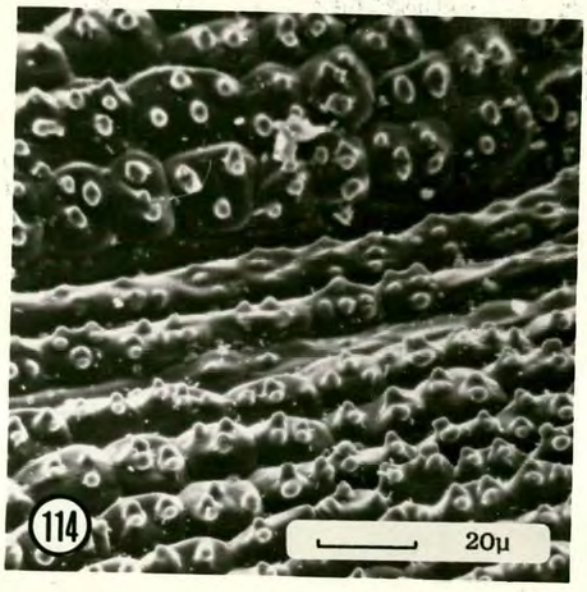
Figure 115 Adaxial nerve surface of a leaf of taxon F. Magnification x 630.

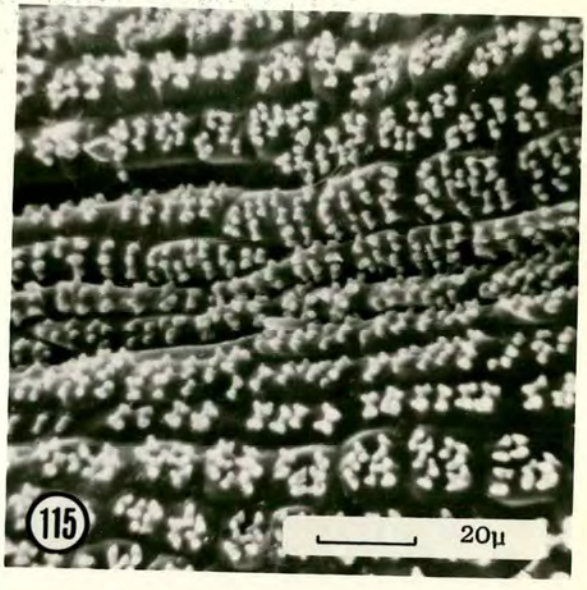
Figure 116 Abaxial nerve surface of a leaf of taxon I. Magnification x 1,200.

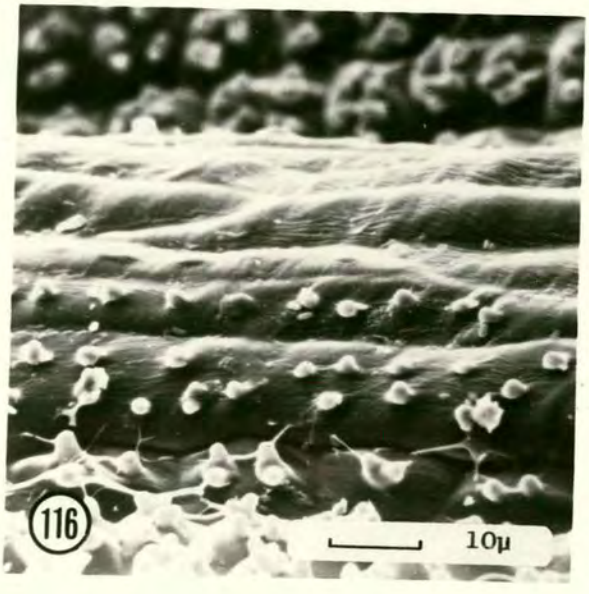
Figure 117 Abaxial nerve surface of a leaf of taxon J. Magnification x 620.

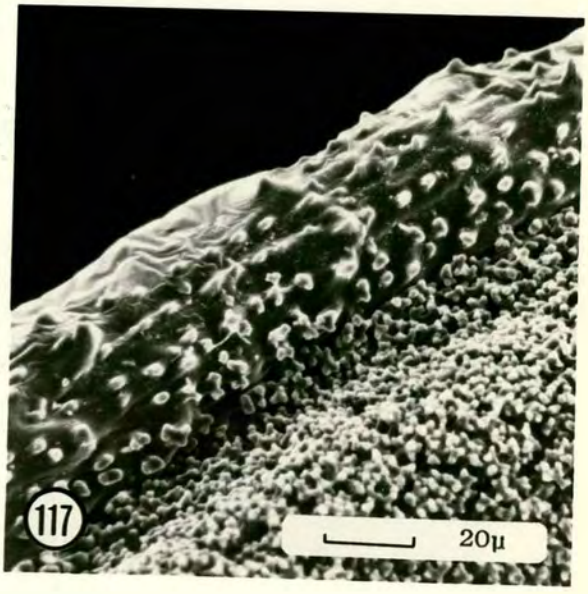

112
10μ


113
10μ


114
20μ


115
20μ


116
10μ


117
20μ

rectangular stereid cells on the abaxial surface. In mid and lower parts of the leaf the abaxial cells were rectangular and papillose (Fig. 119). These were shorter towards the apex and, in leaves in which the nerve disappeared below the apex, were indistinguishable from the quadrate lamina cells (Fig. 120). The thickness of the nerve in such cases decreased to a single layer of cells as it merged into the lamina.

The abaxial nerve surfaces of all other taxa (A, B, C, D, E, F, G, H, J and K) were similar. They were composed of long-rectangular stereid cells which varied from being simply papillose (Figs 121 and 122) to almost smooth or smooth (Figs 123, 124 and 125). When papillae did occur they were usually most prominent near the junction with the leaf lamina (Figs 116 and 126). In some leaves irregular lumps or obscure teeth were also observed (Figs 117, 127 and 128). These were apparently formed by the projection of end walls of cells rather than the projection of cell lumina, which form the papillae. They occurred in the middle to upper region of the nerve and, though more common in some taxa than others, their presence also varied greatly between leaves and between specimens of the same taxon.

6.5 Peristomes

The peristomes of taxon A, non-hair-pointed, and taxon K, hair-pointed, were compared in a search for useful taxonomic characters.

Figure 118 Abaxial nerve surface of a leaf of taxon I showing the quadrate, papillose cells immediately below the leaf apex. Magnification x 1,200.

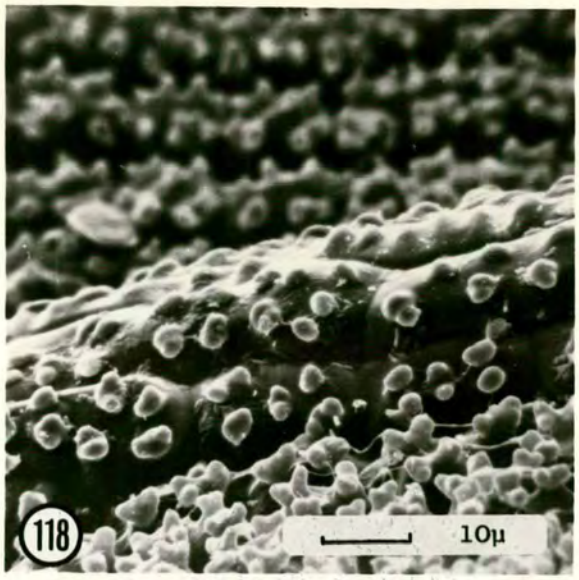
Figure 119 Abaxial nerve surface of a leaf of taxon L in mid-leaf showing rectangular papillose cells. Magnification x 1,000.

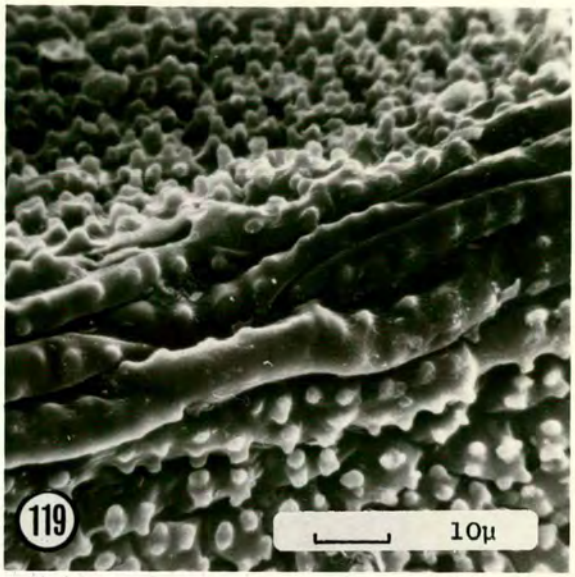
Figure 120 Abaxial cells of a leaf of taxon L between the end of the nerve and the leaf apex. Magnification x 1,920.

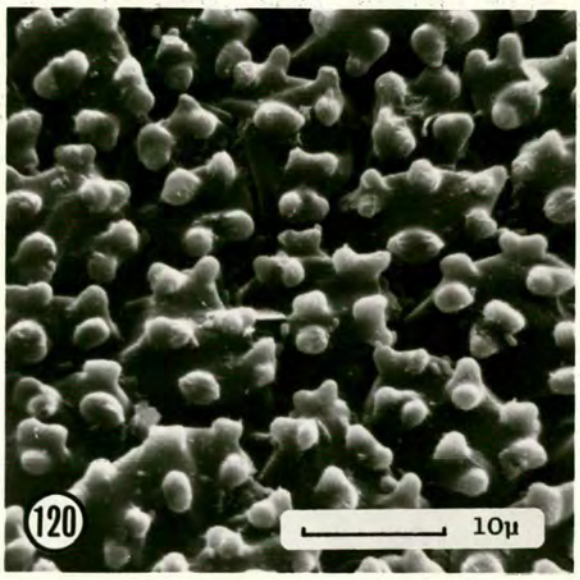
Figure 121 Abaxial nerve surface of a leaf of taxon F. Magnification x 560.

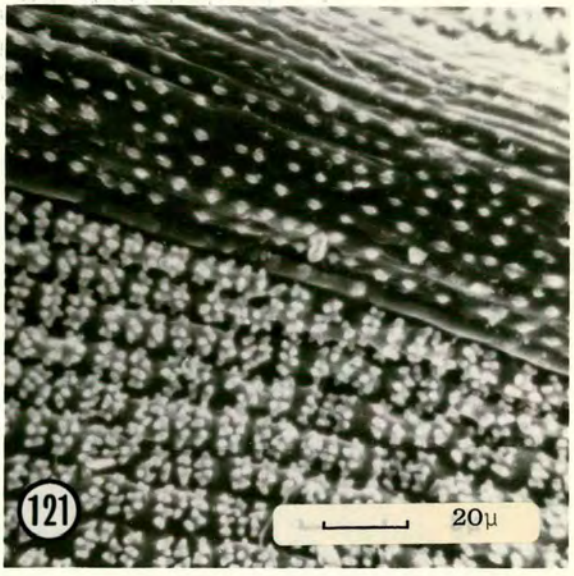
Figure 122 Abaxial nerve surface of a leaf of taxon B. Magnification x 570.

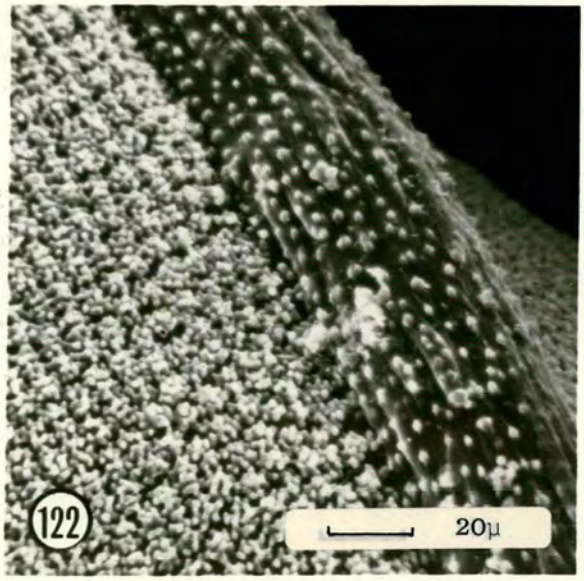
Figure 123 Abaxial nerve surface of a leaf of taxon J. Magnification x 620.


118
10μ


119
10μ


120
10μ


121
20μ


122
20μ

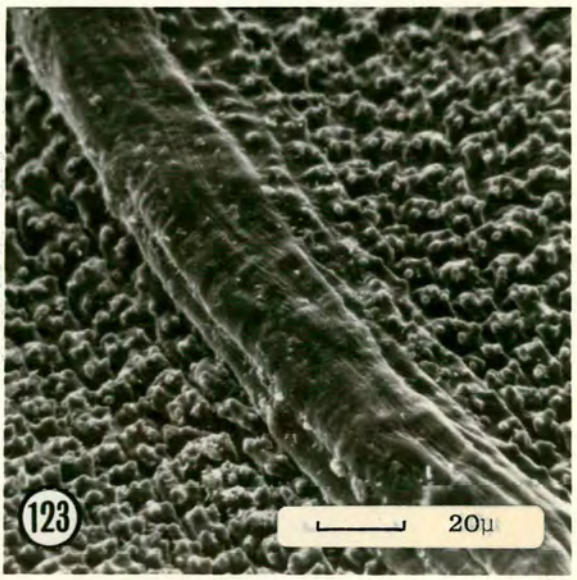

123
20μ

Figure 124 Abaxial nerve surface of a leaf of taxon H. Magnification x 600.

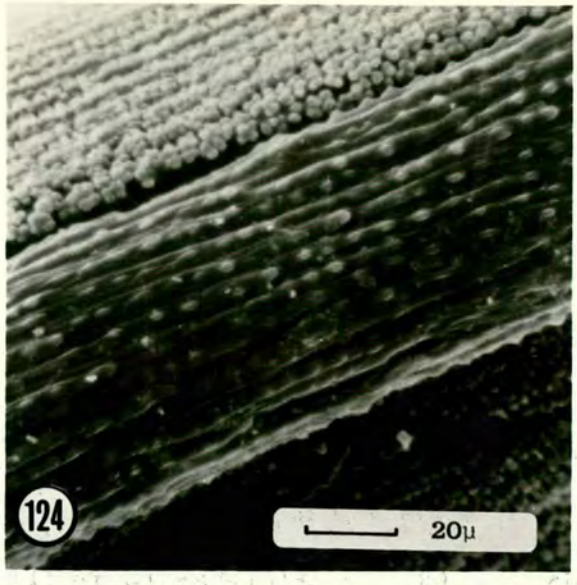
Figure 125 Abaxial nerve surface of a leaf of taxon D. Magnification x 580.

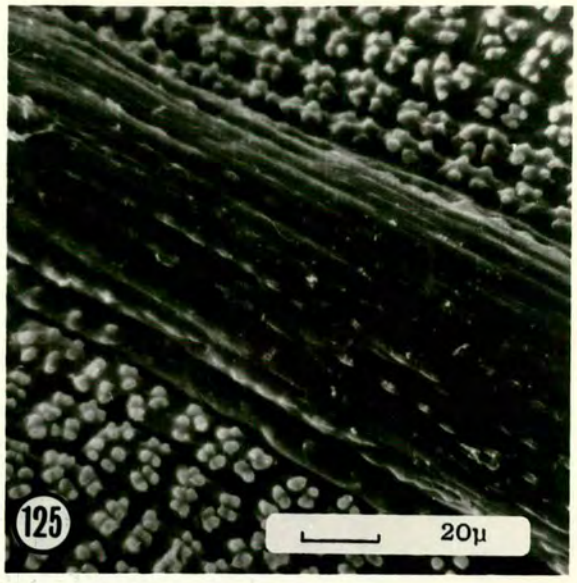
Figure 126 Abaxial nerve surface of a leaf of taxon C. Magnification x 570.

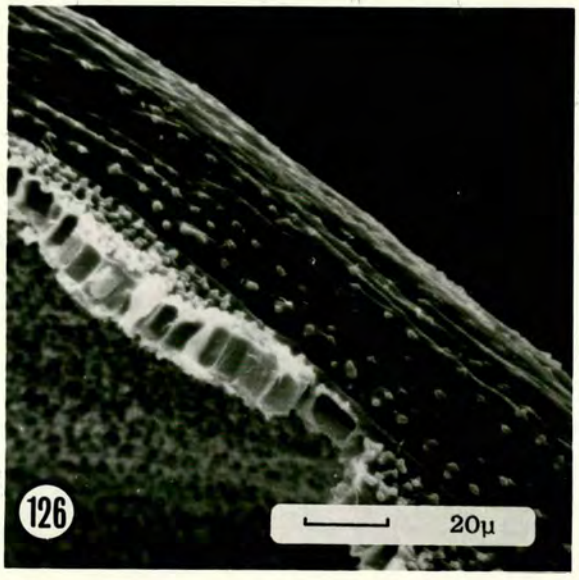
Figure 127 Abaxial nerve surface of a leaf of taxon K showing irregular lumps. Magnification x 680.

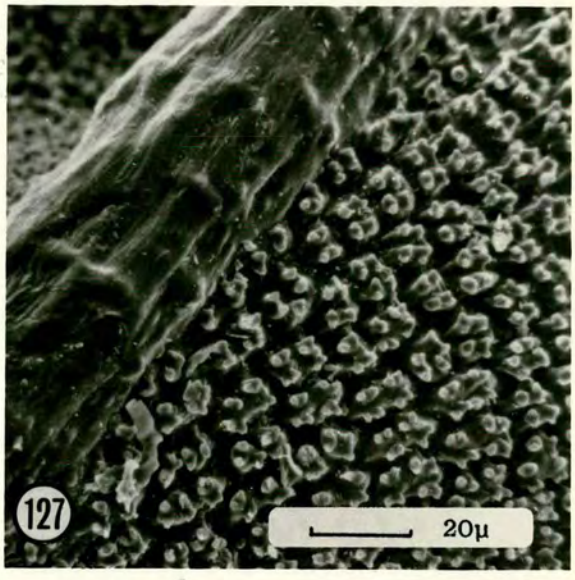
Figure 128 Abaxial nerve surface of a leaf of taxon C showing irregular lumps. Magnification x 570.

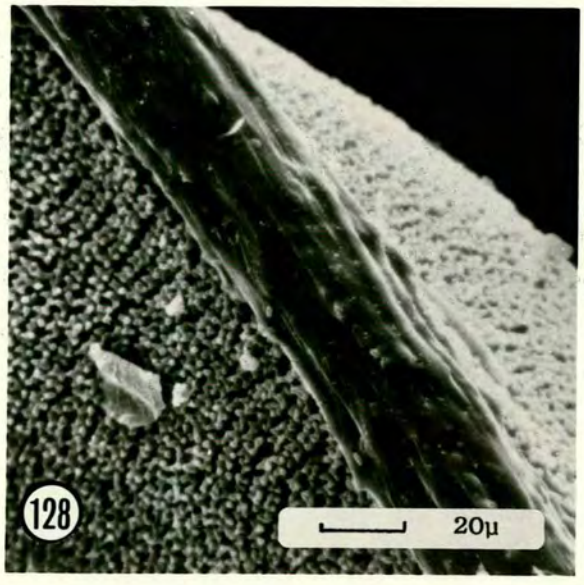
Figure 129 Outer surface of peristome tube of taxon A showing papillae. Magnification x 2,600.

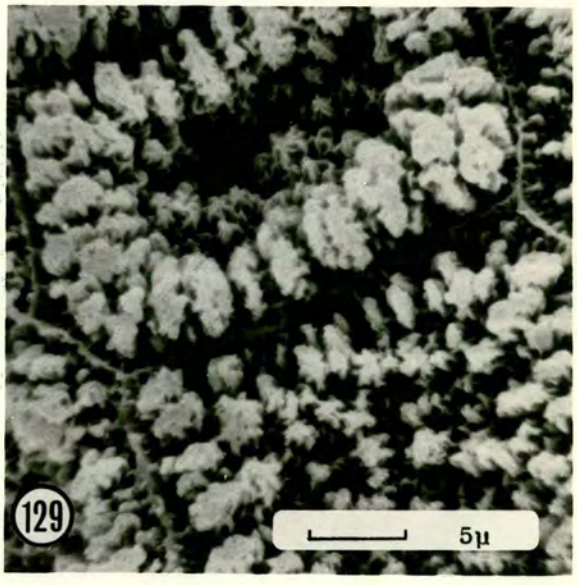

124
20μ


125
20μ


126
20μ


127
20μ


128
20μ


129
5μ

Results. Micrographs of peristomes of taxa A and K are shown in Figs 129 to 132.

Discussion. The outer surface of the peristome tubes of both taxa showed the same arrangement of papillae (Figs 129 and 130). This is also similar to the arrangements in published micrographs of other species, T. norvegica (Lewinsky 1974) and T. ruralis (Robinson 1971), for example. The outer surfaces of peristome teeth in taxa K (Fig. 131) and A were also identical. Comparable micrographs appear to have been published only by Robinson (1971) who shows a peristome tooth of T. ruralis. This is similar to that observed in taxon K (Fig. 132). Lewinsky (1974), after examining the peristome of T. norvegica by SEM, commented that the type of papillae on both peristome tube and peristome teeth were identical. This was also true of the two taxa examined here, and the papillae appeared the same as those illustrated by Robinson (1971) for T. ruralis.

6.6 Spore surfaces

Results. Micrographs of the exine surface of spores of only 2 taxa were obtained due to the scarcity of mature sporophytes. Micrographs of taxon A and taxon K spores are shown in Figs 133 and 134.

Discussion. Spores of taxon A (Fig. 133) appear to be gemmate (Fig. 136) with individual gemmae sometimes converging to form ridges or irregular lumps. Spore surfaces of taxon K (Fig. 134)

Figure 130 Outer surface of peristome tube of taxon K. Magnification x 600.

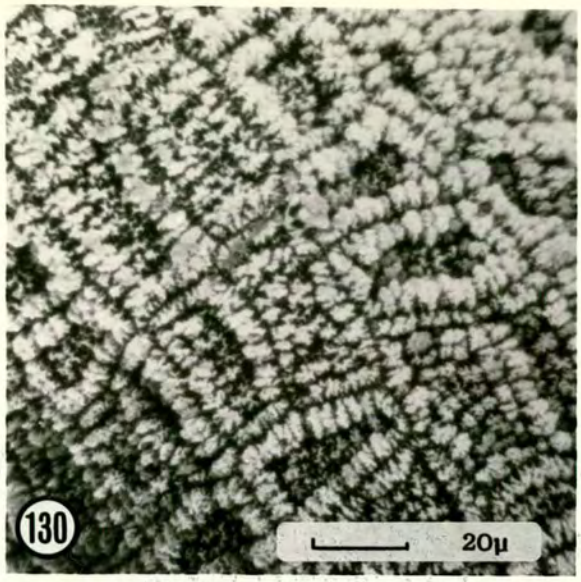
Figure 131 Outer surfaces of peristome teeth of taxon K. Magnification x 1,200.

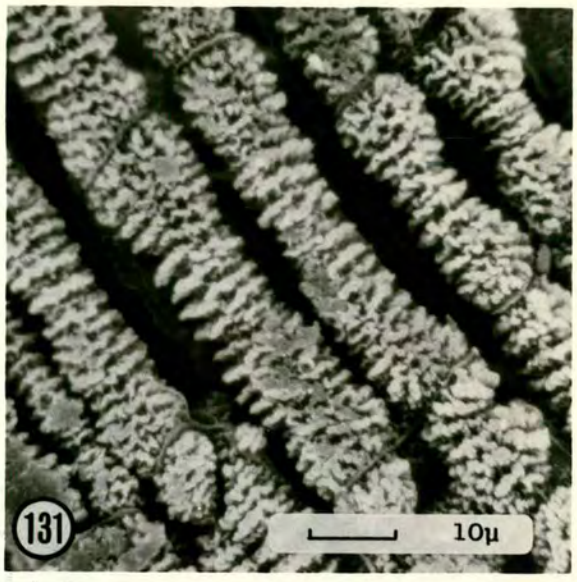
Figure 132 Inner surface of peristome tooth of taxon K. Magnification x 6,000.

Figure 133 Spores of taxon A. Magnification x 6,200.

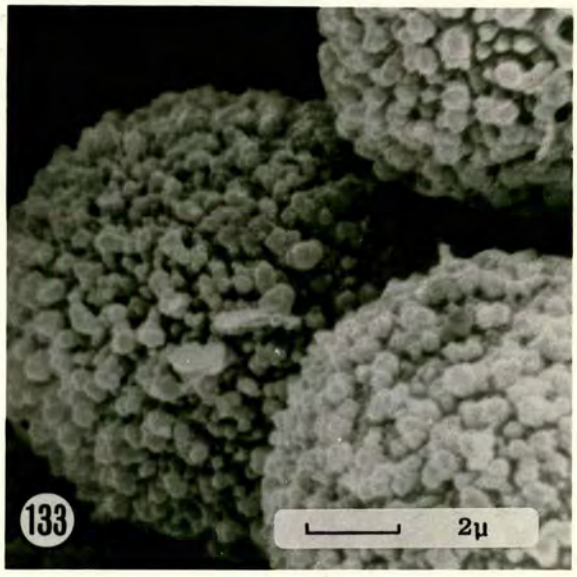
Figure 134 Spores of taxon K. Magnification x 11,200.

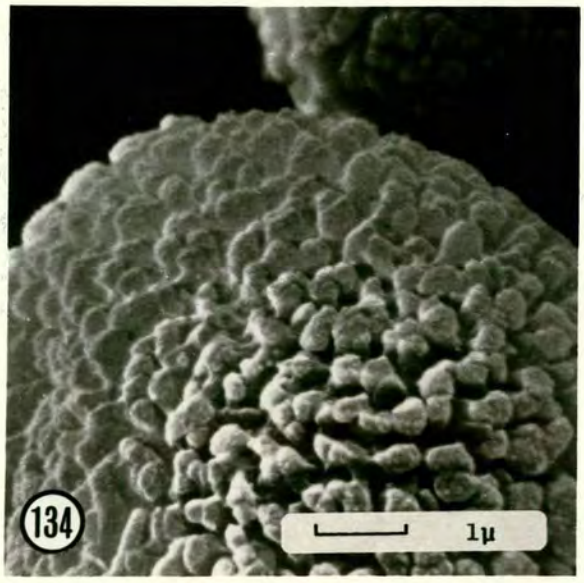
Figure 135 Rhizoids of taxon J. Magnification x 2,400.

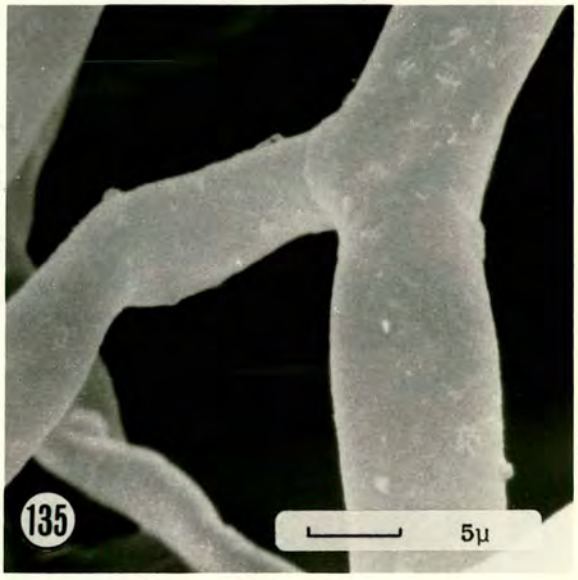

130
20µ


131
10µ


132
2µ


133
2µ


134
1µ


135
5µ

are verrucate (Fig. 136) and also show some convergence of the processes into ridges.

Exine surfaces of many European Tortula species have been examined by Lewinsky (1974) using transmission electron microscopy and were described as finely papillose or papillose with conical or rounded papillae. Using LO-analysis light microscopy (Erdtman, 1969) Boros and Jarai-Komlodi (1975) examined the spores of T. muralis Hedw., T. subulata Hedw. and T. ruralis. All were similar, having pilate processes (Fig. 136) which were confluent to some extent. Saito and Hirohama (1974) studied the surfaces of T. muralis and T. princeps De Not. spores by SEM. T. muralis had densely verrucose spores, but T. princeps spores were described as gemmate, with the gemmae sometimes connecting to form short ridges.

There is therefore evidence of some variation in spore surfaces within Tortula but this is small compared to that in the genus Pottia, for example, where spore surfaces are a valuable means of distinguishing species (Chamberlain 1978).

6.7 Other characters

6.7.1 Rhizoids. Rhizoids of the family Bartramiaceae were studied by Hirohama and Iwatsuki (1980) using SEM techniques. On the basis of rhizoid ornamentation, the genera could be divided into two groups which correlated well with characters such as the branching pattern of stems. Micrographs of Tortula rhizoids obtained during this study (Fig. 135) showed that all

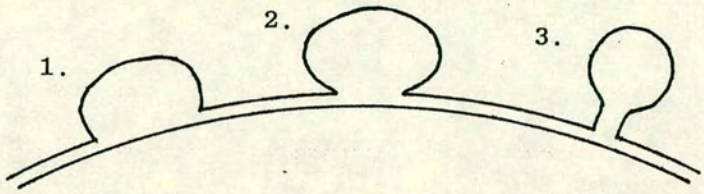


Figure 136 Spore surface processes in cross section:
1. verruca 2. gemma 3. pilum
(from Boros and Járai-Komlódi, 1975)

were smooth and featureless. The SEM clearly showed the origin of the rhizoids, and in taxon J they were found to develop from abaxial nerve cells at the leaf base (Fig. 137).

6.7.2 Leaf margins. Examination of leaf margins by SEM showed that they tended to be recurved (Figs 138 and 139) or revolute (Fig. 140).

Teeth on the upper leaf margin and at the leaf apex were found to be processes of papillose cells (Fig. 141) although the teeth themselves were smooth, sometimes with a single papilla towards the apex (Fig. 142). In some specimens the teeth and upper margins appeared worn and were striate with fine lines (Fig. 143). This could be an effect of desiccation or due to other environmental factors as light microscopy showed that only older leaves were damaged in this way.

6.7.3 Leaf apices. The areolation at the leaf apex was found to be an important character for distinguishing species during herbarium studies. Scanning electron micrographs of leaf apices of several taxa were obtained (Figs 144-147). The apical cusps of taxon B leaves were found to be obscurely toothed and warty with a few simple papillae (Fig. 144). The more finely tapered leaf apex of taxon C was smooth or obscurely crenate (Fig. 145). Hair-points were usually denticulate (Fig. 146) and composed of smooth, long, narrow cells slightly twisted into a helix (Fig. 147).

6.8 Conclusions

Figure 137 Leaf base of taxon J showing rhizoids produced from abaxial nerve surface. Magnification x 190.

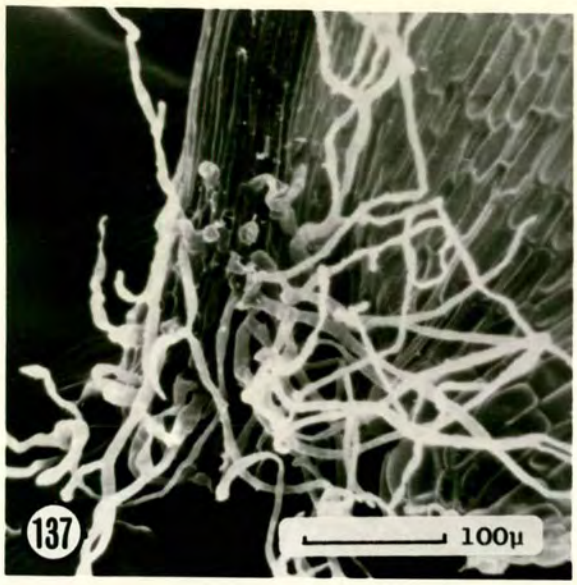
Figure 138 Revolute leaf margin of a leaf of taxon C. Magnification x 2,300.

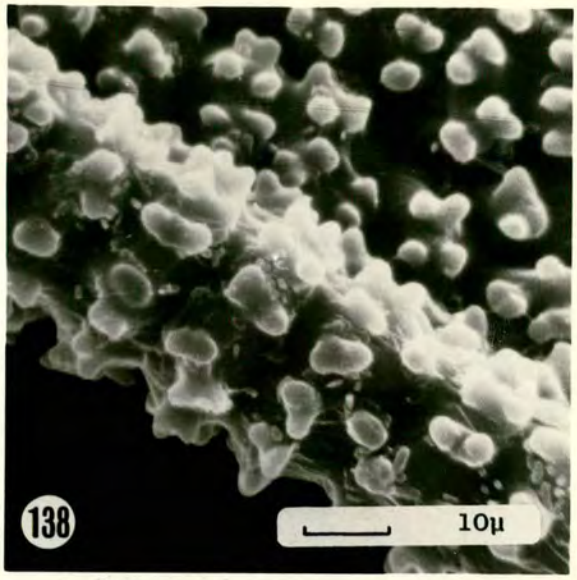
Figure 139 Recurved leaf margin of taxon J. Magnification x 1,150.

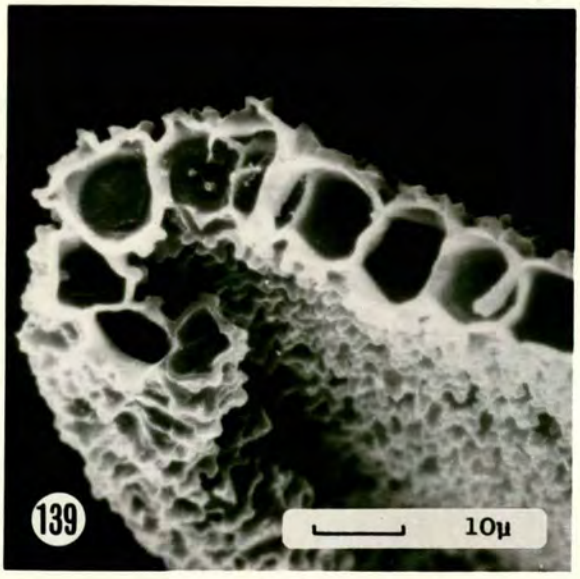
Figure 140 Revolute leaf margin of taxon J. Magnification x 1,000.

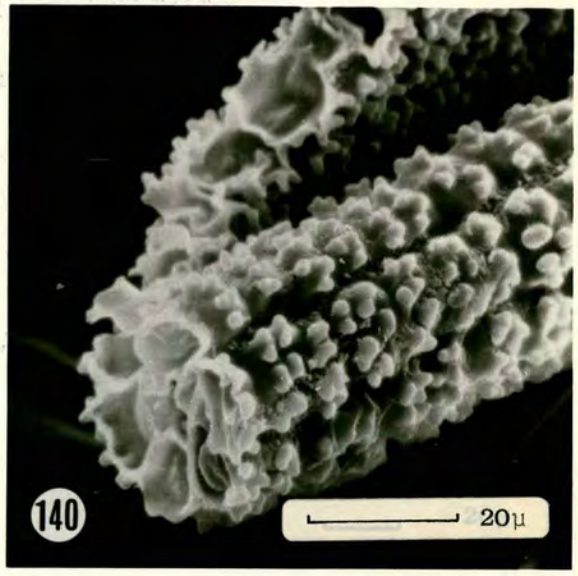
Figure 141 Teeth on upper leaf margin of taxon E. Magnification x 1,200.

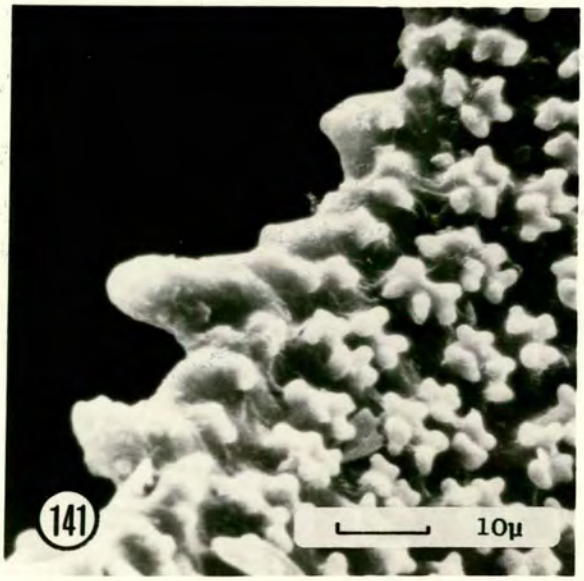
Figure 142 Leaf apex of taxon A. Magnification x 960.


137
100µ


138
10µ


139
10µ


140
20µ


141
10µ

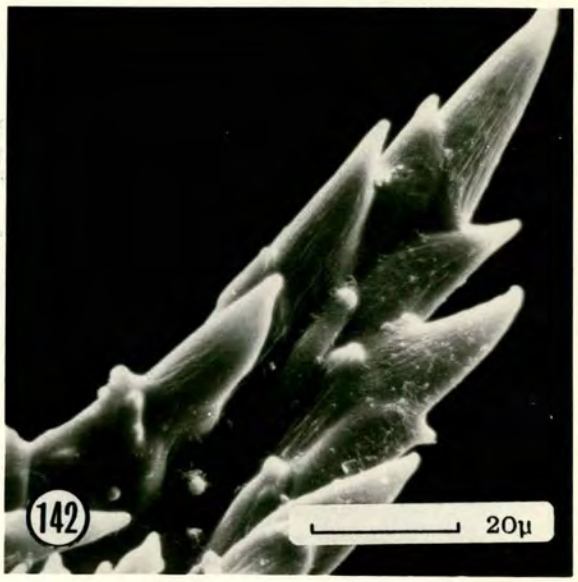

142
20µ

Figure 143 Teeth on upper leaf margin of taxon D. Magnification x 920.

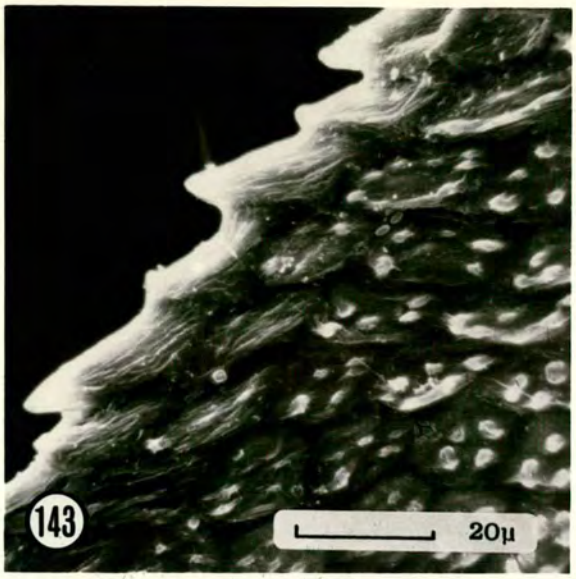
Figure 144 Leaf apex of taxon B. Magnification x 460.

Figure 145 Leaf apex of taxon C. Magnification x 184.

Figure 146 Leaf apex of taxon I. Magnification x 560.

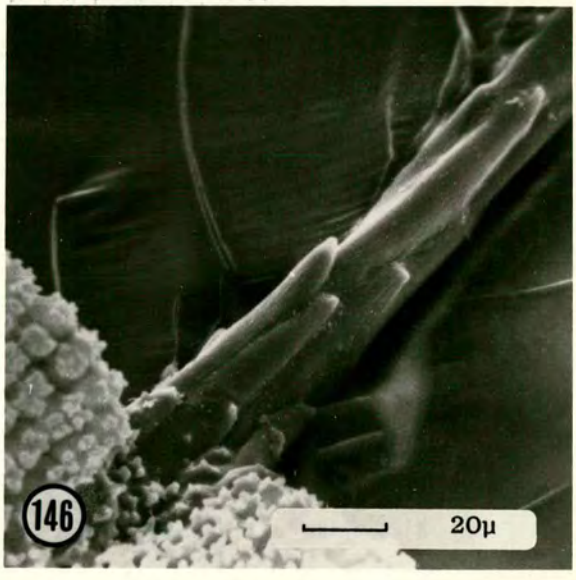
Figure 147 Hair-point of leaf of taxon J. Magnification x 500.

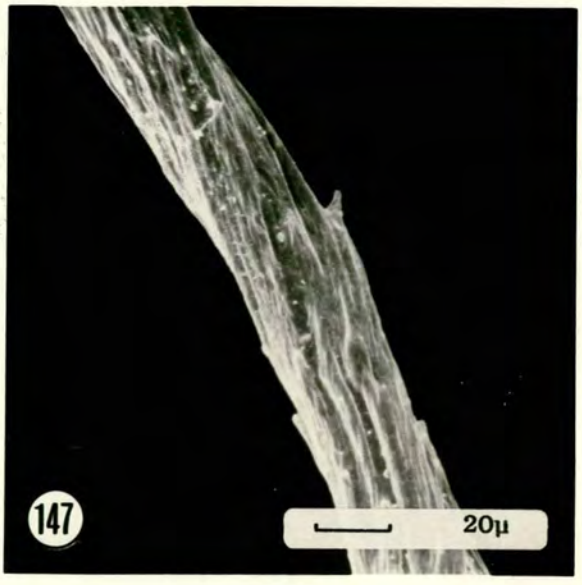
Figure 148 Upper lamina cells of taxon J in an air dried state. Magnification x 1,920.

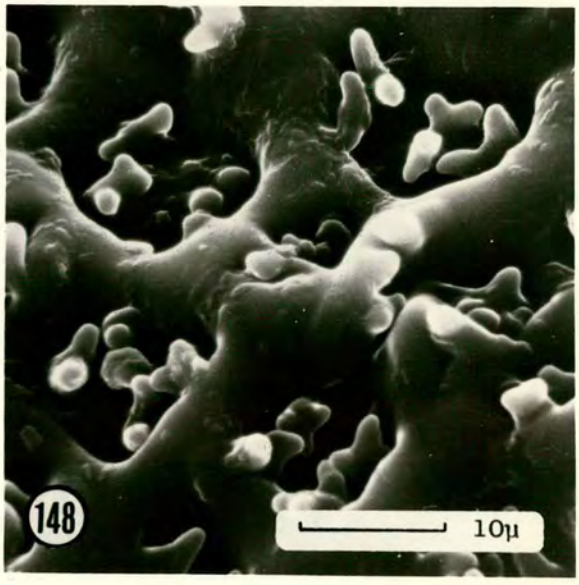

143
20μ


144
50μ


145
100μ


146
20μ


147
20μ


148
10μ

Magill et al (1974) discussed the use of critical-point drying in scanning electron microscope studies of bryophytes. They showed that the results obtained were superior to the simple coating of air-dried material. This was also true in Tortula specimens, air-dried leaves of which are strongly twisted and difficult to examine. Leaf cells in these leaves were collapsed and the papillae shapes were difficult to interpret (Fig. 148). Although the air-dried state is not an unnatural one for mosses of this genus, critical-point dried material of both leaves and spores was found to be the most successful method of preparation.

Scanning electron microscopy was found to be an excellent technique for examining papillae on the leaf and nerve surfaces. Variation in density and complexity of branching of the lamina cell papillae was observed between species, and the density of papillae is now known to be an important taxonomic character in separating taxon H from other taxa. The SEM was also valuable for investigating the internal structure of papillae.

Abaxial nerve surfaces had only simple papillae and obscure teeth in South Georgian taxa, but Kramer (1980) reported branched papillae in European material. This character seems to be taxonomically significant, even though significant variation was found only in taxa I and L. In these taxa differences in the shape and papillosity of the cells were linked to changes in nerve structure which were easily seen under the light microscope. It is likely, however, that

scanning electron microscopy will be important in investigating abaxial nerve surfaces of other sub-Antarctic Tortula species such as T. subantarctica Sainsb., which appears similar to taxon F but is reported to have a highly papillose abaxial nerve surface (Sainsbury 1950).

SEM study of Tortula peristomes can show papillae which are difficult to see using the light microscope. Scanning electron micrographs obtained during this study compared with those given in previous publications (Robinson 1971, Lewinsky 1974) suggest that these papillae are similar in all species. There is a need, however, for future work to compare peristome surfaces of many other species.

Micrographs of Tortula spores obtained here and those given by Saito and Hirohama (1974) do suggest that there is some variation in exine surfaces. Insufficient work has been done to establish whether these differences are constant between species or are part of a non-specific pattern of variation.

Chapter 7 : TAXONOMIC CONCLUSIONS AND DESCRIPTIONS OF SOUTH GEORGIAN *Tortula* TAXA

7.1 Introduction

Conclusions drawn from herbarium studies, measurements, statistics, growth experiments and scanning electron microscopy are combined in the following account of South Georgian *Tortula* taxa. The rank of each taxon is assigned after a summary of the evidence available, the nomenclature is discussed and a final name provided. Descriptions, figures, and habitat and distribution notes are given, and a key for distinguishing the taxa is presented.

The terminology used in the descriptions follows Smith (1978) except in describing papillae and the twisting of setae and peristomes which follows Stearn (1966). Terms used for describing papillae density refer to the patterns discussed in Chapter 6. Unless otherwise stated, all lamina cells described and measured are taken from the upper part of the leaf, about one third from the apex, mid-way between the nerve and the margin. The frequency of species in collections is used as a guide to the relative abundance of the plants on South Georgia. Collectors may gather some species in preferance to others so this is not ideal, but terms such as 'frequent', 'occasional' and 'rare' are not quantifiable and can only have an approximate meaning.

Full details of all type specimens examined are given in the text. Herbarium abbreviations used follow Holmgren *et al* (1981). A full list of specimens examined is given in Appendix 5.

7.2 Taxon A : Taxonomy

7.2.1 Rank Herbarium specimens of this taxon were distinct in their lingulate - spathulate leaves with a border of long-rectangular cells extending up the leaf margin. No other South Georgian species was liable to be confused with it. Growth experiments could not be conducted due to lack of living material, but the differences in characters suggested that the taxon should be recognised as a species.

7.2.2. Nomenclature The earliest name for this taxon appears to be Barbula arenae Besch. which was described by Bescherelle (1885) from material collected in Tierra del Fuego. Type material has been located [Barbula arenae Besch., Punta Arenas de Magellan. 7 Mai 83, Hariot No. 37, Herb. Emil Bescherelle 1900, BM], 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 [Expeditio suecica 1908-09, No. 22 Tortula lingulaefolia Card. sp. nova, Georgia australis: Cumberland Bay, Moraine Fiord. Leg. C. Skottsberg 1909, H-BR two specimens, PC]. All were typical specimens of taxon A and T. lingulaefolia can thus be regarded as a synonym of T. arenae.

New Zealand plants of T. petriei Broth. were found to be similar to this species. The type specimen was examined [Tortula petriei Broth n. sp. Kelly's Hill, Westland, Leg. D. Petrie, BM, FH] which confirmed that the species differed only in having a more strongly differentiated border to the leaf and a nerve which was thicker

in upper leaf and slightly excurrent at the apex. T. petriei appears to be a geographical variant of T. arenae and is therefore considered as a subspecies.

T. arenae ssp. petriei (Broth.) P.J. Lightowlers comb. et stat. nov. in preparation.

The correct name and synonymy for taxon A is therefore as follows:

Tortula arenae (Besch.) Broth. ssp. arenae

syn. T. lingulaefolia Card. et Broth.

7.2.3. Description Stems erect, forming cushions or turves, 0.4-3.0cm high, sparingly branched, with or without a central strand. Leaves 1.9-3.7 (-4.0) mm x 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 a chlorophyllose, papillose upper limb and a hyaline, smooth sheath, the latter sheathing the stem for one quarter - one third of 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 coloured reddish. Abaxial surface of nerve smooth or papillose with simple verrucate papillae. Lamina cells 9.5-17 μ wide, 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 shortly rectangular to longly rectangular, 2 to 8 times as long as wide, hyaline, smooth, sometimes lax

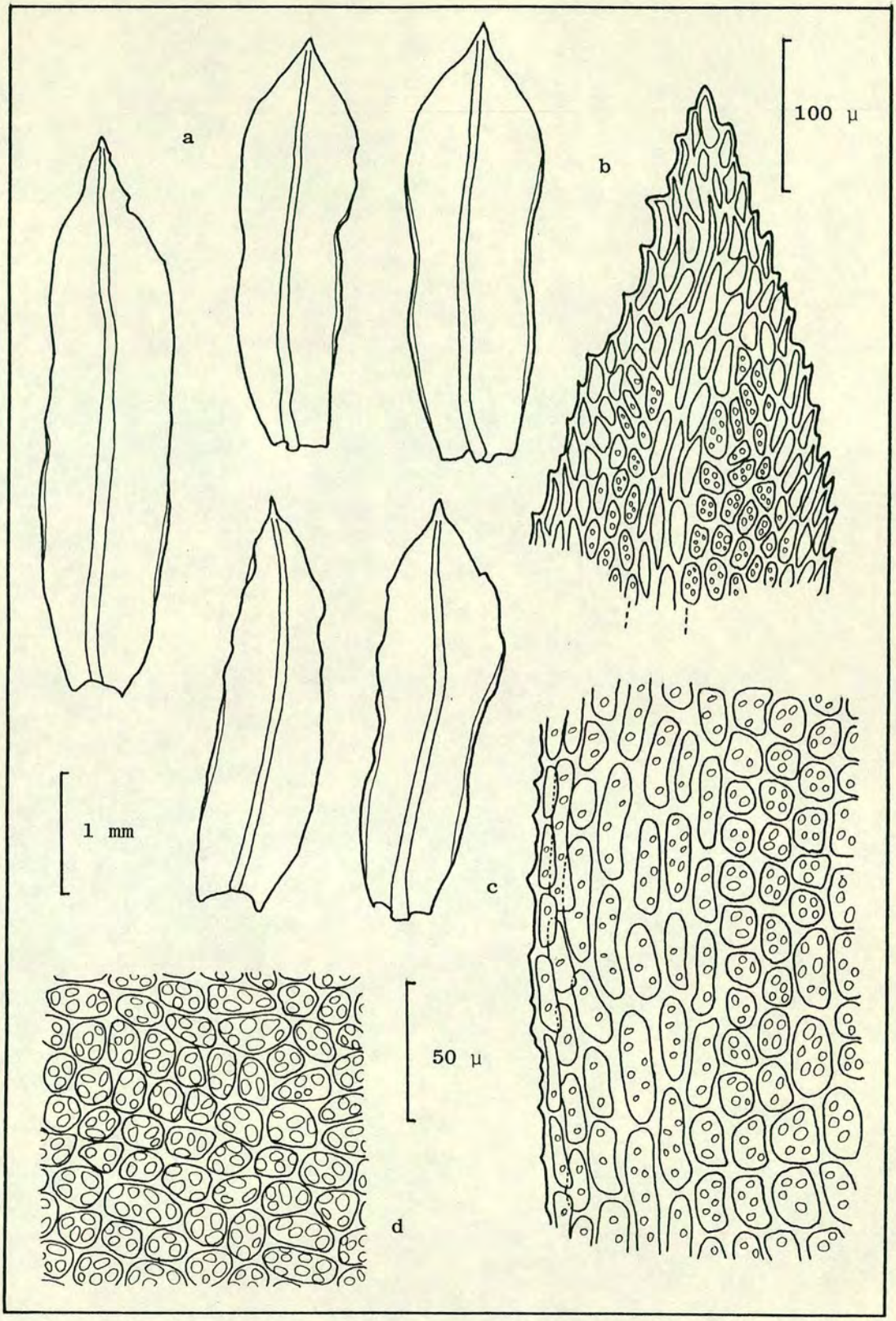


Figure 149. Tortula arenae a. leaves b. leaf apex c. marginal cells at mid-leaf d. lamina cells. Scales: left hand for leaves, upper right hand for leaf apex, lower centre for cells.

and inflated. Rhizoids smooth, brown, sparsely produced on lower parts of stem. Dioecious. Perichaetial bracts similar to the leaves, perigonial bracts shorter and broader at the base. Sporophyte rare. Seta 5-15 mm long, when dry dextrorose (externe visus) above, slightly sinistrorose at base. Capsule erect, cylindrical, 2.0 - 3.0 mm long. Operculum longly subulate Peristome teeth united for about three quarters of their length at the base forming a tube, twisted into a dextrorose helix. Spores 12-14 μ in diameter, exine surface gemmate with gemmae sometimes converging to produce ridges or irregular lumps.

Figure 149. (Micrographs: Figs. 85, 129, 133 and 142).

7.2.4. Habitat notes The majority of South Georgian herbarium specimens were collected from wet, rocky habitats near streams or waterfalls. This species has also been found on mud however, and on bases of tussock grass. These habitats are commonly between 3 and 30 m above sea level but one or two specimens are noted from as high as 300 m. From its frequency in collections, the species appears to be an occasional constituent of the moss flora.

7.2.5. Distribution T. arenae ssp. arenae specimens have been examined from South Georgia, Tierra del Fuego and the Crozet and Kerguelen Islands, while T. arenae ssp. petriei appears to be limited to New Zealand. The species is therefore circum-subantarctic in distribution.

7.3 Taxon B : Taxonomy

7.3.1. Rank This taxon was easily recognised by its lingulate

leaves with no border, ending in a short, often reddish, apical cusp. No other taxon had this combination of characters. Growth experiments were not possible due to lack of material, however, the taxon was clearly defined and is given specific rank.

7.3.2. Nomenclature This taxon has not been described from South Georgia, however a South American species, T. anderssonii Aongstr. (Ångström 1872) is identical to the South Georgian specimens. Type material has been located and examined [Tortula Anderssonii J. Ångstr., Port Famine, fret Magell., N.J. Andersson, NY]. The 5 South Georgian specimens available agree with the type in leaf shape, cell size, type of leaf apex, areolation and papilla density and there is no doubt that the material can be referred to this species.

Material of T. bealeyensis R. Br. ter. (Brown 1898) from New Zealand has been examined and was found to agree in all important characters. There appears to be no reason for maintaining these plants as a separate species and T. bealeyensis, the more recent name, is regarded as a synonym.

The correct name and synonymy for Taxon B is therefore as follows:

Tortula anderssonii aongstr.

syn. T. bealeyensis R. Br. ter.

7.3.3 Description Stems erect, forming cushions 1.0-4.5 cm high, often branched, with or without a central strand. Leaves, 2.1-4.3 mm x 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 spathulate, apex obtuse or broadly acute, cuspidate. Leaves differentiated into a chlorophyllose,

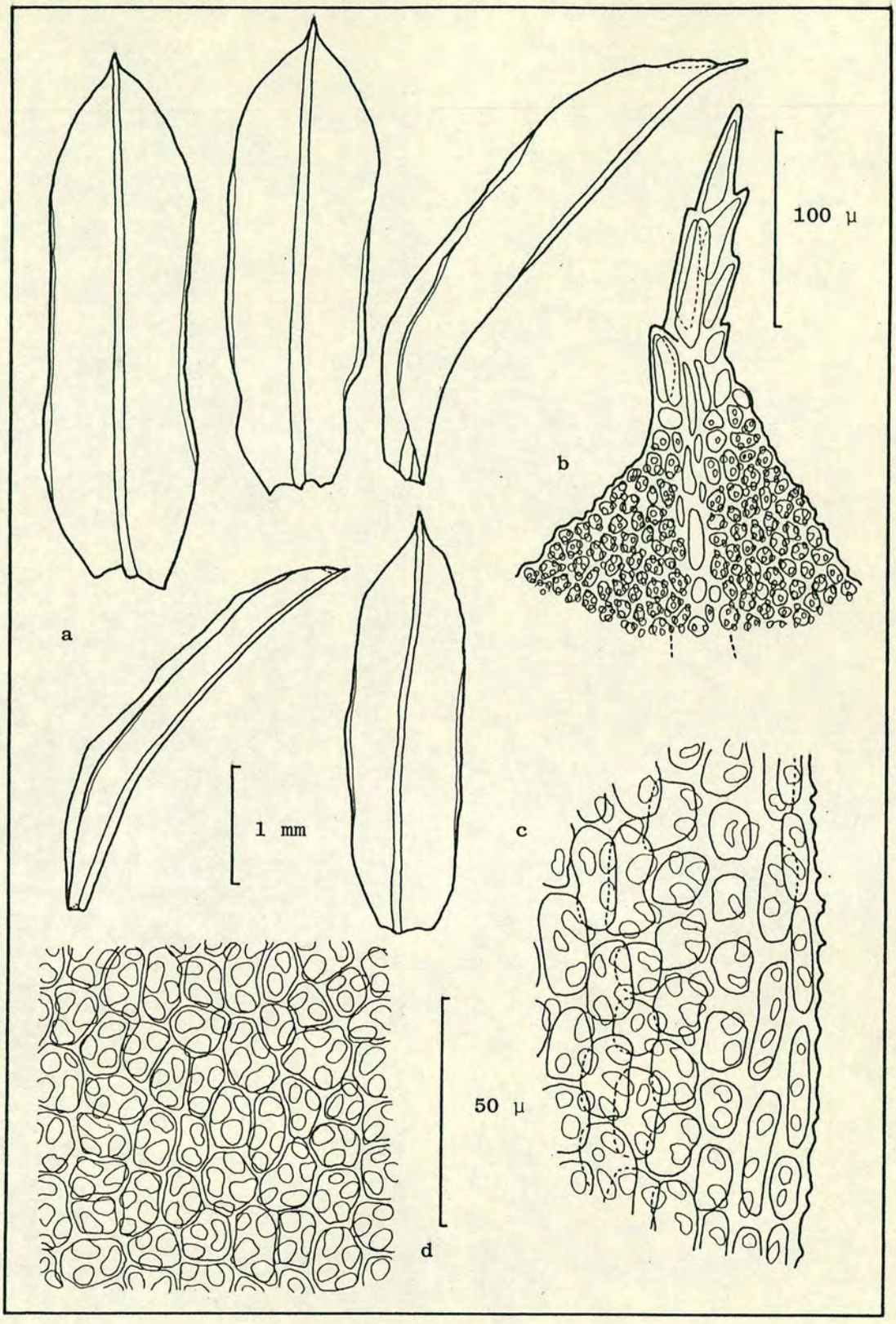


Figure 150. Tortula anderssonii a. leaves b. leaf apex c. cells of upper basal leaf margin d. lamina cells. Scales: left hand for leaves, upper right hand for leaf apex, lower centre for cells.

papillose upper limb and a hyaline, smooth sheath, the latter sheathing the stem for one fifth - one third of leaf length. Leaf margins weakly to strongly recurved or revolute below mid-leaf, plane above, entire, 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 cusp (95-250 μ long in most leaves), nerve sometimes becoming obscure or disappearing below leaf apex. Abaxial nerve surface smooth or papillose with simple verrucate papillae. Lamina cells 8-13.5 μ wide, quadrate, densely papillose with complex papillae. Basal cells 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.

Figure 150. (Micrographs: Figs. 86, 87, 106, 112, 122, 144).

7.3.4. Habitat notes All specimens were collected from moist rock crevices between 30 and 300 m above sea-level. The species appears to be rare on South Georgia.

7.3.5. Distribution In addition to South Georgia and South America, specimens from the Crozet Islands, Macquarie Island and New Zealand have been examined. The species is circum-subantarctic in distribution.

7.4 Taxon C : Taxonomy

7.4.1. Rank This taxon was distinguished by its entire, finely acuminate, lanceolate leaves without a border. Other taxa had leaves of similar shape but possessed teeth on the upper margins and different areolation at the leaf apex. During growth experiments, both of these characters were found to be unchanged in controlled conditions. It is concluded that the taxon is distinct and should be given specific rank.

7.4.2. Nomenclature Cardot (1905) first described this species as T. saxicola Card. from material collected in Tierra del Fuego. Type material has been located [T. 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, S]. 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 T. fuscoviridis Card. from South Georgian specimens. Type material has been examined [T. fuscoviridis Card. sp. nova. South Georgia, Royal Bay, Mount Krokisius usque ad 500 m.s.m. det J. Cardot, Carl Skottsberg, Svenska Sydpolarexpeditionen 1901-03 N:R 298, PC, S] which was referrable to taxon C. T. fuscoviridis thus appears to be a synonym of T. saxicola. Cardot (1906, 1908) however, 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.

The correct name and synonymy fcr taxon C is therefore as follows:

Tortula saxicola Card.

syn. T. fuscoviridis Card.

7.4.3. Description Stems erect forming cushions 0.9-4.0 cm high, often branched, with or without a central strand. Leaves 1.6-4.5 mm x 0.3-0.9 (1.0) mm, when moist erecto-patent to patent with patent to spreading tips, 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 one quarter - one third of leaf length. Leaf margin entire, weakly recurved to revolute for up to two thirds of leaf from base. Nerve percurrent or excurrent as a fine hyaline, reddish or yellow-brown subula c. 0.2-0.3 mm long, rarely becoming obscure above and disappearing before reaching leaf apex. Abaxial surface of nerve smooth or papillose with simple verrucate papillae. Lamina cells 8-12 (-13.5) μ wide, quadrate, densely papillose with complex papillae. Quadrate cells spreading down margin of upper basal region of leaf. Basal cells rectangular to linear, 3-10 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.

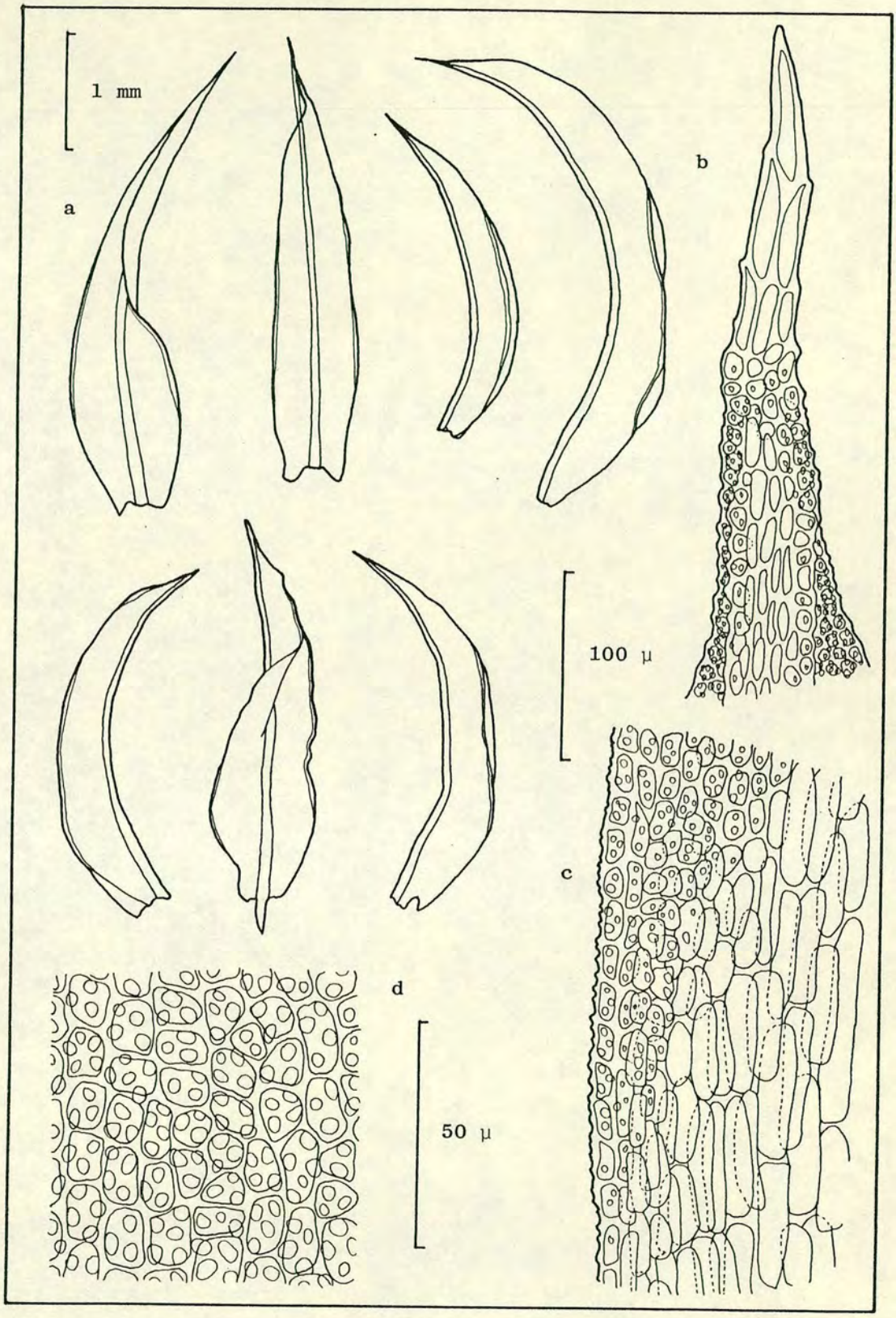


Figure 151. Tortula saxicola a. leaves b. leaf apex c. basal leaf margin d. lamina cells. Scales: upper left hand for leaves, centre right hand for leaf apex and leaf margin, lower centre for lamina cells.

Figure 151. (Micrographs: Figs. 88, 113, 126, 128, 138, 145).

7.4.4. Habitat notes All South Georgian specimens were collected from rock habitats including ledges and crevices. The species is most abundant at low altitudes but extends up to 300 m above sea level.

The number of specimens collected suggests the species is rare to occasional on South Georgia.

7.4.5. Distribution Specimens have been examined from Kerguelen, South America and from many localities on the Antarctic Peninsula and its offshore Islands.

7.5 Taxon D : Taxonomy

7.5.1. Rank Taxon D was found to be distinct from other taxa because of its broadly oblong-pandurate leaves. Measurements showed that these had width/length ratios larger than in any other taxon, but some overlap with Taxon E did occur. During growth experiments however these two taxa remained quite seperate and taxon D should therefore be regarded as a species.

7.5.2. Nomenclature This taxon appears to have been first described by Müller (1890) from South Georgia as *Barbula fontana* C. Muell. An original specimen has been located and examined [*Syntrichia fontana* C. Muell. n. sp. Quelle auf dem Hochplateau, Süd Georgien 14/VII 83. Leg. Will, M]. Although this is not the specimen cited as the type, it is, according to Greene (1973) the only surviving specimen of this species from Will's collections. It is a typical specimen of taxon D and there is no doubt that

the name B. fontana can be applied here. B. fontana was transferred to the genus Tortula by Brotherus (1902).

A further species T. rivularis Dus., has also been examined [Plantae Patagonicae e territoria Sta. Cruz reportatae, Tortula rivularis Dus. Lago Viedma in paudosis, Febr. a 1905 P. Dusen, BM]. This specimen, which is clearly authentic, is within the range of taxon D plants and the type description (Dusén 1906) confirms that this species should be regarded as a synonym.

The correct name and synonymy for taxon D is therefore as follows:

Tortula fontana (C. Muell.) Broth.

syn. T. rivularis Dus.

7.5.3. Description Stems erect forming turves 2.0-10.5 cm high, sparingly branched, without a central strand. Leaves (2.9) 3.9-5.8 mm x 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 one quarter - one third of leaf length. Leaf margin plane or weakly recurved below mid-leaf, denticulate near apex. Nerve narrowing towards the leaf apex, percurrent, abaxial surface smooth or papillose with simple verrucate papillae. Lamina cells 13-23 μ wide, quadrate but becoming shortly rectangular to rectangular towards basal sheath, marginal 1-2 rows usually smaller, papillose with sparse complex papillae. Basal cells 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.

Figure 152. (Micrographs: Figs. 89, 104, 125, 143)

7.5.4. Habitat notes Specimens have been collected from flushes, bogs, stream sides and wet rocks usually below an altitude of 180 m. Its preference for wet habitats appears to be remarkable in the genus Tortula, which is often associated with drought tolerance in the northern hemisphere. The species is rather rare, only 10 specimens from South Georgia are known.

7.5.5. Distribution In addition to the South Georgian material, the species has been identified from South American collections. The species is unlikely to have been overlooked from elsewhere and therefore appears endemic to these areas.

7.6 Taxon E : Taxonomy

7.6.1. Rank Herbarium studies indicated that many of the characters of taxon E were intermediate between taxa D and F. Leaf and cell size measurements confirmed this, showing some overlap between D and E, and taxa E and F. During growth experiments taxon E remained distinct in its stems with spreading leaves which were recurved at the tips and oblong or oblong-lanceolate in shape. Taxon D was also separated by its broad pandurate or spathulate leaves but differences between taxon E and taxon F were not great enough to justify separation at a

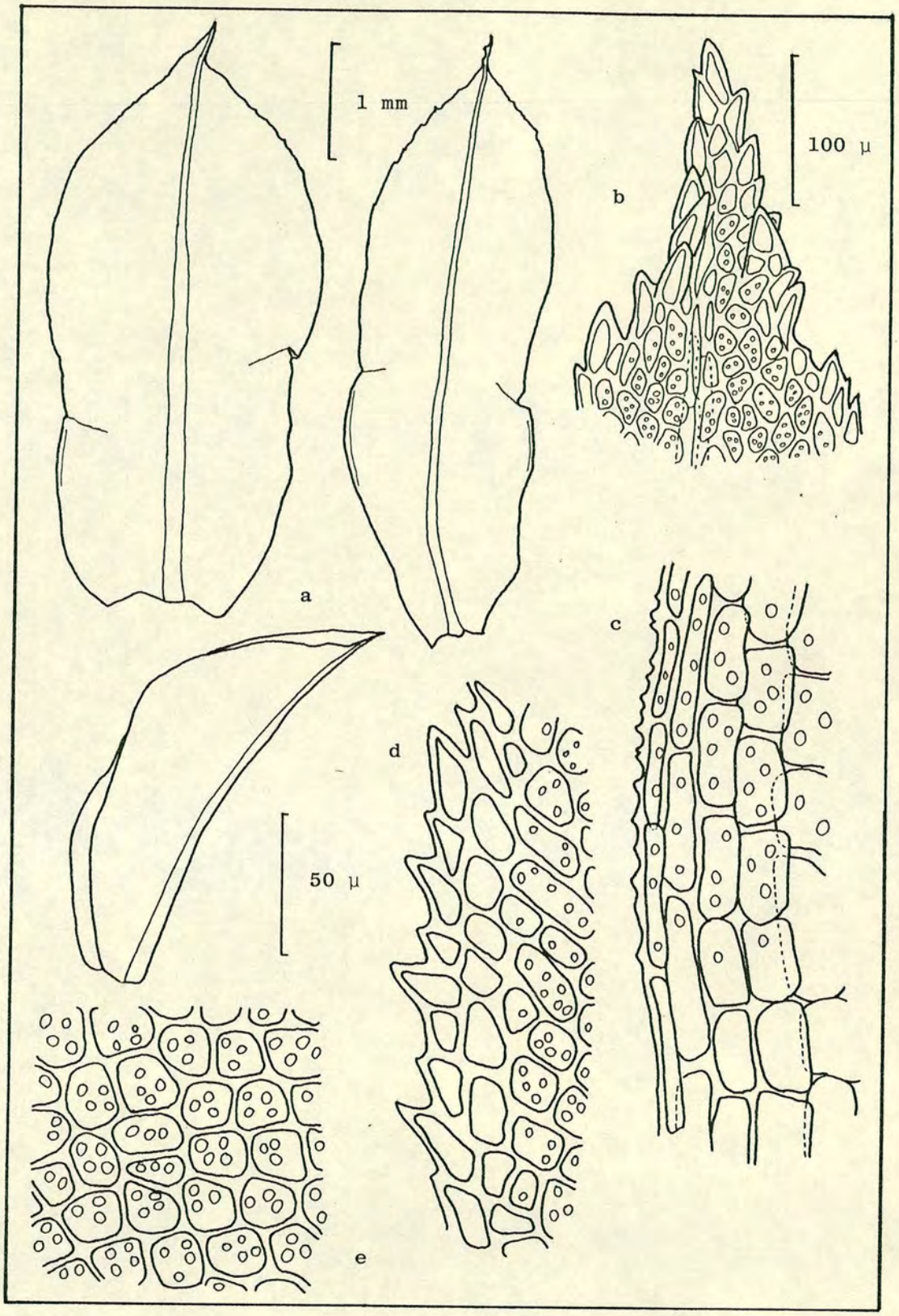


Figure 152. Tortula fontana a. leaves b. leaf apex c. cells of upper basal margin d. upper leaf margin e. lamina cells.

Scales: upper right hand for leaves, upper left hand for leaf apex, lower left hand for leaf margins and cells.

specific level. Taxon E was only sufficiently distinctive to be designated a variety of Taxon F.

7.6.2. Nomenclature Plants of this taxon do not appear to have been described and are therefore placed in a new variety. Further consideration of its nomenclature is given in the account of taxon F (section 7.7.2).

7.6.3. Description Stems erect, forming turves 2.0-7.0 cm high, sparingly branched, without a central strand. Leaves 3.2-4.8 x 1.0-1.6 mm, when moist ~~patent to~~ spreading with recurved tips, when dry curled and slightly twisted. Leaf shape broadly oblong-lanceolate to oblong, narrowing to an acute to obtuse apex. Leaves differentiated into a chlorophyllose, papillose upper limb and hyaline, smooth sheath, the latter sheathing the stem for one quarter to one third of leaf length. Leaf margin plane or weakly recurved below mid-leaf, dentate to denticulate in upper third. Nerve percurrent, abaxial surface smooth or papillose with simple verrucate papillae. Upper lamina cells 12.5-20 μ wide, quadrate but becoming shortly rectangular to rectangular towards basal sheath, marginal row often smaller, sparsely papillose with complex papillae. Basal cells 2-8 times as long as wide, sometimes porose, narrower towards 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 produced on lower parts of stem. Sterile. Gametangia and sporophytes unknown on South Georgia.

Figure 154b. and e. (Micrographs: Figs. 90, 103, 141).

7.6.4. Habitat notes The five herbarium specimens available were all collected from wet rocky habitats at altitudes between 100 and 420 m. R.I.L. Smith (personal communication) has also found this taxon growing with T. fontana in a bog.

7.6.5. Distribution This taxon appears to be limited to South Georgia.

7.7 Taxon F : Taxonomy

7.7.1. Rank Taxon F was distinct from other taxa in its large lanceolate or lingulate-lanceolate leaves with large cells up to 20 μ wide. Cultivation experiments demonstrated that these differences were maintainted in a controlled environment and also showed that a large amount of the variation in leaf size observed in the taxon could be explained by environmental influence. A wide range of variation in many other characters such as cell size and leaf margin recurvature was also observed. In all cases this appeared to be continuous and no basis for splitting the taxon into smaller units was found. Taxon F is therefore regarded as a single variable species.

Taxon E, which was similar to taxon F in all respects except leaf shape and leaf stance, is recognised as a variety of it (section 7.6.1).

7.7.2. Nomenclature The earliest name for taxon F appears to be Tortula robusta Hk. et Grev., a species described by Hooker and Greville (1824). South Georgian material agrees

well with the type description and with a fragment of type material in the British Museum [Tort. robusta sp. novo. Herb. Hookerianum 1867, BM, K]. This specimen is further authenticated by an accompanying diagram which bears the initials 'J.D.' and the date '1817'. The initials probably belong to J. Dickson, who, according to the type description (Hooker and Greville 1824) provided the type specimen. The collector and type locality are unknown but it is probable that the specimen came from a collection made by Menzies in Tierra del Fuego in 1787, as other specimens obtained from Dickson in Hooker and Greville's (1824) publication came from this source.

Three species described by Müller (1890) from South Georgia fall within the morphological limits of this taxon. These are Barbula runcinata C. Muell., B. lepto-syntrichia C. Muell. and B. anacamptophylla C. Muell. All were transferred to the genus Tortula by Brotherus (1902).

Two type specimens of B. runcinata survive in Munich [No. 39 Barbula (Syntrichia) runcinata C. Müller cfr. Oberhalb des magnetischen Observatoriums, Süd-Georgien; 1883. Will, M. No. 39. Barbula (Syntrichia) runcinata C. Müller n. sp. Landzuge ü S. -Rand des Hochplateaus. Sehr häufig, an den Hangen in Wasserrinnen u. sonstigen sehr feuchten Stellen, Süd Georgian, 10/11/83, Will., M]. Both are robust specimens of taxon F with lanceolate leaves and strongly recurved leaf margins. Present knowledge of variation in T. robusta suggests that B. runcinata should be regarded as a synonym. There appears to be no justification for retaining the name as a variety, which was suggested by Brotherus (Cardot and Brotherus 1923).

Three authentic specimens of B. lepto-syntrichia have been found in Brotherus' herbarium in Helsinki (H-BR). These are labelled 'Barbula (or Tortula) lepto-syntrichia C.M. Süd Georgien. Leg. Will' and one specimen is marked 'fo. robusta'. All appear to be fragments extracted from larger specimens, but they are of type significance. All three belong to taxon F, and hardly differ from the type specimens of B. runcinata. The leaves are only slightly denticulate and often worn at the apex, which may have led Müller (1890) to describe them as entire. They are, however, typical specimens of T. robusta. B. lepto-syntrichia is therefore regarded as a synonym.

The type specimen of B. anacamptophylla has not been located and Greene (1973) also failed to find authentic material. Cardot (1906) however, examined Will's material and remarked that B. anacamptophylla was merely a slender form of B. lepto-syntrichia, and 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 it appears reasonable to follow his decision in treating B. anacamptophylla as a synonym of T. robusta.

Bartram (1946) described T. robusta var. laxa Bartr. from specimens collected by Roivainen in Tierra del Fuego. The type specimen has been examined [Bryophyta Fuegiana 1895, Expeditio Fennica 1928-29, 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, FH]. As the description suggests, the leaves are large with

lax cells up to 20 μ wide. This study has found that such specimens are only one extreme of a wide range of variation and there seems to be no justification in retaining the variety. T. robusta var. laxa is therefore reduced to synonymy.

Cox (1961) and Greene (1964a, 1973) considered T. rubra Mitt., a species described from New Zealand (Mitten in Hooker 1867), as a synonym of T. robusta. Type material has been examined [Syntrichia rubra M., Dry Banks, Otago, New Zealand, Hector 37, 1863, BM, NY] together with a range of New Zealand and Australian material. This was found to differ from South Georgian and South American T. robusta specimens in the following respects:

i) leaf shape. T. rubra had leaves which were broader above mid-leaf. The leaves were thus oblong rather than lanceolate in shape.

ii) leaf stance. T. rubra had patent to spreading leaves with recurved tips. The leaves of T. robusta were usually uniformly erecto-patent to spreading.

iii) nerve. The nerve in T. rubra leaves was wider in upper leaf and often excurrent at the apex. In T. robusta the nerve was slender in upper leaf and percurrent at the leaf apex.

iv) nerve papillae. T. rubra leaves had a more highly papillose abaxial nerve surface than T. robusta leaves.

v) lamina cell papillae. The long-rectangular upper basal cells of T. rubra leaves were papillose but in T. robusta leaves these cells were smooth.

vi) teeth. The position of teeth in T. rubra and T. robusta leaves differed. T. rubra leaves were usually denticulate only near the apex on the upper margin, but also produced teeth on the abaxial nerve surface at the leaf apex. In T. robusta leaves, teeth occurred on the upper third of the leaf margin and not on the abaxial nerve surface.

Apart from these differences the two species were similar in leaf size, cell size and areolation. The differences appear great enough, however, to maintain some distinction between the taxa which appear to be geographical variants. It is therefore proposed that T. rubra be considered a subspecies of T. robusta.

T. robusta ssp. rubra (Mitt.) P.J. Lightowlers comb. et stat. nov. in preparation.

The correct name and synonymy for taxon F is therefore as follows:

Tortula robusta Hook et Grev. ssp. robusta

syn. T. robusta var. runcinata (C. Muell.) Broth

(Barbula runcinata C. Muell.)

T. lepto-syntrichia (C. Muell.) Broth.

(B.lepto-syntrichia C. Muell.)

T. anacamptophylla (C. Muell.) Broth.

(B. anacamptophylla C. Muell.)

T. robusta var. laxa Bartr.

The name T. robusta ssp. robusta var. recurva is proposed for taxon E. The new name is intended to refer to the characteristic leaf stance.

T. robusta ssp. robusta var. recurva P.J. Lightowlers var. nov. in preparation

7.7.3. Description Stems erect forming turves 2.0-8.0 cm high, sparingly branched, without central strand. Leaves 4.4-8.0 mm x 0.9-2.0 mm, when moist erecto-patent to patent with spreading tips, when dry slightly curled and twisted, lanceolate to lingulate lanceolate, tapering to an acuminate or acute apex. Leaves differentiated into a chlorophyllose, papillose upper limb and a hyaline, smooth basal sheath, the latter sheathing the stem for one quarter to one third of leaf length. Leaf margin recurved in lower two thirds to one half, sometimes plane, coarsely dentate to denticulate in upper third, very rarely with a border of elongated cells extending up to two thirds leaf length. Nerve percurrent, abaxial surface smooth or papillose with simple verrucate papillae. Lamina cells (9-) 11-21 (-24) μ wide, quadrate but becoming shortly rectangular to rectangular towards the basal sheath, marginal row often smaller, papillose with complex papillae. Basal cells rectangular to long 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. Perichaetial 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 dextrorose (externe visus) in upper part, sinistrorose below. Capsule 2.2-3.9 mm long, cylindrical, erect

or slightly inclined. Operculum subulate. Peristome of 32 teeth united below for about one third of their length and twisted into a dextrorose helix. Spores 9.5-13.5 μ in diameter.

Figure 153 and 154 a, c and d. (Micrographs: Figs. 91, 115, 121).

7.7.4. Habitat notes The species has a wide ecological range. Specimens have been collected from wet places such as bogs with Rostkovia [Juncaceae], flushes, streams and lakesides, on screes with Aceana [Rosaceae], on tussock grass bases, in rocky habitats and even on disturbed ground. It prefers altitudes below about 120 m but specimens have been found as high as 400 m above sea level. The species is very common on South Georgia.

7.7.5. Distribution No material has been collected from the Antarctic Peninsula and its offshore islands but specimens from austral South America have been examined and are abundant in collections from this region. Herzog (1926) reports T. robusta ssp. robusta (as T. runcinata) from as far north as Bolivia, at high altitudes in the Andes.

Specimens of T. robusta ssp. rubra have been examined from New Zealand and Australia. This subspecies is also reported (as T. rubra) from Marion Island and Bouvet Island (Zanten 1971) and from Macquarie Island (Seppelt 1981). Material from Marion and Macquarie Islands has not been seen but the Bouvet Island specimen noted by Zanten (1971) has been examined and found to be a mixed collection of T. filaris and T. princeps.

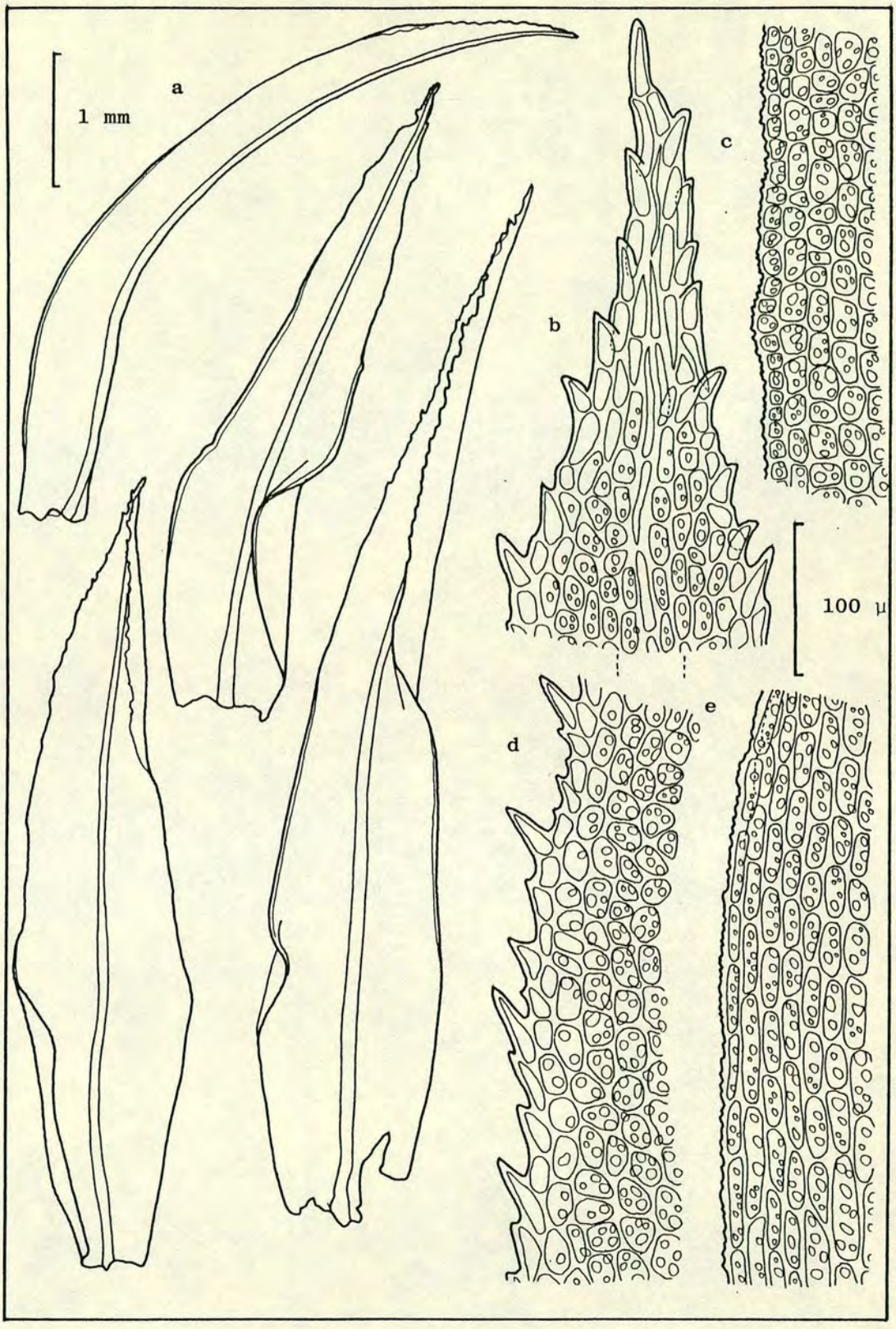


Figure 153. Tortula robusta var. robusta a. leaves b. leaf apex c. marginal cells at mid-leaf d. upper leaf margin e. upper basal leaf margin. Scales: upper left hand for leaves, centre right hand for leaf apex and leaf margins.

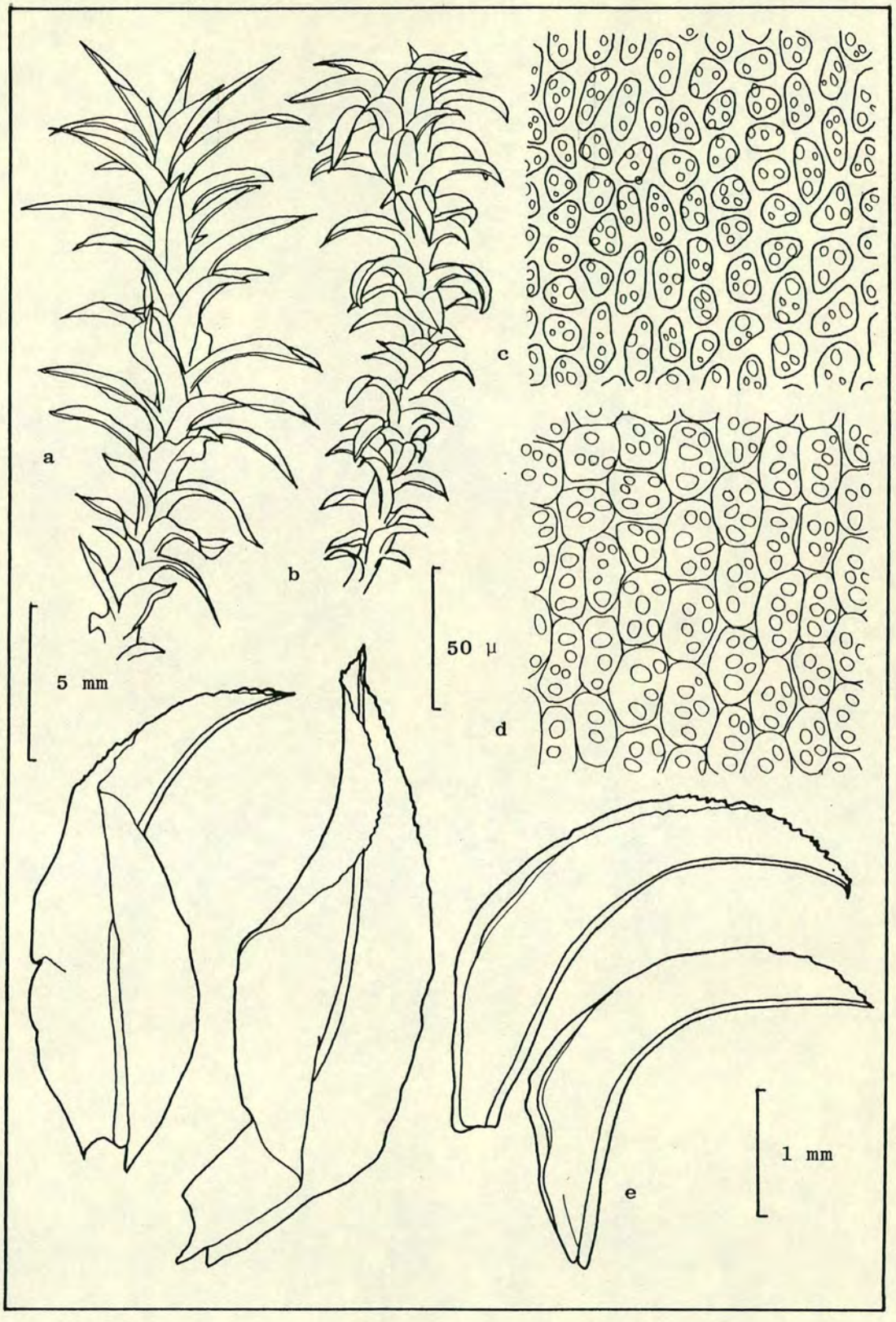


Figure 154. Tortula robusta a. var. robusta shoot b. var. recurva shoot c. and d. var. robusta lamina cells e. var. recurva leaves. Scales: left hand for shoots, centre for cells, lower right hand for leaves.

The distribution of T. robusta therefore appears to be circum-subantarctic but stretching further north into the mountainous regions of Australia and South America.

7.8 Taxon G : Taxonomy

7.8.1. Rank Leaf and cell measurements were found to distinguish taxon G moderately well. The taxon also had a characteristic group of smooth long-rhomboidal cells at the leaf apex. Areolation and leaf and cell dimensions were still diagnostic of this taxon after collateral cultivation with other taxa and it was therefore considered to be a distinct species.

7.8.2. Nomenclature This species appears to have been first described by Müller (1890) as Barbula filaris C. Muell. from material collected on South Georgia in 1882-3 by Will. Type material has been examined [Barbula (Syntrichia) filaris C. Müll. n. sp. Austro-Georgia, oberes Whalerthal in Felsspalten 20.III. 1883, HBG, H-BR, M]. The taxon G material agrees well with these specimens. The type description describes the species as synoecious, but all fertile material examined in this study has been found to be dioecious. Unfortunately only female inflorescences have been seen in the type specimen but it is not unlikely that Müller (1890) was mistaken. B. filaris was transferred to the genus Tortula by Brotherus (1902).

Type material of T. robustula Card. (Cardot 1905) was found to be very similar to this species. Two syntypes have been examined [T. robustula Card. sp. nova. Terre de Feu : Ushuaia. 3.10.1902. Skottsberg 61, Herb. J. Cardot, PC. T. robustula Card sp. nova. Iles Falkland : Port Louis. 6.8.1902. Skottsberg

225, Herb. J. Cardot, PC]. Cardot (1908) noted that T. filaris had more slender stems, leaves equal in size throughout the stem, with more strongly papillose cells and less differentiation at the leaf margin than T. robustula. The range of variation observed in South Georgian material however suggests that these differences are trivial. T. robustula was also described (Cardot 1908) as autoecious rather than dioecious like T. filaris. One of the type specimens of T. robustula (Skottsberg 61) is fertile and appears to be dioecious, male and female inflorescences being closely associated but not found on the same plant. T. robustula is therefore presumed to be dioecious but the sexual state alone is insufficient reason for separating two species which are otherwise identical. T. robustula is thus considered a synonym of T. filaris.

T. excelsa Card. was described by Cardot (1906) who remarked that it was similar to T. filaris. Type material has been examined. [T. excelsa Card. sp. nova. Ile Nelson, Shetland du Sud, Harmony Cove. Leg. Skottsberg 11.1.1902. Svenska Sudpol. Exped. nr. 447, Herb. J. Cardot, PC, BM, BM ex K]. These specimens are robust but otherwise typical specimens of T. filaris. They are similar to South Georgian material in areolation, leaf shape, leaf size and cell size although the stems are taller. A range of Antarctic specimens have been examined and these were found to be generally similar in stature to South Georgian plants. The tall stems of the type specimen of T. excelsa are 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 synonymous

with *T. filaris*.

The correct name and synonymy for taxon G is therefore as follows:

Tortula filaris (C. Muell.) Broth.

syn. *T. robustula* Card.

T. excelsa Card.

7.8.3. *Description* Stems erect forming cushions or turves 0.8-5.2 cm high, sparingly branched, without central strand. Leaves 2.0-4.4 mm x 0.7-1.0 mm, when moist patent with spreading tips, 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 one fifth to one third of leaf length. Margin plane to weakly recurved around mid-leaf, dentate to obscurely denticulate near apex. Nerve ending in apex in a well defined group of several rhomboidal cells, abaxial surface smooth or papillose with simple verrucate papillae. Lamina cells 9-15 μ wide, quadrate, marginal row sometimes slightly smaller, sparsely papillose with complex papillae. Basal cells rectangular to linear 4 to 10 times as long as wide, sometimes porose, narrower towards the leaf margin often forming a weakly differentiated border, smooth, hyaline, sometimes lax and inflated. Longly rectangular cells continuing up leaf margin into limb or not. Rhizoids smooth, brown, sparingly to abundantly produced on lower parts of stem. Dioecious. Perichaetial bracts similar to other leaves but longer. Perigonial bracts shorter with broader base. Sporophyte

uncommon. Plants sometimes polysetous. Seta 10-15 mm, when dry dextrorose (externe visus) in upper part, sinistrorose below. Capsule 1.9-2.5 mm long, cylindrical, erect or slightly inclined. Operculum subulate. Peristome of 32 teeth united below for about half their length and twisted into a dextrorose helix. Spores 11.6-14.1 μ in diameter.

Figure 155. (Micrographs: Figs. 92, 107).

7.8.4. Habitat notes The abundance of this species in collections indicates that it is an occasional component of the moss flora. It is found in a wide range of habitats including wet rocks, streamsides and weedy places such as crevices of concrete, on whale bones or amongst glacial detritus. Specimens have been collected from sea level up to 600 m but, only plants from lower elevations have sporophytes.

7.8.5. Distribution Specimens from austral South America and from a wide range of localities in the Antarctic Peninsula region have been examined. No specimens from other subantarctic islands have been located.

7.9 Taxon H : Taxonomy

7.9.1. Rank Measurements suggested that Taxon H was closest to taxon G in leaf dimensions but could be distinguished by its smaller cells. The papillae of taxon H were characteristically very densely packed when observed under the light microscope or by scanning electron microscope. Unfortunately insufficient material was available for growth experiments but a few plants were grown in the growth chambers with other taxa. Examination

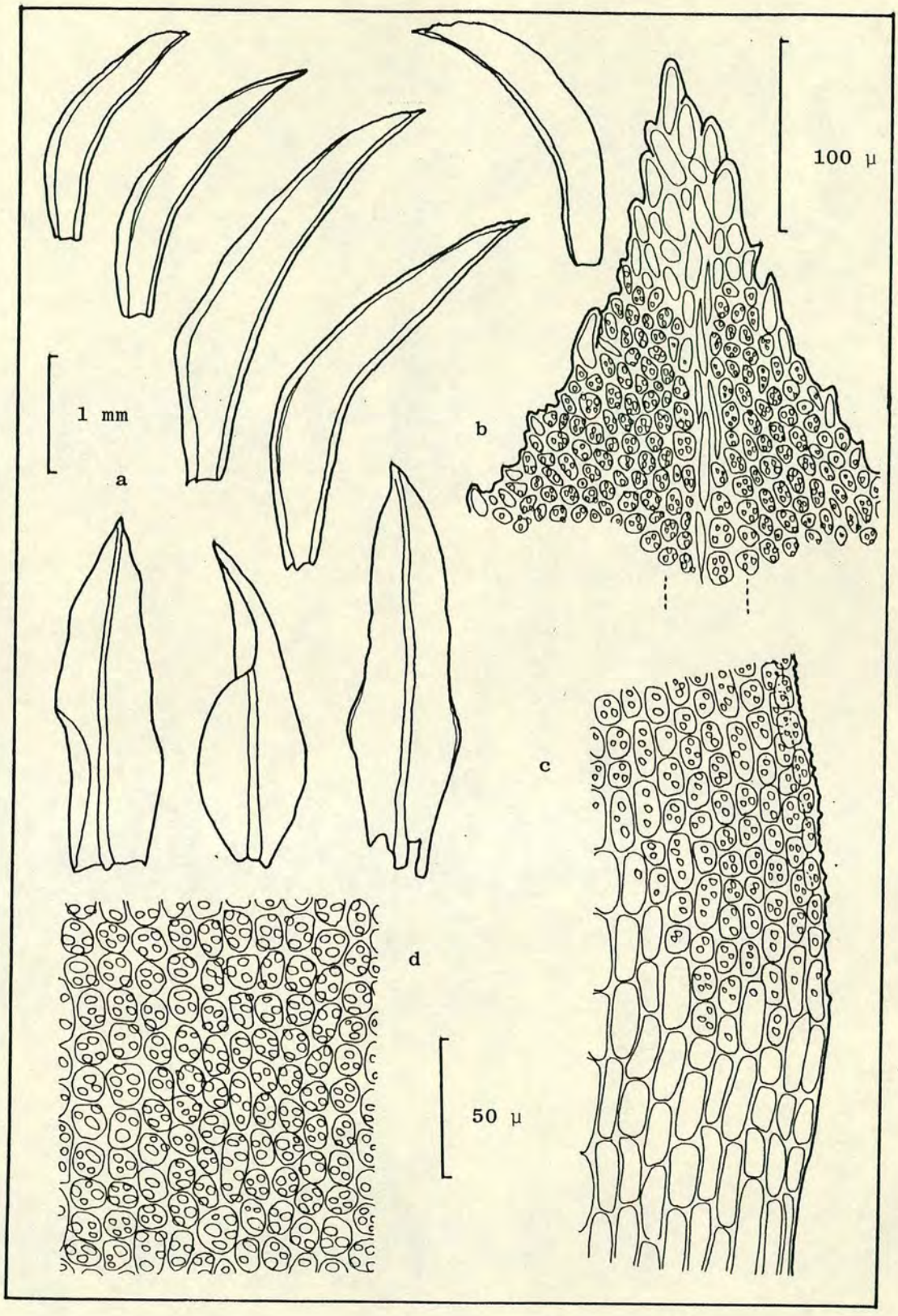


Figure 155. Tortula filaris a. leaves b. leaf apex c. upper basal leaf margin d. lamina cells. Scales: upper left hand for leaves, upper right hand for leaf apex and leaf margin, lower centre for lamina cells.

of these plants suggested that cell size and papillae differences were maintained in cultivation.

Taxon H was easily distinguished from other taxa and is given specific rank.

7.9.2. Nomenclature This species was described from Kerguelen by Müller (1883) as Barbula geheebiaeopsis C. Muell. Transfer to the genus Tortula was made by Brotherus (1902). South Georgian material agrees well with an authentic specimen of B. geheebiaeopsis in Helsinki [Barb. geheebiaeopsis C.M. Kerguelen Leg. Naumann, H-BR]. Much of Müller's original material was destroyed in Berlin during the 1939-45 war (Greene 1973) and this may be the only surviving specimen.

This is the first report of this species from South Georgia. Material was previously referred to a New Zealand species, T. serrata Dix., by Cox (1961) and Greene (1964, 1968a, 1973). According to Cox (1961) this decision was primarily based on the similar cell sizes and papillae densities of the plants. The type specimen of T. serrata has been examined [Herb. H.N. Dixon, Ref. No. 46, T. serrata Dixon sp. nov., Wairarapa, N.Z. Coll. W. Gray 1909, Type, BM] and is identical to South Georgian plants in these respects. However, it differs remarkably 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 a synonym.

Unlike other South Georgian species of Tortula, no additional taxa have been examined which can be reduced to synonymy with T. geheebiaeopsis. However, some authors have mistakenly identified plants of this species from South America and Kerguelen as T. serrulata Hook. et Grev. The type specimen of this species has been examined [H.1731, Terra del Fuego, T. serrulata (J. Dickson), Herbarium Hookeriannum 1867, BM ex K]. It differs from T. geheebiaeopsis in its larger cells and sparse papillae. T. serrulata is thus not an appropriate name for this taxon and is probably a synonym of T. robusta, as Greene (1964a) remarked. However, the leaves of the type are smaller than South Georgian specimens of T. robusta and the nomenclature is therefore left unchanged until a revision of South American taxa is undertaken.

Dixon (1930) transferred Barbula geheebiaeopsis to Leptodontium after examination of a specimen determined by Kaalaas. A specimen of the same collection has been traced [T. geheebiaeopsis (C. Müll.) Broth. det Kaal., Possession Island: Crozetgruppen: Doctor's Bay, Januar 1908. leg. Ring and Raknes No. 246, Ex herb. Univ. Osloensis, BM] which is Leptodontium micro-runcinatum Dus. Dixon's combination was thus based on a mis-identified specimen and should not be followed.

The correct name for Taxon H is therefore

Tortula geheebiaeopsis (C. Muell.) Broth.

7.9.3. Description 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 (-4.4) mm x 0.7-1.1 mm, when moist patent to spreading with recurved tips, 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 one quarter to one third leaf length. Margin recurved for two thirds leaf length, denticulate near apex. Nerve strong, ending in apex or excurrent in a short thick point (c. 0.06 mm), abaxial surface smooth or papillose with simple verrucate papillae. Lamina cells 7.5-12 μ wide, quadrate to shortly rectangular below, usually thick-walled, very densely papillose with complex papillae. Basal cells 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. Perichactial bracts similar to other leaves or longer with an extended basal region. Perigonial bracts shorter with broader bases. Sporophyte uncommon, plants sometimes polysetous. Seta 7-14 mm, when dry dextrorose (externe visus) in upper part, sinistrorose below. Capsule 1.2-2.5 mm long, cylindrical, erect or slightly inclined. Operculum subulate. Peristome of 32 teeth united below for about one third of their length and twisted in a dextrorose helix. Spores 12-13.5 μ in diameter.

Figure 156. (Micrographs: Figs. 93, 94, 105, 124).

7.9.4. Habitat notes From its frequency in collections this is a common plant found in a wide range of habitats including rock

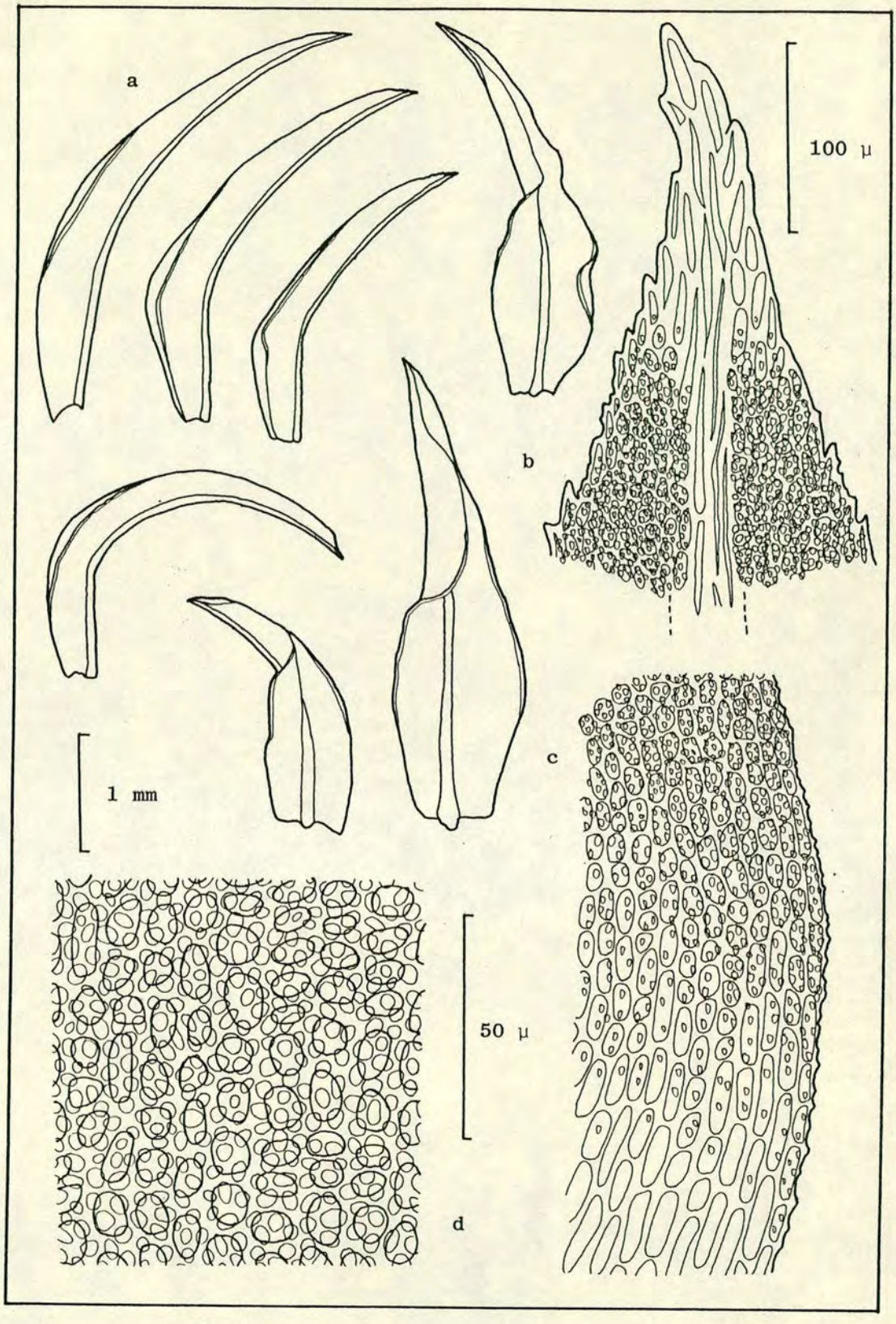


Figure 156. Tortula geheebiaeopsis a. leaves b. leaf apex c. upper basal leaf margin d. lamina cells. Scales: centre left hand for leaves, upper right hand for leaf apex and leaf margin, lower centre for lamina cells.

crevices and ledges, amongst Acaena [Rosaceae], in Festuca grassland, Poa flabellata tussock or in flushes. It occurs from sea level to 550 m but is more abundant at lower altitudes.

7.9.5. Distribution Specimens have been examined from Kerguelen and South Amercia in addition to those from South Georgia. The species appears to be absent from other sub-Antarctic islands and the Antarctic Peninsula. Kaalaas (1912) reported this species from the Crozet Islands but re-examination of this material has shown that this report is based on a mis-identification. Zanten (1971) also reported it from Marion Island, but this determination was made with reference to material determined by Kaalaas from Crozet and is therefore doubtful. On present knowledge T. geheebiaeopsis is found only in austral South America, South Georgia and Kerguelen.

7.10 Hair-pointed taxa I, J, K and L : Taxonomy

7.10.1. Rank Observations on South Georgian hair-pointed material suggested that taxa I, J and K were linked by plants with intermediate characters. Cultivation experiments also indicated that taxon J or taxon K plants produced taxon I phenotypes when grown under experimental conditions. Insufficient taxon L specimens were available from South Georgia to make definite conclusions, but the more abundant Antarctic Peninsula specimens suggested that this taxon intergraded with the other hair-pointed taxa. All hair-pointed taxa are therefore considered to belong to a single species.

The taxa are distinguished by combinations of characters, taxon I by its red hair-points and leaves with recurved profiles,

taxon K by its hyaline hair-points and leaves with cucullate to plane profiles and taxon L by the small size of the plants and the nerve often disappearing below the leaf apex. Principal components analysis showed that taxa I, J and K each formed clusters in a scatter diagram of the first three principal components. Taxon L was too poorly represented in the analysis to enable a conclusion to be drawn about it. Taxa I, J and K were also indentified by cluster analysis, and the various methods employed usually recognised the taxa at the same levels of similarity.

Further evidence from field observations, collateral cultivation experiments and from taxonomic revision of South American material is needed before the hair-pointed taxa can be fully understood. Observations and statistics on South Georgian material suggest that they are valid infra-specific taxa but cultivation indicates they may be only habitat forms. At present they are treated as varieties of the same species. No description or name for taxon I was traced, however, and rather than describing a new, doubtful taxon, it is proposed that no formal taxonomic status be given.

7.10.2. Nomenclature

(a) Taxon J. The earliest name applicable to any of the hair-pointed taxa 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, a later synonym, among collections made by J.D. Hooker on the Falkland Islands.

Original material has been examined [T. mülleri Br. + Sch. Falkland Islands Antarct. Exp. 1839-1843 J.D.H., BM ex K] and is very similar to South Georgian specimens of taxon J.

The Falkland Island plants differ in only two respects, firstly in their larger size, which is perhaps due to the more favourable climate in the Falkland Islands, and secondly they are synoecious and not dioecious or autoecious like South Georgian specimens. Synoecy in European plants has been regarded as a key character of the species, (Dixon 1924, Smith 1978, Kramer 1980). According to Dixon (1923) however, 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. Outside Europe therefore, 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 Island specimens.

An isotype of T. princeps has been examined [T. princeps DNts. in montibus Sardinia australis D.Nts, E] and is identical to Hooker's specimens in leaf shape and stance, recurvature of the leaf margin, sexual state and type of papillae on the abaxial surface of the nerve. The European specimen is slightly larger but the difference is small and there seems no reason to question Wilson's decision to refer the Falkland Island specimens to

T. princeps. This variable, cosmopolitan species has never been the subject of a worldwide monograph which could shed some light on the relationship between its representatives in the northern and southern hemispheres. It is possible that the southern hemisphere plants should be considered as a separate species. There is no doubt however, that South Georgian taxon J plants can be referred to T. princeps as it is currently understood.

South Georgian material of taxon J 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 [T. grossiretis sp. nova, South Georgia, Cumberland Bay, Pot Harbour, D.15/5 1902, Det. J. Cardot, Svenska Sydpolarexpeditionen 1901-03 N:R 299, PC. T. grossiretis var. atrata Card. var. nova, Georgie du Sud : Cumberland Bay. Leg. Skottsberg 1902 No. 300, S]. The type of T. grossiretis is a typical specimen of taxon J and the type of T. grossiretis var. atrata differs only in very minor respects. According to Cardot (1906, 1908) the variety is based on the darker green colour of its leaves, its larger size, its fastigiate branching and leaves with more rounded apices. The range of material available during this study indicates that these differences are trivial and show continuous variation between wide extremes. Both T. grossiretis var. grossiretis and var. atrata are therefore considered to be synonyms of T. princeps.

Cardot (1911b) described T. heteroneura Card. from the Antarctic Peninsula. Type material has been examined [T. heteroneura Card.

sp. nova, Ile Petermann, sur la terre humide, entre les rochers. 2 ème expéd. Charcot. Leg Gain 1909 N. 211. Herb J. Cardot. BM ex K, H, PC] and as the type description suggests, these plants are similar to T. princeps. They differ however in the structure of the nerve in upper leaf, which becomes less distinct and disappears below the leaf apex. Plants with this type of nerve structure have not been found on South Georgia, but sufficient Antarctic material has been examined to be certain that this is merely a forma probably induced by severe climatic conditions. Some leaves in all specimens show normal morphology and no taxonomic significance can be attached to variation in this character. T.heteroneura is treated as a synonym of T. princeps.

The correct name and synonymy for Taxon J is therefore as follows:

Tortula princeps De Not. var. princeps

syn. T. grossiretis Card. var. grossiretis

T. grossiretis var. atrata Card.

T. heteroneura Card.

(b) Taxon I. This taxon does not appear to have been previously named and described and is therefore not given separate taxonomic status. Specimens take the same name as Taxon J, ie. T. princeps var. princeps.

(c) Taxon K. This taxon was first described by Montagne (1850) as T. magellanica Mont. An authentic specimen has been located [T. magellanica Montag. Voy. Pole Sud, PC]. Unfortunately the packet contains plants referable to both taxon J and taxon K. The type description indicates that the plants have smooth hair-points and sporophytes however, which clearly separates the

plants in the packet, since the Taxon J 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 taxon K material agrees well with the type specimen of T. magellanica except that the former often have leaves of an oblong rather than ovate-lingulate shape. Oblong leaves seem to be commoner in sterile and less well developed specimens and most South Georgian collections show both leaf shapes. Taxon K can thus be referred to T. magellanica but it is necessary to give the name new status as a variety of T. princeps.

Müller (1885) and Cardot (1908) noted T. magellanica but neither seem to have examined material closely. The synonymy of other more widely used names has thus been overlooked. South Georgian plants of this taxon 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. Type material has been examined {Svenska Sydpolar-expeditionen 1901-03 N:R 223, T. monoica Card. sp nova. Falkland Islands, Port Louis. D.25/7 1902. Greenpatch in rupibus marit., Carl Skottsberg. Herb. J. Cardot, PC, H-BR}. These specimens have a few weathered sporophytes and have mainly oblong rather than oblong-lingulate leaves, but are well within the range of variation shown by this taxon on South Georgia. T. monoica is therefore considered a synonym.

Type specimens of Syntrichia fuegiana, Mitt. (Mitten 1860) have also been located and examined [Herbarium of William Mitten 1906, Type, Capo negra fret. Magellan. Lechler 1088, NY, BM ex K. Herbarium of William Mitten 1906 Barbula, Sandhills, Uranie bay, Falkland Islands W. 194 J.D. Hooker, NY]. Both undoubtedly belong to taxon K and this species must be considered a synonym. The South American type specimen (Lechler 1088) is more robust than South Georgian material but this might be expected for climatic reasons. The Falkland Island specimen is smaller and within the size range of South Georgian plants. Mitten (1860) described S. fuegiana as dioecious, however both type specimens are autoecious. Cardot (1908) may thus have been misled and did not compare this species with the synonymous T. monoica.

T. pusilla Aongstr. (hom. illeg.) was described by Ångström (1872) from Tierra del Fuego. Type material has been found [Tortula (Syntrichia) pusilla J. Ån, Port Famine fret. Magell. N.J. Anderson, S] and was found to be typical taxon K material. This name should also be reduced to synonymy.

Wijk et al (1969) cite T. monoica as a synonym of T. tenella Broth. described from New Zealand. Type material of this species has been examined [Herb. H.N. Dixon No. 822, T. tenella Broth, Otago, New Zealand, Coll. D. Petrie, Det. Brotherus, BM] and found to differ from the South Georgian taxon in leaf shape and general habit. T. tenella is more densely tufted, the leaves are slightly pandurate and broader above, the nerve is thicker, the hair-point smoother and the leaf lacks the cucullate apex of South Georgian material. Wijk et al (1969) based 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 the Antarctic however, by Pizarro and Sáiz (1977), appears to be based on this false synonymy and refers to T. monoica.

The correct name and synonymy for taxon K is thus:

Tortula princeps var. magellanica (Mont.) P.J. Lightowlers comb. et stat. nov. in preparation.

syn. T. monoica Card.

Syntrichia fuegiana Mitt.

T. pusilla Aongstr. (hom. illeg.)

(d) Taxon L. Bartram (1957) first described this taxon as T. conferta Bartr. from material collected on the Antarctic Peninsula. Type specimens have been examined [Plants of Antarctica, United States Antarctic Service Expedition of 1940-41 No. 335.12, T. conferta Bartr. sp. nov. det. E.B. Bartram, Lysted Island, Melchior Archipelago, P.A. Siple collector, March 1 1941, FH. Plants of Antarctica United States Antarctic Service Expedition of 1940-41 No. 345.1, T. conferta Bartr. and Pohlia cruda var. imbricata det. E.B. Bartram, Lambda Island, NE Landing, Melchior Archipelago, P.A. Siple collector, March 3 1941, FH] and other material from the Antarctic Peninsula, the South Shetland Islands and the South Orkney Islands in the British Antarctic Survey Herbarium (AAS) has also been studied. The small number of South Georgian specimens available seem to fall well within the wide variation shown by this taxon.

The correct name for this taxon, as a variety of T. princeps is therefore:

T. princeps var. conferta (Bartr.) P.J. Lightowlers

comb. et stat. nov. in preparation

7.10.3 Description

(a) General description (all hair-pointed taxa). 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 mm (excluding hair-point) x 0.3-1.3 mm, when moist patent, recurved at tips, 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 one third to one half of leaf length. Leaf margins entire, plane, recurved or revolute at mid-leaf or 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 in some leaves. Leaf apex cucullate to recurved in profile. Nerve reaching leaf apex or becoming obscure or disappearing in upper leaf, abaxial surface smooth or having simple verrucate papillae on long rectangular cells, and complex papillae on quadrate cells, often irregular or obscurely dentate towards apex. Hair-point 0.1-1.6 mm long, very rarely absent, smooth to denticulate, hyaline or reddish. Lamina cells 9-20 μ wide, quadrate, papillose with complex papillae. Quadrate cells spreading down margin of upper basal region of leaf. Basal cells 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 functionally dioecious. Perichaetial bracts similar to other leaves but broader

at base, innermost bract sheathing the seta. Perigonial bracts variable, often shorter and broader than other leaves. Sporophyte occasional. Plants sometimes polysetous. Seta 0.5-1.4 mm long when dry dextrorose (externe visus) above, often slightly sinistrorose at extreme base. Capsule erect, cylindrical 1.9-2.4 mm long. Operculum subulate, Peristome of 32 teeth united in a tube for about half their length and twisted into a dextrorose helix. Spores 11-15 μ in diameter, exine surface verrucate with some verrucae coverging to form ridges.

(b) Taxon I. Stems 0.6-2.0 (3.0) cm high. Leaves 1.2-2.5 mm x 0.6-1.3 mm, when moist spreading, recurved at tips, leaves oblong. Leaf margins almost plane to recurved for about half of the leaf length. Leaf apex recurved in profile. Nerve becoming indistinct above. Hair-point 0.2-0.6 (1.3) mm long, denticulate or crenate, reddish, rarely reduced to an apiculus. Only female inflorescences seen. Sporophyte unknown.

Figure 158a. (Micrographs: Figs. 95, 96, 116, 118, 146).

(c) T. princeps var. princeps. Stems 1.5-5.0 cm high. Leaves 1.8-3.5 mm x 0.7-1.2 mm wide, when moist patent spreading at tips, oblong to lingulate. Leaf margins recurved or revolute for half - two thirds of leaf length. Leaf apex plane or recurved in profile. Nerve continuous to leaf apex, rarely indistinct above. Hair-point 0.4-1.6 mm long, crenate to denticulate, hyaline or brownish towards the base. Autoecious or functionally dioecious. Sporophyte occasional.

Figure 157. (Micrographs: Figs. 97-9, 117, 123, 139, 140, 147).

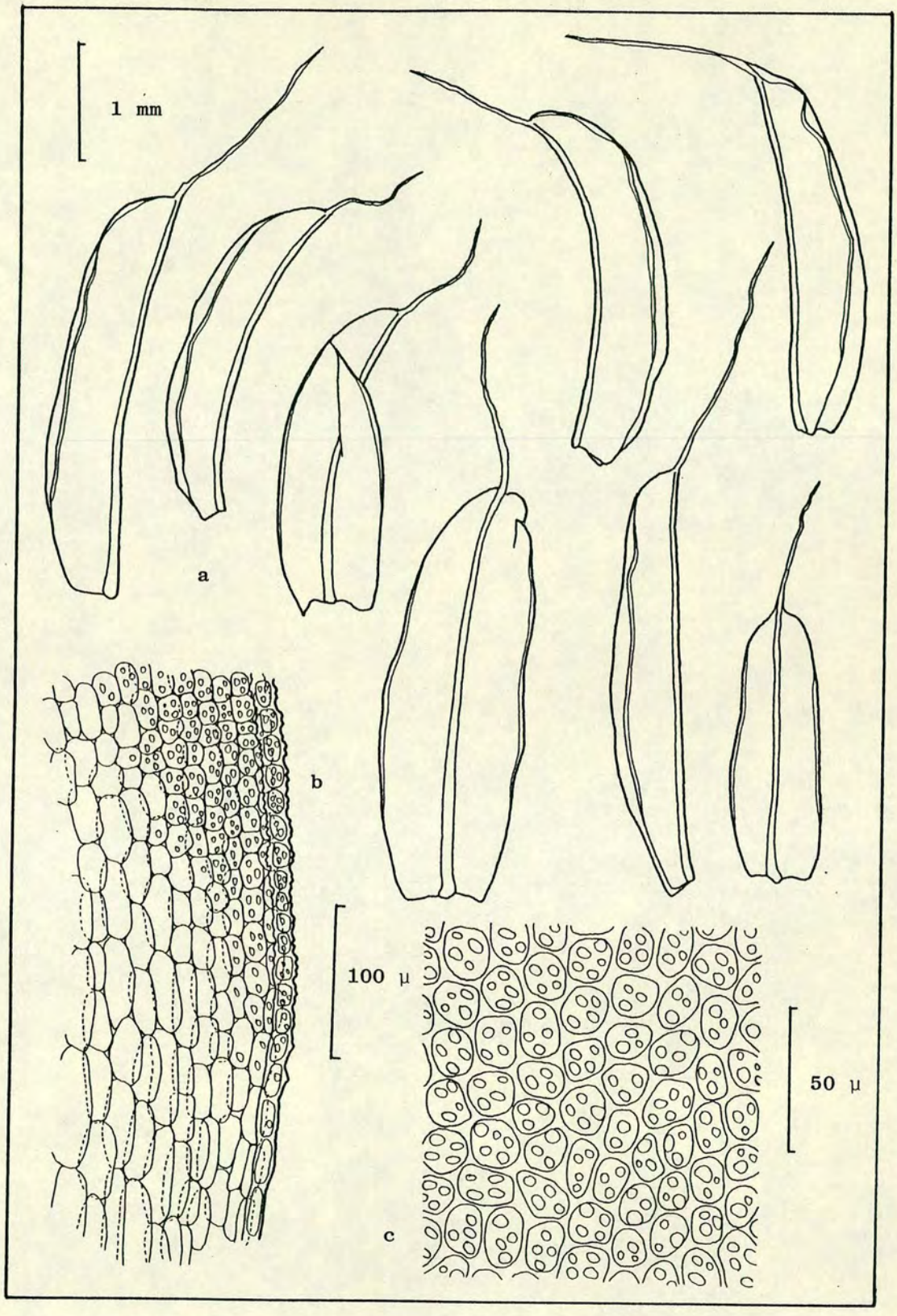


Figure 157. Tortula princeps var. princeps a. leaves b. upper basal leaf margin c. lamina cells. Scales: upper left hand for leaves, lower centre for leaf margin, lower right hand for lamina cells.

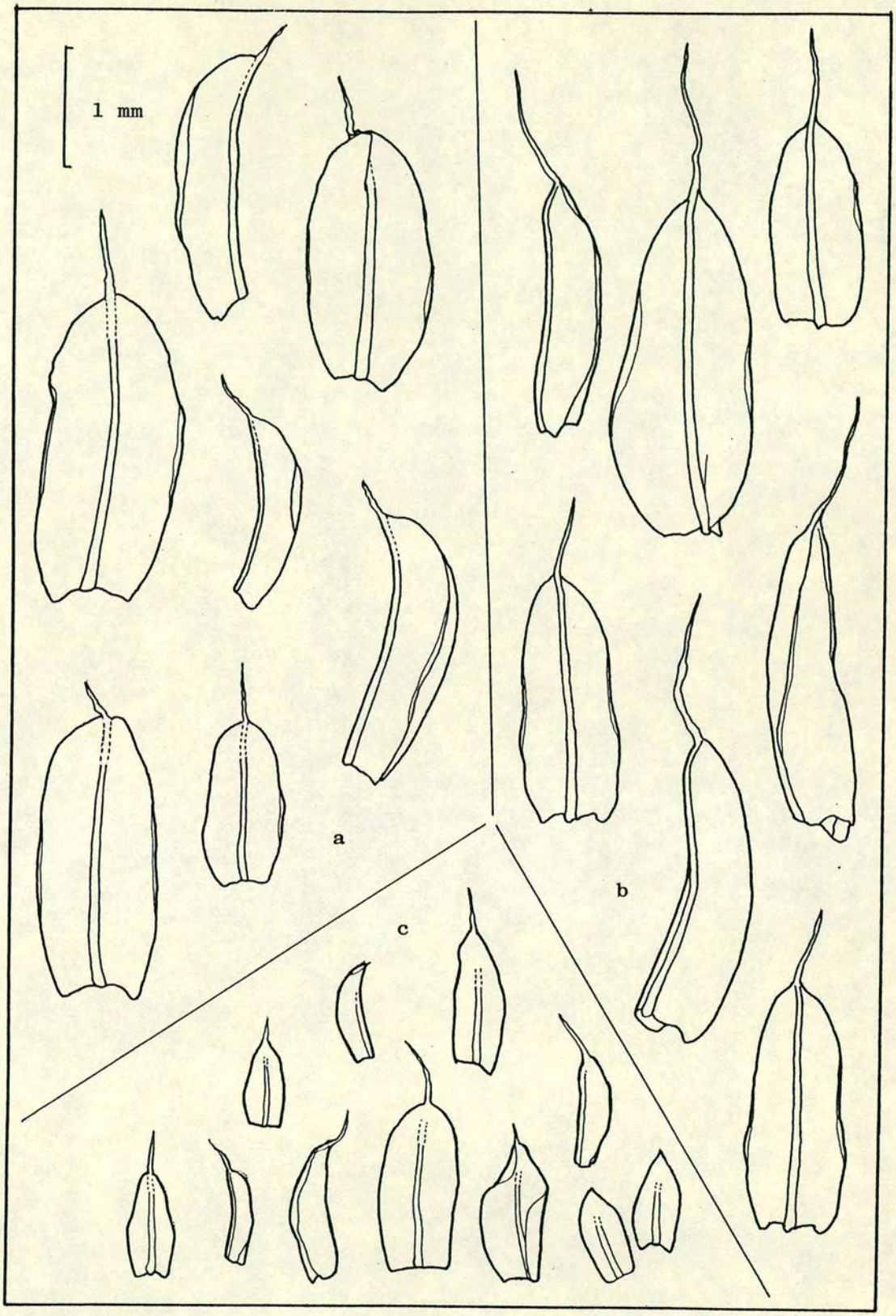


Figure 158 Tortula princeps leaves a. 'Taxon I' b. var. magellanica c. var. conferta. Scale: upper leaf hand for all leaves.

(d) Taxon K. Stems 0.5-1.5 cm high. Leaves (1.0-) 1.4-2.9 mm x 0.5-1.0 mm, when moist, erecto-patent, patent at tips, oblong to ovate lingulate. Leaf margins recurved for about one third to one 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.

Figure 158b. (Micrographs: Figs. 100, 114, 127, 130-2, 134).

(e) Taxon L. Stems slender, 0.2-1.5 cm high. Leaves 0.5-1.4 mm x 0.3-0.75 mm, when moist erecto-patent, spreading at tips, broadly oblong to ovate or lingulate. Leaf margins plane or weakly recurved at mid-leaf. Leaf apex cucullate to plane or rarely recurved in profile. 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 in some leaves. Sterile. Sporophyte unknown.

Figure 158c. (Micrographs: Figs. 101, 119, 120).

7.10.4. Habitat notes. There is little evidence from the specimen information that the hair-pointed taxa have different habitat preferences. All are found in rocky habitats near the coast, on peaty banks, on gravel and on rocks by streams, on whale bones and in man-made habitats such as on waste ground and on walls. Plants with red hair-points may often be found in wetter situations however, and T. princeps var. conferta seems to be commonest on dry rocks and walls. The majority of

specimens have been collected from low altitudes (below 10 m) but this may not be for climatic reasons as hair-pointed plants are frequent on the Antarctic Peninsula. Sea spray may be an important habitat factor influencing pH when most rocks and soils are base-poor. Specimens have been found at 300 m above sea-level growing on basic rocks or concrete.

7.10.5. Distribution. T. princeps sensu lato is worldwide in distribution and specimens from Europe, North America, Australia, New Zealand, Kerguelen, South America and the Antarctic Peninsula have been examined. South Georgian plants are most similar to South American, Antarctic and Kerguelen material in their pattern of variation, but the infra-specific taxa used for South Georgian material are not necessarily appropriate in these regions.

Kerguelen specimens show complete intergradation between the characters of taxa I, J and K within individual collections and sometimes on single stems. It is therefore impractical to recognise infra-specific taxa on these Islands and all hair-pointed material is referred to T. princeps var princeps.

Antarctic Peninsula collections contain many taxon L specimens which appear to intergrade with the other taxa. A large number of specimens are housed in the British Antarctic Survey herbarium (AAS) and it would be unwise to abandon taxon L before this has been thoroughly examined. Taxon L is therefore recognised as T. princeps var. conferta which, though scarce on South Georgia, is abundant on the Antarctic Peninsula. The characters which define taxa I, J and K on South Georgia are often not correlated in Antarctic Peninsula specimens and these taxa are difficult to

define in this region. These taxa are therefore not recognised and all material is referred to T. princeps var. princeps or var. conferta.

Plants with the characters of taxa J and K are most abundant in southern South America but plants approaching taxon I occasionally occur. The latter are not given formal taxonomic status, as with South Georgian material, and are referred to T. princeps var. princeps. Taxon J and taxon K appear distinct in South American material and are therefore referred to T. princeps var princeps and var. magellanica.

The geographical distribution of the varieties of T. princeps are therefore as follows:

var. princeps.	Cosmopolitan, but South Georgian plants are most similar to South American, Kerguelen and Antarctic specimens.
var. magellanica.	South America and South Georgia.
var. conferta.	South Georgia and the Antarctic.

7.11 Key to taxa

The South Georgian taxa of Tortula may be identified as follows:

1. Leaves hair-pointed, apex abruptly producing a hyaline or reddish hair*, leaves oblong to ovate-lingulate 9

   Leaves not hair-pointed, nerve percurrent at apex or if excurrent producing a short cusp or subula (up to 0.3 mm), 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 with a fine acuminate apex, nerve percurrent or excurrent in a tapering subula (Fig. 151b) .. .. T. saxicola

Leaves oblong or lingulate to lingulate-spathulate with an obtuse to broadly acute apex, nerve excurrent in a short cusp. (Fig. 150b.) .. .. T. anderssonii

4. Leaves with 2 to 9 rows of elongated cells extending up leaf margin to at least mid-leaf, leaves lingulate to lingulate-spathulate .. .. T. arenae

Leaves without elongated cells at the leaf margin or with 1 to 2 rows not extending to mid-leaf, leaves lanceolate to broadly oblong but never lingulate-spathulate 5

5. Leaves broadly oblong-spathulate or oblong-pandurate, leaves erect to patent when moist .. .. T. fontana

Leaves lanceolate to oblong-lanceolate, or if oblong then not spathulate or pandurate and leaves spreading

with recurved tips when moist 6

6. Cells in upper leaf very densely papillose (Fig. 156d), 7.5 - 12 µ wide

T. geheebiaeopsis

Cells in upper leaf sparsely papillose (Fig. 155d), 9-23 µ wide 7

7. Nerve ending in a sharply defined group of rhomboidal cells at the leaf apex (Fig. 155b) in most leaves, leaves up to 4 mm long, cells in upper leaf 9-15 µ wide .. .. T. filaris

Nerve ending in rhomboidal cells not forming a sharply defined group (Fig. 153b), leaves (3.2-) 4.4-8 mm long, upper leaf cells 11-21 µ wide 8

8. Leaves lanceolate to lingulate-lanceolate, 4.4-8 mm long, leaves erecto-patent to patent with spreading tips when moist .. .. .. T. robusta var. robusta

Leaves oblong to oblong-lanceolate, 3.2-4.8 mm long, leaves spreading with recurved tips when moist

T. robusta var. recurva

9. Stems slender forming dense tufts, leaves small (less than 1.4 mm long***), hair-point short (less than 0.4 mm long), leaf margin.

T. princeps var. conferta

Stems neither slender nor densely tufted. Leaves larger (over 1.4 mm long***), hair-points longer (over 0.4 mm) leaf margin recurved or revolute .. .. .10

10. 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

Notes to key:

* Hair-point reduced to an apiculus or absent in some leaves of small specimens.

** Leaf apices of young leaves should be examined as erosion of cell walls occurs on the upper margins of older leaves which may remove teeth.

*** Leaf length measurements of hair-pointed leaves do not include the hair-point.

7.12 Summary

The 12 provisional taxa of South Georgia Tortula are

assigned to 8 species and 3 varieties (Table 20). A synopsis of the taxonomy proposed for the genus in the sub-Antarctic is also given in Table 21.

Table 20. Final nomenclature of the twelve provisional taxa of South Georgian Tortula.

Provisional taxon	Final name
A	T. arenae (Besch.) Broth. ssp. arenae
B	T. anderssonii Aogstr.
C	T. saxicola Card.
D	T. fontana (C. Muell.) Broth.
E	T. robusta Hook. et Grev. ssp. robusta var. recurva P.J. Lightowlers var. nov. in preparation.
F	T. robusta Hook. et Grev. ssp. robusta var. robusta
G	T. filaris (C. Muell.) Broth.
H	T. geheebiaeopsis (C. Muell.) Broth.
I	T. princeps De Not. var. princeps.
J	T. princeps De Not. var. princeps.
K	T. princeps De Not. var. magellanica (Mont.) P.J. Lightowlers comb. et stat. nov. in preparation.
L	T. princeps De Not. var. conferta (Bartr.) P.J. Lightowlers comb. et stat. nov. in preparation.

Table 21. A synopsis of nomenclature proposed for sub-Antarctic *Tortula* species.

T. anderssonii Aongstr.

syn. *T. bealeyensis* R. Br. ter.

T. arenae (Besch.) Broth. ssp. *arenae*

syn. *T. lingulaefolia* Card.

ssp. *petriei* (Broth.) P.J. Lightowlers *comb. et stat. nov.* in preparation.

T. filaris (C. Muell.) Broth.

syn. *T. excelsa* Card.

T. robustula Card.

T. fontana (C. Muell.) Broth.

syn. *T. rivularis* Dus.

T. geheebiaeopsis (C. Muell.) Broth.

T. princeps De Not. var. *princeps*

syn. *T. grossiretis* Card. var *grossiretis*

T. grosseretis Card. var *atrata* Card.

T. heteroneura Card.

var. *magellanica* (Mont.) P.J. Lightowlers *comb. et stat. nov.* in preparation.

syn. T. fuegiana (Mitt.) Mitt.

T. monoica Card.

T. pusilla Aongstr. hom. illeg.

var. conferta (Bartr.) P.J. Lightowlers comb. et stat. nov. in preparation.

T. robusta Hook. et. Grev. ssp. robusta var. robusta

syn. T. anacamptophylla (C. Muell.) Broth.

T. lepto-syntrichia (C. Muell.) Broth.

T. robusta var. runcinata (C. Muell.) Broth.

var. recurva P.J. Lightowlers var. nov. in preparation

ssp. rubra (Mitt.) P.J. Lightowlers comb. et. stat. nov. in preparation.

T. saxicola Card.

syn. T. fuscoviridis Card.

Chapter 8 : DISCUSSION

The primary aim of this study was to produce a taxonomic account of *Tortula* for the Island of South Georgia. The results are summarised as a checklist in Table 22. The genus is treated as eleven taxa, that is, eight species and three varieties. The patterns of variation which provide the basis for this classification can be outlined as follows:

i) distinct species with no similar taxa and no intermediates eg. *T. saxicola* and *T. geheebiaeopsis*.

ii) aggregates of species which are similar at their extremes of variation, eg. *T. robusta*, *T. filaris* and *T. fontana*, intermediates are exceptional.

iii) polymorphic species, which consist of two or more forms linked to varying degrees by a series of intermediates, eg. *T. princeps* var. *princeps*; var. *magellanica*; var. *conferta* and the red hair-pointed form 'taxon I'.

The species is, in practice, only a convenient term for a group of individuals 'possessing certain distinctive but not invariable characters' (Best 1905) and, although theoretically defined as a group of populations capable of exchanging genes, bryophyte species have never successfully been tested by breeding experiments. There remains an element of judgement in the delimitation of species. What is regarded in this study as a single polymorphic species may be treated by another author as an aggregate of

Table 22. A revised checklist of South Georgian Tortula species

T. anderssonii Aongstr.

T. arenae (Besch.) Broth ssp. arenae
(syn. T. lingulaefolia Card.)

T. filaris (C. Muell.) Broth.

T. fontana (C. Muell.) Broth.

T. geheebiaeopsis (C. Muell.) Broth.

T. princeps De Not. var. princeps
(syn. T. grossiretis Card.)

var. conferta (Bartr.) P.J. Lightowlers comb. et stat. nov. (in prep.)

var. magellanica (Mont.) P.J. Lightowlers comb. et stat. nov. (in prep.)
(syn. T. monoica Card.)

T. robusta Hk. et Grev. ssp. robusta var. robusta
(syn. Barbula anacamptophylla C. Muell.
B. leptosyntrichia C. Muell.
B. runcinata C. Muell.)

var. recurva P.J. Lightowlers var. nov. (in prep.)

T. saxicola Card.
(syn. T. fuscoviridis Card.)

several species. Perhaps the constraint on the taxonomist to produce workable keys and identifiable species prevents the concept of the species from becoming too broad to include dissimilar plants or too narrow and thus separating plants which are very similar.

One factor affecting the breadth of species concepts is the size of area included in a taxonomic revision. During this study, Tortula species from South Georgia were examined in detail and floras of neighbouring regions were studied less critically. Sufficient research was possible to clarify the taxonomy of sub-Antarctic species and some differences between the study of small and large geographical areas were noted.

In large areas, such as the sub-Antarctic, the variation observed within a taxon is likely to be larger and more complex that in small areas. This is particularly so in the southern hemisphere because gene flow between the widely disjunct land masses is probably small, and the taxa are therefore effectively isolated. Variation patterns were observed which suggested that description and delimitation of a taxon in one area may not adequately define the taxon in another. T. princeps var. magellanica, for example, was shown to intergrade with var. princeps on South Georgia but the same taxon in South America appeared to be distinct. Additionally, characters which were weakly associated with the var. magellanica on South Georgia, such as smooth rather than dentate hair-points, were strongly associated with the variety in South America. In Antarctica, however, the main characters

defining the taxon appeared to lose correlation, particularly stem size, leaf profile and sporophyte frequency. Biologically this pattern of variation can be explained by the presence of barriers to inter-breeding in South America which are weaker on South Georgia and absent in the Antarctic, but taxonomically it is a problem which needs to be considered further. Where two taxa are distinct, different names may be used to distinguish them, but in areas where the taxa intergrade, these names tend to be reduced to synonymy. This has occurred with T. intermedia (Brid.) De Not. in Europe and North America. T. intermedia was originally described from European material and is considered to be a well defined species by European authors (eg. Dixon 1924, Smith 1978), but Crum and Anderson (1981) consider it to be synonymous with the widespread species T. ruralis (Hedw.) Gaertn. et al in North America. The most satisfactory solution seems to be to refer the taxa to different subspecies in the region where they are distinct, and to place all specimens in a single subspecies where they intergrade. The rank of subspecies in this instance is used to denote sympatric taxa which are distinct only in part of their range. It has also been used in this study to indicate similar allopatric taxa in T. arenae ssp. arenae and ssp. petriei, and in T. robusta ssp. robusta and ssp. rubra.

Revisions of large areas, especially world-wide monographs, may result in the reduction to synonymy of taxa which are locally distinct. Bremer (1980b) for example, in a world monograph of Schistidium, reduces Grimmia urnulacea C. Muell. and G. celata

Card. to synonymy with Schistidium apocarpum (Hedw.) B.S.G., although B.G. Bell (unpublished manuscript) considers both to be distinct species on South Georgia. This may be due to local discontinuity being insignificant in the pattern of variation over a large geographical area or, perhaps, to insufficient sensitivity on the part of the monographer. The latter is particularly likely because the amount of work required on the flora of areas like South Georgia is so large that thorough world monographs of anything except very small genera are time consuming. Schistidium, for example, is a small to medium-sized genus of an estimated 20 species (Bremer 1980a, Smith 1978). Bremer's (1980a, 1980b and 1981) monograph of the genus is incomplete as there has been no attempt to examine Schistidium material from its full geographical range and therefore the revision does not describe the variation within species comprehensively. Intergradation may occur, for example, between species in areas where representatives of the genus have not been examined. Another shortcoming of Bremer's (1980a, 1980b and 1981) revision is the failure to trace all relevant species. Bell (personal communication) notes two specific epithets in a revision of South Georgian species which have been omitted. Bremer's (1980a, 1980b and 1981) revision is nevertheless a valuable contribution to the taxonomy of Schistidium, but its limitations should be recognised.

The difficulties of the monographer who encounters complex variation patterns over large geographical areas are made more acute by the absence of local floras in places such as South

Georgia. These floras contribute to world monographs by describing variation at a local level and by resolving problems of synonymy, in addition to their function as manuals for local botanists. These floras are therefore important to the future development of bryophyte taxonomy.

The revision of South Georgian Tortula taxa involved considerable changes in nomenclature. Of the ten taxa previously reported from the Island (Table 4), two have been reduced to synonymy, four have been renamed after the discovery of earlier synonyms and one was found to be a false report. Only three taxa have the same name in both old and new checklists. Extensive changes in the nomenclature appear to be a frequent occurrence in revisions of poorly known moss floras. Touw (1974) for example, estimates that only 32% of species or infra-specific taxa described are maintained in recent revisions of mosses from exotic regions. This emphasises the inadequacy of much bryophyte taxonomy and great care should be taken when considering groups which have not been revised recently.

The distribution of South Georgian species based on specimens examined during this study and recent reports in the literature is given in Table 23. Although inaccuracies may be present due to species having been overlooked by collectors or taxonomists, Table 23 shows that the eight species found on South Georgia are also present in South America and five are common to both South Georgia and the Crozet or Kerguelen Islands. Four species are found on South Georgia and in New Zealand but two of these are

Table 23. The distribution of South Georgian Tortula species, compiled from the specimens listed in Appendix 5 and from Clifford (1953), Seppelt (1981), Vitt (1979) and Zanten (1971).

Key: ● = present ○= present as different subspecies.

? = unverified report

	T. andersonii	T. arenae	T. filaris	T. fontana	T. geheebiaeopsis	T. princeps	T. robusta	T. saxicola
Austral South America	●	●	●	●	●	●	●	●
Antarctic Peninsula	·	·	●	·	·	●	·	●
Marion and Prince Edward Islands	·	·	·	·	?	·	?	·
Crozet	●	●	·	·	·	·	·	·
Kerguelen	·	●	·	·	●	●	·	●
Heard Island	·	·	·	·	·	·	?	·
Macquarie Island	●	·	·	·	·	·	?	·
Auckland and Campbell Islands	·	·	·	·	·	·	○	·
New Zealand	●	○	·	·	·	●	○	·
Australia	·	·	·	·	·	●	○	·

represented by different subspecies in the two areas. Evidence from Tortula species thus suggests strong links between the flora of South Georgia and the flora of southern South America, some links with the floras of the Crozet and Kerguelen Islands and weaker links with the flora of New Zealand.

Phytogeography depends to a great extent on taxonomy and phytogeographers are liable to come to the wrong conclusions if their work is based on inaccurate nomenclature. Zanten (1971), for example, provided a table showing the geographical distribution of moss species from Marion Island. In the genus Tortula two species are provisionally reported as T. geheebiaeopsis and T. rubra. Diagrams of the plant determined as T. geheebiaeopsis show an adaxial stereid band, a character which is never present in Tortula. Zanten (1971) compared his material with a specimen determined by Kaalaas from Crozet, a duplicate of which has been examined during this study and redetermined as Leptodontium microruncinatum Dus. Zanten's material probably also belongs to this species. Records of T. geheebiaeopsis from Marion Island and Crozet in Zanten's (1971) distribution table are therefore erroneous. This species has never been reported from South Georgia or South America and it is not surprising that the table does not show its presence in these areas. The identification of T. rubra (T. robusta ssp. rubra) also appears to be doubtful but cannot be checked from the information provided. Reports of this species from South Georgia and South America appear to be incorrect as all specimens from these areas examined in this study belonged to T. robusta (ssp. robusta).

As a result of misidentifications, failure to recognise synonyms and omission due to inadequate collecting, distribution data can be very misleading. Data based on poor taxonomy does not accurately show the relationships between the floras of different areas and comparisons between floras should only be made after thorough taxonomic revision.

The similarities of the floras of Australia, New Zealand, Tierra del Fuego and the sub-Antarctic Islands, isolated by thousands of miles of ocean, can be explained by long distance dispersal and continental drift. Zanten (1976, 1977 and 1980) investigated the ability of spores of many New Zealand moss species to survive the conditions which might occur during long range dispersal by air currents. This work, despite many errors due to inadequate taxonomy, succeeds in showing that widely dispersed species generally have spores which maintain their viability after various desiccation and freezing treatments. Dispersal may also occur by other means such as propagules carried by birds or other vectors.

Sub-Antarctic species may be relicts of a flora which once covered cool temperate regions of a pan-Antarctic continent in the mesozoic era. About 80 million years ago this continent split up and the various fragments including India, Australia, Africa, South America and Antarctica drifted apart and were subjected to different climates. Cretaceous and tertiary deposits of temperate Fagus - Nothofagus forests are known in Antarctica, South America, Australia, and New Zealand (Du Rietz

1940, Skottsberg 1960) which show that these areas have had a period with a climate conducive to the survival of a rich bryophyte flora since the pan-Antarctic continent fragmented. During the pleistocene, 0.01 to 2 million years ago, severe glaciation affected much of the southern hemisphere, particularly Antarctica, which has remained under ice until the present day. This change probably caused widespread extinction but the temperate flora could have survived by northward migration into South America, New Zealand and Australia. Subsequently a partial amelioration of the climate may have resulted in a southward migration of cold adapted bryophytes, which though possible in South America, could not occur in Australia and New Zealand. Some bryophytes may thus have become extinct in these areas but there is good reason for believing that the present flora of Tierra del Fuego and South Georgia may be rich in ancient species.

Examination of Antarctic collections in the British Antarctic Survey Herbarium (AAS) suggests that the Antarctic moss flora contains only three species of Tortula all of which are common to South Georgia and southern South America. One variety, T. princeps var. conferta is limited to South Georgia and the Antarctic but further work may show that it intergrades completely with larger plants of the species, and is therefore not worthy of separate taxonomic status. The degree of modification and reduction shown in the variety seems to indicate that some adaptation to severe climate has occurred, but this may be a recent event. The evidence from Tortula therefore agrees with Robinson's (1972) suggestion that the flora is modern in origin

and does not contain palaeoendemic species. Palaeoendemics may occur but they appear to be rare and probably survive only in isolated refugia. If most of the flora is recently derived then it is likely to have migrated from southern South America via the islands of the Scotia sea.

Tortula species show some interesting differences between northern and southern hemispheres which may provide a clue to the origin of the genus The southern hemisphere flora includes robust plants with dentate leaves such as T. robusta which are unknown in the northern hemisphere. Together with their longly rectangular cells at the basal margin of the leaf, these species form a distinct group. However, it is not well defined because one species, T. anderssonii, has intermediate characters and appears to form a link with species such as T. saxicola which have entire leaves and quadrate basal marginal cells. The group with dentate leaves also has links with T. subulata Hedw. of the northern hemisphere, which is similar in leaf shape and areolation and sometimes has denticulate leaves. T. subulata is the type species of Tortula section Tortula, and because of the similarities noted above, the southern hemisphere dentate-leaved group has been included in this section of the genus for the purposes of this study.

At least 19 species of Tortula are known to occur in the southern hemisphere, either from specimens examined in this study or from reports by Sainsbury (1955) from New Zealand and Catcheside (1980) from South Australia. Only 4 of these belong to the section Rurales De Not. and 9 to the section Tortula. In the northern

hemisphere Corley et al (1981) and Steere (1939) list 44 species of which 16 belong to the section Rurales and 3 to the section Tortula, the remainder belong to other sections or are of unknown affinities. The section Rurales is thus well represented in the northern hemisphere but poorly represented in the south, where 2 of the 4 species known are cosmopolitan. The section Tortula is abundant in the southern hemisphere but there are relatively few species in the north.

This difference in character between the floras of the two hemispheres may be a result of long isolation. Tortula is a genus which is polar and temperate in distribution and is effectively divided in two by the equatorial tropics. Only a minority of species such as T. muralis Hedw., T. papillosa Wils., T. laevipila (Brid.) Schwaegr. and T. princeps occur in both hemispheres and the distribution of these species can be explained by long distance dispersal or by migration along north-south mountain chains.

The southern hemisphere species of Tortula seem to be least specialised in an evolutionary sense. Miller (1971) noted some primitive and advanced features of mosses and the large size and lack of advanced characters of species such as T. robusta suggest that they are among the most primitive members of the genus. Newton (1971) reported a chromosome number of n = 7 in this species which, with a report by Ramsay (1967) of n = 6 + 1 m for T. papillosa, is the lowest in the genus. Low chromosome numbers are believed to be primitive, larger numbers being derived from them through polyploidy. Counts of n = 12 have also been made for T. robusta and the related species T. filaris and T. fontana

(Newton 1980 and personal communication). T. geheebiaeopsis, another species with dentate leaves, has a chromosome number of n = 13 (Newton 1972, as T. serrata Dix.).

The section Rurales which is well represented in the northern hemisphere, has features which are advanced according to Miller (1971). Most species are adapted to survive drought, have hair-pointed leaves and in some cases have specialised vegetative propagules. Kramer (1980) also described species with bistratose laminae, which is unusual in Tortula and is probably an advanced xerophytic feature. Chromosome numbers in the section Rurales, excluding T. papillosa which has been misplaced in this section (Kramer 1980), vary between n = 12 and n = 36 + 2. The lowest number, n = 12, is found in T. princeps which is the commonest and most widely distributed species in the Southern hemisphere. Kramer (1980) regards T. princeps as primitive and suggests a dioecious species like it to have been the original ancestor of the section Rurales. Austral T. princeps, which may be dioecious, autoecious or synoecious, could thus be a precursor of the section Rurales, which has its present centre of diversity in the northern hemisphere.

It is impossible to make definite conclusions about the genus Tortula in the southern hemisphere because many South American taxa are almost unknown. Schuster (1969) has remarked that he regards the south temperate zone as an ancient centre of many hepatic families such as the Gymnomitraceae, the Blepharostomataceae and the Scapaniaceae, which have since migrated northward and

diversified. There is some evidence from the present study that this may also be the case with Tortula. The southern hemisphere is rich in species with dentate leaves which appear to be primitive and the northern hemisphere by contrast has many species of the section Rurales with advanced features.

The second aim of this study was to test new systematic techniques and apply them to the genus Tortula. Statistical analyses, growth experiments and scanning electron microscopy have been used and the results have contributed to the taxonomic treatment.

Statistical techniques relevant to taxonomic studies can be divided into those that aim to describe the variation pattern and those that aim to classify it using clustering techniques. Descriptive techniques range from scatter diagrams to principal components or other multivariate analyses. They fulfil the need to make taxonomic conclusions open to critical discussion. Variation patterns are the taxonomical equivalent of 'results' in experimental science and data on them should be presented to provide a basis for the conclusions made. There is a tradition of presenting the results of taxonomic work as a key and descriptions alone, with no explanation of how they were arrived at. If more details of methods, variation and discussion of taxa were included in taxonomic treatments this would not only provide a more sound basis for classification but also ensure that the processes and objectives of taxonomy in general were more widely understood.

Numerical classification techniques involving cluster analyses are a superficially attractive way of finding groups by statistical

means. Taxonomy in the past has often not been demonstrably objective and the appeal of clustering lies in the removal of the 'intuitive' group-recognition process. Although cluster analyses are not intuitive in that they do not rely on the pattern recognition capabilities of the human mind, they are not infallible. They are strongly influenced by the choice of characters and as a cluster can only be defined as a subjective blend of internal cohesion and external isolation, the search for objectivity is defeated. Furthermore clustering techniques use algorithms with no formal statistical basis (Cormack 1971) as formal techniques are too time consuming even with the fastest computers.

Despite their limitations, cluster analyses do provide corroborative evidence if they produce a classification which is similar to that achieved by traditional means. This is perhaps not as valuable as that of an independent taxonomist working on the same group, but is nevertheless evidence that the classification is repeatable, and hence objective. If the classification produced by cluster analysis does not correspond with the groups recognised by intuitive means then the analysis 'fails' as a taxonomic exercise. The problem then becomes a statistical one of finding out why the classifications differ. If the groups recognised by numerical methods appeared to have no recognisable logical pattern to taxonomists, then it is inconceivable that they would be accepted as a valid general purpose classification.

Numerical classification techniques therefore are generally only suitable for confirming taxonomic conclusions and are unlikely to

replace intuitive techniques or make up for any lack of thoroughness on the part of the taxonomist. One example of over reliance on numerical techniques is Cox's (1961) study of Tortula. Specimens included in the study were determined as T. robusta, T. rubra or T. serrulata by many different taxonomists and Cox made no taxonomic assessment of the plants herself before measurement. The specimens studied, which are unfortunately not listed, came from a wide geographical area and differences between areas may have confused differences between taxa. Cox (1961) placed too much emphasis on measurements and failed to take into account other characters such as leaf shape and leaf serration, which show discontinuity and can be used to delimit species.

One difficulty with numerical techniques encountered in this study was the initial scoring or measuring process in which characters were converted into numerical values. There are different methods of representing characters which are either continuous, including measuring and scoring in confluent groups, or discontinuous, such as recording the presence or absence of characters or scoring in a series of discrete categories. Different characters are best scored in different ways but it is not always easy to combine different methods in one analysis without giving an undesirable weighting to one type of data (Gordon 1981).

Some characters were difficult to define or measure or were so variable that many replicate measurements had to be made to detect significant variation. Leaf stance, for example, was a complex character which was not included in quantitative

assessments because of the difficulty of definition and measurement. The angle between the leaf base and the stem could be measured by projecting an image of the plant onto a protractor, but this made no allowance for recurvature at the leaf apex which was also a factor in the apparent leaf stance. Many measurements were necessary because of the large variation between leaves on each stem. Leaf shape was also diffficult to represent numerically. Measurements of maximum leaf width/leaf length ratio gave an approximate indication of shape in most cases, but could not distinguish T. robusta var. robusta and var. recurva after cultivation, even though the leaf shapes were distinguishable by eye. Leaf width at 1/3 leaf length from apex/leaf length ratio gave a better separation in this case but was still relatively insensitive. A series of leaf width/length ratio measurements may be necessary to reflect leaf shape differences accurately. In future, computerised image analysis equipment may help solve problems of measurement of complex characters and reduce the time needed to gather data for analysis. At present it is not possible to represent all characters accurately in a quantitative way and the time needed for measuring and scoring imposes limitations on the size of problem which can be tackled.

Cultivation experiments on Tortula plants were successfully carried out in artificial environments. Collateral cultivation of non-hair-pointed species showed that all taxa were constant in cultivation although leaf shape differences between taxa E and F (T. robusta var. recurva and T. robusta var. robusta) were slightly 'levelled out', suggesting that they were partly environmental in origin. Such

experiments have limitations and any conclusions drawn from them must be made with caution. It cannot be assumed that plants which appear different when grown under the same conditions are genetically different and plants which appear identical when grown under the same conditions may not be genetically identical.

Plants with the same genotype grown under the same conditions may produce different phenotypes because of the effects of previous environments. These may be carried over from the parent plant particularly if the material is propagated from fragments or cuttings. Longton (1981) argues that, in bryophytes, material grown from spores may be less susceptible to past environmental effects than vegetatively propagated material. This follows by analogy from seed grown higher plants, which angiosperm taxonomists prefer to use for growth experiments. Durrant (1962) however, working on flax, showed that the environment of the parent affected the progeny through several generations. Although effects of this type have not been demonstrated in bryophytes they may occur. The possibility that previous environment may influence experimental results is unavoidable but may be minimised by growing plants for long periods and propagating from spores when possible.

Plants which have identical phenotypes when grown under the same conditions may have different genotypes which respond in the same way to one particular environment. This principle is called phenocopying (Dobzhansky 1970) and to distinguish phenocopies from genetically identical plants, it is necessary to grow material in a wide range of different conditions so that differences in response to the environment can be detected.

Cultivation of hair-pointed Tortula species in a range of different conditions was attempted but little variation was observed between plants in different environments. Experiments using a range of conditions may be useful not only to help solve taxonomic problems but also to show the effects of environment on morphology. Often taxonomists attribute unusual combinations of characters to an atypical environment, for example, specimens are assumed to be shade forms or wet habitat forms. In Tortula, some plants produce a brown pigment in the cell walls of old leaves, but other plants do not have this pigment, giving the leaves a pale green translucent appearance under the light microscope. Observations on herbarium material and growth experiments suggested that the presence of the brown pigment was associated with desiccation, but this has not been demonstrated by experiment. Evidence of this sort would be useful to taxonomists in interpreting the morphology of many species in the Pottiaceae which produce a similar pigment.

Growth experiments are potentially useful for the investigation of depauperate Antarctic taxa such as T. princeps var. conferta, or plants which are so reduced in morphology that they cannot be identified.

Difficulties were experienced during this study in transporting material. Specimens were often in poor condition on arrival and produced abnormal growth in transit. In future these problems may be solved by moving drought tolerant species in an air-dried state. Hair-pointed Tortula plants survived several months of desiccation with no adverse effects and one South American specimen

which had been dry for 4 years resumed vigorous growth when moistened. The failure of South Georgian herbarium specimens to recover from desiccation is attributed to the method of drying. Heated drying facilities exist on the Island which have been used by most collectors (B.G. Bell, personal communication). The rapid loss of water achieved by the use of heat appears to be harmful and only material which is allowed to dry gradually remains viable. Material allowed to dry slowly may be sent by post and revived on arrival, so the problem of abnormal growth during transit can be avoided.

Growth experiments, despite their theoretical limitations are of importance to the future of bryophyte taxonomy. The techniques necessary for cultivation are poorly developed but further work should remove these difficulties. Growth experiments should be attempted only after a thorough taxonomic evaluation has shown where clarification is most needed. Experimental material can then be chosen which represents these areas of doubt. Experimenters should preferably be able to collect their own specimens in the field or at least have access to a wide range of living specimens. If the material is to be assessed quantitatively, this is best undertaken when the experiment is completed so that measurements most appropriate to show the changes in morphology can be selected.

Scanning electron microscopy produced new information on taxonomic characters such as lamina cell papillae and provided illustrations of structures such as rhizoid surfaces and peristome papillae which have taxonomic potential. There is a need for comprehensive

studies in a range of bryophyte groups to evaluate the significance of new characters visible under the SEM. Although these cannot be used as key characters, their systematic value may be important. As Magill and Horton (1982) remarked, the SEM is not a replacement for the light microscope but should be used in addition to it. Examination of large amounts of material are not practical or economical using the SEM, but only a few specimens need to be examined to provide a new perspective on characters observed by light microscope and micrographs for publication in monographs.

In summary, the priorities for taxonomic study of little known floras of areas such as the Antarctic are as follows:-

i) To define and describe taxa and to produce a means of identification for general use.

ii) To achieve a standardised, stable nomenclature which allows comparisons with floras of other areas.

iii) To recognise any contributions of the flora to existing taxonomic concepts such as the definition of families, genera or species.

iv) To test and improve the classification by contributing further evidence from techniques such as growth studies, cytology, chemotaxonomy and statistics.

This study has taken a small group of species and attempted to take them as far as possible along this course. Although a useful exercise in understanding the development of taxonomic work,

this may not be the most helpful way of continuing the study of the Antarctic flora. Taxonomy is a practical discipline and the results of taxonomic studies are needed by scientists working on other aspects of plant biology. A trained taxonomist could complete the flora more quickly if the depth of study was limited to the definition and description of taxa and the production of a key. This would make information and specimens available more rapidly and allow other taxonomists working on monographs to solve some of the less urgent problems by including Antarctic taxa in their work.

In a study of limited scope, which aims to define, describe and identify taxa, the roles of statistical techniques, growth studies and scanning electron microscopy need to be considered further. Although computer packages are now widely available which can quickly carry out multivariate analyses most of the time in statistical studies is taken up by measurement and scoring of specimens and this is a major limitation of these studies. However, measurements such as leaf length, leaf width and cell sizes are routinely taken during the preparation of descriptions. These could be formalised to provide data for scatter diagrams or even principal components analyses. Extra scoring or measurement may be required to clarify certain variation patterns if these are unusual or complex, as in polymorphic species like T. princeps. In general the number of characters used should be kept to a minimum, involving only those in which variation is known to be important.

Growth experiments are time consuming because techniques for growing particular species have to be developed and tested and at least 6 months or 1 year are needed before significant growth is obtained. Growth experiments are best conducted after a taxonomic revision has been completed so that the areas most in need of study can be included in the range of specimens. Growth experiments are therefore not a suitable method for use during a taxonomic revision of a little known flora, which aims to cover as many taxa as possible in the time available.

Scanning electron microscopy may be used to search for new characters and to give a better understanding of structures examined under the light microscope. The results may prevent characters being misunderstood and misinterpreted or may provide illustrations for publication with a resolution and depth of field difficult to obtain using light microscopy. It is not a time consuming procedure, especially if many specimens are prepared simultaneously and a preliminary examination of the material has been undertaken using a light microscope.

In conclusion, new systematic techniques are not necessarily suited to the needs of the taxonomy of little known areas. Large exercises in numerical classification or formal growth studies are probably better left to taxonomists working on floras in which the basic work of the delimitation and description of taxa is complete. Scanning electron microscopy however is a useful tool for examining the material under study can profitably be used in the preparation of primary local floras such as the 'Synoptic flora of South Georgian mosses' (eg. Greene

1973). Looking to the future of such floristic work, the aim remains the same, that is the production of descriptions and keys as rapidly as possible. Growth experiments and statistics offer opportunities for studies in greater depth once such work is complete.

Appendix 1

J. Bryol. (1981), **11**, 843–845

Bryological Notes

Techniques for mounting fragile tissue in gum chloral solution

Gum chloral and similar gum arabic based mounting media are widely used for making microscope slides of bryophyte leaves and stem sections etc. (Sayre, 1941; Anderson, 1954; Bowers, 1964; Watson, 1968). While such slides are easy to prepare and are invaluable in the rapid examination and comparison of specimens, there are problems in the use of such media. Anderson (1954) noted that distortion occurs when mounting leaves of *Mnium* and *Tortella* species. Zander (1979) encountered the same problem with *Tortula* and remarked that specimens with large cells and thin walls are most susceptible. In the course of recent work on *Tortula* the author has found that many preparations were inadequate because of the severe distortion and collapse of cells in the mountant. In addition, young leaves, stems

and protonemata also seem to be severely affected, the distortion that occurs apparently being similar to the curling and shrinking that takes place when the plants dry naturally. This is perhaps not surprising since the setting of gum arabic mountants involves the loss of water.

Preparations of leaves in pure gum arabic solution are more severely distorted than those made in gum chloral solution, which contains in addition to gum arabic, chloral hydrate as a preservative and glycerol (Watson, 1968). The function of glycerol seems to be to prevent distortion, but it also increases the drying period and results in a less firm final preparation.

After experimenting with various techniques it was found that pre-soaking specimens in certain viscous solutions was a useful way of reducing distortion. The effectiveness of this general method seems to rely on maintaining a high concentration of the viscous solution in the plant tissue which prevents the distorting effects of partial desiccation during setting. Fresh or dry material is placed in an aqueous solution of 50% polyethylene glycol (PEG) 400 grade and left until thoroughly penetrated (*c.* 12 hrs.). Glycerol (50–100%) or lactic acid (100%) can be used instead of PEG but were found to give less effective results. After soaking, the material is removed, blotted thoroughly with tissue paper, placed in a drop of mountant on the slide and dissected as necessary. Thorough blotting is particularly important as an excess of any of the three solutions has deleterious effects. Excess PEG reacts with the gum arabic to produce an opaque precipitate, too much glycerol delays the setting time of the preparation while excess lactic acid crystallises on drying. Any bubbles of air in the mountant can be teased out at this stage before a coverslip is placed over the preparation.

Using a 50% solution of PEG (which can be re-used) all but the most susceptible *Tortula* specimens were mounted satisfactorily. Glycerol and lactic acid produced a considerable but less marked improvement in most material. None of the solutions appear to affect the optical or keeping qualities of the preparations provided the slides are made correctly.

REFERENCES

Anderson, L.E. (1954). Hoyer's solution as a rapid permanent mounting medium for bryophytes. *Bryologist* 57, 242–244.

Bowers, M.C. (1964). A water-soluble, rapid, permanent mounting medium for bryophytes. *Bryologist* 67, 358–359.

Sayre, G. (1941). A gum arabic mounting medium. *Bryologist* 44, 160.

Watson, E.V. (1968). *British Mosses and Liverworts.* 2nd edn. Cambridge University Press.

Zander, R.H. (1979). Techniques for study of Pottiaceae. *Taxon* 28, 643–644.

P.J. LIGHTOWLERS, Institute of Terrestrial Ecology, Bush Estate,
Penicuik, Midlothian EH26 OQB.

Appendix 2

NOTES ON THE ANTARCTIC MOSSES *POHLIA CRUDA* AND *P. INFLEXA*

P. J. LIGHTOWLERS

Institute of Terrestrial Ecology, Bush Estate, Penicuik, Midlothian EH26 0QB, Scotland, UK

ABSTRACT. Cell laxity in specimens of *Pohlia cruda* (Hedw.) Lindb. var *imbricata* (Card.) Bartr. from the Antarctic botanical zone is discussed, a character which has led to confusion with *Pohlia wahlenbergii* (Web. et Mohr) Andrews. Statistical studies on populations of *P. cruda* var. *imbricata* from South Georgia and the South Orkney Islands reveal significant differences in cell shape and leaf length between these areas. *Pohlia inflexa* (C. Muell.) Wijk et Marg., a bulbiliferous species, is reported for the first time from the South Orkney Islands and the Antarctic Peninsula.

The taxonomy of the moss genus *Pohlia* has been revised for the Antarctic continent and its offshore islands by Greene and others (1970) and for South Georgia by Clarke (1973). Consequently identifications of *Pohlia* specimens from this region should be straightforward but some confusion has existed with a small number of specimens from the South Orkney and South Shetland islands. In an attempt to clarify the situation, all *Pohlia* specimens in the British Antarctic Survey Herbarium (AAS) from the South Orkney, South Shetland and South Sandwich islands together with those from the Antarctic continent and its offshore islands have been re-examined. (The AAS bryophyte herbarium is currently located at the Institute of Terrestrial Ecology, Bush Estate, Penicuik, Midlothian.) The taxa involved were *P. cruda* var. *cruda*, *P. cruda* var. *imbricata* (Card.) Bartr., *P. inflexa* (C. Muell,) Wijk et Marg. and *P. nutans* (Hedw.) Lindb.

CELL LAXITY IN *POHLIA CRUDA*

Cell laxity, a bulging and displacement of cell walls perpendicular to the plane of the leaf, (Figs. 1a and 1b) has been used as a key taxonomic character in the distinction of *P. wahlenbergii* var. *glacialis* (Schliech. ex. Brid.) E. F. Warburg. from other South Georgian species by Clarke (1973) and for British species by Smith (1978). Its use in this way assumes a clear-cut difference between lax and non-lax cells. A degree of cell laxity towards the base of the leaf was, however, found to be common in all Antarctic taxa but variable between leaves on the same stem. After the examination of leaf spectra of many specimens it was not possible to infer any relationship between the occurrence of lax celled leaves and seasonal growth patterns. These leaves appeared to be randomly distributed on each stem. *P. cruda* specimens showed a greater tendency to laxity than *P. nutans* or *P. inflexa;* some *P. cruda* var. *imbricata* specimens from all areas except South Georgia also showed laxity in upper leaf cells. In these cases the cells were shorter than typical *P. cruda* leaf cells (Fig. 1a) and could be confused with the areolation of *P. wahlenbergii* var. *glacialis* from South Georgia (Fig. 1b). Specimens showing varying degrees of laxity can, however, be distinguished from *P. wahlenbergii* as at least some leaves have the long rhomboidal cells with a sigmoid curve (Fig. 2a) typical of *P. cruda*. The leaf shape is also different in that the widest point of the leaf occurs at about one-third and one-fifth of the leaf length from the leaf base in *P. cruda* and *P. wahlenbergii* respectively. *P. wahlenbergii* is a streamside and flush species forming swards or deep tall loose turves. *P. cruda* is a short turf forming species of rock ledges and crevices. Herbarium material can often be distinguished

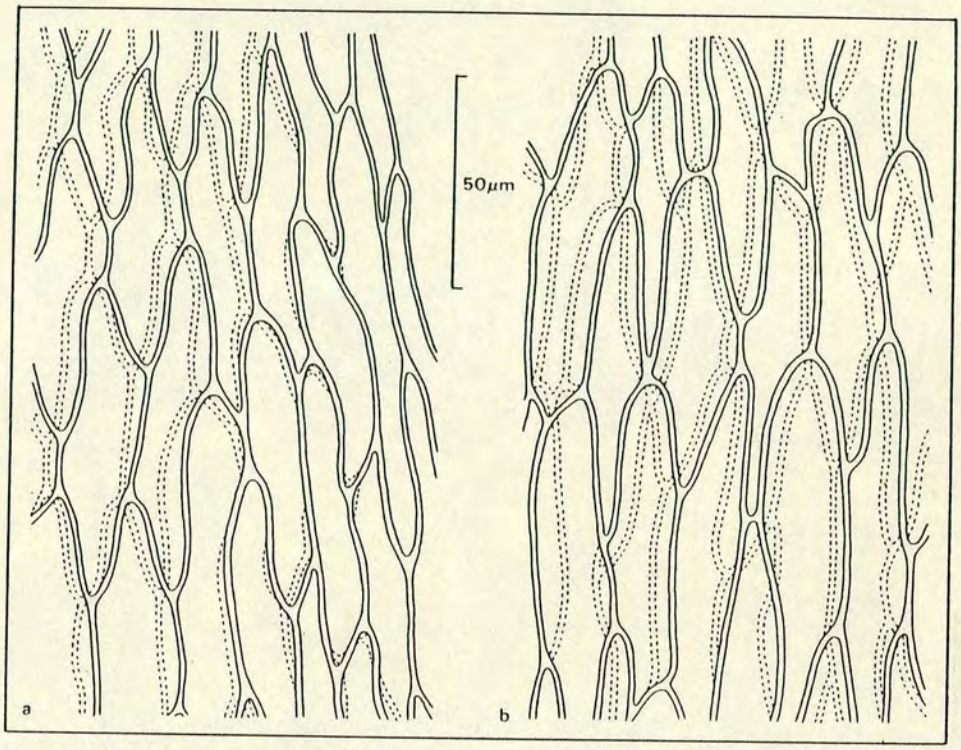


Fig. 1. a. Upper lamina cells of Antarctic *Pohlia cruda* var. *imbricata* showing a degree of laxity.
b. Upper lamina cells of South Georgian *P. wahlenbergii*. showing characteristic lax areolation (from Clarke, 1973).

on sight by the light green, slightly glossy leaves with red nerves characteristic of *P. cruda*. Specimens of *P. wahlenbergii* are dull, however, with leaves varying between pink and green in colour.

P. wahlenbergii is not known from the Antarctic botanical zone, and its preference for habitats between 0 and 100 m on South Georgia suggests that it is unlikely to be found there.

P. CRUDA VAR. *IMBRICATA* POPULATIONS

Differences between *P. cruda* var. *imbricata* populations on South Georgia and in the Antarctic were noted by the author during examination of herbarium material. This variation is reflected in the different ranges of leaf and cell sizes provided for South Georgia by Clarke (1973) and the Antarctic by Greene and others (1970). An investigation of the size and nature of these differences was undertaken by a statistical analysis of leaf and cell measurements.

Sixteen specimens were examined, eight chosen at random from South Georgia and eight at random from the South Orkney Islands. Two stems were taken from each specimen and two leaves were taken from each stem. Leaves to be measured were selected from below the comal tuft to avoid differences arising from the measurement of bracts on fertile stems. Leaf length, leaf width and the point at which the widest part of the leaf occurs were recorded for each leaf. Cell length,

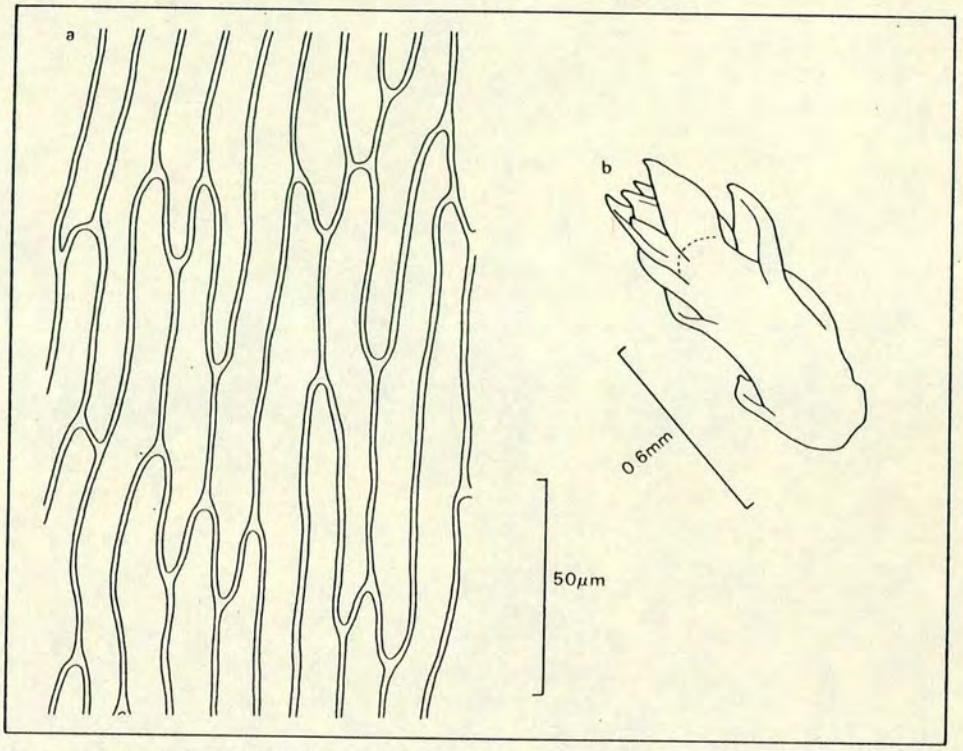


Fig. 2. a. Upper lamina cells of Antarctic *P. cruda* var. *imbricata* showing non lax, sinuose areolation.
b. Bulbil from a South Orkney *P. inflexa* specimen (R. I. L. Smith 424).

cell width and the cell length/width ratio were also measured on two cells per leaf. These cells were taken from approximately one third of the leaf length from the apex, midway between the nerve and margin. The width of lax cells was measured on the upper or lower surface of the leaf to avoid obtaining a high value by measuring the maximum visible (diagonal) width of the cell. In total, 128 cells and 64 leaves were measured from the 16 specimens. A *t*-test conducted on these data produced the results given in Table I.

The results (Table 1) show that the differences between the leaf length and cell length means of the two areas are significant at the 5% level. The difference in cell width/length ratio means is also highly significant at the 0.1% level. Leaves of *P. cruda* var. *imbricata* from the South Orkney Islands are therefore shorter than the same taxon on South Georgia, and the cells are shorter and wider. These results confirm the different ranges of measurements reported for the two areas (Clarke, 1973; Greene and others, 1970). In addition the difference in leaf length, which is one of the defining characters of the var. *imbricata*, together with observations made from herbarium material, have suggested some discussion on variation within *P. cruda* as a whole.

Reports on the flora of South America (Cardot, 1908; Wijk and others, 1967; Seki, 1974) suggest the var. *imbricata* is absent from this area whereas Clarke (1973) reports both var. *cruda* and var. *imbricata* from South Georgia. In addition, he remarks that plants of var. *cruda* are more abundant and notes that a complete

Table I. Means of six variates measured on *P. cruda* var. *imbricata* specimens from South Georgia and the South Orkney Islands. Standard errors and significance levels for the differences between the area means are also given.

Variate	*Mean for South Georgia*	*Mean for South Orkneys*	*Standard error*	*Significance level of difference*
Leaf length/mm	1.879	1.601	0.840	$p < 0.05$
Leaf width/mm	0.746	0.778	0.0341	not significant
Ratio (distance from leaf base to widest point)/(leaf length)	0.252	0.262	0.0093	not significant
Cell width/μm	14.758	16.042	0.4644	not significant
Cell length/μm	127.489	104.533	6.1127	$p < 0.05$
Cell width/length ratio	0.120	0.158	0.0064	$p < 0.001$

intergradation of the two varieties occurs on the island. Greene and others (1970) refer all Antarctic specimens to the var. *imbricata* but mention that non-imbricate plants do occur. Intergradation between the latter and typical var. *imbricata* specimens has been observed during this study. The pattern of variation within the species thus appears to be clinal. There is no discontinuity between *P. cruda* var. *cruda* and var. *imbricata*, and plants with imbricate ovate leaves diagnostic of the latter variety become commoner with increasing latitude. The measurements provided here support this contention by showing that even among plants considered to belong to the var. *imbricata*, variation in diagnostic characters occurs with latitude.

P. INFLEXA

Several specimens of *P. inflexa* (C. Muell) Wijk et Marg. from the Antarctic have come to light and are listed in Table II. This species has not been formally reported from this area although Allison and Smith (1973) listed it in an account of the vegetation of Elephant Island, South Shetland Islands. This record was based on a single depauperate specimen (Allison 171 b, AAS det. G. C. S. Clarke and S. W. Greene) and hence the material reported here is useful confirmation of the

Table II. *Pohlia inflexa* (C. Muell.) Wijk et Marg. specimens from the Antarctic botanical zone.

Locality	*Lat. and Long.*	*Collection/No.*	*Distribution to herbaria*
*Signy Island, South Orkney Islands	60° 43′ S 45° 38′ W	R. I. L. Smith 424	AAS
Coronation Island, South Orkney Islands	60° 38′ S 45° 35′ W	R. I. L. Smith 3228A	BM, CHR, MEL, NY, PC, S
Recess Cove, Charlotte Bay, Danco Coast	64° 30′ S 61° 31′ W	R. I. L. Smith 3986	AAS, ALTA, BA, LE, PRE
Recess Cove, Charlotte Bay, Danco Coast	64° 30′ S 61° 31′ W	R. I. L. Smith 3987	BM, NY
Gamma Island, Melchior Islands, Danco Coast	64° 20′ S 63° 00′ W	R. I. L. Smith 4157A	AAS
Lahille Island, Graham Coast	65° 32′ S 64° 22′ W	R. I. L. Smith 4322	AAS, CHR, S

*Specimen previously determined as *P. cruda* var. *imbricata* by Greene and others (1970).

presence of the species in the Antarctic botanical zone (Greene, 1964). The specimens in Table II also extend the known geographical range of the species to the South Orkney Islands and the Antarctic Peninsula.

Antarctic plants of *P. inflexa* agree well with the descriptions and figures of South Georgian plants given by Clarke (1973). The bulbils, which characterize the species on South Georgia, have also been found in association with several Antarctic specimens (Fig. 2b). In the field, *P. inflexa* is perhaps more likely to be confused with *P. cruda* than *P. nutans*, the latter being distinguished by its slender, densely tufted habit and occasional fertility. *P. cruda* and *P. inflexa* are more similar in coloration and size, but specimens of *P. inflexa* lack the dense tufts and imbricate leaves of typical *P. cruda* from this area.

Acknowledgements

I would like to thank Mr R. I. Smith (Institute of Terrestrial Ecology) for his statistical advice and Dr G. C. S. Clarke (British Museum, Natural History) for confirming determinations. Thanks are also due to Mr B. G. Bell (Institute of Terrestrial Ecology) and Dr R. I. Lewis Smith (British Antarctic Survey) for their help with the manuscript.

MS received 7 March 1983; accepted in revised form 15 April 1983

References

Allison, J. S. *and* Smith, R. I. L. 1973. The vegetation of Elephant Island, South Shetland Islands. *British Antarctic Survey Bulletin*, No. 33 & 34, 185–212.

Cardot, J. 1908. La flore bryologique des Terres Magellaniques, de la Géorgie du Sud et de la Antarctide. *Wissenschaftliche Ergebnisse der Schwedischen Sudpolarexpedition*. 1901–03. Bd. 4 Lf. 8. 298 pp.

Clarke, G. C. S. 1973. A synoptic flora of South Georgian mosses. III. *Leptotheca, Philonotis, Mielichhoferia* and *Pohlia*. *British Antarctic Survey Bulletin*, No. 37, 53–79.

Greene, S. W. 1964. Plants of the land. (*In* Priestley, R. E., Adie, R. J. *and* Robin, G. de Q. *eds. Antarctic Research*. London, Butterworth, 240–53.)

Greene, S. W., Greene, D. M., Brown, P. D. *and* Pacey, J. M. 1970. Antarctic Moss Flora I. Genera *Andreaea, Pohlia, Polytrichum, Psilopilum* and *Sarconeurum*. *British Antarctic Survey Scientific Reports*, No. 64. 118 pp.

Seki, T. 1974. (1976). A moss Flora of Provincia de Aisén, Chile. Results of the second Scientific Expedition to Patagonia by Hokkaido and Hiroshima Universities, 1967. *Journal of Science of the Hiroshima University, Series B, Div. 2 (Botany)*, **15**, (1), 9–101.

Smith, A. J. E. 1978. *The moss flora of Britain and Ireland*. Cambridge, England. Cambridge University Press.

Wijk, R. van der, Margadant, W. D. *and* Florschütz, P. A., 1967. *Index Muscorum, Volume IV*. Utrecht, International Association for Plant Taxonomy.

Appendix 3

NOTES ON ANTARCTIC BRYOPHYTES: XI. *MIELICHHOFERIA AUSTRO-GEORGICA* AND *MUELLERIELLA CRASSIFOLIA*

G. C. S. CLARKE

British Museum (Natural History), Cromwell Road, London SW7 5BD, England

and

P. J. LIGHTOWLERS

Institute of Terrestrial Ecology, Bush Estate, Penicuik, Midlothian, EH26 0QB, Scotland

ABSTRACT. Details of the distribution of *Mielichhoferia austro-georgica* C. Muell. and *Muelleriella crassifolia* (Hook. f. et Wils.) Dus. in the Antarctic botanical zone are provided, together with notes on identification and sporophyte production.

Mielichhoferia austro-georgica C. Muell.

According to Müller (1890), Cardot (1908) and Clarke (1973), *M. austro-georgica* is endemic to the sub-Antarctic island of South Georgia. Smith and Corner (1973) however, recorded the species in their survey of the vegetation of an area of the Graham and Danco coast regions of the Antarctic Peninsula. This extension to its geographical range is particularly significant since it is within the Antarctic botanical zone as defined by Greene (1964).

Smith and Corner's (1973) field observations were supported by a voucher specimen (R. I. L. Smith No. 938, see Table 1) determined by B. G. Bell in 1970. Further specimens have been collected or have come to light during a recent re-examination of all Antarctic material determined as *Pohlia nutans* (Hedw.) Lindb. in the British Antarctic Survey Herbarium (AAS) currently located at the Institute of Terrestrial Ecology, Bush Estate, Penicuik, Midlothian. A list of all known Antarctic specimens of *M. austro-georgica* is given in Table I.

The majority of the specimens have sporophytes, some in profusion, suggesting that the species may be capable of completing its life cycle even at these high latitudes. Its Antarctic distribution appears to be limited to the Graham and Danco coast areas of the Antarctic Peninsula where it is rare but abundant in a few localities such as Rasmussen Island where a single stand is known to cover 2 m^2 (R. I. L. Smith, personal communication). As on South Georgia, it typically forms short turves in rock crevices and on sheltered rock faces near the sea. Surprisingly, it has not been recorded from the more northerly South Shetland or South Orkney islands.

The Antarctic specimens of *M. austro-georgica* agree well with South Georgian material, the fertile plants falling well within the range of stem, leaf and cell measurements given by Clarke (1973). One of the sterile specimens is somewhat smaller, but the key provided by Clarke (1973) identifies this and all other specimens without difficulty. In view of the confusion with *Pohlia nutans*, the major differences between the two species are summarized in Table II.

In conclusion, *M. austro-georgica* is a relatively little-known and local constituent of the Antarctic coastal moss flora. It is possible that specimens exist, in other collections, which have been mis-identified as *P. nutans*.

Muelleriella crassifolia (Hook. f. et Wils.) Dus.

M. crassifolia (as *Orthotrichum crassifolium*) was first noted from the Antarctic botanical zone by Gimingham and Smith (1970), with more precise locations cited by

Br. Antarct. Surv. Bull. No. 59, 1983, pp. 35–39

Table I. All known specimens of *Mielichhoferia austro-georgica* C. Muell. from the Antarctic botanical zone.

Locality	*Lat. and long.*	*Collection/No.*	*With sporophytes*	*Distribution to herbaria*
*Galindez Island, Argentine Islands, Graham Coast	65°15′S 64°16′W	B. G. L. E. 1114a	√	AAS, BM
*Galindez Island, Argentine Islands, Graham Coast	65°15′S 64°16′W	R. W. M. Corner 451	√	AAS, BM, (CHR, IAA, LE, MEL, NY, PC, PRE, SGO, S–PA, TNS)†
*Galindez Island, Argentine Islands, Graham Coast	65°15′S 64°16′W	R. W. M. Corner 561	–	AAS
*Galindez Island, Argentine Islands, Graham Coast	65°15′S 64°16′W	R. I. L. Smith 938	√	BM, BA
*Galindez Island, Argentine Island Graham Coast	65°15′S 64°16′W	R. I. L. Smith 3283	√	AAS, PRE.
Rasmussen Island, Graham Coast	65°15′S 64°06′W	R. I. L. Smith 1924	√	AAS, ALTA, CHR, LE, MEL, NY, PC
Andrée Island, Charlotte Bay, Danco Coast	64°31′S 61°30′W	R. I. L. Smith 4003	√	BM, BA
Andrée Island, Charlotte Bay, Danco Coast	64°31′S 61°30′W	R. I. L. Smith 4017	–	AAS, NY
Andrée Island, Charlotte Bay, Danco Coast	64°31′S 61°30′W	R. I. L. Smith 4019	√	BM, S, TNS
Andrée Island, Charlotte Bay, Danco Coast	64°31′S 61°30′W	R. I. L. Smith 4020	√	BM, ALTA
Andrée Island, Charlotte Bay, Danco Coast	64°31′S 61°30′W	R. I. L. Smith 4036	–	BM

*Specimens previously determined and published by Greene and others (1970) as *Pohlia nutans* (Hedw.) Lindb.

†Duplicate specimens (in brackets) were distributed after their original publication (Greene and others, 1970) and have not been examined by the authors.

Table II. A summary of the differences between *Mielichhoferia austro-georgica* C. Muell. and *Pohlia nutans* (Hedw.) Lindb.

Character	*Mielichhoferia austro-georgica*	*Pohlia nutans*
Outer peristome	Absent	Very conspicuous
Position of inflorescence	On short lateral branches	Terminal on main stems
Perichaetial leaves	Similar to other leaves	Markedly elongate
Leaf shape	Often asymmetric	Rarely asymmetric
Leaf cells	Small hexagonal rectangular with thin walls; the ends of the cells normally pointed	Elongate-rectangular with thick walls (*c.* 3 μm thick); the end walls usually flat or oblique

Smith (1972) (South Orkney Islands), Smith and Corner (1973) (Argentine Islands) and Allison and Smith (1973) (South Shetland Islands). Vitt (1976) unfortunately did not include Antarctic material in his monograph of the genus and therefore the full geographical range of this species is likely to be overlooked. Details of all known material from the Antarctic that has been determined as *M. crassifolia* subsp. *crassifolia* are given in Table III. Cardot (1900, 1908), however, reported two *Orthotrichum* specimens, *O. antarcticum* Card. and *O. rupicolum* C. Muell. from Cape Anna, Danco Coast. Neither specimen has been traced in the present study but they should be considered in any future revision of either *Orthotrichum* or *Muelleriella* for the Antarctic botanical zone.

Table III. All known specimens of *Muelleriella crassifolia* (Hook. f. et Wils.) Dus. from the Antarctic botanical zone. All specimens belong to the subsp. *crassifolia*.

Locality	*Lat. and long.*	*Collection/No.*	*With sporophytes*	*Distribution to herbaria*
Coronation Island, South Orkney Islands	60°38′S 45°35′W	R. I. L. Smith 37	✓	AAS
Coronation Island, South Orkney Islands	60°38′S 45°35′W	R. I. L. Smith 451	✓	AAS
Lynch Island, South Orkney Islands	60°39′S 45°36′W	R. I. L. Smith 506	✓	AAS, ALTA
Matthews Island, South Orkney Islands	60°45′S 45°09′W	R. I. L. Smith 192	–	ALTA, BM, MEL, S, TNS
Powell Island, South Orkney Islands	60°41′S 45°03′W	R. I. L. Smith 255	–	AAS, ALTA, CHR
Powell Island, South Orkney Islands	60°41′S 45°03′W	R. I. L. Smith 281	–	BM
Signy Island, South Orkney Islands	60°43′S 45°38′W	R. E. Longton 1083	–	AAS, PC
Signy Island, South Orkney Islands	60°43′S 45°38′W	R. I. L. Smith 10	–	BM, PRE
Signy Island, South Orkney Islands	60°43′S 45°38′W	R. I. L. Smith 350	–	AAS
Signy Island, South Orkney Islands	60°43′S 45°38′W	R. I. L. Smith 404	–	AAS, BA, BM, LE, NY
Signy Island, South Orkney Islands	60°43′S 45°38′W	R. Webb 87	–	AAS
Aspland Island, South Shetland Islands	61°28′S 55°55′W	J. P. Baylis 75	–	BM
Eadie Island, South Shetland Islands	61°29′S 55°57′W	J. S. Allison 231	–	AAS
Andrée Island, Charlotte Bay, Danco Coast	64°31′S 61°30′W	R. I. L. Smith 4000	–	BM, PC, S
Uruguay Island, Argentine Islands Graham Coast	65°14′S 64°14′W	R. W. M. Corner 596a	–	AAS, BA, CHR, LE, MEL
Berthelot Islands Graham Coast	65°20′S 64°10′W	R. W. M. Corner 618	–	AAS
Cape Tuxen, Graham Coast	65°16′S 64°08′W	R. W. M. Corner 670	–	BM, NY
Between Irizar and Uruguay Islands, Argentine Islands, Graham Coast	65°13′S 64°13′W	R. W. M. Corner 708	–	BM

M. crassifolia is at present known from the South Orkney and South Shetland Islands and the Danco and Graham coast regions of the Antarctic Peninsula. It typically forms loose to dense cushions on coastal rocks often within the spray zone dominated by hygrohaline crustose lichens. Three specimens from the South Orkney Islands have sporophytes and Smith (1972) remarked that the species is often abundantly fertile on sheltered sites in this region. However, Webb (1973) failed to find any fertile plants during his study of bryophyte reproduction on Signy Island. No sporophytes have been seen on specimens collected from more southerly localities, and Smith and Corner (1973) noted that the species is less abundant in the Argentine Islands region of the Graham Coast than on the South Orkney Islands. Thus present information suggests that the species is capable of producing capsules in favourable habitats on the South Orkney Islands (60°S) but is sterile and less abundant in the Graham Coast region of the Antarctic Peninsula (65°S) where it appears to reach the limit of its range.

M. crassifolia is perhaps most likely to be confused with species of *Schistidium*. It can be distinguished by its leaf shape which is generally ligulate from an ovate base, compared with the typical ovate-lanceolate leaf shape of *Schistidium*. The leaf areolation is also different, the longitudinal cell walls of *Schistidium* are characteristically sinuose, if sometimes weakly so, and the leaf margin or patches of the upper lamina are bistratose. In *M. crassifolia*, the cell walls are not sinuose while the lamina is bistratose in the entire upper part and along the margins below, thus giving a much thicker appearance to the leaf. Capsules, when present, differ considerably from those of *Schistidium* in being shortly exserted rather than immersed and bear a much larger calyptra covered in short hairs.

A full description and illustrations of *M. crassifolia* are given by Vitt (1976). *M. crassifolia* is the most widespread of the four species which he considers constitute the genus, being circum-sub-Antarctic in distribution. He divides it into two subspecies; subsp. *acuta* (C. Muell.) Vitt, found on the Îles Crozet and Îles Kerguelen and subsp. *crassifolia* which occurs on most other sub-Antarctic islands (including Auckland, Campbell, Macquarie and Marion islands and South Georgia) and in Tierra del Fuego. It is to the latter subspecies that the Antarctic plants belong. Vitt (personal communication) has confirmed the identifications of three of the Antarctic specimens (Corner No. 670, R. I. L. Smith No. 37, 192) and remarks that they are most similar to Fuegian populations in their small size and rather slender leaves.

Acknowledgements

We are grateful to Dr R. I. L. Smith for information provided and to Dr D. H. Vitt who confirmed identifications and gave the benefit of his observations. Thanks are also due to Mr B. G. Bell and Dr S. W. Greene for helpful comments on the manuscript.

MS received 12 November 1982

References

Allison, J. S. *and* Smith, R. I. L. 1973. The vegetation of Elephant Island, South Shetland Islands. *British Antarctic Survey Bulletin*, Nos. 33 & 34, 185–212.

Cardot, J. 1900. Note préliminaire sur les mousses recueillies par l'expédition antarctique belge. *Revue bryologique*, **27**, 38–46.

Cardot, J. 1908. La flore bryologique des Terres Magellaniques, de la Géorgie du Sud et de l'Antarctide. *Wissenschaftliche Ergebnisse der Schwedischen Südpolarexpedition, 1901–03*, Bd. 4, Lf. 8, 298 pp.

CLARKE, G. C. S. 1973. A synoptic flora of South Georgian mosses: III. *Leptotheca, Philonotis, Mielichhoferia* and *Pohlia. British Antarctic Survey Bulletin,* No. 37, 53–79.

GIMINGHAM, C. H. *and* SMITH, R. I. L. 1970. Bryophyte and lichen communities in the maritime Antarctic. (*In* HOLDGATE, M. W. *ed. Antarctic ecology,* Vol. 2. London, Academic Press, 752–85.)

GREENE, S. W. 1964. Plants of the land. (*In* PRIESTLY, R. E., ADIE, R. J. *and* ROBIN, G. DE Q., *eds. Antarctic Research.* London, Butterworth, 240–53.)

GREENE, S. W., GREENE, D. M., BROWN, P. D. *and* PACEY, J. M. 1970. Antarctic moss flora I. The genera *Andreaea, Pohlia, Polytrichum* and *Psilopilum. British Antarctic Survey Scientific Reports,* No. 64, 118 pp.

MÜLLER, C. 1890. Bryologia austro-georgiae. (*In* NEUMAYER, G. *ed. Die Internationale Polar Forschung 1882–83. Die Deutschen Expeditionen und ihre Ergebnisse.* Bd. 2. Lf. 11, 279–322.)

SMITH, R. I. L. 1972. Vegetation of the South Orkney Islands with particular reference to Signy Island. *British Antarctic Survey Scientific Reports,* No. 68, 138 pp.

SMITH, R. I. L. *and* CORNER, R. W. M. 1973. Vegetation of the Arthur Harbour–Argentine Islands region of the Antarctic Peninsula. *British Antarctic Survey Bulletin,* Nos. 33 & 34, 89–122.

VITT, D. H. 1976. A monograph of the genus *Muelleriella* Dusen. *Journal of the Hattori Botanical Laboratory,* **40**, 91–113.

WEBB, R. 1973. Reproductive behaviour of mosses on Signy Island, South Orkney Islands. *British Antarctic Survey Bulletin,* No. 36, 61–77.

Appendix 4: HISTOGRAMS OF DATA FROM SOUTH GEORGIAN HAIR-POINTED TORTULA SPECIMENS

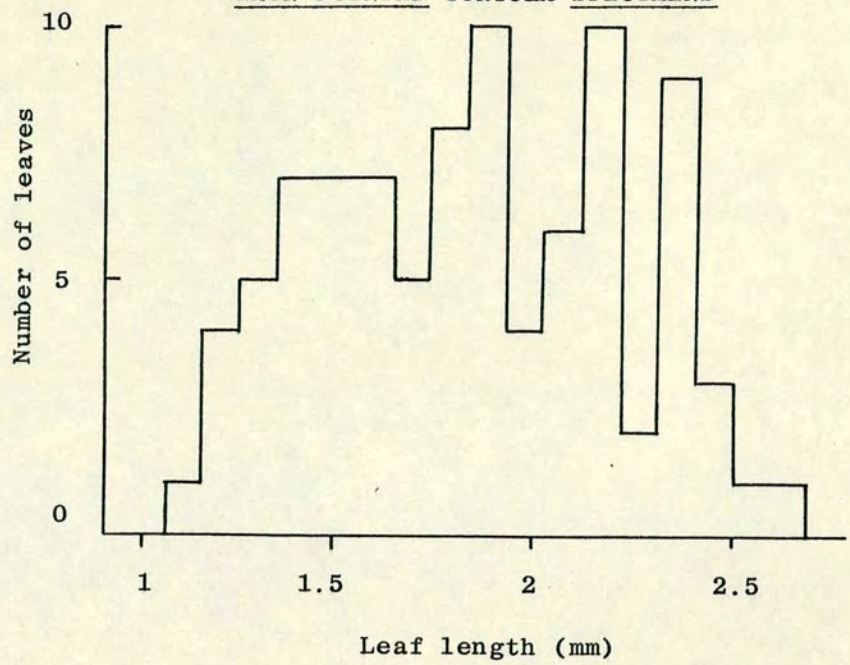


Figure A1. Taxon I : Histogram of leaf lengths of 90 leaves taken from 18 specimens.

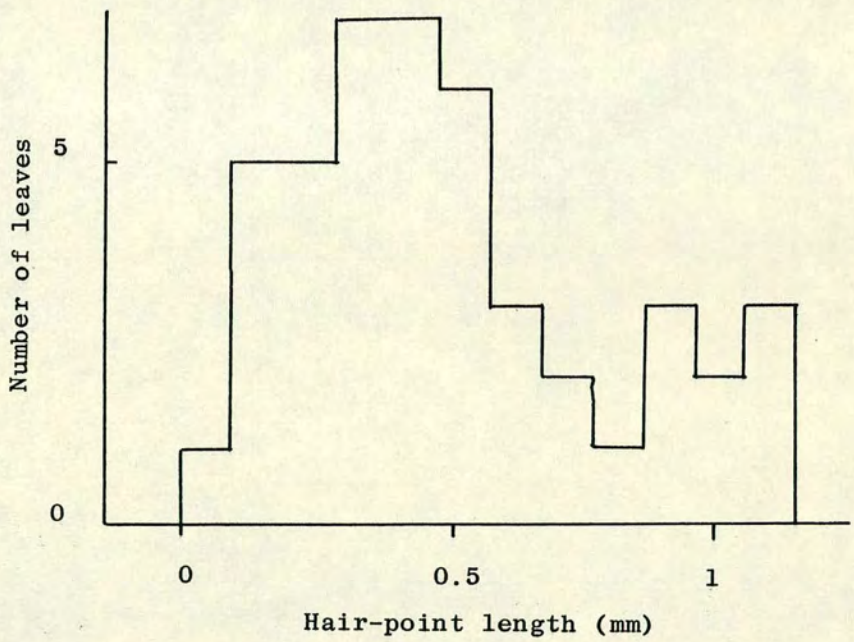


Figure A2. Taxon I : Histogram of hair-point lengths of 45 leaves taken from 9 specimens.

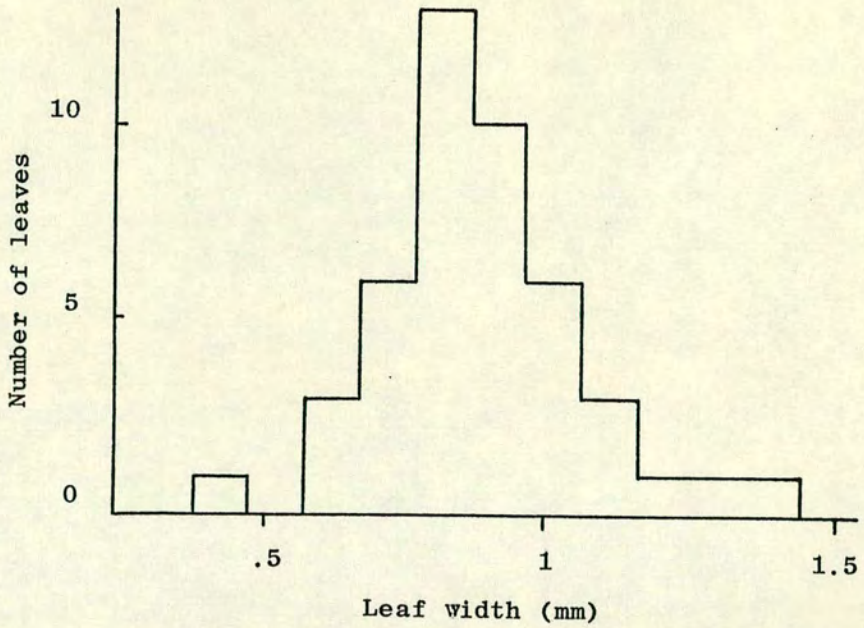


Figure A3. Taxon I : Histogram of leaf widths from 45 leaves taken from 9 specimens

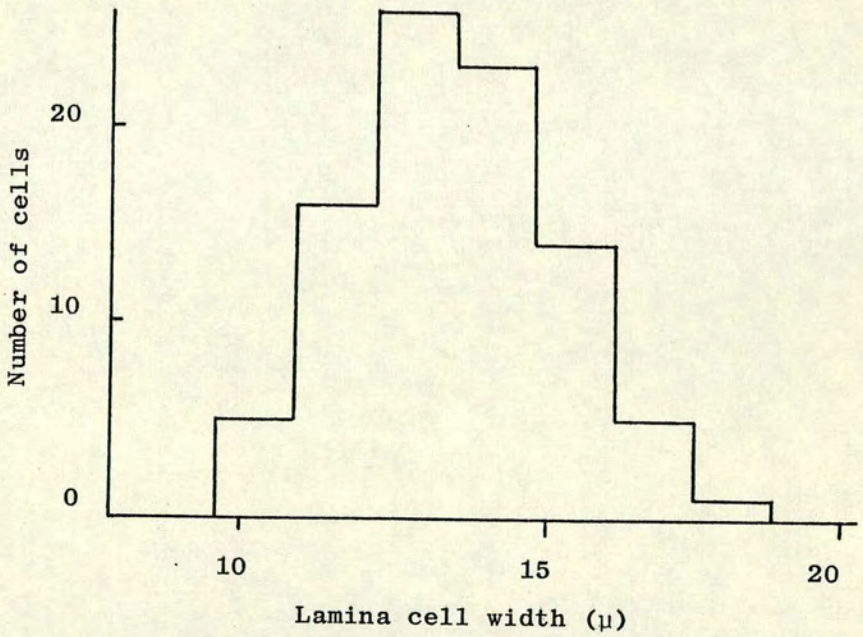


Figure A4. Taxon I : Histogram of cell widths of 90 cells taken from 9 specimens.

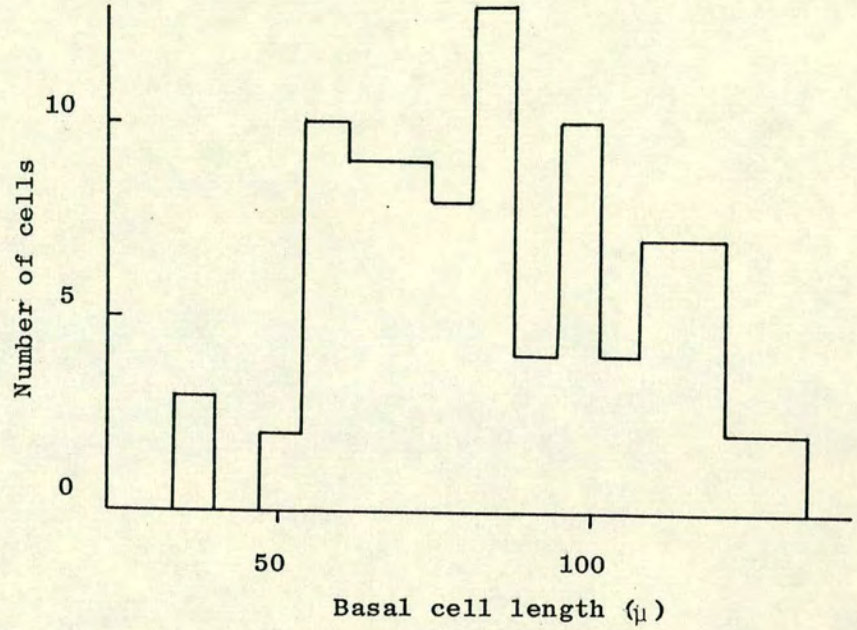


Figure A5. Taxon I : Histogram of basal cell lengths of 90 cells taken from 9 specimens.

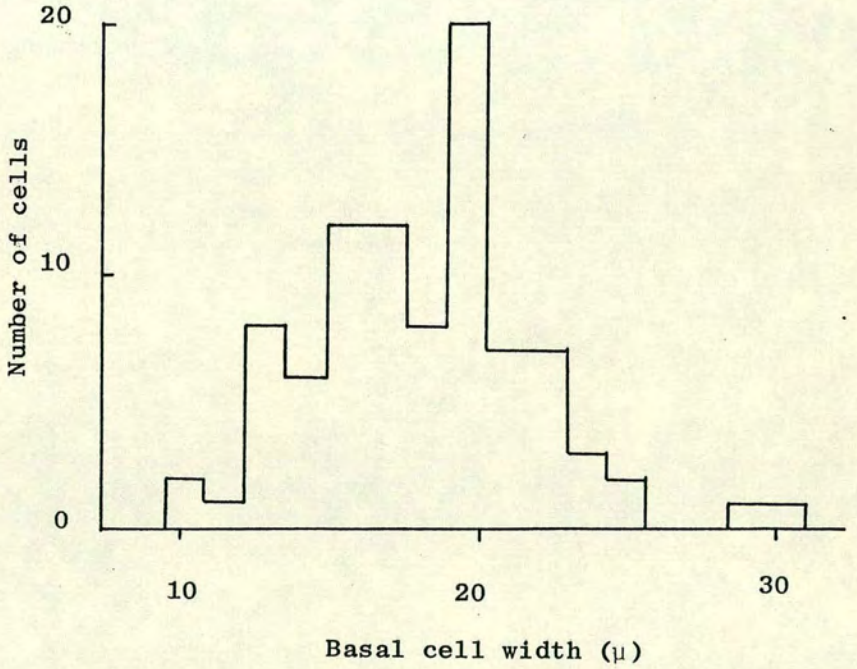


Figure A6. Taxon I : Histogram of basal cell widths of 90 cells taken from 9 specimens.

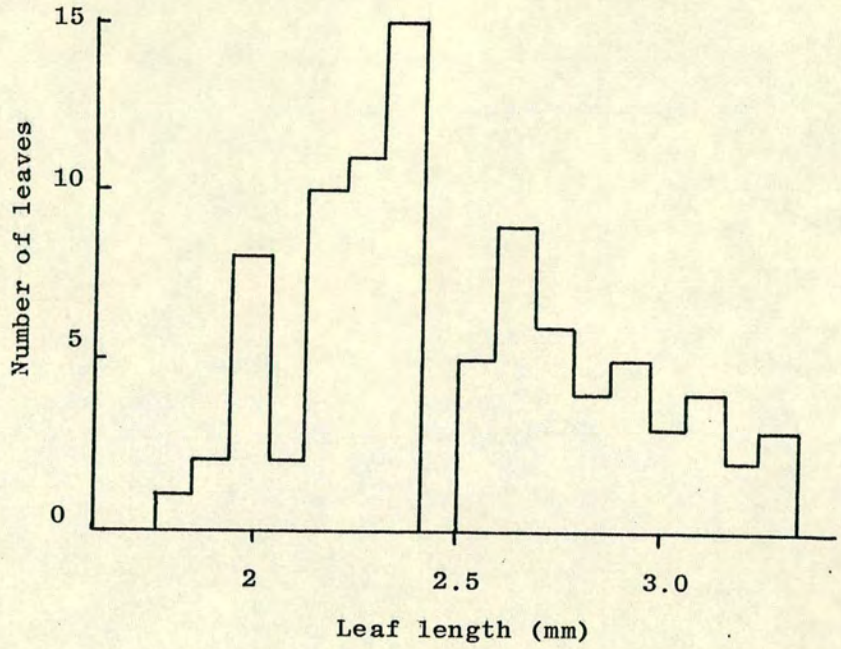


Figure A7. Taxon J : Histogram of leaf lengths of 90 leaves taken from 18 specimens.

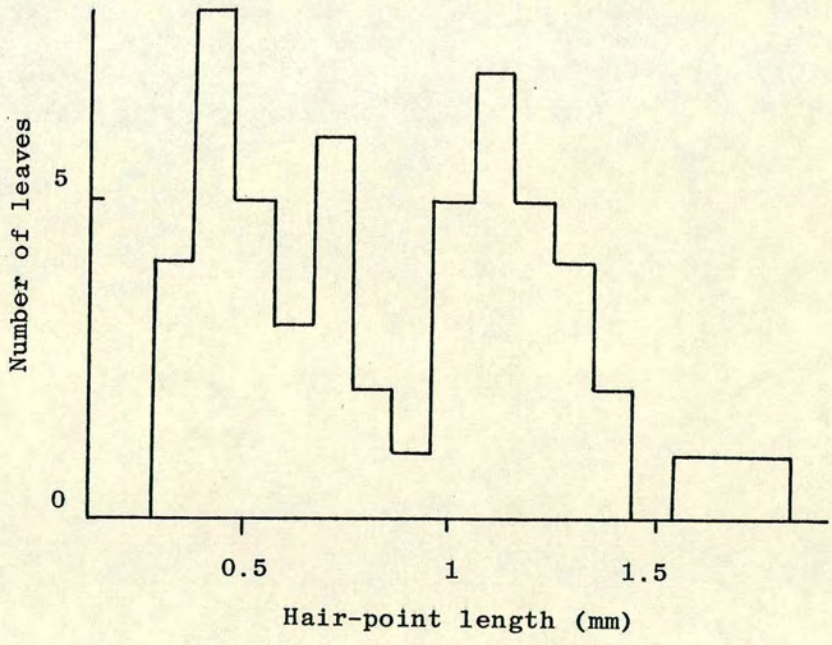


Figure A8 ,Taxon J : Histogram of hair-point lengths of 55 leaves taken from 11 specimens.

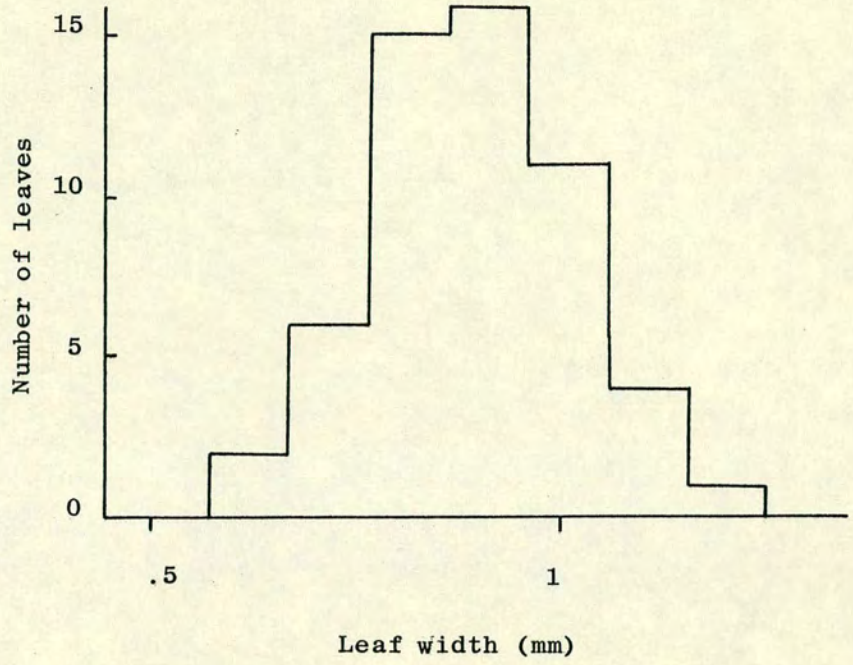


Figure A9. Taxon J : Histogram of leaf widths from 55 leaves taken from 11 specimens.

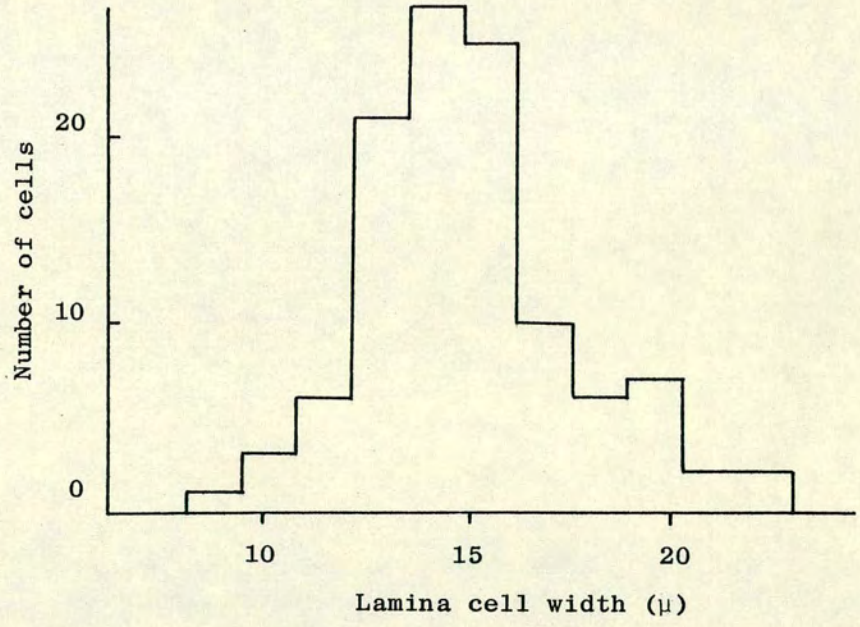


Figure A10. Taxon J : Histogram of cell widths of 110 cells taken from 11 specimens.

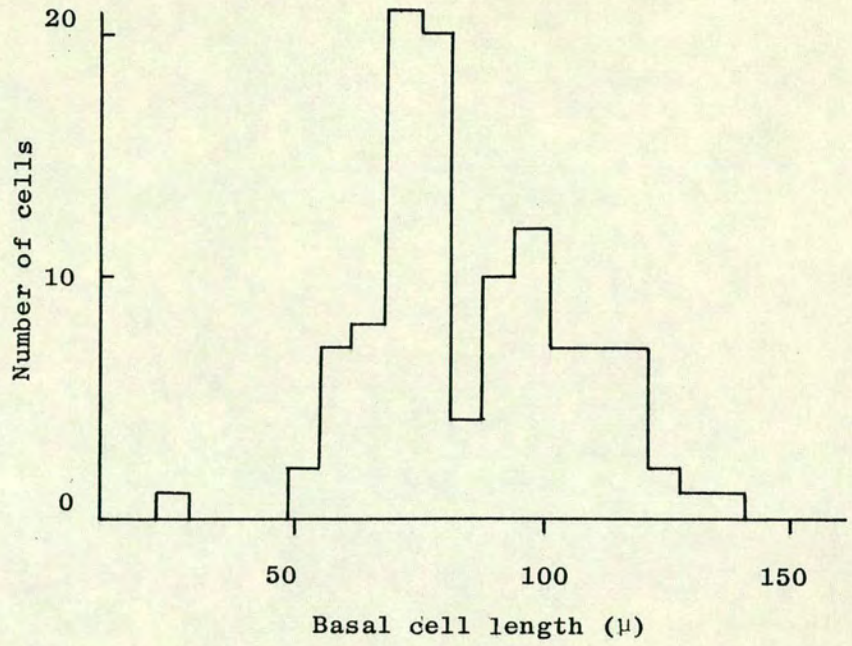


Figure A11.Taxon J : Histogram of basal cell lengths of 110 cells taken from 11 specimens.

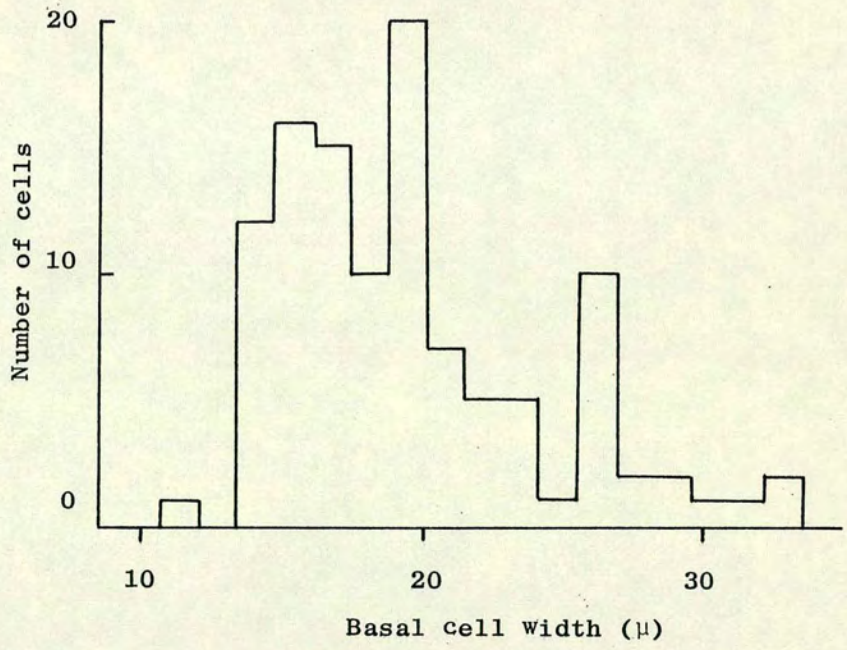


Figure A12.Taxon J : Histogram of basal cell widths of 110 cells taken from 11 specimens.

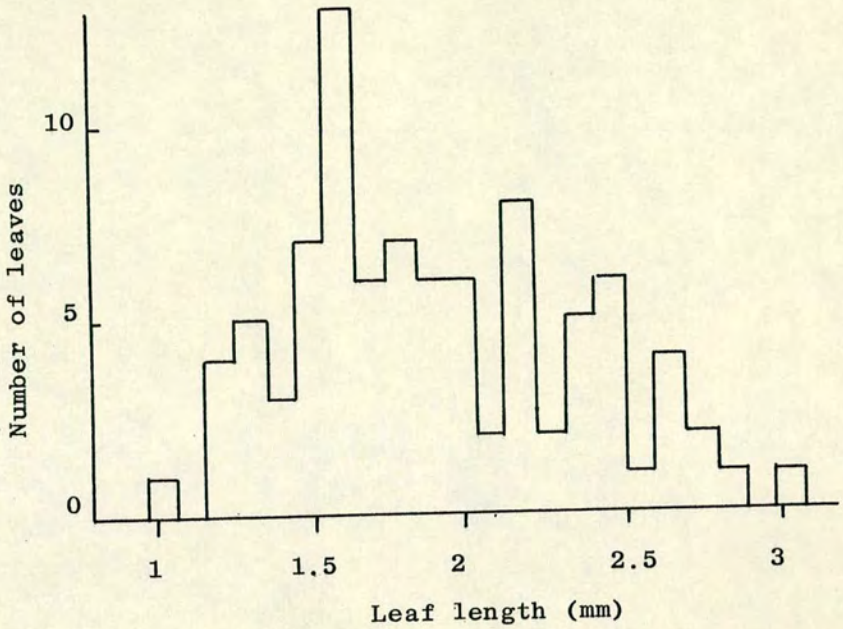


Figure A13. Taxon K : Histogram of leaf lengths of 90 leaves taken from 18 specimens.

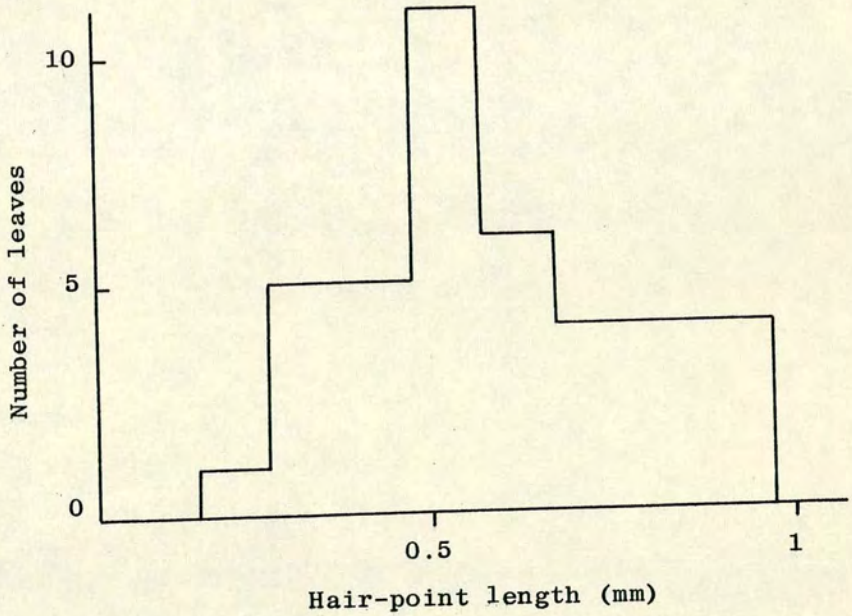


Figure A14. Taxon K : Histogram of hair-point lengths of 40 leaves taken from 8 specimens.

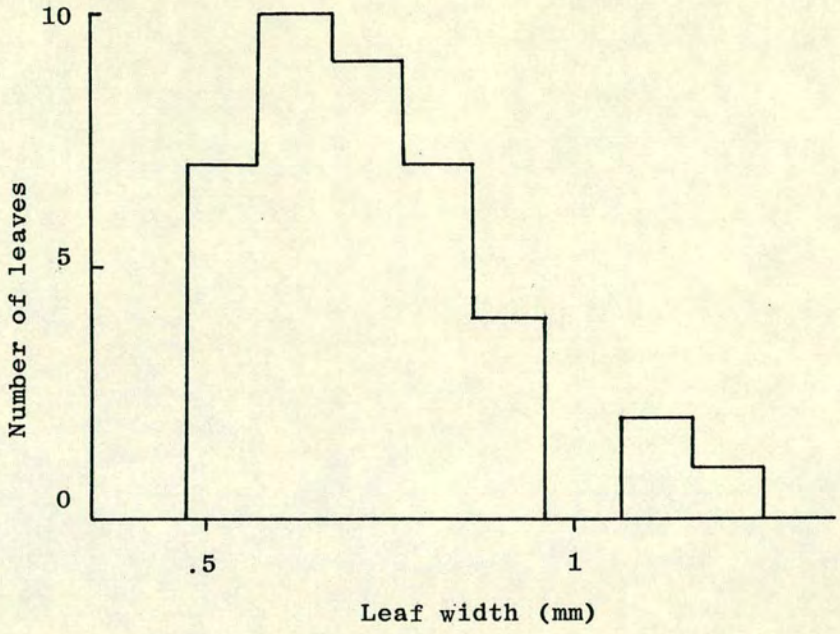


Figure A15. Taxon K : Histogram of leaf widths from 40 leaves taken from 8 specimens.

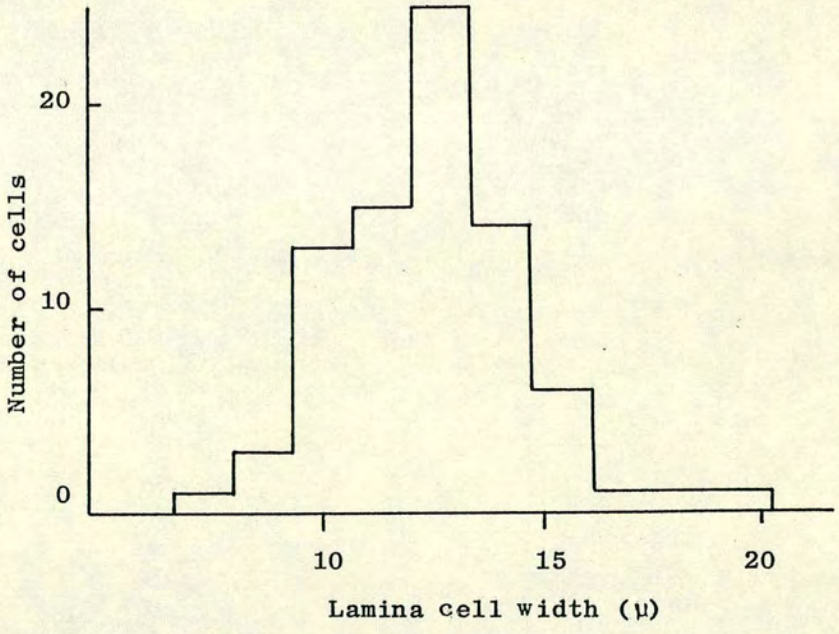


Figure A16. Taxon K : Histogram of cell widths of 80 cells taken from 8 specimens.

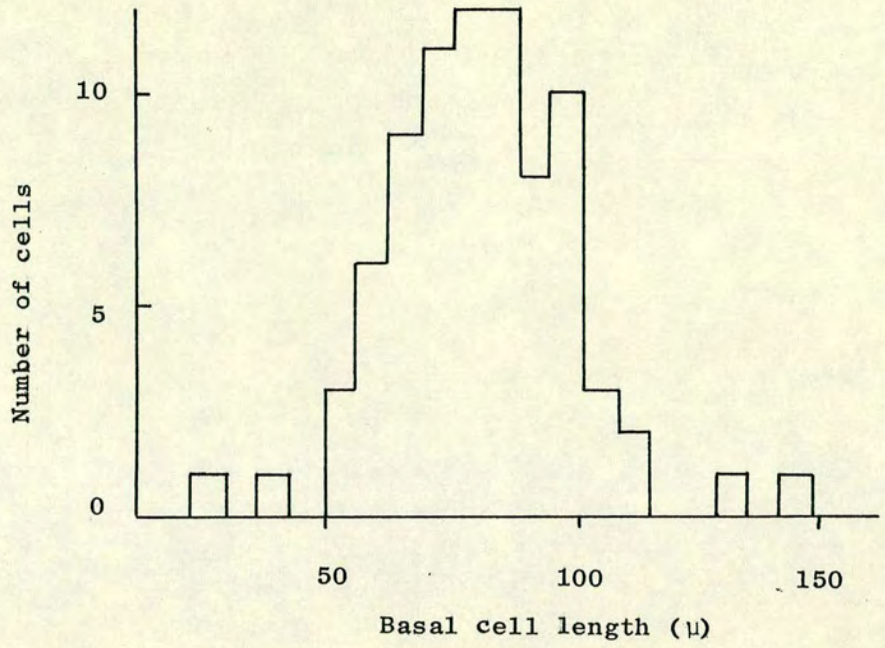


Figure A17. Taxon K : Histogram of basal cell lengths of 80 cells taken from 8 specimens.

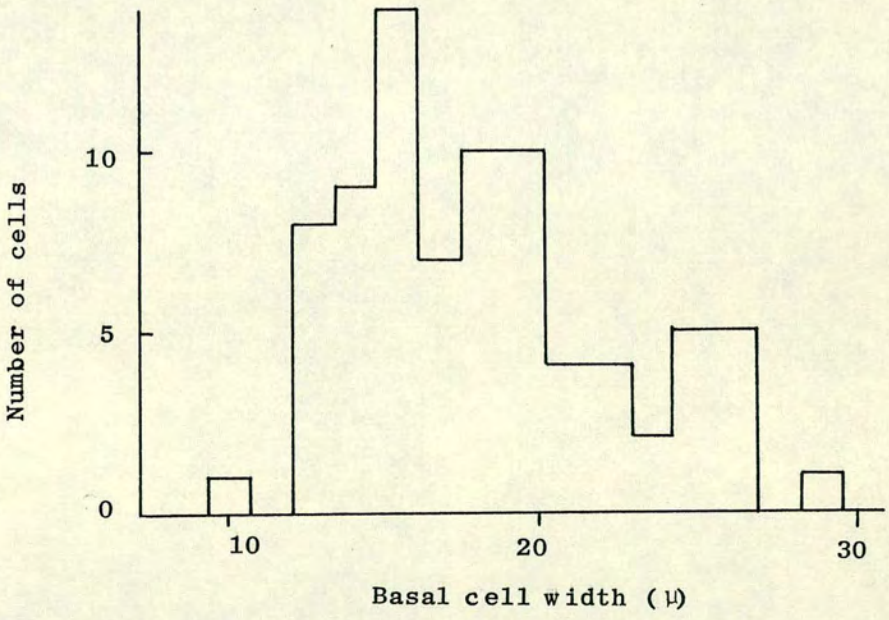


Figure A18. Taxon K : Histogram of basal cell widths of 80 cells taken from 8 specimens.

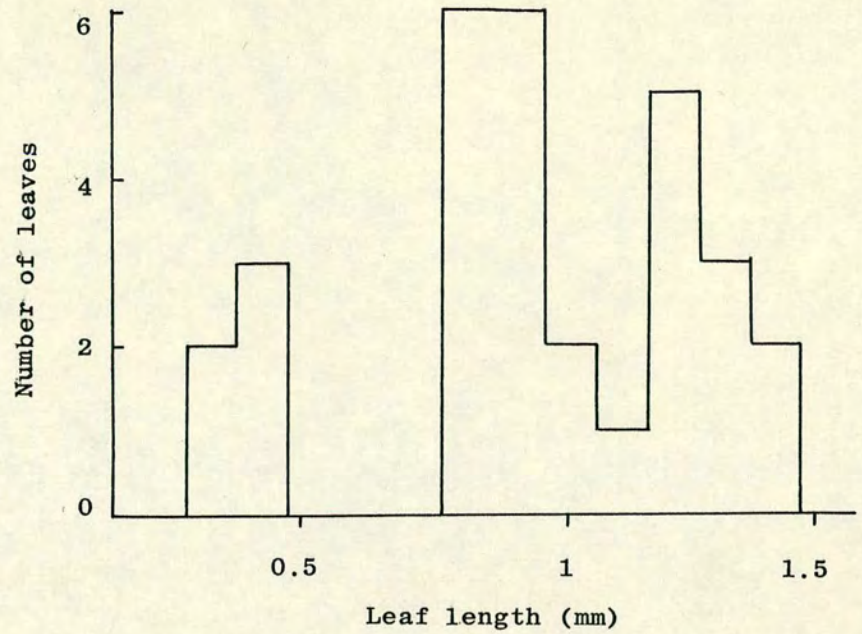


Figure A19. Taxon L : Histogram of leaf lengths of 30 leaves taken from 6 specimens.

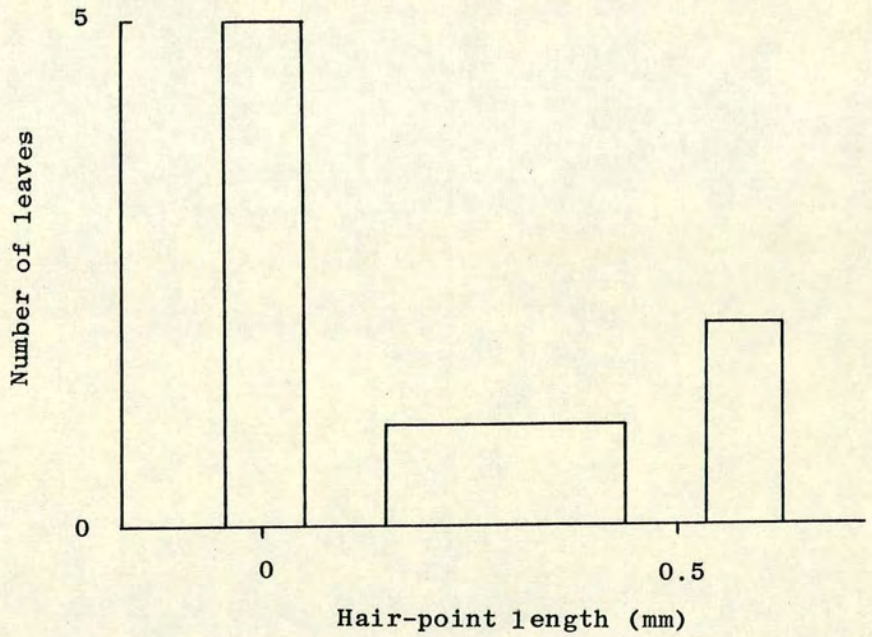


Figure A20. Taxon L : Histogram of hair-point lengths of 10 leaves taken from 2 specimens.

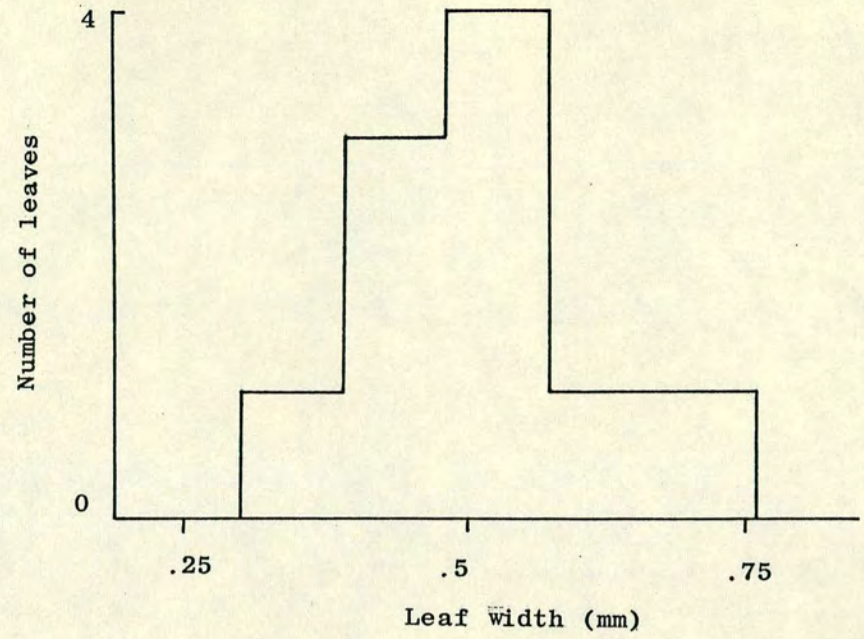


Figure A21.Taxon L : Histogram of leaf widths from 10 leaves taken from 2 specimens.

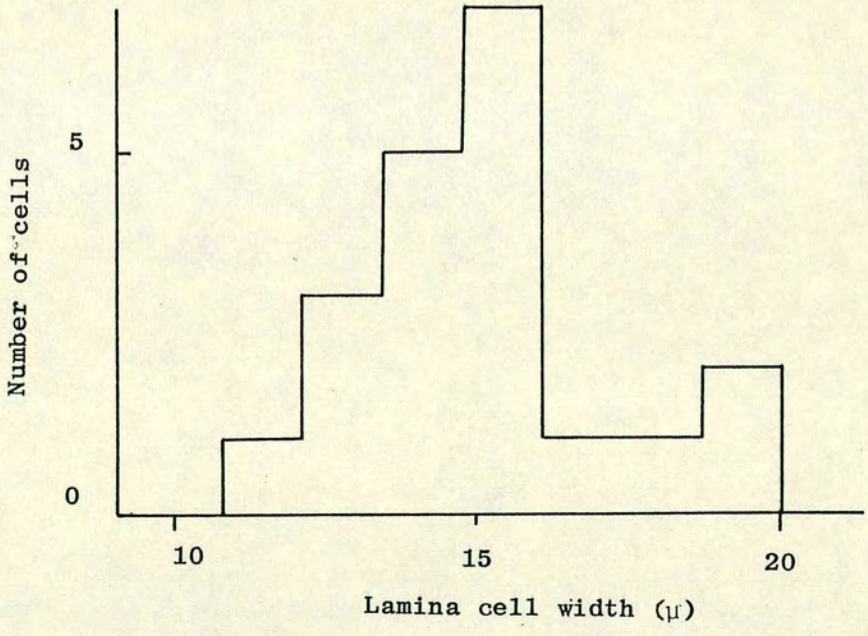


Figure A22.Taxon L : Histogram of cell widths of 20 cells taken from 2 specimens.

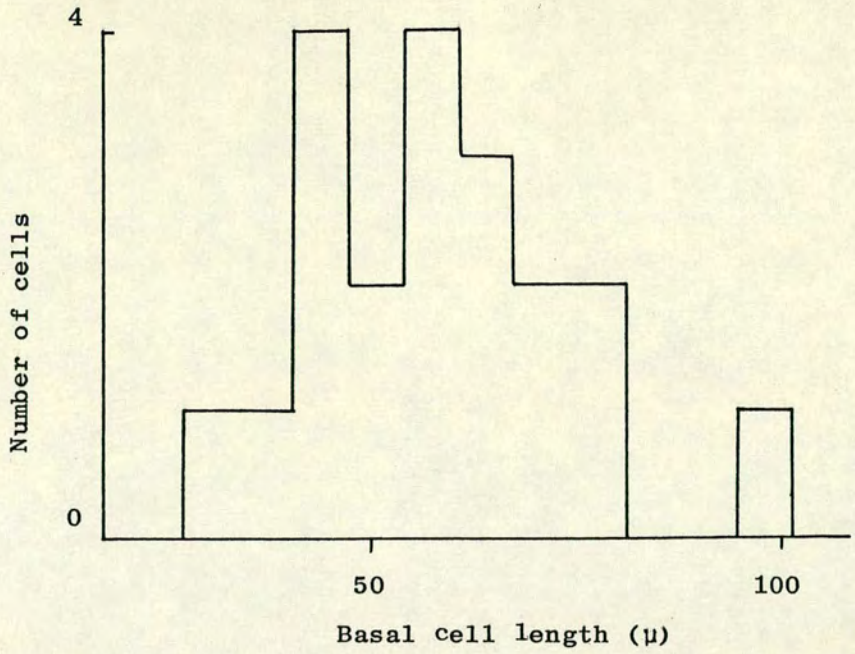


Figure A23.Taxon L : Histogram of basal cell lengths of 20 cells taken from 2 specimens.

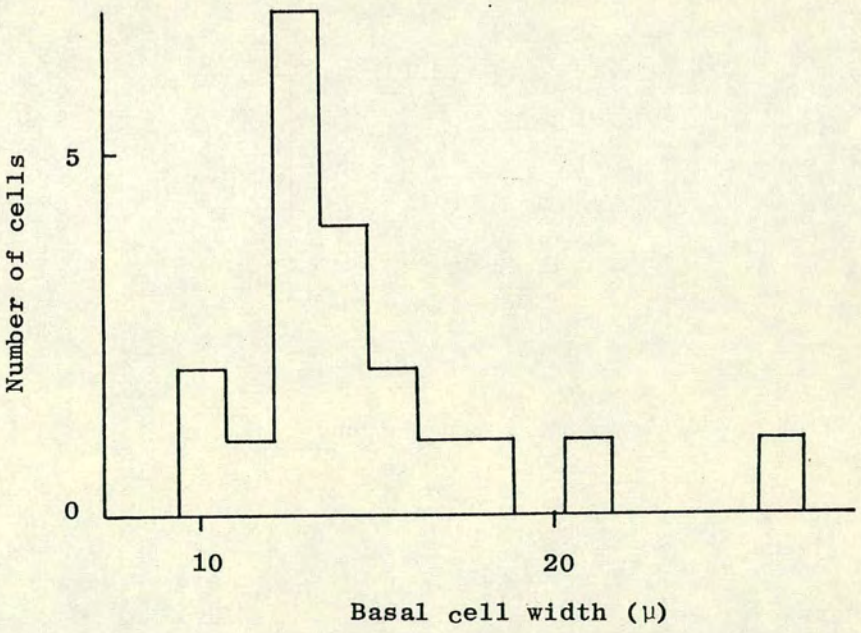


Figure A24.Taxon L : Histogram of basal cell widths of 20 cells taken from 2 specimens.

Appendix 5 : SPECIMENS EXAMINED

Herbarium abbreviations follow Homgren et al (1981)

Tortula anderssonii Aongstr. (Taxon B)

South Georgia

B.G. Bell: 565, 975. (AAS)

G.C.S. Clarke and S.W. Greene: 623, 631. (AAS)

S.W. Greene: 525. (AAS)

South America

Andersson s.n., Port Famine (Type of T. anderssonii) (NY)

Transecta Botanica de Patagonia Austral : 1, 16, 21, 23, 92, 103, 115, 122, 126. (AAS, BA)

Crozet

B.G. Bell: 1448, 1505, 1709, 1713, 1720, 1839, 2748, 2895. (AAS)

Macquarie Island

R.D. Seppelt: 10442.

New Zealand

J. Child: 311, 1579, 2535, 3319, 4100, 4216. (BM)

R. Brown s.n., Bruce's Creek. (Type of T. bealeyensis) (BM).

T. arenae (Besch.) Broth. ssp. arenae (Taxon A)

South Georgia

B.G. Bell: 568, 867, 1164. (AAS)

G.C.S. Clarke and S.W. Greene: 544, 547, 568, 575, 599, 633B. (AAS)

S.W. Greene: 545, 577, 682, 1030, 1200, 1362, 1405, 1569, 1900, 2025, 2380, 2433, 2469, 2546, 2643, 2708, 2765, 2836, 2952A, 3115, 3311, 3393, 3516. (AAS)

R.E. Longton: 161, 394. (AAS)

R.I.L. Smith Field record 1969-70: 476, 478, 544, 552. (AAS)

R.I.L. Smith Field record 1970-71: 838, 996, 1043. (AAS)

South America

Hariot 37, (Type of Barbula arenae) (BM).

Roivainen s.n., Isla Dawson (AAS)

Kerguelen

B.G. Bell: 3115, 3151, 3175, 3180, 3183. (AAS)

Imschaug: 7671, 7957, 7966. (ALTA)

Crozet

B.G. Bell: 2065, 2183, 2246, 2516, 2947, 3087. (AAS)

T. arenae ssp. petriei (Broth.) P.J. Lightowlers

(comb. et stat. nov. in preparation)

New Zealand

R. Brown s.n., Broken River. (BM)

B.E.G. Molesworth s.n., Mt. Egmont. (AUCK)

E.F. Northcroft 30, Mt. Earnshaw. (BM)

D. Petrie s.n., Kellys Hill, Westland (Type of T. petrici) (BM, FH)

T. filaris (C. Muell.) Broth. (Taxon G)

South Georgia

B.G. Bell: 550, 871, 992, 1166. (AAS)

B.G. Bell Field record: 435, 537, 545, 568, 707, 708. (AAS)

G.C.S. Clarke and S.W. Greene: 526, 538, 539A, 585, 592, 595, 616, 621, 626, 628, 637, 641, 651. (AAS)

S.W. Greene: 301, 537A, 593, 607B, 913, 923, 1282A, 1295, 1331, 1424, 1669, 1782, 1826, 2268, 2834B, 3167, 3459, 3502B, 3579A. (AAS)

W.J.L. Sladden: 19/6A, 19/32. (AAS)

R.I.L. Smith Field record 1970-71: 282, 678. (AAS)

South America

R.E. Longton: 1018, 1035, 1044. (AAS)

M. Ostafichuk: 2147. (ALTA)

C.J.F. Skottsberg: 61. (Type of T. robustula Card.) (PC,S)

Transecta Botanica de Patagonia Austral: 220 (AAS,BA)

Antarctic Peninsula

R.E. Longton: 834, 856, 876. (AAS)

T. fontana (C. Muell.) Broth. (Taxon D.)

South Georgia

G.C.S. Clarke and S.W. Greene: 516, 607, 618. (AAS)

S.W. Greene: 2952B, 3460. (AAS)

R.E. Longton: 453. (AAS)

R.I.L. Smith: 1227. (AAS)

R.I.L. Smith Field record 1969-70: 138, 549, 553. (AAS)

South America

Dusén s.n., Lago Viedma in paludosis (BM)

Herb. H.N. Dixon, Chiloe Island, comm. J. Hamilton nos. 426 and 427. (BM)

McWhinnie s.n., Herb. Hookerianum (BM ex K)

T. geheebiaeopsis (C. Muell.) Broth. (Taxon H)

South Georgia

B.G. Bell: 608, 638, 643, 683, 690, 692, 820, 852, 967B, 984, 991. (AAS)

W.N. Bonner: 218, 258, 283. (AAS)

A. Cameron and P. Kennett: 16. (AAS)

G.C.S. Clarke and S.W. Greene: 527, 533, 545, 557, 558, 567, 573, 579, 597, 600, 602, 605, 643, 647, 649- 721. (AAS)

J.B. Cragg: 1A, 2A, 9. (AAS)

S.W. Greene: 104, 222, 415, 563, 633, 654, 741, 769, 893, 1011, 1044, 1143, 1179, 1220, 1263, 1315, 1404B, 1552, 1583, 1659A, 1852, 2288, 2322, 2361, 2456, 2642B, 2730, 2764A, 2900, 2917, 2983, 2984A, 3103, 3224, 3262, 3357, 3383, 3585, 3587. (AAS)

R.E. Longton: 464. (AAS)

W.J.L. Sladden: 18/7, 19/12. (AAS)

R.I.L. Smith Field record 1969-70: 545, 551. (AAS)

South America.

M. Ostafichuk: 1723, 3065 (ALTA)

Kerguelen

Imschaug: 7244, 7285, 7294, 7298, 7303, 7767, 8039, 8043. (ALTA)

Naumann s.n., Kerguelen (Type of Barbula geheebiaeopsis) (H-BR)

T. princeps De Not. var. princeps

Taxon J.

South Georgia

B.G. Bell: 641, 897, 928A, 929A. (AAS)

B.G. Bell Field record: 328, 329B, 562, 1107, 1144. (AAS)

G.C.S. Clarke and S.W. Greene: 589, 598, 646, 653B. (AAS)

S.W. Greene: 771B, 921A, 922, 2176, 3384, 3579B. (AAS)

R.E. Longton: 151, 254, 313. (AAS)

R.I.L. Smith: 1235. (AAS)

R.I.L. Smith Field record 1969-70: 480. (AAS)

South America

Transecta Botanica de Patagonia Austral: 2, 17, 89, 113, 195, 207, 398, 482, 584, 2254. (AAS, BA)

Antarctic Peninsula

R.E. Longton: 11, 833, 899. (AAS)

R.I.L. Smith: 82, 83. (AAS)

Kerguelen

B.G. Bell: 3188, 3198. (AAS)

Imschaug: 7013, 8049, 8051, 8068, 8078. (ALTA)

New Zealand

Macmillan: 80/13, 80/34. (AAS)

Petrie s.n., Omaru 1892. (BM)

Australia

Streimann: 4079. (BM)

Weymouth: 2877. (BM)

North America

P.J. Lightowlers: 821, 823, 845. (Herb. P.J. Lightowlers)

Europe

De Notaris, s.n. In montibus Sardinia australis. (Type of *T. princeps*) (E)

P.J. Lightowlers: 462. (Herb. P.J. Lightowlers)

A. Scott, s.n. Inchnadampf, Scotland. (AAS)

Taxon I

South Georgia

C.J. Barrow Field record: 401. (AAS)

B.G. Bell Field reocrd: 308, 317, 466, 476, 477, 519, 709. (AAS)

G.C.S. Clarke and S.W. Greene: 536, 555. (AAS)

S.W. Greene: 921B, 1294, 1297, 2984B, 3102, 3226, 3261B, 3461A. (AAS)

R.I.L. Smith: 1230. (AAS)

R.I.L. Smith Field record: 1970-71: 1523B. (AAS)

D.W.H. Walton, T.V. Callaghan and T. Gunn Field record: 104B. (AAS)

South America

Transecta Botanica de Patagonia Austral: 22, 106, 255. (AAS, BA)

T. princeps De Not. var. conferta.

P.J. Lightowlers (comb. et stat. nov. in preparation)

(Taxon L).

South Georgia

B.G. Bell: 549.

B.G. Bell Field record: 481.

G.C.S. Clarke and S.W. Greene: 609, 635B.

S.W. Greene: 1648B, 1684, 2599, 2835.

R.I.L. Smith: 3105.

R.I.L. Smith Field record 1969-70: 481.

R.I.L. Smith Field record 1970-71: 1471.

Antarctic Peninsula

J.P. Baylis: 127, 128. (AAS)

R.E. Longton: 1324. (AAS)

R.I.L. Smith: 669. (AAS)

U.S. Antarctic Service Expedition 1940-41: 335.12, 345.1 (Types of T. conferta) (FH)

T. princeps De Not. var magellanica (Mont.)

P.J. Lightowlers (comb. et stat nov. in preparation.)

(Taxon K.)

South Georgia

B.G. Bell: 648, 928B, 929B, 1156, 1165. (AAS)

B.G. Bell Field record: 430, 432, 511. (AAS)

G.C.S. Clarke and S.W. Greene: 537, 588, 601, 620, 635A, 639, 653A. (AAS)

S.W. Greene: 528, 771A, 780, 3170, 3438, 3461B. (AAS)

R.E. Longton: 405, 795. (AAS)

W.J.L. Sladden: 34. (AAS)

R.I.L. Smith: 1240 (AAS)

R.I.L. Smith Field record 1969-70: 477 (AAS)

R.I.L. Smith Field record 1970-71: 1457, 1523A, 1551. (AAS).

South America

Andersson s.n., Port Famine (Type of T. pusilla Aongstr.) (S)

J.D. Hooker s.n., Sandhills, Uranie Bay (co-type of Syntrichia fuegiana) (NY)

Lechler: 1088. (co-type of S. fuegiana) (NY)

M. Ostafichuk: 1808, 1875A, 3262, 3266. (ALTA)

T. robusta Hook et Grev. ssp. robusta var. robusta

(Taxon F)

South Georgia

B.G. Bell: 606, 652, 653, 654, 671, 681, 813, 818, 834, 861, 891, 983. (AAS)

B.G. Bell Field record: 707, 1098. (AAS)

W.N. Bonner: 182, 187, 190, 194, 200, 209, 223, 239, 251, 252, 253, 261, 269.

G.C.S. Clarke and S.W. Greene: 517, 523, 524, 528, 532, 534, 539B, 551, 554, 556, 560, 566, 572, 580, 581, 591, 593, 596,

611, 622, 630, 633A, 648, 650, 652, 656, 722. (AAS)

S.W. Greene: 86, 146, 159, 165, 209, 235, 259, 286, 287, 302, 398, 406, 416, 458, 472, 509, 542, 583, 613, 708, 775, 786, 820, 865, 870, 931, 1080, 1088, 1115, 1130, 1179A, 1262, 1282B, 1298, 1404A, 1517, 1605, 1659B, 1722, 1767, 1958, 2075, 2136, 2276, 2488, 2530, 2689, 2729, 2807, 3010, 3134, 3157, 3389A, 3470, 3502C, 3579B. (AAS)

R.E. Longton: 330, 368. (AAS)

W.J.L. Sladden: 18/3, 19/6. (AAS)

R.I.L. Smith Field record 1970-71: 367A. (AAS)

South America

M. Ostafichuk: 1539, 1800, 1842, 1892, 1913, 2061, 2091, 2111, 2145. (ALTA)

Transecta Botanica de Patagonia Austral: 161, 293, 407, 611, 1390, 2351. (AAS, BA)

T. robusta Hook. et Grev. ssp. *robusta* var. *recurva* P.J. Lightowlers (*var. nov.* in preparation).

(Taxon E)

South Georgia

S.W. Greene: 731, 3114. (AAS)

R.I.L. Smith: 1158. (AAS)

R.I.L. Smith Field record 1969-70: 146, 166. (AAS)

T. robusta Hk. et. Grev. ssp. rubra (Mitt.)

P.J. Lightowlers (comb. et stat. nov. in preparation.)

Australia

Mueller s.n., Cobboras, Victoria. Herb. Hookerianum (BM ex K)

H. Streimann: 5418 (BM)

New Zealand

J. Child: 745, 812, 892, 1203, 1338, 1354, 1368, 1420, 1488, 1643, 2224, 2351, 2988, 3049, 3067, 3076, 3108, 3193, 3436, 3776, 3815, 3898, 4271, 4428, 4704, 4753, 4784. (BM)

T. saxicola Card. (Taxon C)

South Georgia

B.G. Bell: 967A, 974, 1163. (AAS)

B.G. Bell Field record: 431, 434, 1150. (AAS)

G.C.S. Clarke and S.W. Greene: 590, 627, 638, 645. (AAS)

S.W. Greene: 537B, 956, 2246A, 2324, 2413, 2420, 2531, 2764B, 3502. (AAS)

South America

M. Ostafichuk: 1671 (ALTA)

Skottsberg: 62. (Type of T. saxicola) (S)

Antarctic Peninsula

R.E. Longton: 833, 1103B, 1188B. (AAS)

R.I.L. Smith: 81, 150A. (AAS)

Kerguelen

Imschaug: 7975, 7978, 8093. (ALTA)

REFERENCES

ALLEN, D.E. 1966. A list of infraspecific taxa of British phanerogams tested in cultivation. Watsonia, 6 : 205-215.

ANDERSON, L.E. 1954. Hoyer's solution as a rapid permanent mounting medium for bryophytes. Bryologist, 57 : 242-244.

ÅNGSTRÖM, J. 1872. Förteckning och beskrifning öfver mossor, samlade af Professor N.J. Andersson under Fregatten Eugenies verldsomsegling åren 1851-53. Ofvers. K. Vetenskakad. Förh., 29 (4) : 3-29.

BARTRAM, E.B. 1946. New mosses from Tierra del Fuego. Farlowia, 2 : 309-319.

BARTRAM, E.B. 1957. Mosses from the United States Antarctic Service Expedition (1940-41). Bryologist, 60 : 139-143.

BELL, B.G. 1973. A synoptic flora of South Georgian mosses : II. Chorisodontium, Dicranoloma, Dicranum, Platyneurum and Conostomum. Br. Antarct. Surv. Bull., 37 : 33-52.

BELL, B.G. 1974. A synoptic flora of South Georgian mosses: V. Willia and Racomitrium. Br. Antarct. Surv. Bull., 38 : 73-101.

BESCHERELLE, E. 1885. Mousses nouvelles de L'Amérique australe. Bull. Soc. bot. Fr., 32 (2nd series) : 54-69.

BESCHERELLE, E. 1889. Muscinées. II. Mousses in Mission Scientifique du Cap Horn 1882-83, Vol. 5, Botanique 1. Paris. pp. 253-312. 6 plates.

BEST, G.N. 1905. A lesson in systematic bryology. Bryologist, 8 : 16-22.

BIRGER, S. 1926. Nachrufe : Per Dusen. Berichte der Deutschen Botanishen Gesellschaft, 44 : 81-87. 1 plate .

BLACKITH, R.E. and REYMENT, R.A. 1971. Multivariate morphometrics. Academic Press. London.

BORCHGREVINK, C.E. 1901. First on the Antarctic Continent being an account of the British Antarctic Expedition 1898 - 1900. Newnes. London.

BOROS, A. and JÁRAI-KOMLÓDI, M. 1975. An atlas of recent European moss spores. Akadémia Kiadó. Budapest.

BOWERS, M.C. 1964. A water soluble, rapid permanent mounting medium for bryophytes. Bryologist, 67 : 358-359.

BREMER, B. 1980a. A taxonomic revision of Schistidium (Grimmiaceae, Bryophyta) 1. Lindbergia, 6 : 1-16.

BREMER, B. 1980b. A taxonomic revision of Schistidium (Grimmiaceae, Bryophyta) 2. Lindbergia, 6 : 89-117.

BREMER, B. 1981. A taxonomic revision of Schistidium (Grimmiaceae, Bryophyta) 3. Lindbergia, 7 : 73-90.

BRIDEL, S.E. 1800 [1807]. Animadversiones in Muscologiae Recentiorum Tomum secundum, at ipso auctore propositae. Journal für die Botanik, 1 : 268-299.

BRIGGS, D. 1965. Experimental taxonomy of some British species of the genus Dicranum. New Phytol., 64 : 366-386.

BROTHERUS, V.F. 1902. Musci (Laubmoose). III Unterklasse Bryales : II Spezieller Teil, Gruppe I. Acrocarpi. in Engler, A. and Prantl, K., Die natürlichen Pflanzenfamilien. Engelmann. Leipzig. Teil I. Abt. 3, Hälfte I, Lf. 214-215.

BROTHERUS, V.F. 1924. Musci (Laubmoose). III Unterklasse Bryales : II Spezieller Teil. in Engler, A. and Prantl, K., Die natürlichen Pflanzenfamilien. Band 10, Hälfte 1. Engelmann. Leipzig. 2nd Edition.

BROWN, R. 1898. New Zealand Musci : notes on the genus Tortula, with descriptions of new species. Trans. N.Z. Inst., 30 : 399-409 and Plates : XXXV - XL.

BROWN, R.N.R., MOSSMAN, R.C. and PIRIE, J.H.H. 1906. The voyage of the "Scotia". Being the record of a voyage of exploration in Antarctic seas. William Blackwood and Sons. Edinburgh.

BRUCH, P., SCHIMPER, W.P. and GÜMBEL, W.T. 1842. Bryologia europaea seu genera muscorum Europaeorum monographice illustrata. E. Schweizerbart. Stuttgart. Vol. 2. [Fasc. 13-15 : 63-108] Barbula : 1-46.

BRYHN, N. 1902. Sarconeurum, genus muscorum novum. in Wille, J.N.F. Mittheilungen über einige von C.E. Borchgrevink auf dem antarctischen Festlande gesammelte Pflanzen. Nyt. Mag. Naturvid., 40 : 204-208.

CALMAN, W.T. 1937. James Eights, a pioneer Antarctic naturalist. Proc. Linn. Soc. Lond., 149th Session : 171-184.

CARDOT, J. 1900. Note préliminaire sur les mousses recueilles par l'Expédition Antarctique Belge. Revue bryol., 27 : 38-46.

CARDOT, J. 1901. Mousses et coup d'oeil sur la flore bryologique des Terres Magellaniques. Résult. Voyage S.Y. Belgica, 6, Botanique : 1-44.

CARDOT, J. 1905. Notice préliminaire sur les mousses recueillies par l'Expédition Antarctique Suédoise I. Espèces de la Region Magellanique. Bull. Herb. Boissier, 2nd series, 5 (11) : 997-1011.

CARDOT, J. 1906. Notice préliminaire sur les mousses recueillies par l'Expédition Antarctique Suédoise II. Espèces de la Géorgie du Sud. III. Espèces de l'Antarctide. Bull. Herb. Boissier, 2nd series, 6 (1) : 1-17.

CARDOT, J. 1908. La flore bryologique des Terres Magellaniques de la Géorgie du Sud et de l'Antarctide. Wiss. Ergebn. schwed. Südpolarexped., Bd. 4, Lf. 8.

CARDOT, J. 1911a. Les mousses de l'Expédition Nationale Antarctique Écossaise. Trans. R. Soc. Edinb., 48 : 67-82.

CARDOT, J. 1911b. Note sur les mousses rapportées par la seconde Expédition Antarctique Francaise, sou le commandement du Dr. Jean Charcot. Rev. bryol., 38 : 124-127.

CARDOT, J. 1912. Les mousses de l'Expédition National Antarctique Écossaise. Rep. Scient. Results Scott. natn. Antarct. Exped., 3 (5) : 55-57.

CARDOT, J. and BROTHERUS, V.F. 1923. Botanische Ergebnisse der schwedischen Expedition nach Patagonien und dem Feuerland 1907-1909. X. Les mousses. K. svenska Vetenskakad. Handl., 63 : 3-73.

CASAS DE PUIG, C. and MOLINAS, M.L. 1974. Etude an microscope electronique à balayage de la surface de feuilles de Tortula ruralis (Hedw.) Gaertn. var. hirsuta (Vent.) Par. Rev. bryol. lichen., 40 : 267-270.

CATCHESIDE, D.G. 1980. Mosses of South Australia. Handbook of the Flora and Fauna of South Australia, Handbooks Committee, S. Australian Government. Woolman. S. Australia.

CHAMBERLAIN, D.F. 1978. Pottia in Smith, A.J.E. The Moss Flora of Britain and Ireland. Cambridge University Press. Cambridge.

CHEN, P.C. 1942. Studien über die ostasiatischen Arten der Pottiaceae II. Hedwigia, 80 : 141-322.

CLARKE, G.C.S. 1973. A synoptic flora of South Georgian mosses : III. Leptotheca, Philonotis, Mielichhoferia and Pohlia. Br. Antarct. Surv. Bull., 37 : 53-79.

CLARKE, G.C.S. 1979. Spore morphology and bryophyte systematics. in Clarke, G.C.S. and Duckett, J.G. (eds.) Bryophyte Systematics. Systematics Association Special Volume No. 14. Academic Press. London. pp. 231-250.

CLARKE, G.C.S. and LIGHTOWLERS, P.J. 1983. Notes on Antarctic bryophytes : XI. Mielichhoferia austro-georgica C. Muell. and Muelleriella crassifolia (Hook. f. et Wils.) Dus. Br. Antarct. Surv. Bull., 59 : 35-39. (see Appendix 3, this volume).

CLIFFORD, H.T. 1953. The mosses of Macquarie Island and Heard Island. ANARE Rep., Series B, 2 : 1-12.

COOK , J. 1777. A voyage toward the South Pole and round the world performed in His Majesty's ships the Resolution and Adventure, in the years 1772, 1773, 1774, 1775. Strahan and Cadell. London.

CORLEY, M.V.F. 1976. The taxonomy of Campylopus pyriformis (Schultz) Brid. and related species. J. Bryol., 9 : 193-212.

CORLEY, M.V.F., CRUNDWELL, A.C., DÜLL, R., HILL, M.O. and SMITH, A.J.E. 1981. Mosses of Europe and the Azores; an annotated list of species, with synonyms from the recent literature. J. Bryol., 11 : 609-689.

CORMACK, R.M. 1971. A review of classification. Journal of the Royal Statistical Society, Series A (General), 134 : 321-367.

COX, J.F. 1961. Taxonomic studies on the bryophyte flora of South Georgia. M. Sc. Thesis, University of Birmingham.

CROSSLEY, A. 1976. A versatile multi-specimen holder for processing and critical-point drying materials for examination in the scanning electron microscope. J. Microsc., 108 : 349-352.

CRUM, H.A. and ANDERSON, L.E. 1981. Mosses of eastern North America. Columbia University Press. New York.

CRUNDWELL, A.C. 1956. Further notes on Tortula subulata var. graeffii. Trans. Br. bryol. Soc., 3 : 125-126.

CRUNDWELL, A.C. and NYHOLM, E. 1964. The European species of the Bryum erythrocarpum complex. Trans. Br. bryol. Soc., 4 : 597-637.

DE NOTARIS, J. 1838. Specimen de Tortulis Italicis. Memorie della Reale Academia di Torino, 40 : 281-325.

DILKS, T.J.K. and PROCTOR, M.C.F. 1979. Photosynthesis, respiration and water content in bryophytes. New Phytol., 82 : 97-114.

DIXON, H.N. 1923. Studies in the Bryology of New Zealand, Part 3. Bulletin No. 3, New Zealand Institute. Wellington.

DIXON, H.N. 1924. The student's handbook of British mosses. V.V. Sumfield. Eastbourne. 3rd edition.

DIXON, H.N. 1930. Tortula geheebiaeopsis. Rep. Br. bryol. Soc. for 1929, 2 (3) : 191-2.

DIXON, H.N. 1934. More mosses from South Georgia. K. Norske Vidensk. Selsk. Forh., 7 : 1-3.

DOBZHANSKY, T. 1970. Genetics of the evolutionary process. Columbia University Press. New York.

DUCKETT, J.G. and SONI, S.L. 1972a. Scanning electron microscope studies on the leaves of hepaticae I. Ptilidiaceae, Lepidoziaceae, Calypogeiaceae, Jungermanniaceae and Marsupellaceae. Bryologist, 75 : 536-549.

DUCKETT, J.G. and SONI, S.L. 1972b. A scanning electron microscope study of leaf surfaces of some species of Scapania Dum. (Hepaticae) J. Bryol. 7 : 75-79.

DU RIETZ, G.E. 1940. Problems of bipolar plant distribution. Acta phytogeogr. suec., 13 : 215-282.

DURRANT, A. 1962. The environmental induction of heritable changes in Linum. Heredity, 17 : 27-61.

DUSÉN, P. 1903a. Patagonian and Fuegian Mosses. Rep. Princeton Univ. Exped. Patagonia, 8, Botany : 63-126.

DUSÉN, P. 1903b. Beiträge zur bryologie der Magellansländer, von Westpatagonien und Südchile. Teil 1. Arkiv för Botanik, 1 : 441- 465.

DUSÉN, P. 1905a. Beiträge zur bryologie der Magellansländer, von Westpatagonien und Südchile. Teil 2. Arkiv för Botanik, 4 (1) : 1-45.

DUSÉN, P. 1905b. Beiträge zur bryologie der Magellansländer, von Westpatagonien und Südchile. Teil 3. Arkiv för Botanik, 4 (13) : 1-24.

DUSÉN, P. 1906. Beiträge zur bryologie der Magellansländer, von Westpatagonien und Südchile. Teil 4. Arkiv för Botanik, 6 (8) : 1-40.

DUSÉN, P. 1907. Beiträge zur bryologie der Magellansländer von Westpatagonien und Südchile. Teil 5. Arkiv för Botanik, 6 (10) : 1-32.

ERDTMAN, G. 1969. Handbook of Palynology. Munksgaard. Copenhagen.

FLETCHER, M.V. 1978. Growing New Zealand mosses and liverworts. Bull. Wellington Bot. Soc., 40 : 55-58.

FLORSCHÜTZ - DE WAARD, J. and WORRELL - SCHETS, M. 1980. Studies on Colombian cryptogams Vll. Culture studies on the taxonomic relevance of costal anatomy in the Campylopus leucognodes - subconcolor complex and in Campylopus pittieri. Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen, Ser. C., 83 : 37-45.

GODLEY, E.J. 1965. Botany of the southern zone : exploration to 1843. Tuatara, 13 : 140-181.

GORDON, A.D. 1981. Classification methods for the exploratory analysis of multivariate data. Chapman and Hall, London.

GOWER, J.C. 1967. A comparison of some methods of cluster analysis. Biometrics, 23 : 623-637.

GOWER, J.C. 1971. A general coefficient of similarity and some of its properties. Biometrics, 27 : 857-874.

GREENE, S.W. 1964a. Problems and progress in Antarctic bryology. in Carrick, R., Holdgate, M. and Prevost, J. (eds.). Biologie Antarctique, proceedings of the first symposium on Antarctic Biology, Paris 2-8 Sept. 1962. Hermann. Paris.

GREENE, S.W. 1964b. The Vascular Flora of South Georgia. British Antarctic Survey Scientific Reports No. 45. Natural Environment Research Council. London.

GREENE, S.W. 1968a. Studies in Antarctic bryology 1. A basic check list for mosses. Revue bryol. lichen., 36 : 132-138.

GREENE, S.W. 1968b. Studies in Antarctic bryology 2. Andreaea, Neuroloma. Rev. Bryol. Lichen., 36 : 139-146.

GREENE, S.W. 1973. A synoptic flora of South Georgian mosses : I. Dendroligotrichum, Polytrichum and Psilopilum. Br. Antarct. Surv. Bull.,36 : 1-32.

GREENE, S.W., GREENE, D.M., BROWN, P.D. and PACEY, J.M. 1970. Antarctic moss flora. I : The genera Andreaea, Pohlia, Polytrichum, Psilopilum and Sarconeurum. British Antarctic Survey Scientific Reports No. 64. Natural Environment Research Council. London.

GREVILLE, R.K. 1830. Descriptions of some new mosses discovered in South America by Dr. Gillies; with a plate. Edinb. J. nat. geogr. Sci., 2 : 1-4.

HATCHER, R.E. 1967. Experimental studies of variation in hepaticae. I. Induced variation in Lophocolea heterophylla. Brittonia, 19 : 178-201.

HEDWIG, D.J. 1782. Fundamentum historiae naturalis muscorum frondosorum concernens eorum flores, fructus, seminalem propagationem adiecta generum dispositione methodica, iconibus illustratis. Part 2. Siegfried Lebrecht Crusium. Lipsiae.

HERZOG, T. 1926. Geographie der Moose. G. Fischer.Jena.

HERZOG, T. 1954. Zur Bryophytenflora Chiles. Revue bryol. lichen., 23 : 27-99.

HIROHAMA, T. and IWATSUKI, Z. 1980. Surface ornamentation of rhizoids of the species of Bartramiaceae (Musci). Journ. Hattori bot. Lab., 48 : 259-275.

HOLMGREN, P.K., KEUKEN, W. and SCHOFIELD, E.K. 1981. Index Herbariorum Part I. The herbaria of the world. Regnum Vegetabile 106. Bohn, Scheltema and Holkema. Utrecht. 7th Edition.

HOOKER, J.D. 1847. I. Flora Antarctica Pt. 2 Botany of Fuegia, the Falklands, Kerguelen's land, etc. in The botany of the Antarctic voyage of H.M. discovery ships 'Erebus' and 'Terror' in the years 1839-43. Reeve Bros. London.

HOOKER, J.D. 1867. Handbook of the New Zealand flora : a systematic description of the native plants of New Zealand and the Chatham Kermadec's, Lord Auckland's, Campbell's and Macquarrie's Islands. Reeve and Co. London.

HOOKER, W.J. 1818. Musci exotici; containing figures and descriptions of new or little known foreign mosses and other cryptogamic subjects. Vol. 1. Longman, Hurst, Rees, Orme and Brown. London.

HOOKER, W.J. and GREVILLE, R.K. 1824. On the genus Tortula of the order Musci. Edinb. J. Sci., 1 : 287-302.

HOOKER, W.J. and TAYLOR, T. 1818. Muscologia Britannica; containing the mosses of Great Britain and Ireland systematically arranged and described; with plates illustrative of the characters of the genera and species. Longman, Hurst, Rees, Orme and Brown. London.

HORIKAWA, T. and ANDO, H. 1961. Mosses of the Ongul Islands collected during the 1957-1960 Japanese Antarctic Research Expedition. Hikobia, 2 : 160-178.

HORIKAWA, Y and ANDO, H. 1963. A review of the Antarctic species of Ceratodon described by Cardot. Hikobia, 3 : 275-280.

HORIKAWA, Y.and ANDO, H. 1967. The mosses of the Ongul Islands and adjoining coastal areas of the Antarctic Continent. Proceedings of the Symposium on Pacific - Antarctic Sciences, JARE Scientific Reports Special Issue No. 1 : 245-252.

JEFFERS, J.N.R. 1964. Principal components analysis in taxonomic research. Forestry Commission Statistics Section, Paper No. 83.

KAALAAS, B. 1912. Bryophyten aus dem Crozetinseln II. Nyt Mag. Naturvid., L II : 97-119.

KRAMER, W. 1980. Tortula Hedw. sect. Rurales De Not. (Pottiaceae, Musci) in der östlichen Holarktis. Bryophytorum Bibliotheca 21. J. Cramer. Vaduz.

KANDA, H. 1981. Two moss species of the genus Pottia from the vicinity of Syowa station, East Antarctica. Antarctic Record, 71 : 96-108.

KRZAKOWA, M. 1978. Isozymes as markers of inter- and intraspecific differentiation in hepatics. in Suire, C. (ed.) Congress International de Bryologie, Bordeaux 21-3 Nov. 1977. Bryophytorum Bibliotheca 13. J. Cramer. Vaduz. pp. 427-434.

LANJOUW, J. 1952. International Code of Botanical Nomenclature adopted by the seventh International Botanical Congress, Stockholm, July 1950. International Association for Plant Taxonomy. Utrecht.

LECHLER, W. 1857. Berberides americae australis, accedit enumeratio plantarum, quas in america australi auctor detexit. E. Schweizerbart. Stuttgart.

LEWINSKY, J. 1974. An electron microscopical study of the genus Tortula Hedw. with special reference to exine ornamentation. J. Bryol., 8 : 269-273.

LEWIS, K. and SMITH, A.J.E. 1977. Studies on some bulbiliferous species of Pohlia section Pohliella I. Experimental investigations. J. Bryol.,9 : 539-556.

LIGHTOWLERS, P.J. 1981. Techniques for mounting fragile tissue in gum chloral solution. J. Bryol.,11 : 843-844. (see Appendix 1, this volume).

LIGHTOWLERS, P.J. 1983. Notes on the Antarctic mosses Pohlia cruda and P. inflexa. Br. Antarct. Surv. Bull., 60 : 83-87. (see Appendix 2, this volume).

LIMPRICHT, K.G. 1888. Die Laubmoose Deutschlands, Oesterreichs und der Schweiz. in Rabenhorst, L. Kryptogamen - Flora von Deutschland, Oesterreich und der Schweiz. 2nd Edition. Bd. 4 E. Kummer. Stuttgart.

LINDBERG, S.O. 1878. Ukast till en naturlig gruppering af Europas blad mossor md. med töppsittande frukt. (Bryineae Acrocarpae). J.C. Frenckell and Sons. Helsingfors.

LINDBERG, S.O. 1879. Musci Scandinavici in systemate novo naturali dispositi. Officina Iesaiae Edquist. Upsaliae.

MAGILL, R.E., SEABURY, F., and MUELLER, D.J.M. 1974. Evaluation of the critical point drying technique and its application in systematic studies of mosses. Bryologist, 77 : 628-632.

MARDIA, K.V., KENT, J.T. and BIBBY, J.M. 1979. Multivariate Analysis. Academic Press. London.

MATTERI, C.M. 1977. A synoptic flora of South Georgia mosses : VII. Pottia. Br. Antarct. Surv. Bull., 46 : 23-28.

MATTERI, C.M. 1982. Patagonian bryophytes 6 : Fruiting Sarconeurum glaciale (C. Muell.) Card. et Bryhn newly found in southern Patagonia. Lindbergia, 8 : 105-109.

MIDDLETON, R.M. 1909. The first Fuegian collection. J. Bot., 47 : 207-212.

MILLER, H.A. 1971. An overview of the Hookeriales. Phytologia, 21 : 243-252.

MITTEN, W. 1860. Descriptions of some new species of Musci from New Zealand and other parts of the southern hemisphere, together with an enumeration of the species collected in Tasmania by William Archer, Esq.; arranged upon the plan proposed in the 'Musci Indiae Orientalis'. J. Linn. Soc. Botany, 4 : 64-100.

MITTEN, W. 1869. Musci austro-americani. J. Linn. Soc. Botany, 12 : 1-659.

MITTEN, W. 1876. The musci and hepaticae collected by H.N. Moseley, M.A., naturalist to H.M.S. 'Challenger'. J. Linn. Soc. Botany, 15 : 59-73.

LODGE, E. 1959. Effects of certain cultivation treatments on the morphology of certain British species of Drepanocladus. J. Linn. Soc. Botany, 56 : 218-224.

LODGE, E. 1960a. Studies of variation in British material of Drepanocladus fluitans and Drepanocladus exannulatus. I. An analysis of the variation. Svensk bot. Tidskr., 54 : 368-386.

LODGE, E. 1960b. Studies on variation in British material of Drepanocladus fluitans and Drepanocladus exannulatus. II. An experimental study of the variation. Svensk. bot. Tidskr., 54 : 387-393.

LONGTON, R.E. 1981. Inter-population variation in morphology and physiology in the cosmopolitan moss Bryum argenteum Hedw. J. Bryol., 11 : 501-520.

LONGTON, R.E. and GREENE, S.W. 1979. Experimental studies on the growth and reproduction in the moss Pleurozium schreberi (Brid.) Mitt. J. Bryol., 10 : 321-38.

LOOSER, G. 1933-36. Lista de plantas que han sido observadas en Chile en 1828 por el Dr. Carlos José Bertero. Trabajo publicado en "El Mercurio Chileno" en 1828 y 1829 reimpreso con una introducion y notas. Lagunas, Quevedo y Cia Ltd. Santiago de Chile.

MAGILL, R.E. and HORTON, D.G. 1982. The scanning electron microscope and moss taxonomy. in Geissler, P. and Greene, S.W. (eds.) Bryophyte Taxonomy, Proceedings of the International Association of Bryologists taxonomic workshop meeting, Genève, 27 Aug - 2 Sept 1979. J. Cramer. Vaduz. pp. 137-148.

MITTEN, W. 1879. Musci. in An account of the petrological, botanical and zoological collections made in Kerguelen's Land and Rodriguez during the Transit of Venus Expeditions, carried out by order of Her Majesty's Government in the years 1874-75. Phil. Trans. R. Soc., 168 (extra volume) : 24-39.

MONTAGNE, C. 1838. Centurie de plantes cellulaires exotiques nouvelles, Musci. Annls. Sci. nat. (series 2), 9 Botanique : 38-57.

MONTAGNE, C. 1845. Plantes cellulaires in Hombron, M. and Jacquintot, C. Voyage an Pole Sud et dans l'Océanie sur les corvettes l'Astrolabe et la Zélée, exécuté par ordre du roi pendant les années 1837, 1838, 1839, 1840, sous le commandement de M.J. Dumont-D'Urville, Capitaine de vaisseau. Botanique. Vol. I. Gide et Cie. Paris.pp. 281-335.

MONTAGNE, C. 1850. Flora chilena, plantas cellulaires I. Musgos. in Gay, C. Historia física y politica de Chile Vol. 7 Botanica. C. Gay. Paris. Museo de Historia natural de Santiago, Chile. pp. 5-202.

MOORE, C.J. and SCOTT, G.A.M. 1979. The ecology of mosses on a sand dune in Victoria, Australia. J. Bryol.,10 : 291-311.

MÜLLER, C. 1843. De muscis frondosis nonullis novis vel minus cognitis. Linnaea, 17 (5) : 581-601.

MÜLLER, C. 1849. Synopsis muscorum frondosorum omnium hucusque cognitorum. Vol I. Foerstner. Berlin.

MÜLLER, C. 1851. Synopsis muscorum frondosorum omnium hucusque cognitorum. Vol. II. Foerstner, Berlin.

MÜLLER, C. 1879. Prodromus bryologiae Agentinicae I. Schistocarpi. Linnaea, 42 : 220-460.

MÜLLER, C., 1883. Die auf der Expedition S.M.S. "Gazelle" von Dr. Naumann gesammelten Laubmoose. Botanische Jahrbücher fur Systematik, Pflanzengesichte und Pflanzengeographie, Bd. 5 : 76-88.

MÜLLER, C. 1885. Bryologia fuegiana. Flora, Jena, 68 : 391-429.

MÜLLER, C. 1889. Laubmoose (musci frondosi) in Die Forschungsreise S.M.S. "Gazelle" in den Jahren 1874 bis 1876 unter Kommando des Kapitän zur See Freiherrn von Schleinitz herausgegeben von dem Hydrographischen Amt des Reichs-Marine-Amts. IV. Teil Botanik. Ernst Siegfried Mittler und Sohn. Berlin.

MÜLLER, C. 1890. Bryologia Austro-Georgiae in Neumayer, G. Die Internationale Polar Forschung 1882-83. Die Deutschen Expedition und ihre Ergebrnisse, Bd. 2. Lf. 11.pp. 279-322.

MÜLLER, C. 1897. Prodromus bryologiae Argentinicae atque regionum vicinarum III. Hedwigia, 36 : 84-144.

NEWTON, M.E. 1972. Chromosome studies in some South Georgian bryophytes. Br. Antarct. Surv. Bull., 30 : 41-49.

NEWTON, M.E. 1974. A synoptic flora of South Georgian mosses : IV Bartramia and Breutelia. Br. Antarct. Surv. Bull., 38 : 59-71.

NEWTON, M.E. 1977a. A synoptic flora of South Georgian mosses : VI Cheilothela, Dicranella, Distichium, Myurella and Catagonium. Br. Antarct. Surv. Bull., 46 : 1-21.

NEWTON, M.E. 1977b. Heterochromatin as a cyto-taxonomic character in liverworts : Pellia, Riccardia and Cryptothallus. J. Bryol., 9 : 327-342.

NEWTON, M.E. 1979a. A synoptic flora of South Georgian mosses : VIII Calliergon and Brachythecium. Br. Antarct. Surv. Bull.,48 : 133-157.

NEWTON, M.E. 1979b. Chromosome morphology and bryophyte systematics. in Clarke, G.C.S. and Duckett, J.G. (eds.) Bryophyte Systematics. Systematics Association Special Volume 14. Academic Press. London. pp. 207-229.

NEWTON, M.E. 1980. Chromosome studies in some Antarctic and sub-Antarctic bryophytes. Br. Antarct. Surv. Bull., 50 : 77-86.

PIZARRO, C. and SÁIZ F., 1977. Estudio de la taxocenosis muscinal de la península Fildes (isla Rey Jorge, Shetland del Sur). Ser. cient. Inst. Antárct. Chileno, 5 : 81-96.

PODPĚRA, J. 1954. Conspectus muscorum Europaeorum. Československé Akademie Věd. Praha.

PROCTOR, M.C.F. 1979. Structure and eco-physiological adaptation in bryophytes. in Clarke, G.C.S. and Duckett, J.G. (eds.) Bryophyte Systematics. Systematics Association Special Volume 14. Academic Press. London. pp. 479-509.

PROCTOR, M.C.F. 1982. Physiological ecology : water relations, light and temperature responses, carbon balance. in A.J.E. Smith (ed.) Bryophyte Ecology. Chapman and Hall. London. pp. 333-381.

RAMSAY, H.P. 1967. in Löve, A., I.O.P.B. Chromosome number reports XIV. Taxon, 16 : 552-61.

RICHARDS, P.W. 1947. The cultivation of mosses and liverworts. Trans. Br. bryol. Soc., 1 : 1-3.

ROBINSON, H. 1971. Scanning electron microscope studies on moss leaves and peristomes. Bryologist, 74 : 473-483.

ROBINSON, H.E. 1972. Observations on the origin and taxonomy of the Antarctic moss flora. in Llano, G.A. (ed.) Antarctic Terrestrial Biology. American Geophysical Union, Washington D.C.

ROIVAINEN, H. 1933. Contribuciones a la flora de Isla Elisabeth, Rio de Las Minas y Puerto San Isidor de Prov. de Magellanes, de Puerto Barroso de Prov. de Chiloë y de los Alrededores de Termas de Chillan de Prov. de Ñuble, Chile. Ann. Bot. Soc. Zool.-Bot. Fennicae Vanamo, 4 (8) : 1-22.

ROIVAINEN, H. 1934. Musci nonnulli ex Chile austro-centrali. Ann. Bot. Soc. Zool.-Bot. Fennicae Vanamo, 5 (10) : 30-36.

SAINSBURY, G.O.K. 1950. New species of Tortula from sub-Antarctic islands of New Zealand. Svensk bot. Tidskr., 44 : 72-75.

SAINSBURY, G.O.K. 1955. A handbook of the New Zealand mosses. Royal Society of New Zealand Bulletin No. 5. Wellington. New Zealand.

SAITO, K. 1973. Memoir of the Japanese Pottiaceae I. Bull. natn. Sci. Mus., Tokyo, 16 : 61-91.

SAITO, K. 1975. A monograph of Japanese Pottiaceae. J. Hattori bot. Lab., 39 : 373-537.

SAITO, K. and HIROHAMA, T. 1974. A comparative study of the spores of taxa in the Pottiaceae by use of the scanning electron microscopy. J. Hattori bot. Lab., 38 : 475-488.

SAYRE, G. 1941. A gum arabic mounting medium. Bryologist, 44 : 160.

SCHELPE, E.A.C.L.E., 1953. Techniques for the experimental culture of bryophytes. Trans. Brit. bryol. Soc., 2 : 216-219.

SCHIMPER, W.P. 1876. Synopsis muscorum europaeorum praemissa introductione de elementis bryologicis tractante. E. Schweizerbart. Stuttgart. 2nd Edition.

SCHULTZ, C.F. 1823. Recensio generum Barbulae et Syntrichiae. Nova Acta Acad. Caesar Leop. Carol., 11 (1) : 191-232.

SCHUSTER, R.M. 1969. Problems of antipodal distribution in lower land plants. Taxon, 18 : 46-91.

SEPPELT, R.D. 1981. Studies on the bryoflora of Macquarie Island III. Collections, new moss additions and corrections and a revised checklist. Bryologist, 84 : 249-252.

SKOTTSBERG, C. 1960. Remarks on the plant geography of the southern cold temperate zone. Proc. R. Soc., Series B, 152 : 447-457.

SMITH, A.J.E. 1978. The Moss Flora of Britain and Ireland. Cambridge University Press. Cambridge.

SMITH, R.I.L. 1972. Vegetation of the South Orkney Islands with particular reference to Signy Island. British Antarctic Survey Scientific Reports No. 68. Natural Environment Research Council, London.

SMITH, R.I.L. 1981. Types of peat and peat-forming vegetation on South Georgia. Br. Antarct. Surv. Bull., 53 : 119-139.

SNEDECOR, G.W. and COCHRAN, W.G. 1967. Statistical Methods. Iowa State University Press. 6th Edition.

SOKAL, R.R. and MICHENER, C.D. 1958. A statistical method for evaluating systematic relationships. University of Kansas Science Bulletin, 38 : 1409-1438.

SPRAGUE, M.L. 1963-4. Obituary - Carl Johan Fredrik Skottsberg. Proc. Linn. Soc. London, 175 : 189-90.

STAFLEU, F.A. 1972. International Code of Botanical Nomenclature adopted by the eleventh International Botanical Congress, Seattle, August, 1969. International Association for Plant Taxonomy. Utrecht.

STEARN, W.T. 1966. Botanical Latin. Nelson, London.

STEEL, D.T. 1978. The taxonomy of Lophocolea bidentata (L.) Dum. and L. cuspidata (Nees) Limpr. J. Bryol., 10 : 49-59.

STEERE, W.C. 1939. Tortula in Grout A.J. (ed.) Moss flora of North America north of Mexico. A.J. Grout. Newfane, Vermont. Vol. 1, pp. 228-246.

STEERE, W.C. 1961a. A preliminary review of the bryophytes of Antarctica. in Science in Antarctica Part 1. The life sciences in Antarctica. National Academy of Sciences - National Research Council Publication 839. Washington D.C.

STEERE, W.C. 1961b. The bryophytes of South Georgia. in Science in Antarctica Part 1. The life sciences in Antarctica. National Academy of Sciences - National Research Council Publication 839. Washington D.C.

STEERE, W.C. 1965. Antarctic bryophyta. Bio Science,15 (4) : 283-85.

SULLIVANT, W.S. 1859. Musci in United States Exploring Expedition during the years 1838, 1839, 1840, 1841, 1842 under the command of Charles Wilkes, U.S.N. Vol. XVII Botany. C. Sherman and son. Philadelphia. pp. 3-32.

THÉRIOT, I. 1917. Contribution a la flore bryologique du Chili II. Revista Chilena de Historia Natural, 21 : 6-37.

TOUW, A. 1974. Some notes on taxonomic and floristic research on exotic mosses. J. Hattori bot. Lab., 38 : 123-128.

TOWNSEND, C.C. and WHITEHOUSE, H.L.K. 1979. Desmatodon bogosicus C. Muell. hal., an earlier name for Tortula khartoumensis Pettet. J. Bryol., 10 : 475-478.

TURRILL, W.B. 1920. Botanical exploration in Chile and Argentina. Bulletin of Miscellaneous Information, Royal Botanic Gardens, Kew, 6 : 57-66, 223-224.

VITT, D.H. 1976. A monograph of the genus Muelleriella Dusén. J. Hattori bot. Lab., 40 : 91-113.

VITT, D.H. 1979. The moss flora of the Auckland Islands, New Zealand, with a consideration of habitats, origins and adaptations. Can. J. Bot., 57 (20) : 2226-2263.

WATSON, E.V. 1968. British mosses and liverworts. Cambridge University Press. Cambridge. 2nd edition.

WIGH, K. 1975a. Scandinavian species of the Genus Brachythecium (Bryophyta). I. Modification and biometric studies in the B. rutabulum - B. rivulare complex. Bot. Notiser, 128 : 463-475.

WIGH, K. 1975b. Scandinavian species of the genus Brachythecium (Bryophyta). II. Morphology, taxonomy and cytology in the B. rutabulum - B. rivulare complex. Bot. Notiser, 128 : 476-496.

WIJK, R. van der MARGADANT, W.D. and FLORSCHÜTZ, P.A. 1969. Index Muscorum Volume V. International Association for Plant Taxonomy. Utrecht.

WILLDENOW, C.L. 1800. Caroli a Linne Species Plantarum exhibentes Plantas rite cognitas ad Genera relatas cum differentiis specificis, Nominibus trivialibus, Synonymis selectis, Locus natalibus secundum systema sexuale digestas. Tomus III., p.359.

YLI-REKOLA, M. 1980. Infraspecific variation of Polytrichastrum alpinum (Musci, Polytrichaceae) I. Comparison of multivariate methods. Ann. Bot. Fennici, 17 : 277-291.

ZANDER, R.H. 1972. A revision of the genus Leptodontium (Musci) in the New World. Bryologist, 75 : 213-280.

ZANDER, R.H. 1979. Techniques for study of Pottiaceae. Taxon, 28 : 643-644.

ZANTEN, B.O. van 1971. Musci in Zinderen Bakker, E.M. van, Winterbottom, J.M. and Dyer, R.A. (eds.) Marion and Prince Edward Islands. A.A. Balkema. Cape Town. pp. 173-227.

ZANTEN, B.O. van 1976. Preliminary report on germination experiments designed to estimate the survival chances of moss spores during aerial trans-oceanic long range dispersal in the southern hemisphere, with particular reference to New Zealand. J. Hattori bot. Lab., 41 : 133-140.

ZANTEN, B.O. van 1977. Experimental studies on trans-oceanic long-range dispersal of moss spores in the southern hemisphere. in C. Suire (ed.) Congress International de Bryologie, Bordeaux 21-23 Nov. 1977. Bryophytorum Bibliotheca 13.J. Cramer. Vaduz. pp. 715-733.

ZANTEN, B.O. van 1978. Experimental studies on trans-oceanic long range dispersal of moss spores in the southern hemisphere. J. Hattori bot. Lab., 44 : 455-482.