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A Study in the Experimental Taxonomy of some British Sphagha (section Cuspidata),with observations of their ecology.

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A STUDY IN THE EXPERIMENTAL TAXONOMY OF SOME BRITISH SPHAGNA (SECTION CUSPIDATA), WITH OBSERVATIONS OF THEIR ECOLOGY

A THESIS

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A STUDY IN THE EXPERIMENTAL TAXONOMY OF SOME BRITISH SPHAGNA (SECTION CUSPIDATA) WITH OBSERVATIONS ON THEIR ECOLOGY

Summary of Thesis by S. Agnew, April 1958

This thesis is concerned with taxonomic studies on some British members of the genus Sphagnum, and includes an historical survey of their systematics. Those dealt with in detail are S.recurvum P.beauv., S.cuspidatum Ehrh., ex Hoffm. emend., S.pulchrum (Lindb. ex Braithw.) Warnst., S.amblyphyllum Russ., S.fallax von Klinggr., and S.serratum Aust. This study has utilised taxonomic techniques which have not previously been applied to Sphagna including statistical investigations of their morphology and anatomy. These have allowed an assessment to be made not only of the extent to which each variable character is of value in species delimitation, but also of the affinities and number of taxa represented in the material examined. As a preliminary to the statistical work details of the variation in size and shape of branch leaves are given for two species.

Many plants of the species concerned were cultivated under various conditions in the field and in the laboratory to see how the environment could effect the expression of characters.

General conclusions are reached regarding the value of the various characters. Most of these are modified by the environment or vary arbitrarily within one plant. However the shapes of stem and branch leaves seem to be useful in some species and some other characters such as type of stem cortex are highly characteristic of, though not exclusive to, certain species.

It is finally decided to retain specific status for S.cuspidatum, S.pulchrum and S.recurvum, the last of these being divided into subspecies mucronatum and amblyphyllum. Pending further investigation of British material S.recurvum subsp. angustifolium (C.Jens.) Russ. and S.fallax are not recognised as distinct taxa. No evidence is found for recognising any varieties of the accepted species whose ecological relationships have been investigated.

It would appear worthwhile to extend these techniques to other "critical" Sphagnum species.

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I am grateful for loan or gift of specimens to all the people whose names are listed in the Preface.

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PREFACE

This thesis gives an account of a study of the systematics and ecology of certain British Sphagna made by the author during the three years from October 1954 to September 1957. The work was done at the University College of North Wales, Bangor, most of the field observations and all the experiments being carried out in North Caernarvonshire and Anglesey.

Material for cultivation was obtained as follows: specimens of S.recurvum and S.cuspidatum were collected from several localities around Bangor; S. pulchrum was obtained by the author from Tregaron Bog, Cardiganshire, and from Bowness Moss, Cumberland; S. fallax and S. amblyphyllum were gathered from two separate localities in Angus under the guidance of Miss U. K. Duncan.

The herbarium collections of Professor P. W. Richards and the Botany Department, Bangor, were examined by the author and parts of the herbaria of W. R. Sherrin and the British Bryological Society were made available by the South London Botanical Institute and A. H. Norkett at the British Museum respectively. In addition specimens were loaned or given by the following: Miss M. K. Duncan, Miss E. M. Lobley, Dr. M.C.F. Proctor, Dr. D. Ratcliffe, Mr. S.W. Greene and Mr. E.C. Wallace. The majority of the herbarium specimens were British but a few were from Scandinavia or Central Europe, and one was American.

During the preparation of this thesis the recently published 4th edition of Gams' Kleine Kryptogamenflora (1957) was brought

to the author's notice. In this work, which is in the form of an amplified key, Gams has again revised the classification of the Sphagna, including considerably more detail than in the 2nd Edition (1948). The most important change in Gams' classification with regard to the present work is his view that S. recurvum P. Beauv. should now be split into three sub-species. This problem is discussed in Chapter 9, which gives an account of investigations into the distribution and variability of characters cited by Gams (1957) as diagnostic of these sub-species.

However, much of the work was completed before the publication of Gams' new key, and there was not time to include an investigation of his latest ideas in most cases. Fortunately Gams' views on the status of most taxa have remained unchanged so that the present writer's earlier work was not rendered invalid although it failed to consider Gams' new classification. For instance although the study of the relationship and diagnosis of S. pulchrum and S. recurvum (Chapter 4) deals with the latter as a single undivided taxon (as in Gams, (1948)), the status and separation of S. pulchrum from S. recurvum are substantially the same in each of Gams' keys.

CONTENTS

CHAPTER 1

Introduction

The genus Sphagnum was first clearly defined by Ehrhart in 1780, previous workers having included mosses of several other genera with some genuine Sphagnum species. From 1780 onwards, various bryologists published papers and books dealing with the anatomy, systematics and reproduction of mosses, and many useful observations were made on the Sphagna. Schimper in 1858 described several species in detail using a wide range of diagnostic characters, while Lindberg in 1862 suggested a scheme of classification which is similar in outline to the schemes in use at the present time. A few later authors, notably Russow (1865), made valuable contributions to the knowledge of this genus, but the period of intensive study of the Sphagnaceae by European bryologists did not start until after the publication of Braithwaite's monograph in 1880. This was the first work written in English which was devoted entirely to the Sphagnum species of Europe and North America.

Following this, Warnstorf in particular published many papers dealing with Sphagnum systematics; his Kryptogamenflora der Mark Brandenberg (1899) was translated for the benefit of British readers by Herrell (1900). Herrell followed Warnstorf in recognising the following eight sections:- Acutifolia, Squarrosa, Cuspidata, Polyclada, Rigida, Truncata, Subsecunda, Cymbifolia. It is interesting to note that during the preparation of this work Warnstorf revised the Section Cuspidata (presumably for inclusion in Pflanzenfamilien (1900)) and increased the number of European species in this section from 8 to 16.

The next classification due to Warnstorf (1900) resembled his earlier one, except that Cymbifolia was placed by itself in a Section Inophloea, preceding Section Litophloea which consisted of all other groups or sub-sections. A discussion of the taxonomic status of these categories is given by Andrews (1911, p.74).

The next major work on the Sphagna was also due to Warnstorf who published his Sphagnologia Universalis in 1911 as part of Engler's Pflanzenreich. In this, Section Inophloea was placed after Litophloea within which the order of sub-sections was also changed. Sherrin in 1927 published An Illustrated Handbook of British Sphagna, which was in effect a translation of the relevant parts of Warnstorf's work. Thus Sherrin's Section I Litophloea was composed of five sub-sections arranged in the following order:- Acutifolia, Rigida, Squarrosa, Cuspidata, Subsecunda. Sub-sections Truncata and Polyclada were omitted as each is represented by a single species which does not occur in Britain.

While admitting the validity of Warnstorf's grouping, at least as applied to European and non-tropical American forms, Andrews, in the North American Flora (1913, a) rearranged the groups, and divided Litophloea into two Sections. Andrews gives the reasons for this procedure in Notes on North American Sphagnum (1911, p.75). His final classification is as follows:-

Subgenus Inophloea
Subgenus Litophloea
  Section Malacosphagnum (Rigida of Warnstorf)
  Section Acisphagnum

Section Acisphagnum

Group Squarrosa

Group Cuspidata (including Subsecunda of Warnstorf)

Group Acutifolia

The close relationship of the three groups of Section Acisphagnum and the desirability of combining Subsecunda with Cuspidata are discussed by Andrews in further Notes on North American Sphagnum (1913b, p.60, and 1915, p.1 respectively).

Gams (1948) followed Warnstorf rather than Andrews, but did not recognise the Section Rigida; in the latest (1957) edition of his work, however, Gams gives this Section a status equal to that of Sections Cuspidata. Acutifolia etc., Richards and Wallace (1950) followed Andrews' classification into Sections and Groups, but Proctor (1955) maintained Cuspidata and Subsecunda as separate series.

This thesis is concerned with species of Group Cuspidata as defined by Schliephacke (1865), which with the addition of Schliephacke's Mollusca, constitutes the series Cuspidata as understood by Proctor and Gams. The group is represented in the British Isles by eight species, one of which, S.tenellum Pers., is distinct from all the rest in having short oval branch leaves, a character which led Warnstorf (1911) to place it alone in a separate Group Ovalia, the remaining species being placed in Group Lanceolata. The only confusion about S.tenellum has been concerned with nomenclature (Andrews, 1919) and as it seems to be a well defined species it was omitted from the present work. S.lindbergii Schp. and S.riparium Angstr. are distinct species about which there has been little or no question and although the latter is similar to S.recurvum P. Beauv. in some respects,

there is rarely any difficulty in distinguishing these two species. Both are moreover, quite rare, and the difficulty of obtaining herbarium specimens and, more especially, fresh material for cultivation, argued against their being included in this work.

Of the remaining five species recognised by Richards & Wallace (1950), S. obtusum Warnst. is uncommon and can always be distinguished from S. recurvum by the presence in the branch leaves of one or two rows of numerous small "membrane thinnings." (This term is used by Andrews (1913,a) to describe the small round areas which resemble unringed pores except in that they are unperforated, and which are visible only after deep staining.) S. balticium Russ. is also rare, and is distinguished by the presence of oval to lingulate, obtuse, fibrillose stem leaves, a combination of characters not found in any related species.

There remained the species S. recurvum, S. pulchrum (Lindb. ex Braithw.) Warnst. and S. cuspidatum Ehrh. ex Hoffm. emend., which were recorded as having a wide distribution in Sherrin's Census Catalogue (1946). It was decided to investigate these species in detail.

Andrews (1913,b) recognised the following varieties of these species:-

S. recurvum var. tenue Klinggr.

S. cuspidatum var. torreyi (Sull.) Braithw.

S. cuspidatum var. serrulatum Schlieph.

The last two were described as species S. torreyanum Sull. and

S. serratum Aust. by Sherrin (1927), who gave under the latter name parts of Warnstorf's descriptions of both the species and its variety serrulatum Schlieph. Some errors in translation appear to have occurred, thus Warnstorf (1911, p.246) describes the cortical cells of the stem of S. serratum as "bisweilen scheinbar fehlend" (sometimes apparently wanting), whereas Sherrin states (1927, p.38) "cortical cells of the stem apparently wanting." Again Warnstorf (p.247) describes the hyaline cells of the branch leaves of var. serrulatum as "nicht selten zum grössen Teil faserlos" (often for the greater part without fibrils), while Sherrin's description reads "not rarely for the most part fibrillose." There is obviously confusion as to the diagnosis of this taxon, and a re-examination of its status seemed desirable .

The question of nomenclature with regard to S. recurvum var. tenue is fully discussed by Andrews (1917) the important point to note here being his inclusion of small, imbricate-leaved forms of Warnstorf's S. recurvum var. parvulum and S. amblyphyllum var. parvifolium under var. tenue. This leads on to the consideration of S. amblyphyllum Russ. which is accorded specific rank by Warnstorf but which is included by Andrews (1917) under S. recurvum. Similarly S. fallax von Klinggr. is regarded by Andrews (1917) as simply an aquatic form of S. recurvum. The varieties robustum and majus of S. recurvum, and varieties falcatum, submersum, plumosum, plumulosum of S. cuspidatum described by Warnstorf, are not mentioned by Andrews. Although Andrews states that S. pulchrum is easily distinguished from S. recurvum

the former was not accorded specific rank until 1900, and thus it seemed desirable to investigate its relationships. As will be shown later, there has been considerable confusion in this country between S. pulchrum and S. recurvum and a redefinition of these species was certainly needed.

The experimental work, an account of which constitutes the main part of this thesis, was therefore concentrated on the following species and their varieties as recognised by Warnstorf:- S. amblyphyllum, S. pulchrum, S. recurvum, S. serratum, S. fallax, and S. cuspidatum. S. torreyanum was omitted owing to lack of material. Investigation of the value of the taxa so defined was greatly facilitated by the fact that most of the herbarium specimens examined were gathered between 1910 and 1950, and were consequently identified on Warnstorf's system.

Many examples of lack of precise definition can be found in the published systematic descriptions, and one of the primary aims of this work was the improvement of descriptive methods by using quantitative criteria where possible, a further object being the determination of the ranges of variability of diagnostic characters. It was also hoped by the use of culture methods to investigate the effect of environment on variability of characters, and hence to assess the value of previously described taxa, defined on the basis of these characters. During a discussion on biometrics and systematics (Melville et al., 1949-50) many useful comments were made on these aspects of taxonomic investigation. In particular, the remarks of

Heslop-Harrison (p.176) in connection with Dactylorchids are of wide application and could well refer to Sphagnum systematics. Thus "------ not all of the criteria which have been employed in classical description prove to be of equal value when populations rather than individuals are made the object of study. To be of use in critical comparison, the familiar descriptive cliches of species diagnoses require more precise definition in terms of population parameters." Heslop-Harrison also suggests the analyses of populations from ecologically diverse habitats to determine which phenotypic characters show the least intra- and inter- population variability.

Detailed studies of the systematics of Sphagna have been few. Aberg in 1937 published the results of a comprehensive survey of the European Subsecunda, in which he considered the pore structure of stem leaves and type and distribution of branch leaf pores to be the most important diagnostic characters. He refers to the plasticity of stem leaf size and structure under a variety of moisture conditions, drawing attention to the fact that adverse conditions lead to a reduction in vitality and subsequent reversion to the juvenile form, in which stem leaves are not differentiated from branch leaves. The significance of this with regard to variation in fibrillosity and size and shape of stem leaves is at once apparent, as these characters are often used diagnostically. Similar changes were produced in species of the Cuspidata group grown in water by Paul (1932), to whose work Aberg refers. As mentioned above, one aim of this present work has been to show the effect of different conditions of growth on this and other characters.

The next Chapter of this thesis consists of a general account of the morphology and anatomy of the Sphagnum plant, with special reference to features of diagnostic value. Specific differences will be dealt with in subsequent sections dealing with the individual taxa.

CHAPTER 2.

Structure of the Sphagnum gametophyte

Each plant consists of a stem which is capable of indefinite longitudinal growth from division of the apical cell. This is enclosed in a terminal bud formed of spirally arranged leaves borne directly on the stem. Branches arise in this bud, and, owing to delayed elongation of the stem, developing branches and stem leaves are crowded into a dense comal tuft or capitulum. The branches are of limited growth and arise in groups (fascicles) of usually 4 to 6 at the side of every fourth stem leaf. The fascicles are normally composed of comparatively robust divergent (spreading or horizontal) branches, and more slender pendent branches, which may or may not be appressed to the stem. Most stems also show dichotomous branching of the axis, which ultimately leads to an increase in number of plants, as the older parts die and disintegrate. Divergent and pendent branches bear closely set leaves arranged spirally. Sometimes, the spiral arrangement is obscured as when the leaves appear to lie in straight lines, e.g. in S. pulchrum, or when they are secund or falcate in shape. When dry, the leaves, especially those of divergent branches, are often imbricate or recurved or undulate, all these characters being used diagnostically. Stalked antheridia are borne on special branches, each at the side of a branch leaf, which is often different in shape and structure from normal branch leaves. Antheridial branches are usually differentiated and are recognisable as such in the coma, but the antheridia may not mature until much later.

Archegonial branches bear highly specialised perichaetial leaves whose anatomical structure is used by Andrews (1913) in separating the constituent groups of Acisphagnum.

Anatomy

The stem consists of usually three zones: a central thin-walled tissue which passes gradually into a region of thick-walled cells (often inappropriately called the "wood-cylinder") which is surrounded by one or more layers of thin-walled "cortex". The latter term again is hardly applicable, and should strictly be reserved for vascular plants. However, I think it more permissible than "wood-cylinder" which implies histological and physiological properties unknown in Sphagna, whereas "cortex" merely describes the topographical position of the tissue rather than its structure or function. Other terms used include 'cuticle' (Braithwaite), "Stammepidermis" (Warnstorf(1911)), "Rindenzellen" and "Hyalodermis" (Gams (1948)), the last of these probably being the most apt. However, as most of the works written in English use "cortex" which is a concise and descriptive term, this will continue to be used in this thesis.

The thick walled sub-cortical layers are often pigmented and give to the stem the characteristic yellow, brown, red or green colour, which is often used in identification. The degree of differentiation of the cortex from the underlying cell-layers as seen in cross-section is also important.

The branch axis is constructed like the stem of a central tissue and cortex, the latter usually consisting of only one layer of cells. Pigment

is usually found in the subcortical cells of branches when the stem is coloured but apart from a reference by Gams (1957) (which will be considered in detail later) no diagnostic importance appears to have been attached to the presence of pigment in the branches in the absence of pigment in the stem. The value of this feature as a diagnostic character was investigated in this thesis. The presence of two types of cell in the branch cortex was used by Andrews (1913b) as the main feature separating Acisphagnum from Malacosphagnum. Most members of the former have long cells each with an extended "neck" terminated by a pore (retort-cells) only in the axils of leaves, the remaining cortical cells being simple. The shape and size of retort-cells is mentioned by Andrews as being of diagnostic value within the Section Acisphagnum.

Stem leaves and branch leaves are composed of a single layer of two kinds of cell. Andrews (1913a,p.3) describes these as: "narrow linear chlorophyll-cells forming the meshes of a network enclosing the large rhombeidal hyaline cells, the latter being perose and ----- having their walls reinforced inwardly by ring-shaped or spiral fibril-bands; pores round to elliptic, often defined by a fibril ring." The stem leaves do not always have pores and fibrils, but they often have large irregular areas of the hyaline cell-wall reabsorbed during development, leaving resorption gaps. The distributions of these and of similar gaps in the perichaetial leaves are of diagnostic importance.

The branch leaves are usually bordered with a few rows of narrow hyaline cells, similar cells forming a wider border in the stem leaves. The relative position of chlorophyllous and hyaline cells as seen in transverse section or in surface view of the branch leaves has been widely used as a means of separating species, as has the number and distribution of pores.

Each species usually has a distinct facies, and although great variability occurs, with experience, many characters may be successfully used for diagnosis in the field.

Thus colour, size, robustness, direction of branches and proximity of fascicles are generally given as specific characters in systematic descriptions, although precise definition is impossible where the habit of the plant is concerned.

CHAPTER 3

The use of quantitative criteria

A survey of the literature shows that dimensions of stem and branch leaves have been much used as diagnostic characters, particularly by Warnstorf who distinguished many varietal forms on the basis of leaf size and length-width proportion. Andrews does not mention these characters and it is perhaps significant that he also ignores most of Warnstorf's varieties. Sherrin's descriptions closely follow Warnstorf's, although he gives no details of the many "forms" and "sub-forms" recognised by Warnstorf. The main criterion for the separation of varieties of S.recurvum and S.cuspidatum by these authors is the size of branch leaves, stem leaf dimensions sometimes being used as well.

The four varieties of S.cuspidatum described by Warnstorf are further distinguished by their characteristic habits and habitats, which are difficult to define precisely. Preliminary field observation suggested that a range of forms of S.cuspidatum was obtainable near Bangor, and so it was decided to concentrate attention first on this species rather than on S.recurvum which would also involve the consideration of S.amblyphyllum.

Branch leaf dimensions of S.cuspidatum and its varieties are given below (from Warnstorf, 1911).

	Length	Width
	mm	mm
S. cuspidatum	1.6 - 3.0	0.33 - 0.45
var. falcatum	2.0 - 3.0	0.3
var. submersum	1.3 - 1.7	0.5 - 0.6
var. plumosum	2.5 - 5.0	0.5 - 0.6
var. plumulosum	1.5 - 2.5	0.3 - 0.4

Mean values for the dimensions are not recorded, and the ranges for different varieties overlap in some cases, while the range of length given for var. plumosum is very large. It can only be presumed that samples of similar size from comparable parts of plants were examined for the determination of these figures, as Sherrin merely states that only leaves from the lower part of spreading branches should be selected. In order to test the validity of leaf size as a diagnostic character, it was of primary importance to establish a standardised sampling technique. It was hoped by using a suitably large sample (with consequent low variance) from a well defined part of the plant, to obtain mean figures for several gatherings. Comparison of these gatherings would then be valid, and a greater degree of significance could be attached to any differences amongst them.

Melville (1949-50, p.157) has drawn attention to the necessity of confining comparisons to organs removed from corresponding positions on different plants, and Turrill, in discussing Melville's paper, emphasized the importance of taking random samples of the objectively selected comparable areas. Melville worked on Ulmus leaves and

found that series of leaves from short shoots always exhibit the same pattern of variation in size and shape, so that each species has a characteristic leaf "spectrum". Biometric observations were confined to certain of these leaves so that samples were always comparable. These methods were easily adapted for use in the present investigation of Sphagnum, the species of which also have leaf spectra.

Melville used shape rather than size as a diagnostic character, and as long ago as 1937 suggested ways of measuring this. Objectivity in selecting parts to be measured is again essential and he emphasizes that the system of measuring must be such that measurements on different sized leaves are comparable. His leaves were measured by tracing their outlines on to transparent paper and projecting the image from a photographic enlarger to fill lengthwise a 10- unit grid. Breadth could then be read directly at regular intervals as a percentage of length.

In the present work, the author evolved a similar technique in which the images of leaves were projected directly from a microscope slide on to the bench by means of a "Projecterlux" apparatus. By projecting an image of a micrometer slide at a suitable magnification a grid was constructed on a piece of transparent "Perspex", so that images of leaves could then be measured directly in millimetres by using the grid. This technique also facilitated the drawing of leaves

or stem sections and was much quicker and easier than using Camera lucida.

This present chapter is chiefly concerned with the evolution of a sampling technique as a basis for the examination of variability of branch leaf size in S. cuspidatum. A study was made of branch leaf size in a sample showing no marked varietal characters obtained from a non-submerged mixed Sphagnum community in a blanket bog near Bethesda, Caernarvonshire.

The branches borne on a Sphagnum plant are of limited growth and as the number of leaves per branch is more or less constant throughout a plant the branch reaches maturity when it is fully elongated, that is when the youngest (distal) leaves are separated by internodes. The leaves mature very early, no growth taking place after branch elongation has ceased. Various stages of elongation of branches can be seen in the comal tuft, and, usually, all branches appear to be fully extended at about the time they become separated from the coma by elongation of the main stem. Evidence in support of this was obtained by selecting a stem, A, from the sample, and removing the longest divergent branch from each of the first ten fascicles numbered from the base of the coma downwards. Each branch was cut in half at the mid-point by length and all the leaves were dissected in order from base to apex. Branch lengths, number of leaves and number and length of the longest leaf are given in Table 1.

As none of these parameters increased with distance from the coma, all "separated" fascicles were considered to be mature. (In later investigations occasional stems occurred in which some "separated" branches were obviously not fully extended, each having a compact "bud" of leaves at the distal end; these branches were never included in a sample used for leaf measurement.)

The pattern of variation in leaf size and shape

Leaves are of limited growth, and length and width vary along a branch, though not at the same rate, so that changes in shape result. The proximal leaves are short and wide, the median leaves are longer while the terminal ones are shorter and narrower (Fig. 1). Another stem, B , from the same sample was treated in the same way as A , so that complete leaf "spectra" were obtained for a total of 20 branches. The leaves were then sampled by different methods to find the region of the branch giving the least variability within a sample.

Four methods were used:-

(i) 10 leaves per branch about the mid-point by length (M_L)

(ii) " " " " " the mid-point by number (M_N)

(iii) " " " " at a fixed point from the base (leaves number) 30 -39 (F.P.)

(iv) " " " " selected by random numbers (R)

This last method was included for the sake of completeness although it was obvious that it would give a high variance as some smaller basal and terminal leaves would be included in the sample.

All the leaves were measured as follows:-

(i) Length (L)

(ii) Greatest width (W) at

(iii) Height above base (L_B)

For stem B , pooling the data from the first three sampling methods, which usually overlapped to some extent, the following results were obtained.

	Mean	Range
	mm	mm
W	0.54	0.35 - 0.65 (88% between 0.5 and 0.6)
L_B	0.46	0.3 - 0.6 (95% between 0.4 and 0.5)
L	2.24	1.9 - 2.6

Thus the dimensions W and L_B have a low variability and hence any variability in the proportions $L/_W$ or $L/_{L_B}$ is usually a reflection of differences in L. It was then decided to investigate statistically the variability of L using all four methods of sampling. An analysis of variance was carried out on the data for the two stems; thus for each method there were 200 observations.

In all methods, the greatest variance was due to differences between stems, rather than between branches of one stem, or between leaves of a branch. The greatest total variance was obtained by random selection, (V = 0.274), and the least total variance by

selecting leaves about the mid-point by length, ($V = 0.044$).

Selecting leaves about M_N also gave a low value for V ($V = 0.052$) but as it is much easier to find M_L than to find m_N, the former method of selection was adopted.

Next analyses of variance were performed for the two stems, taking

(i) two leaves about M_L from each branch,

(ii) one leaf immediately above M_L,

and (iii) one leaf immediately below M_L.

The results suggested that not much accuracy would be lost by reducing the number of leaves per branch. Table 2 shows the means obtained by taking 1 to 10 leaves per branch from each of the 20 branches. The odd numbers of leaves gave two samples with different means as the "odd" leaf could be taken above or below M_L. The mean for 20 leaves is the same as that for 20 leaves which suggests that 2 leaves per branch is an adequate sample. The minimum numbers of branches and stems per sample were then determined.

Branches

Table 3 shows the means of L calculated from samples of 4, 8, 12 ---40 leaves, 2 leaves about M_L being taken from 1 to 10 branches from each stem. As successive branches from the stem were included in the calculation of the mean, there was a slight rise in mean length and then a gradual fall. Five more stems were selected and 2 leaves about M_L removed from one branch of every fascicle numbered from the coma downwards. Graphs (Fig. 2) of mean leaf length per branch plotted

against number of branch show a similar rise and decline as distance from the coma increases, and in the longest stem, with 44 fascicles, an increase in leaf length was shown in the oldest fascicles. This suggests a periodic variation in length of comparable leaves, but at this stage it is impossible to tell whether the periodicity is internal or a result of fluctuation in environmental conditions.

It was obvious that a random method of selecting branches must be adopted and this was done for all but stems A and B, which only had ten fascicles each. The data obtained for each stem from a sample of from one to at least 15 branches showed that mean leaf length varied considerably until the 10 to 15 branch level was reached, but even at this sample size (20 to 30 leaves) stem means were different.
e.g. 10 branches Stem D, $\bar{L}$ = 2.35 mm. Stem G, $\bar{L}$ = 2.72 mm.

It was apparent that if more than one stem were to be included in the sample, the range of leaf length would be greater and as it would include the variation due to branches of a single stem, it should be possible to reduce the number of branches per stem.

A further five stems were selected, and 2 leaves from each of 15 random branches measured. Means for 1 to 10 stems at three levels (5, 10 or 15 branches per stem) are given in Table 4. At all three levels, little variation occurred after five stems were included, all means between 5 and 10 stems falling within the limits 2.45 to 2.6 mm.

Thus the final sample size was fixed as 5 stems, 5 branches per stem, 2 leaves per branch about M_L. As a check on this, the means for 1 to 10 randomly selected branches for five stems were plotted against number of branches. Fig. 3 shows that the range of variation beyond the 5 branch level did not exceed 0.1 mm., and thus the sample is adequate.

The evolution of this technique has been described in detail because of the importance of using a standardised method in investigations of this sort. Although it was worked out on S. cuspidatum, it was later found to be useful for investigating S. pulchrum and S. recurvum. In these species it was possible to reduce the sample size because of the smaller variability in length shown by the leaves, but in almost all cases, the minimum number of stems examined was 5, and always two leaves were selected from M_L. Actually in some investigations of S. cuspidatum the number of branches per stem was reduced to two or one, partly because of the large number of specimens to be examined in a short time, but also because in comparisons between samples, no advantage is attached to taking large samples when small samples show no significant differences.

Consideration of the use of this technique for the investigation of S. cuspidatum will be deferred until the relationship of this species with S. recurvum is examined in Chapter 6. The method used for assessing the value of qualitative characters in this species complex was first used in an investigation of S. recurvum and S. pulchrum, and so the next Chapter must deal with the relationship of these two last mentioned species.

CHAPTER 4

The relationship between S.recurvum and S.pulchrum

(1) Systematics

The first mention of S.recurvum var. pulchrum seems to have been made by Braithwaite (1880, p.81). This author gives Lindberg as authority for var. pulchrum but does not refer to the place or date of Lindberg's original description. Braithwaite does, however, give a reference under S.recurvum P.Beauv. to a paper of Lindberg's published in 1862 in which the present author has failed to find any reference to S.recurvum var. pulchrum. Until a detailed investigation of all Lindberg's publications has been made it must be assumed that Lindberg described var. pulchrum to Braithwaite in correspondence, and that the latter was thus the first to publish a description of this variety.

Most authors since Warnstorf (1900) have followed the latter in according specific rank to the variety pulchrum. Thus Andrews (1913 a), Sherrin (1927) and more recently Gams (1948) have distinguished the two species S.recurvum P. Beauv. and S.pulchrum (Lindb.) Warnst. The writer suggests that until Lindberg's original description is discovered, this should be amended to S.pulchrum (Lindb. ex Braithw.) Warnst. Dixon differed from the authors mentioned above in that he maintained S.pulchrum as a variety

of S. intermedium Hoffm. even in the third edition of his handbook (1924), as in the first edition, which, of course, preceded Warnstorf's major Work (1911).

A comparative survey has been made of the characters used by different authors in the separation of these taxa. As slight differences of phraseology or emphasis can alter the meaning of diagnostic descriptions, it was decided to set out fully the results of this survey as tabulation would lead to loss of accuracy though generalisation.

Warnstorf (1911, p.180) separates the species in the key on one character, thus (translated):-

1. Hyaline cells on the inner surface of the branch leaves coalescing for some distance along adjacent walls . . . . .

   S. pulchrum (and S. torreyanum)

2. Hyaline cells on the inner surface of the branch leaves not coalescing along adjacent walls .... . .

   S. recurvum (and S. riparioides)

Both species are described as having the chlorophyllous cells superficially enclosed on the inner side of the lower half of the leaf.

The descriptions of the two species by Warnstorf are closely followed by Sherrin (1927), who, however, uses slightly different characters:-

1. "Chlorophyllose cells half the height of the hyaline cells and completely enclosed on the upper surface of the branch

leaf; leaves 5-ranked",

and in the description,

"hyaline cells on the upper surface of the leaf coalescing for some distance along adjacent walls" . . . . S.pulchrum .

2. "Chlorophyllose cells nearly the same height as the hyaline cells and not so completely enclosed on the upper leaf surface; leaves not 5-ranked."

and in the description,

"on the upper surface of the leaf _ _ _ _ the hyaline cells - - - are not united for any distance" . . . . S.recurvum.

Warnstorf refers to the relative heights of hyaline and chlorophyllous cells in his description of S.pulchrum, but no mention is made of this feature in S.recurvum.

Andrews (1913 a) also uses the shape and degree of exposure of the chlorophyllous cells as the main diagnostic feature, but expresses the difference in this way:-

1. "Chlorophyll cells isosceles - triangular in section, the apex of the triangle reaching the inner surface of the leaf . . . . S.recurvum ".

2. "Chlorophyll cells equilateral-triangular in section, the apex of the triangle not reaching the inner surface of the leaf . . . . S.pulchrum".

In the recent key of Proctor (1955), a more precise definition has been obtained by combination of Andrews' and Sherrin's descriptions, but some confusion still exists.
(In the extracts quoted below, the lines within brackets are taken from Proctor's original manuscript of his published key).

Thus "green cells equilateral-triangular in section, completely enclosed on the concave side by the hyaline cells (which are partly fused with each other)" indicates S. pulchrum, while "green cells isosceles-triangular in section, just enclosed on the concave side of the leaf (by the hyaline cells which meet but do not fuse)" is diagnostic of S. recurvum. The present writer suggests that it is subjective if not impossible to distinguish between "just enclosed" and "completely enclosed" cells, and to decide when cells which "meet" become "fused".

Upon consideration of the diagnoses of these four authors, a further source of ambiguity becomes apparent. Proctor and Sherrin imply that the fusion of adjacent hyaline cell-walls is in a plane at right angles to the leaf surface, i.e. as seen in transverse section. Warnstorf writes only of the surface of the leaf, while Andrews does not mention the fusion directly, but refers to the chlorophyllous cell reaching the inner surface or not, i.e. again in sectional view.

Sectional and surface views of various relative positions of hyaline and chlorophyllous cells are shown diagrammatically in Fig. 4. Separation of the two species on the basis of this character will vary according to whether leaves are examined in surface or sectional view. The following table shows the classification of the examples using the keys outlined above.

	S. pulchrum	S. recurvum
Warnstorf	c (e, f, g)	a, b, (d, e)
Sherrin	g	d, e, f
Andrews	f, g	d, e, f
Proctor	f, g	d, e, f

The final diagnosis would of course rest on a combination of characters, but it is obvious that such ambiguity must have led to confusion and uncertainty in identification, and therefore an investigation of the variability and value of these characters was imperative.

Gams (1948), whose work is in the form of a detailed key, does not mention the chlorophyllous cells of these species, but separates them in this way (translated):-

1. Branch leaves spirally arranged. Stem leaves triangular and mostly without fibrils . . .. S. recurvum.
2. Branch leaves in five straight rows. Stem leaves lingulate mostly with fibrils . . . . S. pulchrum.

Now Warnstorf and Andrews mention the five-ranked branch leaves of S. pulchrum, but they both describe the stem leaves of this species as being triangular and usually without fibrils. Fibrillose, lingulate to triangular stem leaves are in fact more characteristic of S. balticum, which is next to S. pulchrum in Gams' 1948 key (and incidentally, in Andrews') and is separated from S. pulchrum by Gams on the basis of the branch leaves being smaller, spirally arranged and secund. In any case, the disagreement suggests that there is uncertainty as to the range of variability of this character, and hence its diagnostic value is suspect.

In his 1957 key, Gams describes both taxa as having triangular, non-fibrillose stem leaves (except S. recurvum ssp. mucronatum Russ.) and separates them as follows (translated):-

1. Branches with 5-ranked leaves. Branch leaves broad lanceolate chlorophyll cells triangular, not reaching the inner surface. Stem brown with 2-4 layered cortex . . . . . S. pulchrum.
2. Branches with spiral leaves. Branch leaves narrow lanceolate. Stem clear with or without partly differentiated cortex . . . . . S. recurvum.

Proctor mentions the shape of branch leaves as another diagnostic feature. In S. pulchrum these are broadly ovate-lanceolate with an abruptly-pointed apex, and in S. recurvum they are narrowly ovate-lanceolate tapering gradually towards the apex. This character,

which is also mentioned by Warnstorf and Andrews, seems to be useful. The abruptly mucronate apex shown by branch leaves in S.pulchrum is also present in the stem leaves, this latter feature, together with the presence of fibrils, being used by Braithwaite (1880) and Dixon (1924) as the main distinction between S.recurvum and its variety pulchrum

A few other characters are listed by Sherrin and Andrews as peculiar to one or the other species. For instance, stems of S.pulchrum are brown, not pale as in S.recurvum, and although cortical cells in both species are small and fairly thick-walled, only in the former are they usually quite clearly differentiated from the underlying cells. Whole plants of S.pulchrum are said to be more often brown in colour than S.recurvum . Branch leaves of both species are undulate when dry, though S.recurvum shows leaves with recurved or spreading, rather than imbricate, tips. The border of the branch leaves is 4-6 cells wide in S.pulchrum and 2-4 in S.recurvum . Retort cells of branches of S.pulchrum have more "conspicuous" necks than in the other species.

Statements of Sherrin and Andrews on the distribution of pores on the leaves of spreading branches can be summarised in a table.

Table 5. Distribution of pores in hyaline cells of branch leaves of S.recurvum and S.pulchrum, as given by Sherrin and Andrews

		Inner surface of leaf			Outer surface of leaf		
		Ends of cells	Sides	Angles	Ends	Sides	Angles
Sherrin	S.recurvum	+ or -	-	+ or -	+ (u)	+	+ (u)
Andrews	S.recurvum	-	+	+	+	+ (u)	+ (u)
Sherrin	S.pulchrum	-	-	+ (u)	+	+ (u)	+ (u)
Andrews	S.pulchrum	-	-	+	-	+ (u)	+ (u)

+ (u) means present in cells in upper part of leaf.

Proctor simply states that for both species there are numerous large unringed pores on the concave side in cell corners close to the margins. It is apparent that any differences in number or distribution of pores are slight, and thus pore structure is almost valueless as a distinguishing feature in this complex. In any case, the number of pores per cell, and the position of porose cells in the leaf varies within a single plant, and if such small differences are to be used diagnostically, there would have to be very exact definition of leaf areas to be compared, and the evolution of a standardised sampling technique would be very difficult.

Having obtained a list of possible diagnostic features for these taxa, it was intended to find out the range of variability of each and hence to redefine the limits within which they could be used to define a particular taxon. A good idea of the range of any character can be gained from the examination of herbarium specimens, which, though they do not constitute a random sample, at least include specimens from different areas, and from different collectors, who presumably did not select samples showing one character rather than another. After

determining which characters remained constant throughout a species, it would be necessary to test their variability by cultivating samples under a range of conditions.

From an examination of several specimens from British localities from the herbarium of professor P.W. Richards, it was seen apparent that the two species are very closely related. In particular, the degree of exposure of the chlorophylleus cells seemed to be a very uncertain character, as many specimens showed a range of conditions in a single leaf section (Fig.5). Shape of branch leaves was also unsatisfactory, as all specimens seemed to have more or less tapering leaves, and similarly it was difficult to decide whether the stem cortex was well or poorly differentiated especially as this feature often varied within a single stem section. In fact, the majority of these specimens which had been determined by such authorities as W. R. Sherrin A. Thompson, E. M. Lobley and U.K. Duncan, could most satisfactorily be placed in a single taxon which would exhibit a wide range of continuous variation in most of its characters.

A specimen of S.pulchrum obtained by M.C.F. Proctor from the regeneration complex of Tregaron bog, (Godwin and Conway, 1939) seemed on superficial examination to agree more closely with the published descriptions of this species than any of the previously examined gatherings. From illustrations in Warnstorf's work (1911), the difference in branch leaf shape in the two species appears to be very well marked. As there was a possibility that leaf shape could be expressed quantitatively, it was decided to investigate this feature more fully.

(ii) The quantitative expression of leaf shape

A mature divergent branch was selected from the Tregaron material, all the leaves were dissected from it in order, and the resultant leaf spectrum was then compared with a similar spectrum prepared from a sample of S.recurvum from Sanford, Florida (det. A. LeRoy Andrews) ex Herb. P.W. Richards. The ranges of leaf length and ranges of width at the widest point seemed to coincide, but there was a distinct difference in shape, which seemed to result from the gradual tapering of S.recurvum leaves from a point about one third the length from the base, while S.pulchrum leaves were more oval. (Fig. 6).

To find the best method of expressing this shape difference quantitatively 38 gatherings identified as S.pulchrum or S.recurvum were examined. Most of these were British specimens, from the herbaria of Professor Richards and the University College of North Wales. Two gatherings from Tregaron bog were included. A quick preliminary survey was made by selecting one branch from each specimen and removing the two leaves about the mid-point by length M_L (cf. S.cuspidatum sampling technique p.17). Although the sample was thus very small it was thought that a quantitative character which was to be of any taxonomic significance should show discontinuous variation even at this sample size, as presumably only two taxa were in question, and the same, if not a greater, population range is covered by taking small samples from a large number of specimens, rather than large samples from a few.

The following four measurements were made for each leaf:-

length (L)

maximum width (W) at height above base (h)

width (W_3) at one third the length from the apex.

The following percentages were calculated:-

$\frac{W}{L}$ 100 and $\frac{W_3}{L}$. 100 (mean for branch i.e. specimen)

If a histogram is constructed showing frequency of occurrence of mean values for these ratios, the distribution in both cases is discontinuous, although the discontinuity is more apparent for $\frac{W_3}{L}$ (Fig. 7).

Then from the original complete leaf spectra, ten leaves about M_L were measured and $\frac{W_3}{L}$. 100 Calculated for each leaf. Within each branch (two S.pulchrum X,Y, and one S.recurvum R,) the values for airs of leaves about M_L were summed and averaged and the final means from two to ten leaves compared (Table 6).

From these figures it appears that six leaves about M_L must be used in calculation of the mean. However by increasing the number of branches it was possible to reduce the number of leaves/branch to two (cf. S.cuspidatum) without altering the final mean (Table 7). Thus for one stem (Y), mean values for $\frac{W_3}{L}$. 100 were as follows:-

		%
5 branches per stem	(2 l./br.	31.5
	(4 l./br.	31.9
	(6 l./br.	31.7

It was seen from inspection of values for stems X and Y that variation between stems of a tuft was greater than between leaves of a single stem, so the final size of sample was fixed at 2 leaves per branch, 5 branches per stem, 5 stems (50 leaves). (The advisability of taking five stems was confirmed on examining the samples, some of which showed great variability between stems).

The next stage in the separation of the two taxa involved the examination of all available specimens using this sampling technique. All specimens determined as S.pulchrum were sampled (total 42) together with 19 specimens of S.recurvum including some samples of each named "variety". For most specimens, a total of 50 leaves was measured, but as most of the S.pulchrum specimens were on loan, and some of them consisted of only two or three stems, the sample size in these was reduced to 40, 30, 20 or even 10 leaves.

In three specimens, random selection of branches led to the inclusion of some antheridial branches. Leaf spectra of such branches show that the shape of antheridial leaves differs from non-antheridial leaves in such a way that the ratio $\frac{W_3}{L_4}$ is increased (Fig. 8). Antheridial branches were therefore neglected in calculating final sample means, but means including these branches are given below for comparison.

Table 8. Comparison of means of $\frac{W_3}{L} \cdot 100$ in three specimens of S.recurvum with and without the inclusion of antheridial leaves

Sample No.	No. of leaves	Range of $\frac{L}{W_3}$	Mean of $\frac{W_3}{L} \cdot 100$ %
12 ♂	50	2.4 - 6.0	26.7
12 non ♂	34	3.1 - 6.0	24.4
13 ♂	50	3.4 - 6.5	21.6
13 non ♂	46	3.4 - 6.5	21.3
56 ♂	50	2.4 - 5.0	29.8
56 non ♂	28	3.4 - 5.0	25.6

The distributions of mean values for $\frac{W_3}{L} \cdot 100$ are given separately for the two taxa in Fig. 9. The distribution for S.pulchrum is discontinuous, peaks occurring at roughly 25% and 35%, whereas S.recurvum shows continuous distribution between 15% and 25% with a peak at 24%. When the data for the two taxa are combined, there are still two peaks, at 24% and 35%.

This suggests that specimens of S.pulchrum with a mean below 27% (afterwards referred to as "false S.pulchrum") fall naturally into the S. recurvum group, leaving a small group with mean above 30% as S.pulchrum. There are two samples with means of 28% - 29%, i.e. falling between the two groups. As one was labelled S.pulchrum and one S.recurvum, and only S.pulchrum has been found to be heterogeneous, both these intermediates were included in the S.recurvum group, as it is more likely that both should belong here rather than both belong to S.pulchrum sens. strict.

This somewhat arbitrary division is inevitable when only one character is considered, but for the moment, all samples were placed in one of two groups.

			Mean of $\frac{W_3}{L} \cdot 100$ %
Group A	S.pulchrum		
	17 specimens		35.1
Group B	S.recurvum	without 2 intermediates (42 specimens)	21.9
	19 specimens		
plus	"false S.pulchrum"	with intermediates (44 specimens)	22.1
	25 specimens		

An analysis of variance was done on the data, which was first converted to the ratio $\frac{L}{W_3}$ for ease of calculation.

	Sum of Squares	Degrees of freedom	Mean square
Groups A & B	34.48	1	34.48
Samples	17.04	59	0.2889
Total	51.52	60	

The result shown above indicates that the greatest variation is due to differences between the groups, variance due to differences within groups i.e. between samples in a group, only forming a small part of the total variance. This also suggests that the two groups are distinct from each other while being individually relatively homogeneous.

To obtain further evidence on this point, the variances of the original three groups of samples - S.pulchrum, "false S.pulchrum" and S.recurvum -

were worked out separately. Then for each pair of groups, a t test was carried out to determine whether the difference between means was significant. Owing to the fact that a t test is founded on the null hypothesis, a non-significant result does not necessarily mean that the groups compared belong to the same population, although of course they may do so.

The same test was also applied to the two groups A and B, the latter formed by pooling the original data from "false S.pulchrum" and S.recurvum. The results are shown below.

Table 9. Probabilities showing significant differences of means of $L/W^{\frac{2}{3}}$ by t test

Groups	Difference of Means	Probability
1. S.pulchrum and "false S.pulchrum"	2.85 - 4.32 = 1.47	< 0.001
2. S.pulchrum and S.recurvum	2.85 - 4.79 = 1.94	< 0.001
3. S.recurvum and "false S.pulchrum"	4.32 - 4.79 = 0.47	0.02 - 0.05
4. Groups A & B	4.85 - 4.52 = 1.67	0.001

The *t*-test is a very sensitive method of indicating real differences between means and therefore it is hardly surprising that the small difference between means of "false S.pulchrum" and S.recurvum should be significant, but as the level of probability for this comparison is so much higher than for the other three: 0.02 compared with 0.001: it was considered to be nonsignificant. Thus the final assessment of the position is that S.pulchrum is a group distinct both from "false S.pulchrum" and from S.recurvum; but these last two may or may not belong to the same population.

Further evidence for this hypothesis is furnished by calculating the population ranges of the three groups.

Now for a normal distribution, $t = \frac{(\bar{x} - x)}{s}$, which is any deviation expressed in units of the standard deviation (whose value depends numerically on the units of the original data). From a table of distribution of *t*, knowing the number of observations used in calculating S and hence the number of degrees of freedom, it is possible to find the probability of occurrence of a deviation of any size expressed in terms of S i.e. 1S, 2S, etc. For the three groups here considered, there is a 1 in 20 chance (5% level of p) of getting a variate (sample mean) with a deviation greater than 2.1S, and a 1 in 100 chance (1% level of p) of getting a variate with deviation greater than 2.9S.

(Value of *t* for 16, 18 or 24 D.F. is about the same at 0.05 and at 0.01 level of p).

Thus 95% of the population in each group will lie within the limits of mean ± 2.1S. However, as the mean of each group is derived from only a single set of samples, the standard error of the mean must also be taken into consideration. As before, true mean of population has only a 1 in 100 chance of lying without the limits (calculated) mean ± 2.9 S.E.

The calculated ranges for the three groups are given in Table 10 and are shown diagrammatically in Fig. 10. When maximum ranges are compared (Fig. 10A) (mean ± 3 S.E. ± 3S) they are seen to overlap considerably. However, it would have been most surprising if they did not, as the taxa would then have been so distinct as never to have been in question. From the start of this investigation it has been obvious that the taxa concerned are very closely related and the purpose of this detailed study has been to determine how far the particular character of leaf shape can be used diagnostically. It was never suggested that this feature alone should be used in placing a specimen in a particular group, any more than any other single criterion is sufficient for identification in such a complex where continuous rather than discontinuous variation is the rule. Bearing in mind these two principles, which are fundamental in this type of work, it would be premature to discard this particular feature because the maximum population ranges overlap, as was done by Redfearn (1956) in his work on leaf size and shape in *Plagiothecium micans*.

On further examination of Fig. 10 (A) and (B) the latter of which shows ranges of 95% of the populations, it is obvious that the range of "false S.pulchrum" falls completely within that of S.recurvum. The ranges of their means also overlap whereas the range of mean in S.pulchrum lies well outside those of the other two groups. Thus there is sufficient justification for the combination of these two groups as before to form Group B, for which the population range is given in Fig. 10 (C), and as the 2 S level (95%) is considered to give a sufficiently large range for the present purpose, so the range of means can be reduced to the 2 S.E level (Fig. 10 (D)).

Now for Group A, only one variate out of 40 will fall beyond the 2 S point which lies in the Group B range, so that for practical purposes, all samples with means greater than this value (3.46) can be considered to belong to Group B.

e.g. Sample with mean 3.65 has 1 in 40 chance of belonging to Group A

and 1 in 7 " " " " Group B

Thus samples with a mean above 3.46 fall into Group B, and similarly, those with a mean below 3.14 fall into Group A, while the intermediates are of doubtful affinity. It will be noted that two samples originally placed in Group A (actually the Tregaron samples) have means of 3.2 (Fig. 9. $\frac{W}{L}_{3.100} = 31 - 32\%$) that is, they lie in

the overlapping parts of the ranges, but as 3.2 is much nearer to 3.14 than to 3.46, it is highly probable that these samples have been correctly placed.

Further evidence on the advisability of separating the samples into these two groups was obtained by considering the remaining diagnostic characters.

(iii) An assessment of the value of qualitative characters.

The best method of obtaining an objective description of a particular character, thus enabling one to set definite limits within which that character is diagnostic of a particular taxon, is to use quantitative data, as was attempted in the last section. However, this is a laborious task, necessitating in each case the determination of a suitable method of sampling besides subsequent collection of data. In addition to this disadvantage, many characters, such as stem colour, undulation of branch leaves, and degree of differentiation of the stem cortex vary in a qualitative way and are unsuited to quantitative definition.

Consequently an objective method was sought whereby the diagnostic value of all characters hitherto used in separating these two taxa could be assessed. The method adopted was that used by Greig-Smith (1954) in work on Lejeunea species and is based on the assumption that a particular set of characters typifies a particular taxon. Within that taxon, every specimen may be expected to show a majority of these characters, but not all of them will be present in every specimen. The association of features in specimens within the taxon will, however, be random. Thus for any group of specimens, expected numbers of joint occurrences of pairs of characters can be calculated and compared with observed numbers. Significant deviation of observed from expected

values, i.e. positive or negative association of characters, indicates heterogeneity in the sample and implies the presence of more than one taxon.

A list was made of all the characters mentioned in published keys and systematic descriptions as useful for distinguishing S. recurvum from S. pulchrum. All available specimens of S. pulchrum and some of each named variety of S. recurvum (a total of 75, a few of which were from non-British localities) were then scored for each character. This first scoring was made as full as possible in that characters were not just marked "present" or "absent". Indeed in most cases this would have been impossible as great variation occurred between the extremes even within a single stem, and for a character such as lateral fusion of hyaline cells on the adaxial side of branch leaves, all conditions were often found in a single leaf (Fig. 11).

To cover these contingencies, and also to lead to a uniform standard of scoring over a period of several weeks, the following subdivisions were adopted:-

+	character shown by all or nearly all sample	
±	"	" more or less by most of sample.
(+)	"	" by some stems or parts of stems.
((+))	"	" occasionally in sample.
-	"	" very rarely or not at all.

Occasionally ($\overset{+}{-}$) was used as intermediate between + and $\overset{+}{-}$ and $\overset{(+)}{-}$ between (+) and ((+)).

Having assembled all the information in this form it was necessary to select the characters which showed a range of variability, and then to express each character in two alternative forms. For this purpose, $\overset{+}{-}$ and ($\overset{+}{-}$) were included with + , and (+), ((+)), and $\overset{(+)}{-}$ with - , for most characters, except where the description of the alternative expressions implies otherwise. A list of the original characters scored is given below, together with comments on the standardised technique of sampling specimens for examination.

1.	Branch leaves oval in shape	Determined by observation of two or three dry whole stems of the specimen.
2.	" " tapering	
3.	" " undulate	
4.	" " with recurved tips	
5.	" " with mucronate tips	
6.	Pendent branches covering stem	Observation of two or three soaked whole stems
7.	Branch fascicles distant or near together	
8.	Branch leaves in five distinct ranks	
9.	Stem brown (red), yellow or green	
10.	Branches brown (red) or pale	
11.	Stem leaves fibrillose	4 or 5 leaves selected at random from two stems and mounted in water under a cover glass.
12.	" " acute	
13.	" " mucronate	
14.	" " obtuse	

15. Branch leaves (flattened under cover slip) inrolled at apex or base or both	Branch leaves sampled for measurement observed for these characters. In specimens not sampled in this way, about five leaves selected at random from about the middle of horizontal branches.
16. Branch leaves inrolled all round margin	
17. Width of border of branch leaves (number of hyaline cells)	
18. Chlorophyllous cells of branch leaves triangular or trapezoid	Sections cut from middle of a branch leaf from M_L with razor blade under binocular microscope.
19. Chlorophyllous cells exposed on adaxial surface of branch leaf	From surface views of middle part of leaf.
20. Hyaline cells fused laterally on adaxial surface of branch leaf	
21. Stem cortex differentiated from inner cells	Section of stem a few cms. below coma.
22. Necks of retort cells of branches evident	Surface view of branch.

It was decided to omit pore structure from this list of characters as it does not seem to differ much in the two taxa. After analysis and final separation of the specimens, it would be possible to examine pore structure within the new taxa and use any differences as confirmatory criteria. Other arguments for omitting it now are that the listed features can all be examined on dry or soaked material, while observation of pore structure necessitates careful staining and this character could not be scored as "present" or "absent". Of these twenty-two characters, three were omitted from the final scoring. Two of these, position of pendent branches, and shape of chlorophyllous cells, showed the same expression in all specimens, and it was found impossible to score objectively the size of the necks of the retort cells.

The final characters are listed here:-

A. Branch leaves oval + or tapering -

B. " " undulate + or not -

C. " " recurved tips or not

D. " " mucronate or not

E. " " 5 - ranked when wet or not

F. Stem leaves fibrillose or not

G. " " acute + or obtuse -

H. " " mucronate or not

I. Branch leaves ever inrolled all round + or never -
i.e. + includes (+)

J. Branch leaf border more than 4 cells + or less -

K. Most hyaline cells fused adaxially + or most chlorophyllous cells exposed -

L. Stem brown + or otherwise -

M. Stem cortex well differentiated or not

N. Fascicles close together or not

O. Branches ever brown + or pale -

Having obtained a table showing positive or negative expressions of these fifteen characters for the 75 specimens, the observed number of joint occurrences of each pair of characters was determined. The difference between observed number and random expectation was tested for significance by calculating a χ^2 corrected for continuity. In many cases, one of the four expected values for a pair of characters

was less than five, so all the probabilities were taken from Fisher & Yates (1943, Table VIII). It should be noted here that on a random basis, a certain number of comparisons is expected to show significance. Thus out of a total of 105 comperisons tested, one may be expected to be significant at the 0.01 level of probability, and 5 to be significant at 0.05 level of p.

Significant correlations between characters in the first analysis are given in Table 11.

Thus ++ or -- indicates that the probability is less than 1 in 100 of the occurrence by chance of an observed value with at least that deviation from the expected value.

The large number of correlations indicates the presence of more than one taxon. All characters except those describing shape of stem leaf (G & H) show more than eight correlations at the lower level of probability. The fact that undulate leaves is positively correlated with recurved leaves, while these two characters show only negative correlations with other characters (which are positively correlated with each other), suggests that undulate recurved leaves together with the alternative (negative) expressions of the other characters are typical of one taxon. The other taxon or taxa, would then be characterised by non-undulate non-recurved leaves plus the positive expressions of the remaining characters. This suggestion follows superficial examination of the results, which must now be assessed in a more objective manner.

The character of oval branch leaves correlates with twelve other characters at the higher significance level. Thus A^+ is correlated with B^- C^- (D E F I J K L M N O) +. Each of the 75 specimens was then given one point for each of these features present in it - a maximum of 13.

The frequency of occurrence of numbers of characters is shown below:-

number of characters out of 13	0	1	2	3	4	5	6	7	8	9	10	11	12	13
number of specimens	7	5	13	11	12	4	5	2	-	-	-	1	5	10

The discontinuity is not surprising when the large number of correlations in the first analysis is considered, and these specimens with 11 or more of the 13 characters were removed as Group X. This Group X was tested for homogeneity by determining significant associations as before. In actual fact, this proved impracticable as 12 of the 15 characters were present in all, or all but one of the specimens, and it is impossible to test for association with so high an occurrence of one of the alternative expressions of a character.

Thus Group X was considered to be homogeneous, and incidently, very well defined.

The remaining 59 specimens were then analysed and showed eight correlations (Table 12, 2nd Analysis). The only correlation significant at $p < 0.05$ was a positive one between acute and mucronate stem leaves, mucronate leaves only occurring once when the leaves were obtuse. It would appear that these characters are virtually mutually exclusive, as they only occur together when a leaf with a broad apex has a point.

Only four of these cases occurred in the first analysis, three of them being removed in Group X. Hence on morphological grounds acute and mucronate leaves may be considered as a single character, and so the positive correlation shown between these features in the second analysis is not valid.

There remain seven correlations significant at 0.05 level of probability. As the characters oval branch leaves and fibrillose stem leaves occurred in only one and three specimens respectively, association of these or their alternatives could not be tested for within the group and so the total number of comparisons made between 13 characters was 78; (12 + 11 + ------1). On a random basis, 3.9 of these are expected to be significant at 0.05 level of p, which is just more than half the number which actually were significant. The group was therefore considered to be heterogeneous although it was obvious that the greatest element of heterogeneity had been removed with Group X.

There are two groups of associations with no common feature:-

(i) Recurved leaves correlates with non-mucronate branch leaves and non-mucronate stem leaves.

(ii) Fascicles near together correlates with five-ranked branch leaves hyaline cells fused adaxially and cortex well-differentiated.

Now as the first group of associations concerns only three characters, as compared with four in the second group, the next assessment of specimens was carried out using the latter. Here the maximum score of characters was only four, and the specimens showing three or four were extracted as Group Y.

Number of characters out of 4	0	1	2	3	4
Number of specimens Total 59	16	17	11	9	6

There is no obvious discontinuity as before but it should be noted that frequency is only a rough method of determining the line of separation into two classes, as the presence of a small number of samples forming a class with a peak at say three characters, may be hidden by the "tail" of a larger class with a peak at, say, one character.

For example, the distribution may actually be as follows:-

Characters.	0	1	2	3	4
Frequency Class 1.	16	17	7	1	0
Class 2.	0	0	4	8	6

with totals as before. Admittedly in a case like this, where the ranges overlap, the eventual separation into two classes would not be as satisfactory as it would if there were obvious discontinuity in the first place.

For the moment, then, an arbitrary separation was made into Group Y, consisting of 15 samples, and a remainder of 44 samples which were subjected to a third analysis. No associations occurred in this remainder, which was thus considered as a homogeneous Group Z, and analysis of Group Y showed that it also was homogeneous. Confirmation of the distinctiveness of the three groups was obtained by taking each

pair of groups in turn, and analysing the combined data. For groups X and Y, and X and Z, oval leaves correlated with several other characters, thus indicating heterogeneity. Groups Y and Z had already been tested in the second analysis.

The presence of three groups has thus been established but it is possible that the separation of specimens into these groups is incorrect due to the arbitrary line of division based on number of correlated characters shown by an individual gathering. As implied above, there is little chance of a specimen properly belonging to group X or not belonging to group X (but to either Y or Z) being wrongly placed with respect to Group X, because of the extremely good definition shown by this group. Confusion between Groups Y and Z is to be expected as they are not so distinct from one another.

As only four characters were used in the separation of Groups Y and Z, a method is required of showing which of the other features are diagnostic of either group. As each group consists mainly of one taxon, the distribution of characters within the group indicates the diagnostic features of that taxon. Thus if a significant majority of specimens allotted to Group X has oval branch leaves, this character may be considered typical of Group X.

The distribution of characters in the three groups is shown in Table 13 a (1st Assessment). Significant departure from a 1 : 1 ratio of the alternative expressions of a character was calculated from the binomial expansion $(\frac{1}{2} + \frac{1}{2})^n$ where n = number of samples in group.

In most cases, the 5% deviation (corrected for continuity) was calculated from the Standard Deviation ($\sqrt{n\ p\ q} = \sqrt{\frac{n}{4}}$) and hence the limits outside which deviations were significant at 0.05 level of probability were obtained. In the case of Group Y, which had the smallest number of getherings, the limit so determined was checked by expansion of the binomial to the 0.05 level of probability. In the table, non-significant deviations from 1 : 1 ratio are indicated by red type. All characters except G^{+} (acute stem leaves) are of value in the diagnosis of at least one group, although where alternative expressions of a character occur with equal frequency e.g. (D) leaves five ranked or not in Groups Y and Z, the absence of five ranked leaves would indicate Y and Z, but their presence would not indicate Group X. Obviously some summation of characters is necessary for correct allocation of a specimen to a particular group. A simple method of assessing the merit of a sample with respect to membership of each group is by addition of characters. In this way, one point is given for a character present in the sample if in the 1st Assessment that character is typically present or indifferent. Similarly, if a character is typically absent in the 1st Assessment (i.e. negative expression of alternative) and is absent in the sample, a point is added. (Greig-Smith, p. 465). As mucronate stem leaves (H^{+}) have been shown to be morphologically associated with acute stem leaves (G^{+}),

character H was omitted from this next assessment together with G, which has no diagnostic value. The maximum possible score for a sample using this system is thus 13, and theoretically a sample should be assigned to the group for which it has the highest rating.

Consideration of the diagnostic values of the characters in the three groups shows however that this system of awarding points is not impartial, but biased in favour of Group Y, because in this group are four characters which are indifferent, which means that a point is added if the expression of the feature in the sample is positive or negative. Similarly, Group Z has two characters which show equal frequency of expression of alternatives and so both Group Y and Group Z have an advantage over Group X. A preliminary assessment of all samples was made by awarding one point for a feature characteristically present or indifferent as described in the last paragraph. All 16 samples belonging to Group X in the 1st assessment were reallotted to this group, and there were no samples with equal scores for X and Y or X and Z. This confirms the distinctiveness of Group X which remained unaltered in spite of the disadvantage mentioned above. However, Group Y now had three samples previously allotted to Group Z, while nine samples had an equal score for these groups.

It was evident that some way must be found of offsetting the bias due to indifferents. The 59 samples were reassessed for Groups Y and Z using only the six characters which distinguish these groups and awarding points as follows:-

Characters	B points	B expression	E		K		M		N		O	
Group Y	1	+	2	+	2	+	2	+	2	+	2	+
	2	-					1	-			1	-
Group Z	2	+	2	-	1	+	2	-	2	-	2	-
					2	-						

The result of this was that Group Y retained the three specimens transferred from Group Z, but eight of the nine which had equal scores for Groups Y and Z were reallocated to Group Z, while the ninth was still uncertain. Inspection of the original scoring for this specimen suggested that it belonged properly to Group Z. The distribution of characters in the groups is shown in Table 13 b, 2nd Assessment. No change in significance of characters has occurred and so this table can be considered to show the characteristic features of the three groups.

The differences and similarities of character expressions in the groups are summarised below, (excluding G & H).

Groups	Absolute differences	Absolute similarities	Similarities involving indifferents
X and Y	6	3	4
X and Z	11	0	2
Y and Z	2	6	5

Groups X and Z are well separated, and although Group Y is in some respects intermediate, it is obviously more closely related to Group Z. It will be remembered that after the second analysis, the separation of Group Y was based on only four correlations, at the lower significance level, and so it is rather doubtful whether Group Y should have taxonomic status.

At this stage it is very illuminating to draw up a table showing the distribution of characters as originally scored, that is, including all intermediate values between + and - (Table 14).

It is at once obvious that Group X specimens show a much smaller percentage of intermediate values than specimens of the other groups. In particular, the large numbers of samples scoring (+) for many characters in Groups Y and Z is noteworthy. Now as the difference between + and (+) is slight and somewhat subjective, Table 13c (third assessment) has been prepared showing the ddistribution of + and - characters with (+) included under + instead of under - . Any changes in the diagnostic value of the characters are indicated (J is excluded because it is quantitative, and I and O already included (+) and +).

Thus five ranked leaves (D) are no longer more suggestive of Group X, and fibrillose stem leaves (F) may now indicate Group Y as well as Group X, although their absence still suggests Y or X. Group X still retains four absolutely diagnostic features: oval branch leaves inrolled all round, with border 4 or more cells broad, and stem brown. It may be noted that brown branches with brown stems denote Group X, while brown branches alone indicate Group Y.

The main significance of moving the line dividing + from - is in relation to the distinction of Groups Y and Z. Thus undulate leaves now predominate in both Groups, and while non-5-ranked leaves, exposed chlorophyllous cells and undifferentiated cortex indicate Group Z, the alternative expressions of these characters have no diagnostic value at

all. Thus they are unsatisfactory for diagnosis of Group X also. This leaves only two characters for the distinction of Groups Y and Z

These are:-

(i) fascicles near in Group Y, distant in Group Z

(ii) branches brown or not in Y, branches not brown in Z,

which can hardly be considered sufficient for separation into taxa. Groups Y and Z then must come together under the name S.recurvum P. Beauv. while Group X is S.pulchrum (Lindb. ex Braithw.) Warnst.

There is a very close correspondence between these taxa as now defined, and those distinguished by leaf shape in the second part of this Chapter. Leaf shape was scored in the analyses just described as "leaves oval or tapering", as the actual measurements were done concurrently and subsequently so that some samples measured were not included in the character analyses.

Group X consisted entirely of specimens with L/W_3 ratio less than 3.2, that is, S.pulchrum (identical with Group A of last section).

Group Y (measured specimens) included:-
10 of "false S.pulchrum" mean 4.16, range 3.5 - 5.1
4 of S.recurvum mean 3.99 range 3.5 - 4.2

Group Z (measured specimens) included:-
15 of "false S.pulchrum" mean 4.48, range 3.9 - 5.05
15 of S.recurvum mean 5.01, range 4.2 - 6.4

Thus there is ample justification for combining Groups Y and Z under S.recurvum (Group B of last section).

The distribution of characters in Groups X and (Y + Z) are shown in Table 15, where (a) and (b) correspond respectively with the 2nd and 3rd Assessments of Table 13. It can be seen that mucronate branch leaves (D) and well-differentiated stem cortex (M) have no diagnostic value when the division between + and - is moved to include (+) with + (Table 15 (b)), while the characters of undulate, recurved branch leaves (B and C) have a decreased significance. Taking this into account, Table 16 overleaf, lists the characters shown by this method to be indicative of one or the other taxon. Only one character of diagnostic value, branches brown, seems to be constantly present in Group X, all other characters showing more or less variability.

The constancy of these characters in plants grown under different conditions is discussed in the next chapter.

It is convenient here to discuss the diagnostic value of the character of fusion of hyaline cells in the branch leaves. Because of the uncertain definition of this character, discussed on p. 26 of this thesis, it was decided to score for the analysis only lateral fusion as seen in surface view. From Tables 14 and 15 it is apparent that although the character as so defined is almost always present in specimens of S. pulchrum, it is also present to a greater or less extent in about half the S. recurvum specimens. Thus lateral fusion of the hyaline cells is of little use for the separation of these taxa. The possibility that fusion in a plane at right-angles to the leaf surface (vertical fusion) might be of diagnostic value was

Table 16. Characteristic features of S.pulchrum and S.recurvum

	S.pulchrum	S.recurvum
Shape of median leaves of divergent branches		
Length	<3.2	>3.5
Width at 1/3 distance from apex to base		
Branch leaves undulate	Sometimes	Almost always
" " recurved	Sometimes	Almost always
" " mucronate	Always	Often
" " 5 - ranked	Almost always	Often
Stem leaves fibrillose	Almost always	Occasionally
Branch leaves inrolled all round (at least one margin)	Almost always	Very occasionally one margin
Border 4 or more cells wide	Almost always	Very occasionally
Most hyaline cells fused laterally on adaxial surface of branch leaf	Always	Often
Stem brown	Almost always	Very occasionally
Stem cortex well-differentiated	Always	Often
Fascides close together	Almost always	Sometimes
Branches brown	Always	Occasionally

examined by cutting transverse sections through the middle of branch leaves of all the 75 specimens.

The results are given below:

	Total number of specimens	Number showing most cells fused in surface view	Number showing some cells fused in surface view	Number showing vertical fusion in section
S.pulchrum	16	16	-	16
S.recurvum	59	32	-	22
		-	17	10

It is interesting to note that of 9 specimens which were scored as showing no fusion at all, 2 showed vertical fusion when sectioned. This illustrates the extreme range of variation which can be shown by different leaves of the same sample. The results show that even vertical fusion of the hyaline cells is not limited to S.pulchrum and that the character, however defined, is of little value for distinguishing these taxa.

CHAPTER 5

Experimental cultivation

(i) General methods

(a) Cultivation

In the early stages of this work, attempts were made to raise plants from spores, but they were all unsuccessful. In any case, the rate of development from spores is slow and it was apparent that it would take far too long to produce by this method mature plants in numbers sufficient for experimental cultivation. Thus in all the experiments, which can be divided into laboratory cultures or field transplants, the original samples consisted of mature plants collected from natural habitats. Direct proof of the homogeneity of the samples was therefore impossible, but owing to the mode of growth of Sphagna it is possible to select clonal material with a fair amount of accuracy.

A single plant can give rise to independent growing points by apparently dichotomous branching of the main stem at the apex, or by the production of young shoots from old parts of the stem. A well-preserved plant may thus consist of several capitula, each terminating a branch of the original stem. Decay of the old parts of the axes eventually results in these capitula becoming completely separated, so that several new independent plants are produced. Thus it is almost certain that at least the central plants of an established tuft have

a common origin (but see discovery of S.amblyphyllum p. 160) Plants growing submerged in pools are usually more diffuse than tufted, but owing to the higher rate of growth in aquatic habitats it is generally possible to find stems showing four or five dichotomies so that common origin of capitula is again assured. Where this was not possible in submerged habitats, stems were taken from a small area to reduce the chance of their being of different origin.

The aim of all culture experiments was to compare the morphology and anatomy of plants grown under different conditions. Comparison with the original necessitated the preparation of a dried specimen of the freshly gathered material, as owing to rather rapid decay under laboratory conditions, it was usually impossible to compare 'new' growth with 'old' growth on the cultivated stems. For each set of experiments, sufficient material was gathered from the centre of a tuft to allow 5-10 stems to be dried, and 20 - 40 stems for each individual experiment. In order to measure rate of growth of samples, five stems were selected at random from the small experimental "tufts" and each was marked by tying coloured thread round the stem about 3 cm. below the coma. Length from top of coma to fascicle immediately below the thread was recorded together with number of fascicles between coma and thread. In this way two aspects of growth - elongation of axis and fascicle production - could be followed for five stems, giving mean values for each experiment. Skene (1915, p.80) used colour,

geotropic curvature, and increase in length as criteria of healthy growth.

Various methods for the cultivation of Sphagna are mentioned briefly in the literature. Skene (1915) grew plants in an unheated room in large conical flasks half-filled with distilled water or various mineral solutions. Bryan (1955) grew them in uncovered flat glass dishes, buried to the tops of the rims in wet cinders, adding distilled water occasionally and maintaining a high humidity. Paton and Goodman (1955) cultivated S. nemoreum in covered glass dishes. These authors studied factors affecting rate of growth and production of anthocyanin, and noted that low light intensities and intermediate temperatures promoted growth. Bryan's experiments were carried out in a cool north-facing greenhouse. In the present work, the greenhouses were artificially shaded in summer but in spite of this, quite high temperatures were reached. This had no adverse effect on the Sphagna apart from an increase in the rate of growth. Plants grown in the laboratory received no direct sunlight and the temperature was usually about 20°C; in some experiments with constant overhead illumination, a water filter was used to maintain this temperature.

Most samples under laboratory or greenhouse conditions were grown in glass tanks 20 x 25 cm. section and 35 cm. deep. The tanks were half filled with tap water and the lower parts of the plants were immersed in this, leaving about 5 cm. exposed. This method was more

satisfactory than "planting" the samples in wet sand or peat. Tap water seemed to have no deleterious effect on these exposed plants as long as the tanks were covered with (transparent) lids to maintain a high humidity. If this was not done, excessive evaporation took place and mineral salts were deposited on the tips of branches. Each experimental tuft, with the five measured stems in the centre, where natural conditions of humidity and shading by adjacent plants were most closely reproduced, was placed in a semi-opaque polythene pot (9cm. deep, top diameter 7 cm., basal diameter 4 cm.) with the bottom cut out to allow the stems to project into the water. The pots were then suspended in the tanks by means of plastic-coated wire. It has been shown by Skene (1915) that small amounts of metallic ions have a harmful effect on Sphagna and thus ordinary wire or earthenware pots (which contain lime) would have been unsatisfactory. Waterproofed cardboard pots were used before plastic ones, but they became soft with continual immersion and also encouraged fungal growth. The water, which was kept at a constant level, was changed about once in three months as there was usually a small amount of algal growth in the tank (cf. Skene, p.86) and the exposed heads of the plants were sprayed with tap water about once a week. The plants were measured every month and replaced in the pot so that the heads were level with the top of the pot; if elongation was rapid, the tuft was pulled down in the pot between measurements to keep the comas at the same height above the water, and to prevent drying due to the more exposed conditions outside the pot.

Growing plants submerged in water in the laboratory presented considerable difficulties. Although tap water did not seem to harm plants with only their lower parts immersed, complete submersion of plants resulted in rapid loss of chlorophyll followed by death. This is curious, as water drawn by capillarity to the upper parts of exposed plants must have the same chemical constitution as that in which they are immersed. An attempt was made to grow plants in continually aerated water, and also in aerated, running water, but neither of these methods was successful. As S.recurvum usually grows with at least the cones exposed, seldom being completely submerged, perhaps the latter condition is fundamentally unsuitable for healthy growth of the species. During later experiments on the laboratory cultivation of S.cuspidatum, distilled water was found to be more suitable than tap water for growth when submerged, but even the use of distilled water did not lead to successful culture of S.recurvum. Most experimental tufts were placed in pots, but where only a few stems were available, they were enclosed in a collar of polythene which was then suspended as before, litre beakers being of a suitable size for these small samples.

All samples transplanted in the field were in pots which were sunk to the level of the surrounding vegetation. Here it did not matter if the stem grew quickly and projected out of the pot, as the surrounding plants maintained the necessary humidity. When pots were submerged in pools, they were weighted with small stones to keep

them immersed and also to maintain an upright position. String was tied across the top of the pot to keep the plants in, as disturbance of the water by sheep or storms could result in the stems floating free and becoming lost. The field pots were examined and stems measured once a month, except from November to April when weather conditions were unsuitable. Actually, little growth takes place in the winter, possibly because of poor light and short days, one particular experimental area in the valley of the Afon Llafar, near Bethesda, Caernarvonshire, being in permanent shadow during these months. The main factor reducing growth at this time however is temperature, most of the plants being frozen for long periods, the occasional warmer wet days being in comparison of negligible influence. Most experiments were replicated, at least in the field samples, as losses due to sheep or drought were high. In some cases, particularly in experiments with S.pulchrum, there was insufficient material to allow of more than one or two samples being set up in similar conditions.

Small samples of five stems were taken from the experimental pots at intervals after the first few months, the marked stems being left for further measurements.

(b) Examination of samples

Because of the peculiar growth form of Sphagnum plants, that is, the aggregation of young fascicles into the coma, a considerable time elapses after the start of an experiment before mature fascicles

produced under the new conditions are available. If a single comal tuft of the original specimen were found on dissection to consist of 20 fascicles in various stages of development, the first 20 fascicles to mature under the experimental conditions would have been differentiated under old conditions. Thus three stages of growth can be distinguished:-

(i) Old growth ---- differentiated and matured under old conditions.

(ii) 'Separated' growth --- differentiated under old conditions but matured i.e. separated from the coma, under new conditions.

(iii) New growth ---- differentiated and matured under new conditions.

In most cases, old growth was examined on the original specimen, or occasionally on the cultivated stems where these had not disintegrated at the base. Separated growth was sometimes examined where a change between old and new growth was shown.

In order to determine the limits of new growth, several comas of each of the original specimens were dissected and the number of differentiated fascicles counted. In most of the cultivated samples, monthly increase in fascicle number was recorded, and where the minimum increase in the five marked stems exceeded the mean number of fascicles in an original coma, the sample was considered to show

new growth. In some experiments, particularly those with S.pulchrum or compact forms of S.cuspidatum, it was impossible to count the fascicles without damaging the plants and so only length increase was recorded. When these tufts were sampled, fascicles were counted in five stems from the base of the coma downwards along a length equal to the minimum increase in length as recorded for the five marked stems. If the mean number of fascicles in the minimum length increment exceeded number of original comal fascicles, the sample must include some new growth.

Having decided which samples had some new fascicles and also the number of these, a detailed investigation was made of this new growth. It should be mentioned here that the method described above of counting comal fascicles is not valid for determination of stage of growth of stem leaves, as a number of these (about 20) are aggregated into a bud around the apical cell above the point where the last distinguishable branch fascicle occurs. However, only about 8 of these stem leaves are well differentiated, the upper ones being very young and small, so that by adding a further two to the number of comal fascicles, the position of "new" stem leaves on a cultivated stem can be determined with reasonable accuracy.

Samples of old and new growth were scored for the characters listed on p. 46 for the analysis, with the addition of branches falcately-curved or not, and coma large and compact or coma small. Branch length and number of leaves were noted, and branch and stem leaf

samples were also measured to see if leaf sizes and proportions remained constant under different conditions. Initially, a sample of 20 stem leaves (4 from each of 5 stems) was taken, together with a branch leaf sample consisting of 20 median and 20 "terminal" leaves (see p. 108) i.e. 2 branches from each of 5 stems. The median leaf sample, 20, was thus less than half the size recommended in the investigation of S. cuspidatum described in Chapter 3, but it was thought that larger samples could be taken later of those samples showing differences after cultivation. However, this was not possible because of lack of time, but as no difference was regarded as significant unless there was a marked change from old to new growth, larger samples would probably not have lessened the significance of the result.

(ii) Cultivation of S.pulchrum and S.recurvum

S.pulchrum was collected from Tregaron Bog, Cardiganshire in July 1955, and from Bowness Moss, Cumberland in April 1956. Some samples of each gathering were grown in the greenhouse and also under different field conditions. All the indoor cultures grew well, and so did the field transplants, except one amongst S.subsecundum which was dead after a year in which the mean increase in length was only 2 cm.. Two cultures which had been "planted" in wet sand in the greenhouse were dying after 6 months; one of these was transferred to a water tank but did not recover; the other was placed in a water tank with constant overhead illumination (from a 60 watt bulb 15 cm. from the comal tufts), and after 8 weeks several green shoots had been produced from the old stems. After another 4 months these shoots had the appearance of mature plants with comas about 1 cm. across, and they continued to grow normally. S.pulchrum was transplanted among S.subsecundum, S.papillosum, S.squarrosum and S.recurvum; samples of the latter from the transplant sites were put in pots in the field under the same conditions as the transplanted S.pulchrum, and further samples were cultivated under laboratory conditions.

In S.recurvum, plants grown indoors were usually more compact than those grown in the field, but this was not true of all S.pulchrum samples, as is shown in Plates 1, 2, 3, and also in Table 17, below.

Table 17. Rate of stem elongation and fascicle production in some cultivated samples of S.recurvum and S.pulchrum

Sample	Condition	Time Months	Increase in length cm.	Increase in fascicle number
(i) S.recurvum	Laboratory	12	14	64
R.IV	Field (Shaded)	12	15.8	45
(ii) S.pulchrum	Greenhouse	14	5.8	28
PII	Field (Shaded)	12	10.8	30
(iii) S.pulchrum	Laboratory	6	7.3	37
P II	Greenhouse	6	5.9	37
	Field (Exposed)	6	3.0	15

The results suggest that compactness is regulated by habitat, in this case by presence of direct sunlight, as the shaded samples (field and laboratory) elongate more rapidly than exposed samples and thus have more distant fascicles. Other exposed samples of S.pulchrum were observed to elongate very slowly - as little as 1 cm. per year - but the fascicles were very close together. This is important because of the conclusion from the character analysis that S.pulchrum and S.recurvum are characterised respectively by close and distant fascicles; it is now apparent that this character can be modified within a single plant by a change of habitat. The effect of shading on rate of elongation of other parts of the plant was shown by S.pulchrum ((iii), above) in which the spreading branches were 1.5 - 2.0 cm. long in the laboratory culture, as compared with 1.0 - 1.5 cm. in the original

specimen and the greenhouse culture, although the number of leaves per branch remained constant at about 100.

Another character which was altered in the shaded, rapidly elongating S.pulchrum specimens was colour. The original Tregaron and Bowness plants were a yellow-green colour with brownish comas, branch axes were red and stems were red to brown. The new growth was green in colour, and although even the comal branches were red, the top 2-3 cm. of stem was pale green. This became pigmented later on, but even the pale stem showed a well-differentiated cortex. This last character seemed to be constant in S.pulchrum specimens although also occurring quite often in S.recurvum, and it appeared to be unaffected by change of conditions.

Several characters which had been difficult to score in the analysis were found to be modified in the samples examined. Thus as shaded or immersed samples of S.pulchrum had longer branches than the compact forms, the branch leaves were not so closely set and thus were more able to spread. The five-ranked arrangement was often obscured because of this, and, particularly in the aquatic cultures, the leaves tended to be secund; this was noticed in herbarium specimens from aquatic habitats. S.recurvum plants also showed the five-ranked arrangement. The border in branch leaves of some indoor cultures of S.pulchrum was never more than 3 cells wide, although the original specimens had borders 3-5 cells wide. No significant changes were

detected in the following characters:-

stem leaves slightly fibrillose in S.pulchrum, occasionally fibrillose in S.recurvum,

branch leaves inrolled in S.pulchrum along at least one margin.

(a) Measurement data

One of the important results of this investigation was the discovery that all samples of S.recurvum cultivated artificially indoors gradually became smaller. This may be attributed to poor light or nutritional deficiency due to growing in tap water, but whatever the causes, there are two major implications.

These are:-

(i) comparisons between laboratory and field cultures are not really valid because of the gradual impoverishment of the former,

(ii) it is possible to alter the size of plants whilst these remain healthy and continue to grow.

The decrease in size was most noticeable in branch leaves, as stem leaves appear to be less affected by any environmental changes; data from such an indoor culture of S.recurvum are given in Table 18. It is apparent from these records that both length and width decrease so that the length/width proportion of median leaves and the difference between length of median and terminal leaves remain constant. Such marked changes were not recorded for S.pulchrum, but it is highly probable that they could be induced.

The proportion length/(width at 1/3 distance from apex to base) was also calculated for both S.pulchrum and S.recurvum. No marked changes of range were recorded, although mean values of this proportion varied as shown by the following figures for S.pulchrum (iii) (as Table 17, above).

Table 19. Values of $L/W_{\frac{1}{3}}$ for some cultures of S.pulchrum

(All sampled leaves 'new' except where stated)

Sample		Mean	Range
Original		3.13	2.7 - 3.5
Laboratory		3.23	2.7 - 3.8
Greenhouse	6 months	3.41	3.0 - 3.75
Field (Separated)		3.05	2.7 - 3.4
Field	14 months	3.3	2.6 - 3.8

Similar variation occurred for S.recurvum, giving, for example, a range of 3.6 - 4.6 in a field sample and 3.3 - 5.0 in a laboratory sample, each with a mean of 4.0. Thus a single sample may contain leaves from the ranges of both taxa as defined in Table 16, but the mean values of this proportion are still useful for indicating the affinities of a plant.

Stem leaves

No significant changes in size, shape or shape of apex were recorded in any of the experiments.

(b) Discussion

The experimental evidence for the distinctness of S.pulchrum and S.recurvum is not great, but these results do show however that certain characters cannot be relied upon as criteria for distinction of these

taxa. Thus colour of plant and of young stem, closeness of fascicles, spreading and undulation of leaves are affected by environment. In all the cultures of S.pulchrum however, even where this was growing amongst S.recurvum and resembled the latter in colour, size of coma, length and position of branches, it had a distinctly different appearance. The branches of S.pulchrum, especially in the coma, are always thicker and tend to be truncate rather than attenuate distally in contrast to S.recurvum. The author suggests that the thicker branches of S.pulchrum are due to the broader leaves, which thus are very important in diagnosis.

The transplanting of samples from Tregaron was followed by a very dry summer, and several samples died or were slow to become established, and again some samples from Bowness which were transplanted to a pool grew well for 12 months and then were lost before the first sample of new growth had been taken. This was very unfortunate, as changes in leaf length and proportion were expected to occur as a result of immersion (see result of immersed culture of S.recurvum, p.122) This would be important particularly with reference to the distinction of these species on the basis of leaf shape, as if length increased without a proportionate increase in width, S.pulchrum leaves would become more tapering and similar to those of S.recurvum. The examination of specimens from different natural habitats indicates however, that the high width/length ratio is maintained in aquatic specimens of S.pulchrum.

It was thought during the early stages of this work that S.recurvum and S.pulchrum might be ecologically if not taxonomically distinct, as their natural habitats seemed to be different. Thus Tregaron bog is a raised bog, with S.pulchrum an important member of the central hummock and hollow regeneration complex; S.recurvum is not found at all on the raised bog proper, being limited to the marginal lagg. Bowness Moss is a flat bog only about 30 ft. above sea level on the shores of the Solway Firth. A true cyclic regeneration complex does not exist here, but as at Tregaron, S.pulchrum is limited to small hummocks and pools (mixed with S.cuspidatum) in the central, slightly raised region of the bog. S.recurvum was not found here either, associated Sphagnum species being S.tenellum, S.papillosum and S.nemoreum.

It would appear from the foregoing that S.pulchrum prefers a habitat with little soligenous influence, as it is mentioned in literature as a typical component of the ombrogenous raised bogs of Ireland also; S.recurvum on the other hand is common in blanket bog, and slightly acid "poor fen". However, Osvald (1949) described an Irish raised bog at Edenberry in which a pool containing S.cuspidatum was bordered by S.pulchrum, this in turn being surrounded by S.apiculatum (S.recurvum var. mucronatum Warnst.); here is an example of the two species growing together and yet remaining distinct. (Is it an indication of the uncertainty of distinction between S.apiculatum

Lindb. and S. angus tifolium C. Jens. (S. parvifolium (Sendt.) Warnst.) (see Chapter 9) that Osvald, in his accompanying sketch, indicates that it is the latter which surrounds the S. pulchrum ?) Proctor (1955) gives poor fen as the typical habitat for both S. pulchrum and S. recurvum, and Rose (1951) describes them as occurring together in the low-lying southern valley-bogs. Although they there occupy slightly different habitats as regards abundance of water and its mineral content, the two species may grow close together. If this is so, their ecological ranges must overlap, and thus it seems doubtful whether the suggestion that they are ecotypes is tenable.

The present author has recently found both species growing in a small area of one bog, though not adjacent to one another. This particular bog, on the Silver Flows of Buchan, Galloway, is a different type again from either the low-lying coastal and valley bogs, or the inland raised bogs of moderate (c. 500 ft.) altitude, as it occupies a large area in a wide mountain valley at about 900 ft. The bog has a flat, or very slightly convex surface but cannot be truly ombrogenous owing to its receiving the drainage water from the surrounding hills; a river borders one side of the bog, but nothing corresponding to a lagg is formed at the foot of the mountain on the other margin. Pools are scattered over the whole surface, S. pulchrum (which is confined to a small area of the bog) growing either in these with S. cuspidatum and S. auriculatum, or in the surrounding flat, wet Sphagnum carpet with S. papillosum, S. tenellum,

S.nemoreum and S.plumulosum. The only well-formed hummocks occur in another part of the bog where S.pulchrum is absent; they consist of S.imbricatum, S.magellanicum, S.tenellum, S.plumulosum, or Rhacomitrium lanuginosum, and appear to be stable and not part of a dynamic regeneration cycle. S.recurvum was only found in one part of the Silver Flowe, in a large eroded peat hollow, where Juncus effusus had become established; curiously, a lax, non-hummock form of S.imbricatum occurred here also.

From these observations on natural occurrences of S.recurvum and S.pulchrum either growing in adjacent tufts or in adjacent areas of the same bog, and from the results of experimental cultures where they remained different under identical conditions one must conclude that taxonomic distinctness does exist. Whether the difference is sufficient to warrant a division into separate species (which could only be proved by genetical studies outside the scope of this thesis) or whether S.pulchrum is best reduced to a variety of S.recurvum is a debatable point, but I think both taxa should probably be accorded specific rank.

It remains to discuss briefly the reasons for past confusion of the species. Certain characters previously used diagnostically have been shown by this work to be of little use for identification because of their variability. Thus differentiation of the stem cortex, exposure of chlorophyllous cells, undulation and recurvature

of leaves were shown by examination of a large number of specimens not only to occur in both taxa, but to vary within individual specimens. Again, a character such as five-ranked branch leaves seems to be fairly constant under cultivation within certain plants, possibly the more robust ones, but as it occurs very often in S.recurvum, it is useless for diagnosis , even though it is almost invariably present in S.pulchrum. Characters such as width of border and particularly habit characters such as colour, robustness and compactness have been shown to be influenced by environment, and so their diagnostic value is greatly reduced. It is significant that almost all the "false S.pulchrum" specimens found to belong properly to S.recurvum were robust, brownish specimens, often with five-ranked leaves and enclosed chlorophyllous cells.

I would suggest that the safest character for identification of S.pulchrum is the shape of branch leaves, although this should never be relied upon alone. Good confirmatory characters are the presence of completely inrolled leaf margins, slightly fibrillose stem leaves (also occasionally in S.recurvum) and red stem turning brown with age. Branches of S.pulchrum are almost invariably red, even in the coma, but this character occurs quite often in S.recurvum and so is not conclusive.

CHAPTER 6

The relationship of S. cuspidatum, S. fallax, S. recurvum and S. amblyphyllum

(i) Systematics

Some introductory remarks on these species were made in Chapter 1. This present chapter is concerned particularly with the taxonomic status of S. fallax and S. amblyphyllum which are given by Andrews (1913, a) as synonyms of S. recurvum. A consideration of the latter must also include S. parvifolium (Sendt.) Warnst., which is accorded varietal rank by Andrews as S. recurvum var. tenue Klinggr. Varieties of S. cuspidatum recognised by Andrews will be considered later together with varieties of this species and of S. recurvum recognised only by Warnstorf.

(a) S. amblyphyllum and S. parvifolium

Horrell (1900), following Warnstorf (1899), recognised S. recurvum and S. parvifolium, there being two varieties of the former species, var. amblyphyllum Warnst. and var. mucronatum Warnst.. S. parvifolium is distinguished by its small stem leaves, as broad as long, usually with obtuse apex, and small, non-undulate branch leaves. The var. amblyphyllum is distinguished by the triangular-lingulate stem leaves with rounded, fimbriate apex.

Sherrin (1927) followed Warnstorf's 1911 classification, in which S. amblyphyllum was given specific rank and S. parvifolium reduced to a variety of this species, presumably because of the similarity in stem leaf apex. This procedure necessitated the creation of S. recurvum

var. parvulum for the small-leaved specimens with triangular acute stem-leaves, and led to considerable confusion. Andrews (1913, a) does not mention stem-leaf shape, but distinguishes the var. tenue as having small, non-undulate leaves. Some confusion may have resulted from Sherrin's mis-translation of part of Warnstorf's description of var. parvifolium (1911, p.213) which reads "Blätter . . . . . trocken häufig nicht unduliert" (branch leaves . . . . when dry, frequently not undulate), whereas Sherrin (1927, p.32) states that they are "usually undulate". Thus Warnstorf's 1911 description of var. parvifolium would accord well with Andrews' conception of var. tenue, in spite of the difference in parent species. The problem is discussed more fully by Andrews (1917).

Richards and Wallace (1950), and Procter (1955), dealing with British Sphagna, have followed Andrews in recognising only two species (S. cuspidatum and S. recurvum) in this complex, but many Scandinavian authors subdivide the latter species. In the graphic keys of Fearnsides (1938) who worked under Du Rietz at Uppsala, S. angustifolium C. Jens. (S. parvifolium), S. spiculatum Lindb. (S. recurvum var. mucronatum), and S. amblyphyllum are recognised as distinct species, the two former having triangular, somewhat fibrillose stem leaves, while the latter has lingulate, obtuse stem leaves. Fearnsides does not illustrate the pore structure of members of the S. recurvum group (including S. balticum and S. pulchrum) as she considers this to be similar in them all.

In contrast to this opinion, Gams (1957) uses pore structure to differentiate between S.recurvum subsp. mucronatum Russ. and subsp. angustifolium (C. Jens) Russ., which he now recognises together with subsp. amblyphyllum (Russ) Warnst.. In his earlier Kryptogamenflora (1948) he described a single taxon, S.recurvum, so this new work is important in that the Scandinavian conception of this group has been applied to the Sphagna of Europe in spite of the rejection of this idea in America. Details of the new classification are given below:

Table 20. Diagnostic characters of S.recurvum subspecies according to Gams (1957) (translated)

Character	subsp. mucronatum	subsp. angustifolium	subsp. amblyphyllum
Stem leaves	Sharply apiculate	Truncate, not longer than broad	Rounded and abruptly fringed
	Equilateral - to isosceles - triangular	Equilateral triangular	Long lingulate
	Fibrils	No fibrils	No fibrils
Size	0.5 - 1.0 mm.	0.4 - 0.8 mm.	up to 1.0 mm.
Branch-axis	Not pink	Mostly pink	-
Spreading branch leaves	1.0 - 3,0 mm.	0.8 - 1.2 mm.	1.2 - 1.8 mm
Pendent branch leaves	Small apical pores	Large apical pores	Large apical pores
Stem cortex	Not or partly differentiated	Not or partly differentiated	Scarcely differentiated

Persson (1952) divided S.recurvum in a similar way, but stated that S.mucronatum stem leaves are apiculate because of the margins being incurved above. With reference to this characteristic, Andrews quotes Warnstorf (1911, p.243) as recommending the examination of leaves on a

slide without cover-glass. Even with a cover-glass it is quite easy to tell the difference between an acute point and an obtuse one where the membrane of the hyaline cells is resorbed (Fig.12) Andrews states that he has found such obtuse leaves on plants determined as var. mucronatum by Warnstorf, but it is possible that these leaves were obtuse through abrasion or erosion which is said by both Andrews and Sherrin to occur occasionally. Obviously old stem leaves, which have been separated from the coma and exposed for a long time, are more likely to be eroded than leaves still protected in the comal tuft, so that in order to determine whether acute or obtuse leaves are characteristic of a particular stem it would seem advisable to examine only the very young stem leaves. Any disadvantage due to non-randomisation because of this limiting of sample area, is outweighed by the advantage of obtaining comparable and reliable results, for although an originally acute leaf may later be abraded, a young obtuse one must remain obtuse.

(b) S. fallax

Horrell (1900) followed Warnstorf in according specific rank to this taxon, which was distinguished from S. cuspidatum by the absence of well-differentiated stem cortex, stem leaf border the same width all round, and branch leaves shorter and wider. It was separated from S. recurvum by the stem leaves being larger and fibrillose, and the chlorophylleus cells of the branch leaves being trapezoid. Sherrin, following Warnstorf's later work, described the stem leaf border in

S.fallax as being of equal width everywhere or widened below, in contrast to Horrell's description, and whereas the latter mentioned that the chlorophyllous cells in branch leaves are sometimes triangular and enclosed as in S.recurvum, Sherrin describes the typical condition thus:

> "Chlorophyllose cells in the lower half of the leaf almost always triangular in section and well enclosed on the upper surface of the leaf; above (very rarely also below) trapezoid and both sides free."

A further character given by Sherrin is that stem leaves of S.fallax are isosceles-triangular, whereas in S.recurvum they are usually equilateral-triangular. The general impression gained from Sherrin's description of S.fallax is that most of its characters are extremely variable sometimes being as in S.cuspidatum and sometimes as in S.recurvum Evidence of the uncertain definition of S.fallax as a taxonomic unit is furnished by some remarks of Warnstorf (1911, p.240) about the naming of certain herbarium specimens as varieties of S.fallax, S.recurvum or of S.cuspidatum by different authors. Andrews believes that S.fallax differs from S.recurvum in characters (presumably length and fibrillosity of stem leaves and exposure of chlorophyllous cells) which are readily modified by an aquatic habitat, and maintains that the character indicating the true and close relationship between these species is the stem-cortex, which is undifferentiated in both, thus differing from that in the (usually) aquatic S.cuspidatum. Most

authors since Andrews have included S.fallax under S.recurvum although admitting that it often resembles S.cuspidatum. Fearnsides considers it to be both taxonomically and ecologically similar to S.recurvum.

The prevalent view of the status of members of this complex can be summarised as follows. There is little question of the distinctness of S.cuspidatum and S.recurvum, the features used by various authors to distinguish these species being given overleaf in Table 21. S.fallax seems to be intermediate in some respects between these two established species, being perhaps nearer to S.recurvum, and considered generally to be a form of the latter. S.amblyphyllum is considered either as indistinguishable from S.recurvum or as a variety or subspecies separated on one or two features.

The next section of this Chapter gives an account of investigations to find (i) the value of characters used in separating S.recurvum from S.cuspidatum;

(ii) the variability of the diagnostic characters of S.fallax;

(iii) the constancy of occurrence of obtuse stem leaves in S.amblyphyllum and the associations between this and other characters.

Table 21. Diagnostic characters of S.cuspidatum and S.recurvum as given by various authors

Authors given as:- D, Dixon (1924) ; S, Sherrin (1927); A, Andrews (1913,a); G, Gams (1957); P, Proctor (1955).

Characters	S.cuspidatum	S.recurvum	Authors
Stem cortex	Large and thin walled	small and thick walled	A
	well differentiated	not or slightly differentiated	S,D,G
Pendent branches	more or less drooping not concealing stem	appressed and concealing stem	S,A D,G
Stem leaf shape	longer than broad	rarely longer than broad	D,P
	isosceles triangular	equilateral to isosceles	S
	triangular-ovate	triangular-lingulate	A
Stem leaf size	more than 1 mm. long	less than 1 mm.long	G
Stem leaf apex	toothed, not lacerate	mucronate, rounded truncate	A,S
	pointed	obtuse-toothed or eroded	D
Stem leaf fibrils	present in upper half	rarely present	D,S,A,P
Branch leaf shape	4-5 times longer than wide	up to 3 times longer than wide	P
	long lanceolate	narrow lanceolate	A
	long lanceolate to subulate	narrow to broad lanceolate	S,D
Branch leaf length	land forms 1½-3 mm. water forms 3-6 mm.	less than 3 mm.	G
Branch leaf position	more or less spreading	imbricate	D
Branch leaf appearance	scarcely undulate	undulate with spreading tips	D,A,S
Branch leaf border width	4-6 cells	2 - 4 cells	S
	2 - 4 cells	2 - 4 cells	A
Branch leaf margin	normally entire	entire	A
Chlorophyll cell shape	trapezoid	triangular	D,S,A,P
Chlorophyll cell exposure	exposed more on outer surface	enclosed on inner surface	D,S,A,P

(ii) Analysis

An assessment of the value of diagnostic characters in this complex was carried out as in Chapter 4. All available herbarium specimens of S.fallax and S.amblyphyllum were examined, together with a number of specimens of each named variety of S.recurvum and S.cuspidatum. Greig-Smith (1952) and Melville (1949-50) have stressed the need for random sampling before the application of statistical and biometric techniques. This was impossible in the case of the first two taxa owing to absence of local material and particularly to the uncertainty of identification in the field, and as the primary aim of the investigation was to determine the status of previously defined groups, it was of course necessary to examine already determined material. Herbarium specimens of S.recurvum and S.cuspidatum were examined in preference to freshly gathered specimens, as more localities were thus represented, and the extent of variability and occurrence of characters used for the distinction of varieties of these species could be determined at the same time, although these results are not discussed until the third part of this chapter.

The characters for which the samples were scored were mostly derived from Table 21, (p.85). Certain others were included for special reasons given below. In order to obtain a quantitative estimate of the occurrence of obtuse stem leaves, 2 leaves were removed from just below the coma from each of 5 stems of a sample,

so that 10 young leaves were examined in each case. The occurrence of obtuse leaves is given below.

Table 22. Frequency distribution of obtuse stem leaves in samples of 10 leaves from 176 named specimens

Specimens determined as	Number of obtuse leaves out of 10											Total number of samples
	0	1	2	3	4	5	6	7	8	9	10	
S. amblyphyllum	4	3	2		1			5	4	13	17	49
S. recurvum	20	7	4		1							32
S. fallax	29	1	3			1		1			1	36
S. cuspidatum	45	5	6		1	2						59
Frequency	98	16	15	0	3	3	0	5	5	13	18	

The discontinuity is well marked and for the analysis, all specimens with 7 or more of the 10 leaves obtuse were regarded as having obtuse leaves. It is interesting to note that 10 specimens determined as S. amblyphyllum have less than 4 out of 10 young leaves obtuse.

The shape of the stem leaves was also scored, but only by eye, as measuring even 5 leaves from each of 176 specimens would have taken too much time at this stage of the investigation. For similar reasons, shape and size of branch leaves were not scored, quantitative observations of these characters being made later on a few samples from each of the final groups defined by the character analysis. Some authors such as Andrews, Bearnsides and Proctor do not give dimensions of stem and branch leaves presumably because they consider these to be of little diagnostic importance.

Serration of branch leaves and position of pendent branches were scored for use in the investigation of varieties of S.cuspidatum and notes were made on the habit and colour of each sample, though these characters could not easily be put in a form suitable for inclusion in the analysis. It was noticed that "terminal" leaves (i.e. about the 9th and 10th leaves from the distal end of a spreading branch) of S.cuspidatum var. serratum were often more serrate than the median leaves, and therefore serration was scored for leaves from both positions.

During an investigation of a mixture of S.recurvum and S.cuspidatum from a pool near Bethesda, Caerns., the author noticed that the bases of branches in S.cuspidatum were often a darker colour than the rest of the branch, being brown or red in contrast to the green or white colour of stems and branches. This colouration was restricted to the subcortical layers of branches, and was absent in the S.recurvum plants, so it was decided to score all specimens for this character. In this connection it is very interesting to see that Gams (1957) uses colour of the branch axis as a diagnostic character for separating S.recurvum subsp. mucronatum from subsp. angustifolium; unfortunately he does not mention this feature under subsp. amblyphyllum.

As mentioned in the Preface most of the work described in this thesis was completed before the publication of Gams' flora in 1957, and the character analysis of the S.cuspidatum / S.recurvum complex

which is discussed in the present chapter was based on systematic descriptions other than Gams'. This is important particularly in relation to his separation of subspp. angustifolium and amblyphyllum from mucronatum partly on the occurrence of large apical pores in the leaves of the pendent branches. Andrews (1913) Gams (1948) and Proctor did not mention this character at all, and Warnstorf's various descriptions (1900 and 1911) lead to uncertainty as to the distribution of large pores in this group of species. Consequently, pore structure was not included as a diagnostic character in the analysis, but has since been studied in detail and is discussed in Chapter 9.

176 specimens were scored for the following 18 characters, first of all using values intermediate between + and -, and then grouping these into + or - as before (Chapter 4, p. 44).

A. Dry branch leaves undulate + or not -

B. " " " spreading + or imbricate -

C. " " " with recurved tips or not

D. Branch leaves 5-ranked when wet or not

E. Pendent branches spreading + or pendent -(soaked whole stem)

F. Stem visible or not - (soaked whole stem)

G. Cortex differentiated or not

H. Stem leaves ever showing fibrils + or never -

I. More than 6 out of 10 stem leaves obtuse + (2 leaves from each of 5 stems removed from just below comal tuft)

J. Stem leaves isosceles + or equilateral triangular -
(predominant shape of 10 leaves; not measured)

K. Branch leaf border of 4 or more cells + or less than 4 cells -

L. Chlorophyllous cells ever trapezoid + or always triangular -
(Section from lower half of branch leaf)

M. Most hyaline cells fused ventrally or not) surface view
N. Hyaline cells ever fused ventrally + or never -) and section

O. Branch bases brown, red or dark + , or green to white (as stem) -

P. Branch fascicles close together + or distant -

Q. Median branch leaves with border serrate + or entire -

R. Terminal branch leaves with border serrate + or entire -
(leaves 9 and 10 from distal end of horizontal branch)

Table 23 (1st analysis) shows the large number of significant correlations between these characters, thus indicating the presence of more than one taxon. A well-differentiated stem cortex (G^+) correlates with 15 other characters, most of which are correlated with each other. Of the 15 correlations, 13 are significant at the 0.01 level of probability, so on the basis of these 15, Group I was extracted.

The characters are:-

$G^+ (B\ E\ F\ H\ J\ K\ L\ O\ P\ Q\ R)^+ (C\ I\ M\ N)^-$

It should be noted here that on morphological grounds a negative correlation is to be expected between trapezoid chlorophyllous cells (L^+) and fused hyaline cells, (M^+ , N^+) and between spreading pendent branches (E^+) and stem not visible, (F^-). The only cases

where E^+ and F^- occur together are where the stem is not visible due to the fascicles being close together. Similarly a high positive correlation between M and N is to be expected. The character of fusion of hyaline cells was expressed in this form to give three alternative expressions instead of the usual two, as it was desired to investigate the variability of this feature as fully as possible.

The frequency of expression of the 15 associated features in the 176 specimens was as follows:-

Number of characters	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Number of samples	2	4	10	21	25	14	15	14	6	6	4	6	17	19	7	6

Although the frequency distribution is continuous, there are peaks at 4 and 13 characters. Specimens scoring 10 or more were removed as Group I, and the 59 specimens concerned were then analysed as a test of homogeneity. Seven characters could not be tested for association as they occurred less than three times, but of the remaining 55 comparisons only two were significant, at $p=0.05 - 0.01$. That between undulate and serrate terminal leaves may be a chance correlation or it may indicate true association of these features, but that between serrate median and serrate terminal leaves is to be expected as presumably the same factor, be it genetic or environmental, influences the development of serrated leaf margins

throughout the plant. Group I was thus considered to be homogeneous.

The remaining 117 samples showed several correlations on analysis, 9 significant at 0.01 level of probability and 8 at 0.05 level of probability (excluding correlations expected on morphological grounds). This number is considerably higher than is expected on grounds of chance from 120 comparisons, and so more than one taxon must be present. It is evident however, that the two or more taxa remaining are not as distinct from each other as was Group I, as no character shows correlations with all the others which are associated in this second analysis (Table 24). As the correlations fall into unrelated groups, the extraction of the next group of samples must depend on only a few characters. Branch leaves not five-ranked (D^-), without recurved tips (C^-), less than 7 out of 10 stem leaves obtuse (I^-), and stem leaves fibrillose (H^+) were associated at the higher significance level with isosceles stem leaves, (J^+) and in addition C^- H^+ and I^- H^+ showed correlations significant at $p < 0.05$.

16 samples had all five of these characters and were extracted as Group II, which was homogeneous.

A third analysis on the remaining 101 samples showed 3 correlations significant at $p < 0.01$ and 9 correlations significant at $p < 0.05$, of which three were only just significant (Table 25). The total number of correlations is not much higher than random expectation, and there is a possibility that undulate leaves A^+ and spreading

leaves B^+ would be associated for morphological reasons. Again, it is to be expected that some non-random associations will occur as Group II was extracted within narrow limits (i.e. only those samples with maximum number of characters, five, were included in Group II) so that some samples rightly belonging to this Group must have been included in the third analysis. However, 8 out of the 12 correlations were between characters showing significant association in the second analysis (Table 24), which implies the existence of an element of heterogeneity other than that due to Group II samples. It would be possible to take out a Group characterised by spreading (B^+), undulate (A^+) leaves with non-recurved tips (C^-), stem visible (F^+) and most hyaline cells not fused ventrally (M^-). 20 samples have all of these characters, and a further 28 have four of the five. However, none of these characters is quantitative, and as only one correlation (spreading and undulate leaves) is significant at the lower probability level, it would seem best at this stage to consider all 101 samples as belonging to a single homogeneous Group III.

It is interesting to note here that character I^+, (7 out of 10 stem leaves obtuse) which has been used to diagnose a 'species', S.amblyphyllum, shows only one correlation, a negative one, with well-differentiated cortex.

The distribution of characters in the three groups is given in Table 26 a, 1st assessment, showing significant departure from 1:1 ratio. The distribution in the 48 samples which can be separated off from Group III (Group III (i)), is also shown for comparison with the remainder, Group III (ii) (Table 26, b). Now III (i) can be separated from III (ii), on the basis of six characters; B and C which show absolute differences in the two sections, and A, F, L and N which are indifferent in one of the sections. However, the minimum significant deviation from 1:1 ratio for alternate expressions of a character is 8 for both sections, so that in III (i) the deviation in character C, (9), and similarly in III (ii), the deviations in characters L and N, (10.5), are only just significant. Thus the only character which remains to distinguish these sections is spreading or imbricate branch leaves, which is hardly sufficient, especially as many plants show both conditions. The advisability of recognising a single Group III will be discussed further when the distribution of intermediate character expressions is considered.

It then remained to define the limits of the groups more clearly. All specimens were assessed for the three groups, points being given for a typically present or indifferent character, in spite of the advantage that this procedure gave to Group II which had four "indifferents". The following characters were omitted as the had the same expression in each groups -

5-ranked leaves, stem visible, most hyaline cells fused, and median leaves serrate.

The 176 specimens were divided into groups according to their ratings for each.

Group	I	II	III	I & II	II & III
Number of specimens	55	36	64	4	17

It is significant that there were no intermediates scoring the same for Groups I and III, indicating good separation, while 17 specimens had equal scores for the closely related Groups II and III. The most striking feature is that while Group I has remained more or less the same, twenty samples have been transferred to Group II from Group III, thus confirming that the criteria used in defining Group II originally were too severe.

In Table 26 c, 2nd Assessment, the distribution of characters is based on these groups, omitting the 21 intermediates. The only change in diagnostic value of the characters is that leaves with recurved tips (C^+) are now characteristically present in Group III instead of being indifferent; otherwise the Groups are defined as before.

It is useful at this stage to compare the numbers of differences and similarities of character expressions in the three Groups, as defined in the 2nd Assessment.

Table 27.

Between Groups	Differences: + ve / - ve	Differences: + ve /indifferent or - ve/indifferent	Similarities: + ve / + ve or - ve/ - ve	Similarities: indifferent / indifferent
I and II	5	3	5	1
I and III	10	3	1	
II and III	3	6	5	

Thus I and III are most distinct, while II has affinities with both I and III. At first sight II appears to have more characters in common with I than with III (6:5) but in only three of these, (characters C, H, J), does Group III have the absolute converse expression, whereas considering Groups II and III together, in all their five similarities (E, G, K, O, R,) Group I has the absolute converse. Also the number of absolute differences is greater between I and II than between II and III.

This second assessment gives equal weight to all characters, so a 3rd Assessment was carried out giving two points for every character which was typically present in a specimen, and one for a character typically indifferent. All the four specimens which had scored equally for Groups I and II then fell into Group I, and certain other specimens were reallotted to different Groups as indicated below.

Table 28. Re-allocation of samples on basis of 3rd Assessment

Group	I	II	III	II and III
Number and origin of samples	53 + 4 (I & II) + 4 (II) + 1 (II & III)	32 + 1 (II & III)	64 + 8 (II & III)	7 (II & III) + 2 (I)

The nine doubtful samples, together with those transferred by this last assessment to other groups, were further examined to see in which of the two groups they fell. This 4th assessment took into account only the absolute character differences, and if a sample was still of uncertain affinity, reference was made to the original data, where values intermediate between "present" and "absent" were recorded.

By these means, all specimens were allotted to one of three groups, the distribution of characters in which is given in Table 26,d, Final Assessment. No further change in the significance of characters has occurred so that this Table may be considered to indicate fairly accurately the diagnostic characters of the three groups. That the groups as so defined are distinct is shown by joint analyses. Groups II and III together consist of virtually the same samples as were tested in the second analysis. (Table 24). When Group I (60 samples) and Group II (35 samples) are considered together, well-differentiated stem cortex correlates with five other characters, and for Groups I and III, this feature correlates with nine other characters, all at the higher significance level.

Analysis of the final Group III alone, which has 20 specimens less than the original Group III, shows the following correlations (from Table 29):-

4 significant at $p < 0.01$ compared with 3 in original Group III

5 " " $p < 0.05$ " " 9 " " " "

Thus the Group is still somewhat heterogeneous but it is impossible to divide it into well defined sections, particularly as there is no means of deciding which correlations result from genuine association of characters typical of one taxon, and which are a result of chance association.

As mentioned above (p. 95), Groups II and III are closely related, the only characters having an absolutely different expression in the two groups being recurved leaf tips, and fibrillose, isosceles stem leaves. The extent of variability of these and other characters is shown in the table of distribution of intermediate scored values (Table 30). If (+) values are included with -, only three changes in the diagnostic value of characters occur, all of these being in Group II (Table 31, below). This is perhaps only a result of there being a smaller number of samples in this Group, but may be a reflection of the lack of definition of this Group as a taxonomic unit.

Table 31 Predominant expressions of three characters in the three Groups, based on different groupings of the original scores

Character	Including (+) with -			Including (+) with +		
	Group I	II	III	I	II	III
A. Leaves undulate	present	indifferent	present	present	present	present
C. Recurved tips	absent	absent	present	absent	indifferent	present
G. Cortex differentiated	present	absent	absent	present	indifferent	absent

It is apparent that character C, recurved leaf tips, is not a good criterion for the distinction of Groups II and III and although a partly differentiated stem cortex (G) is present in about half of Group II samples, it occurs quite often in Group III (see Table 30). The characters of isosceles, fibrillose stem leaves remain to separate Group II from Group III, though intermediate scores are common in both groups for these characters as is shown in the following extract from Table 30.

Table 30. (ex parte) Original scores of two characters in specimens of the Final Groups II and III

		+	+ (-)	+ -	(+)	((+))	-
H. Fibrils present	II	10		5	14	4	2
	III	7			10	14	49
J. Stem leaves isosceles	II	11	1	14		2	7
	III			5		4	72

At this point it is useful to consider the names which should be allotted to these taxa. Group I is obviously S.cuspidatum and is very well-defined by a number of characters. Group II corresponds to S.fallax though it is doubtful whether it is sufficiently distinct from Group III, S.recurvum, to be accorded specific or even varietal rank. S.amblyphyllum is merged with S.recurvum, its primary diagnostic character of obtuse stem leaves being correlated only with an undifferentiated stem cortex (see Table 29), which may or may not

be a true association. The problem of the heterogeneous nature of Group III will be reconsidered in the light of Gams' 1957 classification but for the moment, the occurrence of characters in the three main groups defined by the analyses is given in Table 32, (p.101).

Before going on to consider the quantitative data obtained from these taxa, it is convenient here to discuss an interesting feature of stem cortex differentiation which was noticed during the sample scoring. It soon became apparent that two types of differentiation occur. All transverse sections show that the peripheral layers of the stem consist of slightly larger cells than the inner layers. In the first type of differentiation, found most often in S.cuspidatum specimens, the outer cortical layers consist of usually much larger cells than the sub-cortical layers, which may or may not be thick-walled. The cortical cells appear to have thin walls (cf. Andrews, 1913 a, p.4) because by comparison with the underlying cells, they have much larger lumina, (Fig. 13a). In the second type of differentiation (S.recurvum specimens) the cortical cells are often not much larger than the sub-cortical cells, and the outermost cells may be quite small. Differentiation is apparent when the sub-cortical cells are thick-walled, (Fig.13 b), but when these are thin-walled and thus of larger lumen, they grade into the outer layers and the cortex is apparently undifferentiated, (Fig. 13 c). Fig. 13 d, shows a stem section of S.pulchrum in which differentiation of the cortex is of this second (S.recurvum) type.

In the character analysis, no distinction was made between these two types of differentiation, though it was noted in the initial scoring. It is significant that in the final groups, of the samples with differentiated cortex, 27 out of 28 in Group III, 14/16 in Group II, but only 2/59 in Group I were of the second type. The two "odd" samples in Group I were not originally determined as S.cuspidatum and this suggests that they are incorrectly placed in this Group.

Table 32 Characters of the Groups defined by the analysis

Characters	Group I S.cuspidatum	Group II S.fallax	Group III S.recurvum
Branch leaves undulate	almost always	almost always	very often
" " spreading	almost always	very often	often
" " recurved	sometimes	often	very often
" " 5-ranked	very rarely	very rarely	sometimes
Pendent branches spreading	often	rarely	sometimes
Stem visible	always	very often	almost always
Cortex differentiated	almost always	often	sometimes
Stem leaves fibrillose	almost always	very often	sometimes
Stem leaves more than 6/10 obtuse	never	very rarely	often
Stem leaves isosceles	almost always	very often	very rarely
Branch leaf border of 4 cells	almost always	very rarely	very rarely
Chlorophyllous cells trapezoid	almost always	often	sometimes
Most hyaline cells fused	never	very rarely	rarely
Hyaline cells ever fused	very rarely	often	very often
Branch bases brown	almost always	very rarely	rarely
Fascicles close	often	sometimes	sometimes
Median leaves serrate	sometimes	never	never
Terminal leaves serrate	very often	very rarely	never

(iii) Varieties of S. cuspidatum

Warnstorf recognised five varieties of S. cuspidatum, four of which were British and therefore described by Sherrin. These were var. falcatum Russ., var. submersum Schimp., ver. plumulosum Schimp., and var. plumosum Schimp.. The latter variety was credited by Braithwaite (1880) and Warnstorf (1911) to Nees and Hornschuch who published the name in Bryologica Germanica in 1823; Schimper described the variety in 1857. S. serratum Aust. will also be considered here; it is accorded specific rank by Warnstorf (1911) and varietal rank by Andrews (1913,a) as S. cuspidatum var. serrulatum Schlieph..

These varieties are separated partly on branch leaf dimensions, as given on p. 14 , and partly on various morphological characters such as position of branches, serration of the branch leaf margins, and whether or not the branches are falcately curved. The variability of branch position was examined during the S. cuspidatum - S. recurvum analyses. Sherrin's descriptions (p. 42-43) are as follows:-

var. falcatum Pendent branches slightly weaker than spreading branches and directed downwards at an acute angle.

var. submersum Two stronger branches slightly curved downwards or straight and spreading nearly horizontally, the pendent branches obliquely directed downwards from the stem.

var. plumosum) All branches nearly equal, spreading almost
var. plumulosum) horizontally from the stem.

When the specimens were scored for the analyses, the pendent branches were noted as "spreading" + , or "pendent, near to stem" - , with intermediate values. The distribution of scores in the final Group I (S. cuspidatum) is shown below.

	Pendent branches spreading			Branches pendent	
	+	+ (-)	+ -	(+) -	-
Number of specimens	27	6	16	6	5

There is a high proportion of intermediate values showing that this is a variable character difficult to score objectively. Table 33 below, shows that all varieties had a majority of specimens with spreading branches.

Table 33. Distribution of scores of pendent branch position within the named varieties of S. cuspidatum

	Branches spreading			Branches pendent	
	+	+ (-)	+ -	(+) -	-
var. falcatum	2	3	2	-	4
var. submersum	4	-	3	3	1
var. plumosum	10	1	2	2	-
var. plumulosum	4	1	3	-	-
S. serratum (including var. serrulatum)	6	4	-	1	-

The character was thus considered to be of little value for distinction of taxa, particularly as it showed no correlations with other characters within the Group I specimens.

Falcate branches and serration of branch leaves

These two characters have been considered diagnostic of var. falcatum and S. serratum respectively, but remarks by various authors suggested that they might be directly influenced by habitat conditions, especially the presence of water. Thus Warnstorf states of var. falcatum (1911, p.265) that it is "Häufige Sumpf -, selten Wasserform" and of var. submersum (p.267) that it is "Häufige Wasserform, die den Übergang von var. falcatum zu var. plumosum bildet" (often a water-form, forming a transition between var. falcatum and var. plumosum). Braithwaite (1880) however, stated that both var. plumosum and var. falcatum were usually submerged in deep pools, but that the latter did show transitions to the type. Braithwaite mentioned the form with serrate leaf margins only as S. laxifolium var. serrulatum Schlieph., giving this as a synonym for S. cuspidatum var. plumosum; this suggests that only the immersed forms have serrate leaves. Andrews (1919) remarked that serration is characteristic of some, but not all, aquatic S. cuspidatum, and in some regions, the serrate-leaved form is dominant to the exclusion of the normal form; Bryan (1955) commented on the abundance of var. serrulatum in roadside ditches of the coastal plain of North Carolina.

The distribution of the characters of falcate branches and serrate leaves was first examined in the Group I specimens, (a total of 59, as one specimen placed there in the analyses was found to have stem

and branch leaf dimensions much more typical of Group III). Of the 59 specimens, 27 had falcate branches, 16 had both median and terminal branch leaves serrate, and a further 20 had just the terminal leaves serrate. As only 11 specimens each of labelled var. falcatum and S. serratum had been examined, it was abundantly clear that these characters were not limited to their respective taxa as previously determined. If however, the characters are diagnostic of different taxa, they should show a negative correlation within Group I specimens. Joint occurrence of falcate branches and serrate leaves was calculated, and it was found that a negative correlation ($p = 0.05 - 0.01$) did in fact exist.

Because of the possibility that these characters might be correlated with environmental conditions, habitat data were collected from 33 of the Group I specimens; unfortunately details were not recorded for the remainder. The distributions of the characters in specimens from different habitats are given below:-

	Submerged	Not submerged
Number of samples	25	8
Number with falcate branches	7	8
Number with serrate leaves	19	4

It appears as though serration is linked with submergence and falcation with exposure, but comparison between the habitats is difficult because of the greater number of submerged samples. A further 16 samples of S.cuspidatum gathered from exposed habitats were scored for the two characters, the final distributions of which are shown below -

	Submerged	Not submerged
Number of samples	25	24
Falcate branches	7	23
Serrate leaves	19	5

Any character can be considered typical of plants from a particular habitat if it occurs in significantly more than half the samples from that habitat. On this basis it was calculated that all the distributions tabulated above would occur by chance less than 1 in 20 times, so that serrate leaves can be considered characteristic of submerged plants and uncharacteristic of exposed ones, while the opposite is true for falcate branches. It should be noted that in only one of the exposed specimens were the median as well as the terminal branch leaves serrate, while this was so in 8 of the submerged ones. In addition, 9 exposed samples showed very rudimentary serration of the terminal leaves, which does not affect the significance of the result as it would be unusual to have no intermediate stages. The difference between rudimentary and distinct serration is illustrated in Fig. 14.

It is impossible to define any varieties of S. cuspidatum on this evidence. A character such as branch position seems to be very variable, and falcation and serration are suspected of being regulated by environment. Other characters such as compactness of habit, leaf length and size generally are also likely to be influenced by habitat, as suggested by cultivation of S. recurvum. For the moment then, S. cuspidatum is regarded as a single taxon, and quantitative data discussed overleaf were obtained from Group I specimens without attempting to subdivide these.

(iv) The value of quantitative criteria in this complex

Quantitative measurements used diagnostically fall broadly into two groups; those referring to size of organs, given usually as ranges of length (e.g. Gams), and those describing shape, i.e. proportion, without reference to size (e.g. Proctor). Some authors, such as Warnstorf, give ranges of various dimensions so that both size and shape are recorded. Most authors give these details for branch and stem leaves.

(a) Branch leaves

Because of the large number of samples involved in the study of this species-complex, the sample size was reduced from that recommended in Chapter 3 of this thesis. Initially, 22 specimens were selected from each of the three final Groups, and five stems selected at random from each specimen. From one random branch from each stem, the two median leaves and leaves numbers 9 and 10 from the distal end were removed. Thus 10 median leaves per sample were measured, and although the dimensions cannot properly be compared with those given by other authors because of not knowing which leaves the latter measured, such data are comparable throughout the present investigations. The sub-terminal leaves were measured because from superficial examination it was thought that these were longer than median leaves in S.cuspidatum and shorter than median leaves in S.recurvum. In all cases, length

and breadth at widest point were measured with a micrometer eye-piece. (The use of the Projectorlux and grid mentioned on p. 15 was only quicker when width at a point other than the widest was needed).

Three sets of data were calculated from these measurements, and *t* tests performed using sample means of the three Groups, to determine the significance of deviation of Group means from one another. These will be discussed individually.

1. Median leaf length

The frequency distributions of lengths of median leaves for the three Groups are shown in Fig. 15, where values have been grouped into classes at 0.5 mm. intervals. There are two points of interest, the first being that although Group means differ slightly (*S. recurvum*, $\bar{L}$ = 1.78 mm.; *S. fallax*, $\bar{L}$ = 2.22; *S. cuspidatum*, $\bar{L}$ = 3.05;) the ranges overlap considerably, particularly for the two first-mentioned taxa which both have peaks at 1.5 - 2.0 mm. *S. cuspidatum* shows a peak at 2.0 - 2.5 mm. and has part of its range above 4.0 mm., which is the greatest length reached by median leaves of the other Groups. Because of the overlapping of ranges, *t* tests were not worked out for these data, as leaf length alone can be of little diagnostic value. It is appropriate to mention here that ranges of length of leaves from four specimens of each named variety of *S. cuspidatum* also overlapped, so that separation of varieties on this character was impossible.

The other interesting feature is the occurrence of several leaves longer than 3.0 mm. in S.recurvum and S.fallax, in contrast to Gams' statement (1957, p.83) that S.recurvum s.lato (including S.fallax) has leaves less than 3 mm. long. Habitat details were recorded for about half of these samples with long leaves, which were found in all cases to be aquatic. The influence of a submerged habitat on leaf length will be discussed later.

2. Median leaf length / width

Histograms (Fig. 16) of values of length / width of individual leaves were constructed as before. They conform to the same general pattern as histograms of leaf length distribution; the only noticeable difference being the greater range of length /width ratio, particularly in S.cuspidatum. This is to be expected because of the smaller variability of leaf width compared with length; a feature which was noticed in preliminary investigations of S.cuspidatum (see Chapter 3 p. 18) The results of t tests between Group means are given below:-

	Groups means	t	p
S.cuspidatum S.fallax	5.5 3.5	7.97	<0.001
S.cuspidatum S.recurvum	5.5 3.1	9.97	<0.001
S.recurvum S.fallax	3.1 3.5	3.06	<0.01

Thus all Group means of median leaf length / width proportion are significantly different from each other, although S.recurvum and S.fallax

are significant only at the lower probability level. Because of the overlapping of ranges this feature cannot be considered to be very important diagnostically but with reference to its use by other authors, it is interesting to see what a large range is covered by the present, comparatively small sample.

Proctor (1955) gives figures for the proportions of leaf length to width; these are shown below, together with figures obtained from the present investigation.

	Proportion given by Proctor	Percentage of sample means falling within Proctor's limits	Percentage of sample means falling outside Proctor's limits
		%	%
S.cuspidatum	4.0 - 5.0	36.4	18.2 below 45.4 above
S.fallax		13.6	86.4 above
S.recurvum	up to 3.0	50	50 above

3. Median leaf length minus terminal leaf length within individual branches

These values were calculated for each branch (mean of two leaves in each position) and then sample means were derived from these. Group means and values of t with corresponding probabilities are given below:-

	Group mean mm.	t	P
S.cuspidatum S.fallax	- 0.15 + 0.79	7.6	<0.001
S.cuspidatum S.recurvum	- 0.15 + 0.72	6.9	<0.001
S.recurvum S.fallax	+ 0.72 + 0.79	0.69	>0.4 N.S.

The frequency distributions of values for individual branches (110 per Group) are shown in histograms in Fig. 17, where the values have been grouped into classes at 0.5 mm. intervals.

It can be seen both from the histograms and the t tests that S.cuspidatum differs from S.recurvum and S.fallax in that the sub-terminal leaves in the former are often as long as, or longer than the median leaves. From this evidence, it is tentatively suggested that this character usually indicates S.cuspidatum, but that the converse has no diagnostic importance. Because of the usually greater length of median leaves in S.cuspidatum as compared with the other taxa, it is possible that frequency distribution diagrams of terminal leaf length for the three groups would show greater discontinuity than is shown by either median length, or median - terminal length distribution. This point was not investigated further here, partly because of questions of time, but particularly because of the suspected influence of environment on leaf length. The cultivation experiments described in Chapter 7, included investigations on changes in median and terminal leaf length as well as changes in leaf proportion.

(b) Stem leaves

Most authors refer to the shape of stem leaves as "isosceles-triangular", "equilateral-triangular" or "lingulate" and in the character analysis, stem leaf shapes were scored on these definitions. Andrews describes S.cuspidatum leaves as triangular-ovate and S. recurvum

as triangular-lingulate but these terms are rather vague and it was impossible to score samples objectively on this basis. Gams (1957) separates S.recurvum subsp. amblyphyllum from the other subspecies and from S.cuspidatum by the former having long lingulate leaves, whereas in the latter group, the stem leaves are distinctly tapered towards the apex. In the 176 specimens examined, all the stem leaves tapered towards the apex, and only a few could be described as even "triangular - lingulate", if the latter term means that for the greater part of the leaf, the sides are straight and parallel, as in S.rubellum. Indeed, the gradation of leaf shape from equilateral-triangular to triangular - lingulate (as is illustrated in Fig. 18) makes it difficult to score shape at all.

All specimens of stem leaves were therefore scored as isosceles - or equilateral-triangular in shape, but even this terminology is an approximation as will be shown. Strictly speaking, the word equilateral means all sides of equal length, and isosceles means two sides equal and different from the third. In practice, it is assumed that when a leaf is described as "isosceles-triangular", the two sides are equal to each other and longer than the base where the leaf is attached, as the sides are rarely shorter than the base. Thus judging by eye alone, it is usually the maximum length of leaf (i.e. height of the triangle) which is compared with the width of the base, and if length greatly exceeds width, the leaf is described as isosceles. In an equilateral triangle, height is less than width of the base, but this

was so in only a very few of the hundreds of leaves measured for this study, and leaves were scored as equilateral when the length equalled or only slightly exceeded the width.

It was important to know how accurate the eye-judgement actually was and so 5 leaves (one per stem) were measured from each of the same 22 specimens in each Group. Length and width were recorded for each leaf, and then shape was expressed as length/width. Histograms of frequency distribution of length/width proportions within each Group showed almost complete overlapping of ranges (Fig. 19a); combination of these figures gave a distribution showing a peak at 1.2 - 1.3 and one at 1.6 - 1.7 (Fig. 19 b). The high variance within each Group showed that some leaf shapes had been incorrectly judged by eye, but the absence of a sharply discontinuous distribution in Fig. 19 b, suggests that in any case the character is of little diagnostic value. With respect to S.recurvum and S.fallax, the incorrect scoring may have some importance, as leaf-shape was one of the characters used to separate S.fallax as a Group and thus some specimens of S.fallax found to have a low length /width ratio may properly belong to S.recurvum. These specimens were re-examined with this in mind, but in only one or two cases did the change of leaf-shape scoring from "isosceles" to "equilateral" result in the transfer of the specimen from S.fallax to S.recurvum. The same was true of specimens of S.recurvum found to have somewhat isosceles-triangular leaves. Again, in S.cuspidatum the high

variability of leaf shape within the taxon is genuine, and not a result of wrong inclusion of specimens due to incorrect scoring for this character, because all the specimens of this Group show a number of other highly correlated characters.

There remained the problem of deciding what significance might be attached to leaf shape. As almost all leaves are strictly isosceles an attempt was made to fix a value dividing "equilateral" (width almost equalling length) from "isosceles" (width much less than length). Five leaves were measured from each of the other specimens of Groups II and III (S.fallax and S.recurvum) and from 11 more specimens of S.cuspidatum. Shape was here expressed as length-width as this was easier to calculate, and Fig. 20 shows the frequency distribution of sample means. The pattern of distribution is the same as shown in Fig. 19 a, the most striking feature being that values for S.recurvum fall within much narrower limits than those of the other taxa, 84% of the samples of this Group having leaves only 0.1-0.3 mm. longer than broad. That changes in shape are almost entirely due to changes in length is shown by comparing the ranges of leaf width in the three Groups. These are almost identical, and the mean values are as follows:-

	Mean width mm.
S.recurvum	0.76
S.fallax	0.75
S.cuspidatum	0.79

Thus leaves more than 0.3 mm. longer than broad are about half as long again as broad, and this arbitrary point was fixed as dividing equilateral - from isosceles - triangular leaves. This is convenient, because, of the sample taken, most of the S.recurvum specimens thus have equilateral leaves. The distribution of values in the Groups is given below for comparison with the original visual scoring of intermediate values.

Table 34. Occurrence of isosceles and equilateral stem leaves

(a) By visual scoring

Group	+	(±)	±	(+)	((+))	-
I	32		3	1		
II	11	1	14	2		7
III			5	4		72

(b) By measurement (L-W) mm.

Group	above 0.4	0.3-0.4	0.2-0.3	0.1-0.2	below 0.1
I	32	3		1	
II	10	17	7	1	
III	2	8	31	36	4

It can be seen from Table 34 that correspondence of the two methods is good, the most important feature with reference to diagnostic value, being the large number of leaves in Group III Table 34 (b) which are somewhat isosceles, so that the discontinuity suggested in Table 34 (a) must be a result of subjective scoring. This is important

in relation to the separation of Groups II and III in particular, and all that can be said is that stem leaves of the former are "more isosceles", which it will be admitted is even less precise than distinguishing between isosceles and equilateral. Because of the arbitrary division mentioned above, this character cannot be considered to be of much value in separating Groups II and III, though one is justified in regarding samples with leaves more than 0.5 mm. longer than broad as probably belonging to S. cuspidatum (Group I).

The influence of an aquatic environment on stem leaf shape in samples of the three groups was investigated by culture experiments.

CHAPTER 7

Cultivation of S.recurvum and S.cuspidatum

(i) General

The assertion by Watson (1955, p.106) that S.recurvum "usually grows submerged in pools and deep ditches" is misleading, as the present author has found this species in habitats which are almost always drier than those in which S.cuspidatum typically occurs. Thus in North Wales, a large area of bog is often covered with a mosaic of S.recurvum, S.papillosum, S.nemoreum and Polytrichum commune, with S.cuspidatum limited to the wetter hollows. In pools, ditches and gentle waterlogged slopes, S.cuspidatum is usually found to be the dominant Sphagnum species (replaced by S.squarrosum and S.subsecundum in less acid waters), although it may not occur at all in the surrounding drier areas. However, S.recurvum and S.cuspidatum often do grow together, but in the author's experience, they only grow completely intermixed in permanently wet places. More often, a shallow channel or hollow, which usually contains free water, is filled in the centre with S.cuspidatum which gives way abruptly at the higher, well-drained edges to pure masses of S.recurvum. Such a well-marked transition is shown in Plate 4.

It is convenient here to mention a detailed study which was made of the occurrence of these two species in one small area near Llyn Idwal.

The area was 50 yards long by 15 yards wide and sloped along its length. The highest part had a 7° slope, the next part had a 12° slope and was covered with scattered, not clumped Juncus effusus, which ceased abruptly as the slope flattened out again to an angle of 9° with the horizontal. On preliminary inspection it was noticed that S.recurvum was present throughout the whole area, S.cuspidatum occurred everywhere except amongst J.effusus while Polytrichum commune was limited to the area of the latter. The whole area was sampled by random quadrats 25 cm. square and joint occurrence of species worked out, and it was found that S.cuspidatum did actually show a high negative correlation with J.effusus and P.commune. It might be supposed from this that S.cuspidatum is not a member of the commonly occurring Juncus - Polytrichum - S.recurvum community, but all four species have been found growing together in several other places, notably one in Anglesey where the community borders a shallow lake. It would appear then that the over-riding factor in the distribution of S.cuspidatum is the presence of abundant free water for at least the greater part of the year; this situation does in fact exist in the Idwal area studied, where the upper and lower slopes are usually more waterlogged than the J.effusus slope which is steeper and thus better drained.

Arising from such ecological studies is an observation which is of great importance to the systematics of these Sphagnum species.

Wherever S.recurvum and S.cuspidatum have been found growing together, whether intermingled or in adjacent tufts, they have always been quite distinct from each other, and accurate identification in the field has been possible. The only exceptions to this have concerned certain submerged specimens, as mentioned later in the Chapter on S.fallax. Braithwaite in 1880 (p.83) referred to the two species growing together yet each retaining its special features.

Because of this retention of individual characters by the two species naturally growing under the same conditions, there was no point in cultivating them artificially or in field experiments under similar conditions to see if they became more alike. The culture experiments were therefore concentrated on discovering how much certain characters could be affected by a few conditions, the most important of which was presence of water.

(ii) S.recurvum

Cultivation of specimens of S.recurvum in an exposed condition in the field and laboratory has been discussed in connection with S.pulchrum; the main changes being a decrease in size of the plant and branch leaves, compaction of fascicles, and possibly greater enclosure of the chlorophyllous cells of the branch leaves in the indoor cultures. 4 Samples of exposed S.recurvum were submerged in pools in the field, controls being maintained in situ; the indoor culture of submerged S.recurvum was unsuccessful. Of the four field experiments one was lost, one showed no change and two showed the same changes; one of these will be described in detail.

Plate 5 shows the habit of the specimen, (i) as originally collected, (ii) after 2, and (iii) after 5 months immersion in a pool. The small comas, distant fascicles and short ('separated') branches shown in Plate 5 (ii), seem to be produced in all specimens of S.recurvum after sudden immersion, but after a few more weeks, the coma enlarges and new branches are longer and appear plumose as in S.cuspidatum. After 5 months, 30 fascicles had been produced and the average increase in length of the stem was 13 cm. Branches were the same length (1.0 - 1.5 cm.) as in the original and number of leaves per branch was constant at 90-100. Branch leaves were more spreading and not as recurved when dry, and the pendent branches showed a slight tendency to spread away from the stem. No change was shown by the stem leaves which remained equilateral (length-width = 0.2 mm.) and fibrillose. Measurement of branch leaves

showed that mean lengths of median and terminal leaves had increased, but widths had remained constant at 0.3 - 0.6 and 0.2-0.3 mm. repectively. Ranges of length of old and new median leaves overlapped, but the upper limit and mean had increased by about 50% of the original; for the terminal leaves, mean length had increased over 100% and the ranges did not overlap.

These quantitative changes are given in detail in Table 35 which includes comparable figures obtained from a specimen of S.cuspidatum; it is evident that used alone, neither length nor length/width proportion of branch leaves is a reliable criterion for the distinction of S.recurvum and S.cuspidatum. An interesting feature is that in spite of the great increase in terminal leaf length, this is still less than median length, so that $L_M - L_T$ remains positive, as in all previously sampled S.recurvum specimens. It may be thought from these results that terminal leaves are more affected by the aquatic environment than median leaves, but it is probable that the former show a greater increase in length because they are differentiated later than median leaves in the comal branches. Thus after 5 months, it was calculated that only 4 'new' fascicles had been produced, so it was quite likely that when the plants were transferred to the pool, the median branch leaves of these fascicles were already partly differentiated and therefore less easily affected by the new environment. Unfortunately, the pool dried up in the summer of 1957, and so no further samples could be taken, but it was

shown later (p.134) for S.cuspidatum that on transference to water terminal leaves responded more quickly than median leaves.

As mentioned earlier, S.recurvum is typically found in an exposed condition, but it is quite often found partly submerged at the edges of shallow pools. These plants show the characters of long branch leaves and distant fascicles which were produced in the sample artificially submerged, but only one specimen found by the author was considered to agree sufficiently well with Warnstorf's description of var. robustum; this taxon will now be discussed.

(iii) S.recurvum var robustum

Warnstorf gave the following characters for the distinction of var. robustum Breidler:-

robust, usually lax and submerged
cortex usually well-differentiated
branch leaves 1.6-4 mm. long and 0.5-1 mm. broad

Comparable dimensions for the other varieties of S.recurvum are given below.

var. majus Angstr. 1.4-1.6 x 0.4-0.6 mm.
var. parvulum Warnst. 1.0-1.3 x 0.3-0.4 mm.

As these varieties can also have a well-differentiated cortex, the diagnosis of var. robustum seems to rest almost entirely on the greater size of some plants, which may be linked with a submerged habitat.

A specimen of S.recurvum was found growing in a ditch in September 1955. The plants were very large and brownish-green in colour and in the centre of the ditch they were submerged or just breaking the water surface. At the edge of the ditch only the lower parts of the plants were submerged, about the upper 5 cm. being exposed and more green in colour. These marginal plants were not as robust as the central ones (Plate 6).

Microscopic examination of central plants showed that they accorded well with the description of var. robustum, having median branch leaves 2.4 - 3.0 mm. long and 0.7-0.9 mm. broad. The cortex was not noticeably differentiated and all the other characters were as in typical exposed S.recurvum. Both lower (submerged) and upper

(exposed) parts of the marginal plants were next examined, and it was found that all characters except size of branch leaves were constant throughout the length of a stem, and were the same as in the completely submerged central plants. Branch leaves from the lower parts of the stem were 2.5 - 3.1 mm. x 0.7 - 0.9 mm., that is, the same as those from the central stems, but the upper branches had smaller leaves, 1.8 - 2.2 mm. x 0.6 - 0.7 mm.. This difference was also shown by the sub-terminal leaves, which were 1.6 - 2.2 mm. long in central and lower marginal stems, and 1.1 - 1.7 mm. long in upper marginal stems. Width of terminal leaves in all samples was between 0.2 and 0.4 mm..

Several of the submerged plants were cultivated in the laboratory with the comas 7 cm. above water level. After two months the mean increase in length was 17 cm. and 25 fascicles had been separated from the coma in this time; Plate 7 shows the difference in habit produced by the change of conditions. The comas had become smaller, and the plants were more slender and were green with no trace of brown colouration. Branches were thinner, but were the same length as in the original plant (1.5 - 2.0 cm.), although they had rather fewer leaves (70 compared with 90 in original). Tips of branch leaves were more recurved than before, and the stem cortex was slightly better differentiated, but because of the variability of this character, any change in it cannot definitely be attributed to change of

conditions. Stem leaves showed a slight decrease in length, from 1.2 - 1.4 mm. in the old to 1.0 - 1.2 mm. in the new; width remained constant at 0.8 - 1.1 mm. so the new leaves were less isosceles-triangular in shape. Branch leaf length and width had decreased as was expected; median leaves were 1.6 - 1.9 x 0.5 mm. after 2 months, and 1.35 - 1.8 x 0.5 mm. after 5 months.

The ditch from which the original sample was taken was visited again in September 1956. The water was not as deep as previously, probably owing to the accumulation of Sphagnum plants, including a lot of S. subsecundum which was rapidly replacing the S. recurvum. Samples were again taken of the completely submerged central plants and the partly exposed marginal plants. Upper and lower branches of the former had leaves of the same size as before, i.e. 2.9 - 37 x 0.8 - 0.9 mm., but upper and lower branches of marginal stems had short leaves within the range 1.9 - 2.2. x 0.5 - 0.7 mm. (All measurement data are given in greater detail in Table 36).

This difference from the previous year's sample in which lower leaves of marginal stems fell in the central stem range, can be explained as follows. Branches of the marginal stems were differentiated in the exposed comal tufts and therefore had short leaves; by continued growth of the plants, the lower parts became submerged but this could not affect the already matured leaves. It must be assumed therefore

that marginal plants of the earlier sample had become exposed only a short time previously, as the lower branches must obviously have been differentiated in submerged comas. This assumption would fit in with the observation that the pool was becoming shallower due to building up by dead plants; but the comparatively sudden change in the earlier sample from submerged to exposed conditions may well have been due to the exceptionally dry summer of 1955. It is interesting to note that by June 1957, no open water was present in the ditch, which was filled with S.subsecundum, most of the submerged S.recurvum having disappeared. Some plants of S.recurvum persisting at the edges were green and fairly robust but did not differ in any respect from typical non-aquatic S.recurvum.

(iv) S.cuspidatum

The experiments with this species fall into two groups, depending on whether the original samples were from submerged or exposed habitats. In nearly all experiments using exposed material, field and laboratory cultures were set up under submerged and exposed conditions, the latter being in the nature of controls; the submerged material was cultivated only under exposed conditions. It must be stated at the outset that the submerged indoor cultures were not really successful, as although a method was eventually found in which the plants were still healthy and growing after several months, they then invariably showed a reduction in branch length and in number of leaves, the comas were much smaller than before, and they were obviously in a degenerate state. Under such conditions valid comparison between old and new growth could not be made.

It is interesting at this stage to describe briefly the methods of submerged indoor culture. Plants from either submerged or exposed habitats survived no longer than two months when submerged in tap water, even when this was changed regularly. Growth was rapid at first, and after a month, marked changes in habit were evident, as is shown in Plate 8. Thus the centres of the comal tufts became much smaller in submerged plants, branches became less falcate, and branch leaves tended to be more spreading. Although tap water had no adverse effect on exposed plants, it was thought that the high pH (8.8) might be

responsible for the rapid death of submerged plants.

An experiment was set up using an exposed form of S. cuspidatum, samples of which were submerged in beakers containing water of varying pH. This was altered quite easily, without introducing undesirable minerals or organic buffers, by mixing fresh Sphagnum peat with tap, distilled or rain water. A series of culture media from pH 3.95 - 8.8 was obtained and Table 37 gives the experimental results. It is apparent that pH alone does not control the healthy growth of Sphagnum, as plants became bleached and ceased to grow after a fortnight in rain water (pH 7.0), whereas they grew for a month in tap water (pH 8.8). The addition of peat to rain or tap water delayed death for another few weeks, but the only healthy plants were growing in distilled water with or without peat.

Similar numbers of fascicles (44-45) were produced in 4 months by stems in distilled water or in this with peat (not filtered), but in the latter culture, the stems grew almost 10 cm. more. This was thought to be a result of reduction in light intensity due to the presence of peat which gave a dark brown colour to the water. A subsequent experiment in which 6 different gatherings of S. cuspidatum were submerged in distilled water was disappointing. Only 4 samples grew sufficiently in 6 months to produce 'new' fascicles, and two of these were then bleached and dying; one of the remaining healthy green samples was of the same material as used in the pH experiment,

which suggests it was particularly robust or resistant to death by submersion. However branch length had decreased in this cultured specimen from about 2.0 cm. to 1.2 cm., and number of leaves per branch was reduced from 85 to 45; further investigation was therefore abandoned.

Of the successful experiments, those involving originally submerged material will be described first. It was suggested by the S. recurvum experiments that an aquatic environment caused an increase in branch leaf length; the reverse effect was demonstrated by cultivating submerged S. cuspidatum under exposed field and laboratory conditions. Several field samples, although transplanted to wet (but not submerged) places where S. cuspidatum was already established, were lost in the summer of 1957, when such places were completely dried up for several weeks. Plates 9 & 10 shows the results of one indoor culture, in which the comal tufts have become smaller and yet more compact and the branch leaves are less spreading than before; the whole effect is that the plant appears less plumose. In all these experiments, branch leaves became smaller, width decreasing as well as length, but stem leaves were hardly affected. Table 38 gives the dimension data in detail, a particularly interesting feature being the ratio of length of median and terminal leaves. In only one of the three original samples did L_T exceed L_M, and in this after exposure, L_M exceeded L_T. In the two other samples,

$L_M - L_T$ was positive in the original, but decreased under cultivation.

Other character changes resulting from exposed conditions were a decrease in branch leaf border width in one sample from 5-6 (-9) to 3-4, and an increase in branch curvature, so that originally straight branches were succeeded by falcate ones. Another important feature was a decrease of leaf serration on exposure, so that in one case, median leaves were no longer even slightly serrate, while originally distinctly serrate terminal leaves were replaced by leaves with rudimentary serration. Both this and the change in branch curvature have an important bearing on the status of varieties of S. cuspidatum; further evidence was gained from cultivation of exposed samples under submerged conditions.

Altogether 6 samples under submerged conditions in the field survived long enough to produce new growth. In all of them, the fascicles became more distant, and the comas smaller and less compact, even though comal branches were the same length as before. This attenuation was most evident in cultures of originally compact plants, as illustrated in Plate 11. The reduction in size of the comal tuft is interesting, and is presumably a result of rapid elongation of the stem, and separation of fascicles, although increase in rate of elongation exceeds that of fascicle separation as is shown by the increased distance between the fascicles (about 1 cm. compared with less than 0.5 cm. in the original). Eventually a new equilibrium

must be reached by increasing the rate of differentiation of fascicles so that this equals rate of separation from the coma, although the number of fascicles in a submerged comal tuft at any time will then be less than in an exposed plant. This idea was supported by comparing numbers of fascicles dissected from comas of submerged and exposed specimens; submerged S. recurvum and S. cuspidatum usually had less than 16 differentiated but immature fascicles whereas exposed plants had 20-30 comal fascicles. Further evidence was gained from experiments on one sample of exposed S. cuspidatum which originally had 20-25 comal fascicles. Exposed and submerged field transplants of this material after several months showed 20-28, and 9- 14 comal fascicles respectively.

Submerged plants usually became more plumose in appearance, because the branch leaves tended to be longer and more spreading (Plate 12), and for this reason, submerged leaves were rarely recurved when dry, but were frequently undulate and twisted. The tendency to spread in an aquatic habitat was also shown by the pendent branches, which usually became more like the horizontal branches in appearance as well as in position. In some cases the pendent branches became very short or even disappeared altogether, the fascicles then consisting of two or three similar spreading branches. As noted in the indoor cultures, falcate branches seemed to be produced only in exposed conditions; although falcate branches were present to some extent in all originally exposed samples, new branches were straight in each

of the 6 submerged cultures. Similarly an increase in serration of branch leaves was shown by the submerged cultures. Table 39 below summarises these changes with details of exposed controls for comparison.

Table 39. Serration of branch leaves in some submerged (S) and exposed (E) cultures of S. cuspidatum

Date	Sample		Serrate leaves: Median	Serrate leaves: Terminal
6.56	CII	Original E	(+)	(+)
3.57	(f)	Indoor E	-	(+)
8.56	(a)	Field S	-	(+)
11.56	(a)	" S	(+)	+
10.56	(c)	" S	-	+
10.56	(d)	" S	(+)	+
4.57	(m)	" S	(+)	+
6.56	CVIII	Original E.	-	+
2.57	(b)	Indoor E	-	(+)
6.57	(k)	Field E	-	(+)
10.56	(a)	Field S	-	+
4.57	(a)	Field S	+	+
6.56	C V	Original E	-	-
4.57	(b)	Field S	(+)	+

Before considering the changes in leaf size induced by aquatic conditions, it is of interest to note that branch leaf border width was increased by submersion, from 3-5 to 6-8 cells. This variation, and its converse, seemed to be limited to S. cuspidatum; it was not observed in S. recurvum.

Table 40 gives details of branch leaf dimensions of several cultures of one originally exposed specimen of S. cuspidatum. As expected, significant changes occurred only in the submerged

cultures, in which after 10 months, branch leaves were more than twice as long as in the original plants. Even after only four months immersion, growth had been sufficient to produce 'new' fascicles, and comparison of these with the 'separated' fascicles is interesting. Thus median leaves of separated, new (4 month) and new (10 month) branches show a gradual increase in mean length from 2.3 (as in original) to 4.0 to 6.6 mm.; terminal leaves from the same branches however do not show any further increase in length after the 4 month sample, the mean lengths corresponding with those given above for median leaves being 2.9, 5.0 and 5.0 mm. This supports the view mentioned on p. 123 with reference to S. recurvum, that as terminal leaves are differentiated later than median leaves within a comal branch, they can respond earlier to changes in the environment. This time lag effect is responsible for the large difference between $L_M - L_T$ in the 4 and 10 month samples, (-1.1 and + 1.6 mm. respectively); after 4 months the terminal leaves have increased enormously, and only after a few more months do the median leaves show a proportionate increase. Further reference to Table 40 indicates that although leaf width increases slightly on immersion, the length/width proportion is greatly increased and is thus not a constant feature of even a single specimen.

Exposed cultures in field and laboratory showed no significant changes in leaf length, except possibly a slight reduction in maximum

length of terminal leaves (3.3 - 2.5 mm.) although ranges of old and new were coincident; this reduction may have been due to the new exposed conditions being rather more dry than the old exposed conditions. Branch leaves are very sensitive to slight changes in environment as is shown by another set of experiments using a very compact form of S.cuspidatum. The general results were the same as described above, that is, elongation on submersion and no change in the indoor exposed cultures, but the result of one exposed field culture was puzzling.

In this, mean length of median branch leaves increased to 2.9 mm., which was more than the original (2.1 mm.) and separated (2.3 mm.) leaves on the same plants, and also more than the indoor exposed culture (2.4 mm.); it was however below the values of mean length in several submerged samples (3.3, 3.5, 4.7 mm.). A possible explanation is that the new exposed site to which the sample was transferred was more liable to flooding after rain than its original habitat, and during the very wet summer of 1956, the plants may have been immersed for considerable periods. This would also explain the increase in serration of branch leaves shown by this sample (CIIm) (see Table 39, p.153). It is convenient to mention here that increases in branch leaf length were found to be due to an increase in number of cells.

Stem leaves showed little response to change in environment except in one submerged culture in which maximum leaf length was increased from 1.5 to 1.9 mm.. However the ranges overlap to such

an extent that the variation has no significance.

It is curious that no striking reductions in size such as occurred in indoor cultures of S.recurvum were recorded for S.cuspidatum although actually none of the latter was cultivated for as long as S.recurvum. In some indoor experiments, an increase in size was recorded for S.cuspidatum. Thus a very small, compact, exposed specimen with branches less than 0.6 mm. long, and median and terminal leaves 2.1 - 2.8 mm. and 2.4 - 2.8 mm. long respectively was grown indoors in an exposed position for 8 months. New branches were then 0.7 - 0.1 cm. long (leaves per branch constant at 40), median leaves 2.2 - 3.6 mm., and terminal leaves 2.1 - 3.5 mm. The fascicles were also much further apart after cultivation.

Another sample of this specimen was immersed in a pool and showed a similar response. This particular specimen is interesting because of its very small compact growth form, which was thought to be due to its habitat. It was growing on very shallow peat overlying the edges of a low, flat boulder and the plants in some places were spreading over the bare rock. Such small plants were found in several similar situations and were very often associated with Campylopus atrovirens. They only occurred in low lying flat bogs which would be almost always waterlogged, but even so, the plants on the rock itself must often be dried in the summer. It is suggested that available water and possibly nutrients in such situations are below the optimum

for growth of S.cuspidatum so that on transfer to more favourable conditions, such as a pool, or even an artificial indoor culture, the plants show an increased vigour. Most other field samples however are taken from optimum or above optimum conditions, so that on cultivating them indoors where light and possibly nutrients are below average, a decreased vigour is shown (as in S.recurvum cultures).

It is interesting to note that S.cuspidatum seems to dry out very quickly. It does of course grow in places which remain wet after others have dried up, but in cases of severe drought, it certainly becomes completely desiccated in a very short time. This is possibly because of its loosely tufted habit as the denser S.recurvum does not lose water as quickly, but the rapid desiccation of the Cuspidata generally is for the most part due to the lack of pores in their leaves, hummocks of S.papillosum (Group Cymbifolia), being quite moist even on the surface after several weeks without rain. S.cuspidatum does however, show a remarkable recovery after desiccation as indeed all Sphagna do. A pool which had been dry for eight weeks in the summer of 1955 and in which the S.cuspidatum has formed a hard dry, bleached mat on the bottom, was filled again with healthy growing plants by October. Even though the uppermost exposed plants may die, the plants underneath remain green and moist, and under favourable conditions new sheets are produced from old stems.

(v) Discussion

There seems to be no doubt that S.cuspidatum and S.recurvum are sufficiently distinct to be ranked as species. Characters such as type of stem cortex differentiation and fibrillosity of stem leaves seem to be constant under different environmental conditions and as they also show discontinuous variation they are useful in diagnosis. Size of stem leaves is also a fairly reliable character, as leaves in S.cuspidatum are always isosceles, and usually more than one and a half times as long as broad.

The character of brown (or red) branch bases seems to be constant in S.cuspidatum. All freshly collected samples, and all but a few of the herbarium specimens examined had brown branches; the absence of colour in old dried specimens is not surprising. Certain of the indoor submerged cultures of this species did not retain the brown colouration in the new branches, but this was probably a result of the peculiar conditions which produced rapid growth in poor light. However, the discovery of several red branched specimens of S.recurvum, particularly subsp. amblyphyllum (see Chapter 9), has reduced the value of this character for separating S.cuspidatum from S.recurvum, although branches of the former tend to be brown, not red or pink, the pigment usually being restricted to the proximal 1-2 mm. of the branch. This is an example of a character being of almost universal occurrence within one taxon, yet occurring occasionally in other taxa; similarly distributed characters are the constant brown branches and five-ranked leaves of

S. pulchrum, each of these features being present in some S. recurvum plants.

Although the quantitative data discussed in the last part of Chapter 6 suggested that branch leaf dimensions and proportions might be of diagnostic value, the culture experiments have shown these characters to be greatly influenced by environment. Measurement of leaves of several S. cuspidatum samples taken since the preliminary studies showed that terminal leaves were not longer than median leaves in the majority of cases, although they were usually nearly the same length. Thus although terminal exceeds median leaf length only in S. cuspidatum as far as is known, (in aquatic cultures of S. recurvum median leaves were still longer than terminal leaves), in fact that median leaves are longer than terminal does not necessarily indicate S. recurvum .

Leaf proportion varies with leaf length, and so proportion is a character of neither more nor less diagnostic value than absolute length. The latter has a limited use when considered in conjunction with other characters, so that a plant with median branch leaves more than 3 mm. long is more likely to belong to S. cuspidatum than S. recurvum (S. fallax is discussed in Chapter 8). Although aquatic cultivation of S. recurvum produced leaves in the length range of S. cuspidatum (Table 35 and p. 122) it must be pointed out that this was a comparison between aquatic S. recurvum and exposed S. cuspidatum; within any one habitat S. cuspidatum will invariably be found to have longer leaves

than *S. recurvum*.

There is no evidence from these results for recognising varieties of *S. cusnidatum*, as size, serration of leaves and branch position and curvature have been found to be controlled by environment. Some further work on leaf serration would be advisable to see if all non-serrate plants could have serration induced by submersion.

CHAPTER 8

S.fallax

(i) Preliminary observations

During an investigation in October 1955 on a small circular pool in the blanket bog mentioned previously (p.16) some plants showing several S.fallax characters were discovered. The pool was surrounded by S.recurvum, S.cuspidatum was dominant in the centre, and in order to find out what distance from the edge the latter replaced S.recurvum, a transect 70 cm. long and 3 cm. broad was taken along a radius. Starting from the margin, this strip was divided into 14 samples each 5 cm. long, which were then examined macroscopically, and divided into S.recurvum and S.cuspidatum, the latter being identified by its "spiky" appearance due to the long branch leaves. Samples 6-12, which consisted of both species, were difficult to determine, and on microscopic examination it was found that all plants in the S.cuspidatum sections of these samples were not alike. Some had a poorly defined stem cortex and shorter, less fibrillose, stem-leaves, although their branch leaves were very long; they were tentatively assigned to S.fallax. It was found possible to separate them from S.cuspidatum plants as the latter showed a brown colouration of the branch-bases. (cf. p.88).

Several stem leaves were taken from all S.cuspidatum samples, and from all "non-S.cuspidatum" (i.e. S.recurvum and S.fallax) samples. There was some evidence that in the latter group, length of stem leaf

and degree of fibrillosity increased along the transect, that is from exposed to submerged conditions, but even the innermost samples differed from the S.cuspidatum in these respects. It is very unlikely that all "non-S.cuspidatum" samples in this investigation were of common origin, and thus the evidence is far from conclusive for a gradual change from S.recurvum to S.fallax with increased submergence. However, it is mentioned here because the characters involved, increase in branch leaf length, stem leaf size and fibrillosity, were later investigated by cultivating S.recurvum in water.

(ii) Detailed study of one specimen from Ethie Wood, Arbroath

In November 1956, Miss U. K. Duncan obtained for me a fresh specimen of a plant identified a few years ago by A. Thompson as S.fallax . The plants were growing in a small pool in a birch wood, their comas just breaking the surface of the water. The general appearance was very like S.cuspidatum as the leaves, particularly of the upper branches, were very long. Some plants were cultivated in the laboratory and some in an exposed (i.e. non-submerged) position in a S.recurvum community; other stems were examined in detail and the results of these investigations will now be described.

(a) Examination of fresh specimen

Leaves in the branches of the upper 5 cm. of stem were green and fairly long; the fascicles were distant. About 7 or 8 cm. from the coma, the fascicles were more compacted, and the leaves, which were bleached of chlorophyll, seemed shorter than those in the upper branches. Dimensions of leaves from branches from these two regions of one stem are given below:-

Distance of spreading branch from coma mm.	Dimensions of median leaves mm.	Length of sub-terminal leaves (9 & 10) mm.
2	2.83 x 0.6	1.98
	2.88 x 0.6	2.07
8	1.80 x 0.6	1.39
	1.84 x 0.6	1.40

The shorter leaves and closely compacted fascicles of this region

suggest that it was formed under conditions different from those prevailing when the specimen was gathered. Miss Duncan informed me that the pool often dries up in the summer; this alternation of submergence and exposure could explain the different growth forms. Median and terminal leaves from every fascicle were removed from each of two stems. The pattern of variation in leaf length down the stem was similar for both stems, and in the longer stem (13 cm.) mean leaf length increased from about the 10 cm. level i.e. beyond the 6-9 cm. compact region with shorter leaves, (Fig.21). This variation closely resembles that described earlier for a sample of S.cuspidatum, (p. 19 and Fig. 2).

A further five stems were selected and leaf samples taken from branches at 1.5, 5.0, 6.0, 8.5, 10.5, 13.0 cm. from the coma, to see if the pattern of variation was constant. In actual fact, there were no stems longer than 10.5 cm. and so the suspected increase in leaf length beyond this point could unfortunately not be confirmed. The changes in leaf length up to this point were similar in all seven stems, even though the sample was small. An interesting feature shown by five out of the seven stems, and illustrated in Fig.21 was the sharp decrease in length (to 1.35 - 1.7 mm.) shown by median leaves about 5-6 cm. from the coma, so that in branches from this region, terminal leaf length often exceeded median leaf length. On

examining these branches the 6 or 7 median leaves were found to be shorter than leaves on either side of them; they were not antheridial leaves, and it is difficult to explain why they should be so short. However, branches beyond about 6 cm. showed normal leaf spectra, and the anomaly at 5-6 cm. does not alter the general pattern of variation in leaf length. It should be mentioned here that leaf width remained more or less constant at 0.55 - 0.7 mm., the most important variation being in length (3 mm. at 1 cm., 2 mm. at 8 cm., 2.7 mm. at 13 cm.).

Next the stem leaves were examined to see if any comparable changes in size occurred. One leaf was removed from each inter-fascicular stem portion, i.e. every fourth leaf. Length and width were noted and also presence of fibrils, using the following notation:-

4 well developed fibrils in apical part of leaf

3 4-10 cells with well-developed fibrils

2 a few cells with poorly-developed fibrils

1 rudimentary fibrils appearing as projections of the lateral walls of the hyaline cells

0 no fibrils

Values of leaf length for one stem are shown in Fig. 22 (a). Even allowing for the smaller size of stem leaves and hence their lower variability, there is slight evidence that leaves of the compact region of the stem (fascicles 15 +) are significantly shorter than the upper leaves.

Examination of six other stems, taking one leaf from every fifth interfascicular region, did not show any significance variations within any one stem, and, paradoxically, in the longest stem, leaves in the central, compact region were longer than those either in the upper region or in the lower region of long branch leaves. Mean lengths of leaves from comparable positions on the 7 stems are given in Table 41, which also shows the "fibril index" of each leaf. It does seem from Fig. 22 (b) as though the lower leaves are less fibrillose than the upper leaves within that particular stem. Table 41 confirms this for 4 of the other 6 stems, but again in the longest stem, (no.2), all leaves are fibrillose.

It is difficult to draw any reliable conclusions from these investigations, and it is doubtful whether collection of additional data from other stems would elucidate the problem further. I think it is reasonable to assume that the alternation of compact and diffuse regions with short and long branch leaves respectively is due to a change from an exposed to a submerged, or at least, partly immersed, condition, but the influence of these supposed conditions on the stem leaves is far from clear.

(b) Experimental cultivation

Both cultures were set up in November and after 4 months, mean increase in length was 1.8 cm. in the field sample, and 7.6 cm. in the indoor culture; during the next three months mean length

increments were 3.5 cm. and 9.4 cm. respectively, showing that growth rate in the field is slower than indoors particularly during the winter. Samples were taken in July 1957, the field sample having about 4 new fascicles, and the indoor sample about 25.

Both cultures had altered in appearance after only four months growth in the new exposed conditions. All plants were a lighter green colour, the comas were compact and composed of a large number of unseparated fascicles and branches were more rigid. Branch leaves were shorter and less spreading, and particularly in the field sample were distinctly recurved when dry. Measurement of branch leaves showed that mean width had decreased from 0.7 to 0.5 mm. in both cultures, but mean length had decreased more in the field than in the indoor sample; Table 42 below shows however that lengths of all new median and terminal leaves fall within the range of length of normal exposed S.recurvum leaves.

Table 42. Branch leaf measurement data from exposed cultures of originally submerged S.fallax

Date	Sample	$L_M - L_T$ mm.	L_M/W_M	L_M mm.		L_T mm.	
			mean	range		mean	range
11.56	Original	+ 1.2	4.45	3.2	4.05 - 2.6	2.0	2.9 - 1.65
7.57	Indoor	+ 0.6	3.5	1.65	2.15 - 1.45	1.0	1.2 - 0.9
7.57	Field	+ 0.6	2.85	1.4	1.8 - 1.3	0.8	1.1 - 0.6

Branches were longer in the indoor culture (1.2 - 2.0 cm., as in the original) compared with 1.2 - 1.5 cm. in the field culture, but this is presumably the effect of poor light, rather than an intrinsic characteristic.

After 7 months cultivation, stem leaves of neither the indoor nor the field sample showed any appreciable change in size or fibrillosity, but after a further 2 months, the field culture had produced much shorter and less fibrillose leaves. Table 43 below gives values of length, length-width and fibril index (see p. 145) for both old and new stem leaves of the 9-month sample. This shows that the change actually occurred within individual stems, and was not a result of the sampling method.

Table 43. Stem leaf data from exposed cultures of originally submerged S. fallax

Date	Sample	Fibril index	Mean dimensions mm.	Range of L - W mm
11. 56	Original	4	1.2 x 0.7	0.7 - 0.35
7. 57	Indoor	4	1.1 x 0.7	0.5 - 0.3
7. 57	Field	4	1.2 x 0.6	0.75 - 0.5
9. 57	Inddor (old	4	1.25 x 0.55	0.8 - 0.45
	(new	4	1.0 x 0.6	0.5 - 0.25
9. 57	Field (old	4	1.2 x 0.7	0.7 - 0.35
	(new	2	0.8 x 0.7	0.2 - 0.05

Little significance can be attached to the slight reduction in size of stem leaves from the indoor culture as the range of L-W for

new leaves overlaps with the range for old leaves of the same stem and for leaves of the original specimen. In addition, the minimum value of L-W (0.25 mm.) is higher than the minimum recorded for all S.recurvum cultures (0.1 mm.). The result of the field culture is more important as here a significant change in size, shape and fibrillosity of leaves has been demonstrated. In all cases, length-width of new leaves was less than the minimum value recorded for old leaves from the same stems, the change in shape being due to a decrease in length rather than in width.

It seems strange that this change should not take place until the eighth and ninth months after transplanting, but growth in the field was slow at first and when the first sample was examined in July, only 4 new fascicles had been produced and presumably the then uppermost stem leaves had been differentiated before transplantation. This would explain the comparatively sudden appearance of leaves which had been influenced by the new exposed environment.

It is harder to explain why no similar changes in the stem leaves occurred in the indoor culture, which already had 25 new fascicles by July. Unfortunately this experiment could not be repeated because of lack of material, and though far from conclusive, it does show that changes in size, shape and fibrillosity of stem leaves can occur. Also there is a strong suggestion that these characters are influenced

by the environment prevailing during the very early stages of differentiation of the stem leaves, which are later unaffected by subsequent habitat changes.

(iii) Discussion

As branch leaf size and curvature have been shown to be a direct result of presence or absence of water, there are at most two characters which can be used to separate this taxon from S.recurvum; isosceles and fibrillose stem leaves. Neither of these is very satisfactory for four reasons:-

(i) Many plants with equilateral-triangular leaves (L-W <0.2 mm.) have fibrils,

(ii) a decision on degree of fibrillosity is somewhat subjective,

(iii) the division into equilateral- and isosceles - triangular leaves is arbitrary, as continuous variation in shape occurs,

and (iv) one experiment suggested that growth in a non-submerged habitat resulted in decrease in length of leaf with a consequent trend from isosceles to equilateral - triangular shape, and a decrease in number of fibrillose hyaline cells.

These reasons argue that S.fallax should not be distinguished from S.recurvum, even as a variety, but against them must be set certain facts. Thus not all naturally submerged S.recurvum plants have more isosceles or fibrillose stem leaves than naturally exposed ones, and in cultivation experiments with S.recurvum, submersion did not lead to an increase in size or a change in shape or fibrillosity, so there is a possibility that these characters are genetically controlled.

This work has thrown some light on the problem of the status of *S.fallax* but the author suggests that until more culture work has been done, it would be advisable to recognise only a single taxon, *S.recurvum*.

CHAPTER 9

S. amblyphyllum

(i) Investigation of herbarium specimens of S. recurvum "S. lato"

The question of the existence of this taxon is closely connected with the rather heterogeneous nature of Group III as defined in the character analysis (Chapter 6, (ii)) The shape of stem-leaves seems to be almost constant, if the method of sampling described on p.86 is adhered to, that is, for the majority of stems, all young stem leaves are obtuse, or all are acute. One or two stems with young obtuse leaves were further examined by dissection of the comal tuft, and in all cases, the stem leaves up to the base of the apical "bud" (where branch rudiments are very small) were also obtuse. It will be remembered that this character correlated only with undifferentiated stem cortex, which is variable within Group III, and so the possibility of correlation with large apical pores on the leaves of the pendent branches was next investigated.

Gams (1957) emphasises these characters as distinguishing S. recurvum subspp. amblyphyllum and angustifolium from subsp. mucronatum which has acute stem leaves and small apical pores. The two former subspecies are seperated from each other on shape of stem leaves, and size of branch leaves. Now as Andrews' var. tenue corresponds in part to subsp. angustifolium, the latter would

be expected to have small non-undulate branch leaves, but the character of undulation is not mentioned by Gams. Gams' use of stem leaf shape also seems rather doubtful as he gives comparable size ranges for the two taxa (0.4 - 0.8 mm. in ssp. angustifolium and up to 1 mm. in ssp. amblyphyllum (1957, p.84) whereas the main difference in shape of the leaves in his illustration (p.82, figs.24,25) is due to the much greater length of ssp. amblyphyllum leaf. The present author suggests that similar sized leaves of both taxa would be indistinguishable on the basis of leaf-shape. Again, as mentioned on p.113 of this thesis, none of the obtuse leaves of scored specimens was strictly lingulate, but all showed a somewhat triangular outline.

It is extremely interesting to note that in the analysis of Group III specimens (Table 29) red branch bases correlated with non-undulate leaves; the former character is given by Gams for subsp. angustifolium, and the latter by Andrews' for var. t nue. It was decided to investigate Group III specimens again for the following characters:-

(i) Shape of stem leaves (length - width)

(ii) Size of stem leaves (length)

(iii) Size of median branch leaves (length)

(iv) Presence of large apical pores on the outer side of leaves of the pendent branches

With regard to the last character, a few preliminary investigations were made, and it was found that there were two types of large apical pores. In many cases, the pores were rounded but larger than corresponding pores in the spreading branch leaves (8-12μ in pendent, $< 8\ \mu$ in spreading), but in other samples, the pores in the pendent branches were much larger (12-16μ) and were oval to irregular in outline; this latter type was scored as apical "gaps", which often coincided with smaller pores on the upper leaf surface so that complete perforation of the leaf resulted. (Three minutes staining in 1% aqueous crystal violet was adequate to show up all types of pores).

The following characters were then analysed for correlations:-

(i) More than 7/10 young stem leaves obtuse

(ii) Fibrils present in stem leaves (even slightly fibrillose (+) leaves were scored as "Fibrils present"; Fearnsides (1938) indicates fibrils in S. angustifolium leaves.)

(iii) Branch bases red or pink

(iv) Branch leaves not undulate (including very slightly undulate leaves)

(v) Apical "gaps" on lower side of pendent branch leaves

(vi) Large apical pores on lower side of pendent branch leaves

Significant positive correlations were shown as follows:-

$p < 0.01$ Obtuse leaves with apical gaps

$p < 0.05$ Red branch bases with obtuse leaves,
non-undulate branch leaves,
and apical gaps.

Thus Gams' view of the existence of a taxon (or taxa) characterised by obtuse stem-leaves and large apical gaps seems to be confirmed by these results. Fibrillose stem leaves and large apical pores (not gaps) do not however show any correlations and it remains to be seen whether it is possible to distinguish two taxa within the obtuse leaved specimens. Of the 81 Group III specimens, 26 had obtuse leaves and apical gaps, and 8 of these also had red branch bases.

Next, 5 stem leaves from each of the 81 specimens were measured and shape expressed as (length-width) as before. Table 44, below, shows the distributions of values within four sub-groups distinguished on various combinations of the three intercorrelated characters listed above.

Table 44. Frequency distribution of mean values of length - width (mm.) for stem leaf samples of Group III specimens

Characters of specimens	>0.4	0.3–0.4	0.2–0.3	0.1–0.2	<0.1	Total number of specimens
Acute stem leaves	1	6	18	18	1	43
Obtuse stem leaves						
(i) Apical gaps absent	1	1	5	5		12
(ii) Gaps present		2	7	7	2	18
(iii) Gaps and red branches present			1	6	1	8

The ranges of leaf shape overlap considerably, all sub-groups showing peaks at 0.1 - 0.3 mm.. In the sub-group characterised by obtuse leaves, apical gaps and red branches, 7 of the 8 specimens have leaves less than 0.2 mm. longer than broad. All specimens were then scored as follows:-

Mean leaf length - width < 0.2 mm. (shape 1) +

" " " " > 0.2 mm. (shape 2) -

and associations between this and other characters were tested for in the usual way. A positive correlation ($p < 0.05$) was shown with red branch bases which accords with Gams' definition of subsp. angustifolium, but this single correlation is insufficient for the formation of a separate taxon. Again, the fact that red branches correlate with obtuse leaves and apical gaps, which are given by Gams as characteristic of both subspp. angustifolium and amblyphyllum, suggests that red branches may not be confined to the former subspecies. Within the 28 obtuse leaved specimens with apical gaps, "shape 1" leaves correlated with non-undulate branch leaves, but not with red branches. There are slight indications of a taxon with some characters of Gams' subsp. angustifolium and some of Andrews' var. tenue, but much more evidence is required.

Absolute lengths of stem leaves showed comparable variability so that ranges of the sub-groups coincided as before; none of the samples had leaves less than 0.7 mm. long, and all but one had a mean length of over 0.8 mm.

Branch leaf length of Group III specimens was ne t investigated. Two median leaves were taken from one branch from each of five stems per sample. All 28 specimens with obtuse stem leaves and apical gaps were sampled, together with 13 specimens with only one or neither of these characters. Further data were taken from 15 acute-leaved S.recurvum specimens already examined in the S.recurvum - S.pulchrum investigation (Chapter 4). Table 45 below shows the distribution of sample means.

Table 45. Frequency distribution of mean lengths (mm.) of branch leaves within various sub-groups of S.recurvum

Characters of specimens	1.1-1.2	1.3	1.4	1.5	1.6	1.7	1.8	1.9	2.0	2.1	3.5-3.6
I Acute stem leaves		1	5	5	7	1	5	2		1	1
II Obtuse leaves and apical gaps											
(i) Red branches absent	1	1	1	4	6		3	1	1		
(ii) Red branches present		1	3	3		1					

There is some evidence that plants with small stem leaves (see Table 44) tend to have small branch leaves, but as both these characters are likely to be similarly affected by environmental factors, no taxonomic significance can be attached to the association. The continuous distribution of sample means of branch leaf length

is significant, because the ranges of length within samples of comparable leaves overlap even more, and it is impossible to separate the samples into distinct groups on the basis of this character.

A comparison of these figures with those given by Gams is not strictly valid, because of the difference in sampling technique, but a similar distribution curve would be expected. Perhaps some comparison can be made however, as Gams gives 1-3 mm. for subsp. mucronatum (including the often longer-leaved S.fallax) which accords well with sub-group I (Table 45, $\bar{b}$ = 1.2 - 3.6 mm.), and similarly the range given for subsp. amblyphyllum, 1.2 - 1.8 mm., corresponds with 1.1 - 2.0 mm. in sub-group II (i). The most important evidence arising from this is that there are no specimens corresponding with subsp. angustifolium ($\bar{L}$ = 0.8 - 1.2 mm.) All specimens showing the other correlated characters given by Gams for this taxon i.e. obtuse, small stem leaves, large apical pores (only the largest "gaps" according to the present author) and red branches, have branch leaves 1.2 - 1.7 mm. long and therefore cannot be separated on this character from other specimens of S.recurvum.

Thus altho gh the results suggest the presence of a taxon characterised by obtuse stem leaves and large apical gaps, there is no justification for the distinction within this of a taxon whose members have very small branch leaves.

(ii) Investigation and cultivation of field samples

These results were supplemented by field investigations and examination of fresh and cultivated plants. In November 1956, the author discovered three separate tufts of S.recurvum showing red branches, and in addition several plants in each tuft had red stems. The pigmentation occurred in large irregular patches about 2 - 5 cm. long in these stems, which were the normal green colour elsewhere, but the appearance was unlike that of young S.pulchrum plants, in which the upper parts of the stems are often greenish, only becoming pigmented with age. The irregular nature of the red patches and the fact that they were not universally present suggested some relationship to growth rate and environmental conditions as the investigations of Paton and Goodman (1955) have shown for S.nemoreum. The tufts were removed to the laboratory for experimental cultivation and were first examined microscopically.

Two of the tufts were alike in the following respects:-

All branch bases red

Some stems red

Cortex undifferentiated

Stem leaves { obtuse (including those dissected from the coma) shape 1(L - W $<$ 0.2 mm.) and short (L $<$ 1.0 mm.) feebly fibrillose

Pendent branch leaves with large apical gaps

They were from different habitats and differed in appearance. The tuft from a large exposed Sphagnum carpet (1) consisted of rather

compact plants with orange-brown comas; that from a shaded place among Juncus effusus (2) was composed of taller green plants with more distant fascicles. Tuft (3) was from a similar habitat to tuft (1) and resembled it in appearance but had only a few red stems. On microscopic examination, plants of tuft (3) were found to have the following characters:-

All branch bases red

Cortex undifferentiated

Stem leaves { acute (including comal leaves)
shape 2 and short (L< 1.1 mm.)
feebly fibrillose

No apical gaps.

This simple investigation showed (a) that obtuse stem leaves are correlated with apical gaps, and (b) that red branch bases are not confined to obtuse-leaved plants.

Tufts (2) and (3) were grown for 6 months in the laboratory and were then re-examined; plants of the latter had become greener, though still showing a few brownish comas, and the fascicles were as distant as tuft (2) fascicles. None of the new stem growth was red, and of six stems of (2) examined in detail, three no longer had red branch bases. New stem leaves were even less fibrillose than the old ones, but were still obtuse in (2) and acute in (3). Stem leaves of (2) within each of the 6 stems studied, showed a slight increase in (L-W), which was due to a decrease in width rather than to an increase in length.

One stem of tuft (2) provided good evidence that obtuse stem leaves do not occur solely by chance or through erosion of acute leaves. During the period of cultivation the original apical cell of this stem had been killed by some means, growth had ceased, and the comal branches were dying. As often happens in similar cases under natural conditions, a new shoot was produced from the stem just below the dying coma, and after a few months was about 5 cm. long. Now all the leaves and branches on this shoot had been differentiated under the conditions of cultivation, which were constant, so that any changes within the shoot must be intrinsic and not caused by the environment. One stem leaf from each interfascicular stem portion was removed and measured and the degree of fibrillosity and shape of apex were noted. After a few very short, cucullate, fibrillose leaves at the extreme base of the shoot there was a gradual change in leaf size and shape to the coma. These changes are summarised in Table 46 which shows that the first-formed large, acute, fibrillose stem leaves which resemble branch leaves are in fact a juvenile type, and after about 10 rudimentary fascicles, they are replaced by typical short, obtuse, scarcely fibrillose leaves. It is of interest to note that red branches first appeared in the thirteenth fascicle from the base, that is, just before the appearance of obtuse stem leaves.

Because the character of red branches occurred in both acute and obtuse-leaved plants, and was not constant under cultivation, no

importance was attached to it during this small investigation. The primary aim was to see if plants under similar conditions continued to produce only acute or obtuse leaves, and this seems to be confirmed. However, after Gams cited the red branch character for the distinction of subsp. angustifolium among the obtuse-leaved plants, it seemed important to investigate this further.

Ten samples of S. recurvum showing red branches were collected from a single area, each sample being separated from the next by a distance of at least 20 yards. Even in the field it was easy to see that very few tufts, each of which was taken from the centre of a large uniform clump, were actually homogeneous as regards the single character of red branches. Unfortunately, all the red-branched specimens seemed to grow in rather dry situations where growth is slow and disintegration fairly rapid, so that stems showing more than one "dichotomy" were not found. Thus within a tuft it was impossible to be sure of the common origin of all but a few stems, and so genetical heterogeneity could not be disproved. Of the ten samples, only four were found to consist entirely of red-branched plants; all the others consisted of red-branched stems mixed with completely green plants, and the stems were divided into two groups on this character. The red-branched plants appeared rather more delicate than the green plants, and had smaller comas which were a yellowish colour, probably due to the red colouration showing through the green leaves.

All samples were scored for several characters, and it was soon

evident as before that red branches were not confined to obtuse leaved plants, and that leaves on a single stem were either all obtuse or all acute. From 10 samples a total of 46 stems with red branches were examined. Of these, only 31 stems had obtuse leaves, and only 26 of these also had apical gaps in the pendent branch leaves. Some of the obtuse leaved stems had large apical pores, not gaps, but the difference between small and large pores is so slight and the change so gradual, that it is difficult to define objectively, and is therefore of little taxonomic value. Fibrils were confined to obtuse stem leaves but were not always present. There was some evidence that red-branched plants with obtuse leaves and apical gaps had shorter stem leaves than other stems (0.8 mm. compared with 0.95 mm.) the leaves often being somewhat broader than longer. However, all leaves sampled were "shape 1", that is less than 0.2 mm. longer than broad.

All branch leaves were undulate, and length showed no correlations with stem leaf size and shape or apical gaps. Means of length, (10 median leaves per sample), fell within the limits 1.33 - 1.62 mm. except for one sample with mean of 1.15 mm., which was an acute leaved specimen without apical gaps and red branches; this as before is a strong argument for recognising at most two taxa within these specimens.

A specimen from a boggy wood near Rescobie Loch, Angus, identified by Miss Duncan as S. amblyphyllum was cultivated in the laboratory and also among S. recurvum near Bethesda. All stems had obtuse leaves, including those dissected from the comas, and some were feebly fibrillose. Many upper branches of the fresh specimen had faintly pink bases, but the predominant colour was green. After 9 months cultivation, both samples had new fascicles; plants were green, but red branches were present only in the field culture, and even in this, the pigmentation was very faint. Length of median branch leaves of the indoor culture was the same as in the original specimen (1.1 - 1.5 mm.) but new branch leaves of the field culture showed an increase in length (1.3 - 2.0 mm.). This may have been a result of the new exposed habitat being wetter than the original habitat. Stem leaves were all obtuse and the same size as before, all were less than 0.2 mm. longer than broad, and most of them were slightly fibrillose. Large apical gaps occurred in pendent branch leaves of old and new fascicles of the five sampled stems.

(iii) Discussion

The results described in this chapter seem to indicate the existence of more than one taxon within S.recurvum , the principle diagnostic character being shape of stem leaf apex. This is acute or obtuse, with very rare occurrence of intermediate shapes, which are almost always produced by abrasion of leaves which are acute when young. Examination of young comal leaves and cultivation of acute and obtuse-leaved stems has shown that shape of apex remains constant, and this must be a genetically controlled character. This is supported by the natural occurrence of both types of plant intermixed in the same tuft. The association of this character with others presents more difficulty. Thus red branches, although showing a strong correlation with obtuse leaves, also occur in acute-leaved plants and are not always constant under different conditions of cultivation. Again obtuse leaves are nearly always slightly fibrillose, but fibrils occur quite often in acute leaves. Obtuse leaved stems usually but not always have pendent branch leaves with apical gaps but these sometimes occur in acute leaved stems.

All the plants examined during this work can be placed in one of two divisions of S.recurvum, one with obtuse stem leaves, usually with apical gaps in the pendent branch leaves, and often with red branches, or the other with acute stem leaves, and usually without apical gaps and red branches. These correspond with subspp. amblyphyllum and mucronatum respectively. Size ranges of stem and branch leaves of

both these subspecies are almost identical except that larger leaved plants usually belong to subsp. macronatum. However the size ranges overlap sufficiently for these characters to be of no use for seperating the taxa.

There is no evidence from these results of the occurrence of a taxon characterised by small branch leaves, i.e. subsp. angustifolium. Non-undulation of branch leaves, given by Andrews as a diagnostic character for var. tenue, is a variable character difficult to define objectively, and the present author tentatively suggests that for mechanical reasons it is correlated with size of leaves. The present work has shown that branch leaf size is n t necessarily correlated with stem leaf size, as plants wh ch have small short stem leaves, with width equalling or exceeding length (given by Gams as diagnostic of subsp. angustifolium) usually have branch leaves more than 1.2 mm. long, which is in the range of leaf length of the other subspecies.

There is little ecological information about the occurrence of these taxa in Britain. Osvald (1949) states that S. angustifolium is common in the wooded raised mosses of Eastern Europe with Ledum palustre, and S. magellanicum, and as this type of bog is absent in Britain, perhaps S. angustifolium is rare because of lack of suitable habitats. Osvald also remarks that this species occurs sometimes in the bottom layer of blanket bogs, with S. apiculatum and

S. plumulosum , Eriophorum angustifolium and Juncus effusus forming the field layer. The present author has found subsp. mucronatum and subsp. amblyphyllum growing together in blanket bog with J. effusus in the field layer, but as mentioned above, no plants corresponding with subsp. angustifolium have been found at all.

GENERAL CONCLUSIONS

As discussions of the value and interpretation of experimental results have been included in the relevant chapters of this thesis, it is proposed here to limit the remarks to a brief criticism of the methods used in the investigation.

It is highly important that samples used for observation of qualitative or measurement of quantitative characters should be comparable. To this end it is worth while spending some time in preliminary investigation to find a) the region of the plant in which the character being studied varies least, and b) the smallest possible size of sample which gives a consistent mean. As regards the possibility of using quantitative characters in other Groups of Sphagna, for example Subsecunda or Acutifolia, it would seem advisable to investigate shape rather than size of branch leaves, as the latter in the Cuspidata is greatly influenced by the environment especially the presence of water. Both shape and size of stem leaves may be found to be useful diagnostic criteria in other Groups since these leaves do not seem to be as readily affected by the habitat conditions. However, care should be taken to examine sufficient samples to find out the overall range of variation of these characters.

The method of assessing the value of diagnostic characters by determining correlations between them has many advantages and it is in the main an objective method. The collection of data

in a form which gives any feature two or at most three alternative expressions is useful in that it avoids lengthy subjective descriptions of shades of difference difficult to communicate in writing to other investigators. A superficial examination of such data shows immediately which characters are continuously variable and hard to define even with a single sample, so an early pointer is provided as to the relative values of characters for distinguishing taxa.

The analysis of correlations and subsequent assessment of their significance indicates the good diagnostic characters, and enables a number of samples to be divided into groups, each showing features which are common to more or less all members of that group, and which differ from features of other groups. The comparative reliability of the useful features is also indicated. Thus although several characters may occur in all specimens of one taxon (i.e. all specimens of the taxon examined in this study), they usually appear to some extent in other taxa as well.

The methods of cultivation used in the field were mainly successful, when sufficient protection was given against sheep and bad weather conditions. With regard to indoor cultivation, more work could be done on the effect of light and temperature using the basic culture method as described. Methods of cultivating Sphagna under water should be developed, but for the

purpose of this work, which was to show that changes are possible (that is, the plasticity of characters) rather than to find the extent of change, field experiments under natural conditions were more suitable and incidentally more successful.

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Table 1. Maturity of branches and branch leaves in S.cuspidatum

Longest branch of each fascicle below coma of Stem A

Fascicle number	Branch length cm.	Number of leaves	Position of longest leaf. Number from base	Length of longest leaf mm.
1	1·15	75	47 - 54	3·1
2	1·1	67	54	3·15
3	1·05	65	45	3·3
4	1·1	61	48 - 51	3·2
5	1·2	69	45	2·95
6	1·25	73	54	3·2
7	1·1	74	37 and 61	2·5
8	1·25	66	54 - 55	2·95
9	1·2	74	56 - 58	2·8
10	1·15	57	51	2·65

Table 2. Means of leaf length for 1 - 10 leaves/branch about M_L taking 10 branches/stem from stems A and B of S.cuspidatum

Number of leaves per branch	Total number of leaves	Position of leaves about M_L Number	Mean leaf length mm.
1	20	5	2·41
		6	2·44
2	40	5 - 6	2·42
3	60	4 - 6	2·41
		5 - 7	2·43
4	80	4 - 7	2·42
5	100	3 - 7	2·41
		4 - 8	2·43
6	120	3 - 8	2·42
7	140	2 - 8	2·41
		3 - 9	2·43
8	160	2 - 9	2·42
9	180	1 - 9	2·40
		2 - 10	2·43
10	200	1 - 10	2·42

Table 3. Means of leaf length for 1 - 10 successive branches per stem taking 2 leaves/branch about M_L from stems A and B of S.cuspidatum

Number of branches per stem	Total number of leaves	Mean leaf length mm.
1	4	2.46
2	8	2.50
3	12	2.53
4	16	2.54
5	20	2.50
6	24	2.49
7	28	2.47
8	32	2.46
9	36	2.43
10	40	2.42

Table 4. Means of leaf length for 1 - 10 stems of S.cuspidatum taking 2 leaves/branch about M_L from 5, 10 or 15 branches/stem

No. of stems	Total no. of leaves at 5 branches/stem	Mean length mm.	Total no. of leaves at 10 branches/stem	Mean length mm.	Total no. of leaves at 15 branches/stem	Mean length mm.
1	10	2.61	20	2.45	30	2.48
2	20	2.40	40	2.40	60	2.43
3	30	2.46	60	2.45	90	2.47
4	40	2.44	80	2.45	120	2.43
5	50	2.46	100	2.50	150	2.52
6	60	2.47	120	2.50	180	2.52
7	70	2.50	140	2.54	210	2.54
8	80	2.52	160	2.55	240	2.55
9	90	2.50	180	2.56	270	2.59
10	100	2.50	200	2.55	300	2.58

Table 6. Means of $\frac{W_3}{L} \cdot 100$ for successive pairs of leaves about M_L

Stems X, Y (S.pulchrum) and R (S.recurvum)

Position about M_L	Number of leaves	Means of $\frac{W_3}{L} \cdot 100$		
		Y	X	R
1	2	32.75	34.5	20.35
1 and 2	4	30.55	35.5	20.65
1, 2, 3	6	32.07	36.2	20.35
1, 2, 3, 4	8	32.26	36.5	20.21
1, 2, 3, 4, 5	10	32.25	36.54	20.07

Table 7. Means of $\frac{W_3}{L} \cdot 100$ for 2, 4 and 6 leaves about M_L from 1 - 10 random branches from stem Y (S.pulchrum)

Number of branches	Means of $\frac{W_3}{L} \cdot 100$		
	2 l./br.	4 l./br.	6 l./br.
1	31.1	30.9	32.1
2	31.7	31.75	31.85
3	32.1	32.36	32.16
4	31.85	32.36	32.15
5	31.5	31.9	31.7
6	31.0	31.6	31.3
7	31.3	31.5	31.2
8	31.0	31.5	31.3
9	30.95	31.4	31.2
10	31.6	31.8	31.4

Table 10. Population ranges of $\frac{L}{W_3}$ for S.pulchrum
"false S.pulchrum"
S.recurvum
Group A
Group B

(Fig. 16)

$\bar{V}$ - variance; S - Standard deviation; S.E. - Standard error of mean;
$\bar{x}$ - mean

	"False S.pulchrum"	S.recurvum	S.pulchrum = Group A	"False S.pulchrum + S.recurvum = Group B
	4.32	4.79	2.85	4.52
	0.150	0.553	0.061	0.374
	0.387	0.744	0.247	0.611
E.	0.077	0.171	0.060	0.092
ation				
E. 3 S	2.93 - 5.71	2.05 - 7.53	1.93 - 3.77	
E. 2 S	3.31 - 5.32	2.79 - 6.79	2.18 - 3.52	
E. 2 S			2.18 - 3.52	3.04 - 6.00
E. 2 S			2.24 - 3.46	3.14 - 5.90

Table 11. 1st Analysis of S. recurvum - S. pulchrum complex showing significant correlations between characters

75 specimens

	A	B	C	D	E	F	G	H	I	J	K	L	M	N		
O	++	-	—	++	++	++	·	·	++	++	++	++	++	++		
N	++	-	·	+	++	++	·	·	++	++	++	++	++		++	p = 0.05 - 0.01
M	++	—	—	++	++	++	·	·	++	++	++	++			—	
L	++	—	—	++	++	++	·	·	++	++	++					
K	++	—	·	·	++	·	·	·	++	+					+	p < 0.01
J	++	—	—	++	+	++	·	·	++						-	
I	++	—	—	++	·	++	·	·								
H	·	·	·	·	·	·	+									
G	·	·	·	·	·	·										
F	++	—	—	++	+											
E	++	-	·	++												
D	++	-	—													
C	—	++														
B	—															

Table 12. 2nd Analysis of S.recurvum - S.pulchrum complex showing χ^2 values and significant correlations between characters

59 specimens

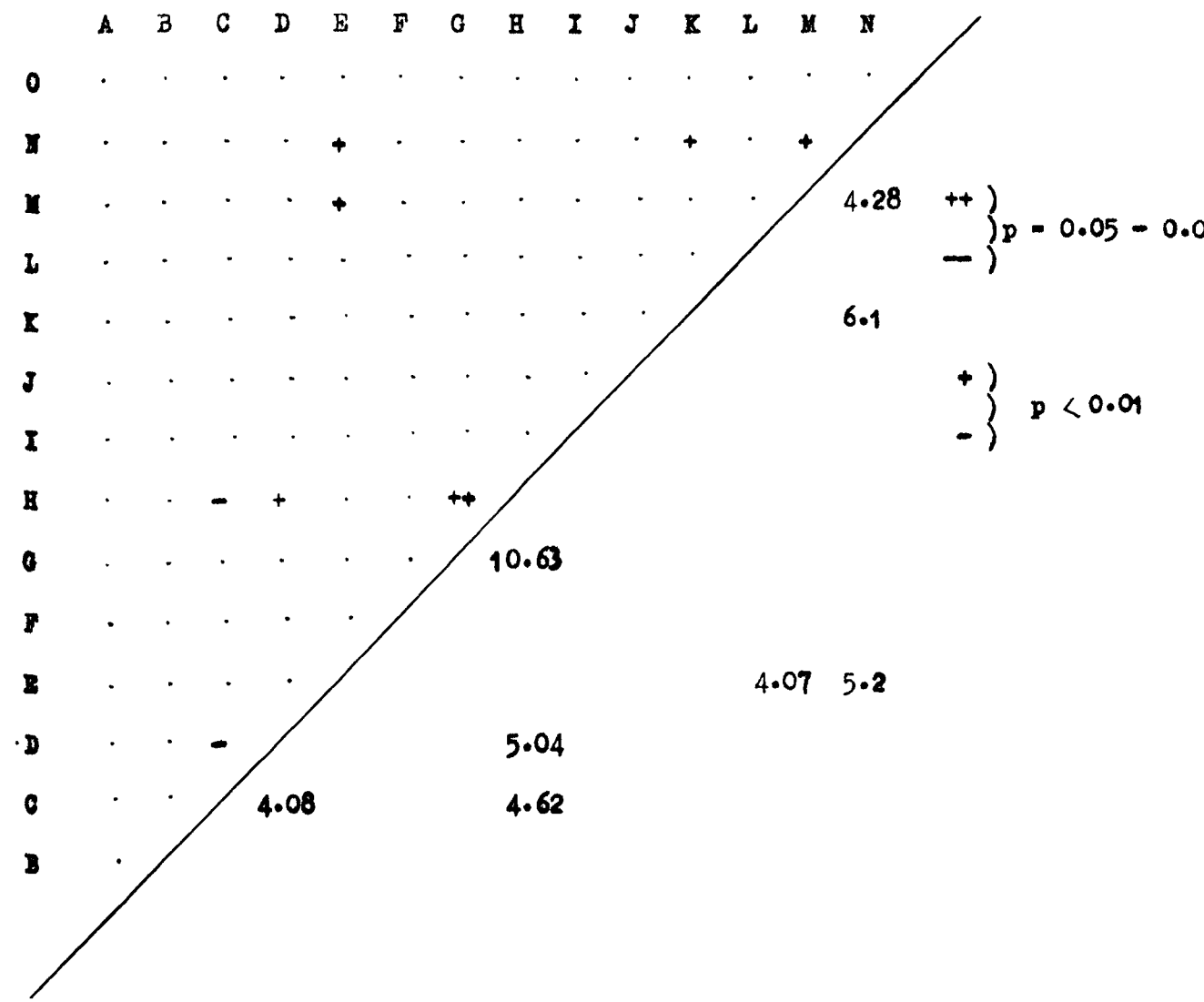

Table 13. Distribution of characters of samples within Groups X, Y and Z

Characters		(a) 1st Assessment: No. of samples with +ve or -ve character in Groups X	Y	Z	(a) 1st Assessment: Predominant expression of character in Groups X	Y	Z	(b) 2nd Assessment X	Y	Z	(c) 3rd Assessment X	Y	Z	(c) 3rd Assessment X	Y	Z
A	+	16	1	0	+	-	-	16	1	0	16	1	0			
	-	0	14	44				0	17	41	0	17	41			
B	+	1	11	36	-	±	+	1	13	34	10	18	40	±	+	+
	-	15	4	8				15	5	7	6	0	1			
C	+	1	12	29	-	+	+	1	14	27	12	16	37	±	+	+
	-	15	3	15				15	4	14	4	2	4			
D	+	16	6	17	+	±	±	16	8	15	16	15	33	+	+	+
	-	0	9	27				0	10	26	0	3	8			
E	+	15	13	10	+	+	-	15	15	8	15	16	20	+	+	±
	-	1	2	34				1	3	33	1	2	21			
F	+	13	1	2	+	-	-	13	1	2	15	6	7	+	±	-
	-	3	14	42				3	17	39	1	12	34			
G	+	13	12	40	+	+	+	13	14	38	13	15	38			
	-	3	3	4				3	4	3	3	3	3			
H	+	14	9	34	+	±	+	14	11	32	14	11	33			
	-	2	6	10				2	7	9	2	7	8			
I	+	16	3	4	+	-	-	16	3	4	16	3	4			
	-	0	12	40				0	15	37	0	15	37			
J	+	15	0	5	+	-	-	15	1	4						
	-	1	15	39				1	17	37						
K	+	16	14	18	+	+	±	16	16	16	16	16	16			
	-	0	1	26				0	2	25	0	2	25			
L	+	16	2	3	+	-	-	16	2	3	16	2	3			
	-	0	13	41				0	16	38	0	16	38			
M	+	16	11	7	+	±	-	16	12	6	16	16	24	+	+	±
	-	0	4	37				0	6	35	0	2	17			
N	+	16	13	4	+	+	-	16	14	3	16	14	4			
	-	0	2	40				0	4	38	0	4	37			
	+	16	5	8	+	±	-	16	7	6	16	7	6			
	-	0	10	36				0	11	35	0	11	35			

Non-significant deviations ($p > 0.05$) from 1:1 ratio for alternative expressions of a character are shown by red type. Predominant expressions of characters under (b) and (c) are only shown where they differ from (a).

Table 14. Distribution of characters as originally scored for samples within Groups X, Y and Z

	+			-				Division for analysis
	+	(±)	±	(+)	(±)	((+))	-	Detailed scoring divisions
Group X								
A	11	5						
B	1			9			6	
C	1			11			4	
D	16							
E	11		4					
F	13			2		1		
G	10	1	2				3	
H	14						2	
I	4		12					
J	6		9	1				
K	12	4						
L	9	1	6					
M	16							
N	13	2	1					
O	16							

	+	±	(+)	(±)	
			3		Score
J	4+	3-4	2-3	2	No. of border cells

Group Y								
A			1		5		12	
B	13			5				
C	13		1	2			2	
D	8			7			3	
E	7		8	1		2		
F			1	5		2	10	
G	11		3	1			3	
H	11						7	
I					3			
J			1	11	6			
K	1	8	7		1		1	
L			2		3		13	
M	8		4	4			2	
N	5		9		2		2	
O	1		1	5			11	
Group Z								
A					4		37	
B	32		2	6		1		
C	25		2	10		1	3	
D	14		1	18		1	7	
E	5		3	12	1	2	18	
F	2			5		5	29	
G	34	1	3		1		2	
H	31		1	1			8	
I					4		37	
J			4	31	6			
K		5	11		16		9	
L			3		4		34	
M	5		1	18		6	11	
N		2	1	1	5		32	
O			2	4			35	

Table 15. Distribution of characters of samples within Groups X and (Y + Z)

Character		(a) 2nd Assessment: No. of samples with +ve or -ve character in Groups X	(a) 2nd Assessment: No. of samples with +ve or -ve character in Groups YZ	(a) 2nd Assessment: Predominant expression of character in Groups X	(a) 2nd Assessment: Predominant expression of character in Groups YZ	(b) 3rd Assessment X	(b) 3rd Assessment YZ	(b) 3rd Assessment: Predominant expression X	(b) 3rd Assessment: Predominant expression YZ
A	+	16	1	+	-	16	1		
	-	0	58			0	58		
B	+	1	47	-	+	10	58	±	+
	-	15	12			6	1		
C	+	1	41	-	+	12	53	±	+
	-	15	18			4	6		
D	+	16	23	+	±	16	48	+	+
	-	0	36			0	11		
E	+	15	23	+	±	15	36		
	-	1	36			1	23		
F	+	13	3	+	-	15	13		
	-	3	56			1	46		
G	+	13	52	+	+	13	53		
	-	3	7			3	6		
H	+	14	43	+	+	14	44		
	-	2	16			2	15		
I	+	16	7	+	-	16	7		
	-	0	52			0	52		
J	+	15	5	+	-				
	-	1	54						
K	+	16	32	+	±	16	32		
	-	0	27			0	27		
L	+	16	5	+	-	16	5		
	-	0	54			0	54		
M	+	16	18	+	-	16	40	+	+
	-	0	41			0	19		
N	+	16	17	+	-	16	18		
	-	0	42			0	41		
O	+	16	13	+	-	16	13		
	-	0	46			0	46		

Non-significant deviations ($p > 0.05$) from 1:1 ratio for alternative expressions of a character are indicated by red type.

Predominant expressions of characters under (b) are only shown where they differ from (a).

Table 18. Branch leaf dimensions in a specimen of S.recurvum cultivated under different conditions

Date	Sample	$L_M - L_T$ mm.	L_M/W_M	L_M mm. mean	L_M mm. range	W_M mm. mean	W_M mm. range	Branch length cm.
10.55	RIV Original	0.6	2.8	1.8	2.0–1.7	0.6	0.7–0.6	1.8–2.0
6.56	(a) Indoor (sep.)	0.7	3.3	1.5	1.7–1.4	0.5	0.6–0.4	1.4–2.0
6.56	(a) Indoor (new)	0.6	3.0	1.4	1.5–1.2	0.4	0.5–0.4	1.0–1.5
11.56	(a) Indoor	0.6	2.8	1.1	1.3–0.9	0.4	0.5–0.3	1.0–1.3
9.56	(b) Field (new)	0.6	2.6	1.5	1.7–1.3	0.6	0.6–0.5	1.7–2.1

Table 23. 1st Analysis of S.recurvum - S.cuspidatum complex showing significant correlations between characters

176 specimens

++) —) p = 0.05

+) -) p < 0.01

	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q
R	++	++	—	-	++	·	++	++	—	++	++	++	·	—	++	·	++
Q	·	·	—	·	++	·	++	++	-	++	++	++	·	—	++	·	
P	-	·	-	·	++	·	++	++	·	·	·	·	·	·	·		
O	·	++	—	·	++	++	++	++	-	++	++	++	·	—			
N	·	—	++	+	—	—	—	—	·	—	—	—	++				
M	·	—	+	·	·	-	-	·	·	·	—	—					
L	·	++	—	-	++	++	++	++	·	++	++						
K	·	++	—	-	++	++	++	++	—	++							
J	·	++	—	—	++	++	++	++	—								
I	·	—	++	·	—	·	—	—									
H	·	++	—	·	++	++	++										
G	·	+	—	·	++	+											
F	+	++	-	·	++												
E	·	++	—	·													
D	·	·	·														
C	·	—															
B	++																

Table 24. 2nd Analysis of S.recurvum - S.cuspidatum complex showing significant correlations between characters

117 specimens

++ / −− p = 0.05 - 0.01

+ / − p < 0.01

	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q
R	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Q	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	
P	·	·	·	+	·	−	·	·	·	·	++	·	·	·	·		
O	·	·	·	·	·	·	·	·	+	·	·	·	·	·			
N	·	·	·	·	·	·	·	·	·	·	−	−−	++				
M	·	·	·	·	·	·	·	·	·	·	·	−−					
L	·	·	·	·	·	·	·	·	·	·	·						
K	·	·	·	·	·	·	·	·	·	·							
J	·	·	−−	−−	·	·	·	++	−−								
I	·	·	·	·	·	·	−−	−									
H	−	·	−	·	·	·	·										
G	·	·	·	·	·	·											
F	+	++	·	·	·												
E	·	·	·	·													
D	·	·	·														
C	·	−−															
B	++																

Table 25. 3rd Analysis of S.recurvum - S.cuspidatum complex showing significant correlations between characters

	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	
R	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	++	p = 0.05 - 0.01
Q	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	—	
P	.	.	.	++	.	.	.	.	.	.	.	.	.	.	.			
O	—	.	.	.	.	.	.	.	+	.	.	.	.	.			+	p < 0.01
N	-	.	.	.	.	.	.	.	.	.	.	.	.	.			-	
M	.	—	.	.	.	.	.	.	.	.	.	.	.					
L	.	.	.	.	.	+	.	.	.	.	.	.						
K	.	.	.	.	.	.	.	.	.	.	.							
J	.	.	.	.	.	.	.	.	.	.								
I	.	.	.	.	.	.	—	.										
H	-	.	.	.	.	.	.											
G	.	.	.	.	.	.												
F	+	+	.	.	.													
E	.	.	.	.														
D	.	.	.															
C	.	-																
B	++																	

Table 26. Distribution of characters of samples within Groups I, II and III

Character		(a) 1st Assessment No. of samples with +ve or -ve character in Groups I	II	III	(a) 1st Assessment Predominant expression of character in Groups I	II	III	(b) 1st Assessment Division of Group III 1.	2.	(c) 2nd Assessment 1.	2.	(d) Final Assessment I	II	III
A	+	44	9	70	+	±	+	44	26	+	±	42	20	48	45	22	56
	-	15	7	31				4	27			13	16	16	15	13	25
B	+	55	12	54	+	+	±	43	11	+	-	47	29	30	55	29	37
	-	4	4	47				5	42			8	7	34	5	6	40
C	+	1	0	55	-	-	±	15	40	-	+	1	5	41	2	4	50
	-	58	16	46				33	13			54	31	23	58	31	31
D	+	0	0	16	-	-	-	8	8	-	-	1	2	11	1	2	13
	-	59	16	85				40	45			54	34	53	59	33	68
E	+	48	3	22	+	-	-	13	9	-	-	46	8	14	49	7	17
	-	11	13	79				35	44			9	28	50	11	28	64
F	+	59	13	66	+	+	+	44	,22	+	±	55	29	41	60	28	50
	-	0	3	35				4	31			0	7	23	0	7	31
G	+	56	4	19	+	-	-	6	13	-	-	54	10	10	57	9	13
	-	3	12	82				42	40			1	26	54	3	26	68
H	+	59	16	30	+	+	±	15	15	-	-	54	30	7	59	29	17
	-	0	0	71				33	38			1	6	57	1	6	64
I	+	0	0	41	-	-	±	18	23	±	±	0	3	31	0	3	38
	-	59	16	60				30	30			55	33	33	60	32	43
J	+	58	16	15	+	+	-	9	6	-	-	53	27	1	58	26	5
	-	1	0	86				39	47			2	9	63	2	9	76
K	+	53	2	8	+	-	-	6	2	-	-	51	4	4	54	4	5
	-	6	14	93				42	51			4	32	60	6	31	76
L	+	51	8	39	+	±	-	23	16	±	-	48	21	18	53	20	25
	-	8	8	62				25	37			7	15	46	7	15	56
M	+	0	2	11	-	-	-	0	11	-	-	0	2	9	0	3	10
	-	59	14	90				48	42			55	34	55	60	32	71
N	+	3	10	62	-	±	+	25	37	±	+	2	17	45	3	16	56
	-	56	6	39				23	16			53	19	19	57	19	25
O	+	51	0	11	+	-	-	4	7	-	-	48	3	8	51	2	9
	-	8	16	90				44	46			7	33	56	9	33	72
	+	27	5	26	±	±	-	9	17	-	-	2	14	11	26	12	20
	-	32	11	75				39	36			32	22	53	34	23	61
Q	+	17	0	0	-	-	-	0	0	-	-	16	0	0	17	0	0
	-	42	16	101				48	53			39	36	64	43	35	81
R	+	38	0	2	+	-	-	0	2	-	-	36	1	0	39	1	0
	-	29	16	99				48	51			19	35	64	21	34	81

Non-significant deviations ($p > 0.05$) from 1:1 ratio for alternative expressions of a character i.e. "indifferents" are indicated by red type.

Predominant expressions of characters under (c) and (d) are only shown where they differ from (a)

Table 29. Analysis of Final Group III of S.recurvum - S.cuspidatum complex showing significant correlations between characters

81 specimens

	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q		
R	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.		
Q	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	++	p = 0.05 - 0.01
P	.	.	.	++	.	.	.	.	.	.	.	.	.	.	.	.		—	
O	—	.	.	.	.	.	.	.	.	.	.	.	.	.	.				
N	.	.	.	.	.	.	.	+	.	.	.	.	.					+	p < 0.01
M	.	-	.	.	.	.	.	.	.	.	.	.	.					-	
L	.	.	.	.	.	.	.	-	.	.	.	.							
K	.	.	.	.	.	.	.	.	.	.	.								
J	.	.	.	.	.	.	.	.	.	.									
I	.	.	.	.	.	.	.	--	.										
H	-	.	.	.	.	.	.												
G	.	.	.	.	.	.													
F	.	+	.	.	.														
E	.	.	.	.															
D	.	.	.																
C	.	.																	
B	++																		

Table 30. Distribution of characters as originally scored for samples within Groups I, II and III

		+	(+)	±	(-)	(+) or (+)	-	Division for analysis: Detailed scoring divisions
Group I	A	37		8	13		2	
	B	36	4	15		4	1	
	C	2			14		44	
	D	1					59	
	E	27	6	16		6	5	
	F	60						
	G	47		10	2	1		
	H	48	2	6	3		1	
	I						60	
	J	55		3			2	
	K	44	10		6			
	L	39			14	4	3	
	M							
	N							
	O	38		5	8		9	
	P	15	1	9	3	2	29	
	Q	12			5	2	41	
	R	35			4	1	20	
Group II	A	15		7	11		2	
	B	19	1	9		1	5	
	C	2		2	12	2	17	
	D	1		1	3	2	28	
	E	3	2	2		4	24	
	F	20		8	1		6	
	G	5		4	7	1	18	
	H	10		5	14	4	2	
	I	3					32	
	J	11	1	14		2	7	
	K	4					31	
	L	16			4		15	
	M							
	N							
	O	2					33	
	P	7		5		2	21	
	Q						35	
	R				1	1	33	
Group III	A	38		18	14	2	9	
	B	12	7	18		12	32	
	C	38		12	17	2	12	
	D	6		7	15	4	49	
	E	3	1	12		6	59	
	F	41		9	20	2	9	
	G	5		8	15	2	51	
	H	7			10	15	49	
	I	38					43	
	J			5		4	72	
	K		5				76	
	L	16			9		56	
	M							
	N							
	O	6		3	2		70	
	P	3		17	4	1	56	
	Q					1	80	
	R						81	

Table 35. Branch leaf measurement data from a submerged culture of S.recurvum, and from a sample of S.cuspidatum

Date	Sample	$L_M - L_T$ mm.	L_M/W_M mm.	L_M mm. mean	L_M mm. range	W_M mm.	L_T mm. mean	L_T mm. range	W_T mm.
	S.recurvum R III								
6.56	Original exposed	+ 0.7	3.45	1.6	1.9–1.3	0.5	0.8	1.1–0.7	0.2
11.56	Submerged	+ 0.3	4.7	2.2	2.7–1.4	0.5	1.9	2.4–1.3	0.2
	S.cuspidatum C II								
	Original exposed	+ 0.2	4.9	2.2	2.3–2.0	0.5	2.1	2.3–1.8	0.3

Table [illegible]. [illegible] data of S. [illegible] var. robustum

Date	Sample	$L_M - L_T$ mm.	L_M/W_M	L_M mm. mean	L_M mm. range	W_M mm. mean	L_T mm. mean	L_T mm. range	W_T mm. mean
9·55	Central plants								
	(i) lower stem	+ 1·1	3·3	3·0	3·0–2·9	0·9	1·9	2·2–1·6	0.3
	(ii) upper stem	+ 0·7	3·3	2·6	2·8–2·4	0·8	1·9	2·1–1·9	0.4
	Marginal plants								
	(i) lower	+ 0·8	3·5	2·9	3·1–2·5	0·8	2·0	2·2–1·8	0.4
	(ii) upper	+ 0·6	3·2	1·9	2·2–1·8	0·6	1·3	1·7–1·1	0.3
9·56	Central								
	(i) lower	+ 0·6	3·7	3·0	3·1–2·9	0·8	2·4	2·7–2·1	0.3
	(ii) upper	+ 1·1	4·1	3·6	3·7–3·6	0·9	2·5	2·6–2·4	0.4
	Marginal								
	(i) lower	+ 0·6	3·2	2·0	2·2–1·9	0·6	1·4	1·8–1·1	0.3
	(ii) upper	+ 0·5	3·0	1·9	2·0–1·9	0·6	1·4	1·5–1·3	0.3
11·55	Indoor cultivation (exposed) of central submerged plants	+ 0·6	3·4	1·7	1·9–1·6	0·5	1·1	1·35–0·9	0.2
2·56				1·5	1·8–1·35	0·45			

Table 37. Growth of S.cuspidatum submerged in various water cultures

Water source	pH	1 month		pH	2 months		3 months			4 months			pH
		F	B		F	B	F	B	L cm.	F	B	L	
Tap	8.8	20	(+)	6.0	0	+							3.85
Rain	7.0	12	+	7.15	0	+							-
Distilled	5.6	19		5.5	8		7		12.8	10		3.1	3.35
Distilled + peat	4.65	21		4.9	7		8		14.1	0	(+)	0.2	3.6
Distilled + peat (not filtered)	4.6	18		5.05	10		9		20.1	8		4.3	3.35
Tap + peat	4.5	25		4.95	1	(+)	0	+					4.0
Rain + peat	3.95	22		4.6	7		0	+					3.7

F - Fascicle increase

B - Bleaching

L - Length increase

Table 38. Branch leaf measurement data from three exposed (E) cultures of originally submerged (S) S.cuspidatum

Date	Sample	$L_M - L_T$ mm.	L_M/W_M	L_M mm. mean	L_M mm. range	W_M mm.	L_T mm. mean	L_T mm. range	W_T mm.
3.56	CIV Original S	+ 0.9	6.9	4.8	5.3-3.3	0.65	3.9	5.2-3.0	0.3
4.56	Indoor E	+ 0.1	5.6	2.7	3.4-2.2	0.5	2.6	2.9-2.2	0.3
5.57	Indoor E	+ 0.2	6.6	2.2	2.9-1.8	0.35	2.1	2.5-1.7	0.25
4.56	CXIII Original S	- 0.7	6.5	4.0	5.3-3.0	0.6	4.7	5.9-3.7	0.35
6.57	Indoor E	+ 0.4	7.1	3.0	4.0-2.3	0.4	2.6	3.4-2.0	0.3
6.56	CIII Original S	+ 1.2	6.1	4.7	6.1-3.0	0.8	3.5	6.2-2.8	0.45
4.57	Field E	+ 0.05	5.5	3.7	4.2-3.1	0.7	3.65	4.75-2.8	0.35

Table 40. **Branch leaf measurement data from exposed (E) and submerged (S) cultures of one specimen of originally exposed S.cuspidatum**

(sep.) = separated fascicles only; all other measurements are of new growth

Date	Sample	$L_M - L_T$ mm.	L_M/W_M	L_M mm.		W_M mm.		L_T mm.		W_T mm.
				mean	range	mean	range	mean	range	
6.56	CVIII Original E	+ 0.5	6.9	2.5	3.1–1.7	0.4	0.45–0.3	2.5	3.3–1.6	0.25
2.57	(b) Indoor E	- 0.3	5.6	2.5	2.7–2.3	0.45	0.5–0.35	2.8	3.1–2.4	0.2
5.57	(b) Indoor E	+ 0.2	7.2	2.8	3.1–2.3	0.4	0.5–0.3	2.7	3.2–2.0	0.2
10.56	(d) Field E (sep.)	+ 0.4	4.1	2.5	2.9–2.1	0.6	0.65–0.55	2.1	2.4–1.6	0.3
6.57	(d) Field E	+ 0.45	5.5	2.4	3.4–1.75	0.45	0.5–0.4	1.95	2.65–1.45	0.3
10.56	(a) Field S (sep.)	- 0.5	4.1	2.3	2.7–1.9	0.6	0.75–0.45	2.9	3.7–1.6	0.25
10.56	(a) Field S	- 1.1	7.5	4.0	4.9–2.9	0.55	0.65–0.4	5.0	6.2–3.9	0.25
4.57	(a) Field S	+ 1.6	12.1	6.6	7.3–6.1	0.55	0.65–0.45	5.0	6.4–4.2	0.25

Table 41. Fibril index number for stem leaves (1 out of 20) along 6 stems of S.fallax

Position of leaf: between fascicles numbers	Stem Number 2	3	4	5	6	7	Mean leaf length mm.	
4 and 5	4	4+	4	4	4	4+	1.18	
9 10	1	4+	4+	4	4	4+	1.30	
14 15	4	4+	4	4	3	3	1.29	Mean of 7 stems
19 20	1	4	2	1	0	1	1.03	
24 25	3	4	4	0	2	4+	0.97	
29 30	1	0	0	-	0	4	1.06	
34 35	3	2	0	-	0	0	1.04	Mean of 6 stems
39 40	0	0	0	-	0	0	0.95	
44 45	4	-	0	-	0	0	0.95	Mean of 5 stems
49 50	3	-	-	-	0	0	0.94	Mean of 4 stems

Table 46. Sequence of changes in stem leaves of a new shoot of S.recurvum (Tuft 2) from base to coma

Number of fascicle	Length	Length-width	Shape of leaf	Shape of apex	Fibrils
1	0.4	0.05	Triangular	Cucullate	All leaf
	0.7	0.7	"	"	"
	1.1	0.55	Round concave base	"	"
	1.4	0.7	"	Acute	Upper half
5	1.55	0.8	"	"	"
	1.5	0.7	"	"	"
	1.4	0.7	"	"	"
	1.4	0.7	"	"	"
	1.3	0.65	"	"	"
10	1.3	0.6	Triangular	"	"
	1.2	0.55	"	"	Upper third
	1.15	0.45	"	"	"
	1.0	0.35	"	"	"
	0.95	0.3	"	"	5 - 8 cells
15	0.95	0.3	"	Obtuse	"
	0.9	0.2	"	"	"
	0.9	0.15	"	"	"
	0.85	0.1	"	"	"
	0.85	0.15	"	"	"
20	0.85	0.15	"	"	None
	0.8	0.1	"	"	"
	0.9	0.15	"	"	"
	0.85	0.2	"	"	Very few

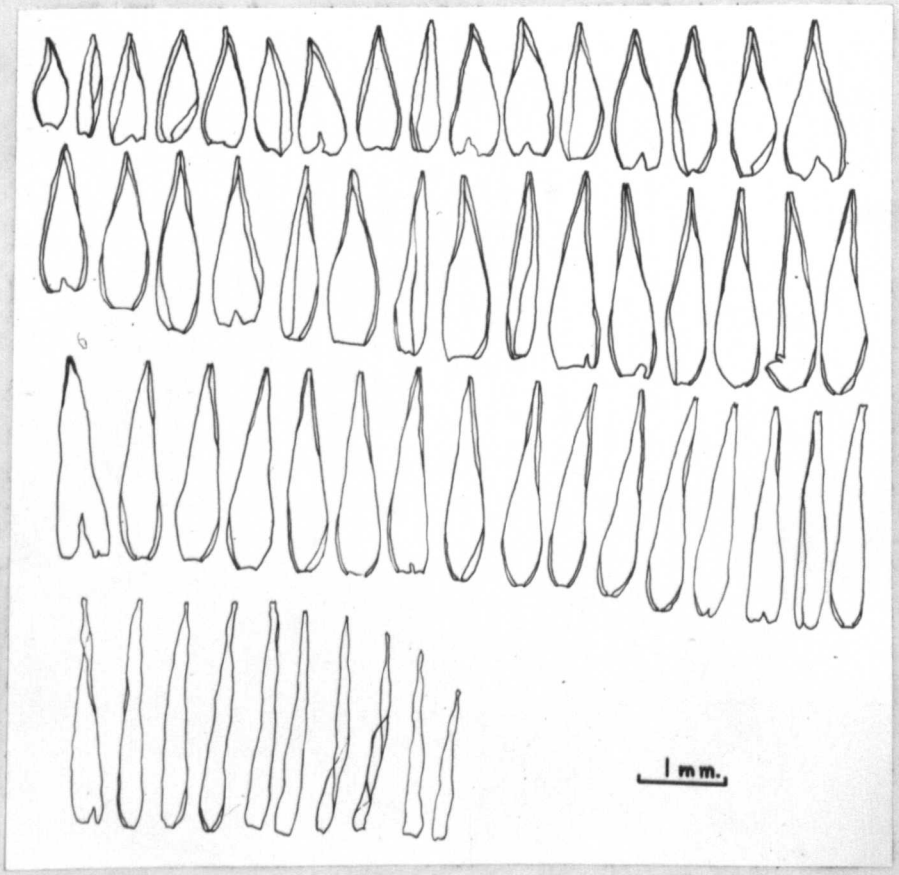

Fig. 1. Leaf spectrum of S. cuspidatum ; leaves removed in order from base to apex of a mature spreading branch.

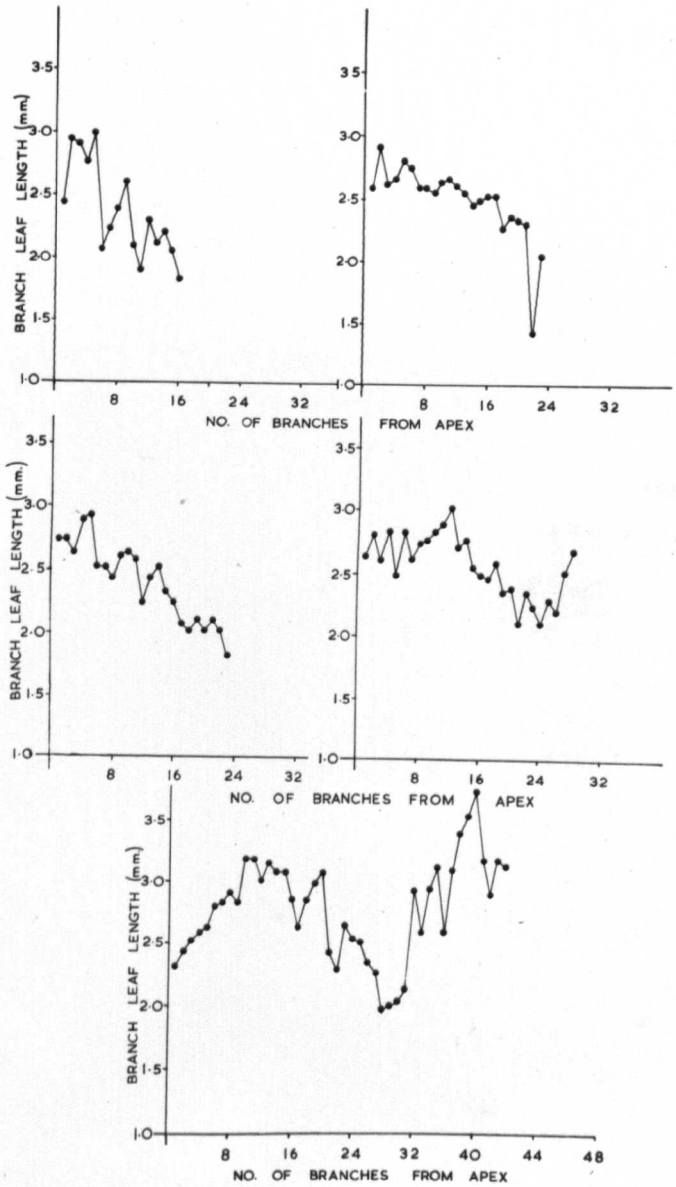

Fig. 2. Variation in length of median branch leaves with increasin g distance from the coma in 5 stems of S. cuspidatum.

The median branch leaf length is given as the mean length of two leaves re removed from about the mid-point by length of one spreading branch per fascicle.

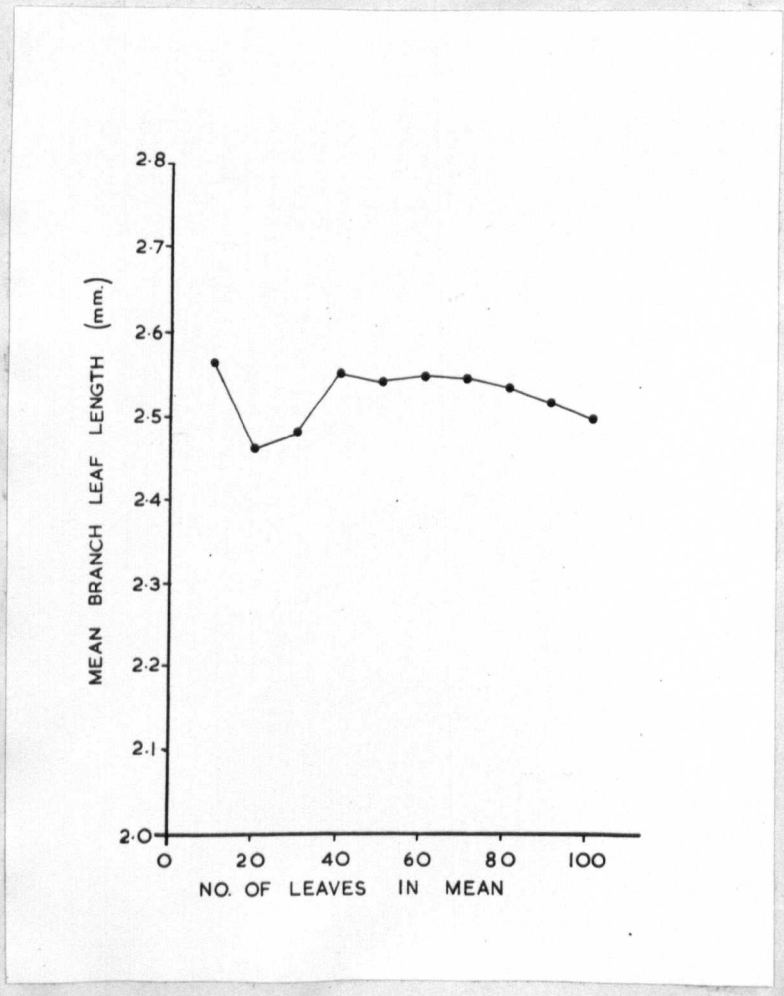

Fig. 3. Mean length of increasing numbers of branch leaves of S. cuspidatum. These means are from two leaves per branch from 1-10 random branches from each of 5 stems. The graph shows that variation in mean leaf length is negligible after the 5 branch level, i.e., after 50 leaves.

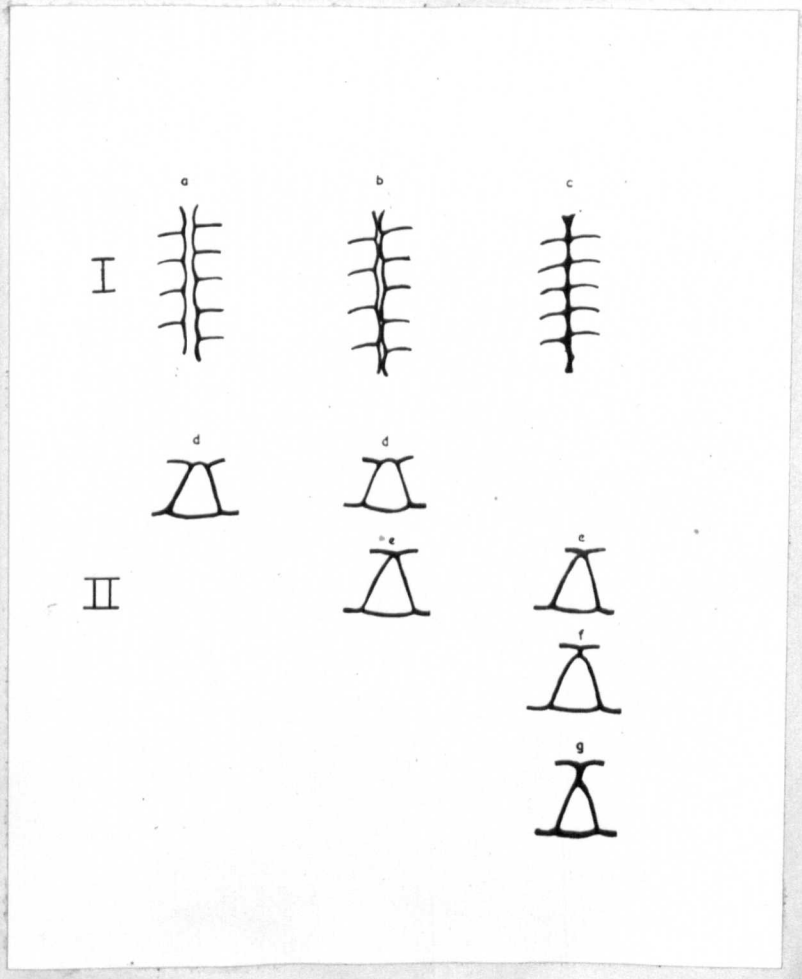

Fig. 4. Diagrams illustrating the various relative positions of Hyaline and chlorophyllous cells in branch leaves of S. recurvum.

I - adaxial surface of leaf

II - transverse section of leaf, adaxial surface uppermost

In II the sectional views given are all those which can be derived from the surface view directly above them.

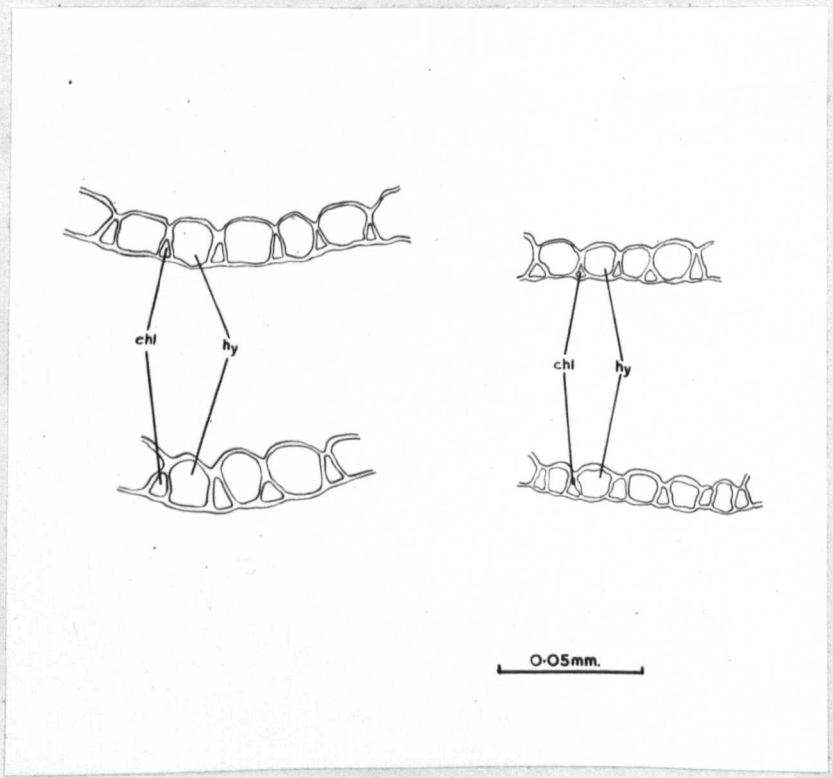

Fig. 5. Transverse sections of branch leaves of 4 specimens of S. recurvum showing the variation in degree of exposure of chlorophyllous cells within a single section.
chl, chlorophyllous cell. hy, hyaline cell.
The adaxial surface is uppermost.

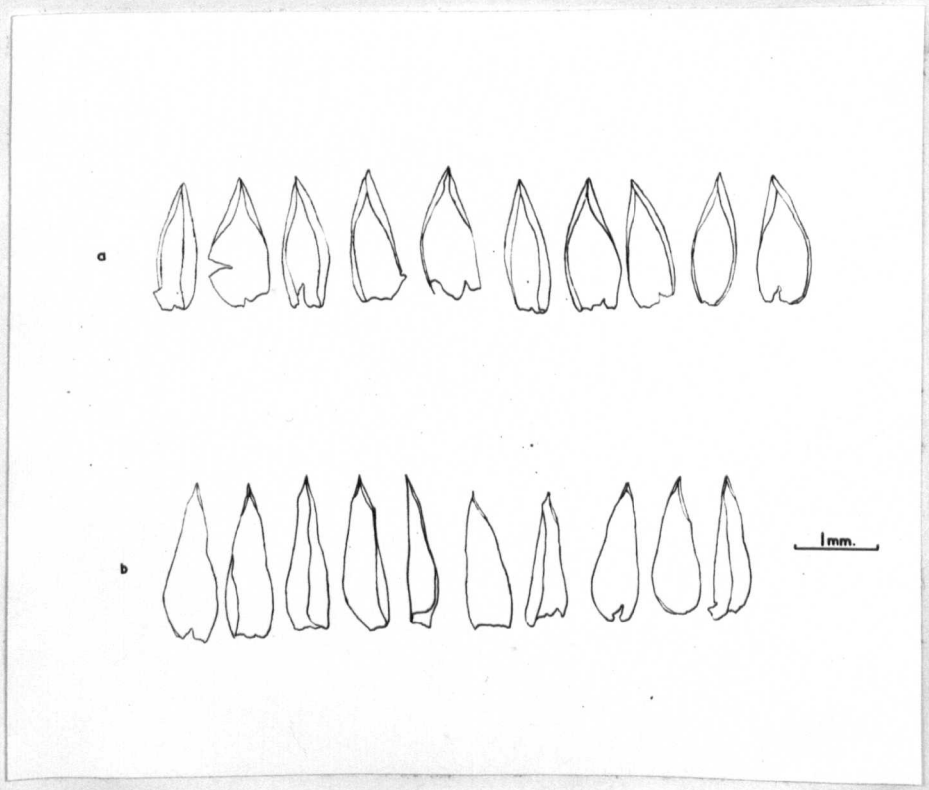

Fig. 6. Comparison of parts of leaf spectra of S. pulchrum (a) and S. recurvum (b), showing the difference in leaf shape. (10 leaves about the mid-point by length of a spreading branch)

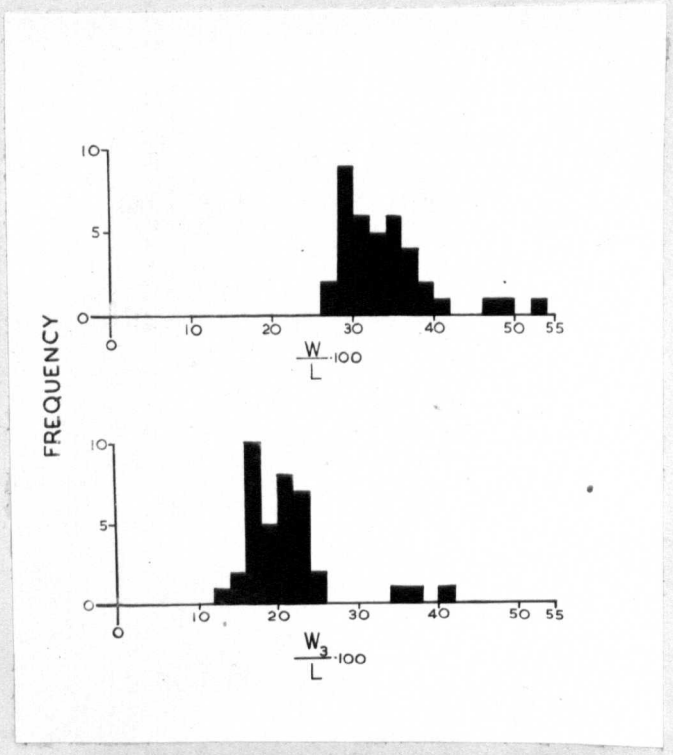

Fig. 7. Distribution of means of $\frac{W}{L} \cdot 100$ and $\frac{W_3}{L} \cdot 100$ for 38 samples of S. recurvum and S. pulchrum. The means are of 2 median leaves from one randomly selected spreading branch per sample.

W - maximum width , L - length ,

W_3 - width at one third the length from the apex

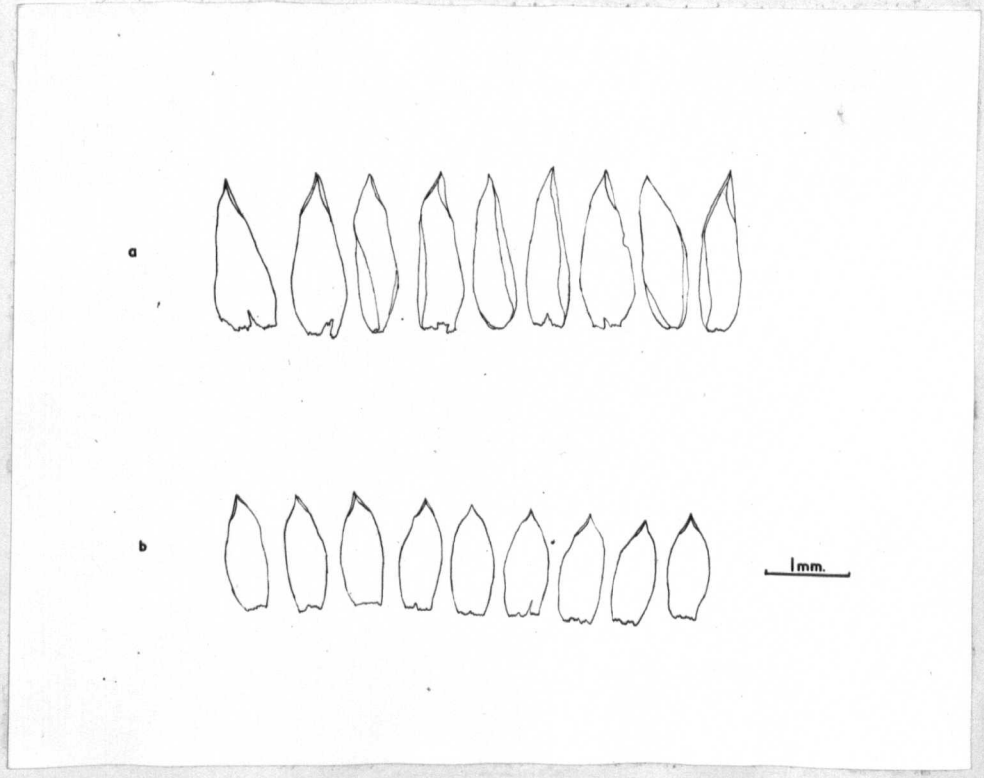

Fig. 8. Comparison of the shapes of antheridial and non-antheridial leaves from a sample of S. recurvum.

b - antheridial leaves

a - leaves from the corresponding position on a non-antheridial branch of the same stem

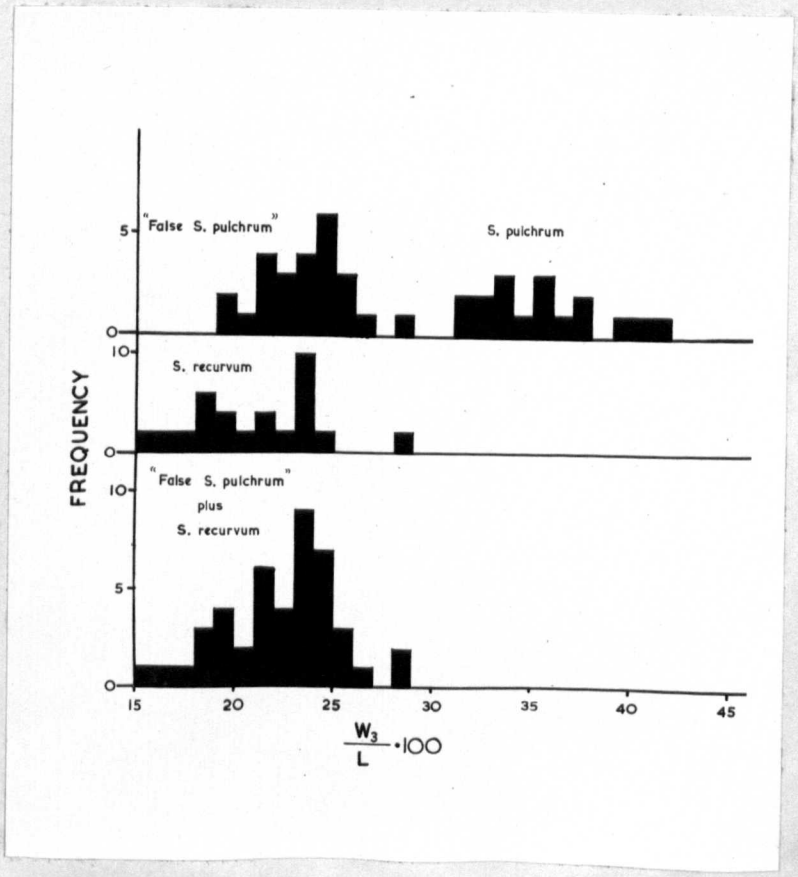

Fig. 9. Distribution of means of $\frac{W_3}{L} \cdot 100$ for 61 samples of S. recurvum and S. pulchrum; histograms for the two species are given separately, and a further histogram combines part of the S. pulchrum data with the S. recurvum data. Most samples consisted of two median leaves from each of 5 branches from each of 5 stems - total 50 leaves.

W_3 - width at one third the length from the apex, L - length

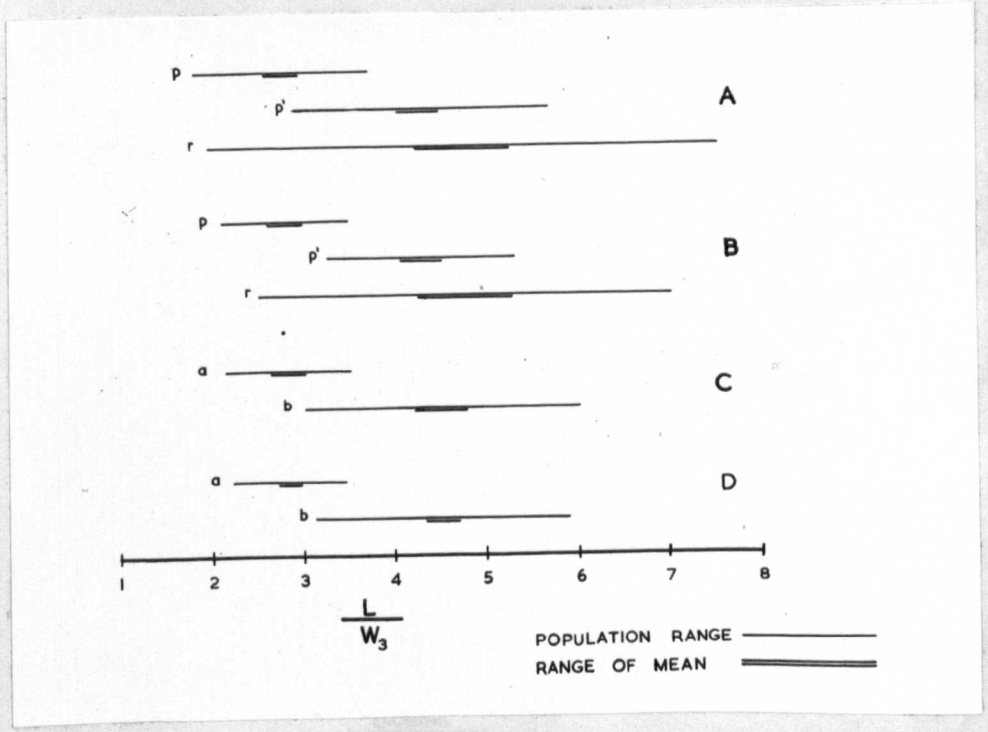

Fig 10. Calculated ranges of variation of $\frac{L}{W_3}$ in populations of S. pulchrum,(p); "false S. pulchrum", (p'); S. recurvum, (r); Group A, (a); Group B, (b); For explanation see Text p 39 .

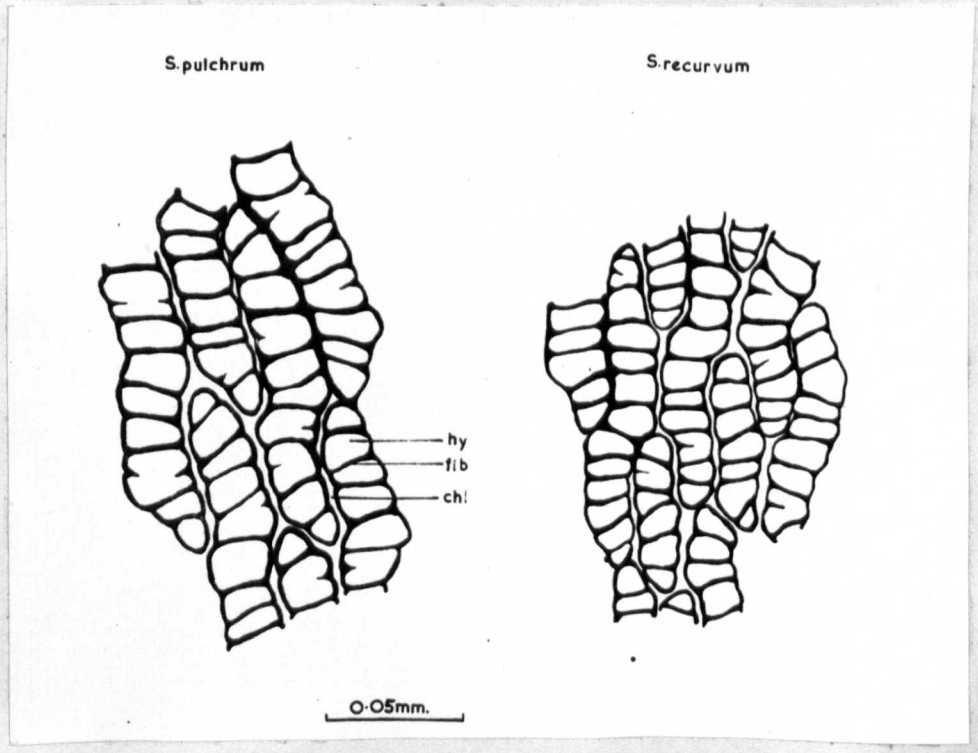

Fig. 11. Surface views of the adaxial side of parts of branch leaves of S. pulchrum and S. recurvum showing various degrees of fusion of the hyaline cells in a single leaf.

hy, hyaline cells; chl, chlorophyllous cell; fib, fibril.

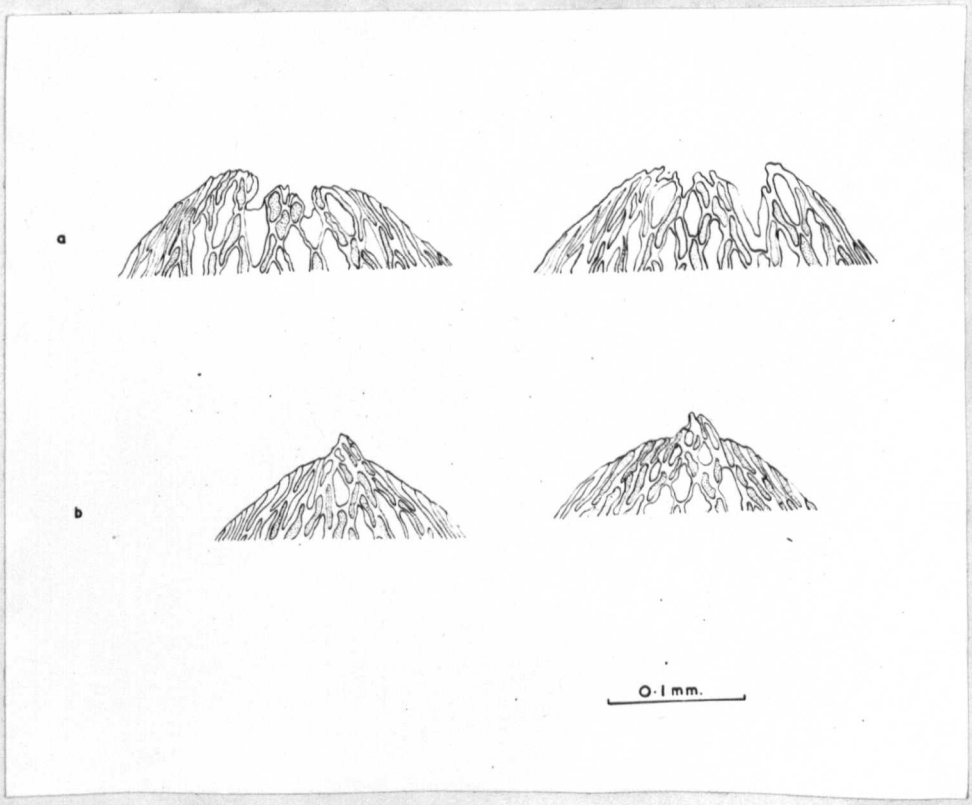

Fig. 12. Apices of stem leaves of (a), S. amblyphyllum, and (b), S. recurvum, showing obtuse and acute apices respectively. Chlorophyllous cells stippled.

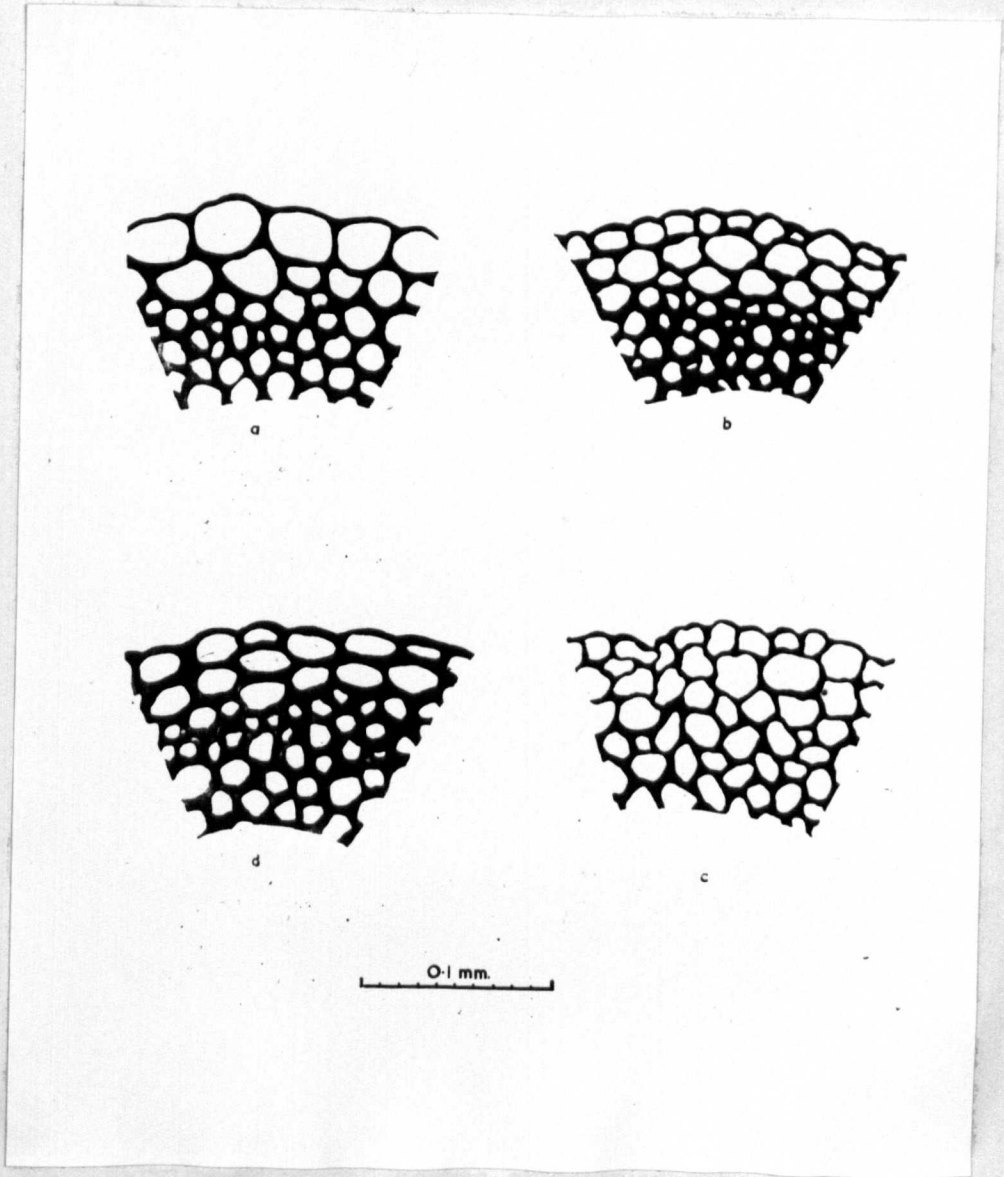

Fig. 13. Transverse sections of stems showing degrees of differentiation of the cortex. a, S. cuspidatum; b & c, S. recurvum; d, S. pulchrum.

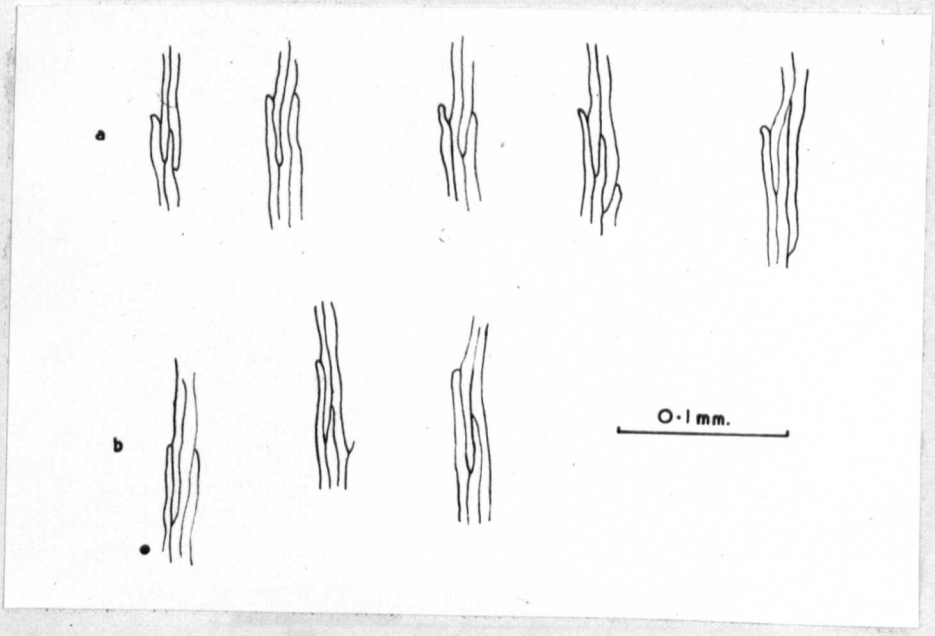

Fig. 14. Margins of branch leaves of S. cuspidatum showing serration due to projecting ends of cells. The leaf margin is at the left hand side of the figures.

a, distinct serration; b, rudimentary serration.

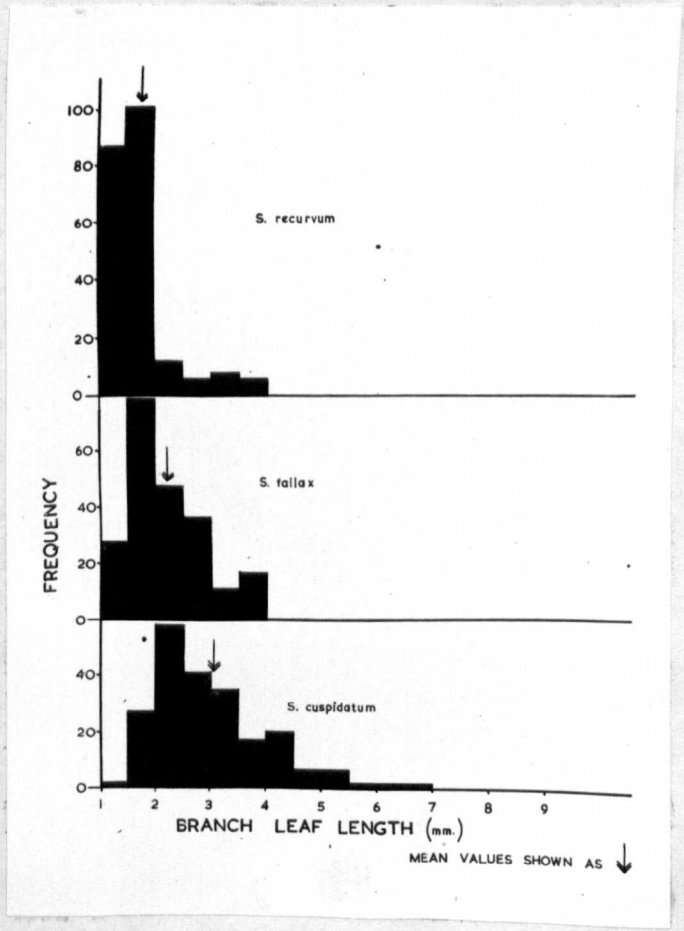

Fig. 15. Frequency distribution of lengths of median branch leaves of samples within Groups I, II and III, that is S. cuspidatum, S. fallax and S. recurvum respectively. (22 samples from each Group, 50 stems/sample, 2 median branch leaves/ stem)

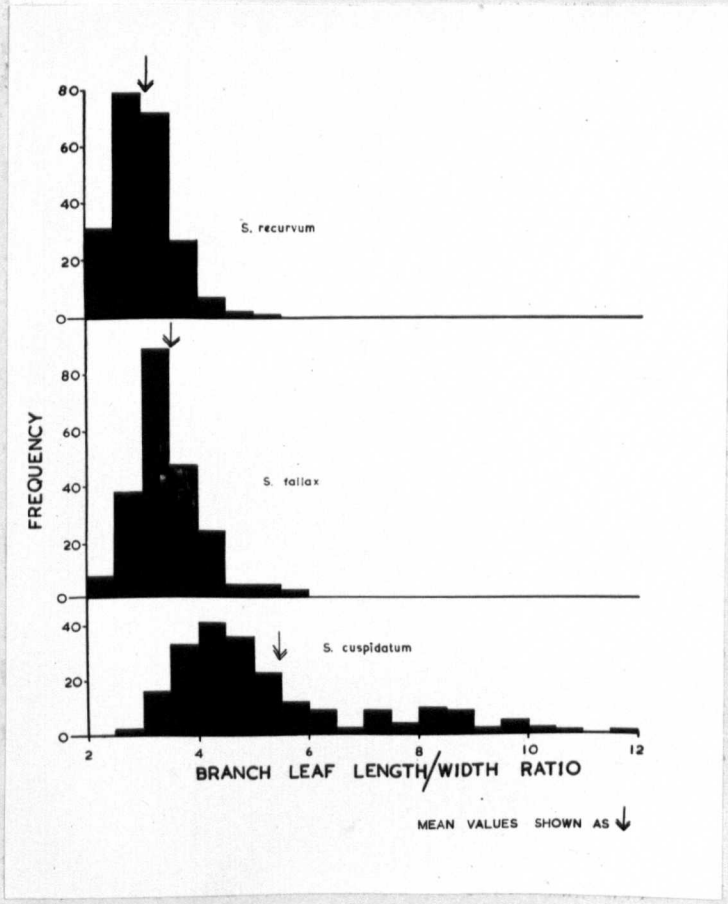

Fig. 16. Frequency distribution of length/width ratios of median branch leaves within Groups I, II & III (samples as in Fig. 15).

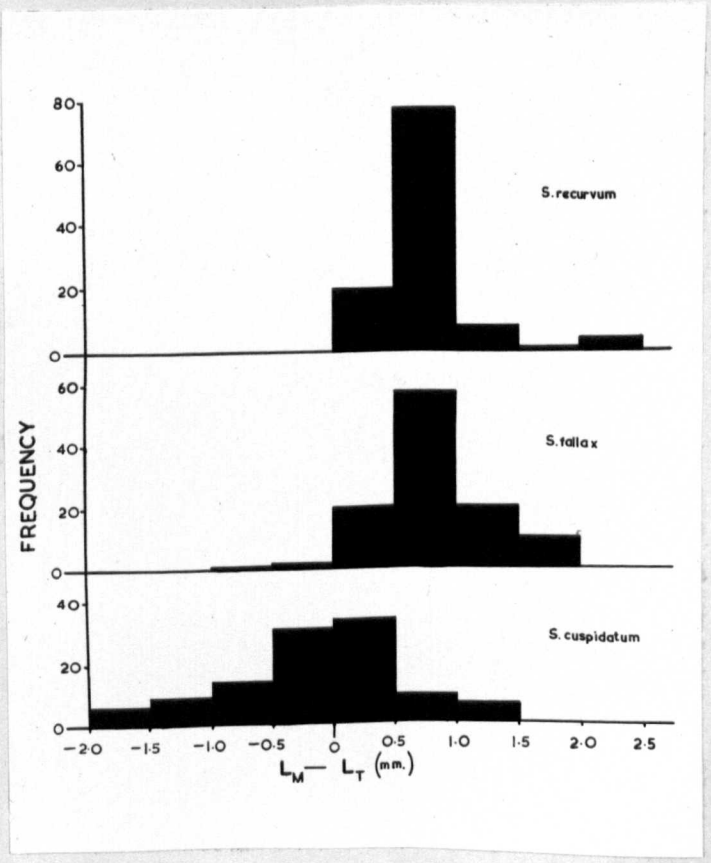

Fig. 17. Frequency distribution of values of median-terminal leaf length for individual branches of samples within Groups I, II & III. (22 samples/Group, 5 stems/sample, 2 median and 2 sub-terminal leaves from one random branch/stem)

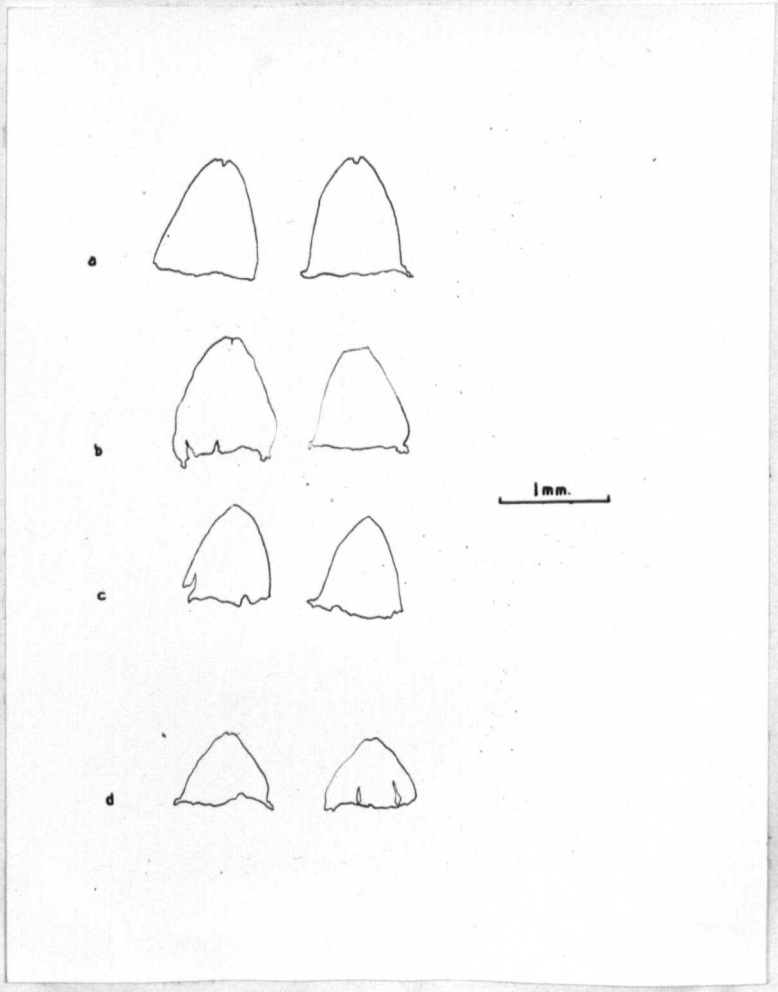

Fig. 18. Variation in shape of stem leaves of S. recurvum and S. amblyphyllum samples.

a -- triangular-(lingulate), obtuse apex

b -- isosceles-triangular, obtuse apex

c -- isosceles-triangular, acute apex

d -- equilateral-triangular, obtuse apex

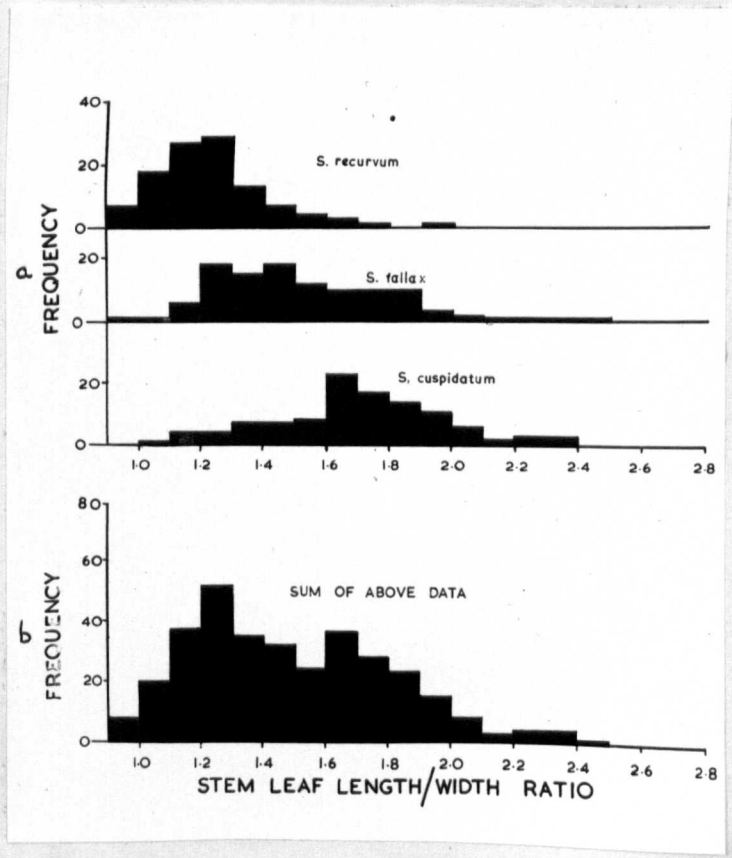

Fig. 19. Frequency distribution of length/width ratios of stem leaves of samples within Groups I, II & III. (22 samples/Group, 5 stems/sample, one leaf/stem)

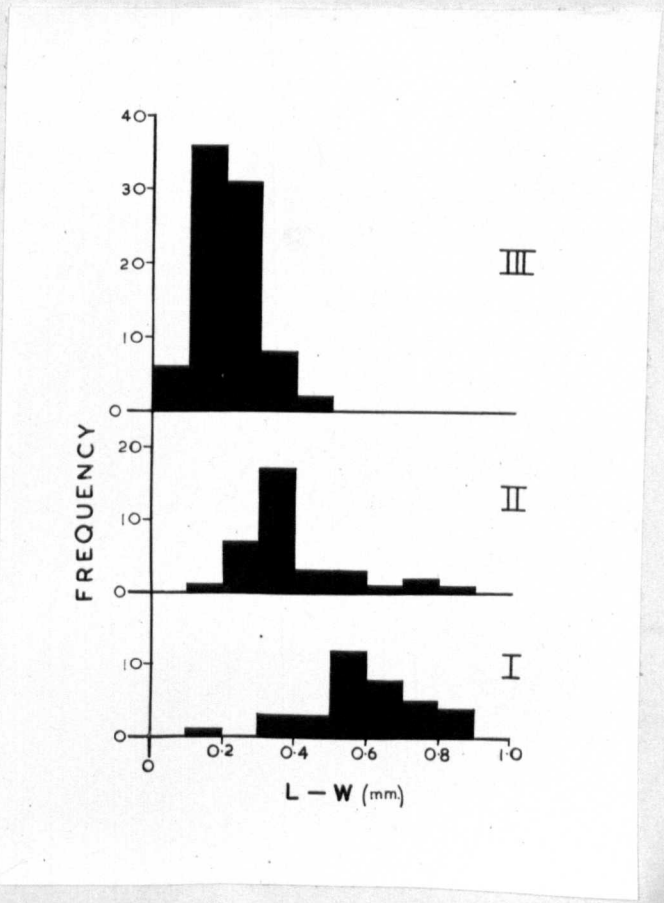

Fig. 20. Frequency distribution of sample means of length-width of stem leaves within Groups I, II & III. (33, 35 and 81 samples from Groups I, II and III respectively, and 5 stems/sample, one leaf/stem)

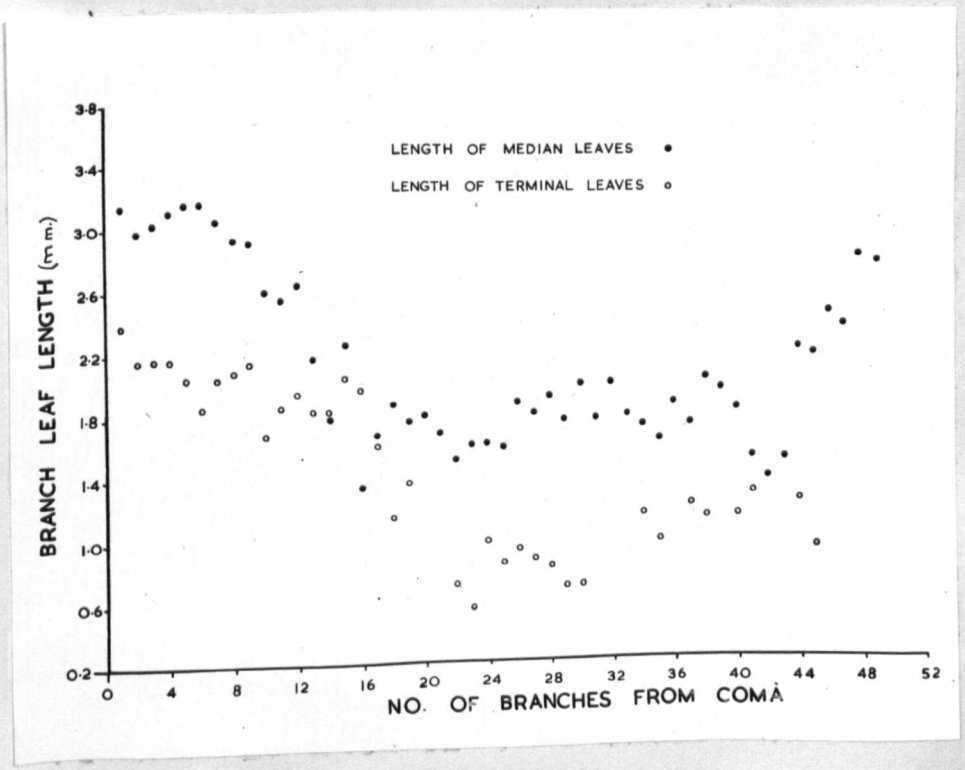

Fig. 21. Variation in length of median and terminal branch leaves with increasing distance from the coma in a stem of S. fallax. (given as the mean length of two leaves from the mid-point by length of a branch and of the 9th and 10th leaves from the distal end of the same branch; one branch per fascicle analysed)

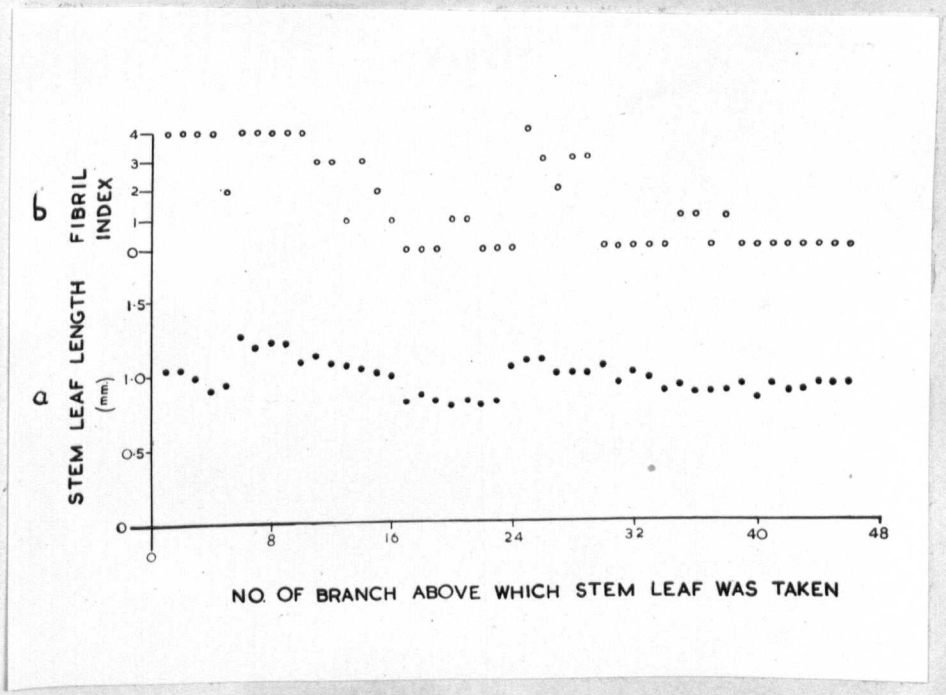

Fig. 22. Variation in fibril index and length of stem leaves with increasing distance from the coma in a stem of S. fallax. Fibril index is a measure of the number of fibrillose hyaline cells in a leaf - for key see p. 145. (One leaf was measured from each interfascicular stem portion, i.e., every fourth leaf.)

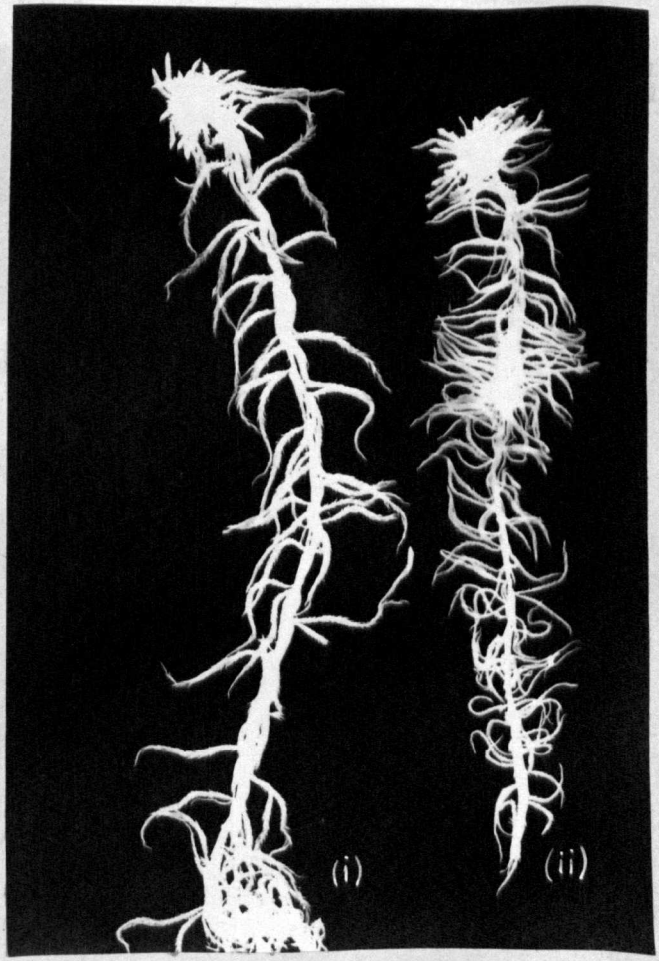

Plate 1. S. recurvum ((RIV) of Table 18) from an exposed habitat. (x 1)

(i) After 12 months exposed cultivation in field

(ii) After 12 months exposed cultivation in laboratory

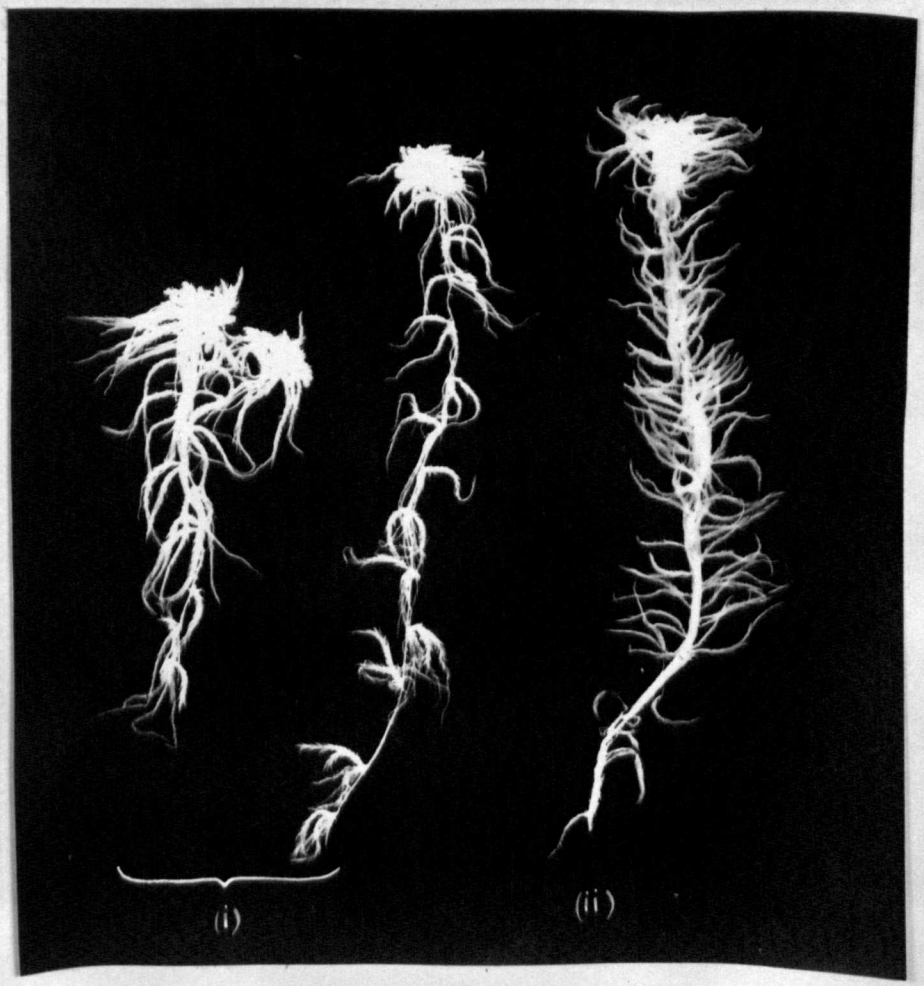

Plate 2. S. recurvum (RII) from an exposed habitat.(x 1)

(i) Original field sample (2 stems)

(ii) After 12 months exposed cultivation in laboratory

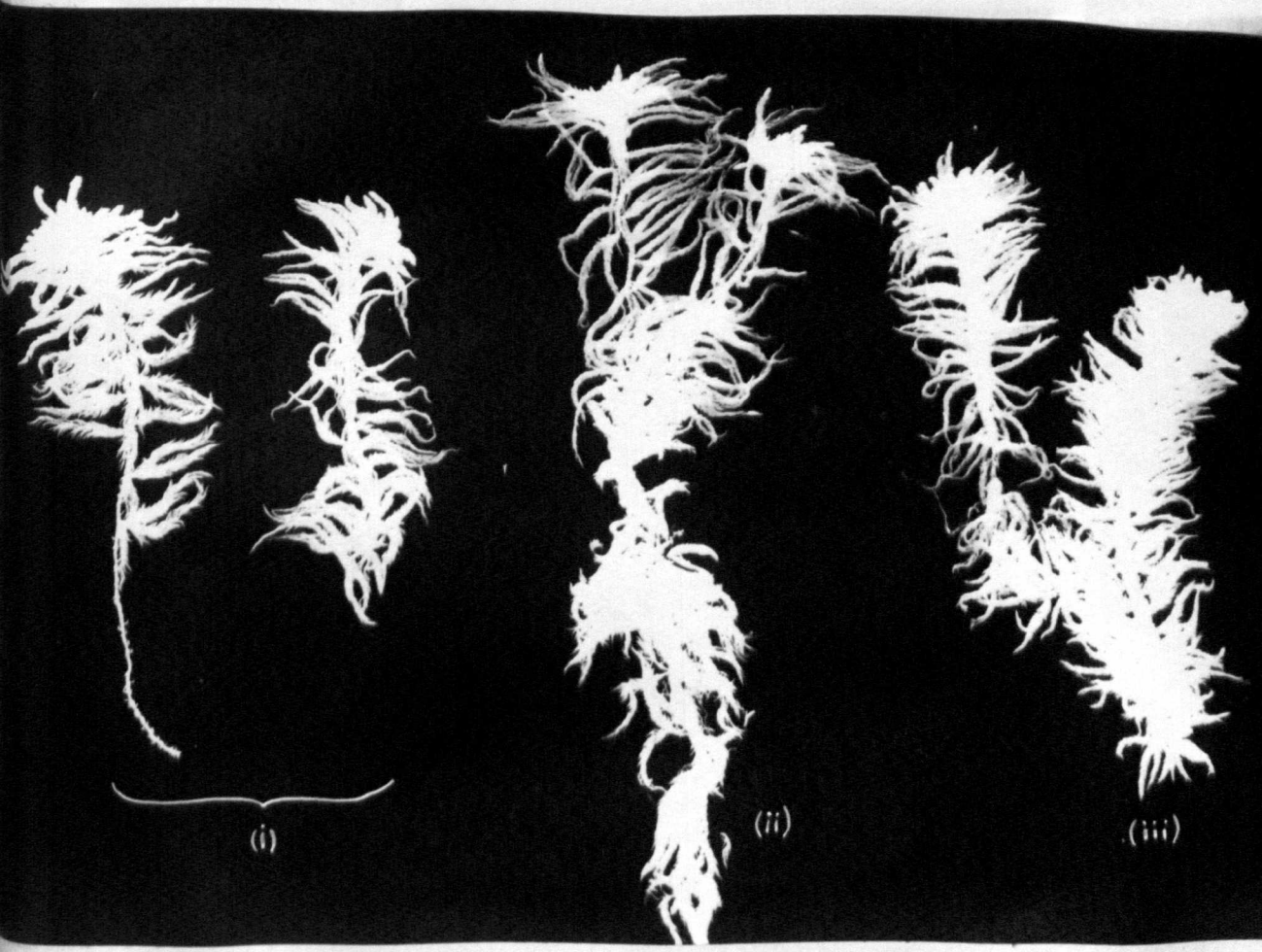

Plate 3. S. pulchrum ((PII) of Table 18) from an exposed habitat. (x 1)

(i) Original field sample (2 stems)

(ii) After 6 months exposed cultivation in laboratory

(iii) After 6 months exposed cultivation in green house

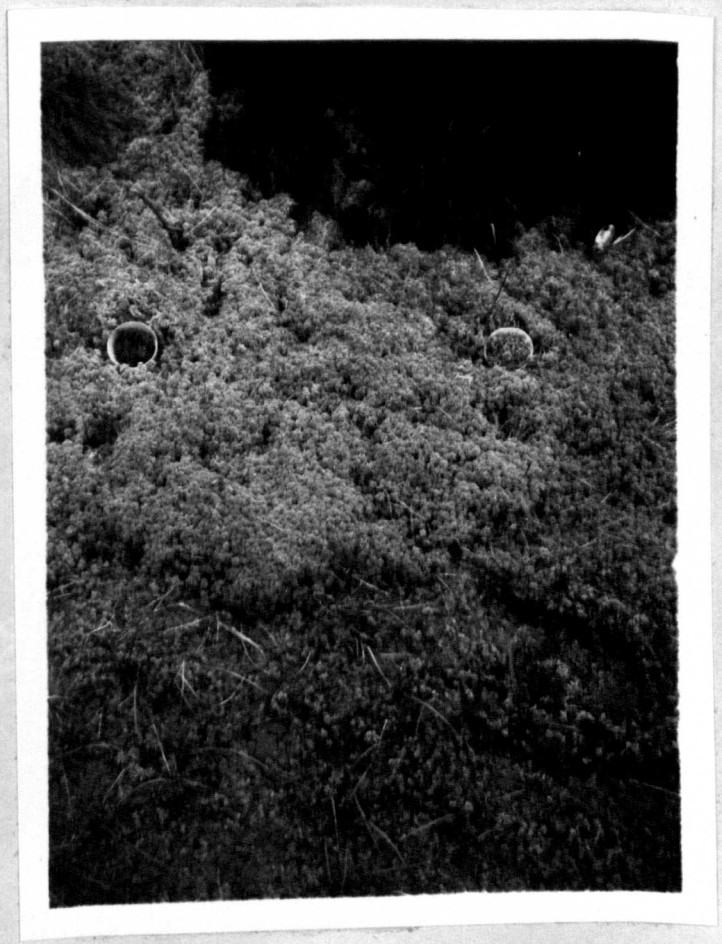

Plate 4. Part of bog behind Moel Wnion, near Bethesda, Caernarvonshire, showing transition from S. recurvum on a well drained margin (upper, light coloured part of plate) to S. cuspidatum in waterlogged channel. Two experimental pots (diameter 7 cm). are shown sunk in the S. recurvum.

Plate 5. S. recurvum (RIII) from an exposed habitat. (x 1)

(i) Original field sample

(ii) After 2 months immersion in a pool

(iii) After 5 months immersion in a pool

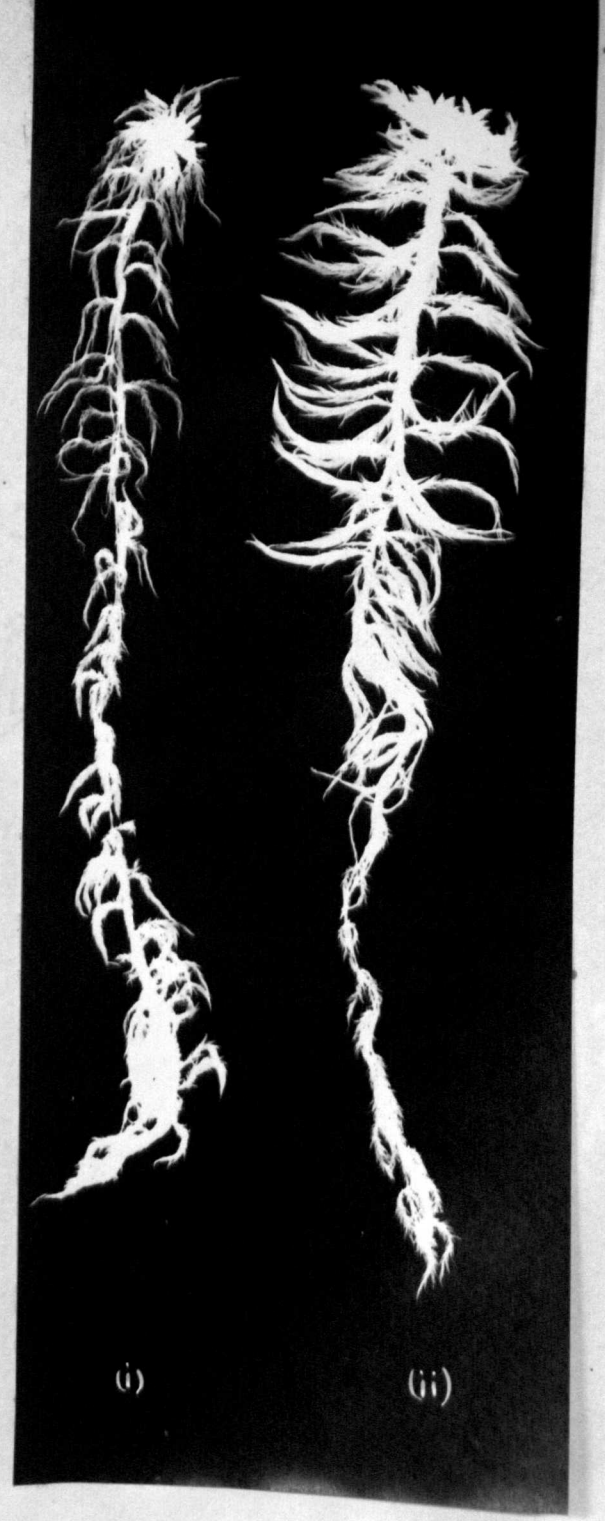

Plate 6. S. recurvum var. robustum (RV) froma a ditch. (x 1)
(i) Marginal plant with top 5 cm. above water level
(ii) Completely submerged central plant

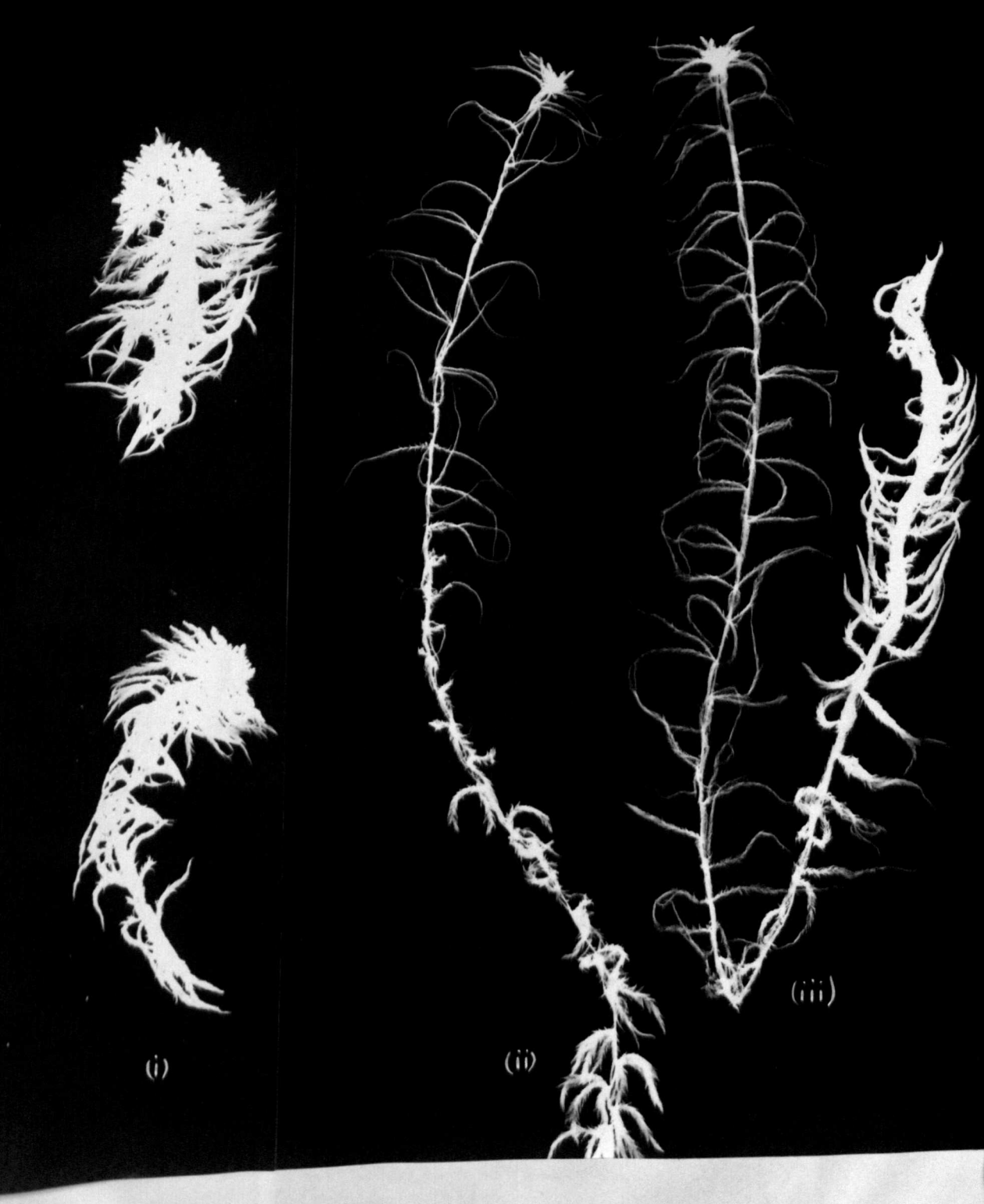

Plate 7. S. recurvum var. robustum (RI) from the same locality as that shown in Plate 6. (x 1)

(i) Original field sample (2 submerged stems)

(ii) After 2 months exposed cultivation in laboratory

(iii) After 5 months cultivation as in (ii)

(a)

(b)

Plate 8. S. cuspidatum (CVIII) from an exposed habitat after 1 month in (a) submerged indoor culture and (b) exposed indoor culture. The comas are viewed from above. (x 1)

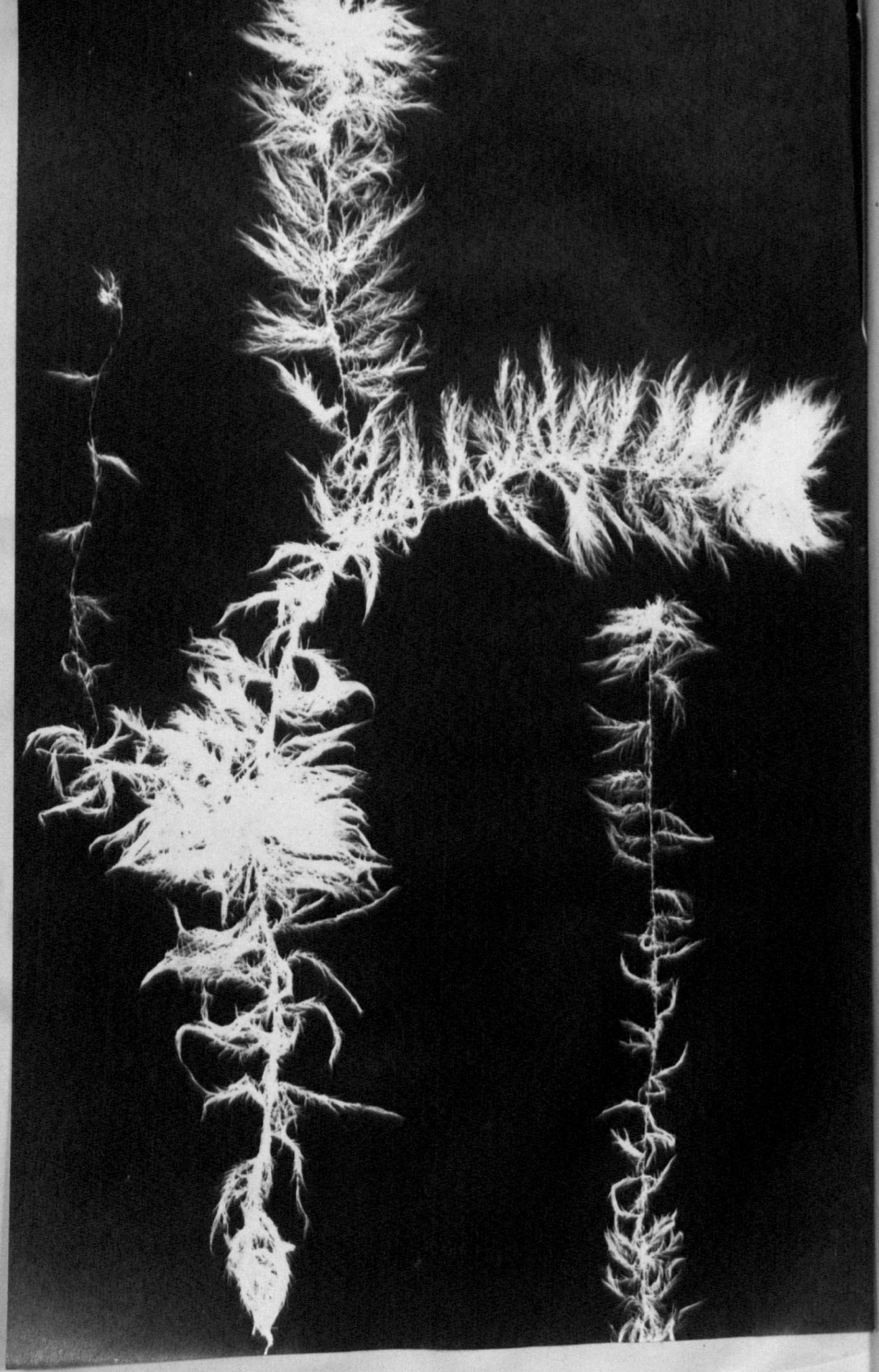

Plate 9. S. cuspidatum (CIV) from a submerged habitat. Two stems are shown the larger of which bears a slender new shoot produced from an old part of the stem - a method of vegetative reproduction referred to on p. 60. (x 1)

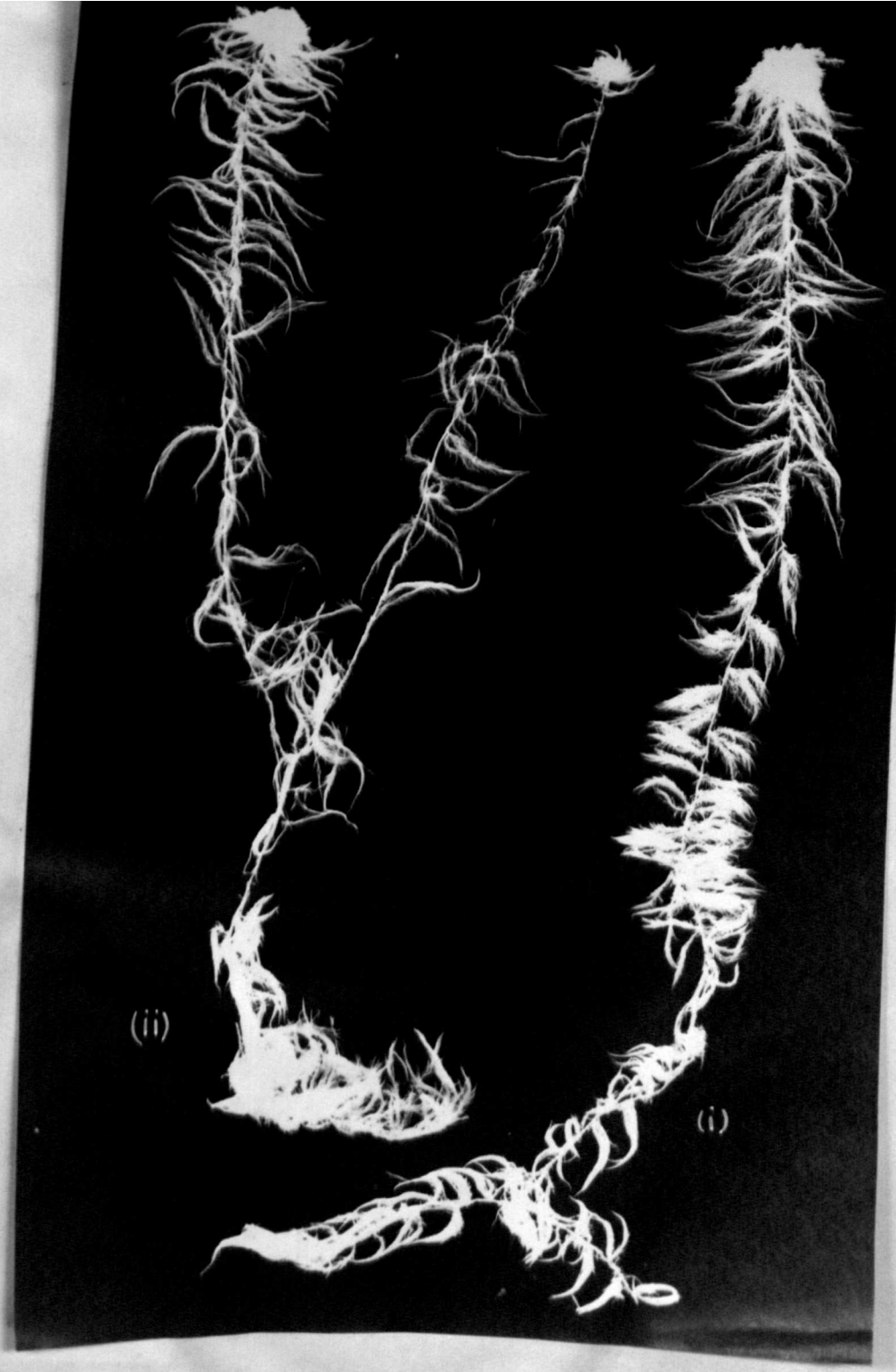

Plate 10. S. cuspidatum (CIV) as in Plate 9. (x 1)

(i) After 3 months exposed cultivation in green house

(ii) After 8 months exposed cultivation in green house

Plate 11. S. cuspidatum (CII) (x 1)

(i) Original sample from an exposed habitat

(ii) After 2 months submergence in a pool

(iii) As (ii) after a further 3 months submergence

(iv) Replicate of (ii) in another pool after 4 months

(v) Replicate of (ii) in another pool after 4 months

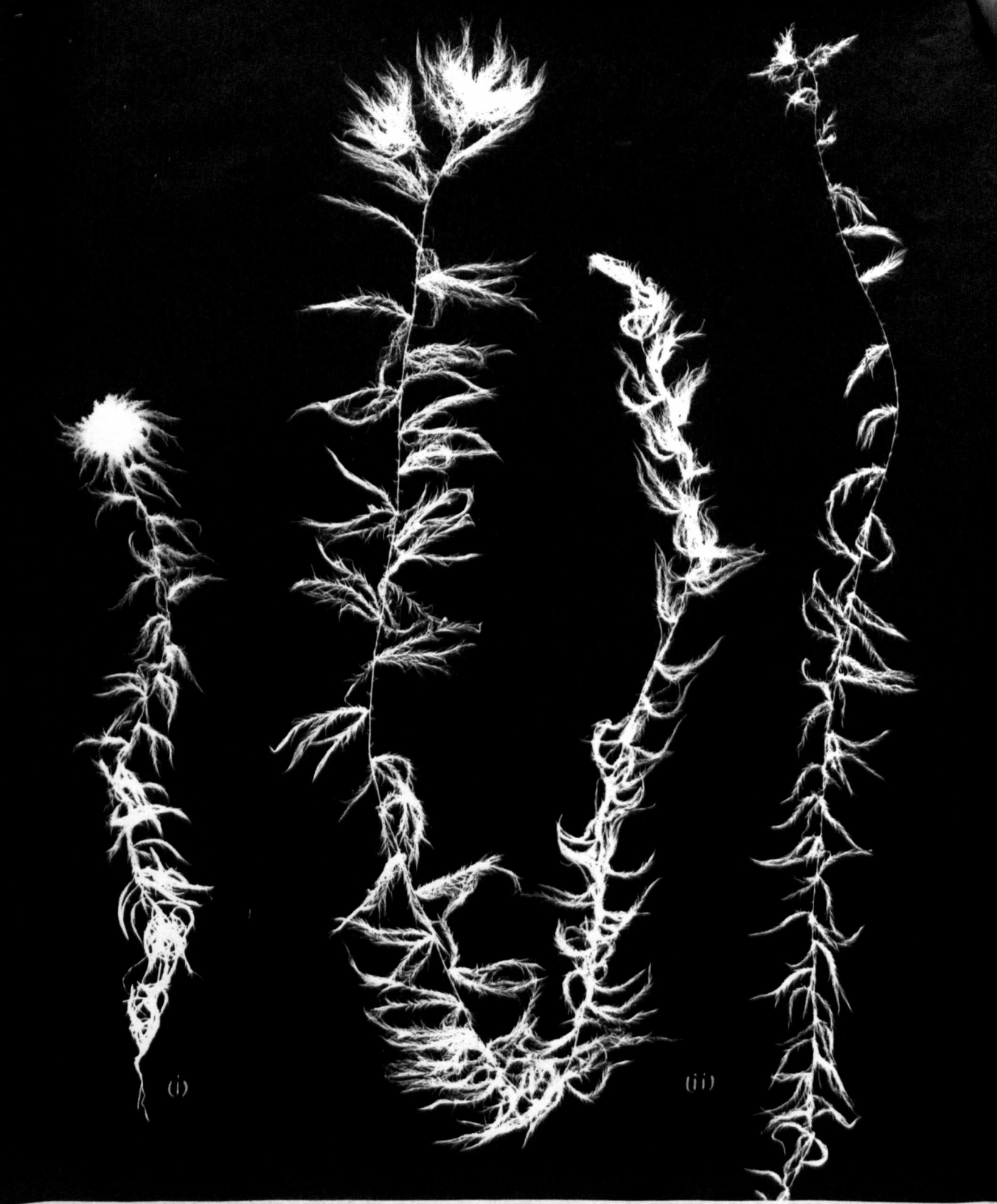

Plate 12. S. cuspidatum (CVIII) from an exposed habitat. (x 1)

(i) Original sample

(ii) Two stems from a sample grown for 4 months submerged in a pool