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EXPERIMENTAL TAXONOMY OF SOME DICRANUM SPECIES

By

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CONTENTS.

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INTRODUCTION.

The experimental taxonomy of flowering plants is now firmly established, and major advances in our knowledge of the Pteridophytes have come from similar studies. The present study is an attempt to apply the methods and approach of experimental taxonomy to a group of mosses which have not yet been investigated in this way.

The genus *Dicranum*, with its four common British species *D. scoparium* Hedw., *D. bonjeanii* De Not., *D. majus* Turn., and *D. fuscescens* Turn., was chosen for experimental study, as the problems of intra-specific variation and species boundaries are difficult to resolve by classical herbarium taxonomy. These difficulties are evident in herbaria, where misidentifications are sometimes found. Considerable confusion is experienced in naming the very variable *D. scoparium*, which sometimes appears to overlap or come close to the other three species. At the outset therefore, experiments were started to estimate to what extent the variation was genotypic, or environmentally controlled, and to determine the ecological background to the problem.

The results of the work will be presented as follows:-

(a) Chapter 1. An account of the four species and their variation as reflected in the literature.

(b) There will then follow sections on the main experimental approaches used in this study:-

Chapter 2. Ecology.
Chapter 3. Morphology and biometrical studies.
Chapter 4. Culture experiments (and further biometrics).
Chapter 5. Cytology.
Chapter 6. Reproductive Biology of the *Dicranum* group.

The experimental taxonomic sections will include detailed resumés of published information on mosses, applicable to the problems in *Dicranum*.

Finally, Chapter 7, a synthesis, based on all the information available, will be attempted.

CHAPTER 1.

ORTHODOX TAXONOMY.

Four species of the genus *Dicranum* have been studied in this investigation, *D. scoparium*, *D. majus*, *D. bonjeanii*, and *D. fuscescens*. The taxonomic treatment of these species in the literature has been carefully examined. Original descriptions have been consulted as well as more recent bryological literature. Various descriptions and interpretations of the four species, from the nineteenth century onwards, will be considered, then the problems of intra-specific variation will be reviewed.

A general description of typical plants, of each species, has been produced, to give an idea of the main diagnostic features mentioned in bryological works in general use. Table 1, 1. British and other floras in English are quoted, as they are easier to handle than German etc. The compound descriptions are largely from Braithwaite (1887), Dixon (1896), Grout (1928), and Nyholm (1954). Important key characters are underlined in the descriptions, which do not refer to intraspecific variation in any detail.

TABLE 1, 1. GENERAL DESCRIPTION OF SPECIES.

DICRANUM SCOPARIUM.

2-5" lax rigid tufts[1], *leaves shorter than D. majus*[3] up to *9 mm long*[2], leaves typically falcato-secund[2] also erecto-patent[3], (contradicted by Braithwaite, in which the leaves are stated to be rarely straight), serrated leaf margin[1] and back of nerve[1], rarely undulate[3], cells in upper part of leaf porose[4], leaf apex subulate with nerve reaching extreme tip, nerve 1/9-1/7th width leaf base[5], seta solitary, red[1], capsule subarcuate, not striate[1], exannulate[4].

Transverse sections of leaf show four serrated lamellae at the back of the nerve, lamina cells quadrate in cross section[4].

Habitats. Shady banks, rocks and heaths[1], decaying wood[2], bogs[3]. FOUND IN ALL V-C's.[1]

Male plants. Male plants distinct, more slender, with infl. terminal, or gemmiforme and nidulant in the tomentum below the perichaetium, bracts from an ovate base, narrowly linear[1].

D. BONJEANII.

4-6" lax tufts[1], leaves 4-6mm[3], erecto-patent[1], rarely curved[2], with serrated leaf margins[1], back of nerve only faintly toothed or smooth[1], upper leaf cells porose[1], nerve 1/13-1/11th width leaf base[5], nerve vanishing below apex[1], acuminate to acute (to obtuse[2]) leaf apex.

Seta solitary or 2 [4], yellow above, red below bearing striated slightly curved capsule[1]. Capsule exannulate.

Transverse sections of leaf show 2 (-4) low, smooth or serrated lamellae at back of nerve[4].

Habitats. Shady banks, bogs[1], calcareous districts on ground[1]. MAP 3.

Male plants. Male flower usually on separate plant[3].

D. MAJUS.

2-5" lax tufts[1], leaves very long up to 15 mm[2], (6-10 mm[3]), falcato-secund[1], serrulate leaf margin and back of nerve[1], with porose cells in the upper leaf[4], non-undulate[1], nerve c. 1/9 leaf base[5], leaf aristate with nerve reaching apex[1], polysetous with pale setae. Capsule scarcely striate, cernuous with a long beak[1], exannulate[4]. Lamina cells rectangular in cross section[4].

Habitats. Banks and rocks in alpine woods. MAP I.

Male plants. Male infl. gemmiforme, nidulant in the cauline tomentum[1].

D. FUSCESCENS.

1-4" dense tufts[1], leaves up to 7 mm[2], subsecond falcate crowded[1], secund or falcato-secund[3], leaf apex subulate, serrulate, non-undulate[1], with non-porose cells[4], nerve toothed at the back, reaching apex of leaf[1]. Seta solitary, dull yellow bearing striated arcuate capsule[1]. Annulate[4]. Nerve c. 2/5 leaf base[5].

Habitats. Wet rocks amongst grass in mountain districts[3]. MAP 2.

Male plants slender, intermixed with female[1].

Key to authorities.

BRAITHWAITE (1887)[1], GROUT (1928)[2], DIXON (1954)[3],
NYHOLM (1954)[4], JENSEN (1939)[5].

The main features of typical material of the four species may be summarised as follows. D. majus is the largest with falcato-secund leaves and differs from the other three in having many setae developing from one perichaetium, each seta bearing an exannulate cernuous capsule. Dicranum scoparium, with its variable leaf stance, usually has markedly serrate leaves with well developed lamellae at the back of the nerve.

and unlike *D. bonjeanii* is only rarely found with transversely undulate leaf apices. *D. bonjeanii* lacks the prominent lamellae of *D. scoparium* and has a wider leaf apex. Unlike the other species, in *D. bonjeanii* the nerve vanishes below the tip of the leaf and is weaker, occupying a small proportion of the leaf base, 1/13-1/11th compared with up to 2/5 in *D. fuscescens*. Both *D. scoparium* and *D. bonjeanii* have slightly curved exannulate capsules. *D. fuscescens* is usually the smallest species, often with falcato-secund leaves and it differs from the other three species in having non-porose upper cells in its serrated leaves. The striated annulate capsule is also distinct.

Taxonomic Opinion on the position of the species within the genus *Dicranum*.

An analysis of the taxonomic characters shows that there is a strong similarity between all four species. Hagen (1915) divided the genus *Dicranum* into several sections and all four species appeared in the Section *Dicrana scoparia*, (as quoted by Podpera (1954)). Recent work by Nyholm (1953) on the Fennoscandian *Dicranums* has suggested that *D. fuscescens* may be sufficiently dissimilar to warrant the formation of a separate group. The two sections containing the four species are characterised as follows:

Section 1. *Dicrana scoparia*.

Capsule without large-celled ring, nerve with ridges or stripes on dorsal side, cells in upper part of leaf with pores, cross section of lamina shows thickening between cells - *D. bonjeanii*, *D. majus*, *D. scoparium*.

Section 2. *Dicrana fuscescentia*.

Capsule with large-celled ring, leaves ± crispy, cells in the upper part of the leaf quadratic regular or irregular, lamina in cross section with slight thickenings between cells - *D. fuscescens*. Further evidence on the position of the four species in relation to each other will be discussed below.

Nomenclatural and Historical aspects.

Dicranum scoparium is described in Hedwig (1801), from a species in Linnaeus (1753). As the starting point of bryological nomenclature is Hedwig's 'Species muscorum frondosorum' (1801), his name appears as the authority. The species diagnosis reads '*Dicranum* trunco ascendente ramoso, foliis secundis recurvatis, pedunculis aggregatis, sporangiis erectiusculis = *D. scoparium*.' It should be noted that the leaves are described as falcato-secund and that the setae are aggregated. The habitats given by Hedwig are woods and fields and the distribution of the species is recorded as European and North American. The other three species under review were described after 1801 and at this date would undoubtedly have been placed in the Hedwigian *D. scoparium*.

The first description of *D. fuscescens* appears in Turner (1804) and the authority for *D. majus* is most often ascribed to Turner in the same work, but sometimes to Smith (1804). Martensson (1956), who investigated this nomenclatural problem thinks that it was most likely that Turner described D. majus first, and reported it to Smith. The characters used by Turner to separate these two species from D. scoparium are:

(a) D. fuscescens - seta solitary, capsule cernuous, nerve of leaf broad,

(b) D. majus - leaves falcato-secund with long acuminate serrulate leaf apex. Many setae produced from single perichaetium.

It is of interest to note that D. scoparium, as it is now recognised, has solitary setae, not aggregated, as stated by Hedwig in his original description, which included the polysetous D. majus Turn.

The fourth species under review was given the name D. bonjeanii by De Notaris in 1837. It had been described earlier under the name D. undulatum by Turner (1804), but this name is invalid. The name undulatum was used in 1804, by Turner, for what is now D. bergeri. (Personal communication from Dr. E.F. Warburg.) D. undulatum is in fact the correct name for this latter species. D. palustre Br. Eur. is also a name given to D. bonjeanii, it was first used however in 1847, 10 years after D. bonjeanii. The characters, used to separate bonjeanii from scoparium, in the 1837 description included: wider transversely undulate leaf apex and reduced lamellae at the back of the leaf. D. bonjeanii is also characterised by the fact that the nerve vanishes below the leaf tip.

Further species have been described within the original D. scoparium Hedw. but they are now, by general consent, reduced to synonymy within the appropriate species. Podpera (1954) has collected this information together in his 'Conspectus Muscorum Europaeorum' and it is summarised below:-

D. scoparium Hedw.

- D. recurvatum Schultz (1806)
- D. reflectens Brid. (1826)
- D. Dillenii Tayl. (1843)

D. fuscescens Turn.

- D. rupestre Bridel (1806)
- D. congestum Hubener (1833)
- D. Kinlayanum Schimper

D. bonjeanii De Not.

- D. subpalustre C.M. et Kindb. (1892)

D. spadiceum Zetterst. (1865) has been variously placed in the synonymy of the four species. Podpera places it in D. muehlenbeckii Bryol Eur. (1847), but this treatment is open to criticism and further discussion of this problematical taxon will follow below.

Before passing to a discussion of the variation within the species the question of the validity of the individual species must be raised. Differences in interpretation of the four species are found in the literature. For instance, W.J. Hooker in Vol. I of 'The English Flora of Sir James Smith' placed *D. majus*, *D. congestum* and *D. fuscescens* as varieties within *D. scoparium*, with the footnote 'Most authors consider the three varieties, above noticed, as distinct species, but I must confess myself unable to draw any decided line of distinction, they seem to pass gradually into each other.' Another example is given by Grout (1928) in the 'Moss Flora of North America', where *D. bonjeanii* is reduced to subspecific rank within *D. scoparium*. Generally however the validity of the taxa as four species is recognised by bryologists.

TABLE 1. 2.

WORLD DISTRIBUTION FROM PODPERA (1954).

DICRANUM SCOPARIUM

Europe - widespread

Asia - Caucasus, Kashmir, China, Japan.

N. America - widespread.

New Zealand

DICRANUM BONJEANII

Europe - widespread.

Asia - Caucasus, Siberia, Himalayan mounts.

N. America - Canada, Great Lakes, Rockies, West Coast.

DICRANUM FUSCESCENS

Europe - Spitzbergen, Iceland, common in European Mountains rarer in lowland. Carpathians, Tartra, Rumania, Bulgaria, Urals, Spain, Portugal.

Asia - Caucasus, Siberia, Japan.

N. America - Greenland to New England States, Alaska, West Coast to California.

DICRANUM MAJUS

Europe - N. widespread, rare in Spain and Czechoslovakia.

Asia - Caucasus, Siberia, Japan, China.

N. America - Greenland, New England, West Coast.

The Problem of Intraspecific Variation.

Podpera (1954) cites the European named forms, varieties, subspecies etc. and the following list shows the number of named taxa in each species:-

D. fuscescens	10
D. majus	3
D. scoparium	31
D. bonjeanii	14

The material used in this thesis, is mostly British and the study of the intraspecific variation will be mainly concerned with a limited part of the general distribution of the group. The Table 1. 2.of distribution indicates the narrow range of material under review, but it is hoped to clarify some of the problems by intensive studies of populations from various experimental, as well as taxonomic angles. The following is a list of intraspecific units (Table 1. 3.) commonly encountered in British herbaria, together with the main features which delimit them from typical forms, fitting the descriptions given above.

TABLE 1. 3. Intraspecific Units

(source of information shown after description.)

A. Dicranum scoparium.

1. Var. alpestre Hueben. - stem straight, leaves broader, straight or slightly secund, erecto-appressed, leaf margin entire or with a few obtuse teeth. Subalpine woods. (ex Braith.)

2. Var. *turfosum* Milde. - leaves erecto-patent, elongated, almost entire or with few obtuse teeth. Moorland bogs. (ex Braith.) These two varieties are found in Braithwaite (1887). Dixon (1954) unites the two taxa:-

3. Var. *spadiceum* Zett. - leaves erecto-patent appressed and rigid when dry, varying in length and acumination, entire, smooth at the back above or faintly denticulate, channelled or tubular in the upper part. Mountain woods, heaths and rocks on moorland. (ex Dixon.)

4. Var. *recurvatum* (Schultz) Brid. - slender, stem geniculate-ascending, falcato-secund leaves. Amongst grass on sandy ground. (ex Braith.)

5. Var. *orthophyllum* Brid. - leaves erect or subsecund, rigid, entire or distinctly serrated towards apex. Heaths. (ex Braith.) (Dixon states - leaves distinctly toothed. Bridel (1806), in his original description - leaves scarcely secund.)

6. Var. *paludosum* Schimp. - strongly radiculose, (usually white with tomentum Dixon), leaves short, broad, subsecund, (hardly falcate Dixon), sharply serrate, rugose at apex. Moorland bogs. (ex Braith.)

Varieties, 1, 2, 4, 5, and 6 appear in Braithwaite (1887).
3, 5 and 6 appear in Dixon (1954).
3 and 6 appear in the Check List of Bryophytes produced by the British Bryological Society - Richards and Wallace (1950).

B. Dicranum bonjeanii.

1. Var. juniperifolium (Sendt.) - densely leaved, robust rigid. Sandpit. (ex Braith.) (leaves broader erect, straight. Dixon)

2. Var. calcareum Braith. - shorter, leaves secund, subfalcate, with incurved margins, undulate only at apex and slightly serrated towards point. Calcareous ground. (ex Braith.)

3. Var. rugifolium Bosw. - leaves spreading, rugose above, undulate throughout greater part of length, contorted and twisted. Rare, bogs. (ex Dixon.)

4. forma falcata - material in the Oxford Herbarium, with falcato-secund leaves.

Varieties 1 and 2 appear in Braithwaite.
1, 2 and 3 in Dixon.
2 in BBS check-list.

C. Dicranum fuscescens.

1. Var. congestum Husnot.
(D. congestum Brid. in Braithwaite.)
leaves broader, with narrower nerve and irregular apical cells, leaf smooth or remotely serrate at apex. (ex Dixon.)

2. Var. falcifolium Braithw. - leaves all falcato-secund. (ex Dixon.)

Varieties 1 and 2 are found in all three sources.

D. *Dicranum majus*.

No varieties described in British material. (Forms with erect leaves, without serration, and with nearly quadrate cells are known from Scandinavia.)

Review of Intraspecific Variation.

A close examination of the varieties shows that they may be divided into several groups:-

1. UNDULATE FORMS.

Undulate specimens, within the group, are commonly regarded as *D. bonjeanii* and in many herbaria misidentifications are found. *D. scoparium* var. *paludosum* comes close to *D. bonjeanii* in form. Roell (1892-93), working in the North West United States concludes that *D. bonjeanii* is just as variable as *D. scoparium* and that it is impossible to distinguish between the two, 'naming is an arbitrary path'. Few bryologists would agree with this verdict, maintaining that the nerve-width to leaf-width ratio and the lamellar structure would separate specimens in practically all cases. Rugose forms of *D. bonjeanii* var. *rugifolium*, appear to be plants with extreme undulation involving the whole of the leaf and not just the leaf apex. Undulate *D. majus* is known from a Scandinavian locality and is described as var. *undulascens* Kindb. No specimens have been recorded from Britain. Undulate material of *D. fuscescens* has never been described; this is another respect in which *D. fuscescens* seems to be distinct from the other three species in the group.

2. LEAF STANCE VARIETIES.

D. scoparium contains populations with two extreme types of leaf stance, erecto-patent and falcato-secund, together with intermediates. The falcato-secund specimens can often approach D. majus in macromorphology and some difficulty exists in deciding the correct name for a herbarium specimen. Pilouz (1958) has shown that many of the specimens of D. majus from Czechoslovakia are in fact D. scoparium var. recurvatum. Nyholm (1954) suggests that doubtful D. majus and doubtful D. scoparium may be separated by examining cross sections of the leaves, the lamina cells of D. scoparium are quadrate, while those of D. majus are rectangular. No difficulty exists with fertile material as D. majus is polysetous.

Leaf sections are suggested too by Nyholm (1954), as a means of distinguishing between falcate forms of D. bonjeanii and D. scoparium, which are similar in appearance. In comparison with cross sections of leaves of D. scoparium, those of D. bonjeanii have fewer guide cells and only two lamellae which are less well developed.

Small specimens of falcato-secund D. scoparium also approach D. fuscescens. The areolation of the upper leaf is however different, D. scoparium having porose cells, as distinct from the quadrate cells of D. fuscescens.

In addition to falcato-secund types it should be noted that erecto-patent populations of D. bonjeanii and D. scoparium (vars.

juniperifolium and *orthophyllum* respectively) are described. Separation is accomplished by using the characters of the type viz. weak nerve and less well developed lamellae in *D. bonjeanii*. Erecto-patent forms without teeth will be dealt with in the next section.

It should be noted that it is forms of *D. scoparium* which cause confusion. By and large *D. bonjeanii*, *D. fuscescens*, and *D. majus* do not have interconnecting populations.

3. SERRATION VARIETIES.

Non-serrated or slightly serrated forms of all four species have been described and several of these occur in the British Isles, usually in upland areas, the var. *spadiceum* of *D. scoparium* and var. *congestum* of *D. fuscescens* being commonly found. No smooth varieties of *D. majus* are described but *D. bonjeanii* var. *calcareum*, which is slightly serrated towards the tip of the leaf, is known from several localities. *D. fuscescens* var. *congestum* and *D. scoparium* var. *spadiceum* can be distinguished by examining the upper areolation; the former has non-porose cells in the upper leaf. *D. bonjeanii* var. *calcareum* has the weak nerve of the type.

British material does not however reflect the enormous taxonomic difficulties in understanding the variation in the non-serrated forms of the four species. The variation must be viewed in a wider context to understand the full scope of the problem.

For instance, in Scandinavia all four species have non-serrated populations. Dixon (1954) reflecting upon British material writes that '*D. majus*, unlike its near allies, is not a very variable species'. But in Fennoscandia Nyholm (1954) reports that 'it is very variable perhaps the most variable of all, especially in the mountains'. High in the alpine regions are forms of this plant with short ± erect, very nearly smooth leaves, the upper cells almost quadrate, as distinct from the porose cells of the lowland material. *D. scoparium* has very similar variation, the leaf lamellae being extremely reduced and smooth. The var. *congestum* of *D. fuscescens* in Fennoscandia is also variable, and its forms include populations with irregular upper cells and ones with ± porose upper cells. The most important feature of upper areolation, porosity and non-porosity, breaks down with this sort of variation. Less difficulty is found with *D. bonjeanii* as its non-serrated populations are rarely found above the wooded region in Fennoscandia and it occupies a less varied range of habitats. Similar problems occur in the high Alps and Arctic regions, where non-serrated reduced forms of *Dicranum* grow, instead of the familiar serrated forms of the British Isles.

Another series of problems relating to these plants concerns the nomenclature and description. *D. scoparium* var. *spadiceum* was originally described as *D. spadiceum* Zett. (1865) and has been the cause of much argument. It is most commonly placed as a variety in *D. scoparium*, as in Dixon (1954) but since its original description has been included as var. spadiceum in D. congestum, D. majus, D. scoparium, D. fuscescens and D. muehlenbeckii, as well as a species in its own right. Nyholm (1954) regards it as a doubtful species having seen specimens from the Pyrenees identified by Zetterstedt. The description given by her is substantially that of D. scoparium var. spadiceum given above, with the additional information that the upper cells can be porose or irregular. It is seen that this variation cuts across the Dicrana scoparia/fuscescentia boundary suggested by Nyholm (1954) and reported above. Another difficult series of specimens are contained in D. angustum Lindb. (1891) described from Fennoscandian material and known too from N. America. One of its chief features is that the leaf has a weak nerve, which does not reach the leaf apex. They may be reduced forms of D. majus (see Nyholm 1954) or D. bonjeanii (supported by Podpera (1954)).

This review of the non-British material illustrates the difficulties of working with a limited range of material.

TABLE 1. 4.

UNDULATE FORMS

D. bonjeanii

D. scoparium v. *paludosum*

D. majus v. *undulascens*

FALCATE FORMS

Proportion of falcate leaves	Exclusively falcate leaves
D. bonjeanii f. *falcata*	
D. scoparium type	v. *recurvatum*
D. majus	*D. majus* type
D. fuscescens type	v. *falcifolium*

RUGOSE FORMS

D. bonjeanii v. *rugifolium*

NON SERRATED FORMS

D. bonjeanii v. *calcareum* in part

D. scoparium v. *spadiceum*

Orthophyllous specimens from Scandinavia of

D. majus

D. congestum (*D. fuscescens* v. *congestum*)

ECOLOGICAL CONSIDERATIONS.

The habitats of the species will be analysed in a later section but it is perhaps interesting to note that the four species are not recorded as ecologically separated. *D. scoparium* is reported from mountain woods as are *D. majus* and *D. fuscescens* and in bogs *D. bonjeanii* and *D. scoparium* may both be found.

The possibility of hybrids cannot be ruled out, if species are ecologically equivalent within communities and can occur in mixed tufts. No reference to hybrids, as a possible explanation for intermediates, has been found in the literature referring to *D. scoparium* and its allies.

CONCLUSION

So far as can be judged from the literature, the four species are generally regarded as good species. Intraspecific variation is said to be marked, especially in *D. scoparium*, which appears to overlap the other taxa to some extent. Table 1. 4 summarises the diagnostic characters. In the following sections the validity of the characters, as tested both by examination of herbarium material and by experimental methods, will be discussed in detail.

EXPERIMENTAL TAXONOMIC APPROACH.

INTRODUCTION.

Studies on the genus Dicranum, using classical taxonomic methods, have revealed considerable intraspecific variation and the underlying causes of this are largely speculative. Nyholm (1954) has stressed the need for experimental taxonomic work in Dicranum.

The following questions therefore have been the basis of this thesis:-

(a) Is the 'ecology' of each species different, do they occur in the same environment, if so do the 'problem' taxa occur in areas where the species grow together?

(b) Is the variation due to phenotypic plasticity or is it genetically controlled; are both types of variation found together? Do residual differences remain, if the samples are grown under the same conditions or does convergence continue until all the samples are alike?

(c) Do the species have cytological differences; can the variation be explained in terms of chromosomal variation in number or morphology?

(d) What is the breeding system in the group? Do populations in the same area cross, or are populations distinct entities?

The succeeding sections will show how far answers to the questions are possible.

CHAPTER II.

ECOLOGY.

Introduction.

Early in this investigation it was decided to concentrate on the cytology of the group, and this bias is reflected in the ecological results. A large number of fruiting populations has been collected, and the proportion of these in the ecological tables in no way reflects the frequency of fruiting in natural populations. A further range of habitats, containing sterile material, has also been studied to throw light on the morphological variation in different habitats. It was hoped too to provide information on whether the species are ecologically separated. To make the ecological picture of the *Dicranum* species clearer, literature accounts of communities, not specially studied, have been included in the review of the ecology.

Information on fruiting behaviour will be presented in the section on reproductive phenomena. Chapter VI.

Method.

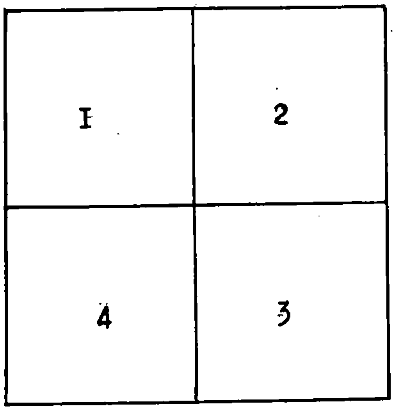
The ecological information about each population was collected in the following way:-

1. An area, with a good stand of *Dicranum*, was chosen, and a quadrat placed to include an area representative of that in which the moss was growing. The quadrats were usually 10 cm for tree boles and dead wood and 50-100 cm in woodlands and grasslands. The plants within each

quadrat were listed and each species was given an index of cover-abundance, according to the scale of Braun-Blanquet, see Poore (1955),

5 - covering more than 75% area
4 - 50-75%
3 - 25-50%
2 - 5-25%
1 - plentiful, but of small cover value
+ - sparsely present, cover small
x - present in habitat, not present in quadrat area

The quadrat was then doubled-up to give a total area four times as large as the original quadrat area:



any additional species were noted in 2, 3 and 4 and indexed according to their cover-abundance, within the appropriate quadrat. In this way a measure is obtained of whether the initial quadrat is typical of the surrounding areas. If only a few species are added to the list for the original quadrat, it is probably typical, but if a large number are found a transitional habitat could be involved. Any further additional species, not present in the four quadrats, but typical of the stand, were then listed.

2. A soil pit was prepared under the *Dioranum* tuft and details taken. Samples of soil were brought back to the laboratory and the pH value was determined using a pH meter (glass electode type), on a reconstituted airdry sample. (A carefully prepared soil/distilled water mixture was used; sufficient water was added to wet the soil thoroughly, but with no standing moisture on its surface.)

3. Slope, aspect and altitude were recorded for each site.

4. Notes on the communities, in which the *Dicranum* facies are a part, were taken, with particular reference to shading etc.

5. Details of fruiting behaviour, distribution of males, condition of capsules were then collected.

6. A herbarium specimen, composed of tufts from several clumps of *Dicranum*, was selected, and living material packed in 'polythene' bags for cultivation in the laboratories.

Results.

The results of the ecological investigations are presented as a series of tables. The species are arranged in the following order:- trees, shrubs, Ericoids, Monocotyledons, Dicotyledons, Pteridophytes, Bryophytes, and lichens. Ecological data are summarised too and full details are given of the localities. The tables are not 'association tables' in the sense of Poore (1955), where marked similarity in species composition is the main criterion, but are loose collections of quadrats united by some common factor. The following groups have been distinguished.

1a. Dune habitats.
2. Other habitats with basic soils.
3. Woodlands.
3a. Communities on dead wood.
3b. Living tree habitats.
4. Upland communities.
5. Samples with watertable at ground level.
6. Other communities, rocks etc.

Nomenclature. Clapham, Tutin and Warburg (1952) - Flowering plants and Ferns.
Richards and Wallace (1950) - Mosses.
Jones (1958) - Liverworts.
Duncan (1959) - Lichens.

1. <u>Dune Quadrats</u> (a distinct group of habitats with basic soils). TABLE 2.1.

<u>D. scoparium</u> has been found on several dune systems, always on fixed sand. The three quadrats show that the amount of bare sand is relatively small in one case, in the other two the vegetation was

completely closed. The large number of accompanying bryophyte species also indicates the fixed nature of the dunes; many of the species are recorded by Watson (1918) for 'somewhat' stable sandhills along the West Coast of England. Richards (1929) records *D. scoparium* var *orthophyllum* as locally abundant on grey dunes at Blakeney Point, Norfolk but it does not feature in his lists for yellow dunes. Similar results are found in Robertson (Ph.D. thesis unpubl.) for stabilised and mobile dunes at Ross Links in Northumberland.

The soil details, for all three samples, show upper layers with roots and humic material, above relatively unchanged sand. The depth of this humic layer showed considerable variation, being 9 cm on Newburgh Dunes and only 2-3 cm at Morfa Harlech. *D. scoparium* has never been found growing directly on unchanged sand, a humic layer is always found beneath the moss. An examination of the pH values for the three soil profiles shows a high pH in the lower sand of 355 and 488 (458 not recorded), but a more acid pH for the upper dune layers. The high pH of the lower samples is probably correlated with the considerable proportion of shells in the sand. The pH gradient is almost certainly due to leaching and is recorded by several workers as a major feature in the evolution of a dune soil. Salisbury (1922) showed that the pH of the youngest ridges at Blakeney Point was 7.1 (with max. 7.4), while surface samples from the oldest ridges had a pH of 6.4.Moore (1931) obtained comparable figures on a dune system in the Isle of Man; embryo dunes had a pH of 7.6 and dune heath a pH of 5.8.

D. majus has been recorded from fixed dunes at Morar, Invernessshire by E.C. Wallace, (specimen in Professor Richards' Herbarium) and D. bonjeanii from dune slacks Nr. Tain, E. Ross coll. A.C. Crundwell 28-6-51. It is unusual to find these species in this series of habitats.

The performance of D. scoparium, in the three areas, was not uniform. In 355 and 488 large patches of the moss were found, (with capsules in 355), whereas at Morfa Harlech, popn. 458, it was found in small quantity, in isolated tufts. This is probably correlated with the different water relations in the sand-hills; 355 and 488 were both much moister than 458.

TABLE 2. 1.

	355	458	488
Ulex europaeus	-	-	+
Aira praecox	+	-	-
Ammophil~~l~~a arenaria	3	2	-
Anthoxanthum odoratum	-	-	2
Carex arenaria	2	2	1
Festuca ovina	3	-	-
Festuca rubra	-	4	2
Luzula campestris	+	+	1
Poa pratensis	+	-	-
Anthyllis vulneraria	-	-	+
Arenaria serpyllifolia	-	-	+
Armeria maritima	-	-	3
Bellis perennis	-	2	-
Cardamine flexuosa	-	2	-
Cerastium vulgatum	2	-	2
Cirsium vulgare	+	-	-
Galium verum	-	1	2
Heracleum sphondyl~~l~~ium	+	-	-
Hypochaeris radicata	+	1	-
Lotus corniculatus	-	1	1
Ononis repens	+	1	-
Plantago lanceolata	-	1	-
P. maritima	-	-	2
Polygala serpyllifolia	2	-	-
Ranunculus bulbosus	-	2	-
Rumex acetosella	-	-	+
Sedum album	+	-	-
Senecio jacobaea	1	-	+
Succisa pratensis	-	+	-
Taraxacum officinale	+	2	-
Teucrium scorodonia	2	-	-
Thymus drucei	2	+	-
Trifolium repens	-	-	1
Veronica chamaedrys	+	-	-
Viola riviniana	2	-	-
Morella esculenta	-	+	-
Brachythecium albicans	-	+	-
Climacium dendroides	-	+	-
DICRANUM SCOPARIUM	3	2	2
Hylocomium splendens	-	3	+
Hypnum cupressiforme	1	-	-
Mnium undulatum	+	-	-
Pleurozium schreberi	1	-	-
Pseudoscleropodium purum	-	1	-
Rhodobryum roseum	2	-	-
Rhytidiadelphus squarrosus	-	2	3
R. triquetrus	-	+	-
Tortula ruraliformis	-	2	-
Calypogeia trichomanis	-	+	-
Lophocolea cuspidata	-	+	-

	355	458	488
Bare sand	-	2	-
Quadrat size	100	50	50
Aspect	NE	NW	E
Slope	5	5	-
Soil depth cms	20	2	15+

1. Dune samples.

(with Grid Ref.)

355 Warkworth, Northumberland.
coll. 29-6-59 NJ 260/056

458 Morfa Harlech, Merionethshire.
coll. 23-4-60 SH573/310.

488 Newburgh dunes, Aberdeenshire.
coll. 23-6-60.NK 005/252.

also Coll MJH. Tentsmuir dunes, Fife.
489 27-6-60.

Details of dune soils.

355 upper layers, 5 cm dark, many roots. pH 7.4.
lower 15+ cms dark humic on pure sand pH 8.0

458 2-3 cm humic layer pH 7.8.
lower, unchanged sand.

488 9 cm dark humic upper layers pH 6.2.
6+ sand. pH 7.0

(for localities see community lists.)

2. Other basic habitats. TABLE 2.2.

The quadrats given are representative of only a limited number of basic habitats in which Dicranum spp. are known to occur, and such communities as chalk grassland have not been studied.

Firstly samples 346, 352, and 353 will be considered as they are a distinct group collected on various Pennine limestone communities. All three are Festuca ovina-dominated with high Carex cover, and many calcicole bryophytes are present especially Ctenidium molluscum, Ditrichum flexicaule, Tortella tortuosa, and Camptothecium sericeum. Both Dicranum scoparium and D. bonjeanii were found in the Long Fell (346) sample and were exceedingly difficult to distinguish in the field. Watson (1960) studying chalk grassland also notes the difficulties of field identification. The pHs of the upper soils in these quadrats are relatively high in 346 and 353, but sample 352 shows evidence of leaching, with a surface pH of 6.4, especially as there were unaltered pieces of limestone below soil level. Calcicole flowering plants in the quadrats include Helictotrichon pratense, Galium pumilum, Gentiana verna, Myosotis alpestris, and Primula farinosa. Ratcliffe (1959) records D. scoparium from basic grasslands in N. Wales and further localities are given in Proctor (1958) and Pigott (1955) for different parts of Britain.

Sample 354 was taken from calcareous hummock systems on Widdybank Fell, Upper Teesdale, and was found on examination to be a mixed gathering of D. scoparium and D. bonjeanii. Both species occur on the hummock tops. Pigott (1956) has described the vegetation of these hummocks, famous for their rich flora of rare species, including *Primula farinosa*, *Bartsia alpina*, *Saxifraga aizoides* and *Tofieldia pusilla*. The pH of the soil immediately below the *Dicranum* tufts was 7.1, which together with the presence of *Calluna* probably indicates a certain amount of leaching.

Samples 440, 446 and 448 collected at lower altitudes are from communities in Shropshire, Merionethshire and Denbighshire. All were from communities on boulder-scree of basic rocks, all on steep slopes. The chief characteristics of these populations was the high cover of bryophytes, with relatively few flowering plants.

TABLE 2.2.

Basic Habitats	Grasslands			Hummocks	Scree Communities			Woodland
Species	346	352	353	354	440	446	448	495
Crataegus monogyna	-	-	-	-	-	-	x	x
Calluna vulgaris	-	-	-	2	-	-	-	-
Vaccinium mytillus	x	-	-	-	-	-	-	-
Agrostis tenuis	x	-	-	-	-	-	-	2
Brachypodium sylvaticum	-	-	-	-	-	-	x	3
Briza media	-	1	2	3	-	-	-	-
Carex capillaris	-	-	2	-	-	-	-	-
C. caryophyllea	1	3	2	3	-	-	-	-
C. flava	-	x	-	-	-	-	-	-
C. hostiana	-	-	-	x	-	-	-	-
C. lepidocarpa	-	-	x	-	-	-	-	-
C. panicea	-	2	-	2	-	-	-	-
C. pulicaris	-	2	2	1	-	-	-	-
Dactylis glomerata	-	-	-	-	-	-	x	-
Deschampsia caespitosa	4	-	-	-	-	-	-	-
Festuca ovina	5	5	3	5	-	-	-	3
Helictotrichon pratense	-	-	2	-	-	-	-	-
Kobresia simpliciuscula	-	-	2	-	-	-	-	-
Luzula campestris	2	-	-	-	-	-	-	-
Sesleria caerulea	-	-	3	1	-	-	-	x
Sieglingia decumbens	-	1	-	2	-	-	-	-
Tofieldia pusilla	-	-	-	+	-	-	-	-
Achillea millefolia	x	x	-	-	-	-	-	-
Alchemilla vestita	x	x	x	-	-	-	-	-
Bartsia alpina	-	-	-	2	-	-	-	-
Bellis perennis	-	1	x	-	-	-	-	-
Campanula rotundifolia	1	1	-	-	-	-	-	-
Cardamine flexuosa	-	-	-	-	-	x	-	-
Cerastium vulgatum	x	-	-	-	-	-	-	-
Cochleria alpina	2	-	-	-	-	-	-	-
Digitalis purpurea	-	-	-	-	-	1	-	-
Epilobium montanum	-	-	-	-	-	x	-	-
Euphrasia officinale agg.	-	x	-	+	-	-	-	-
Galium aparine	-	-	-	-	-	x	-	-
G. pumilum inc. sterneri	1	2	1	-	-	-	-	-
G. verum	-	-	-	-	-	-	-	2
Gentiana verna	-	2	2	-	-	-	-	-
Geranium robertianum	-	-	-	-	-	1	-	-
Glechoma hederacea	-	-	-	-	-	-	-	-
Helianthemum chamaecistus	-	-	1	-	-	-	-	2
Hieracium pilosella	-	2	x	-	-	-	-	2
Hypericum perforatum	-	-	-	-	-	-	-	+
Linum catharticum	-	1	+	1	-	-	x	-
Lotus corniculatus	-	x	x	-	-	-	-	-
Malva sylvestris	-	-	-	-	-	-	-	x
Minuartia verna	-	x	-	-	-	-	-	-
Myosotis alpestris	x	-	-	-	-	-	-	-
Oxalis acetosella	-	-	-	-	-	-	x	-
Plantago lanceolata	-	2	x	-	-	-	-	-
P. maritima	-	x	+	-	-	-	-	-
Polygala vulgaris	-	-	-	+	-	-	-	-
Potentilla erecta	-	2	+	1	-	-	-	-
Primula farinosa	-	-	-	2	-	-	-	-
Prunella vulgaris	-	1	x	2	-	-	-	-
Ranunculus acris	-	x	-	-	-	-	-	-
Rubus fruticosus	-	-	-	-	-	x	-	-
Saxifraga asoides	-	-	-	2	-	-	-	-
S. hypnoides	x	-	-	-	-	-	-	-
Succisa pratensis	-	-	-	3	-	-	-	-
Taraxicum officinale	-	+	-	-	-	-	x	x
Teucrium scorodonia	-	-	-	-	+	2	-	-
Thymus drucei	2	2	2	-	-	-	x	2
Trifolium repens	2	1	-	-	-	-	-	-
Umbilicus rupestris	-	-	-	-	-	x	-	-
Urtica dioica	-	-	-	-	-	x	-	-
Verbascum thapsus	-	-	-	-	-	-	x	-
Viola lutea	-	1	-	-	-	-	-	-
V. riviniana	2	1	1	-	-	-	x	+
Asplenium trichomanes	-	-	-	-	+	-	2	-
Selaginella selaginoides	x	2	2	+	-	-	-	-
Bare ground	-	3	-	-	-	2	-	-
Bartramia pomiformis	-	-	-	-	-	x	-	-
Brachythecium rutabulum	-	-	-	-	-	2	-	-
Breutelia chrysocoma	-	-	-	x	-	-	-	-
Bryum capillare	-	-	-	-	-	-	2	-
B. pallens	-	-	-	x	-	-	-	-
Camptothecium sericeum	+	-	-	-	-	-	3	-
Campylium stellatum	-	-	-	x	-	-	-	-
Cratoneuron commutatum	-	-	-	x	-	-	-	-
Ctenidium molluscum	+	-	+	x	+	-	-	-
<u>Dicranum bonjeanii</u>	+	-	-	}2	-	-	-	2
<u>D. scoparium</u>	2	2	2		2	3	3	2
Ditrichum flexicaule	+	2	-	-	-	-	-	-
Fissidens adiantoides	-	-	+	x	-	-	-	-
F. cristatus	-	-	-	-	+	-	-	-
Grimmia pulvinata	-	-	-	-	+	-	1	-
Hylocomium splendens	-	-	-	-	-	-	-	2
Hypnum cupressiforme	+	-	-	x	-	+	2	-
Isothecium myosuroides	-	-	-	-	-	3	-	-
Neckera crispa	-	-	-	-	+	-	2	-
Pleurozium schreberi	+	x	-	-	-	-	-	-
Polytrichum formosum	-	-	-	-	-	x	-	-
Pseudoscleropodium purum	+	-	-	-	-	-	2	2
Rhacomitrium heterostichum	-	-	-	-	-	2	-	-
R. lanuginosum	x	1	2	2	-	-	-	-
Rhodobryum roseum	-	-	-	-	-	-	-	+
Rhytidiadelphus loreus	+	-	-	-	-	-	-	-
R. squarrosus	-	-	-	-	-	-	-	2
R. triquetrus	-	-	-	-	+	+	2	-
Thuidium tamariscinum	+	-	-	-	-	-	-	-
Tortella tortuosa	x	-	+	-	+	-	x	-
Tortula subulata	-	-	-	-	+	-	-	-
Frullania tamarisci	x	-	-	-	-	-	2	-
Lophocolea cuspidata	-	-	-	-	-	1	-	-
Quadrat size cms.	400	1000	1000	1000	-	1000	1000	1000
Aspect	WSW	W	W	-	NW	W	NW	S
Slope	20°	5°	2°	-	30°	34°	25°	c10°
Altitude	2350'	1650'	1650'	1300'	650'	500'	c1000'	300'
Date	10/6/59	26/6/59	26/6/59	26/6/59	10/4/60	11/4/60	12/4/60	30/11/60

TABLE 2. 2. continued

2. Other Basic habitats.

Popn. No.	Locality	Grid Ref.
200/210/211	Boulder scree, Ebbor Gorge, Somerset.	ST 528/492
274	Grassland, Burington Combe, Somerset.	ST 482/583
346	Limestone grassland, Little Fell, Westmorland.	NY 780/223
348	Limestone rock, Little Fell.	
349	Lead spoil heaps, Hilton Beck, Little Fell.	
352	Limestone grassland, Widdybank Fell, Durham.	NY 815/300
353	Sugar limestone, Widdybank Fell.	NY 820/293
354	Calc. hummocks, Widdybank Farm, Durham.	NY 837/298
440	Rocks, Llanymynech Hill, Oswestry, Montgomeryshire.	SJ 267/221
446	Scree, Breidden Hill, Nr. Shrewsbury, Shropshire.	SJ 290/144
448	Eglwyseg Rocks, Llangollen, Denbighshire.	SJ 22-/44-
460	Winchester Hill, Hampshire. 5/60. Coll. J. Paton.	
495	Woodland clearing, Wychwood, Nr. Whitney, Oxford.	SP 347/172

SOIL DETAILS.

* 346 6 cm dark, homogenous soil. pH 7.2

352 19 cm brownish soil with a few unaltered limestone fragments. pH 6.4.

o 353 20-35 cm dark soil, unlayered, with limestone fragments. pH 7.2

o 354 10 cm upper layers, very tenacious, many roots, pH 7.1,
15 cm lower, as above but more gritty.

440, 446, 448, very small amount of dark powdery soil.
440. pH 6.9. 446. pH 5.8. * 448. pH 7.9.

* 495 2 cm brown loam. 10 cm clay.

* Effervescence with dilute HCl.
o No reaction with HCl.

Pockets of shallow soil were found under the *Dicranum* turf with the following pHs,

440 6.9, 448 7.9, 446 5.8. In 446, with the lowest pH a certain amount of leaching is further indicated by the presence of *Digitalis*, a pronounced calcifuge species. These three populations contained only *D. scoparium*.

A mixture of *D. scoparium* and *D. bonjeanii* is however recorded in quadrat 495 from Wychwood, Oxfordshire. The *Festuca ovina*/*Brachypodium sylvaticum* dominated slope is the site of an old stone quarry and is partially shaded by *Corylus* and *Crataegus monogyna*. Effervescence when dilute HCl is added to a soil sample shows that there is free carbonate in the upper layers of the soil, which had a pH of 7.5 for the surface loam.

It is clear from the results that *D. scoparium* and *D. bonjeanii* can occur in close proximity to highly basic rocks, but almost invariably a layer of humic material is found, between the tuft and the rock. Nevertheless they cannot be regarded as calcifuge species, as the pH results quoted are measured on soil samples collected at the base of the *Dicranum* tuft. Tansley (1939) points out that 'as it (*D. scoparium*) is more generally found on acid soils its frequent occurrence in chalk grassland is presumably to be attributed to its loose attachment to the herbage'. Experience has shown however that the attachment is not always loose and that the tuft can be intimately associated with the soil below it, at least as intimately as in such a recognised calcicole species as *Camptothecium lutescens*.

In further studies separate examination of pH and mineral balance may prove more informative than pH readings alone.

Fruiting material is relatively uncommon in basic habitats, and only 440 and 446 had Dicrana cfr. The general performance of the two species found in these areas is as follows. In closed grasslands scattered tufts are often present, on open rocky habitats large patches of Dicranum are more common. The hummock systems of Widdybank Fell, with their eroding unstable surfaces, always present exposed areas and larger mats of Dicranum are found than occur in the surrounding closed Festuca grasslands.

3. Woodland communities. TABLE 2.3.

As D. scoparium, D. fuscescens and D. majus all fruit in woodlands many samples have been collected. The ground flora of several types has been examined and each type will be considered individually, followed by an account of the communities on living trees, dead wood and rocks, found within woods.

First, however, a few general points may be made. The altitudinal range is large, from 50-1300 ft. The higher woods are of Quercus petraea and Betula pubescens, the lower are more varied in species composition. All have a fairly high cover of bryophytes and are generally found on steep sloping habitats in the North and West of Britain. These areas have a high rainfall, the relative humidity in the floor of the woodlands being high for much of the year. The marked angle of slope, combined with the heavy rainfall often produces instability in the upper surface of the soil. An examination of the bryophytes shows that frequently large pleurocarpous mosses are found with the *Dicranum* species e.g. *Hypnum cupressiforme*, *Thuidium tamariscinum*, *Pleurozium schreberi* and *Rhytidiadelphus* spp. Another feature of the results is the lack of other large densely tufted mosses in the *Dicranum* stands; exceptions to this are scattered records of *Campylopus flexuosus*, *Leucobryum glaucum*, and *Mnium hornum*. It is interesting to note that ferns of various species are present in all the communities, except 358 and 451, *Dryopteris* spp. and *Pteridium* being particularly important.

The following types of woodland have been studied:-

A. *Quercus robur* dominant.

Quadrats 486 and 390. The former had a *Deschampsia flexuosa*/Ericoid herb layer with scattered tufts of *Dicranum scoparium* and *D. fuscescens*; the latter woodland, also contained occasional *Corylus* and *Betula*, was dominated by *D. flexuosa* alone. Tansley (1939) lists *D. scoparium* as typical of *Quercus robur* woodlands.

B. *Quercus petraea* dominant.

Other trees were often found in this type of community including *Fagus* and *Fraxinus* in a lowland Lake district wood 320, and *Betula pubescens* in more upland woods e.g. 450. An interesting series of ground floras has been found:-

TABLE 2.3.

	QUERCUS ROBUR		QUERCUS PETRAEA											BETULA							PINUS	LARIX		CORYLUS
	486	390	320	429	374 369	328	330	392	411 412	428 /9	444	450	455 456	333	358	357	391	400	408	451	371	396	399	329
Acer pseudoplatanus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Betula pubescens	-	x	-	-	-	x	x	-	-	-	-	x	x	x	x	x	+	x	x	x	x	-	-	-
Corylus avellana	-	x	-	-	-	-	x	-	-	-	x	-	x	-	-	x	x	-	-	-	-	x	-	4
Fagus sylvatica	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-
Fraxinus excelsior	-	-	x	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-	-	-	-
Ilex aquifolium	-	-	-	-	-	-	x	x	-	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-
Juniperus communis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-	-	-
Larix decidua	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	x	-
Pinus sylvestris	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-
Quercus petraea	-	-	x	x	x	x	x	x	x	x	x	x	x	-	-	-	-	-	-	-	-	-	-	-
Q. robur	x	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Salix caprea	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-
Sorbus aucuparia	+	x	-	-	-	-	-	+	x	-	-	-	x	x	-	-	-	-	x	-	-	-	-	-
Taxus baccata	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-	-	-
Calluna vulgaris	3	-	-	-	-	-	-	+	-	-	-	2	-	x	-	-	x	-	-	-	2	-	-	-
Erica cinerea	3	-	-	2	-	-	-	2	-	-	-	-	-	-	-	-	2	+	-	-	-	-	-	-
E. tetralix	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Vaccinium mytillus	x	-	2	3	2	-	2	2	-	-	-	+	2	x	-	-	-	-	-	2	1	-	-	-
Agrostis canina s. montana	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-
A. tenuis	-	2	-	2	-	2	2	-	x	-	-	-	-	-	-	x	2	-	-	x	-	-	-	-
Allium ursinum	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Anthoxanthum odoratum	x	-	-	3	-	+	+	-	2	-	-	-	-	-	1	2	-	-	1	-	-	2	-	-
Brachypodium sylvaticum	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-
Dactylis glomerata	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	-	-
Deschampsia caespitosa	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	1	-
D. flexuosa	3	3	5	+	x	-	x	+	-	x	x	-	2	2	-	x	-	2	1	2	3	2	-	-
Endymion nonscriptus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	+	3
Festuca ovina	-	-	-	5	-	3	-	-	2	4	-	x	-	-	-	-	-	-	-	-	-	-	2	-
F. vivipara	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	-	-	x	-	-	-	-	-	-
Holcus lanatus	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-
H. mollis	-	2	-	-	-	-	1	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	4
Juncus effusus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+
Luzula campestris	-	-	-	-	-	-	-	-	2	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-
L. multiflora	-	-	-	-	2	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	x	-	-	-
L. sylvatica	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Anemone nemorosa	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2
Conopodium majus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2
Campanula rotundifolia	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Digitalis purpurea	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	3
Galium hercynicum	-	-	-	2	-	2	-	-	-	3	-	x	-	-	-	2	-	2	2	-	-	-	-	-
G. saxatile	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Hedera helix	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-	-	-	x	-	-	-	-
Hypericum perforatum	-	-	-	-	-	-	2	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
H. pulchrum	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-
Hypochaeris radicata	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Lapsana communis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-
Lonicera periclymenum	-	x	-	-	x	-	2	x	-	-	-	x	-	-	-	-	x	-	-	-	x	-	-	+
Lysimachia nemorum	x	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Melampyrum pratense	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Oxalis acetosella	-	2	x	-	x	-	2	-	-	-	+	-	x	-	2	+	-	-	2	-	+	+	2	3
Potentilla erecta	2	1	-	-	-	-	-	x	x	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-
Primula vulgaris	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	2
Rubus fruticosus	-	x	-	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4
Rumex acetosa	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Sanicula europaea	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	-	-
Solidago virgaurea	-	-	-	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Succisa pratensis	-	-	-	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Taraxicum officinale	-	-	-	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Teucrium scorodonia	x	-	-	-	-	-	-	-	2	-	x	-	-	-	-	-	1	-	-	-	-	-	-	-
Veronica officinale	x	-	-	-	-	-	-	-	2	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-
Viola riviniana	x	-	-	-	-	-	2	-	-	-	x	-	-	-	2	+	-	-	-	-	-	x	2	2
Blechnum spicant	-	2	-	-	3	-	-	x	-	-	-	-	-	-	-	-	x	2	-	-	x	x	-	-
Cystopteris fragilis	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Dryopteris dilatata	-	-	x	-	-	-	x	-	-	-	-	-	-	x	x	-	-	-	-	-	2	-	x	3
D. felix-mas	-	+	-	-	x	-	-	-	-	-	-	-	-	x	x	-	-	-	-	-	-	x	x	3
D. spinulosa	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-
Hymenophyllum wilsoni	-	-	-	-	-	-	-	-	-	-	-	-	x	x	-	-	-	-	-	-	-	-	-	-
Polypodium vulgare	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	x	x	-	-	-	-	-	-	-
Pteridium aquilinum	x	-	2	x	-	4	-	3	5	-	x	2	x	-	-	x	x	-	x	-	-	3	-	-
Acrocladium cuspidatum	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-
Atrichum undulatum	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Campylopus flexuosus	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Dicranella cerviculata	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-
D. heteromalla	-	-	-	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-
Dicranum fuscescens	x	-	-	+	2	-	-	-	-	x	-	-	-	-	-	1	-	-	2	-	-	-	-	-
D. majus	-	4	3	2	+	4	4	3	3	3	5	2	4	5	2	4	1	3	3	2	3	-	5	-
D. scoparium	3	-	-	-	1	-	-	-	3	3	x	4	2	2	-	1	3	-	-	2	-	2	-	1
D. scottianum	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-
Eurynchium praelongum	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-
Hookeria lucens	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-
Hyocomium splendens	2	-	-	-	-	-	-	3	1	-	-	-	-	-	-	-	-	3	2	1	1	-	-	-
Hypnum cupressiforme	2	x	2	-	-	2	x	2	-	-	-	2	-	2	-	+	+	-	-	+	-	-	1	-
Isothecium myurum	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-
I. myosuroides	-	x	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-
Leucobryum glaucum	-	-	-	-	+	3	-	-	-	-	-	2	-	-	-	-	-	-	-	2	-	-	-	-
Mnium hornum	-	+	+	-	-	2	-	+	-	-	x	+	x	-	-	2	-	+	2	-	-	-	-	1
M. undulatum	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	+	-
Plagiothecium denticulatum	-	-	-	-	-	-	-	-	-	-	-	x	2	-	-	+	-	-	-	-	-	-	-	-
P. undulatum	-	1	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	1	2	1	-	-	-	-
Pleurozium schreberi	2	2	-	3	-	-	-	2	-	2	x	x	2	-	2	-	-	2	-	1	-	-	-	-
Polytrichum commune	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-
P. formosum	-	-	2	-	-	3	2	-	-	-	-	2	2	x	-	+	-	-	2	+	-	-	-	-
Pseudoscleropodium purum	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-
Ptilium crista-castrensis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-
Rhacomitrium lanuginosum	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-
Rhytidiadelphus loreus	-	1	-	3	-	-	2	1	-	3	+	-	-	-	2	-	-	2	2	-	x	4	-	-
R. squarrosus	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	2	-	+	1	-
R. triquetrus	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-
Sphagnum palustre	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	-	-	-	-
S. quinquifarium	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	2	-	-	-
Thamnium alopecurum	-	3	-	-	-	-	-	-	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-
Thuidium tamariscinum	-	x	-	-	-	-	1	-	-	-	x	-	2	-	1	1	+	-	-	1	-	2	2	1
Bazzania trilobata	-	-	-	-	-	-	-	-	-	-	-	x	+	-	-	-	-	-	-	2	-	-	-	-
Calypogeia trichomanis	-	x	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Conocephalum conicum	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Diplophyllum albicans	-	2	-	-	-	-	x	-	-	-	-	x	-	-	+	+	-	-	-	x	-	-	-	-
Lepidozia reptans	-	x	-	-	-	-	-	-	-	-	+	-	+	3	-	-	-	-	-	-	-	-	-	-
Lophocolea cuspidata	-	x	-	-	-	-	x	-	-	-	-	+	-	2	-	-	-	-	-	-	-	-	x	-
Mylia taylori	-	-	+	-	-	-	-	-	-	-	-	-	x	2	-	-	-	-	-	-	-	-	-	-
Plagiochila asplenioides	-	-	-	-	-	-	-	+	-	-	-	-	-	-	+	-	-	-	-	-	-	-	2	-
Saccogyna viticulosa	-	x	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cladonia squammules	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	+	-	-	+	+	-	-	-	-
C. sylvatica	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Hypogymnia physodes	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-
KEY + by eye																								
Altitude ft.	750	100	250	1300	550	500	300	50	750	1300	300	350	750	500	900	900	50		1200	300	550	200	200	400
Quadrat size cms.	1000	1000	1000	1000	1000	1000	1000	1000	1000	100	100	1000	1000	800	1000	1000	1000	1000	1000	1000	1000	1000	1000	by eye
Aspect	N	N	SE	SE	S	SE	N	NNE	SE	SE	N	N	W	NE	NE	NE	S	W	SE	NNE	N	SSE	SW	NW
Slope	30°	10°	20°	34°	35°	33°	16°	30°	25–30°	34°	20°	25°	30°	50°	steep	35°	30–40°	20°	30°	5°	36°	35°	35°	20°
Soil depth cms.	20	10	15	16	24	23	16	30	30^{+}	16	18	37^{+}	7	2	15	14	12	30	14	3–4	23	5–10	5	-
pH upper soil	4.2	5.2	4.2	5.1	3.8	-	-	5.2	5.0	5.1	-	4.8	5.2	4.8	-	4.2	4.8	5.6	4.9	4.8	3.8	6.0	5.4	4.5
pH lower soil	4.2	4.8	-	-	4.6	-	-	-	5.3	-	-	5.2	-	-	-	-	4.7	-	-	-	4.6	-	-	-
Bare surface/dead leaves	-	-	-	+	3	-	-	-	-	-	-	2	3	-	-	2	-	-	-	-	-	+	2	-

TABLE 2.3. continued

3. Woodland samples.

	Localities, grid ref., altitude[1], date.
165/6/8	Alfreds Tower, Bruton, Somerset. ST 743/351. Alt. 800 ft. 3-4-59.
290	Belstone Cleave, Devon. 20. 605/945. Alt. 750 ft. 11-4-59.
295/6/7	Wistmans wood, Two Bridges, Devon. 20. 612/771. Alt. 1250 ft. 10-4-59.
320	Lake-side, Grasmere, Westmorland. NY 345/063. 28-8-59.
329	Below Longbarrow Hill, Nr. Hawkshead, Lancashire. SD 364/997. 29-5-59.
330	Arthur Wood, Nr. High Wray, Windermere, Lancashire. SD 377/998. 28-8-59.
332/333	Stybarrow Crag, Ullswater, Cumberland. NY 388/178. 28-8-59.
328	Loughrigg Fell, Ambleside, Westmorland. NY 348/044. 26-9-59.
358/57	High Force, Upper Teesdale, Yorkshire. NY 888/284. 20-10-59.
360/64	Hareshaw Linn, Bellingham, Northumberland. NY 84-/84-. Alt. 500'.
369/371/374	West Dipton Burn, Hexham, Northumberland. NY 906/616.
390/91/92	Morar, Inverness-shire. 390 NM 682/922. 28-7-59.
	391 NM 678/923. 29-7-59.
	392 MN 683/920. 29-7-59.
396	Rha Valley, Uig, Isle of Skye. NG 396/645. 4-8-59.
399	same data.
400	Near Broadford, Isle of Skye. NG 632/208. 5-8-59.
408	Lakeside, Killin, Perthshire. NW 579/354. 11-8-59.

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[1] See also Table 2. 3.

411/12	Near Killin, Perthshire. NW 575/350. 11-8-59.
428/29	Keskadale Woods, Near Keswick, Cumberland. NY 206/195. 28-8-59.
486	Near Ballater, Aberdeenshire. 382/962. 22-6-60.
444	Near Llandderfel, Merionethshire. SH 913/332. 10-4-60.
450	Kings Valley, Near Dolgelley, Merionethshire. SH 683/163. 21-4-60.
451	Cwm Bychan, Near Harlech, Merionethshire. SH 620/294.
455/6	same data. SH 649/310.

1.	392	*D. scoparium*	*Pteridium/Holcus*
	328	*D. majus*	*Pteridium/Festuca*
	411/12	*D. majus* and *D. scoparium*	
2.	320	*D. majus*	*Deschampsia flexuosa*
3.	369/374	*D. scoparium*, *D. fuscescens*	*Luzula sylvatica*
4.	428/29	*D. scoparium*	*Festuca/Vaccinium*
5.	444	*D. majus*	All Moss Rich
	450	*D. scoparium*	
	455/6	*D. scoparium*, *D. majus*	
	330	*D. majus*	

A large range of mosses is found in 5 including *Leucobryum glaucum* (male plants) and the oceanic species *Bazzania trilobata*. Literature records of *Dicranum* for this woodland type include Tansley (1939), Devils Bridge, Wales and Richards (1938) Killarney.

C. *Betula pubescens* dominant.

Seven quadrats, 391, 400, 408, 451, 333, 357, and 358, were taken in birch woodlands. A moss rich ground flora is also shown in several of these communities, especially in 400, which had a well developed bryophyte flora with *Hylocomnium splendens*, *Plagiothecium undulatum*, *Pleurozium schreberi*, *Ptilium crista-castrensis*, *Rhytidiadelphus loreus* and *Sphagnum quinquifarium*. Quadrat 358 was less bryophyte rich having a sward of Festuca vivipara below the Betula. Quadrat 451 is notable for the presence of the Western species Dicranum scottianum.

D. Pinus sylvestris dominant.

371. This stand was very moist and together with the enormous tufts of D. majus were patches of Sphagnum quinquifarium. Dicranum scoparium and D. majus are well known in this type of woodland, Tansley (1939) records them from Dee Valley Pine forest in Scotland.

E. Larix plantation.

A community was examined on the Isle of Skye, sample 396/99, and was found to have abundant Dicranum tufts in a Pteridium/Deschampsia caespitosa herb layer.

Communities, containing Dicranum spp., not specially studied include:-
Beech woodland e.g. Paulson (1926) D. scoparium and D. majus, in Epping Forest.
Also Ash woodland e.g. Moss (1907) D. scoparium in various lists from Derbyshire examples.

Soil details.

Examination of the pH data shows that the soils are all acid with evidence of leaching, e.g. 3.8 upper layers, 4.6 lower layers — quadrat 391

Generally the Dicranums were on shallow soils, the maximum being c 30 cms in depth. An important feature of most of the quadrats, is the broken nature of the ground. The woodland floors often had rocks at the surface and the Dicranums were especially abundant as a fringe between the rock and the surrounding vegetation. In such cases the soil was extremely shallow e.g. 451 only 3-4 cms in depth. The instability of many of the soils must be further stressed. Pure tufts of Dicranum are often found where competition is reduced by this factor.

Performance of the group in woodlands.

The quadrat lists are an important source of information on the reproduction of three of the species. D. fuscescens and D. scoparium have been collected with capsules in a single metre quadrat in 369/374. D. scoparium and D. majus are often found fruiting within close range of each other, e.g. 444, 391, 455, 428. D. majus cfr. and D. fuscescens cfr. have never been seen in close proximity and from field observations it appears that D. fuscescens favours drier conditions, with more open vegetation, than D. majus.

3a. Dead wood samples. TABLE 2.4

Three of the four species of Dicranum species under study occur on rotting logs. Quadrats on dead wood from various sites are reported in the lists. They may be interpreted as stages in a successional sequence.

368B shows similar bryophytes to those found growing at lower heights on living trees, together with the characteristic liverwort of dead wood Lophocolea cuspidata. Probably the tufts of mosses have originated from the epiphytic colonies present on the living tree.

Later stages in the disintegration of the timber are shown by the presence of flowering plants e.g. Vaccinium, Anthoxanthum, Holcus, Galium, and Geranium. Several bryophytes typical of the woodland floor also appear in the species lists e.g. Plagiothecium undulatum, Pleurozium schreberi, Polytrichum formosum and Rhytidiadelphus loreus.

Richards (1938) notes the importance of Dicranum scoparium as climax with Hylocomnium splendens on dead wood in the Killarney Oak woodlands. Similar communities with D. scoparium have been recorded by Gams (1927) for Abies and Picea timber in Switzerland.

3b. Living tree samples. TABLE 2.5

Dicranum fuscescens and D. scoparium are both epiphytes and have been collected in several localities. The communities, in which they occur, reach their maximum development in upland woodlands in the North and West of the British Isles. A small number have been examined in detail and are presented here to illustrate points in the ecology of the epiphytic Dicranums. D. majus is recorded from tree boles in Ireland Tansley (1939) but has rarely been found during this work on epiphytes.

Vertical zonation.

Considering first the Skye samples taken from one tree at different heights above the ground, the following species were found.

TABLE 2. 4.

DEAD WOOD HABITATS.

	368A	368B	395a	395b	425/6/7
Vaccinium mytillus	+	-	-	-	1
Anthoxanthum odoratum	-	-	-	-	+
Holcus lanatus	-	-	-	+	-
Galium hercynicum	-	-	-	-	2
Geranium robertianum	+	-	-	-	-
Oxalis acetosella	1	1	+	+	-
DICRANUM FUSCESCENS	-	-	5	+	3
D. MAJUS	4	-	-	-	+
D. SCOPARIUM	-	2	2	3	3
Hypnum cupressiforme	3	3	2	2	-
Isothecium myosuroides	2	2	-	-	-
I. myurum	-	-	2	2	-
Mnium hornum	1	2	-	-	-
Plagiothecium undulatum	-	-	+	-	-
Pleurozium schreberi	-	-	-	-	2
Polytrichum formosum	-	-	-	-	2
Rhytidiadelphus loreus	-	-	-	-	3
Thuidium tameriscinum	+	-	+	+	-
Lophocolea cuspidata	-	2	-	+	-
Quadrat size. x 4 in cm	10	10	10	10	10
Slope	-	-	30	30	34
Aspect	-	-	SSE	SSE	SE
Date of collection	26/9/59		4/8/59		28/8/59

Details of Collections.

= 166 Alfreds Tower, Bruton, Somerset.
= 363 Hareshaw Linn, Bellingham, Northumberland.
= 368 Dipton Burn, Hexham, Northumberland.
= 395/7 Rha Valley, Uig, Isle of Skye.
= 425/6/7 Keskadale Woods, near Keswick, Cumberland.
481 Old Picea stump, Sallanches, Haute Savoie, France. Coll. TTE. 1-6-60.

= more details see Table 2. 3.

Maximum height of the *Dicranum* 15 ft.

394A	5 ft.	*D. fuscescens*, *D. scoparium*, *Isothecium* present, cover less than 100%.
394B	2 ft. 6 inches.	Additional spp. *Oxalis*, *Mnium hornum*, *Pleurozium*. Diminution in the cover of *D. scoparium* and *D. fuscescens*, increase in *Isothecium*. Total cover of spp. 100%.
394C	0 ft.	Many less tolerant spp. present, *Mnium undulatum*, *Thuidium*, *Plagiochila asplenioides* var. *major*. Total cover of all spp. 100%. Reduction in *D. scoparium* and *Isothecium*; *Mnium hornum* increased, *D. fuscescens* absent.

This series of quadrats illustrates the relative performance of *D. scoparium* and *D. fuscescens* at different heights. *D. fuscescens* is less tolerant of competition than *D. scoparium* and is mainly found in the upper open communities. *D. scoparium* is however commonly found on splayed out tree bases, together with more mesic species, as well as high on tree trunks. Generally, in the N. and W., if both species are present on the same tree, *D. fuscescens* is found at a greater height than *D. scoparium*. Circa 30 feet is the maximum height recorded for both species in this investigation.

Another series of quadrats (357) taken at High Force, Upper Teesdale, shows a common modification of simple vertical zonation. The highest cover of *Dicranum* occurs on horizontal limbs of *Corylus* in these communities, which have a similar species list to the Skye samples.

Epiphytic Dicranums	327	357			372			394/8			402/3			407	410
		A	B	C	A	B	C	A	B	C	A	B	C		
Festuca ovina	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Oxalis acetosella	-	-	-	-	-	-	-	-	+	+	-	-	-	-	-
Polypodium vulgare	-	-	-	-	-	-	-	-	-	-	1	4	-	+	-
Dicranum fuscescens	-	5	5	+	2	x	2	2	+	-	-	4	-	5	-
D. scoparium	4	3	3	-	-	2	-	2	+	+	5	4	2	-	5
Hypnum cupressiforme	+	-	2	+	2	-	3	-	-	-	+	+	2	2	-
Isothecium myosuroides	-	-	-	-	-	1	2	2	5	2	-	-	-	-	2
Mnium hornum	-	-	1	-	-	3	2	-	+	2	-	-	-	+	-
M. undulatum	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-
Pleurozium schreberi	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Polytrichum formosum	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Thuidium tamariscinum	-	-	-	-	-	-	-	-	+	2	-	-	-	-	-
Ulota phyllantha	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Frullania dilatata	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2
Lepidozia reptans	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-
Lophocolea cuspidata	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-
Mylia taylori	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Plagiochila asplenioides	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-
Cetraria glauca	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-
Cladonia squammules	1	-	-	-	-	-	-	-	-	-	-	-	-	-	2
C. sylvatica	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-
Graphis sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Hypogymnia physodes	3	-	+	5	2	-	-	-	-	-	-	-	-	1	-
Lobaria pulmonaria	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x
Pertusaria amara	-	-	-	-	1	-	-	-	-	-	+	-	-	-	-
High incidence	NEW							N			N	N	N	NNW	N
Low incidence	S							S			S	S	S	S	S
Bare wood	-	-	-	3	2	-	+	3	-	-	-	2	2	-	4
Quadrat size	10	40	40	40	10	40	40	40	40	40	40	10	40	40	40
Aspect	S	N	N	N	SW	S	S	N	N	N	N	N	S	W	NW
Maximum height of Dicranum tufts								15			30	30		8	
Height above ground of quadrat	0	6'	6'	6'	4'	3'	3'	5'	2'6"	0	6'	10'	7'	8'	6'
Altitude	550'	900'	900'	900'	550'	550'	550'	200'	200'	200'	350'	350'	350'	1200'	1200'

TABLE 2.5. continued

Samples of Dicranums from trees.

+	168	Alfreds Tower, Bruton, Somerset.
	217	Cranmore Tower, Dean, Somerset. Alt. 850 ft. ST 674/457. 5-4-59.
+	297	Belstone Cleave, Devon.
+	362	Hareshaw Linn, Bellingham, Northumberland.
+	327	Loughrigg Fell, Ambleside, Westmorland. 27-4-59.
+	357	High Force, Upper Teesdale, Yorkshire. 20-10-59.
+	367/72	West Dipton Burn, Hexham, Northumberland. 26-9-59.
+	394/98	Rha Valley, Uig, Isle of Skye. 4-8-59.
+	401	Ben Suardal, Near Broadford, Isle of Skye.
	402/3	Killin, Perthshire. Alt. 350 ft. 9-8-59.
+	407/410	Killin, Perthshire. 11-8-59.
+	430/31	Keskadale Woods, Keswick, Cumberland.

+ further details see Table 2. 3.

Tree species involved.

Quercus petraea	327, 372A.
Corylus avellana	357.
Fraxinus excelsior	372B and C.
Larix decidua	394/8 A, B, C.
Alnus glutinosa	402 A, B, and C.
Betula pubescens	407.
Quercus robur	410.

Aspect.

Communities on Loughrigg Fell, 327, showed high D. scoparium cover on tree bases. Records of cover in relation to aspect for this woodland indicate that Dicranums occurred all round the tree bole but extended highest on North, East and West aspects, with little on the South side of the trunk. This is a common phenomenon recorded too in other localities:- 394, 402, 407, and 410.

Performance of the species.

In very humid upland woods, epiphytic communities are extremely well developed and the Dicranums are often present in large tufts. Drier woodland has small Dicranum tufts; the species are absent from many lowland woods. This is especially true of D. fuscescens which is typically a montane plant. Fruiting material of both D. scoparium and D. fuscescens has been collected from trees. D. scoparium cfr. has been collected 30 ft. above the ground at Bellingham, Northumberland, but usually fruiting material is found near the ground with sterile tufts higher on the tree. It was interesting to find D. scoparium cfr. in this position, as Barkman (1958) studying epiphytes in the Netherlands describes, 'the Scoparieto-Hypnetum filiformis (community) in which isolated tufts of D. scoparium occurs to a height of 5 metres or more above the ground. Colonisation takes place by spores from fruiting specimens on the forest floor, ... D. scoparium does not fruit on trees and also lacks vegetative means of propagation. Hence the Scoparieto-Hypnetum filiformis is dependant on soil vegetation for a constant supply of spores of this, and other of its component species.'

This is clearly not the case in the more oceanic woodlands of upland Britain, where fruiting clumps of Dicranum are quite common on trees; it may apply however in the drier woods of lowland districts.

The zonations illustrated above seem to fit the general principles established by Barkman (1958), who describes a horizontal zonation by aspect together with a vertical zonation. He thinks that humidity is the most important factor governing the distribution of the bryophytes. Evaporation is at a minimum on the North side, where there is high bryophyte cover, and at a maximum on the South side which is exposed to the full effects of sunlight. Field observations during this study support his hypotheses; invariably the most luxuriant growth of epiphytic Dicranum species is found on the North side of the tree, and to the greatest height in this aspect. They occur only as isolated tufts on the South side and do not ascend much above the tree base. The distribution is no doubt complicated by differences in the prevailing winds and local topography. The more mesic flora of the tree bases has been linked to several factors by Barkman (1958), all of which seem applicable to British communities. Snow cover at the base of trees, the slackening of speed in water run-off due to roughness of the bark and the protection offered by woodland floor species, such as tall growing Pteridophytes, all seem important.

4. Upland acid communities. TABLE 2.6.

The quadrats included in this group give only a very incomplete picture of the range of upland communities in which Dicranums are found.

The species lists will be considered in the context of the altitudinal zonation given in Poore and McVean (1957), with additional material drawn from literature records to give a more complete picture of the ecology of the group.

A. *Middle Alpine zone.*

Includes communities:-

Juncus trifidus, *Festuca vivipara*/*Gymnomitrium*, snow bed communities.

Altitudinal range in Cairngorms 3600 ft - to highest peaks.

B. *Low alpine zone.*

Communities:-

Rhacomitrium heath, *Nardus* grasslands, *Empetrum-Vaccinium*.

Altitudinal range in Cairngorms c 2400-3600 ft.

C. *Sub-alpine zone.*

Communities:-

Calluna moor, blanket bog, *Trichophorum-Molinea*, *Nardus* and *Agrostis-Festuca* grassland.

Altitudinal range in Cairngorms up to c 2400 ft.

A. *Middle Alpine Zone.*

No quadrats have been taken at this altitude. *Dicranum* species are important members of the communities, as is reflected in the literature, e.g. *D. fuscescens* var. *congestum* is prominent in the *Juncus trifidus* zone, Ingram (1958); and Tallis (1957) records *D. scoparium* from summit vegetation in Snowdonia. Snow patch communities are often found at high altitude on the Scottish mountains and several Dicranum species are recorded, D. starkii, D. schisti, and D. falcatum, all outside the scope of this work.

It is possible that quadrats 422A, 422B and 422C are within the Middle Alpine zone, which has been shown, Poore and McVean (1957), to be at different altitudes in different areas. These quadrats were characterised by having abundant Festuca ovina/vivipara on thin acid soil.

B. Low Alpine Zone.

None of the samples fall within this zone. Communities recorded in the literature having Dicranum species in their lists include the following. Burges (1951) records D. scoparium and D. fuscescens in the moss layer of Empetrum-Vaccinium stands and notes that above 3000 ft. D. fuscescens tends to replace D. scoparium. Details of the Rhacomitrium/Carex bigloweii nodum, Poore (1955), include both D. scoparium and D. fuscescens and both too are found in Nardus snowbeds in North Scotland. The latter communities are developed in shallow depressions where snow lie is relatively long. Rock-ledge floras are often well developed in this zone; Watson (1925) records D. fuscescens in a list of typical species. Sample 381, D. fuscescens cfr., and D. majus both collected by T.T. Elkington from rock ledges on Ben Lawers, Perthshire, have been studied, but no species list is available.

TABLE 2.6.

Montane Acid Communities	Lower Alt. Festuca		Agrostis-Festuca Stands						Peat		Callunetum	High Alt. Festuca		
	326	445	347	420	423	424	442	404	405A	B	393	432A	B	C
Calluna vulgaris	-	-	-	-	-	-	x	-	-	-	4	-	-	-
Erica cinerea	-	-	-	-	-	-	-	-	-	-	2	-	-	-
Empetrum nigrum	-	-	-	-	-	-	1	-	-	-	-	-	-	-
Vaccinium mytillus	-	-	2	-	-	x	1	-	-	-	-	-	2	-
V. vitis-idaea	-	-	-	-	-	-	1	-	-	-	-	-	-	-
Agrostis tenuis	-	-	-	2	-	3	x	-	-	-	-	2	x	-
Aira praecox	3	-	-	-	-	-	-	-	-	-	-	-	-	-
Anthoxanthum odoratum	-	-	-	-	+	x	-	-	-	-	-	-	-	-
Carex caryophyllea	-	-	+	-	-	-	-	-	-	-	-	-	-	-
Deschampsia caespitosa	-	-	2	-	-	-	-	-	-	-	-	-	-	-
D. flexuosa	2	-	-	-	-	-	-	-	-	-	2	-	-	-
Endymion nonscriptus	-	2	-	-	-	-	-	-	-	-	-	-	-	-
Eriophorum vaginatum	-	-	-	-	-	-	-	-	-	2	-	-	-	-
Festuca ovina	4	2	5	-	3	4	2	-	-	-	-	x	3	5
F. vivipara	-	-	-	3	x	x	-	x	-	-	-	-	-	-
Juncus squarrosus	-	-	-	-	-	-	-	-	-	-	x	-	-	-
Luzula campestris	-	2	2	1	-	-	-	-	-	-	-	-	-	-
Molinia caerulea	-	-	-	-	-	-	-	-	-	-	+	-	-	-
Nardus stricta	3	-	-	-	-	-	-	-	-	-	1	-	-	-
Narthecium ossifragum	-	-	-	-	-	-	-	-	-	-	x	-	-	-
Trichophorum caespitosum	-	-	-	-	-	-	-	-	2	-	2	-	-	-
Achillea millefolia	-	-	1	-	-	-	-	-	-	-	-	-	-	-
Alchemilla alpina	-	-	-	2	2	-	-	x	-	-	-	-	-	-
A. glabra	-	-	-	-	-	-	-	x	-	-	-	-	-	-
Campanula rotundifolia	-	-	+	-	-	-	-	-	-	-	-	-	-	-
Cochleria alpina	-	-	x	-	-	-	-	-	-	-	-	-	-	-
Digitalis purpurea	-	x	-	-	-	-	1	-	-	-	-	-	-	-
Galium hercynicum	2	x	1	2	2	2	1	x	-	-	-	2	-	3
Minuartia verna	-	-	-	-	-	-	-	+	-	-	-	-	-	-
Oxalis acetosella	-	2	-	-	-	2	-	-	-	-	-	-	-	-
Potentilla erecta	-	-	-	-	-	-	1	-	-	-	2	-	-	-
Rumex acetosa	-	x	-	-	-	-	-	-	-	-	-	-	-	-
R. acetosella	+	x	-	-	-	-	-	-	-	-	-	-	-	-
Saxifraga hypnoides	-	-	+	-	-	-	-	-	-	-	-	-	-	-
Sedum acre	2	x	-	-	-	-	-	-	-	-	-	-	-	-
Succisa pratensis	-	-	-	-	-	-	-	-	-	-	2	-	-	-
Teucrium scorodonia	-	-	-	-	-	-	1	-	-	-	-	-	-	-
Thymus drucei	-	-	+	-	-	-	-	-	-	-	-	-	-	-
Veronica officinalis	-	-	-	-	-	-	x	-	-	-	-	-	-	-
Viola lutea	-	-	x	-	-	-	-	-	-	-	-	-	-	-
V. riviniana	-	-	1	-	-	-	1	-	-	-	-	-	-	-
Cryptogramme crispa	-	-	-	-	x	2	-	-	-	-	-	-	-	-
Lycopodium selago	-	-	-	-	-	-	-	-	-	-	-	-	-	x
Pteridium aquilinum	-	x	-	-	-	-	2	-	-	-	-	-	-	-
Bare ground	3	-	-	-	-	-	-	-	-	-	1	-	2	-
Blindia caespitosa	-	-	-	-	-	-	-	x	-	-	-	-	-	-
Campylopus flexuosus	-	-	-	-	-	-	-	-	-	+	-	-	-	-
C. pyriformis	-	-	-	2	-	-	-	-	-	-	-	-	-	-
Dicranella heteromalla	-	x	-	-	-	-	1	-	-	-	-	-	-	-
Dicranum majus	-	2	-	-	-	4	-	-	-	-	-	-	-	-
D. scoparium	3	3	2	2	3	-	3	5	2	2	2	3	3	3
Hylocomium splendens	-	-	-	-	-	+	-	-	-	-	-	-	-	-
Hypnum cupressiforme	-	1	1	2	x	2	1	-	-	-	1	2	-	-
Leucobryum glaucum	-	-	-	-	-	-	-	-	-	-	+	-	-	-
Mnium hornum	-	-	-	-	-	+	-	-	-	-	+	-	-	-
Plagiothecium undulatum	-	2	-	-	-	-	-	-	-	-	+	-	-	-
Pleurozium schreberi	2	1	-	2	-	-	1	-	-	-	+	-	-	-
Pohlia nutans	-	-	-	-	-	-	-	-	-	-	2	-	-	-
Polytrichum commune	-	-	-	-	2	2	-	-	-	-	-	-	-	2
P. formosum	-	2	-	-	-	-	4	-	-	-	-	-	-	-
P. gracile	-	2	1	-	-	-	-	-	-	-	-	-	-	-
P. juniperinum	-	-	-	-	-	-	-	2	-	-	-	-	-	-
P. piliferum	2	-	-	-	-	-	-	-	-	-	-	-	-	-
P. urnigerum	-	-	-	2	-	-	-	-	-	-	-	3	-	-
Rhacomitrium heterostichum	2	-	-	-	-	-	-	-	-	-	-	-	-	-
R. lanuginosum	2	-	-	-	+	-	-	2	-	-	-	2	+	2
Rhytidiadelphus loreus	-	-	-	-	-	2	-	-	-	-	+	-	-	+
R. squarrosus	3	2	-	+	+	x	1	-	-	-	-	-	-	-
Sphagnum acutifolium	-	-	-	-	-	-	-	-	3	-	-	-	-	-
S. papillosum	-	-	-	-	-	-	-	-	2	-	-	-	-	-
Thuidium tamariscinum	-	+	-	-	-	x	-	-	-	-	-	-	-	-
Aplozia pumila	-	-	1	-	-	-	-	-	-	-	-	-	-	-
Diplophyllum albicans	-	-	-	2	-	+	1	-	-	-	+	-	-	-
Frullania tamarisci	x	-	-	-	-	-	-	-	-	-	-	-	-	-
Lophozia ventricosa	-	x	-	-	-	-	-	-	-	-	-	-	-	-
Marsupella emarginata	2	-	-	-	-	-	-	x	3	2	-	-	-	-
Mylia taylori	-	-	-	-	-	-	-	-	-	-	+	-	-	-
Orthocaulis floekii	-	-	-	1	-	-	-	-	-	-	-	-	-	-
Habitat details														
Quadrat size cms.	50	50	100	50	10	10	50	10	10	10	10	10	10	10
Slope °	10	25	6	30	35	35	40	20	5	5	25	10	10	10
Aspect	NW	NNE	ENE	NW	NNE	NNE	ENE	S	N	N	NNW	NW	NW	NW
Soil depth	10	7	30	36	11	10	15-30	10	?	?	45	10	10	10
pH upper soil	4.2	5.1	4.2	-	4.9	-	5.3	-	4.5	-	5.2	5.1	5.1	5.1
lower soil	-	-	5.1	-	-	-	5.1	-	-	-	-	-	-	-
Altitude ft.	500	300	2200	1500	2000	2000	1000	2800	2800	2800	250	2900	2900	2900
Date of collection	29/8/59	10/4/60	10/1/59	26/8/59	26/8/59	26/8/59	10/4/60	10/8/59	10/8/59	10/8/59	7/59	26/8/59	26/8/59	26/8/59

TABLE 2. 6. continued

Montane acid Communities.

218 Cranmore Tower, Dean, Somerset. Alt. 850 ft. ST 677/454. 5-4-59.

270 Acid bog, Burrington Combe, Somerset. Alt. 600 ft. ST 476/586. 7-4-59.

298 Heathland, Belstone Tor, Devon. Alt. 1500 ft. 20. 614/918. 11-4-59.

317 *Nardus* grassland, Sickle Tarn, Langdale, Westmorland. Alt. 1500 ft. SD 285/076. 25-4-59.

318 *Deschampsia flexuosa* grassland, Sickle Tarn, Langdale, Westmorland. Alt. 2300 ft. SD 284/078. 25-4-59.

\+ 326 Loughrigg Fell, Ambleside, Westmorland. NY 347/042.

\+ 347 Little Fell, Near Brough, Westmorland. NY 780/223.

350 Under *Calluna*, Mukur, Swaledale, Yorkshire. 18-6-59.

376 Schist. Glen Lui, Perthshire. Alt. 1750 ft. TTE. 8-7-59.

380 Schist. West Corrie, Ben Lawers, Perthshire. Alt. c 3250 ft. TTE. 1-7-59.

381 Rock ledges, Glen Lyon, Perthshire. Alt. c 2000 ft. TTE. 3-7-59.

382 Gulley, Lawers, Perthshire. 1-7-59.

385 Gulley, Cam Creag, Lawers, Perthshire. Alt. c 3000 ft. 2-7-59.

\+ 393 Mallaig, Inverness-shire. NM 676/967.

\+ 405 Redistributed peat, Ben Lawers, Perthshire. NW 643/428.

\+ 404 Same locality on rocks.

\+ 420 Wastdale screes, Cumberland. NY 151/034.

\+ 422 Pillar, Ennerdale, Cumberland. NY 172/120.

\+ 423 High Level Path, Pillar, Ennerdale, Cumberland. NY 172/120.

\+ 424 Same locality as 423.

\+ 445 Lakeside, Bala, Merionethshire. SH 913/332.

\+ 442 Pennant Melangell, Llangynog, Montgomeryshire. SJ 008/273.

\+ Further details see above.

C. Sub-Alpine Zone.

Agrostis/Festuca grassland is a major ecological feature of the lower slopes of upland areas. Quadrats 424, 420 and 442 show typical stands. Developed on steeply sloping exposed slopes, they have only small amounts of Dicranum scoparium, 424 with D. majus. Tallis (1957) records similar lists for N. Wales and quotes the following constant species, besides the D. scoparium and the Festuca/Agrostis species: Galium hercynicum, Vaccinium mytillus, Hypnum cupressiforme, Pleurozium schreberi, Polytrichum alpinum, and Rhacomitrium lanuginosum. This list is very similar to the ones presented. Population 347, showing dominant Festuca-Vaccinium without Agrostis is probably a variant of typical stands of Festuca/Agrostis. Poore (1955) records similar communities in the Breadalbanes and this paper is the source of the suggestion on the relationship between various facies of Festuca grasslands.

Communities on peat are represented by 405 A and B, found on Ben Lawers, with Trichophorum and Eriophorum. Pearsall (1941) records D. scoparium from several peat mosses in the Stainmore District, Durham, dominated by Eriophorum vaginatum and/or Calluna. Similar communities with D. scoparium are described by Ratcliffe (1959) from Carneddau, N. Wales, the same survey also records this species from Juncus squarrosus bog.

393 is a typical example of wet Callunetum, showing a rich understory of acidophilous bryophytes. With the D. scoparium, in this

unshaded habitat, were Leucobryum glaucum, Plagiothecium undulatum, Pleurozium schreberi, and Hypnum cupressiforme. Gimmingham (1960) records much information on Calluna and shows that D. scoparium is a common associate in both wet and dry Callunetum. Very similar communities to 393 are often found in open woodland and they intergrade with the vegetation developed below the trees.

D. Other Samples.

Samples 326 and 445 were both collected on well developed Festuca ovina grassland at low altitudes. Polytricha are prominent in the species lists and Rhytidiadelphus squarrosus.

Summarizing the performance of the species in montane regions the following general points may be made.

D. bonjeanii is not generally found in wide range of habitats, see section 5.

D. majus is only found in tall Callunetum just above the tree line, and on moist shaded ledges or amongst shady rocks.

D. scoparium is found throughout most of the drier communities, often in conspicuous mats, but in closed vegetation as small isolated tufts.

D. fuscescens is found commonly at high altitudes in open communities, and replaces D. scoparium at higher altitudes.

A fruiting specimen of D. fuscescens has been obtained from c 2500 ft. on Ben Lawers but usually sterile material is found of all four species above the sub-alpine zone.

TABLE 2.7.

Species	319	322	421	443	454	485
Calluna vulgaris	-	-	-	-	-	3
Empetrum nigrum	-	-	1	-	-	x
Erica tetralix	2	-	x	-	1	-
Vaccinium vitis-idaea	-	-	-	-	-	2
Agrostis sp.	-	-	-	x	-	-
Anthoxanthum odoratum	2	+	-	-	-	2
Carex curta	-	-	-	-	-	x
C. echinata	-	1	x	-	-	-
C. flacca	-	2	-	-	-	2
C. hostiana	2	3	-	-	-	-
C. nigra	-	2	-	-	-	2
C. panicea	-	-	-	1	2	-
Coeloglossum viride	-	-	-	-	-	x
Eriophorum angustifolium	-	-	-	x	2	2
Festuca ovina	-	-	-	2	-	-
F. vivipara	-	x	-	-	-	-
Holcus lanatus	-	-	1	-	-	2
Juncus acutiflorus	x	2	-	-	-	-
J. articulatus	-	-	-	x	x	-
J. bulbosus	2	-	-	-	-	-
J. effusus	-	-	-	-	x	x
J. squarrosus	-	-	-	x	x	x
Luzula campestris	-	-	-	-	-	x
Molinia caerulea	2	-	1	x	x	-
Nardus stricta	-	2	+	x	3	2
Narthecium ossifragum	2	1	2	-	-	-
Orchis ericetorum	-	-	-	-	+	-
Rhynchospora alba	2	-	-	-	-	-
Sieglingia decumbens	-	x	-	-	-	-
Trichophorum caespitosum	-	-	2	-	-	-
Achillea ptarmica	-	-	-	-	-	+
Anagallis tenella	2	2	-	-	-	-
Cirsium palustre	1	2	-	1	-	3
Drosera rotundifolia	2	2	x	-	-	-
Epilobium palustre	-	-	-	-	-	+
E. pedunculare	-	-	-	-	2	-
Euphrasia officinalis agg.	1	x	-	-	-	-
Galium uliginosum	-	-	-	-	-	1
G. verum	-	-	-	-	-	x
Hydrocotyle vulgaris	2	-	-	-	-	-
Linum catharticum	-	-	2	-	-	-
Oxalis acetosella	-	-	-	1	-	-
Oxycoccus palustris	-	-	-	-	x	-
Pedicularis sylvatica	2	-	1	-	-	-
Pinguicula vulgaris	-	2	-	-	1	-
Plantago lanceolata	-	-	-	1	-	-
P. maritima	-	-	1	-	-	-
Polygala serpyllifolia	-	-	-	-	+	-
Potentilla erecta	2	2	2	1	2	1
Prunella vulgaris	-	-	+	2	-	-
Ranunculus acris	-	-	2	-	-	-
R. ficaria	-	x	-	-	-	-
R. flammula	x	-	-	-	-	-
Succisa pratensis	2	1	-	x	2	-
Viola palustris	-	-	-	?	1	-
V. riviniana	-	-	-	-	-	x
Taraxicum officinale agg.	-	x	2	-	-	x
Equisetum fluviatile	-	-	-	-	-	1
E. palustre	-	-	-	-	-	+
Pteridium aquilinum	-	-	-	3	-	-
Selaginella selaginoides	-	x	-	-	-	-
Acrocladium cuspidatum	-	-	?1	+	-	-
Aulocomnium palustre	2	x	x	x	2	2
Breutelia chrysocoma	2	3	2	1	2	-
Campylopus atrovirens	+	-	-	-	-	-
Ctenidium molluscum	-	1	3	-	-	-
Dicranum bonjeanii	3	3	3	5	3	3
D. scoparium	-	-	-	-	x	-
Drepanocladus revolvens	3	-	-	-	-	-
Hylocomium splendens	-	-	-	1	+	x
Hypnum cupressiforme	-	+	-	-	-	-
Mnium punctatum	-	-	-	-	-	2
Philonotis fontana	-	-	-	-	-	1
Pleurozium schreberi	-	-	?	-	2	2
Polytrichum commune	-	x	-	-	x	-
Rhytidiadelphus squarrosus	-	-	-	-	-	2
R. triquetrus	-	-	-	-	-	2
Scorpidium scorpioides	x	2	-	-	-	-
Sphagnum palustre	-	-	-	-	3	-
S. papillosum	-	3	-	-	-	-
S. ? plumulosum	3	-	-	-	-	-
S. rubellum	-	-	-	3	x	x
Thuidium tamariscinum	-	x	-	-	+	1
Calypogeia trichomanis	-	-	-	-	-	2
Lophocolea bidentata	-	-	-	+	-	+
Riccardia multifida	-	-	-	-	-	+
R. pinguis	x	+	-	1	-	-

Habitat details

Aspect	SSW	N	NW	ENE	WNW	WSW
Slope	5°	28°	20°	27°	5°	5°
Quadrat size (cms)	50	50	50	50	50	50
Soil depth (cms)	50^{+}	25	37^{+}	30^{+}	30^{+}	28^{+}
Date of collection	8/59	8/59	8/59	9/4/60	21/4/60	21/6/60
Altitude	500'	450'	500'	1000'	300'	1550'
Standing water	✓	✓	✓	✓	✓	✓

TABLE 2. 7. continued

Populations from Communities with a High Water Table.

220	Cranmore Tower, Downhead, Somerset. Alt. 850 ft. ST 677/454.
319/25	High Close, Elterwater, Westmorland. NY 338/054.
322	Lake side, Grasmere, Westmorland. NY 345/059.
421	Wastdale, Cumberland. NY 144/035.
441	Whix~~h~~all Moss, Shropshire. SJ 49-/36-.
443	Pennant Melangell, Llangynog, Montgomeryshire. SJ 008/273.
454	Cwm Bychan, Merionethshire. SH 620/294.
471	Flushed grassland, Moorhouse Nature Reserve, Co. Durham. Coll. AE. 10-6-60.
485	Kirkton-of-Glenbucket, Aberdeenshire. NJ 362/152.

Soil details.

319	Upper 6 cm very fibrous, black. pH 5.9. Lower 42 cm lighter mineral soil.
322	Upper black humic. pH 5.5. Lower more silty.
421	Upper 9 cm silty, many roots. pH 6.5. Lower 9 cm black tenacious, plastic.
443	Homogeneous black. pH 6.8.
454	Black, plastic. pH 6.0.
485	Upper 7 cm roots, soupy, black silt. pH 6.3. Lower 28+ cms.

5. Communities with water table at ground level.

TABLE 2.7

The six communities, with D. bonjeanii, found between 300-1550 ft., were all on hill slopes. No exact equivalents have been found in the literature. The most characteristic feature of the group is the high water table; even in the summer months these communities are permanently wet, often with evil-smelling sub-soil. They occur on sloping ground (421, 485, 322, and 319), in slight hollows between ridges (454), or at the edges of flushes (443); in all cases the constant water supply is from seepage rather than from direct surface flow. D. bonjeanii has never been found, during these investigations, in the bryophyte flush habitats associated with upland streams. D. scoparium also occurred in 454 examined on Cwm Bachan, Merionethshire, but was restricted to the drier parts of the habitat. Potentilla erecta and Aulocomnium palustre are constant associates of the D. bonjeanii and Breutelia chrysocoma is also commonly present. Other important species were Molinea caerulea, Nardus stricta, Cirsium palustre and Succisa pratensis, together with Carex spp., and Juncus spp.

Community 485 was of great interest as it contained D. bonjeanii cfr. Details of the fruiting behaviour will be given in a later section.

The performance of the D. bonjeanii was interesting, as large pure clumps of the moss were found, excluding other bryophytes. This is in marked contrast to the isolated stems or small tufts found in the dry calcareous habitats.

TABLE 2.8

Samples of Dicranum from rocks.

300	Walls, Yeo, Devon. 20. 675/876. 12-4-59.
+ 361	Rocks, Hareshaw Linn, Bellingham, Northumberland.
+ 370/73	Rocks, Dipton Burn, Hexham, Northumberland.
404	Rocks, Ben Lawers, Perthshire. Alt. 2800 ft. NN 643/428.
406/9	Rocks, Killin, Perthshire. NN 579/354. 11-8-59.

+ For further details see Table 2. 3.

6. Communities on rocks. TABLE 2·8.

D. scoparium and D. fuscescens are commonly found on rocks in montane areas. The Killin samples were taken from exposed rocks above the tree line. The Dipton Burn and Bellingham samples, on the other hand, were found within open woodland in less exposed conditions. Both species are never seen in direct contact with the rock face, but usually have a layer of humic material between the tuft and the rock. This may have collected around the original growth of Dicranum, as experiments in the laboratories have shown that spores will germinate on sterilised damp gritstone surfaces.

Closed rock communities occur in more sheltered places or on shaded faces of rocks, and show marked species differences on the exposed faces of the same boulder. Such species as Polypodium vulgare, Geranium robertianum, Oxalis acetosella and various grass species appear on closed boulders, while Cladonias and other lichens are important on open facies.

Other rock communities.

A. Isolated specimens of D. scoparium have been collected from Millstone Grit walls in S.W. Yorkshire and Tallis (1957) records considerable cover of this species on Welsh walls. D. scoparium is also common on acid boulder scree, Tallis (1957). Lists for scree of basic rocks see Section 2.

B. Population 228.

This sample of *D. scoparium* was growing on the floor of disused andesite quarry, Downhead, Somerset. On the rocky substrate large swards of fruiting material were present, with the following species:-

Potentilla sterilis	2
Festuca ovina	2
Holcus mollis	2
Achillea millefolia	+
Hypochaeris radicata	3
Rubus fruticosus	3
Taraxacum officinale	2
Viola odorata	+
V. riviniana	+

Quadrat details.

size 1 m.
soil depth 5 cm.
pH of upper soil 6.1.
slope 0
altitude 700 ft.

TABLE 2. 9.

PERFORMANCE OF DICRANUM SPECIES IN VARIOUS HABITATS

Habitat	D. scoparium	D. bonjeanii	D. majus	D. fuscescens
Dunes	++	-	-	-
Basic grassland	++ often +	+	-	-
Acid woodland				
1. floor	++ cfr.	-	++ cfr.	++ cfr.
2. dead wood	++ cfr.	-	++	++ cfr.
3. trees	++ cfr.	-	++ tree bases	++ cfr.
Basic woodland	++	++	-	-
Montane Ericoid	++	-	++	+
Grasslands	++	-	-	+
High Alt. Communities	++	-	-	++
Rocks, walls	++ cfr.	-	-	++ cfr.
Montane communities with high water table	+ rare	++ cfr.	-	-

Key		
	cfr.	with capsules
	++	large tufts
	+	smaller tufts

Conclusion.

The communities, in which Dicranum species have been found, are described with reference to literature records. Table 2. 9 has been prepared to show the overall performance of the various species in the different habitats.

The species overlap considerably in ecological amplitude, with D. scoparium showing by far the largest range. Optimum conditions for all species occur, where local topography, heavy rainfall or extreme exposure produce open communities with reduced competition. They also occur in the open series of seral systems such as dunes and rock habitats.

It is of considerable interest that D. bonjeanii is the sole Dicranum species found in the communities with a very high water-table. D. scoparium is also found but only on the drier areas in the same locality. It is perhaps notable also that D. bonjeanii has two such markedly different habitats, dry basic conditions, and extremely waterlogged acid ones. Intermediate habitats are known but they occur much less frequently than in D. scoparium, where a continuous series, of almost the same range, is found.

In conclusion it may be stated that, in these field studies it has been found that, D. bonjeanii is ecologically isolated from D. majus and D. fuscescens and that D. scoparium shows ecological overlap with the other three species. Careful collection of specimens have been made to investigate the variation in relation to habitat and especially to discover whether the 'morphologically difficult' specimens occurred where two or more of the species were growing together.

CHAPTER III.

VARIATION.

The main problems investigated in this study of Dicranum variation are firstly, that of species separation and secondly, the origin and extent of the diversity of forms found within each species.

Two methods of approach have been used to investigate herbarium samples of the populations under study.

1. The material has been divided into ecological groups to find out whether any morphological types are found in particular habitat conditions. Often several of the Dicranum species have been found growing together and special note has been taken of whether problem taxa occur in such situations. By comparing data for each ecological group a picture of the variation within each of the species has been developed. This method of approach casts some light on both the problems posed above; on the intra-specific variation and the problem of species separation. To examine some of these problems more closely another analysis was also carried out.

2. A biometrical analysis of a selected number of populations has been undertaken. The fine details of variation become apparent by this means, and not only has the intra-specific variability been more clearly defined but such problems of the variation of male and female plants in the same population has been investigated.

STUDIES IN THE VARIATION IN DIFFERENT ECOLOGICAL GROUPS.

Methods.

Each population was examined and if mixed separate numbers were given for each taxon. The material was then scored, by eye in some cases, for the following characters:-

1. Depth of tuft in cms.
2. Zonation in leaf size (between upper and lower leaves).
3. Falcation class in upper leaves using following key -
    1. Erect 0-26°.
    2. Patent 26-45°.
    3. Patulous 46-90°.
    4. Falcate.
    5. Secund.
    6. Falcato-secund.

    LEAVES STRAIGHT.
    1 - 3.

    LEAVES NOT STRAIGHT.
    4 - 6.
4. Falcation class of lower leaves using same key. In both cases the dominant falcation class is recorded.
5. Tomentum class

    Slight 1
    Well developed 2

    Colour also recorded

    R - red.
    W - white.
6. Upper cell porosity + or - .

7. 8. 9. Teeth at apex, at edge of lamina, and at back of nerve.

10. Undulation:

Absent - 0

Slight - 1

Rugose - 2

11. Leaf size, whether 9 mm or more in length.

12. Nerve proportion at widest part of the leaf. Jensen (1939) calculated nerve proportion data using the nerve width and leaf base measurements, see Chapter I. During preliminary examination of the samples it was found that in preparing slides the leaf base was often damaged and that the nerve was less distinct in this region. These two difficulties were not encountered if the leaf and nerve width were measured at the widest point of the leaf.

CHARACTERS of fruiting material.

13. Polysety + or -.

14. Seta colour; R - red, G - green, Y - yellow.

15. Capsule inclination:- 1. Erect, 2. Suberect, 3. Horizontal.

16. Capsule striate + or -.

17. Type of male plant if determinable.

Identification.

Each population in the tables has been assigned to one of the four Dicranum species. The following characters, recorded in tabular form, have been used in identification. A combination of characters has always been used in deciding to which species a specimen belongs.

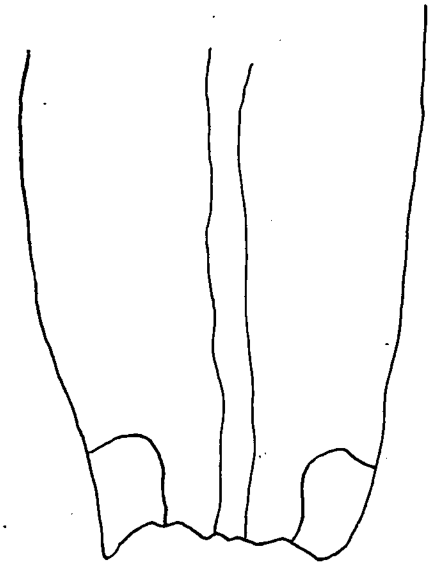
	Upper cell porosity	Undulation	Nerve	Polysety	Striate capsule	Seta colour	Capsule inclination
D. scoparium	+	+	S	-	-	R	Suberect
D. majus	+	-	S	+	-	G	± horizontal
D. fuscescens	-	-	S	-	+	Y	Arcuate
D. bonjeanii	+	+	W	-	-	R	Suberect

R = red, Y = yellow, G = green.

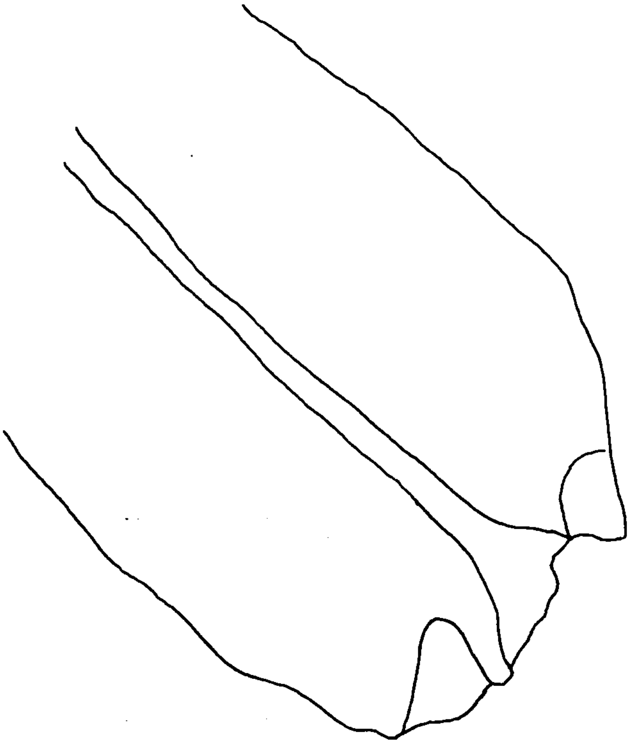
Specimens 9 mm or more in leaf length were suspected of being D. majus, as accounts in floras indicate that this is the upper limit of Dicranum scoparium, the largest of the remaining three species, and 9 mm is near the lower limit for D. majus. The range of the length of the various species has been the subject of biometrical study and will be reported on below.

Some difficulty in using nerve proportion characters has been found. In Tables 3. 2 - 3. 6 single proportions are given, calculated from a typical leaf. Some variation in proportion was noted within populations and in Chapter VII details of this variation will be summarised. Fig. I shows typical leaf bases of the four species.

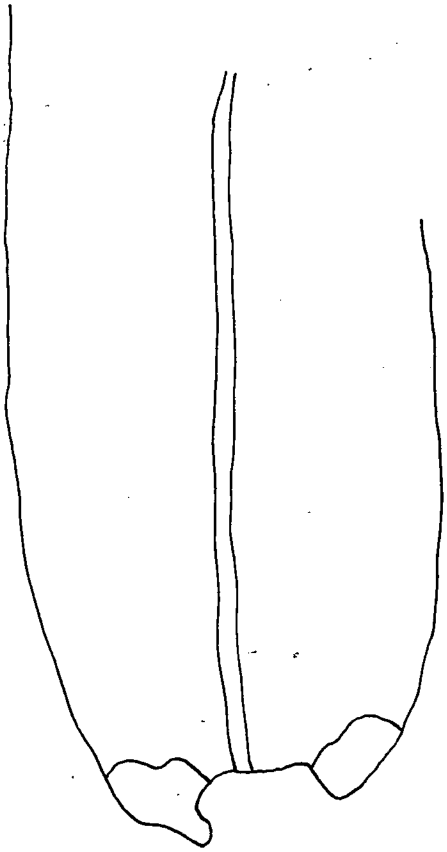
LEAF BASES OF DICRANUM SPECIES TO SHOW NERVE PROPORTION.



D.scoparium population 395.



D.majus population 444.



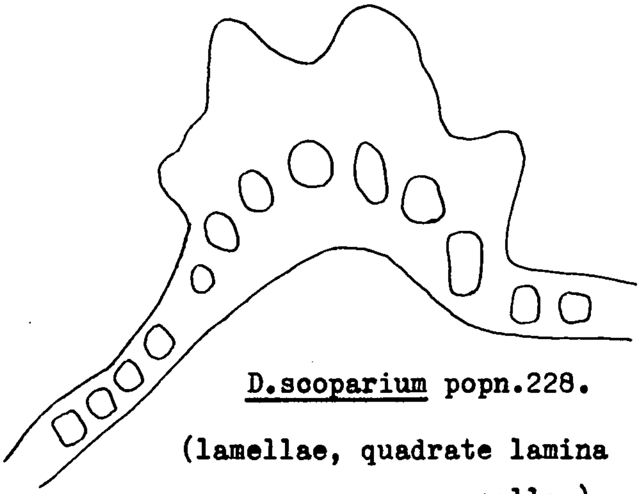
D.bonjeanii population 454.

D.fuscescens population 357.

Imm.

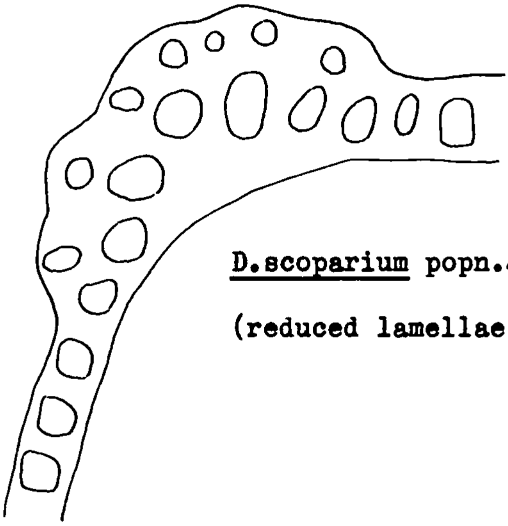
FigI.

LEAF SECTIONS OF THE FOUR DICRANUM SPECIES.



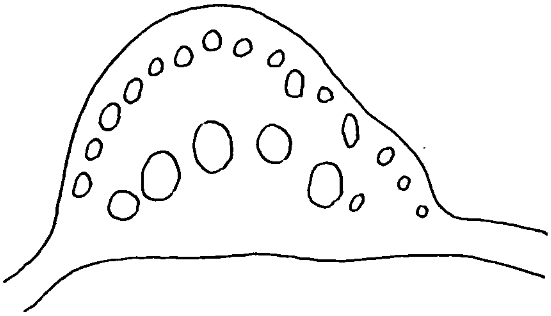
D.scoparium popn.228.

(lamellae, quadrate lamina cells.)



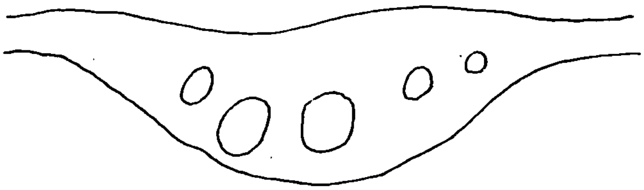
D.scoparium popn.486.

(reduced lamellae.)



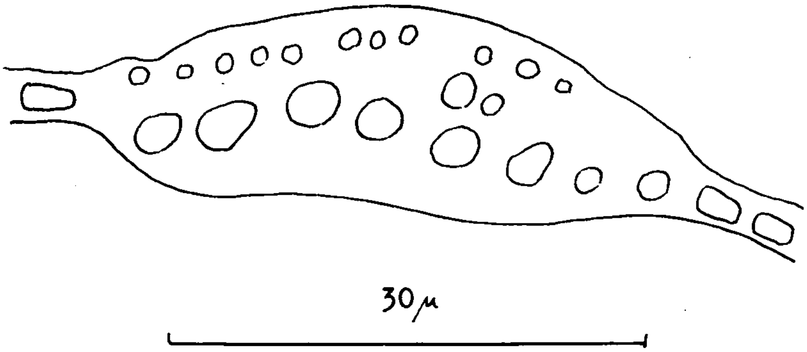
D.fuscescens popn 357.

(no lamellae.)



D.bonjeanii popn.485.

(no lamellae.)

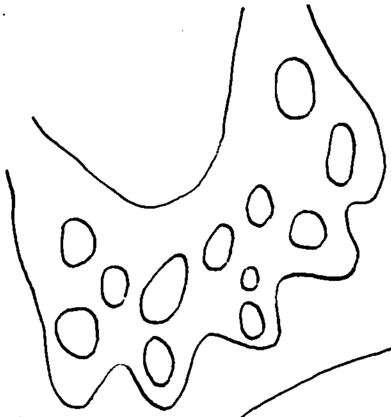


D.majus popn 37I.

(rectangular lamina cells.)

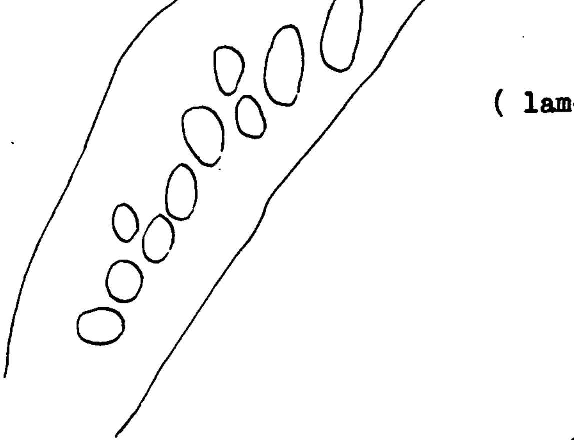
Fig.2.

LEAF SECTIONS OF DIFFICULT MATERIAL.



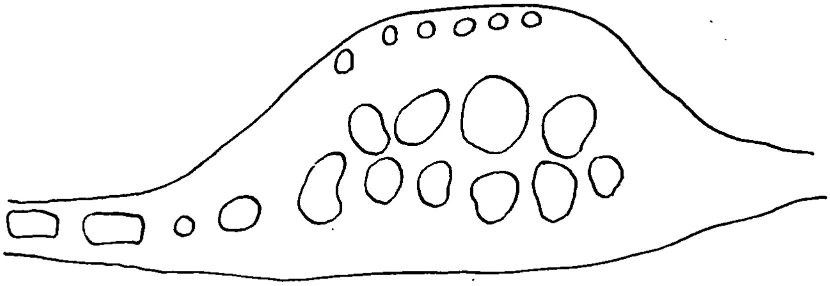
Popn. 217. a). D.scoparium or b). D.fuscescens.

(clearly a) as lamellae present.)



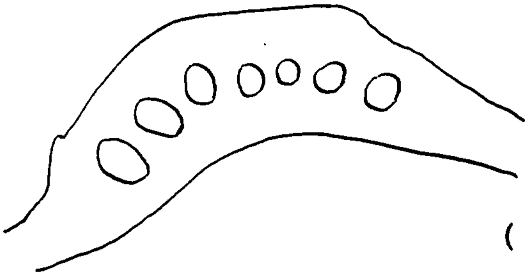
Popn. 426. a) D.scoparium or b). D.fuscescens.

(lamellae absent, leaf margin serrated, therefore not a).)



Popn. 328. D.majus.

(not D.scoparium var. recurvatum as lamina cells rectangular.)



Popn. 325. D.bonjeanii.

(no lamellae, leaf margins serrated, not D.scoparium with this combination of characters.)

30 μ.

Fig.3.

Leaf sections of any particularly difficult material have been prepared. Reference sections of standard material are given in Fig. 2 and 3 together with a selection of difficult specimens, comments on which will be given below. The leaf section characters, mentioned in Chapter I, are briefly summarised in Table 3. 1.

	No. lamellae	Shape of lamina cells in cross section
D. majus	Several, irregular	Rectangular
D. scoparium	4 serrated	Quadrate
D. bonjeanii	2-(4) serrated or smooth	Quadrate
D. fuscescens	-	Quadrate

Results.

The variation shown in each ecological type is summarised in Tables 3. 2 etc. with comments upon the identification of difficult specimens and the range of material found in each group of habitats. Details of sporophytes are not included; the four species were found to conform to the descriptions in Chapter I. The material is divided into sub-units in accordance with the criteria given in Chapter II.

1. Dunes.
2. Basic Habitats.
3. Woodlands.
4. Dead wood.
5. Tree epiphytes.
6. Rock and Walls.
7. Acid communities.
8. Communities with a high water-table.

TABLE 3. 2.

POPULATIONS FROM BASIC SOILS

	DUNE MATERIAL																			
POPN. NO.	355	458	488	489	200	210	211	274	346	348	349	352	353	354A	354B	354C	440	446	448	460
Depth cms.	4	4	5.5	1.5	4	6	7	5	3	1.5	2	1.5	1	1.5	1.5	1.5	3	1.5	2	2
Zonation in leaf size	+	+	+	+	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–
F. class of upper leaves	2	2	2	2	2	2	4	6	1–2	1–2	1–2	1–2	1–2	6	2–6	1–2	1–2	1–2	1–2	2
F. class of lower leaves	2	2	2	2	2	2	4	3	–	–	6	–	–	2	2	–	6	6	–	2
Other F. types	–	–	–	–	–	6	2	–	–	–	–	–	–	–	1	–	–	–	–	–
Tomentum	+	+	–	–	–	+	+	+	–	–	–	–	–	–	–	–	–	–	–	–
Upper cell porosity	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Teeth at apex of leaf	+	+	+	+	+	–	+	+	+	–	–	–	+	+	+	+	+	+	+	+
Teeth edge lamina	–	–	+	–	+	–	+	–	+	–	–	–	–	+	–	–	+	+	+	–
Teeth back nerve	–	–	+	–	+	–	+	–	+	–	–	–	–	+	–	–	+	+	+	–
Leaf undulate	–	–	–	–	1	–	2	–	–	–	–	–	–	2	1	–	–	–	1	1
Leaf length 9 mm^{+}	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Nerve propn.	$\frac{1}{9}$	–	$\frac{1}{9}$	$\frac{1}{11}$	$\frac{1}{10}$	$\frac{1}{10}$	$\frac{1}{17}$	$\frac{1}{11}$	$\frac{1}{10}$	$\frac{1}{10}$	$\frac{1}{10}$	$\frac{1}{9}$	$\frac{1}{12}$	$\frac{1}{16}$	$\frac{1}{16}$	$\frac{1}{11}$	$\frac{1}{8}$	$\frac{1}{13}$	$\frac{1}{7}$	$\frac{1}{15}$
Conclusion	D.s	D.s	D.s	D.s	D.s	D.s	D.b	D.s	D.s	D.s	D.s	D.s	D.s	D.b	D.b	D.s	D.s	D.s	D.s	D.b

1. Dune Material.

All the gatherings are attributable to D. scoparium. No difficulties were experienced in dealing with this material. It is of interest to note that the leaf stance is predominantly patent with a zonation in leaf size. Serration is very variable within populations, the predominant type being recorded. Sometimes teeth are found at the apex, on the back of the nerve, and also on the lamina of the leaf as in 488, but in the other three populations only a few teeth were present at the extreme tip of the leaf. The variation in tomentum is also shown in the tables, two populations being without tomentum, the others having a mixture of red and white.

Large and dwarf male plants were found in 355, which also had a single specimen showing disety.

Using the subspecific nomenclature given in Chapter I, the D. scoparium specimens can probably be referred to the following taxa.

355, 458, 489 var. spadiceum Zett.
488, var. orthophyllum Brid.

2. Other Basic Habitats.

An interesting feature of the material collected from basic habitats is the high incidence of erecto-patent leaves recorded for D. scoparium. Both var. orthophyllum and var. spadiceum appear to be present, e.g. 461, 464 and 352, 349, respectively. Reduction in serration again appears to be associated with high altitude; the higher altitude quadrats invariably have entire leaved plants. Undulate specimens of *D. scoparium* and *D. bonjeanii* are recorded.

354 appears to contain three taxa. One approaching *D. bonjeanii* var. *calcareum*, 354B; another being D. *bonjeanii* of type morphology, 354A; and the third *D. scoparium*, 354C. The features of 354B which indicate var. *calcareum* are the reduced serration and the small amount of undulation of the leaf lamina in comparison with the material of 354A.

3. Woodland material.

Identification.

The populations of sterile *Dicranum*, 320, 328, 330, 333, with large falcato-secund leaves, attributed to *D. majus*, were carefully checked, as they may have been specimens of *D. scoparium* var. *recurvatum*. The irregular lamellae and rectangular lamina cells seen in cross sections of the leaves pointed to *D. majus*. The sections illustrated in Fig. 3 are very similar to 371, which was undoubted *D. majus*. Other populations presented little difficulty, and in habitats with more than one species, (see Table 3. 3), the difficulties were usually reduced.

Variation.

D. majus (16 gatherings), shows great homogeneity of leaf stance, serration, porosity and other characters. *D. fuscescens* (4 gatherings) also shows a regular type of leaf stance but the serration of the leaf is a variable character. In three cases teeth are found throughout the recorded zones of the leaf in 332 however serration is confined to the

TABLE 3. 3.

POPULATIONS FROM WOODS

POPN. NO.	165	290	294	295	296	320	329	330	331	332	333	357	358	360	364	369	371	374	390	391	392
Depth cms.	25	5	3	3	3	7	4	12	2.5	2.5	4	2	4	3	5	4	5	2	3	3	3
Zonation in leaf size	+	-	+	+	+	-	+	-	-	-	-	-	-	+	-	+	-	-	-	+	-
F. class upper leaves	6	6	6	2	6	6	6	6	2	6	6	6	6	6	6	6	6	6	6	6	6
F. class lower leaves	2	6	2	1	2	6	2	6	2	-	6	-	6	2	6	2	6	6	6	2	6
Other F. types	3.4	-	3.4	-	4	-	3.4	-	-	-	-	-	-	3.4	-	3	-	4.2	-	-	-
Tomentum	+	+	-	-	+	+	-	+	-	+	-	-	-	+	+	+	+	+	-	-	-
Upper cell porosity	+	+	+	+	+	+	+	+	+	-	+	-	+	+	+	+	+	-	+	+	+
Teeth at leaf apex	+	+	-	+	+	+	+	+	-	+	+	+	+	+	+	+	+	+	+	+	+
Teeth edge lamina	+	+	-	+	+	+	+	+	-	-	+	+	+	+	+	+	+	+	+	-	+
Teeth back nerve	+	+	-	+	+	+	+	+	-	-	+	+	+	+	+	+	+	+	+	+	+
Leaf undulate	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-
Leaf length 9 mm$^+$	-	+	-	-	-	+	-	-	-	-	+	-	+	-	+	-	+	-	-	-	+
Nerve propn.	$\frac{1}{11}$	$\frac{1}{12}$	$\frac{1}{10}$	$\frac{1}{10}$	$\frac{1}{10}$	$\frac{1}{10}$	$\frac{1}{10}$	$\frac{1}{10}$	$\frac{1}{10}$	$\frac{1}{4}$	$\frac{1}{10}$	$\frac{1}{4}$	$\frac{1}{10}$	$\frac{1}{10}$	$\frac{1}{10}$	$\frac{1}{10}$	$\frac{1}{10}$	$\frac{1}{4}$	-	$\frac{1}{13}$	$\frac{1}{16}$
Conclusion	D.s	D.m	D.s	D.s	D.s	D.m	D.s	D.m	D.s	D.f	D.m	D.f	D.m	D.s	D.m	D.s	D.m	D.f	D.s	D.s	D.m

TABLE 3. 3. continued

POPN. NO.	396	399	400	408	411	412	428	429	444	450	451	455	456	486L♂	486D♂	487	495	496	497
Depth cms.	3	4	6	2	5	2	3	4	7	2	2.5	3	7	1.5	1.5	1.5	5	6	5
Zonation in leaf size	+	–	–	–	–	+	+	–	–	+	–	+	–	+	+	–	–	–	+
F. class upper leaves	2	6	6	6	6	2	6	6	6	2	6	2	6	6	6	6	6	6	1
F. class lower leaves	2	6	6	6	6	2	6	6	6	2	6	2	6	2	2	–	6	6	2
Other F. types	–	–	–	–	–	6	2	–	–	6	–	6	–	3	4	–	1,2	2	–
Tomentum	1W	–	–	–	–	1R	–	–	–	–	–	–	1W	–	–	1W	–	1W/R	–
Upper cell porosity	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	–	+	+	+
Teeth at leaf apex	+	+	+	+	+	+	+	+	+	–	+	+	+	+	+	+	+	+	+
Teeth edge of lamina	–	+	+	+	+	–	–	+	+	–	+	–	+	+	+	+	+	+	+
Teeth back of nerve	–	+	+	+	+	–	–	+	+	–	+	–	+	–	–	+	–	+	+
Leaf undulate	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2
Leaf length 9 mm^{+}	–	+	+	+	–	–	–	+	+	–	–	–	+	–	–	–	–	–	–
Nerve propn.	$\frac{1}{8}$	$\frac{1}{13}$	$\frac{1}{13}$	$\frac{1}{10}$	$\frac{1}{13}$	$\frac{1}{10}$	$\frac{1}{12}$	$\frac{1}{16}$	$\frac{1}{12}$	$\frac{1}{7}$	$\frac{1}{9}$	$\frac{1}{11}$	$\frac{1}{15}$	$\frac{1}{10}$	$\frac{1}{9}$	$\frac{1}{6}$	$\frac{1}{16}$	$\frac{1}{9}$	$\frac{1}{16}$
Conclusion	D.s	D.m	D.m	D.m	D.m	D.s	D.s	D.m	D.m	D.s	D.s	D.s	D.m	D.s	D.s	D.f	D.b	D.s	D.b

extreme tip. Two distinct types of D. bonjeanii were collected in 495/7, 495 with falcato-secund leaves showing only limited undulation, and 497 with erecto-patent leaves more markedly undulate. D. scoparium shows great variability in the woodland populations, especially in leaf stance and serration.

Leaf Stance.		
	Falcato-secund throughout	3
	F-S above patent below	10
	Patent throughout	5
	Patent above erect below	1

No. of Popn.	Teeth at APEX	EDGE LAMINA	NERVE BACK
8	+	+	+
2	+	+	-
1	+	-	+
5	+	-	-
3	-	-	-

These groups of characters will be dealt with below when the whole range of variation within each species is discussed. Undoubtedly within woodlands however, serration (at first sight), appears to be related to altitude, as entire forms are found in the highest woods.

From an ecological view point the variation shown by the Dicranums in leaf stance is very interesting. Falcato-secund forms of all four species predominate in shaded communities with more erecto-patent forms, except in D. majus, in more exposed facies of the woodlands.

Zonation in leaf size is common in woodland *D. scoparium* and is due to different growth patterns at different times of year. This seasonal phenomenon will be discussed below. It is of interest to note that *D. fuscescens* and *D. majus* do not show these marked zones; in *D. bonjeanii* 497 they are developed. Stem tomentum is found in some populations of the three commonest species. No clear cut reason for the irregularity of distribution of tomentum within the samples has been found, though usually it is associated with well developed specimens.

Examination of the fruiting populations has revealed little variation in the sporophyte of any of the three species which produce capsules within woodlands. The male plants recorded show that large males are found in *D. scoparium* and *D. fuscescens* and dwarf males in *D. majus* and one population of *D. scoparium* 486.

An examination of Table 3.3 of variation in woodlands, for all the *Dicranum* species, shows that variation within the species does not fall into groups related directly to the dominant tree species. Reduced serration forms are however found in the higher woodlands especially in the North and West of Britain. These include forests with several different dominants.

Using the nomenclature and characters given in Chapter I the following variants are found to occur in woodlands:-

D. majus type material only.

D. fuscescens. type e.g. 374

cf var. congestum 332

D. bonjeanii type 497

forma falcata 495

D. scoparium type 165

var. paludosum 360 in part

var. orthophyllum 295

var. spadiceum 331, 450

Certain populations of D. scoparium are extremely difficult to place within a variety. Forms with few serrations and falcato-secund leaves do not appear to be covered by the varieties e.g. 294.

4. Dicranum samples from decaying timber.

D. majus, 428, has been found in one quadrat taken on dead wood. The material was indistinguishable from gatherings made from the ground flora of the same woodland. It occurred in this quadrat together with D. fuscescens and D. scoparium. D. fuscescens, 426, was confirmed by leaf sections and was a difficult specimen. This difficulty was unusual; throughout this study material has been easiest to deal with if more than one species was present within the sample area.

The specimens of D. fuscescens closely resembled type material. The variation in D. scoparium is most marked in leaf stance, where both falcato-secund and erecto-patent forms have been found; no great variation has been found in serrature. The material of all the species conforms to the type description.

TABLE 3. 4.

POPULATIONS FROM DECAYING TIMBER AND EPIPHYTIC

	SAMPLES FROM DECAYING TIMBER									EPIPHYTIC DICRANA														
	166	363	368	395	397	426	427	428	481	168	217	297	304	362	367	372	394	401	402	403	407	410	430	431
Depth cms.	2.0	1.5	3	3	1	1.5	3	4	4	3	3	2	1	3	2.5	1	2	3.5	4	1	2	1.5	1.5	2
Zonation in leaf size	–	–	+	+	–	–	+	–	+	+	–	–	–	+	+	–	–	+	+	–	–	–	–	–
F. class of upper leaves	2	6	6	1	6	6	6	6	6	4	6	6	6	6	6	6	2	6	6	6	6	2	2	6
F. class of lower leaves	2	–	2	2	–	–	2	–	2	4	–	–	–	2	2	–	–	2	6	–	–	–	–	–
Other F.types	6	2	–	–	–	–	–	–	1	6,2	–	–	–	–	–	–	–	–	2,4	–	–	6	6	–
Tomentum	1W	–	–	1W	1W	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1W
Upper cell porosity	+	+	+	+	–	–	+	+	+	+	+	+	–	+	+	–	+	+	+	–	–	+	+	–
Teeth at leaf apex	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	–	+	+
Teeth edge lamina	+	+	+	+	+	+	+	+	+	–	–	+	–	+	–	+	–	–	–	+	+	–	–	+
Teeth back of nerve	+	+	+	+	+	+	+	+	+	–	+	+	+	+	–	+	–	–	–	+	+	–	–	+
Leaf undulate	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Leaf length 9 mm$^+$	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Nerve propn.	$\frac{1}{8}$	$\frac{1}{10}$	$\frac{1}{10}$	$\frac{1}{10}$	$\frac{1}{5}$	$\frac{1}{4}$	$\frac{1}{7}$	$\frac{1}{10}$	$\frac{1}{9}$	$\frac{1}{10}$	$\frac{1}{7}$	$\frac{1}{7}$	$\frac{1}{7}$	$\frac{1}{10}$	$\frac{1}{10}$	$\frac{1}{5}$	$\frac{1}{10}$	$\frac{1}{11}$	$\frac{1}{8}$	$\frac{1}{5}$	$\frac{1}{4}$	$\frac{1}{8}$	$\frac{1}{10}$	$\frac{1}{3}$
Conclusion	D.s	D.s	D.s	D.s	D.f	D.f	D.s	D.m	D.s	D.s	D.f	D.s	D.f	D.s	D.s	D.f	D.s	D.s	D.s	D.f	D.f	D.s	D.s	D.f

5. Dicranum populations epiphytic on trees.

The material in this group presented little difficulty except population 217, in which porosity of the upper cell seemed to vary, a few leaves had irregular not strictly porose cells. A leaf section, see Fig. 3, showed four marked lamellae at the back of the leaf, which clearly establishes it as *D. scoparium*.

D. fuscescens, represented by five populations shows falcato-secund leaves predominantly, with a reduced type of serration in population 304 only. All the material fits the type description and is clearly very similar to woodland floor specimens of 372/374.

The leaf stance of *D. scoparium* is variable but with falcato-secund forms commonly found. Similar forms are found in the dry ground flora of woods. Three populations had patent leaves however, these were from moister trunks and tree bases. Serration is again variable, two samples showing typical leaves 297, 362, but others had reduced serration of various types, six populations had only apical serration and often resembled ground flora gatherings. (e.g. 410 is very similar to 412.) All the samples were non-undulate and the rarity of tomentum is worth recording.

Fruiting material of *D. scoparium* had large males in quadrat 367, 401, and 362, but in 402 dwarf males were discovered.

The material of *D. scoparium* falls mostly within the type but population 410, from moister habitat, approaches var. *spadiceum*.

No variation has been noted in samples collected from different tree species, except in luxuriance of growth.

TABLE 3. 6.

COMMUNITIES WITH HIGH WATER TABLE; AND ROCKS.

	HIGH WATER TABLE										ROCKS AND WALLS						
	220	322	325	421	441	443	A 454	B 454	471	485	300	361	370	373	404	406	409
Depth cms.	8	6	3	2	2	4	2	2	4	5	2	3	6	1.5	1.5	1.5	2
Zonation in leaf size	+	-	-	-	-	-	-	-	-	-	+	+	-	-	-	-	-
F. class upper leaves	2	2	2	2	3	3	2	2	2	2	6	6	6	6	2	6	2
F. class lower leaves	2	-	-	-	-	-	-	-	-	-	2	2	6	-	2	-	2
Other F. types	-	-	-	1	-	6,2	-	-	-	-	3	3	4	-	-	-	-
Tomentum	-	-	-	-	-	-	-	1R	-	2R	1W	-	-	1W	-	-	-
Upper cell porosity	+	+	+	+	+	+	+	+	+	+	+	+	+	-	+	-	+
Teeth at leaf apex	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	-
Teeth at edge lamina	+	+	+	+	+	+	-	+	-	+	+	+	+	+	-	-	-
Teeth at back nerve	+	+	+	-	-	-	-	+	-	-	+	+	+	+	-	-	-
Leaf undulate	2	+	+	+	+	+	-	-	+	+	-	-	-	-	-	-	-
Leaf length 9 mm$^+$	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Nerve proportion	$\frac{1}{10}$	$\frac{1}{16}$	$\frac{1}{21}$	$\frac{1}{12}$	$\frac{1}{15}$	$\frac{1}{14}$	$\frac{1}{21}$	$\frac{1}{10}$	$\frac{1}{22}$	$\frac{1}{14}$	$\frac{1}{14}$	$\frac{1}{9}$	$\frac{1}{10}$	$\frac{1}{4}$	$\frac{1}{12}$	$\frac{1}{6}$	$\frac{1}{13}$
Conclusion	D.s	D.b	D.b	D.b	D.b	D.b	D.b	D.s	D.b	D.b	D.s	D.s	D.s	D.f	D.s	D.f	D.s

6. Rock and Wall specimens.

Material collected in this group of habitats includes both main leaf stance types of D. scoparium, falcato-secund and erecto-patent, and also specimens showing reduced serration, 404 approaching var. spadiceum. The gatherings of D. fuscescens show closely similar variation in these two characters, the less serrulate being close to var. congestum 406.

Fertile material shows little variation. The erect capsules recorded for 300 were immature, the usual suberect inclination being assumed later in development.

Ecologically the group is heterogeneous, shaded woodland rocks 361, 370/373 on the one hand, and on the other more exposed upland rocks 404/409. There is a marked division of the material into two groups morphologically, the erecto-patent reduced serration forms being upland and the more typical material being shaded woodland.

7. Acid communities, mostly montane.

Gatherings of D. scoparium from acid unshaded habitats show marked variation in serration of the leaf apex, the high altitude types having entire leaves, similar in this respect to forms in high woodland and upland basic communities.

These approach D. scoparium var. spadiceum e.g. 420, 422, 423. Others e.g. 318 are nearer to var. orthophyllum. Leaf stance variation in D. scoparium is considerable in these quadrats, both falcato-secund and erecto-patent forms being found.

The specimens of D. fuscescens 381, 382, 385 had falcate leaves, 382 and 385 having reduced serrature. A single population of D. majus has been collected, 424, and is very similar to woodland material, with falcato-secund leaves and no reduction in the serrature.

8. Communities with High Water Table.

Specimens included in this group have been specially checked as both D. scoparium and D. bonjeanii can have undulate leaves. Leaf sections clearly show small development of lamellae in 322, 325, 421, and 443 and very similar sections are found in 485 which is undoubtedly D. bonjeanii. All are therefore assigned to D. bonjeanii. The phenomenon of reduction in serration at high altitude is probably found also in D. bonjeanii, 471 from Moor House Nature Reserve has only a few teeth at the leaf apex.

The leaf stance of the samples is extremely regular being patent in most cases but with some plants showing patulous leaves and in 443 deflexed leaves.

All the material of D. bonjeanii is of the type except 454A which is near D. bonjeanii var. calcareum; D. scoparium is also represented by type material in 454 with var. paludosum in 220.

Fruiting material of D. bonjeanii has been collected at 485 and it was noted that there was a gradation in size in the male plants, both large and small plants being found (see below).

TABLE 3. 5.

ACID COMMUNITIES MOSTLY MONTANE.

	218	228	270	298	317	318	326	347	350	376	380	381	382	385	393	420	422	423	424	442	445?
Depth cms.	1.2	4.0	5	2	2	3	1.5	2	1	2.5	2	2	1.5	1	1.5	1	2	2	2	1	
Zonation in leaf size	+	-	-	-	+	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	
F. class upper leaves	6	6	2	1-2	6	6	1-2	1-2	1-2	1-2	1-2	4	4	4-5	1-2	1-2	1-2	6	6	1-2	
F. class lower leaves	2	6	6	-	2	-	-	-	-	6	-	4	4	-	-	-	-	1-2	-	-	
Other F. types	-	-	-	-	-	2	-	-	6	-	-	6,2	-	-	6	-	-	-	-	-	
Tomentum	1R	1R	1R	-	-	-	-	-	-	-	-	1W	-	-	-	-	-	-	-	-	
Upper cell porosity	+	+	+	+	+	+	+	+	+	+	+	-	-	-	+	+	+	+	+	+	
Teeth at leaf apex	+	+	+	+	+	+	+	+	-	-	+	+	+	-	+	-	-	+	+	+	
Teeth edge lamina	+	+	-	+	-	+	-	-	-	-	-	+	-	-	-	-	-	-	+	-	
Teeth back of nerve	+	+	-	+	-	+	-	-	-	-	-	+	-	-	+	-	-	-	+	-	
Leaf undulate	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Leaf length 9 mm$^+$	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	
Nerve proportion	$\frac{1}{10}$	$\frac{1}{8}$	$\frac{1}{11}$	$\frac{1}{7}$	$\frac{1}{10}$	$\frac{1}{10}$	$\frac{1}{8}$	$\frac{1}{10}$	$\frac{1}{9}$	$\frac{1}{12}$	$\frac{1}{7}$	$\frac{1}{4}$	$\frac{1}{7}$	$\frac{1}{8}$	$\frac{1}{10}$	$\frac{1}{12}$	$\frac{1}{11}$	$\frac{1}{10}$	$\frac{1}{17}$	$\frac{1}{9}$	
Conclusion	D.s	D.s	D.s	D.s	D.s	D.s	D.s	D.s	D.s	D.s	D.s	D.f	D.f	D.f	D.s	D.s	D.s	D.s	D.m	D.s	

Discussion.

It has been shown that species delimitation can be accomplished using the criteria mentioned in Chapter I. Certain characters such as nerve width, and leaf length which are very important have been investigated using biometrical methods to test their reliability as key features. It has also been pointed out that species are usually distinct when growing together, though difficulties arise often with poorly grown material.

Summarizing the variation patterns in relation to ecology it may be stated that certain morphological types are of regular occurrence. In D. majus type material is found throughout the communities recorded. On the other hand in the other three species falcato-secund leaves are predominately found in such shaded habitats as in woods, and related communities on trees, dead wood, and rocks within woodland. Also found regularly are various straight leaved forms with and without teeth.

An interesting feature of the variation in leaf stance shown by the four species in a single habitat has been mentioned above and must be further stressed and that is the phenomenon of parallel variation. D. fuscescens, D. scoparium and D. majus all show somewhat similar leaf stance in shaded woods, e.g. 369/371/374. Exceptions to this do occur however e.g. 455/456. (D. scoparium, D. majus).

The forms with falcato-secund leaves are found in shaded habitats, erecto-patent forms in exposed habitats with intermediates and mixtures of both. The significance of this is not easy to understand but one possibility is that falcato-secund leaves are a xerophytic feature of the plant, developed in habitats where rainfall is low or where the habitat is extremely quickly drained such as rocks and trees and woodlands on steep slopes; many examples of this are given in the habitat lists. The predominance of erecto-patent forms in upland areas may, on this hypothesis, be due to two features; impeded drainage and high rainfall, which falls on a large number of days per year, (figures of more than 200 rain-days are recorded for Highland Wales, Scotland, N. and S.W. England. Climatological Atlas (1952)).

This hypothesis is open to experiment. If the falcato-secund forms are maintained when grown in high humidity, the character would probably be genotypically fixed; if however erecto-patent leaves can be produced from falcato-secund specimens, the species could be regarded as being phenotypically plastic for the character, the amount of falcato-secund or erecto-patent leaves indicating the water relations of the habitat. Such an experiment has been carried out, using the standard habitat of a cold frame with frequent watering, and will be reported on in a later section.

The suggestion has been made that altitude has an important bearing upon serration; any theory which suggests that the number of teeth per leaf decreases with increase in altitude, must take into account specimens collected at sea level, (on dunes,) which have similar reduction in teeth number. Also an examination of Maps 4, 5 and 6, giving the distribution of entire-leaved forms, indicates that they are not restricted to the highest altitudes in D. scoparium and D. bonjeanii, though probably so in D. fuscescens. A fuller discussion of serration problems appears below.

An examination of the lists for the various habitat groups shows that variation amongst and between populations is much more marked in some, than in others. E.g. woodlands contain a number of different types of leaf stance in marked contrast to the more constant forms found in basic habitats. This may well be connected with micro-climatic differences within the habitats, a wide range being found in the heterogeneous tree dominated communities loosely called woodland, whereas quadrats from a number of basic grasslands probably have less habitat variation of this kind. The type of ecological data recorded at the time of collection of the sample is of little use in assessing the micro-climatic differences. Experiments in which samples have been grown under standard conditions will be described below.

Certain difficulties in applying the intraspecific categories commonly mentioned in the floras have been mentioned, especially in relation to falcato-secund types which show reduced serration. These too will be discussed below.

The different habitat groups studied all have tomentose specimens but best development appears to be found in moist habitats in well grown material. More work is required to explain the different colours produced and to account for their distribution.

BIOMETRICAL ANALYSIS.

Detailed measurements on several populations of Dicranum, of all four species, have been carried out. Besides material from cytologically studied populations representative herbarium specimens taken from the various habitats studied, have been measured. These results will be used to examine, from another angle, the problems of species separation and the status of the various named intraspecific units.

Methods.

From soaked-out herbarium material of each population 30 stems were chosen at random and the largest leaf from each stem mounted in gum chloral. Six slides were produced for each sample, each with five leaves. The following measurements were made, using a micrometer eye piece and low magnification microscope, on the first 25 intact leaves.

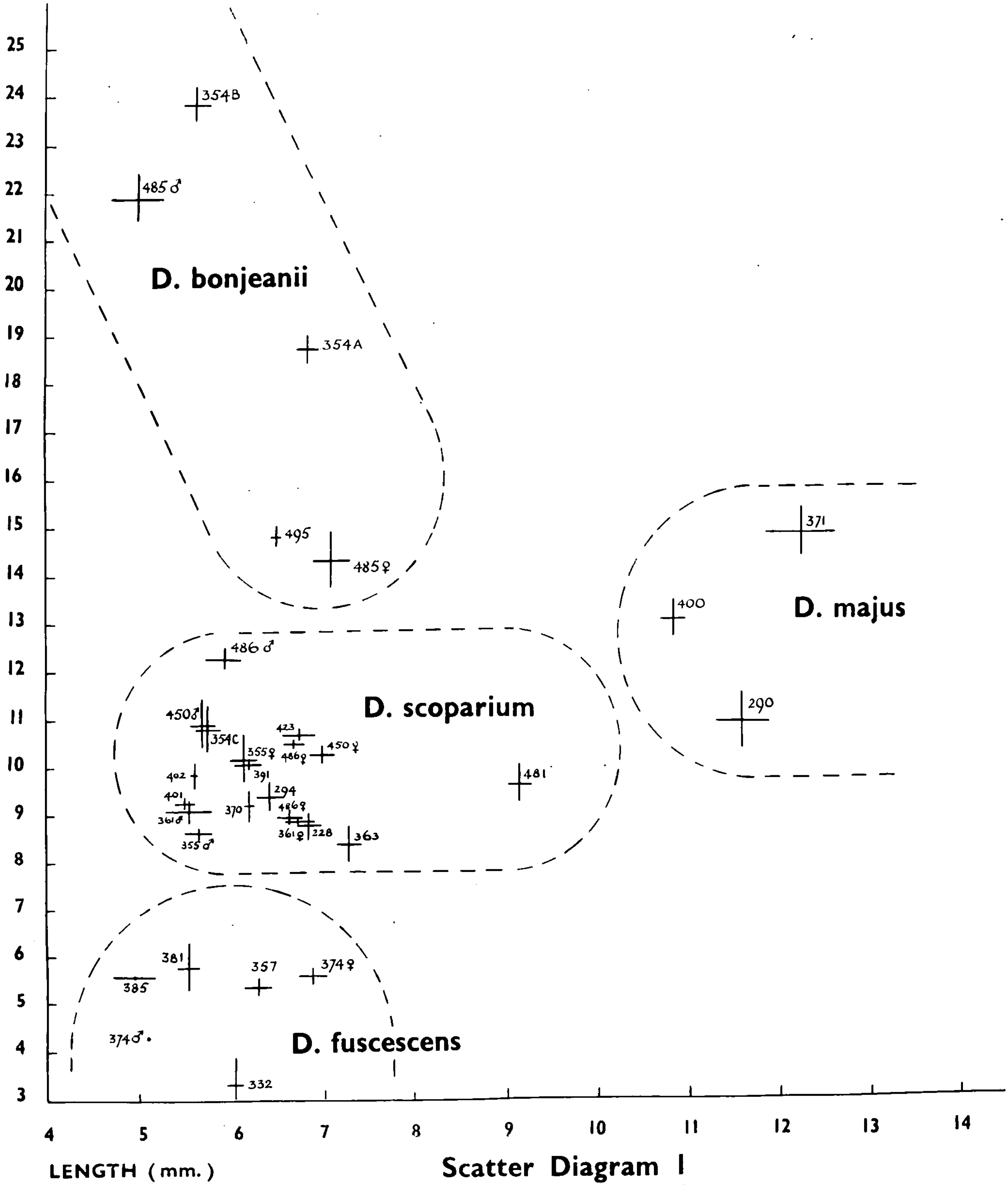
A. Length.

B. Breadth, at widest point.

C. Nerve width, at same point as B.

D. Number of teeth on one edge of the lamina from apex to leaf base. Care was taken not to include nerve serration.

Length/breadth and leaf width/nerve width proportions were calculated from the data, together with mean values for all measurements and Standard Errors for important characters. The following tables of results have been prepared, Tables 3.7, 3.8, 3.9, and 3.10.



Scatter Diagram I

Leaf length / width / nerve width

Standard errors and mean values

SPECIES SEPARATION.

Leaf Length.

Mean length and leaf width/nerve width have been prepared as a scatter diagram, with Standard Errors incorporated. Separation of D. majus from the other three species is clearly shown in the samples measured. No separation is seen between the other species.

Leaf Breadth.

No significant difference between the four species is seen in the Table, D. majus has the largest mean values, D. fuscescens the smallest, with D. bonjeanii and D. scoparium in an intermediate position.

Nerve Width.

D. bonjeanii has the lowest mean values for this character amongst female plants but overall male plants of D. scoparium closely approach D. bonjeanii. D. majus and D. scoparium have closely comparable nerve width with D. fuscescens showing, generally but not invariably, higher mean values. The value of this feature for identification is extremely clear if the results are expressed as a proportion of the leaf width.

$\frac{\text{Leaf Width}}{\text{Nerve Width}}$

Examination of the scatter diagram I shows that the mean values for this character separate D. bonjeanii, D. scoparium and D. fuscescens which have closely similar leaf length means. The standard errors have been included in the diagram and the separation of the three species is statistically significant. It is interesting to note that D. majus is intermediate in respect of this character, between D. scoparium and D. bonjeanii. Taking width/nerve width alone separation of the four species could not be accomplished.

Serration.

The four species can not be separated by this character. D. majus has a high number for the teeth on half the leaf lamina but population 481, D. scoparium, mean 39.58, is more serrated than D. majus, 371, mean 31.4. D. scoparium, D. fuscescens and D. bonjeanii do not approach separation.

Conclusions.

It would appear from the data, on a limited number of specimens, that species separation is best accomplished by using two criteria, leaf length and leaf width/nerve width proportion. Taking all the material investigated specimens falling near 9 mm in leaf length would present most difficulty. Small specimens of D. majus e.g. 390, 411 would have to be checked using leaf sections. The differences in the lamellae and lamina cells should prove conclusive.

TABLE 3. 7.

DICRANUM SCOPARIUM

No. Popn.	Leaf Length mm.	SE Length	Leaf Width Units	Nerve Width Units	L/W	W/NW	W/NE SE	
	Mean		Mean	Mean				
228	6.89	.175	1.512	.58	6.58	8.82	.276	
294	6.45	.186	1.56	.56	6.02	9.42	.373	
354C	5.78	.168	1.572	.52	5.31	10.80	.513	
355♀	6.17	.156	1.48	.50	6.11	10.16	.529	
355♂	5.69	.156	1.2	.45	6.90	8.65	.22	1
361♀	6.77	.178	1.604	.59	6.09	8.85	.254	
361♂	5.53	.273	1.329	.49	5.97	9.11	.317	
363	7.32	.175	1.776	.73	5.94	8.40	.401	
370	6.24	.044	1.44	.57	6.25	9.27	.347	
391	6.22	1.69	1.638	.53	5.45	10.04	.26	
401	5.50	.122	1.4	.53	5.75	9.21	.241	
402	5.63	.039	1.496	.50	5.57	9.83	.247	
423	6.79	.150	1.88	.57	5.21	10.66	.251	
450♀	7.0	.155	1.6	.52	6.37	10.24	.274	
450♂	5.71	.176	1.524	.47	5.47	10.96	.532	
+486♀	6.7	.145	1.60	.52	6.09	10.45	.155	
+486♂	5.95	.23	1.62	.45	5.47	12.24	.371	
*486♀	6.69	.215	1.52	.56	6.38	8.98	.295	2
481	9.18	.143	1.711	.64	7.78	9.648	.422	

+ Large Male popn.

* Dwarf Male popn.

1 Male plants also found .6 mm - 3-4 mm in leaf length.

2 Dwarf male plants mean leaf length .678 mm.

TABLE 3. 8.

No. Popn.	Leaf Length mm. Mean	SE Length	Leaf Width Units Mean	Leaf Width mm Mean	Nerve Width Units Mean	Nerve Width mm Mean	L/W Mean	W/NW Mean	W/NW SE
D. FUSCESCENS									
332	6.05	.126	1.1	.6	.9	.16	8.40	3.36	.576
357	6.39	.143	1.05	.6	.69	.11	8.85	5.4	.226
374♀	6.91	.177	1.3	.73	.82	.16	7.61	5.56	.235
374♂	5.09	-	.9	-	.74	-	8.16	4.32	-
381	5.54	.151	1.08	.61	.64	.10	7.44	5.78	.506
385	4.9	.316	-	.65	-	.15	8.10	5.58	-
D. BONJEANII									
354A	6.89	.169	1.94	-	.36	-	5.11	18.72	.266
354B	5.64	.171	1.87	-	.26	-	4.39	23.83	.342
485♀	7.09	.226	1.78	-	.40	-	6.09	14.82	.602
485♂	5.02	.314	1.49	-	.31	-	4.80	21.96	.572
495	6.51	.032	1.68	-	.41	-	5.68	14.84	.222
D. MAJUS									
290	11.62	.293	2.06	-	.62	-	7.81	10.9	.561
371	12.25	.413	2.34	-	.51	-	7.63	14.8	.485[1]
400	10.85	.169	2.08	-	.54	-	7.54	12.97	.384

[1] Dwarf Males mean leaf length .327 mm.

Popn. 364. Dwarf male mean leaf length .419 mm.

TABLE 3. 9.

SERRATION

POPN. NO.	MEAN	SE
D. SCOPARIUM		
228	19.3	2.56
294	7.24	3.55
354C	7.09	4.88
355♀	12.5	3.89
355♂	11.0	3.66
361♀	16.08	6.25
361♂	6.82	4.67
363	13.6	6.22
370	1.2	.55
391	18.69	2.17
401	.96	.45
402	11.28	5.27
422	.06	-
423	.4	.26
450♀	5.76	3.96
450♂	19.58	4.09
486♀	12.08	4.53
486♂	9.78	4.05
+ 486♀	4.84	3.59
481	39.58	2.48

POPN. NO.	MEAN	SE
D. FUSCESCENS		
332	9.36	5.91
357	14.64	2.81
374♀	15.28	2.22
374♂	5.0	-
381	12.24	1.16
385	1.29	-
D. BONJEANII		
354A	9.0	4.01
354B	6.52	4.59
485♀	6.92	3.61
485♂	11.2	5.54
495	20.6	6.28
D. MAJUS		
290	62.2	3.88
371	31.4	3.53
400	30.72	2.5

\+ Dwarf male population

INTRASPECIFIC VARIATION AS REFLECTED IN BIOMETRICAL SURVEY.

A. VARIATION IN SIZE OF PARTS AND PROPORTIONS.

D. scoparium.

No significant differences in leaf length are found between populations showing low serration values and the rest of the material, i.e. low serration means are not accompanied by a characteristic length of leaf. It is important to note however that the highest serration number 39.58, in population 481 is also from the longest leaved plant of this species. Other high serration populations however do not appear to be different in length from the bulk of the material. The other characters of nerve width and leaf width do not appear to divide the species; continuous variation in the mean values is found. Length/breadth ratio is interesting in that population 481 again stands out as different from the other material. Its mean value for this character is close to that of D. majus, which it also resembles in its high serration number. The mean leaf breadth/nerve width results show no significant breaks in the variation of D. scoparium.

Of great interest is the variation of the male and female plants in populations. Details of dwarf and large male plants are found in Chapter VI and as no detailed measurements have been found in the literature special attention has been paid to sex differences.

Length - Male plants in two cases (450 and 361) are significantly shorter than the female plants. In 355 and 486 no significant difference was found, although the mean values for the male plants were smaller than the female.

Breadth - Only means have been calculated for this character and in three cases the leaves were on the average narrower in the male than in the female, but in 486 males were marginally greater in width than the females.

Nerve width - A study of the mean values shows that the males had a narrower leaf nerve than the female plant.

Length/Breadth ratio - In three instances lower mean values are found in the male plants but in 355 the males show a larger mean value than the females.

Leaf Breadth/Nerve width - In three cases the figures for this value are larger in the male than the female, only marginally so in 361. They are however smaller in 355.

From the results it can be seen that the male plants appear to be shorter in leaf length than the females, often significantly, and narrow in leaf nerve with much variation in the other characters. These details refer to the large male plants, (see Chapter I). Dwarf males have also been measured for population 486 and the mean value for leaf length was .678 mm, clearly a good deal outside the range of length of the large male material. Dwarf male plants have also been found in population 355. The range of sizes is much larger than in 486. (Leaf length .6 mm to 3.0 mm.).

D. fuscescens.

Consideration of all the mean values for the various characters shows wide variation in leaf length, nerve width mean, with very little variation in leaf width. The ratio characters, width/nerve width and length/breadth show some variation but taking all the means there is no reason to give any of the populations varietal rank, (see comments on 332 and 385 below). 332 had been placed near var. congestum in the initial analysis see Table 3.3, but the plant does not agree with the details given in Chapter I. The leaf is on average less wide than 374, which appears to be typical, yet it is described by Dixon (1954) as having broader leaves with narrower nerve. Population 332 has however the widest average nerve width of the four species. It must therefore be considered as falling within the variation of the type. Population 385, showing almost entire leaves did not fully agree with the description of var. congestum in Chapter I. The leaf base was not on the average broader and the leaf nerve figures are within the range shown by the other material, see Table 4.7. Upper leaf cells were irregular in some specimens but quadrate cells were found in others.

On a limited amount of material of male plants of 374, (5 plants), the males are on average shorter leaved than the females with narrower leaves and leaf nerves, and higher L/B and W/NW ratios.

D. bonjeanii.

In the initial analysis the material 354 was thought to contain D. bonjeanii var. calcareum and D. bonjeanii type, as well as D. scoparium. The variety is described by Braithwaite (1887) as 'shorter in the leaf, and slightly serrate near the apex'. Measurements carried out to investigate this population 354 involved dividing the D. bonjeanii into the two taxa followed by separate measurements. The 'calcareum' portion of the gathering was found to have a significantly smaller leaf length and also to have an enormous value for the W/NW ratio (23.83 as against 18.72) for the portion referred to D. bonjeanii. Serration values underline this impression, as 354 (var. calcareum) has a mean value of 6.52 as against 9.0 for the remainder. Other differences between the two taxa include, smaller average nerve width, leaf width and L/B ratio in the var. calcareum. It seems extremely likely that two distinct taxa are present, the type, and the variety calcareum.

The male plants of population 485 are very interesting. They are significantly smaller than the female plants and the standard error of length is very high. There appeared to be a wide range of sizes of longest leaves on male stems. The difference in length of the leaves between male and female plants, noted in the initial analysis, is clearly brought out in the present study.

D. majus.

Some differences in leaf size and other characters are shown in the figures but there is no reason to suppose that any one of the three populations is different from type material. The sizes of the male plants are shown in Table 3.8 and it can be seen that they are smaller than the dwarf males of D. scoparium in leaf length.

TABLE 3. 10.

SERRATION. ACTUAL COUNTS OF TEETH (PER HALF LEAF). 25 LEAVES PER POPN.

D.SCOPARIUM

Popn.	Mean	Counts/25 leaves	SE
228	19.32	(23,21,25,18,30,26,22,34,22,0,25,14,15,31,14,16,11,26,18,8,14,29,18,7,16)	2.56
294	7.24	(1,14,3,9,7,12,3,6,0,10,6,12,0,5,14,12,10,16,17,0,8,13,2,0,0)	3.55
354C	7.09	(5,17,4,13,0,0,3,8,20,9,0,9,0,12,24,7,5,3,0,10,0 21 counts)	4.88
355♀	12.5	(2,1,0,13,4,0,4,12,25,3,0,12,0,2,0,0,4,11,3,2,10,1,3,12,1)	3.89
355♂	11.0	(23,15,19,16,8,12,7,10,15,10,11,2,3,16,9,11,12,14,19,9,3,3,2,15)	3.66
361♀	16.08	(30,32,18,9,27,27,29,21,0,19,9,21,13,4,5,32,12,2,27,8,14,11,14,13,6)	6.25
361♂	6.82	(0,0,0,0,3,3,14,0,6,7,10,15,9,16,5,16,12 17 counts)	4.67
363	13.6	(14,22,7,9,0,34,11,24,20,11,34,10,13,10,0,21,13,7,22,11,27,1,3,15,0)	6.22
370	1.2	(6,0,0,0,0,0,0,0,7,0,1,0,0,0,1,0,0,0,0,0,3,0,1,11,0)	.551
391	18.69	(37,15,18,8,18,37,34,18,28,18,27,12,31,15,9,5,8,8,22,11,32,0,0,27,32,15)	2.17
401	0.96	(0,0,0,0,0,0,2,0,0,2,1,3,3,0,0,0,0,0,9,4 20 counts)	.458
402	11.28	(10,16,23,3,18,30,2,10,23,12,13,6,0,1,5,2,2,4,12,13,15,27,14,13,8)	5.27
423	0.4	(4,0,0,0,0,0,0,3,0,0,0,0,0,0,0,0,0,0,1,0 20 counts	.258
450♀	5.76	(0,7,3,14,0,28,0,6,0,0,5,6,16,3,6,12,6,4,7,5,0,4,3,4,5)	3.96
450♂	19.58	(10,13,15,24,14,0,15,14,3,7,8,10,21,8,12,24,5,0,4,12,14,14,6,10 24 counts)	4.09
486♀	12.08	(14,25,8,5,7,36,14,14,10,9,9,5,21,16,12,15,17,12,8,11,6,10,9,3,6)	4.53
486♂	9.78	(14,17,26,1,8,5,0,13,5,3,12,6,8,11,4,5,12,7,9,8,16,11,17,12,13)	4.05
486♀*	4.84	(0,7,2,3,4,0,5,6,12,0,1,1,3,5,4,2,2,9,0,2,14,26,4,3,6)	3.59
481	39.58	(37,49,58,36,18,63,33,52,39,25,40,47,45,50,44,54,26,31,23,55,21,50,36,39,23,35)	2.48

* dwarf male clumps

TABLE 3. 10. CONTINUED.

SERRATION. ACTUAL COUNTS OF TEETH (PER HALF LEAF). 25 LEAVES PER POPN.

Popn.	Mean	Counts/25 leaves	SE
D.FUSCESCENS			
332	9.36	(14,1,25,2,17,5,17,0,3,7,26,3,7,16,0,12,2,3,8,4,1,3,7,11,7,6)	5.91
357	14.64	(7,25,1,10,3,11,14,9,3,16,7,20,12,13,14,0,2,7,11,9,31,46,9,26,60)	2.81
374♀	15.28	(40,5,4,4,25,20,13,21,23,16,4,35,5,3,29,27,8,14,8,22,12,3,11,2,28)	2.22
374♂	5.00	(8,0,2,4,11 5 leaves only)	
381	12.24	(12,6,15,14,33,18,30,47,12,4,9,17,6,4,16,18,1,8,2,24,6,0,5,0)	1.16
D.BONJEANII			
354A	9.0	(1,9,3,20,1,5,20,6,8,6,11,4,8,4,12,12,10,2,3,17,20,19,6,15,3)	4.01
354B	6.52	(4,1,6,11,0,3,5,0,14,0,9,20,9,0,0,18,0,0,8,0,12,3,17,23,0)	4.59
485♀	6.92	(4,5,2,18,18,2,4,14,15,15,13,3,3,5,5,9,9,0,10,7,3,0,1,7,0)	3.61
485♂	11.2	(5,15,18,2,12,0,11,18,2,16,7,14,15,23,10 15 counts)	5.543
495	20.6	(19,43,25,32,15,16,45,40,20,14,4,20,19,20,23,12,24,13,15,16,9,17,20,18,18)	6.28
D.MAJUS			
290	62.2	(100,67,44,53,70,52,42,70,53,41,38,57,85,78,59,81,68,83,89,99,42,52,41,56,35)	3.88
371	31.4	(18,13,17,34,40,65,24,9,34,21,14,28,50,18,14,30,12,42,9,48,51,45,70,50,39)	3.53
400	30.72	(18,20,23,19,18,16,63,20,24,16,25,35,35,33,32,31,42,39,23,48,15,46,29,50,48)	2.57

B. VARIATION IN SERRATION.

The populations of *D. scoparium* show high and low values for serration; from .06 in population 422 to 39.58 in population 481. Discounting the highest value there is continuous variation between the lowest mean value and 19.3.

		POPULATIONS
Average no. teeth	1 - 5	423, 370, 486D male, 401, 422.
	6 - 10	354, 294, 450.
	11 - 15	363, 355, 486L male.
	16 - 20	228, 361, 391.
	20+	481

There is no break in the variation in tooth number and the very high standard errors for the populations, (as high as 6.25) shows that there is much variability between individual leaves on different stems of the same population. An examination of the actual counts of teeth, see Table 3.10, shows that low numbers occur in populations with predominately high serration counts and vice versa.

The possibility that forms of *D. scoparium* can be characterised by serration differences becomes very remote when these results are examined. If a continuous series of types are found, separation of the populations with low numbers as different varieties on serration alone is invalid. The descriptions of *D. scoparium* var. *orthophyllum* show that some confusion occurs. Dixon (1954) states that the variety 'is distinctly toothed' yet Braithwaite (1887) includes specimens in this taxon which are entire.

More information will be presented on serration types in the section dealing with material grown under standard conditions. The fundamental question to be solved is whether this continuous series of serration values is genotypically fixed as regards a given population or whether variation in number of teeth is possible, if a population is grown under different conditions. In other words does the mean remain fixed, or will a completely different mean value be obtained, indicating phenotypic plasticity for the character?

Variation in the serration of the male plants shows that in some cases the mean value is near that of the female as in:

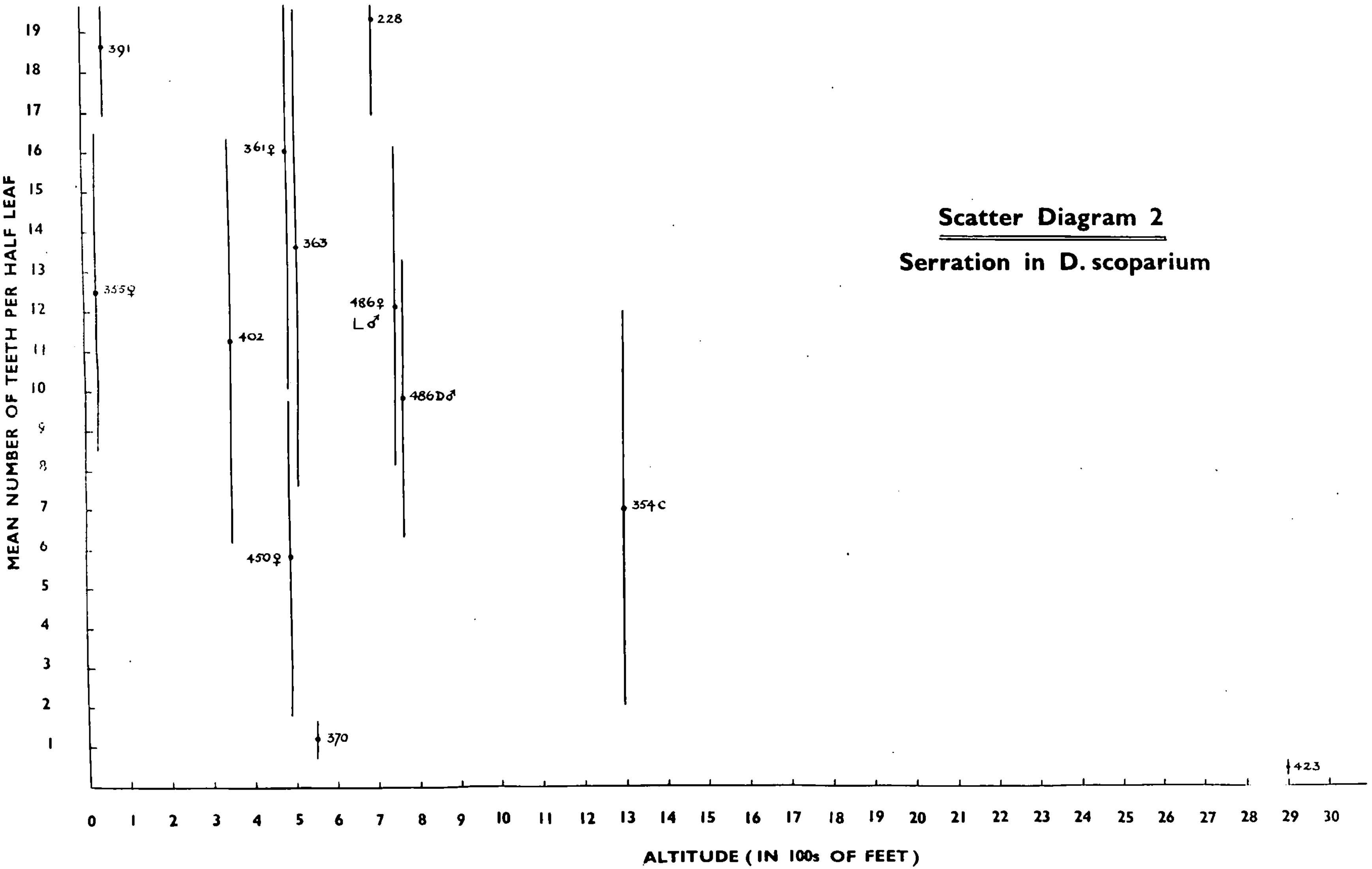
486 (large male)	12.08 female	9.78 male
355	12.5 female	11.0 male

or it may be substantially different,

450	5.76 female	19.58 male
361	16.08 female	6.82 male

These figures add weight to the contention that serration alone cannot be used as a satisfactory method of characterising varieties. The males of population 361 clearly have a very low figure for serration, perhaps approaching var. *spadiceum*, but the female plants have a much larger figure and definitely do not fit this variety.

Variation in serrature is also found in *D. fuscescens*. All the specimens appear, on average, to be of the type, (except 385) but examination of the actual serration counts shows some leaves with



Scatter Diagram 2

Serration in D. scoparium

numbers much below the mean values. Population 385 has some of the characters of var. congestum but does not fit the full description of the variety. D. bonjeanii too has variation in serration, the lowest value being for the var. calcareum mean 6.52, with standard error of 4.59. As in D. fuscescens, Table 3. 10 also shows low values for D. bonjeanii for some leaves, and within the same population, higher values. D. majus differs from the other three species in that no entire leaves have been found in any of the populations studied. The serration counts show considerable variation about the mean value however.

Discussion of the serration problems.

Altitude has been suggested as having an important bearing on serration in Dicranums. The following remarks refer to D. scoparium, as more information is available on this species.

Examination of the Scatter Diagram 2 for serration distribution in relation to altitude, in D. scoparium shows that the relationship is not a simple one. See also Table 3.9. Standard Errors have been plotted with the mean values and it is obvious that there is an enormous amount of variation in serrature in each population. It is also interesting to note that the Standard Errors of 423 and 370, the least serrate of the D. scoparium populations, show the smallest standard error values.

An explanation of the distribution of entire or very reduced leaves must take into account the presence of these in serrated populations. One hypothesis is that they are developed in response to conditions similar to those at high altitudes, i.e. under conditions of exposure. The extreme statement of this view is that environment is the controlling factor in the development of serration. An alternative to this hypothesis is that the variation is genotypic and the plants comprising a highly variable population have different propensities to serration. Or both environmental and genotypic influences may operate together.

A. Environmental hypothesis.

The leaves sampled were always the largest on the stems and were without doubt of comparable age within a population. An explanation involving phenotypic plasticity must account for the production of leaves with different serration numbers at the same time of year. It may easily be that microclimatic factors vary considerably over a tuft of mosses and that the peripheral shoots may be more exposed than the central ones.

B. Genotypic hypothesis.

The basis of this hypothesis is that the variation has a purely genetic foundation. It would be expected that in areas where Dicranums fruit more variability would be found, due to segregation, than would be present in the purely "vegetative" populations encountered above the treeline. On this thesis the variability in serration would be expected to be large in fruiting populations and small in "vegetative" ones. An examination of the figures for the standard errors of the populations studied shows that the variation in 423, with the smallest mean value, is of the same order as population 370 gathered in woodlands where there was abundant fruiting material. Another sterile population 354 has a SE of the same order as 355 cfr. The highest values for SE of variation were however found in fruiting populations 361 and 363.

Judgement is reserved until data are presented on serration values of samples collected from standard environment experiments. By this means it should be possible to show whether the variation is genotypic or environmental.

There are not enough data for the other three species to make any firm statement on serration variation within populations. They are closely related spp. to D. scoparium and if the principles could be established which govern variation in this spp. they may provide a basis for an explanation of the phenomenon found within the genus as a whole.

CONCLUSIONS.

The bases of the separation of the four species have been discussed and the most reliable have been pointed out. Biometrical studies have shown the importance of some features. Most of the characters are concerned with the nerve, its length, (equal to leaf length), width as a proportion of the leaf width, and its cross sectional structure, especially its lamellae.

The ecological pattern of variation has been surveyed and parallel and non-parallel variation have been described. Microclimatic variation is postulated as a cause of the differences in morphology within the broad ecological groups.

Finally intra-specific variation has been studied, both intensively and extensively and the validity of taxonomic separation on grounds of leaf stance and serration has been questioned.

CHAPTER IV.

CULTURE EXPERIMENTS.

Introduction.

In Chapters I and III the variation of the four *Dicranum* species is surveyed and it is very clear that some experimental evidence of the nature of the basis of this variation would be most valuable. Thus the variation may be entirely conditioned by the environment or it may have, at least to some extent, a genetic basis. This Chapter reports experiments which were designed with three objectives in view.

A. To review the variation in male and female plants in the same population.

B. To bring immature capsules to the meiotic state and beyond, to spores.

C. To investigate under controlled conditions the variation shown by samples of populations, after a growth period in a standard environment.

In deciding on the type of standard environment to use, literature reports of bryophyte cultures were examined. Richards (1947) reports simply that mosses growing in pots could be maintained with various degrees of success, depending upon the extent of algal and bryophyte infection. Schelpe (1953) used sterile sand cultures and many workers have used agar plates, e.g. Vaarama and Taren (1959), Gorton and Eakin (1957), Whitehouse (1961), while others have resorted to liquid cultures on glass cloth, (see Voth (1941) for experiments with Marchantia). Early experiments were set up using sterile sand and Knop's agar cultures, and glass wool cultures were also attempted. In all these, abnormal growth of new leaves was often found or the leaves did not develop the normal characteristics. Finally pot experiments were set up using the methods described below.

Methods.

The Dicranum samples, including as many variants as possible, were all sown on John Innes Potting soil (JIP), made with local Durham loam, and having a final pH of 6.1. 5 inch pots were used, with soil 1 inch from the top of the pot. The material was grown in a north-facing cold-frame, with "summer-cloud" shading in the summer. As was reported in chapter II, several tufts of Dicranum were sampled from each habitat and the material planted, (as well as that dried as a herbarium specimen) was not all from one tuft. The material was therefore a population sample, not a piece from a possible clone.

Early attempts were made to control the environment around the pots of JIP soil. At the suggestion of Dr. H.L.K. Whitehouse the pots were placed in polythene bags, wired at the open end. This method was successful for some time, but the material was extremely difficult to examine and it was finally abandoned in favour of open pots.

Watering was first of all carried out with distilled water, later, experiment showed that Durham tap-water was suitable. Water given to each pot was not measured but as far as possible, all the pots were watered to the same extent. A glass vessel was used for watering as mosses are very sensitive to zinc.

The planting methods used for each *Dicranum* are very important. It was found by experience that the tuft structure of the plant had to be preserved on planting. Isolated shoots of *Dicranum* died. This is possibly due to the break down of the capillary system of water movement within the normal tuft. Growth was most successful where the tufts were closely packed, and rubber bands were sometimes used to keep the shoots together. Closely packed shoots also proved more competitive against *Funaria hygrometrica* and *Leptobryum pyriforme*, which were common weedy species about the garden. Periodically the algae on the sides of the pot were washed away.

Open pots present the possibility of cross colonisation of one population by another. It was found however that detached leaves and shoots on soil produced protonema slowly and it was thus considered that the danger was negligible.

Having found a successful cultivation method which gave considerable extension growth in the planted shoots, the problem of sampling arose. When should samples be taken from material planted at different times and thus cultured for differing lengths of time? Work by Hagerup (1935) on the mosses of Denmark suggests that there are two growth periods in most European species, (a) December to March and (b) June or July to August or September. It was thought that the growth behaviour of *Dicranum* species in culture would probably be of this kind. It was noted however that uninterrupted growth appeared to occur as was reported by Romose (1940) for continually moistened Camptothecium sericeum carpets. Much growth appeared to be made in the spring period and it was decided to sample material in April after as long a period of growth as possible. Only a limited amount of material was available for sampling but collections were made at random, as far as possible.

As in chapter III, two methods of analysing the variation in the resulting new growth of leaves have been used. First an extensive review has been made of all the populations cultured, and secondly an intensive biometrical analysis made of various important features, on a selected group of populations.

1. EXTENSIVE SURVEY OF VARIATION AFTER CULTIVATION.

The characters investigated were those listed in chapter III. Gum chloral slides were made from the leaves of one shoot for microscopic leaf characters, other characters were judged on the bulk sample of material. New growth only was sampled. The results are presented in Tables 4.1, 4.2, 4.3.

Results.

(a) Broad Effects of Cultivation.

From Tables 4.1 and 4.2 the following general observations may be made.

1. Falcation of the leaves.

Most of the material of D. scoparium is found to have erecto-patent leaves. Some specimens have falcato-secund leaves at the apex of the stems. An interesting feature is the variability present. In D. majus falcato-secund leaves are invariably found at the tip of the shoots, but

TABLE 4. 1.

D. SCOPARIUM

	Acid communities								Trees				Dead Wood			Dunes	
Popn. No.	228	270	326	442	350	393	422	423	362	367	394	401	368	395	481	355	489
No. months cultivation	12	12	24	17	22	20	19	19	21	21	20	20	21	20	10	21	9
Upper leaf stance	1-2	1-3	1-2	1-2	1-3	1-2	1-2	1-2	1-2	1-2	1-2	1-2	1-2	1-2	1-2	1-2	1
Lower leaf stance	1-2	1-3	1-2	2	1-2	1-3	1-3	1-3	2-3	2-3	2-3	2-3	2-3	2-3	2-3	2-3	2-3
Other types	-	-	-	-	-	-	-	4	-	-	-	-	-	-	6	-	-
Strength of nerve	$\frac{1}{8}$	$\frac{1}{12}$	$\frac{1}{8}$	$\frac{1}{8}$	$\frac{1}{8}$	$\frac{1}{7}$	$\frac{1}{10}$	$\frac{1}{10}$	$\frac{1}{7}$	$\frac{1}{10}$	$\frac{1}{9}$	$\frac{1}{10}$	$\frac{1}{9}$	$\frac{1}{11}$	$\frac{1}{9}$	$\frac{1}{10}$	$\frac{1}{9}$
Undulation	1	1	-	-	-	-	-	-	-	-	-	-	1	-	1	-	-
Tomentum	-	-	-	-	-	-	-	-	1R	-	-	1R	-	-	-	-	-
Upper cell porosity	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Serration	+	+	+	+	+	-	-	-	+	+	+	+	+	+	+	+	+

TABLE 4. 1. continued

D. SCOPARIUM

	Ground Flora Woodlands													Rocks			Basic Habitats			
Popn. No.	294	295	360	369	391	396	412	445	450	451	486L	486D	496	361	370	409	354	353	354	446
No. months cultivation	24	24	21	21	20	20	20	10	9	10	9	9	5	21	21	20	12	12	12	9
Upper leaf stance	1–2	1–2	1–2	1–2	1–2	1–2	1–2	1–2	1–2	1–2	1–2	6–1	6	1–2	1	1	1–2	1–2	1–2	1–2
Lower leaf stance	2–3	2–3	2–3	2–3	2	2–3	2–3	2	2–3	2	2–3	2	2	2–3	2	2	2–3	1–2	1–2	1–2
Other types	6	–	–	6	–	–	4	–	–	6	6	–	1	3,6	–	–	3	3	–	3
Strength of nerve	$\frac{1}{10}$	$\frac{1}{13}$	$\frac{1}{9}$	$\frac{1}{11}$	$\frac{1}{10}$	$\frac{1}{15}$	$\frac{1}{11}$	$\frac{1}{11}$	$\frac{1}{11}$	$\frac{1}{11}$	$\frac{1}{10}$	$\frac{1}{10}$	strong	$\frac{1}{10}$	$\frac{1}{9}$	$\frac{1}{9}$	$\frac{1}{10}$	$\frac{1}{7}$	$\frac{1}{8}$	$\frac{1}{10}$
Undulation	1	1	1	1	1	1	1	–	–	–	1	–	–	–	1	–	+	–	–	–
Tomentum	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1R	–	–	–	–
Upper cell porosity	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Serration	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	–	+	–

TABLE 4. 2.

D. FUSCESCENS

	Trees			Ground Flora					Rocks		Dead Wood
Popn. No.	334	372	403	332	357	374	487	381	373	406	397
No. months cultivation	24	9	20	19	23	9	10	19	9	20	20
Upper leaf stance	6	6	6	6	6	6	1	1	4	6	2
Lower leaf stance	6	6	6	6	6	1	1	4	1	6	2
Other types	-	-	-	-	-	-	6	2	-	1,2	1
Strength of nerve	$\frac{1}{3}$	$\frac{1}{4}$	$\frac{1}{4}$	$\frac{1}{3}$	$\frac{1}{4}$	$\frac{1}{4}$	$\frac{1}{5}$	$\frac{1}{5}$	$\frac{1}{4}$	$\frac{1}{5}$	$\frac{1}{3}$
Undulation	-	-	+	-	-	-	-	-	-	+	-
Tomentum	-	-	-	-	-	-	-	-	-	-	-
Upper cell porosity	-	-	-	-	-	-	-	-	-	-	-
Serration	+	+	+	+	+	+	+	+	+	+	+

TABLE 4. 2. continued

D. BONJEANII

	Basic Habitats						Other Popns.						
Popn. No.	211	354A	354B	460	495	497	322	325	441	443	454	471	485
No. months cultivation	10	9	9	9	5	5	19	19	9	9	9	10	9
Upper leaf stance	1	1	1	1	1	1	1	1	1	1	1	1	1
Lower leaf stance	3	3	3	3	2	2	3	3	2	3	3	3	3
Other types	2	2	2	6,2	3	1	2	2	2	2	2	2	2
Strength of nerve	$\frac{1}{14}$	$\frac{1}{14}$	$\frac{1}{14}$	W	$\frac{1}{25}$	$\frac{1}{25}$	$\frac{1}{18}$	$\frac{1}{19}$	$\frac{1}{20}$	$\frac{1}{18}$	$\frac{1}{18}$	$\frac{1}{20}$	$\frac{1}{18}$
Undulation	2	2	2	2	2	2	2	2	2	2	2	2	2
Tomentum	-	-	-	-	-	-	-	-	-	-	-	-	-
Upper cell porosity	+	+	+	+	+	+	+	+	+	+	+	+	+
Serration	+	+	+	+	+	+	+	+	+	+	+	+	+

TABLE 4. 3.

D. MAJUS

Popn.—No.	290	320	328	330	333	358	364	371	383	390	392	399	400	424	429	444
No. months cultivation	24	24	24	24	24	21	21	21	21	20	20	20	20	19	19	10
Upper leaf stance	6	6	6	6	6	6	6	1	6	6	6	6	6	6	6	6
Lower leaf stance	64	24	4	6	6	3	3	3	3	4	3	4	3	3	3	3
Other types	4	3	32	–	–	–	–	4	–	3	–	3	4	4	4	4
Strength of nerve	$\frac{1}{15}$	$\frac{1}{13}$	$\frac{1}{11}$	$\frac{1}{13}$	$\frac{1}{11}$	$\frac{1}{15}$	$\frac{1}{13}$	$\frac{1}{12}$	$\frac{1}{14}$	$\frac{1}{12}$	$\frac{1}{14}$	$\frac{1}{11}$	$\frac{1}{14}$	$\frac{1}{11}$	$\frac{1}{12}$	$\frac{1}{13}$
Undulation	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–
Tomentum	1R	1R	1R	–	–	–	–	–	–	–	R	–	–	–	–	–
Upper cell porosity	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Serration	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+

the uniformity in leaf stance, of the lower leaves, noted in the field collections is not preserved after cultivation. Falcato-secund leaves are often replaced by erecto-patent and other types. In polythene covered cultures, apical leaves were erecto-patent. D. fuscescens shows falcato-secund apical leaves in many cases, but with great variation in lower leaves. D. bonjeanii shows uniformly erecto-patent leaves.

2. Porosity of the upper cells.

New growths of D. fuscescens maintained the non-porose upper leaf cells characteristic of the original herbarium material. The new leaves of the other three species had porose cells. Sometimes it was noticed that the cell walls were thinner in cultivated samples and this sometimes masked the pores.

3. Undulation.

All the specimens of D. bonjeanii are clearly markedly undulate, and some had contorted rugose leaf apices. In D. scoparium a few specimens were undulate, but in earlier experiments with polythene enclosed pots, Table 4.4, more specimens had undulate leaves. The leaves of D. fuscescens have a different structure from that found in the other species. The apex of the leaf is more aristate, and it is perhaps mechanically less prone to undulation. It is of interest to note that undulation of the lower lamina was shown by one or two cultivated samples. D. majus (popn. 290) in polythene covered cultures produced undulate leaves, but no undulate specimens were found in the open pot cultures.

TABLE 4. 4.

UNDULATION - SHOWN BY SPECIMENS IN POTS ENCLOSED BY POLYTHENE BAGS[2].

	No. specimens examined	No. undulate
D. scoparium	8	7
D. fuscescens	4	-
D. majus	1	1
D. bonjeanii	3	3[1]

[1] Specimens all rugose and leaf apex twisted.

[2] Cultures of various ages 3½ - 7 months.

4. Nerve strength.

Statistical examination of this feature will follow, but it is interesting that the examination methods used in routine study of herbarium specimens showed that the nerve proportions in cultivated material were of the same order as those of the original material.

5. Leaf length

Individual leaves of D. scoparium and D. bonjeanii were commonly in excess of 9 mm e.g. in popns. 369, 228, 486, 443, 454, 471. All the populations of D. majus had leaves greater than 9 mm in length. The proportions of the sizes were important. D. majus leaves were almost invariably all larger than 9 mm, only occasionally were such long leaves found in the other three species.

6. Leaf serration.

An examination of this follows below. General observations showed that serrated leaves could be found in almost every population.

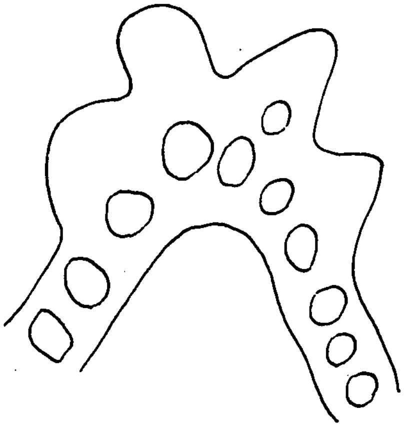
7. Leaf sections.

The lamina and nerve characters listed in chapter 1 were found to remain constant in culture, D. majus had rectangular lamina cells, while D. scoparium showed quadrate lamina cells in leaf section, Fig. 4. Leaves of D. bonjeanii could be distinguished as before, and sections showed only small development of lamellae, compared with marked lamellae in the D. scoparium samples, see below.

8. Other characters.

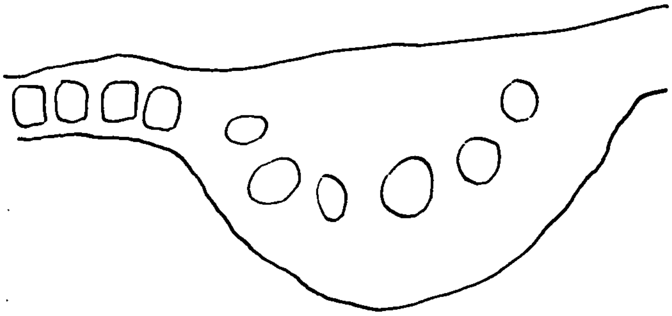
Many cultures of D. scoparium and D. bonjeanii showed a very wide

LEAF SECTIONS OF CULTIVATED MATERIAL.



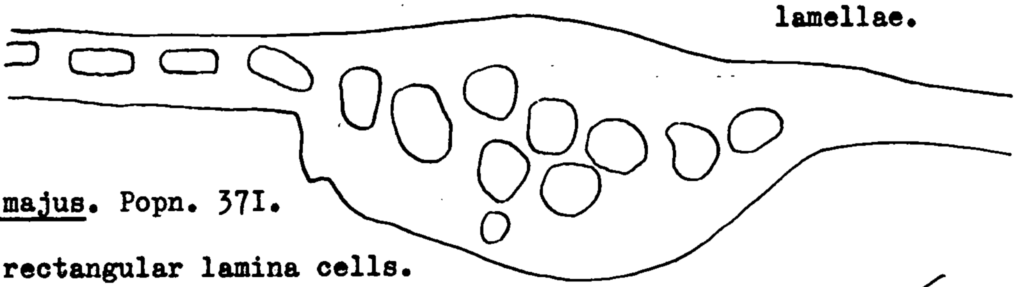
D.scoparium. Popn.228.

- lamellae present.



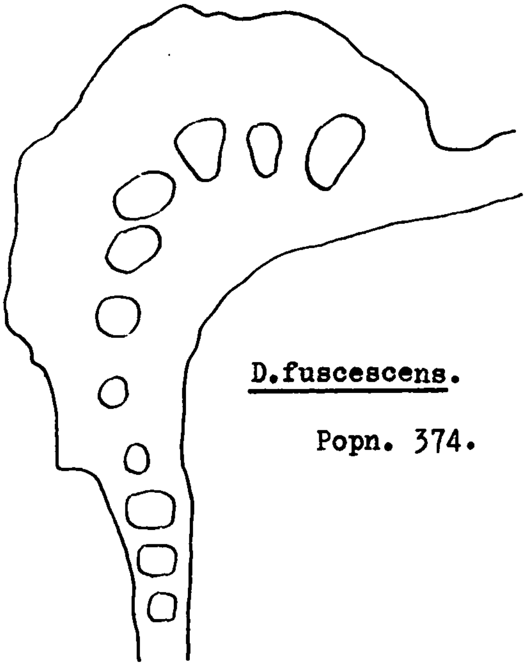
D.scoparium. Popn. 450 female.

- quadrate lamina cells,no lamellae.



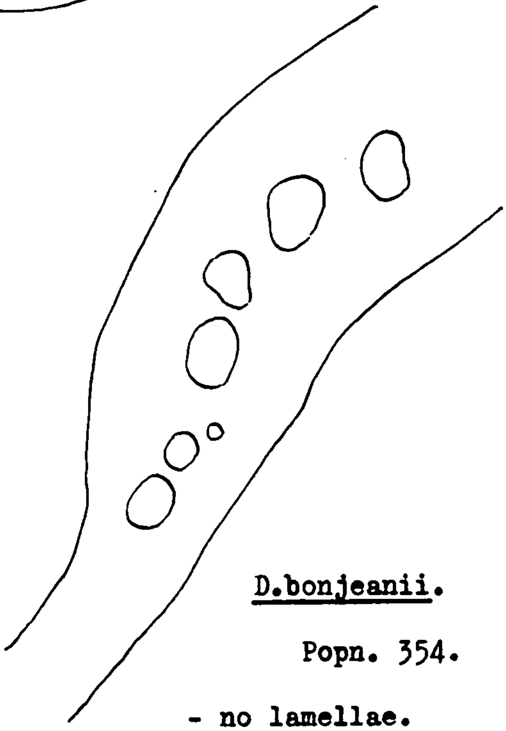
D.majus. Popn. 371.

- rectangular lamina cells.



D.fuscescens.

Popn. 374.



D.bonjeanii.

Popn. 354.

- no lamellae.

30 µ.

Fig.4.

leaf apices, Fig. 5. This feature was not examined in detail but it is interesting to note that a wide apex is listed, in chapter I, as a characteristic of D. bonjeanii. The development of lamellae has not been examined in great detail, invariably D. scoparium samples show more development of these than in D. bonjeanii samples. Poor development was found in some of the entire leaved forms of D. scoparium after cultivation, but they lacked the serration, characteristic of D. bonjeanii.

Very little tomentum has been found on any of the specimens; cf. data in Chapter III. Perhaps in a continually moist atmosphere the stimulus to develop such a capillary system is not very strong.

(b) Maturation of Capsules and Reproduction.

Cytological preparations, from capsules maturing in pot cultures, show that development continued normally to give spores. Sporophytes developing from very early stages, before seta elongation in some cases, have successfully matured under the cultivation conditions used.

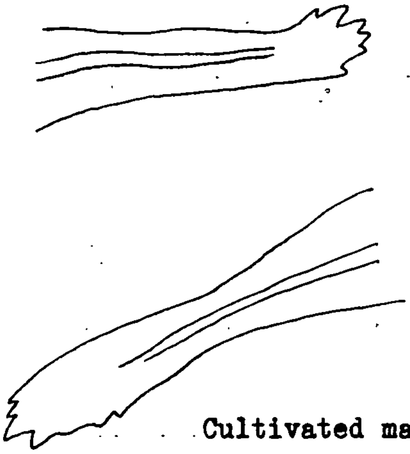
It is of interest to note that no reproduction took place in the pots even when male and female plants were present. Antheridial heads matured in population 329, D. scoparium, (the year after collection), but the plants did not complete their lifecycle in the pots. Maturation of newly fertilized archegonia was the most that was accomplished.

(c) Performance of Dicranum specimens in culture, (comments on unsuccessful populations).

This is a difficult subject to elucidate as there can be so many reasons why cultures fail. Fungi and algae were common infestations

THE EFFECT OF CULTIVATION ON THE LEAF APEX OF D.SCOPARIUM

POPN. 40I.



Cultivated material.

Original herbarium

material.

Fig.5.

TABLE 4. 5.

PERFORMANCE OF DICRANUM SPECIMENS IN CULTURE.

NUMBER OF CULTURES WHICH DIED (OR POOR GROWTH) EXPRESSED AS FRACTION OF TOTAL NO. OF POPNS. FROM A GIVEN HABITAT TYPE.

	Habitat					
	Woodlands					
Species	Ground Flora	Trees	Dead Wood	Basic Communities inc. dunes of high pH	Acid Communities inc. acid dune	Rocks and Walls
D. scoparium	3/19	4/10	4/7	18/24	3/18	1/5
D. bonjeanii	-	-	-	1/5	1/8	-
D. fuscescens	1/6	3/6	2/2	-	-	0/2
D. majus	3/18	-	1/1	-	0/1	-

in the pots but only one or two cultures died of fungal attack, perhaps following compression in transit from the field. Algae were ineffective in competing with the moss. Specimens kept for two years are still vigorous and the bulk of material remained healthy and vigorous throughout the experiments.

Table 4. 5 has been prepared to show the number of populations which failed during the experiment. In D. scoparium some of the specimens from basic soils would not grow in the JIP soil watered with Durham tap water. The pH of the soil was 6.1 and the water was of pH 7.65. The failure of these populations is an indication that different populations of the moss may tolerate different pH ranges or mineral balances. The death of the plant was sometimes sudden and the results are perhaps evidence of genetic variability with regard to substrate variation. Much more evidence is required before this problem can be understood.

In D. majus excellent growth was made in most pots. D. bonjeanii samples were also vigorous and in this case the specimens from basic soils were especially successful, suggesting tolerance of the new pH and mineral conditions. A sample of fire-scorched material from Whixhall Moss, Shropshire, revived excellently. This species is obviously extremely vigorous vegetatively. This is perhaps not surprising in a species which rarely reproduces sexually in Britain. Pots of D. fuscescens only made good growth if the cushions were not broken apart. The cultures which failed were planted with stems divided from the large tufts.

The overall impression of the cultivation of the four species is that D. scoparium is not as tolerant of different soil conditions as the other three species. Perhaps the species has populations with differing soil preferences, (with restricted tolerance of different soil types), giving a total species tolerance of considerable magnitude. The other three species may be less exacting in their requirements.

Discussion.

Brief comments on a few of the criteria studied are recorded above. Two of the most important ones will now be considered in detail. Those involving measurement will be reported below (page 124).

Firstly some theoretical points must be made. Ideally several culture experiments should be set up with varying environmental conditions, with all the contributing factors carefully under control. Though it has not proved possible to provide such a series, it is clear that a start can be made in understanding the problems of Dicranum variation by growing material from as many environments as possible, in the standard conditions referred to above. Major difficulties involved are firstly that material was collected at different times and was therefore grown for differing lengths of time; and the process of adjustment to the new conditions may be slow. Nevertheless, even though the population samples may not have been fully in equilibrium with the new conditions, much of interest has been found on examination. Another difficulty is that the lower parts of the plant may influence the new extension growths which have been sampled and that the effect may not be the same in all populations. On final sampling however the original leaves and stem were often dead and their effect is probably negligible. It may be concluded that it is valid to compare material sampled from the pots with the herbarium material of the same population, but that comparison between samples grown for different times may be rather less reliable.

Leaf Stance Variation.

In D. scoparium, field collections with predominately falcato-secund leaves often produced erecto-patent leaves in culture; or falcato-secund leaves are found at the tip of the stems with a variety of leaf stances below. It is obvious that the leaf stance characters are not constant.

It has been reported in chapter II that falcato-secund forms are commonly found in shaded communities, often in dry habitats, such as on trees and rocks. Wilczek (1948) has suggested that illumination of the plants is of major importance in determining leaf stance, together with humidity. The following facts must be incorporated into any theory. First, in deciduous forests a good deal of the growth of Dicranum tufts takes place in the winter and spring when there are open lighting conditions. In shaded habitats specimens are often found in which the best illuminated parts of the tuft, the apical leaves, are falcato-secund, and the lower leaves, which are in deeper shade are of various stances. If illumination was the most important factor the lower leaves would all tend to be falcato-secund. These points, particularly the latter, are incompatible with the theory that illumination is the most important factor.

Before the factor of humidity is considered, other possible factors must be considered. Temperature variations within the frame were probably not considerable and yet different leaf stances were found. Soil factors can also be discounted as all the samples were growing on the same soil. The possibility that falcato-secund forms are only formed on vertical or steeply sloping habitats and that erecto-patent leaves are only a feature of horizontal cushions is not substantiated by field observations.

It seems clear from the culture experiments that humidity is the most important factor. Developing a hypothesis on these lines, falcato-secund leaves are regarded as a xeromorphic feature, developed on well drained or impervious substrata or in localities with only a small number of days per year on which rain falls. The leaf surfaces pressed together reduce the area of leaf exposed. Under conditions of high relative humidity the leaf stance predominating is the erecto-patent. This leaf position is probably photosynthetically more efficient, than the falcato-secund form, as a greater leaf surface is exposed. All combinations of leaf stance can be found in ecological studies of different habitats. Often the apical leaves are falcato-secund. These project beyond the moss turf into a drier atmosphere; the lower leaves in the capillary moisture system of the turf are often in a higher relative humidity and are commonly erecto-patent. The leaf stance of the leaves in different parts of the stem will indicate the range of moisture conditions prevailing at the time of their growth. A series of culture experiments with different relative humidities maintained around tufts of D. scoparium would help towards a final solution of these problems.

On the evidence available it would seem that humidity is extremely important in determining the leaf stance in D. scoparium. It follows that the falcato-secund forms, and varieties given in chapter I are probably without value. No stock has preserved its falcato-secund leaves. It does not follow however that erecto-patent forms would produce falcato-secund leaves under the appropriate environmental conditions. Culturing with conditions favouring falcato-secund leaves will be necessary before the problem of leaf stance can be fully elucidated.

The variation shown by D. bonjeanii closely parallels the situation found in D. scoparium. Falcato-secund forms of D. bonjeanii are not constant in culture and erecto-patent leaves are produced throughout. The humidity hypothesis can probably be applied to D. bonjeanii.

The results for D. majus show that falcato-secund leaves are invariably produced at the apex of the shoot, in open pots. This character is not disturbed by conditions which gave erecto-patent leaves in D. scoparium and D. bonjeanii. In polythene covered cultures however erecto-patent leaves were produced. It seems possible that D. majus is sensitive to different and higher relative humidity ranges than D. scoparium and D. bonjeanii.

In D. fuscescens some populations retained falcato-secund leaf stance of upper leaves in open pots and polythene covered cultures; others produced different leaf stances. Obviously much variation is found, some of it possibly genotypically determined. Lower leaf stance in the cultivated plants was often different from that of the apical leaves and different too from that found in herbarium material. Here plasticity in leaf character seems to occur. In other cases falcato-secund leaves were found throughout the stems of the pot samples and may therefore be genotypically determined.

Variation in Undulation.

Field observations suggest that in D. bonjeanii slightly undulate leaves are found on plants growing on drier areas and in the same locality moister niches have more markedly undulate specimens. Experimental increase in relative humidity has been found to increase undulation in the four species. Polythene enclosed pots and open pots had similar environmental conditions with the obvious exception of higher humidity. Other factors may modify the effect of moisture, for instance low light intensity will reduce evaporation. The evidence so far available suggests that humidity is primarily responsible for leaf undulation and that other factors take effect only by influencing humidity. This hypothesis will now be elaborated.

In D. bonjeanii polythene bag cultures, undulation may involve the whole leaf and the tip may become contorted and twisted, as was described for var. rugifolium in chapter I. Specimens which fitted the description of var. calcareum, in having little or no undulation, could easily be "converted" to type material by growth in an atmosphere of high humidity. Some leaves of var. "calcareum" became almost rugose. It is suggested therefore that a whole series of undulation types can be produced under field conditions, and that as different grades of undulation are not constant in culture, varieties based mainly on this feature are of little taxonomic importance. It is not known whether highly rugose samples collected in the field would give non-undulated leaves in the appropriate environmental conditions.

In *D. scoparium* the degree of relative humidity, necessary to a ~~e~~ffect the new growth of leaves, is probably higher. In open pot cultures a few specimens produced undulate leaves. In polythene bag cultures most populations produced undulate leaves. As in the case of *D. bonjeanii*, undulation appears to vary continuously with the relative humidity. Production of undulate leaves in natural populations may depend upon weather conditions prevailing at the time of leaf growth. It is doubtful whether var. *paludosum* is more than a habitat modification. One possible explanation of the higher humidity requirement for undulation in *D. scoparium* is that the nerve is relatively thicker than in *D. bonjeanii*. The leaf is more rigid than in *D. bonjeanii*.

Undulation in *D. fuscescens* has already been commented upon above, and the suggestion made that mechanically the leaf apex is less liable to show the phenomenon. The lower leaf lamina can show undulation under growth conditions of high humidity.

D. majus in open pots did not produce undulate leaves. In polythene covered pots popn. 290 produced undulation. The highest humidities used gave specimens which fit the description of var. *undulascens*, from material collected in Scandinavia. This variety is almost certainly a habitat modification, and not a genotypically distinct taxon.

A final discussion at the end of this chapter, after the biometrical results have been presented, will draw together all the conclusions of this section of the work.

TABLE 4. 6.

POPN. NO.	LEAF LENGTH m.m.	SE.	$\frac{W}{NW}$ MEAN	SE.	SERRATION MEAN	S.E.
D. SCOPARIUM						
228	8.98	.629	11.92	.4394	38.2	4.78
294	6.82	.5391	10.75		16.48	4.02
354	7.2	.6708	10.53	.588	11.6	4.5
355	6.08	.7887	11.32	.762	4	-
361♀	6.2	.5916	13.17	.859	8.72	2.37
361♂	4.8	.7149	12.6	.655	10.0	4.25
370	6.62	.3913	9.01	1.00	8.92	4.78
391	6.10	.5323	10.35	.620	9.56	3.51
401	5.86	.5205	10.57	.759	6.32	2.7
422	5.36	.4233	12.9	-	7.56	3.963
423	5.97	.698	11.03	.580	1.86	.496
450 ♀	6.66	.82	12.9	.4827	2.12	.414
450 ♂	4.7	.8803	15.28	1.452	1.43	.16
486♀ L♂	6.64	.6199	13.45	.669	10.2	3.24
486♀ D♂	7.92	.4973	10.27	.394	15.16	4.56
481	7.98	.5736	9.2	.407	39.24	2.25
D. FUSCESCENS						
332	8.56	.273	4.23	.403	43.08	5.3
357	7.5	.507	4.37	.693	55.96	5.71
374	8.12	.569	5.14	.607	36.6	3.47
381	6.68	.2289	5.01	.803	36.54	3.53
385	5.94	.5938	4.36	-	8.76	1.744
D. BONJEANII						
354A	7.1	.7071	20.1	.517	13.72	5.02
354B	7.4	.7633	16.78	.869	20.88	5.62
485♀	7.1	.616	17.77	.799	15.46	4.77
495	7.28	.4412	16.22	1.127	16.22	3.45
D. MAJUS						
290	9.44	.292	13.57	.658	78.74	4.568
371	11.70	.324	13.67	.529	76.39	5.107

2. BIOMETRICAL STUDIES ON CULTIVATED MATERIAL.

Methods.

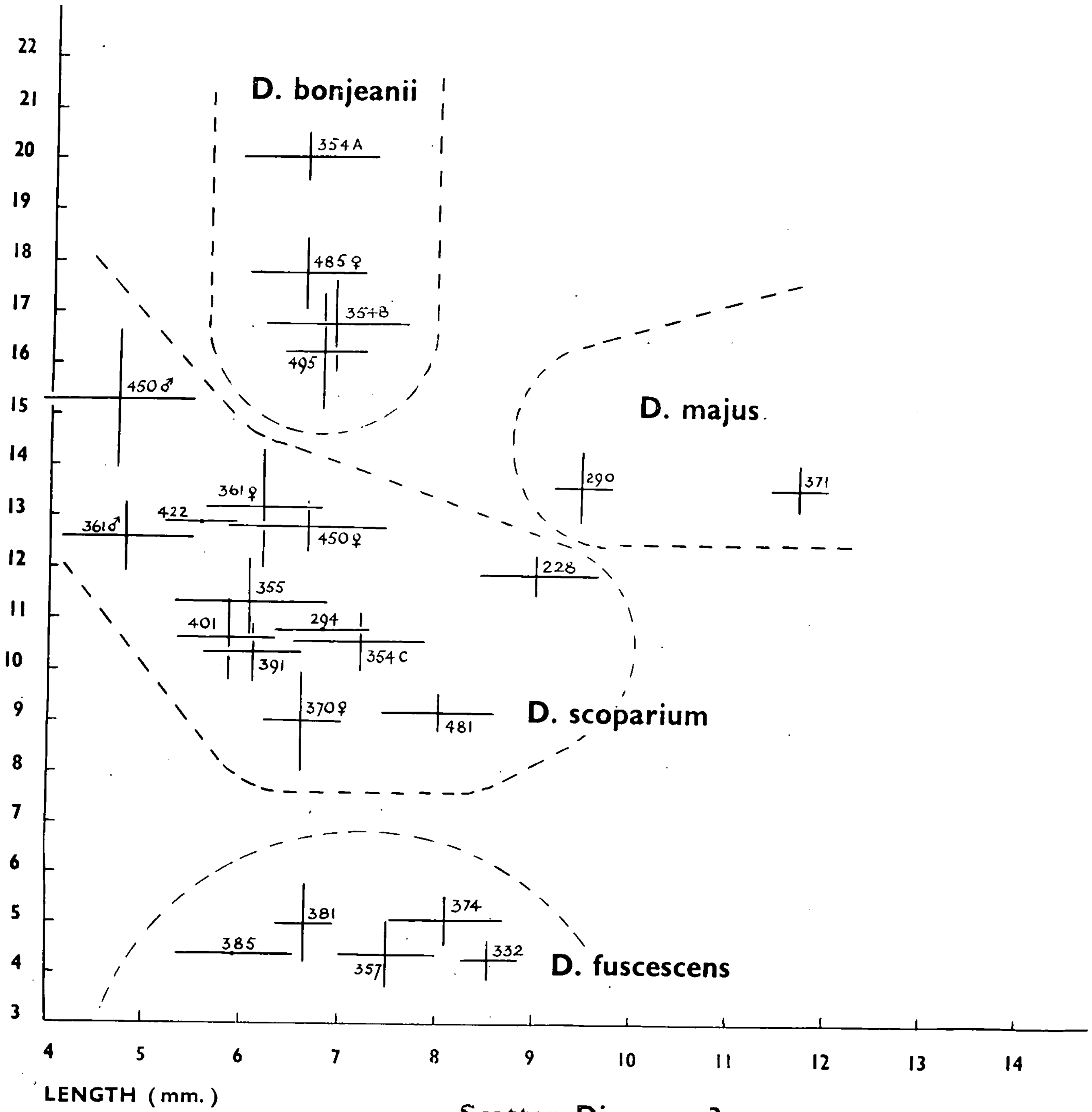
The populations studied in chapter III were re-examined after a period of cultivation. 30 leaves, each the largest on a stem picked at random from the available material, were mounted in gum chloral. Length, breadth at the widest point and nerve width were measured and tooth number of one edge of the lamina counted. 25 leaves were examined where this number was available. Sometimes the material was scanty and the data are not from a truly random sample, as in the investigations of the field collections. The ratios which proved interesting in the biometrical analysis of the original herbarium material were again calculated, as well as mean values and standard errors for important data. The results are given in Table 4. 6.

Results.

As in chapter III two problems are illuminated by the results, firstly that of species separation and secondly the extent and nature of intra-specific variation.

A. Species separation.

In the original study it was found that the leaf length and width: nerve width ratio (W/NW) could be used to separate the samples investigated. The data for these two features from the pot samples are plotted on scatter diagram 3. As can be seen D. majus (popn. 290) and D. scoparium (popn. 228) are very close in mean length and the difference is not statistically significant. The W/NW ratios show



Scatter Diagram 3

Leaf length / $\frac{\text{width}}{\text{nerve width}}$

Standard errors and mean values

clearly that D. fuscescens is distinct from the other three species. The highest value 5.14 (popn. 381) is statistically different from the lowest D. scoparium value of 9.01 (popn. 370 female). The separation of D. scoparium and D. bonjeanii on this ratio, which was significant in the herbarium material, breaks down. D. bonjeanii has the highest mean value but 16.22 D. bonjeanii (popn. 495) is clearly close to 15.28 D. scoparium (popn. 450 male). D. scoparium 13.45 (popn. 486) is also close to the D. bonjeanii value.

Conclusions.

Cultivation has shown that D. majus may produce small leaved stems and that leaf length is not an absolute guide to the species if the mean value is of the order of 9 mm. The nerve strength characteristics of D. fuscescens are clearly useful as a taxonomic character. In the case of D. bonjeanii, at the other extreme of the observed range of W/NW, the nerve strength means are higher in some cases, but as the lower range approaches closely to the values for D. scoparium, the character is best used in combination with others.

B. Intraspecific taxa and sex differences.

D. scoparium.

Length means for cultivated material are a continuous series (Table 4. 6) and as in chapter III there is no break in the variation. It is interesting to note that popn. 481, which had the largest mean value for leaf length in the herbarium material is no longer the longest leaved. Popn. 228 has the highest value of 8.98 mm.

The herbarium studies on populations 450 and 361 of female and large male plants showed that the males were significantly shorter in the leaf. The males were only marginally shorter leaved in cultivated samples. Breadth measurements indicate that the males were only slightly narrower in the leaf than female plants. This was the case in the original studies. The W/NW ratios for pot samples of male and female plants clearly demonstrate the variability of the sexes. The mean for male plants may be higher (as in popn. 450) or lower (as in popn. 361). Dwarf males in popns. 486 and 355 have been cultivated on soil. Detached males soon died; presumed male plants of 486 produced leaves 2 mm long. As no antheridial heads were produced in these males grown in situ on the females, the sex could not be determined positively. The shoots had however grown in the position occupied by dwarf males in the planted material. The cultivation of marked males must be observed to get conclusive results, but the data so far suggests that dwarf plants may develop into larger plants.

D. fuscescens.

It was considered in chapter III that most of the material fitted the 'type' description. Population 385 did however have entire leaves, but not the other characters of D. fuscescens var. congestum. The mean serration value for cultivated material of this population is clearly significantly higher than in the herbarium material. At the same time it is still much lower than that of the other populations. Examination of the leaf and nerve breadths of cultivated leaves, Table 4. 7, shows that 385 is not distinct from the other populations in these characters.

Further comment on the serration details will be given below. The upper leaf cells of 385 were quadrate in some of the cultivated material, or irregular. The original material did not appear to be mixed, and further studies are essential.

No male plants have survived in cultivation.

TABLE 4. 7.

WIDTH AND NERVE WIDTH MEASUREMENTS - mm.

POPN.	332		357		381		374		385	
	W	NW	W	NW	W	NW	W	NW	W	NW
Herbarium values	.61	.16	.60	.11	.61	.10	.73	.16	.65	.15
Cultivated material	.8	.18	.7	.18	.8	.18	.9	.2	.60	.1

D. bonjeanii.

Population 354 was thought to contain D. bonjeanii var. calcareum, see page 91. The calcareum portion under cultivation however had a similar mean leaf length to the typical material, from the same locality, grown under the same conditions. Also very similar leaf width results are shown by the two samples and the serration mean for the "calcareum" portion is higher than for the material conforming to the "type". Clearly this does not conform to the description given by Braithwaite (1887) "shorter in the leaf (than typical material) and slightly serrate near the apex".

In cultivation sex differences have been under observation. The male plants have not produced antheridial heads and as a profusion of little shoots has been developed, within the cultivated shoots, which could be either male or female it is not clear whether the male plants remain smaller than the female. Further work is essential involving marked male plants.

D. majus.

The original survey of material indicated that all the samples fitted the description of typical plants, given in chapter I.. Very similar new growth has been produced in all cases. Dwarf males (in situ on the female plants) were planted but no trace of these could be found in the following year. It is not clear whether males are ephemeral or whether they can produce larger leaved forms under cultivation.

SERRATION PROBLEMS.

To interpret the results presented in Table 4. 8 it is assumed that the experimental conditions used in growing the samples were closest to those found in sheltered humid Dicranum communities. Data in chapters II and III indicate that under these conditions the leaves are often strongly serrated. It is therefore considered that the experimental environment favoured serrated types.

TABLE 4. 8.

SERRATION VALUES

D. SCOPARIUM	ORIGINAL (CHAPTER III)		CULTIVATED		SIGNIFICANTLY DIFFERENT	DECREASE
	m	SE	m	SE		
228	19.3	2.56	38.2	4.78	+	
294	7.24	3.55	16.48	4.02		
354C	7.09	4.88	11.6	4.5		
355	12.5	3.89	4.0	–		+
361♀	16.08	6.25	8.72	2.37		+
361♂	6.82	4.67	10.0	4.25		
370	1.2	.55	8.92	4.78	+	
391	18.69	2.17	9.56	3.51	+	+
401	.96	.45	6.32	2.7	+	
422	.58	–	7.56	3.936	+	
423	.4	.26	1.86	.496		
450 ♀	5.76	3.96	2.12	.414		+
450 ♂	19.58	4.09	1.43	.16	+	+
486♀ L ♂	12.08	4.53	10.2	3.24		+
486♀ D ♂	4.84	3.59	15.16	4.56	+	
481	39.58	2.48	39.24	2.25		
D. FUSCESCENS						
332	9.36	5.91	43.08	5.3	+	
357	14.64	2.81	55.96	5.71	+	
371	15.28	2.22	36.6	3.47	+	
381	12.24	1.16	36.54	3.53	+	
385	1.29	.322	8.76	1.74	+	
D. BONJEANII						
354A	9.0	4.01	13.7	5.02		
354B	6.52	4.59	20.88	5.62	+	
485♀	6.92	3.61	15.46	4.77		
495	20.6	6.28	16.22	3.95		
D. MAJUS						
290	62.2	3.88	78.74	4.568	+	
371	31.4	3.53	76.39	5.107	+	

Two hypotheses are put forward in chapter III which might explain the variation; it might or might not have a genotypic basis. If not, then one would expect new leaves produced in the cold frame to be serrated in conformity with the new conditions. In this case entire leaved forms should produce serrated leaves. If there are genotypic differences, then all the populations should remain at about the mean serration value for the herbarium material. The possibility that both processes could operate together was also mentioned and will be considered.

The results for D. scoparium will be considered first, and populations conforming to each hypothesis will be noted. In 228, 370, 422, and 486 dwarf male significant increases in serration means have been noted in comparison with the herbarium material, (see Table 4. 8). In such cases as 228 the increase in mean value is a large one. This group supports the first hypothesis, i.e. serration is behaving as a plastic character.

Another group of specimens 423, and 481 show very close agreement of the old and the new values. 423, a non-serrated population remained almost entire leaved after 19 months cultivation. 481, the most highly serrated D. scoparium under study, gave two almost identical mean values for serration. Population 423 furnished some evidence of genetic control of serration, with its persistent growth of entire leaves in an environment in which other populations showed significant increases in serration. As for population 481, under the cultivation conditions it was probably in an environment very close to its natural state; and its peak serration mean, for that particular set of conditions, was already expressed in the herbarium mean value, and no increase therefore occurred on cultivation.

A further group of samples 294, 354, and 361 male plants, showed increased serration but the results were not significantly different from those of the herbarium material. This suggests the possibility that the plasticity of the plants is limited in its expression by some factor, which may be genetic. The possibility that the cultures were not in equilibrium with the new environment is not very strong; for instance, population 294 had been in cultivation for two years.

A puzzling group remains to be considered. In 355, 361 female, 450 female, and 486 female a decrease in serration occurred, though the values for cultivated material are not significantly different from the herbarium data. In 391 and 450 male the two values are significantly different. One explanation is that the material collected in the field was very much more variable than is reflected in the herbarium data and that plants poorly represented in the original sample were grown in the laboratories. The possibility that the culture conditions in the frame were not uniform and that this group of plants were in a distinctly different environment is not valid, as they were in different positions, not in a group together.

Standard error values for the new means have been worked out and it is interesting to note that they are often of the same order as those for the herbarium data. Variation about new means is evidently quite as great as in natural variation. In some cases however the new values are smaller as in 361 female and 450 male. This may be due to differential survival of the planted material or the action of natural selection reducing the variation in the habitat conditions of the frame.

Summarizing the serration details for D. scoparium, it is clear that genetic factors play a part in the variation patterns. Of particular interest are the high altitude populations 422 and 423. Both were entire leaved in the field, conforming to the description of var. spadiceum. 423 showed persistent low serration under humid sheltered conditions, 422 on the other hand produced serrated leaves. The original serration figures for 422 show that such large serration counts were not represented in the population in its original state. This is clear evidence for phenotypic plasticity. If entire leaved material is so variable in its behaviour it is doubtful whether var. spadiceum is of any taxonomic value. Taking the lowland samples, the results suggest some phenotypic plasticity but the objection that the pot samples have been depleted of some of the variation by differential survival cannot altogether be ruled out. The two more highly serrated populations 228 and 481 are clearly distinct from the others and evidence of a break in variation in serration is presented.

D. fuscescens. Examination of the results obtained for this species shows that all the populations increased in serration means but that 385 remained much lower than the others. The original material was almost entire-leaved; the new growth was distinctly serrated but to a lesser degree than the other populations. Experiments on a number of entire-leaved D. fuscescens populations would be extremely interesting; some plasticity appears to be shown by population 385.

D. bonjeanii. 354B was originally thought to be near var. calcareum and it is interesting to note that after cultivation it was more serrulate than the type material from the same locality. The results as a whole indicate that some plasticity of serration expression is found in natural populations.

D. majus. Two populations of this species both maintained highly serrated leaves in culture.

In all the four species much more data are required before the serration phenomena can be fully understood. Especially instructive would be transplant experiments at high altitude to see if serrated forms can produce entire leaves; (population 422 may be an exceptional population, of D. scoparium). It would also be interesting to find out if the populations at high altitude are derived from spores of a certain genetic character or whether vegetative reproduction from fragments of lowland populations, showing plasticity, can produce entire leaved plants.

Comments on the W/NW ratio results.

Table 4. 9 has been prepared to show the full results for this character. It is clear that a wide range of ratios is possible within each species and measurement of a few leaves may not be a reliable guide

to the species concerned. Means of samples of 25 or more plants are more reliable but may not be conclusive. The character is best used with others. The results obtained differ from those of Jenson (1939) who quotes ratios of the nerve width as a proportion of the leaf base. His values did not suggest the closeness of the extreme values for each species, which I have found.

TABLE 4. 9.

$\frac{W}{NW}$

	D. scoparium	*D. bonjeanii*	*D. fuscescens*	*D. majus*
Herbarium 'mean' values	$\frac{1}{8} - \frac{1}{12}$	$\frac{1}{15} - \frac{1}{23}$	$\frac{1}{3} - \frac{1}{6}$	$\frac{1}{11} - \frac{1}{14}$
Extreme individual values	$\frac{1}{5} - \frac{1}{20}$	$\frac{1}{10} - \frac{1}{30}$	$\frac{1}{3} - \frac{1}{8}$	$\frac{1}{7} - \frac{1}{19}$
Cultivation 'mean' values	$\frac{1}{9} - \frac{1}{15}$	$\frac{1}{16} - \frac{1}{20}$	$\frac{1}{4} - \frac{1}{5}$	$\frac{1}{13}$
Extreme individual values	$\frac{1}{6} - \frac{1}{20}$	$\frac{1}{10} - \frac{1}{30}$	$\frac{1}{3} - \frac{1}{7}$	$\frac{1}{9} - \frac{1}{18}$

TABLE 4. 10.

The effect of cultivation on the morphology of Dicranum

	D. scoparium	D. bonjeanii	D. fuscescens	D. majus
Leaf length mean	To 9 mm.	To 9 mm.	Less than 9 mm.	More than 9 mm.
Leaf stance:				
- apical leaves	Variable	Variable	Some F.S.	All F.S.[1]
- lower leaves	Variable	Variable	Some variable Some F.S.	Variable
Porosity of upper cells	+	+	-	+
Undulation of leaf	+	+	+[2] rare	+[2] rare
Serration[3]	Genotypic and phenotypic	Phenotypic	Genotypic and plasticity	Plasticity
Leaf section detail unchanged[4]	+	+	+	+
Width/Nerve width details changed	+	+	+	+

Notes:

1 Except under high relative humidity.

2 Only under high relative humidity.

3 Data so far.

4 Details in Chapter III.

Conclusions.

Table 4. 10 has been prepared to show the effect of one series of cultivation experiments on the morphology of Dicranum leaves. The main conclusions are as follows:

A. In respect of species separation certain characters, leaf length, undulation and nerve strength are not fully reliable. D. majus is predominately the longest leaved species. D. bonjeanii is commonly undulate, and evidence has been put forward which suggests that it can become so at a lower relative humidity than D. scoparium. As regards nerve strength, it may be stated that D. fuscescens has the widest nerve and D. bonjeanii the narrowest (as a proportion of the leaf base), but examination of only one or two leaves from a population can be very misleading as is shown above. Characters of leaf sections and porosity, or otherwise, of the upper leaf cells do appear to remain constant in culture. This is evidence that they are more useful taxonomically than leaf stance etc.

B. With regard to intra-specific variation, the cultivation experiments have been most interesting. Evidence that entire leaved forms of D. scoparium may be genotypically fixed or phenotypically plastic has been presented and the var. spadiceum is rejected on the grounds that it is impossible to determine beforehand what the behaviour of a particular population will be in culture. The status of D. fuscescens var. congestum is not clear. 385 comes close to this variety and showed slightly increased serration on cultivation. It is clearly not as constant as one of the entire leaved populations of D. scoparium. The variety calcareum of D. bonjeanii seems to have no permanence in culture and is almost certainly a habitat modification. This is true too of var. paludosum of D. scoparium and D. majus var. undulascens. The evidence suggests that the variation in leaf stance depends upon relative humidity in D. scoparium, D. bonjeanii and D. majus. In D. fuscescens falcato-secund leaves may be genetically fixed, although the lower leaves show different leaf stances in different humidities. The leaf stance varieties of D. scoparium and D. bonjeanii on this evidence seem to be habitat modifications, but the problem of D. fuscescens with regard to var. falcifolium is not fully worked out.

Only in D. scoparium were the male plants examined in any detail and they appear to show considerable variability. Further comments on this and final comments on the taxonomic problems will be dealt with below in the final discussion, chapter VII.

CHAPTER V.

CYTOLOGY.

Introduction.

The cytological study of mosses is a relatively recent development but already much light has been cast on the relationships of species in difficult groups. It was hoped, at the outset of these studies, to see if the four species of Dicranum were distinct cytologically; either by virtue of having different haploid numbers or by showing different karyotypes. The cytological aspects of this study also promised to provide data on the problem on intraspecific variation; was the large morphological variation correlated with an underlying chromosomal variation? Another series of problems which could be illuminated by cytological data were those concerned with sex determination.

Methods.

The results presented were obtained from spore-mother cell meiosis stages, from immature sporophytes. Meiosis takes place in Dicranum capsules at about the same time as pigmentation of the cells at the junction of the operculum and the capsule proper.

The sporophytes have been fixed in 1:3 acetic-alcohol or 1:1:1 acetic acid, ethyl alcohol, chloroform. Ferric acetate has been used as a mordant, in some cases. The most successful preparations were made using 1:1:1 mixture and the fixation was much improved if the capsules were slightly broken, with forceps, as they were placed in the fixative. It has been found also that better fixation could be obtained if only a few capsules were placed in each tube. The tubes have been stored at

-10°C. in a deep freeze and satisfactory preparations have been made on material stored for well over a year. The minimum fixation time was several days. Material fixed at different times of day, range midmorning to late evening, has yielded meiotic stages.

The SMC preparations were prepared using aceto-carmine squash techniques very similar to those used by Lewis (1957), Anderson and Crum (1958) and other workers in the field of bryophyte cytology. The capsule was first removed from the fixative and was then split longitudinally with a razor blade, after first cutting off the operculum region. From each capsule half the sporogenous tissue was removed with mounted needles, and placed in a drop of carmine, on a grease-free slide. This material was then thoroughly macerated with the needles, the iron from these instruments acting as an excellent mordant. If on examination with a microscope, x 40 the drop was found to contain tetrads or spores, then the slide was rejected. If on the other hand SMC, containing small stained areas, could be seen, then the preparation was continued. The drop of stained macerate was divided between 3-4 slides and all large fragments of columella etc. were removed. Both these precautions enabled easier squashing of the material. A coverslip was added to each slide and after tapping to spread the cells, the slide was heated, almost to boiling, over a spirit lamp. Digital pressure was then applied to the coverslip, the slide having been placed within a folded filter paper. The process of heating and squashing was sometimes continued until the spreading of the chromosomes was satisfactory. Next the slide was ringed with "Philisol", a proprietary brand of rubber solution, and most of the microscopic examination and photography was carried out on these temporary mounts. It has been found that slides treated in this way can be kept for about a week, if stored in a moist atmosphere. Attempts to make the slides permanent failed, an alcohol-acetic acid series to final mounting in Euparal, from absolute alcohol was amongst the methods attempted. It was found that as soon as the pressure on the coverslip was altered, the SMCs distorted. During the course of the work however Dr. A. Schmidt from Munich, recommended the use of CELODAL I a highly viscous fluid, which when placed undiluted at the edge of the coverslip gradually replaces the evaporating acetic acid, making a permanent mount. Care was taken to cover the slides during Celodal treatment to prevent dust being drawn under the coverslip.

The slides were carefully examined using a Reichert Biozet binocular microscope oil immersion x 1000. The photographs were taken with a Reichert plate camera using Ilford cut film. Ilford Contrast FF developer was used to develop the film.

Attempts to prepare slides of gametophytic chromosomes have not been successful. Young leaves, stem tips, protonemal cells and antheridial heads, have been tried using aceto-carmime squash methods on macerated material. Hydrolysis with concentrated hydrochloric acid/alcohol mixtures was found to hinder staining, but if boiling aceto-carmine was used as the hydrolysing agent, staining was not impaired. The main obstacles however were the small number of plates obtained and the great difficulty of squashing the plate sufficiently to count the chromosome complement.

Pre-treatments with 8-hydroxy-quinoline, colchicine and p-dichlorobenzene did not give any apparent increase in the number of plates available for study.

RESULTS.

PREVIOUS COUNTS IN THE GENUS DICRANUM.

The following list of chromosome numbers for the genus *Dicranum* is mainly from Wylie (1957), with additional data from Anderson and Crum (1958), and Holman (1958).

TABLE 5. 1.

Species	n.	Locality	Author
D. caeisum	11	Japan	Yano 1951
D. condensum	12	N. Carolina	Bryan 1956
D. elongatum	13	Alaska	Steere 1954
D. fuscescens	12	Canadian Rockies	Anderson & Crum 1958
D. fuscescens	24	Canadian Rockies	Anderson & Crum 1958
D. groenlandicum	12	Canadian Rockies	Anderson & Crum 1958
D. japonicum	11	Japan	Schimotomai 1932, Yano 1951
D. nipponense	11	Japan	Yano 1951
D. majus	11	Japan	Yano 1951
D. majus	12 + 2-3m	Finland	Vaarama 1950
D. majus	12 + 2-3m	Alaska	Steere 1954
D. rugosum	10 - 12	C. Europe?	Heitz 1928
D. rugosum	11	Japan	Yano 1951
D. rugosum	12	Finland	Vaarama 1950
D. rugosum	12	Denmark	Holmen 1958
D. scoparium	10 - 12	C. Europe?	Heitz 1928
D. scoparium	11	Japan	Yano 1951
D. scoparium	12	Finland	Vaarama 1950
D. spurium	12	Finland	Vaarama 1950
D. strictum	12 + 2m	Canadian Rockies	Anderson & Crum 1958

General observations on the results of the cytological preparations.

Several difficulties in the interpretation of meiotic plates have been recorded in the literature, and some of these have been encountered in this work. Firstly there is the problem of precocious division of bivalents in the meiotic groups. This phenomenon has been described in mosses, by Vaarama (1949), and may lead to erroneous results. Considerable care has been exercised in interpreting the aneuploid series found in this work. Another difficulty is that of "stickiness" of the chromosomes. Anderson and Crum (1958) have shown that the chromosomes of D. fuscescens are sticky, so that it is sometimes difficult to determine the exact number of bivalents. In several plates small bivalent, univalents or fragments have been found. The terminology of small chromosomes is much confused. They have been known as 'm' chromosomes, Heitz in Bryan (1955); accessory chromosomes by Vaarama (1949); and small bivalent for the "non-minute" type by Anderson and Crum (1958). The term accessory chromosome has been criticised by Anderson and Crum (1958), as it implies that these chromosomes are in some way extra to the chromosome set. It appears that these small chromosomes are a constant feature of the meiotic complement of many mosses and in this case are not "extra" chromosomes, comparable with B chromosomes and other types of supernumaries. The term "small chromosome s.c." has been used in this account and it includes fragment-like bodies not fully understood. The behaviour of these chromosomes has not been studied throughout meiosis, as more emphasis has been placed on determining the chromosome number. There appears to be "all degrees of smallness", from the thin type in D. majus 364, to the minute fragments found in D. scoparium 228.

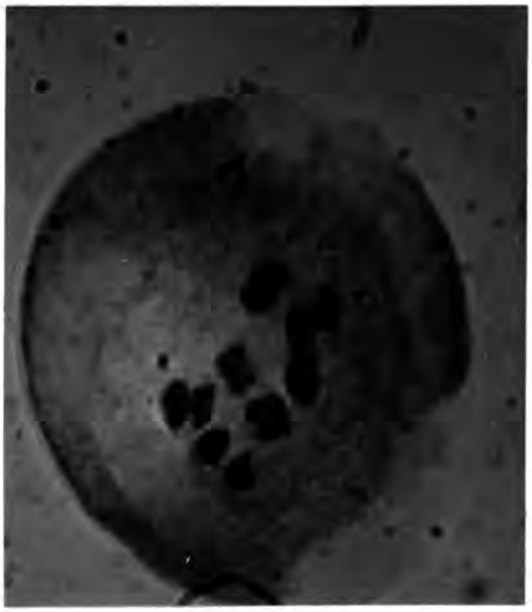
Cytology of individual species.

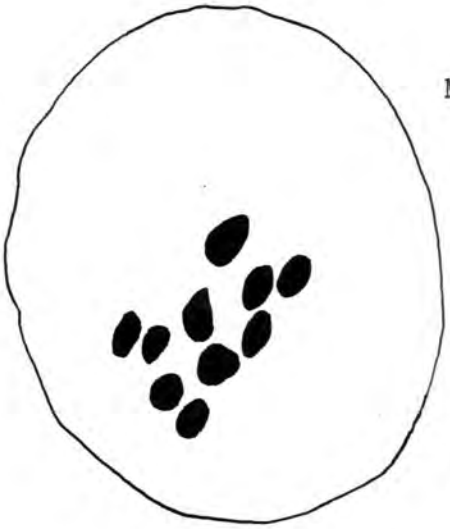
D. fuscescens.

In all three cases the haploid number appears to be 10. In population 332 this is clearly shown in fig. 6. Fig. 7 shows a plate with precocious division of one chromosome pair. This phenomenon is common in all four species and much care had to be exercised in interpreting plates. In population 357 a small chromosome pair or fragment is present, fig. 8. The nature of this body is not fully understood. It has not been possible to find out if it divides during meiosis, behaving as a bivalent, or whether it behaves as a fragment. Population 374 fig. 10 presents some difficulties in interpretation. The group x x is interpreted as two bivalents showing precocious division with the small chromosome pair or fragment apposed to the larger precocious pair. Fig. 11 shows clearly the 10 bivalents with the slightly smaller chromosome or bivalent.

More work is essential to understand this species, especially in respect of the smaller chromosomes found in 357 and 374. It is of interest to note that in 357 a capsule was discovered which had a polyploid sector, fig. 9, a small proportion of the SMC showed the high number illustrated.

This species has been the subject of cytological study by Anderson and Crum (1958), and the numbers given from material collected from localities in the Canadian Rockies are clearly different from those given above. No polyploid material has been found in my work, with the





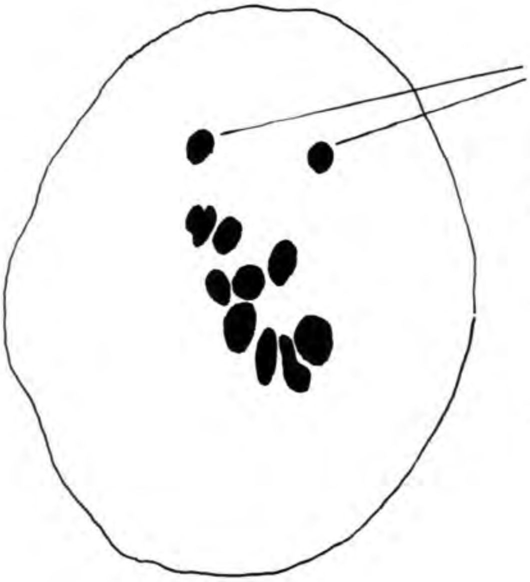
Metaphase I

n = 10

Fig. 6

Camera lucida drawings

x 1000



Metaphase I

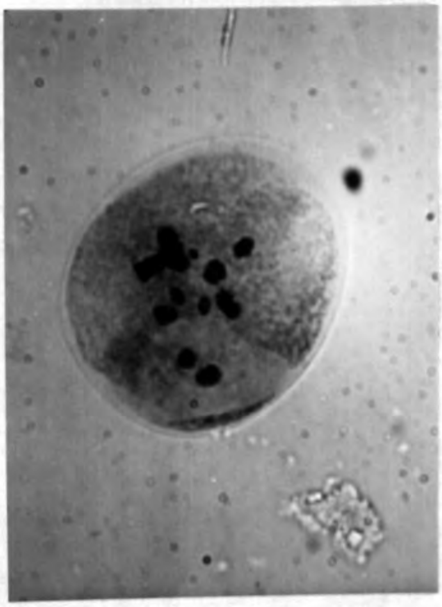
n = 10

Fig. 7

POPULATION 332 Dicranum fuscescens.

Metaphase I

n = 10 + 1



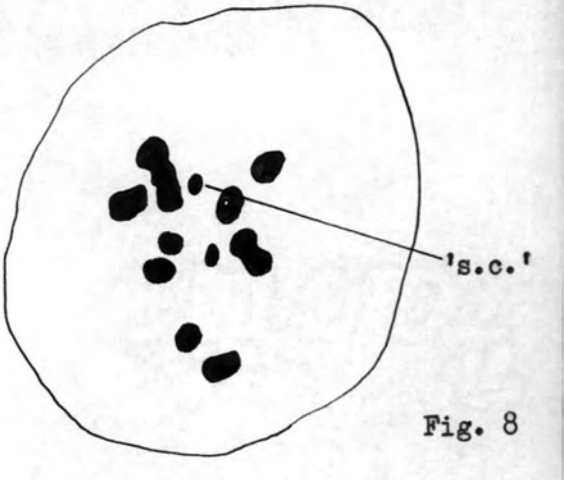


Fig. 8

Camera lucida x 1000

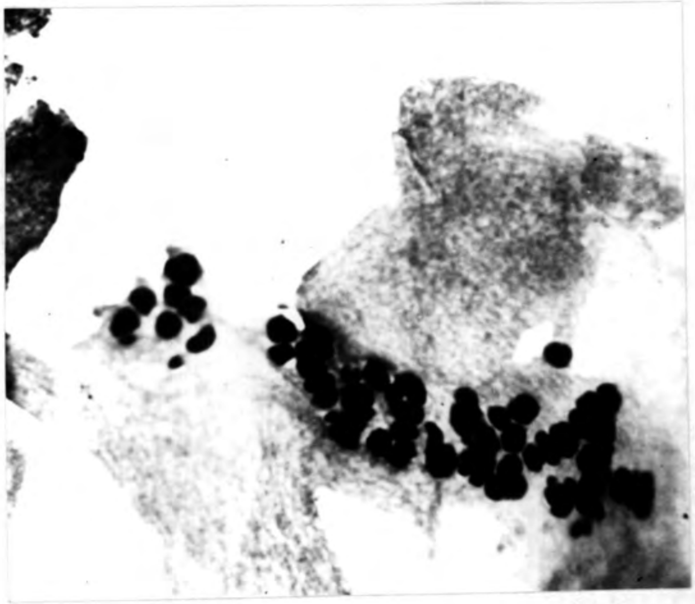


Fig. 9

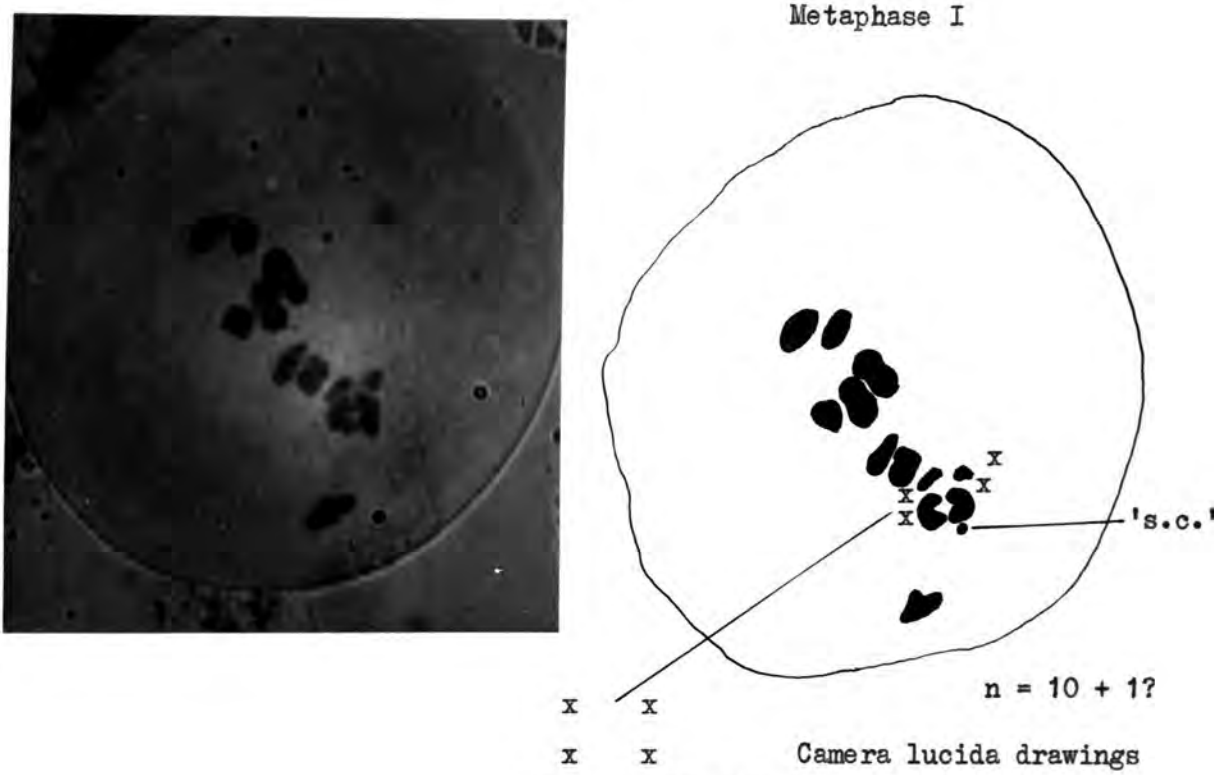
Cell of
Polyploid Sector

(Different capsule to
cell above)

POPULATION 357 Dicranum fuscescens.

Fig. 10

Metaphase I

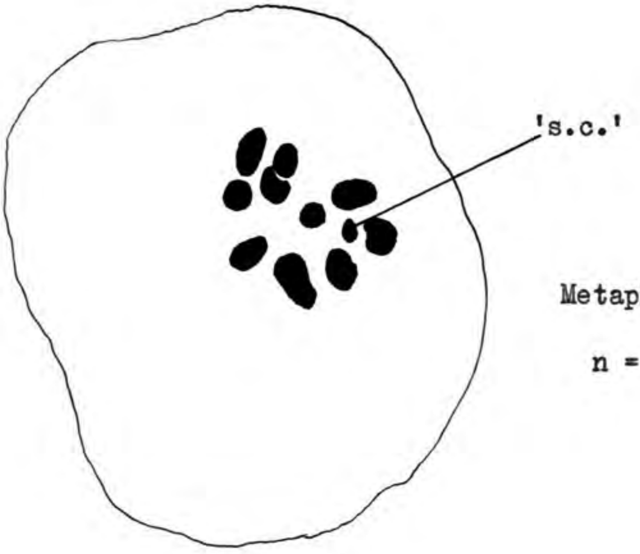


n = 10 + 1?

Camera lucida drawings

Two precociously dividing bivalents

x 1000

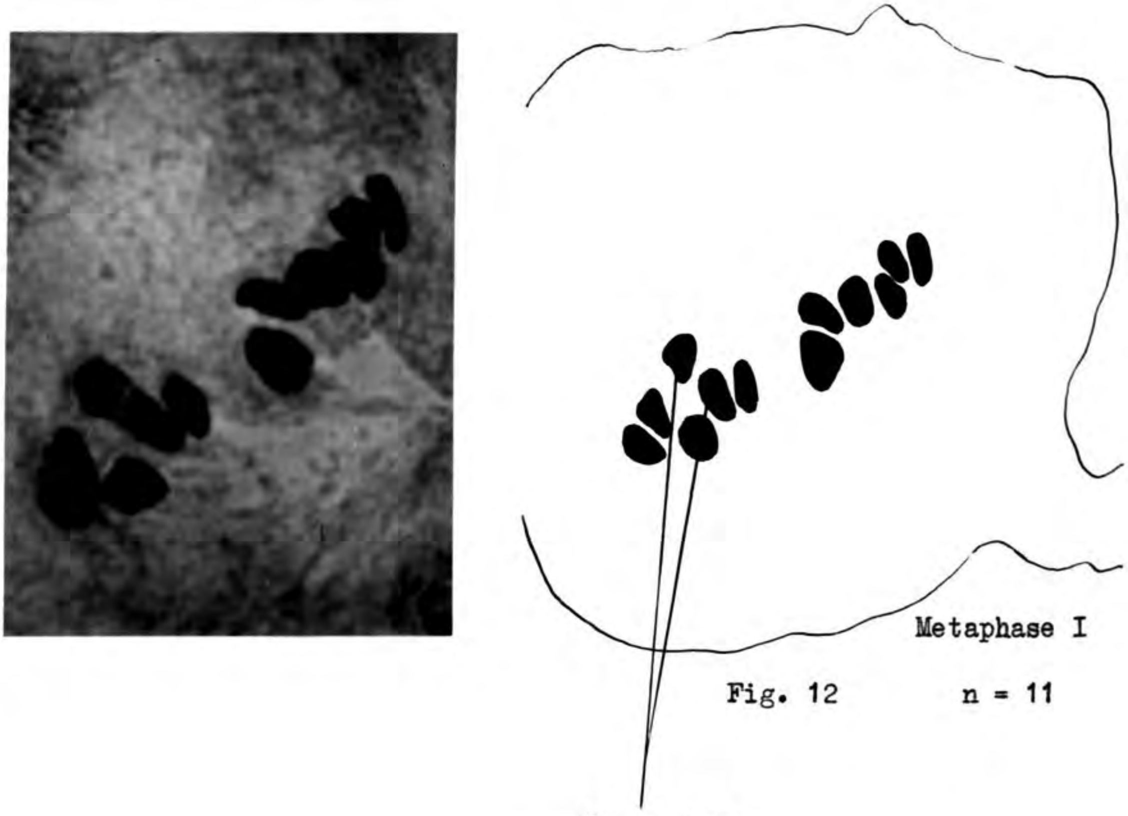


Metaphase I

n = 10 + 1

Fig. 11

POPULATION 374 Dicranum fuscescens.



Metaphase I

Fig. 12 n = 11

Camera lucida
drawings
x 1000

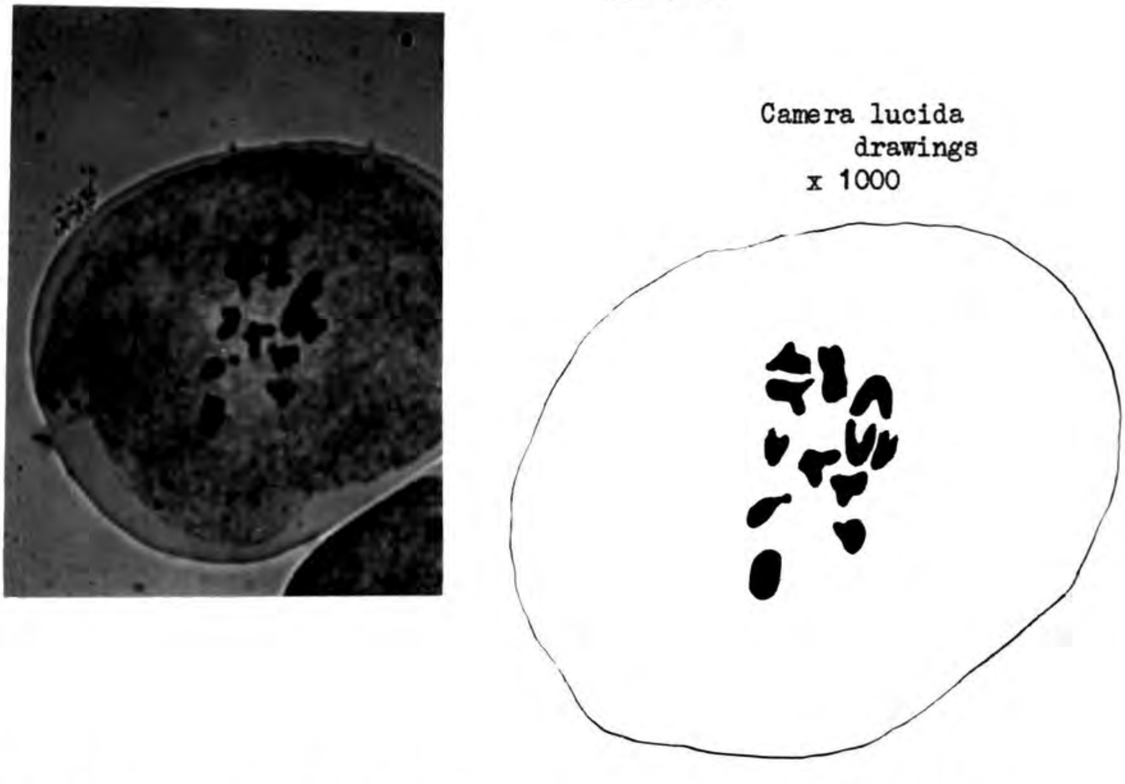


Fig. 13

POPULATION 485 Dicranum bonjeanii.

exception of the polyploid sector in 357. One tetraploid population is recorded by Anderson and Crum from Banff National Park. The tetraploid is recorded as being indistinguishable from the diploid plant in most characters; the SMC were however smaller than those of the diploids.

The possibility exists that American and European plants have different haploid numbers and on this account would probably be reproductively isolated.

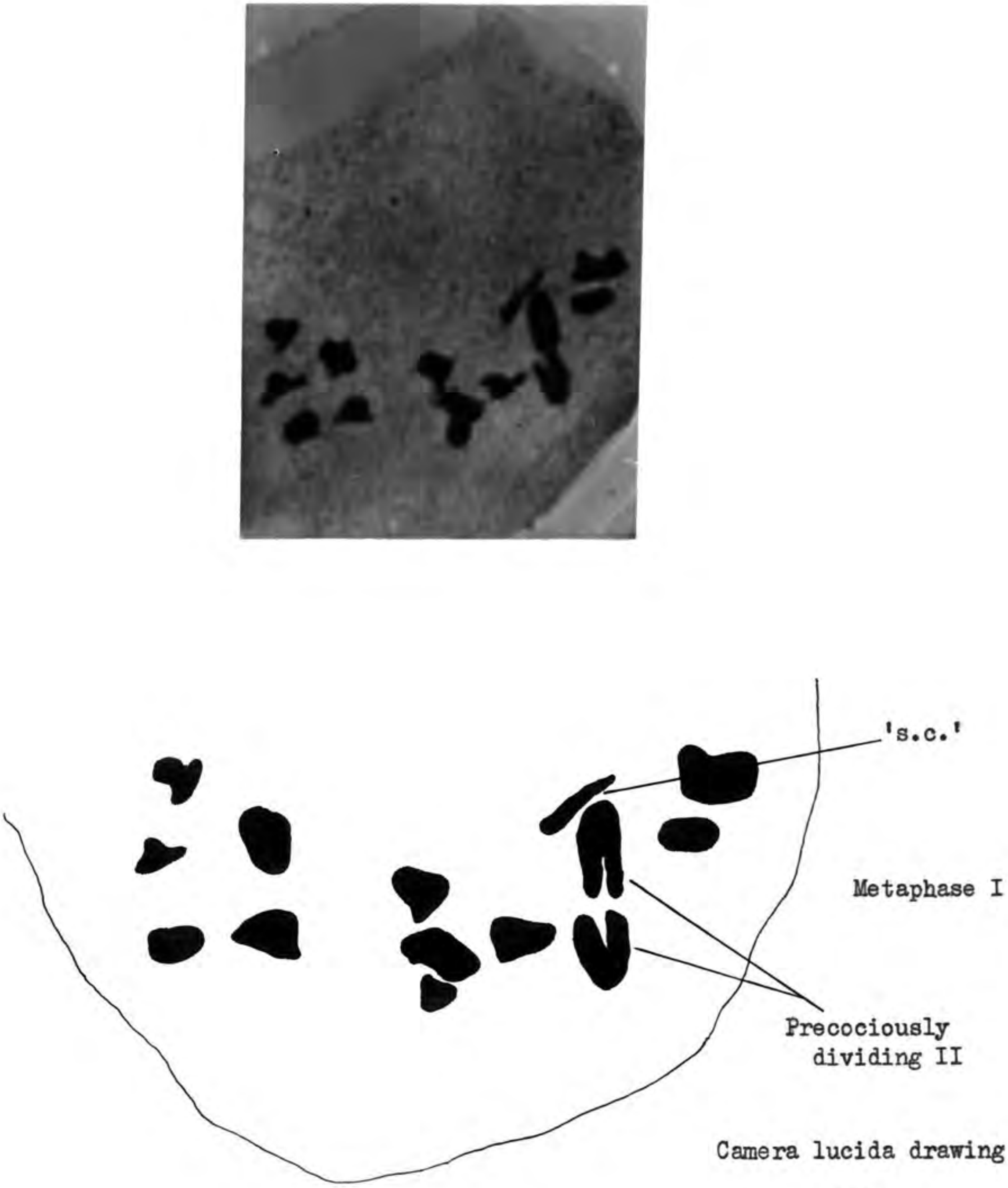
The existence of chromosomal variation in this widespread and variable species is perhaps not unexpected.

D. bonjeanii.

One fruiting population has been studied, and appears to have n = 11. This species is very rare in fruit and this is the first attempt to count its chromosomes. Fig. 12 clearly shows 12 stained bodies of similar size but as fig. 13 indicates there is a large bivalent in the chromosome complement. This is represented in both plates as a precociously dividing bivalent. A cytological feature of interest in this species, is the presence of a satellite see fig. 13.

D. majus.

The interpretation placed on the meiotic plates of this species is that the haploid number is 12, with the addition of a small chromosome in 364, 371, and 290. The small chromosome was not found in 400, a fragment type body was found. See figs. 14, 15, 16, 17 and 18.



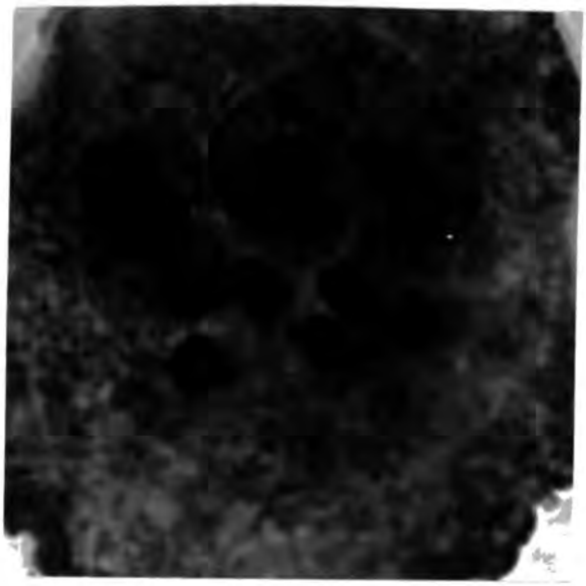
Camera lucida drawing

x 2000

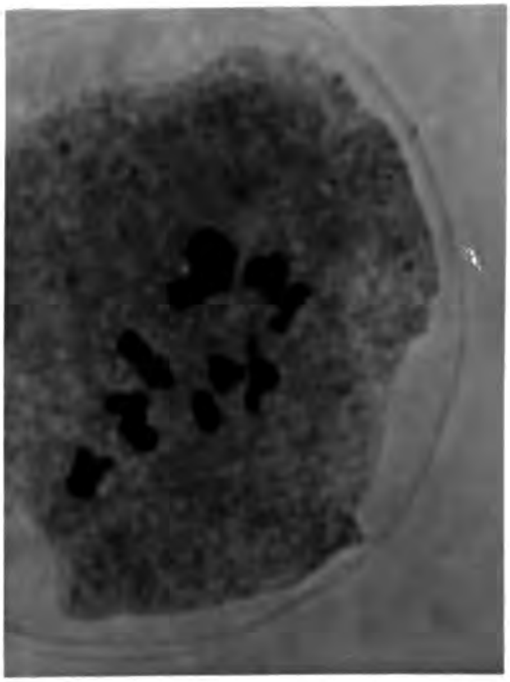
POPULATION 364 Dicranum majus.

Fig. 14

Fig. 15



Camera lucida drawings
x 2000



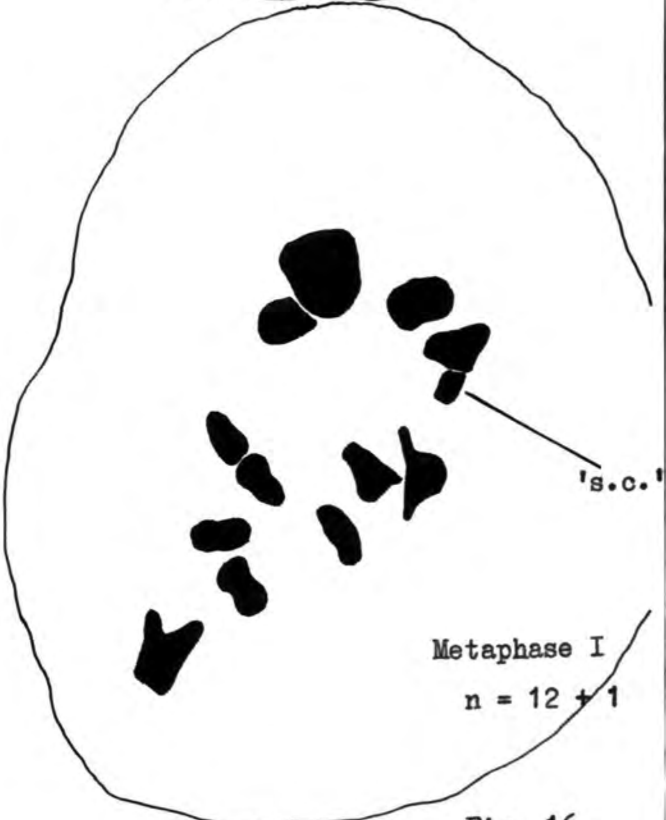
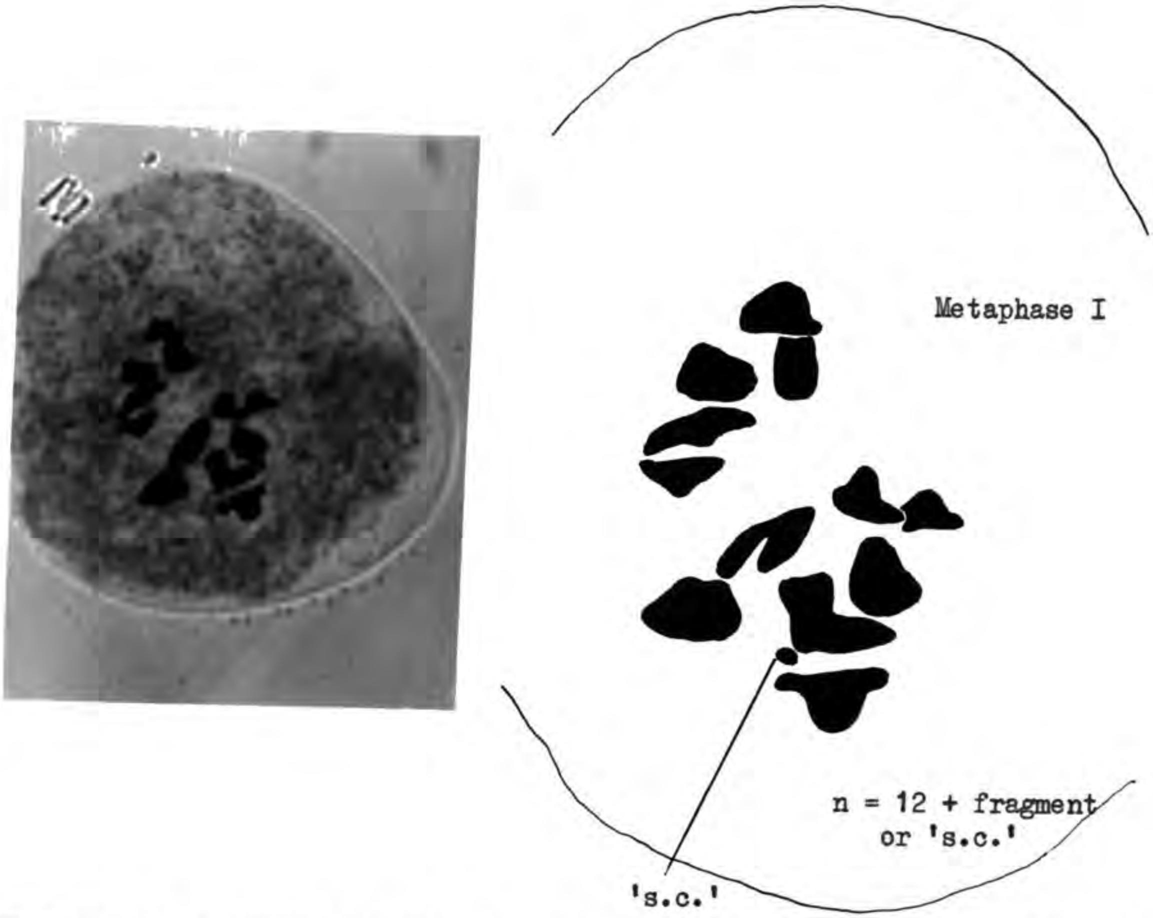


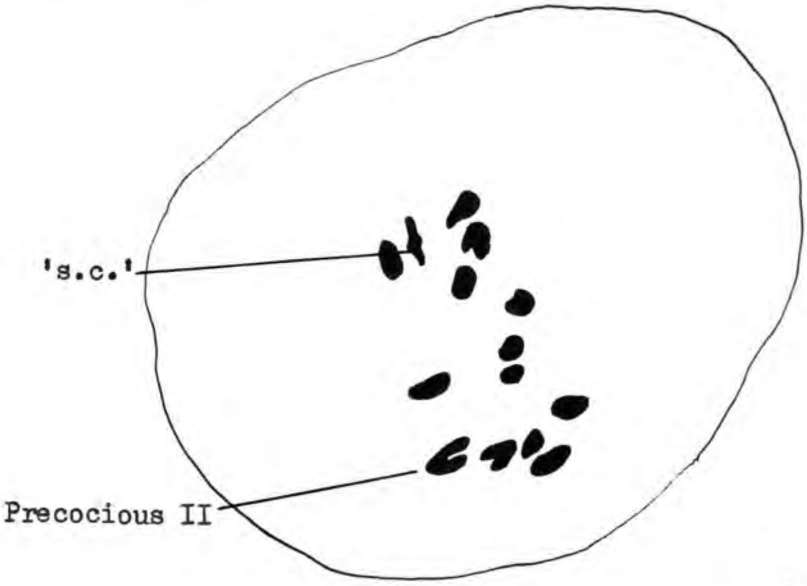
Fig. 16

POPULATION 290 Dicranum majus.

Both S.M.C. from one capsule.



POPULATION 400 Dicranum majus. Camera lucida x 2000 Fig. 17



Metaphase I

n = 12 + 1

Camera lucida x 1000

POPULATION 371

Fig. 18

Examining all the plates presented, it can be seen that there is always a large bivalent in the chromosome complement of this species and as shown in 371 and 364 it is often found precociously dividing. Figs. 14, and 18.

The various other counts of D. majus, recorded above, also show n = 12, with the exception of Yano (1951) who reports n = 11. Yano's results were obtained from gametophytic counts and the possibility exists that small chromosomes would not be detected in somatic cells (see Bryan (1955)) and this may account for some of the variation in numbers reported.

The variation in the small chromosomes within the species is most interesting. This variation is from minute bodies, as in 400, which may be fragments, to the elongated bodies in 364 and 371. Vaarama (1950) has recorded five accessory chromosomes in a population from Finland. They were heterochromatic and conjugated with each other. It is possible that the small chromosomes recorded above are equivalent to Vaarama's isochromosomes.

D. scoparium.

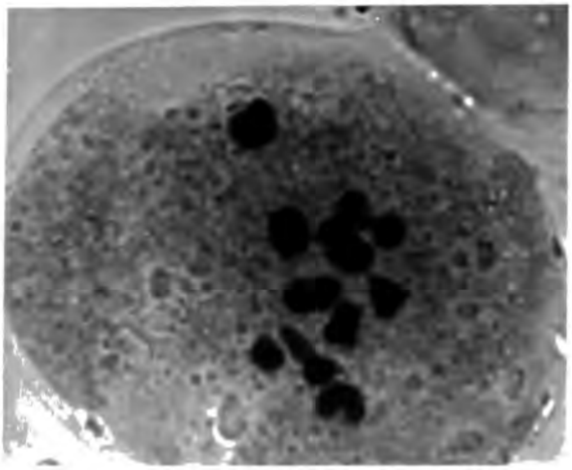
There is the possibility of intraspecific variation in chromosome number in this species. Four populations have been counted with n = 12, 294, 486, 361 and 445. The 12 bivalents are clearly shown in 294, fig. 19, with a large bivalent, found in all the populations studied. Population 481 appears to have 12 + 1 sc, see figs. 20 and 21. No small chromosomes have been recorded before in D. scoparium.

D. scoparium cont.

Population 361 was very interesting in that some of the capsules had SMCs which appeared to have n = 10. Two such cells are illustrated in fig. 22 and fig. 23. Other plates from other capsules show distinctly the 12 bivalents, figs. 24, 25 and 26. One explanation of the lower number is the association of some of the bivalents into multivalent groups or the association may be due to the sticky nature of the chromosomes. Heitz (1928) records D. scoparium as having n = 10-12 and the possibility arises that 10 may be a valid number. In this case variation within populations would have to be explained.

Population 486 was carefully investigated cytologically as two distinct types of tuft were found. One type had dwarf males only and the other large males. No mixed male types were found, fruiting tufts had either one or the other. It was thought that as the tufts were scattered throughout the woodland community sampled, the chances of 'cross' fertilisation between the two different types of tuft, would be slight and separate collections of capsules were made to see if there was any cytological difference. As is shown in figs. 27 and 28 both had n = 12 and there is no reason to suppose that they are different cytologically.

Two particularly difficult populations are included in this species. Population 228 is probably best interpreted as n = 12 with obscured precocious division of one of the bivalents. The possibility that n = 13 cannot be ruled out especially in fig. 31 where 13 bodies are



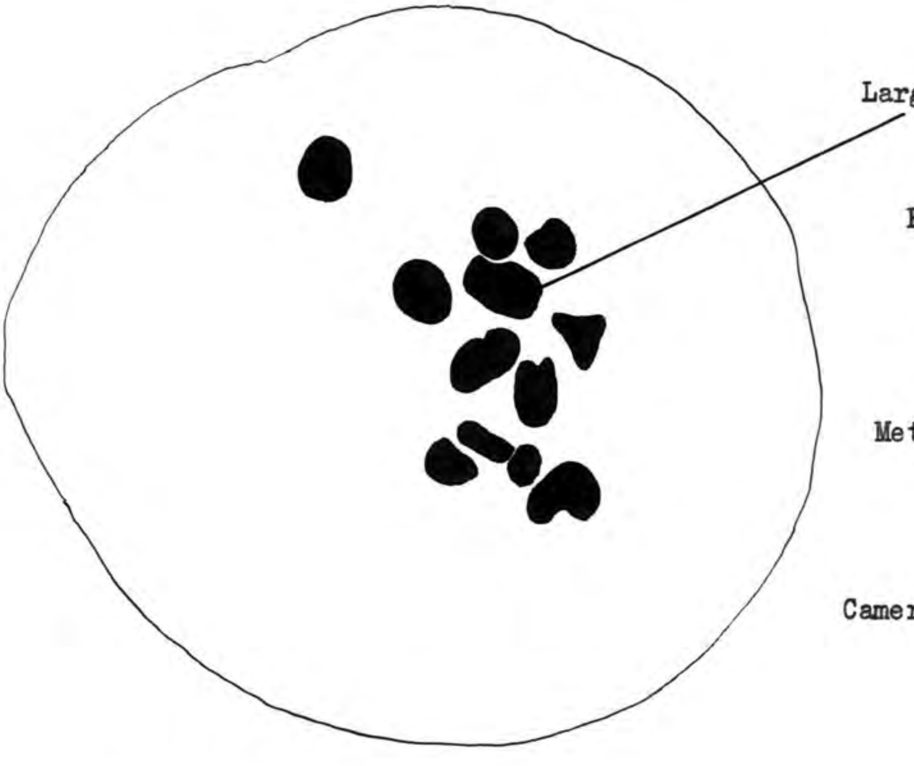


Fig. 19

n = 12

Metaphase I

Camera lucida x 2000

POPULATION 294 Dicranum scoparium.

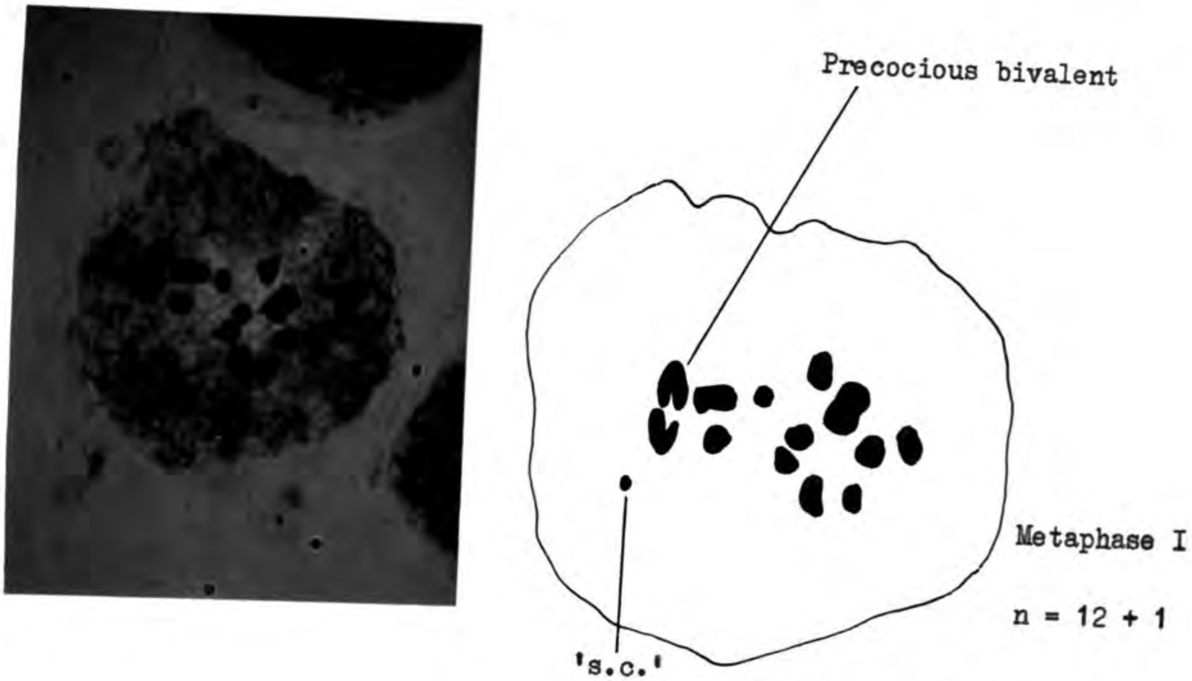
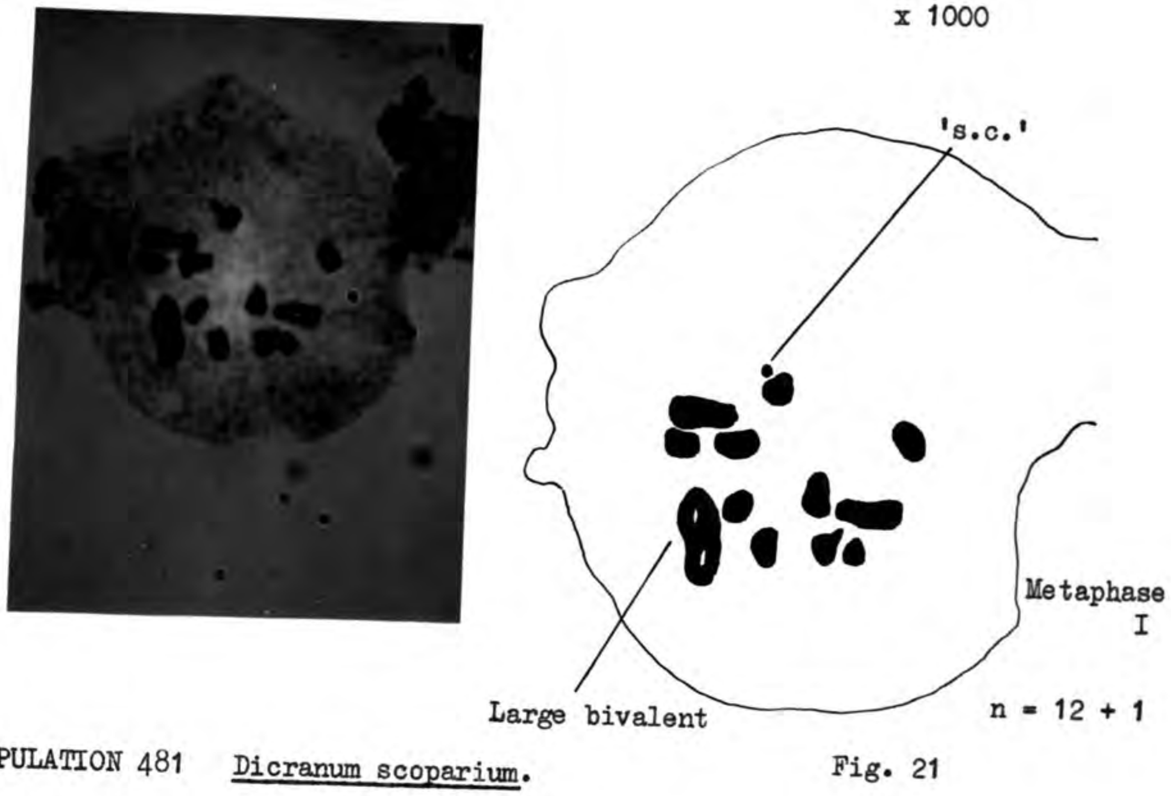


Fig. 20

Camera lucida
drawings

x 1000

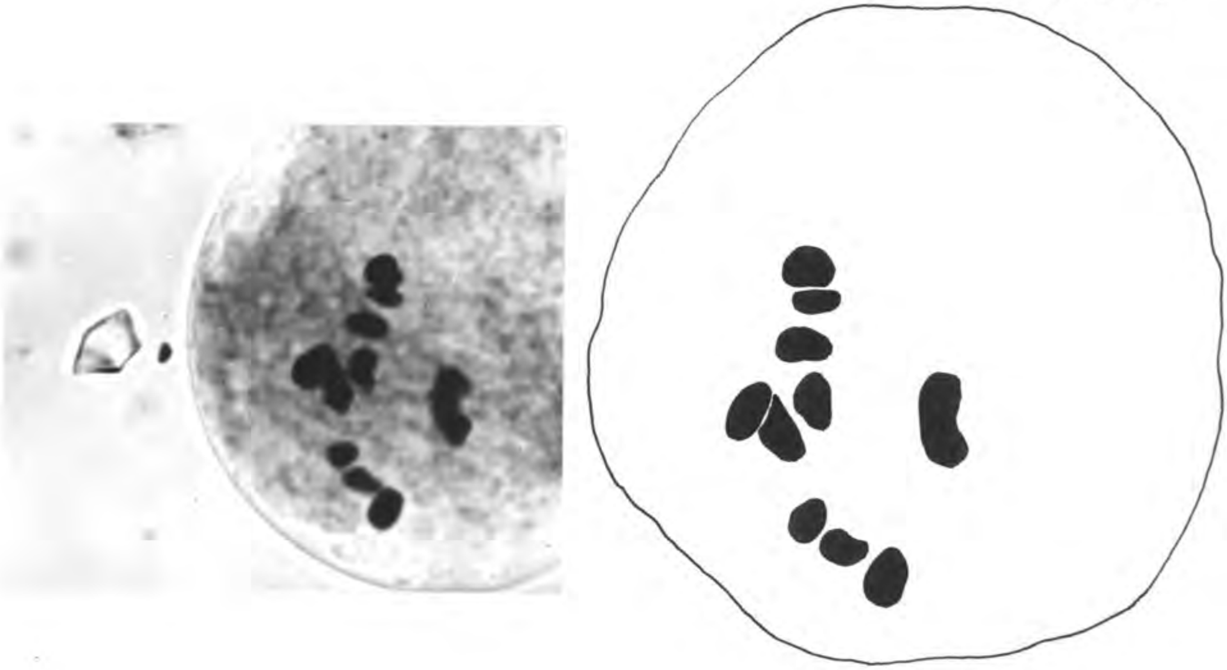


POPULATION 481 Dicranum scoparium.

Fig. 21

Fig. 22

n = 10?



Camera lucida x 1500

Metaphase I

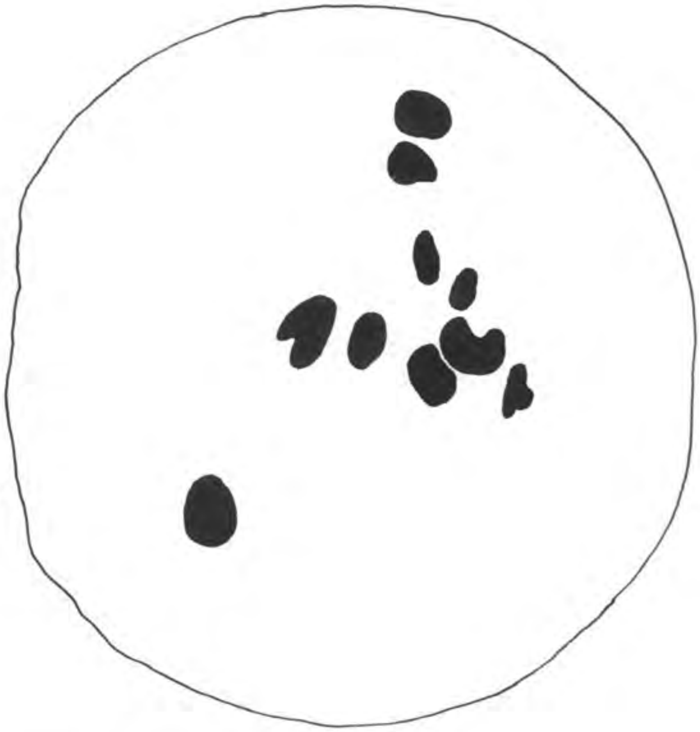


Fig.
23

Camera lucida

x 1500

Metaphase I n = ?10

POPULATION 361 Dicranum scoparium.

Both plates from one capsule.

Camera lucida drawings

x 1000

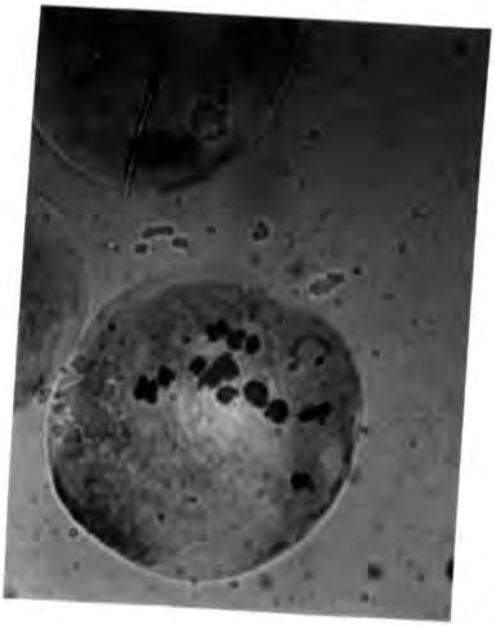


Fig. 24

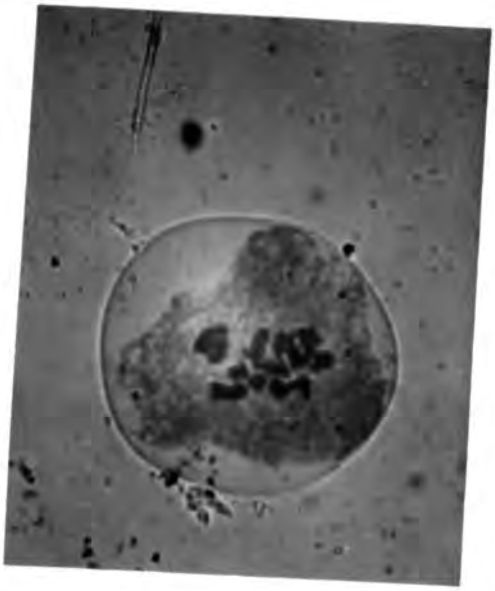


Fig. 25

Metaphase I groups n = 12

From another capsule of 361

POPULATION 361 Dicranum scoparium.

Fig. 26

DWARF MALE TYPE

Metaphase I

n = 12

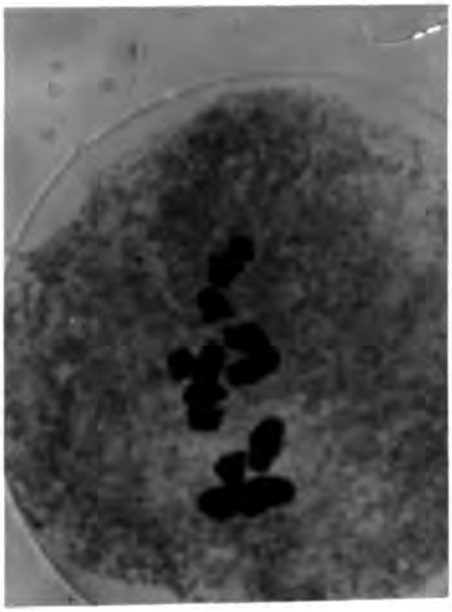
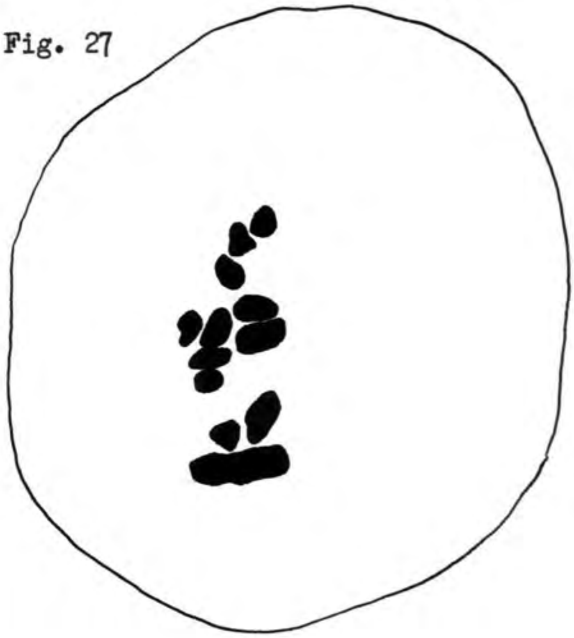


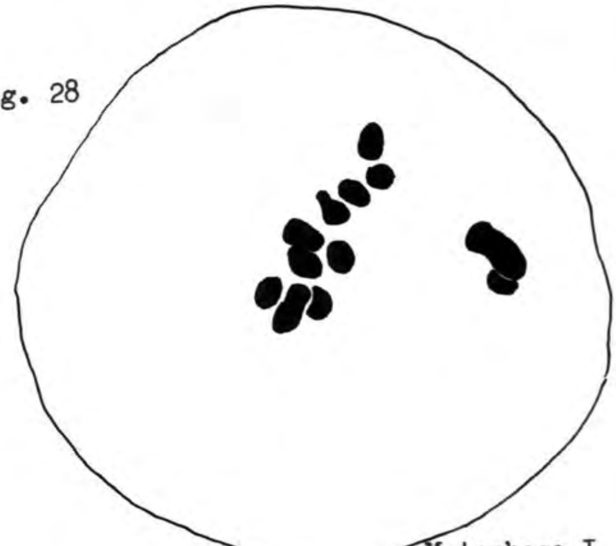
Fig. 27



Camera lucida drawings

x 1000

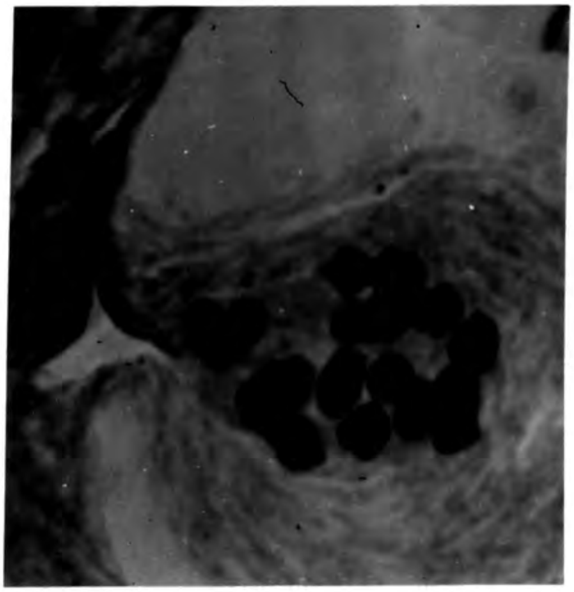
Fig. 28

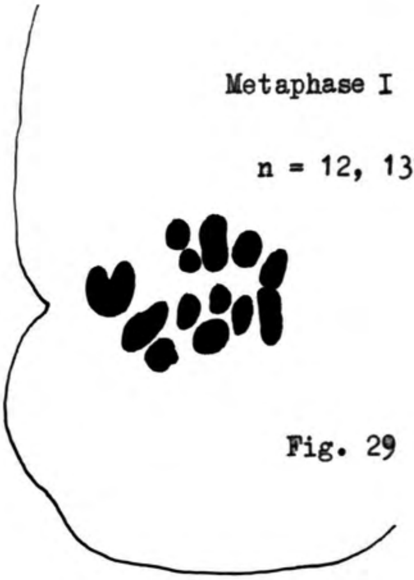


Metaphase I

LARGE MALE TYPE n = 12

POPULATION 486 <u>Dicranum scoparium</u>.





Metaphase I

n = 12, 13?

Fig. 29

Camera lucida x 1000

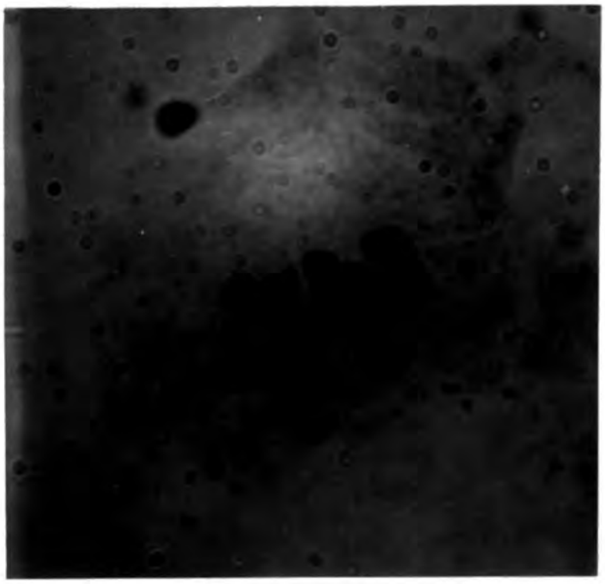


Fig. 30

Metaphase I

n = 12, 13?

POPULATION 228 Dicranum scoparium.

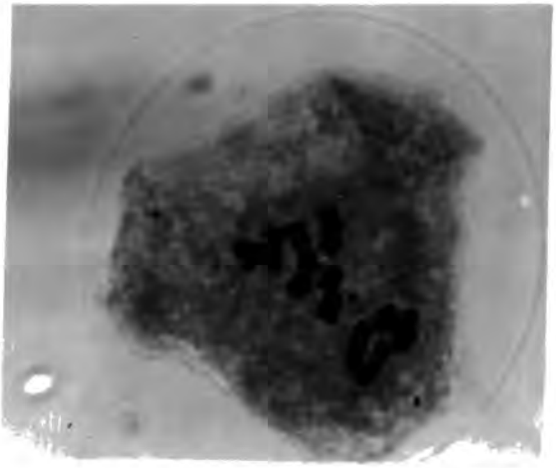
clearly defined. See also figs. 29 and 30. Population 355 offers considerable difficulties in interpretation. Early counts figs. 32 and 33 show 10 distinct bodies. In fig. 32 the best explanation is given in the camera lucida drawing and shows a univalent and two possible quadrivalent associations. Chromosome group + is clearly not a bivalent as four distinct foci of chromosome movement are seen instead of two.

Vaarama (1954) however has described, in Pleurozium schreberi, bivalents with more than two foci of movement, and he uses this information to postulate a theory of centromere evolution in which moss chromosomes appear as more highly evolved than diffuse centromere types and less evolved than in most flowering plants which have a localised centromere. If Vaarama's theory is correct, much care is necessary in interpreting the 355 plates.

Another capsule of 355 has been prepared which can be interpreted as showing 12 bivalents, one precociously divided, fig. 35. Fig. 34 however from the same capsule shows 10 'bivalents'. If n = 12 then multivalents must be involved in the latter plate.

Judgement must be reserved on populations 228 and 355 until more sensitive techniques are developed. Gametophytic counts particularly would be of great value.

Several interesting cytological features have been discovered during these studies. In 361, 355, and 486 lagging chromosomes have been found at anaphase I. In some cases they would probably have been



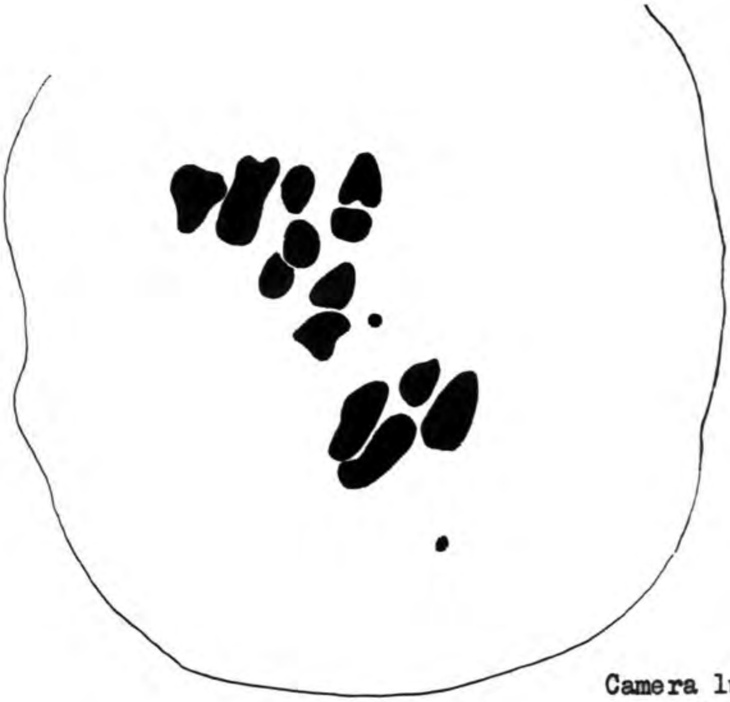


Fig. 31

Metaphase I

n = 12, 13?

+ fragments

Camera lucida
x 2000

POPULATION 228 __Dicranum scoparium.__

Camera lucida drawings x 1000

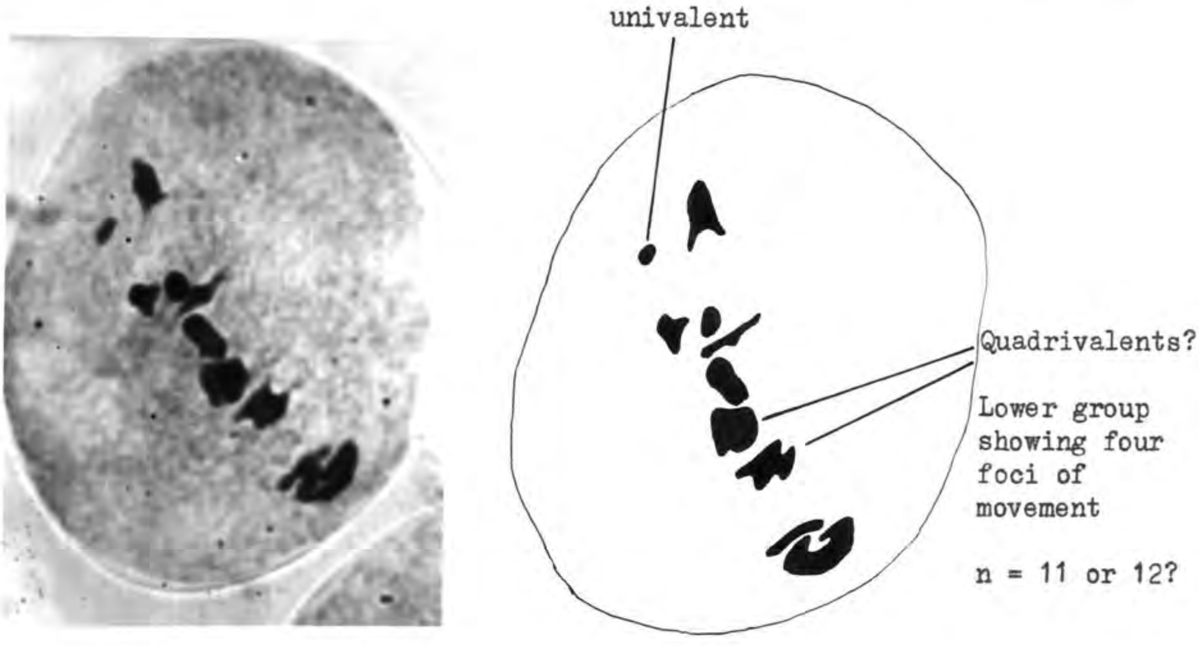


Fig. 32 Metaphase I

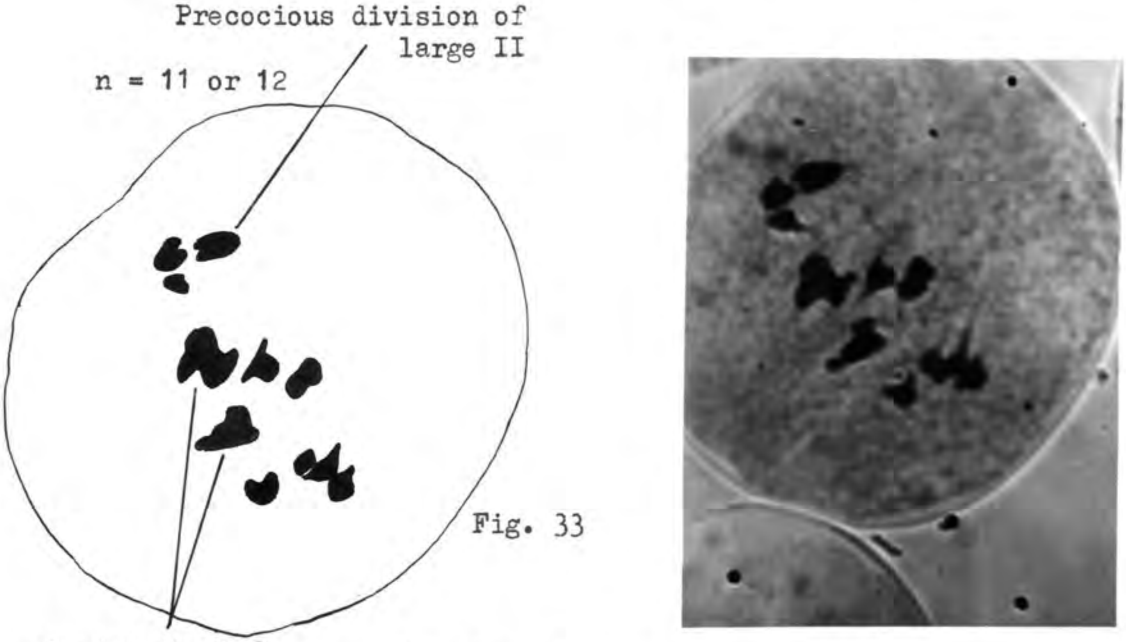
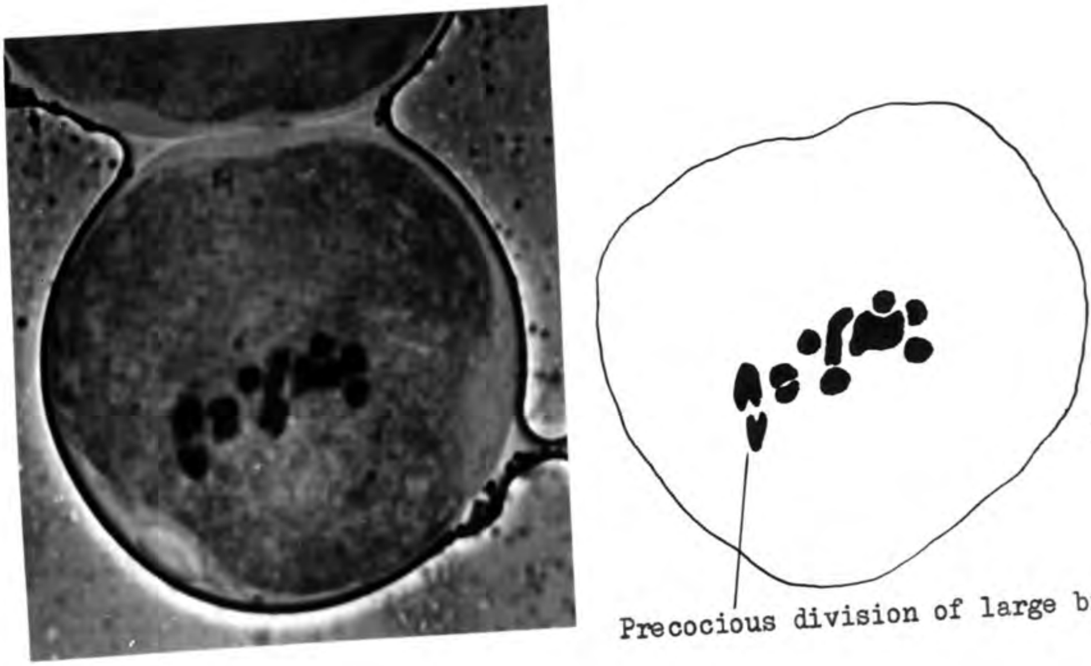


Fig. 33

Metaphase I

POPULATION 355 <u>Dicranum scoparium</u>.



n = 10?

Fig. 34

Precocious division of large bivalent

Camera lucida drawings

x 1000

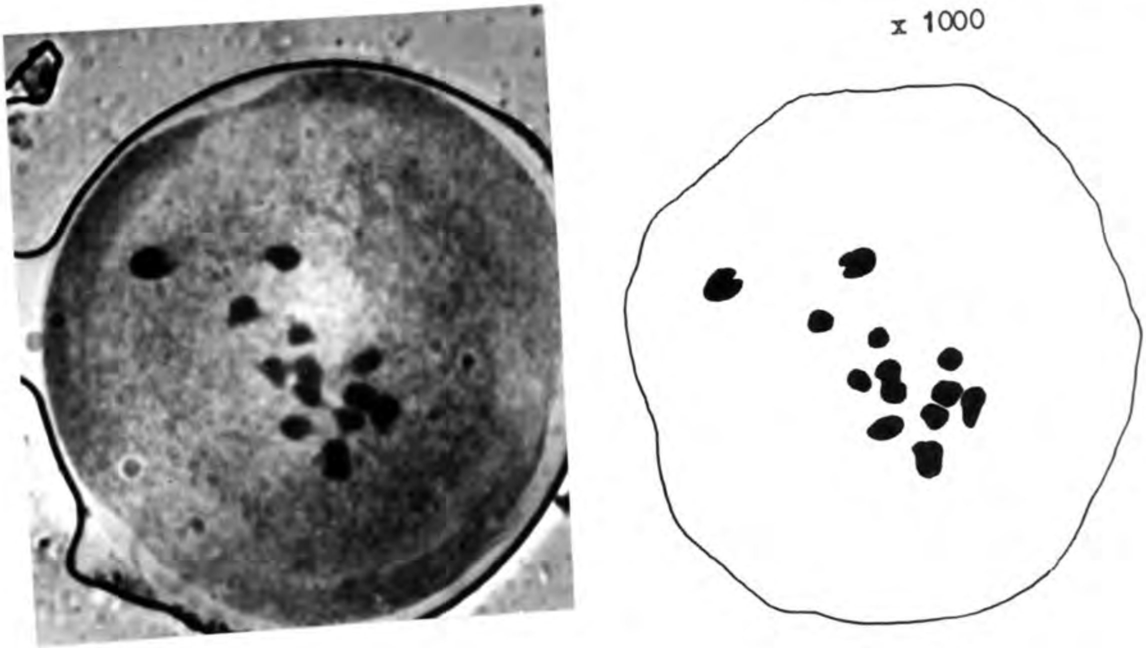


Fig. 35

POPULATION 355 *Dicranum scoparium*.

Metaphase I groups

excluded from the interphase nuclei, giving rise eventually to infertile spores. An anaphase bridge has been discovered in 486. This was probably an inversion bridge as fragments were also seen.

The chromosome counts made during the study are recorded in Table 5. 2.

Examination of the Karyotypes of the four species.

The karyotypes given in fig. 36 are from camera lucida drawings and in all cases there is a wide range of chromosome size within each complement. In all four species there is a large bivalent. It has been suggested Vaarama (1950), that the site of the sex determining genes is probably this large bivalent. He records that the large bivalent in D. majus is slightly asymmetrical. Examination of all the plates recorded in this work has not shown any marked asymmetry. Gametophytic chromosome studies are essential if the process of sex determination is to be understood.

DISCUSSION.

CHROMOSOMAL EVOLUTION IN DICRANUM.

Firstly the origin of the range of numbers in Dicranum will be discussed followed by comments on the variation in chromosome numbers in the Family Dicranaceae.

As can be seen in Tables 5. 1 and 5. 2 a full sequence of numbers from 10-14 is found in the Genus Dicranum. Within the four species investigated the following range has been found; (including my own results).

TABLE 5. 2.

CHROMOSOME COUNTS ON BRITISH DICRANUM MATERIAL.

(plus one count of European *D. scoparium*)

	n.	Locality
D. fuscescens		
332	10	Rocks, Stybarrow Crags, Cumberland.
357	10 + 1 sc.	High Force, Yorkshire.
374	10 + 1 sc.	Dipton Burn, Northumberland.
D. bonjeanii		
485	11	Kirkton of Glenbuchat, Aberdeenshire.
D. majus		
290	12 + 1 sc.	Belstone Cleave, Devon.
364	12 + 1 sc.	Hareshaw Linn, Bellingham, Northumberland.
371	12 + 1 sc.	Dipton Burn, Hexham, Northumberland.
400	12 + fragment.	Ben Suardal, Isle of Skye.
392	12?	Morar, Inverness-shire.
408	12?	Killin, Perthshire.
D. scoparium		
228	13?	Downhead, Somerset.
481	12 + 1 sc.	Sallanches, France.
294	12	Wistmans Wood, Devon.
486	12	Ballater, Aberdeenshire.
361	12	Bellingham, Northumberland.
355	11-12	Warkworth, Northumberland.

D. MAJUS POPN. 408 x 2000

D. FUSCESCENS POPN. 374 x 2000

D. SCOPARIUM POPN. 361 x 1000

D. BONJEANII POPN. 485 x 1000

X LARGE BIVALENT

SELECTED KARYOTYPES

Fig. 36

D. fuscescens	10.	10 + 1.	12.	24.	
D. bonjeanii	11.				
D. scoparium	10–12.	11.	12.	12 + 1.	13?
D. majus	11.	12.	12 + 1.	12 + 2.	12 + 5.

It can be seen that polyploidy is found only in *D. fuscescens*. All the other results fit into an aneuploid series. It is interesting to note that no point in the aneuploid series is monopolised by any one species. The close relationship of the four species from a taxonomic point of view is thus underlined by the cytological results. The intraspecific variation is also better understood when one finds that the gross chromosome number may vary within a species and that 'small' chromosomes and fragments may be present or absent.

One possible origin of the aneuploid series involves the breakage of chromosomes. As has been recorded above fragment-like bodies have been discovered in *D. scoparium*, *D. majus* and *D. fuscescens*. These vary in size from the tiny fragments in population 228 to the multiple associations described by Vaarama (1950) in *D. majus*. The process postulated as giving rise to new polyploid levels requires interchange of chromosome segments. The theoretical principles of the process were formulated by Darlington (1937) and recorded in Stebbins (1950).

Two non-homologous chromosomes with centromeres near the ends of the chromosomes exchange segments, resulting in a large chromosome with a median centromere, and a very small chromosome. A homozygous individual for this interchange would have a very large bivalent and a small one. If both pass to the same pole in meiosis, gametes will be produced without the small fragment like bivalent. Darlington postulated that if the small bivalent was of genetically inert material, gametes lacking it would perhaps be viable and if two such gametes fused a true-breeding strain, with a reduced basic number, would be obtained. An increase in the basic number is also possible by the same mechanism. If the small chromosomes are genetically active then gametes without them would be inviable and reduction in the basic number, as above, would be impossible. But individuals with increased number due to the presence of several small chromosomes would be possible and modification of these could occur by further unequal translocations, and by mutations.

This process may have operated in Dicranum where fragments are often found. It is however complicated by the fact that all the species are dioecious and that both males and females, of the new basic number, would have to be produced, unless cross breeding is possible between plants of different basic numbers. No information is available on intraspecific breeding patterns, and experiments in which species crosses were attempted were unsuccessful (see below, page 184).

The theory of Darlington presupposes the principle of Nevashin (1932) that centromeres cannot be formed de novo but the work of Vaarama (1954) in mosses, working with Pleurozium schreberi, suggests an interesting alternative theory. Vaarama has suggested that there might be a less evolved centromere system in mosses, as he has found bivalents with more than two foci of chromosome movement. If these studies also apply to Dicranum chromosome numerical change may be a less complicated process. Breakage could give rise to a wide range of chromosome numbers containing exactly the equivalent genetic material. This theory gains support if the problematical chromosomes of 355, are shown to be bivalents with more than two foci of movement rather than multivalent associations.

Much more work is essential before answers to these questions can be given, especially in deciding the base number from which the aneuploid series began.

CHROMOSOMAL VARIATION IN THE FAMILY DICRANACEAE.

Crum and Anderson (1958) have collected together all the information on the chromosome numbers in this group and the range is most revealing. Additional information, from my own work, is given in Table 5. 3. Anderson and Crum (1958) note that there is not a strong similarity in number amongst genera of the same subfamily, but taking the numbers as a whole, most fall within the range of 10-16, forming an aneuploid series. A few polyploids are known e.g. in Bruchia and Dicranum.

It seems highly likely that the system postulated for chromosome numerical change in the genus Dicranum may have been involved throughout the whole family Dicranaceae.

TABLE 5. 3.

CHROMOSOMAL VARIATION IN THE FAMILY DICRANACEAE.

A. SUBFAMILY TREMATODONTOIDEAE		
	Bruchia	n = 14. 15. 28.
	Trematodon	n = 28.
B. SUBFAMILY ANISOTHECIOIDEAE		
	Anisothecium	n = 14. 15.
C. SUBFAMILY CAMPYLOPODIOIDEAE		
	Dicranella	n = 13. 15.
D. SUBFAMILY PARALEUCOBRYOIDEAE		
	Paraleucobryum	n = 12.
E. SUBFAMILY RHABDOWEISIOIDEAE		
	Amphidium	n = 16.
	Rhabdoweisia	n = c. 12.
F. SUBFAMILY DICRANOIDEAE		
	Cynodontium	n = 14. 15.
	Dicranoweisia	n = 11.
	Oncophorus	n = 14.
	Dicranum	n = 10. 10 + 1. 11. 12. 12 + 1. 12 + 2. 12 + 5. 13? 14. 24.

CONCLUSION.

Taking all the results recorded, both in the literature and in the present study, it has been shown that the four species are not at different numerical levels in the aneuploid series. In fact species with more than one count available the diploid number is often found to vary. The counts of n = 11 from Japan and the counts of 12 from Europe for the same species should be noted, as indicating a regional variation in haploid number. Knowledge of the chromosome number of any population of the four species under study, would not lead to certain identification of the species. Neither would details of chromosome morphology, as it has been found that the karyotypes are closely alike especially in having a large bivalent.

Studies of the cytology of the four species have shown variation in small types of chromosomes within species and this, together with differences in haploid number, could easily account for the wide morphological range of types described above. An attempt to see how the chromosome variation is linked to the morphology will be made in the final discussion.

Much more work is essential to a study of this difficult group. Gametophytic counts are essential to check the SMC data. Modified fixing and staining techniques could also give valuable information; this especially applies to meiotic plates.

CHAPTER VI.

REPRODUCTIVE BIOLOGY OF THE DICRANUM SPECIES.

INTRODUCTION.

There is a lack of information on the general biology of mosses. Records of dates and details of the most obvious stages in the lifecycle are not mentioned in the literature. A preoccupation amongst active bryologists with uncommon and rare mosses, and with problems of distribution, probably accounts for the paucity of information on the common species. The following account of the four species of *Dicranum* is largely from my own observations. It will take the form of a lifecycle.

1. ADULT SPOROPHYTE.

(a) Date of meiosis.

Table 6. 1 gives the dates at which meiosis was taking place in the various populations I have studied cytologically. It can be seen from the data that within a species there is variation in the date of meiosis, for different localities, in the same year. Material from the South and West of Britain undergoes meiosis much earlier than Northern and Scottish specimens. This is very clear for the *D. scoparium* data. Another interesting feature of the results is the difference in meiotic dates for the four species. *D. fuscescens* is definitely the first species to undergo meiosis in a given locality, as shown by observations at Dipton Burn, Northumberland, 16-6-60:-

TABLE 6. 1.

DATE OF MEIOSIS.

SPECIES	POPN. NO.	1959	1960	1961	LOCALITY
D. scoparium					
	228	3-6	25-6	-	Somerset.
	294	3-6	-	-	Devon.
	355	8-7	24-6	-	Northumberland.
	361,2,3	6-7	-	23-6	"
	368,9,70	12-7	-	-	"
	391	29-7	-	-	W. Coast Scotland.
	401	5-8	-	-	Isle of Skye.
	402	9-8	-	-	Perthshire.
	445	-	1-6	-	Merionethshire.
	481	-	15-6	-	Switzerland.
	486	-	10-7	-	Aberdeenshire.
D. majus					
	290	4-6	-	-	Devon.
	358	3-7	-	-	N. Yorkshire.
	364	6-7	-	-	Northumberland.
	371	12-7	30-6	-	"
	392	29-7	-	-	W. Coast of Scotland.
	400	5-8	-	-	Isle of Skye.
	408	11-8	-	-	Perthshire.
D. fuscescens					
	332	-	-	9-4	Cumberland.
	357	2-7	-	14-5	N. Yorks.
	374	12-7	-	-	Northumberland.
D. bonjeanii					
	485	-	16-7	-	Aberdeenshire.

TABLE 6. 2.

TIME OF FRUITING

SPECIES	AUTHORITY			
	Braithwaite	Rabenhorst	Grout	Dixon
D. scoparium	7-8	Early year to summer.	Late summer to autumn.	Late summer.
D. majus	7-8	Midsummer.	-	Late summer.
D. fuscescens	8	Midsummer.	Autumn.	Autumn.
D. bonjeanii	7-8	Midsummer.	-	Late summer.

BRAITHWAITE (1887), RABENHORST (1890), GROUT (1928), DIXON (1954).

D. fuscescens, plants on ground-capsule apices fully pigmented and so judged post meiotic. A few capsules on trees and rocks, in drier habitats, premeiotic.

D. scoparium and D. majus premeiotic.

The observations that meiosis is later in the drier habitats has been made in many populations. The humidity factor may apply over small distances; often the capsules at the margins of a tuft are later in meiosis than the centre ones.

In Table 6. 1 the 1959 records for D. fuscescens do not appear to be different from the other species but in the populations sampled almost all the capsules were post-meiotic, while in D. scoparium and D. majus most were premeiotic. The more 'characteristic' position of meiosis is shown in the 1961 records for D. fuscescens. Here the meiosis is clearly earlier than in 361, D. scoparium.

(b) Time of capsule maturity.

In Table 6. 2 the dates for fruiting given in four well known bryological works are tabulated. The details almost certainly refer to dates when fully mature capsules can be found and bear no relation to the time of first maturity. Some of the variation, between Grout (N. American observations), and Rabenhorst (European), may be due to real differences in the developmental time sequences in different geographical areas. Comparison of Braithwaite's figures with those in Table 6. 1 show that they approximate to the time of meiosis.

One serious inaccuracy in the Table concerns D. fuscescens. It would appear that the capsules mature later than in the other three species. This was not the case in my experience. Meiosis takes place in D. fuscescens before capsule enlargement in the other species. Capsules with mature spores are found in the autumn but they can also be found earlier in the year. One explanation for this inaccurate information is that the authors are comparing material from different altitudes or latitudes. It is essential to compare specimens from the same area if possible.

(c) Dispersal of the spores.

Part of the difficulty of recording data on fruiting arises because the capsules remain closed for a considerable period after spore formation. In the populations I have studied the calyptra has often remained in position for several months; e.g. in dune D. scoparium, 355, some capsules were still not open on 29-3-60, circa 8 months after meiosis. In woodland populations of D. scoparium the capsules may be closed even longer. At Bellingham there were sheltered areas with Dicranum scoparium, the capsules of which had their calyptrae intact circa 9 months after meiosis.

It is an interesting feature that capsules in exposed situations, which are often the last to undergo meiosis, are often the first to open and disperse their spores.

Experiments in the laboratory have pointed to the fact that the peristome mechanism in Dicranum may be relatively insensitive to changes in atmospheric humidity. Peristomes of intact capsules, opened by drying the air near them with a hot needle, did not close when air saturated with water vapour was blown over them. If however liquid water was placed at the mouth of the capsule, closure took place. Similar observations have been made by Tallis (1957) for Rhacomitrium lanuginosum. This insensitivity of the peristome is probably important ecologically; it may confer selective advantage in very humid habitats.

(d) Mortality of capsules.

Details are given in Table 6. 3 of the mortality of D. majus and D. scoparium capsules in part of a wood at Bellingham, Northumberland. The high number of abortive capsules in D. majus is most interesting. It is not at all clear why there should be such wastage. As other parts of the wood did not show such a large figure, it is suggested that it is probably correlated with environmental factors in the area sampled. The large number of setae with no capsules is also interesting in D. majus 371, and D. scoparium 363. The capsules may be taken by birds but no observations have been made which would help to elucidate the problem.

2. SPORES.

(a) Percentage infertility of spores, as tested by germination.

The results given in Table 6. 4 were obtained by growing the spores on Knop's agar, in a petri dish. (The techniques used will be given below). Each population was represented by 5 capsules and a drop of spores from each capsule was placed on the agar. Extreme care was taken to prevent mixing of the spores from different capsules. Separate counts of fertility were made on each drop.

TABLE 6. 3.

CAPSULE MORTALITY

DATA FROM HARESHAW LINN, BELLINGHAM, NORTHUMBERLAND. 9-1-60.

SPECIES	POPN. NO.	ABORTIVE CAPSULES	CAPSULE LESS SETAE	NORMALS	TOTAL
D. MAJUS	371	80	93	184	357
D. SCOPARIUM					
ROCKS	361	2	10	110	122
TREES	362	-	3	33	36
GROUND	360	2	5	49	56
DEAD WOOD	363	-	13	14	27

It is very clear that a wide range of infertility is shown in populations of all four species. One possible explanation was that germination was occurring over a protracted period. It was found by examining the cultures regularly that germination of the spores was by no means simultaneous, but that it was clearly apparent, at an early stage, which would germinate. Infertile spores had no green contents and were often irregularly shaped, in contrast to the dark green regularly shaped fertile spores. All the green spores did eventually produce protonema.

Another possible cause of infertility could have been immaturity of the capsules, but as they were collected in November from pots kept in a cold frame, this objection can be discarded.

From Chapter V, on the cytology of *Dicranum* species, it will be clear that even though a few cytological irregularities were found, the number of these would be very small in total and could not be responsible for the huge percentage infertility counts on the spores.

The most reasonable explanation of the results seems to be that in maturation and retention within the capsule, loss of fertility may result from environmental factors. If this is so, it is very interesting that a plant with such a resistant gametophyte, should be so sensitive to environmental influences during its spore phase.
The figures for infertility of the spores represent yet another example of variation within populations.

TABLE 6. 4.

PERCENTAGE INFERTILITY OF SPORES

(COUNT OF 200$^+$ SPORES GERMINATED ON KNOPS AGAR).

	CAPSULE NO.				
D. scoparium	1	2	3	4	5
228	3.0	12	18.6	28	34
355	22	35	57	40	30
362	73	4	7	28	15
361	44	8	13	5	42
370	14	11	36	99	11
450	47	37	29	41	32
451	18	15	6	16	4
486 D♂	17	15	5	18	6
486 L♂	18	10	99	48	14
D. majus					
364 (4 capsules)	4	12	10	18	
371	5	62	28	9	10
D. fuscescens					
357	18	31	99		
374	26	20	22	28	
D. bonjeanii					
485	4	11	14	7	5

The fertility of moss spores has received very little attention from bryologists and only a few records can be found in the literature. Dening (1935) records infertility in a few species, including D. scoparium:

Funaria hygrometrica c 5%, Bryum caespiticium very small number, Mnium hornum numerous, Diphyscium foliosum very few, Buxbaumia aphylla very few, Pogonatum aloides c 6%, Dicranum scoparium many dead spores.

Tallis (1957) records that 25-40% of the spores of Rhacomitrium lanuginosum are abortive.

(b) Size of spores.

The Dicranum species under study are recorded as dioecious and there is usually a size difference between the male and female plants. It was considered that this difference might be reflected in spore dimensions. No pronounced differences were detected by ordinary microscope examination and no measurements were made. Dening's work (1935) was later disovered in which Dicranum scoparium spores measurements were recorded. c.400 spores were measured and produced a histogram with only one peak. He concluded that heterospory was not shown by D. scoparium. A bimodal curve has been found in some dioecious species. It is recorded by Ernst-Schwartzenbach (1942) in Macromitrium salakanum and several Schlotheimia species. Macromitrium has dwarf males as in D. scoparium and D. majus.

3. PROTONEMAL STAGES.

The filaments produced from spores are known as primary protonema in contrast to the secondary protonema produced by regeneration from parts of the gametophyte. Secondary protonema will be discussed in section (e).

(a) Methods.

The observations on protonemal growth were made on cultures growing on Knop's agar, in petri dishes and tubes. The Knop's formula used was as follows:-

.25 gm $MgSO_4.7H_2O$; 1 gm $Ca(NO_3)_2$; .25 gm KH_2PO_4; 5 drops 1% $FeCl_3$ soln.; and 20 gm agar per litre aqua dist. Sterilisation was in bulk, at 15 lb/sq. ins. for 15 minutes. Dishes and tubes were heated in an oven for 2 hours at 160°C. Pouring of plates and tubes was carried out in the most sterile conditions.

Capsules for experiments were surface sterilised with dilute calcium hypochlorite solution or bromine water for 2-10 minutes and then washed in sterile water. After crushing the capsules into sterile water in tubes, the spores were centrifuged until concentrated at the bottom of the tube. Pipetting of the spores on to the agar surface was then carried out using alcohol cleaned tubes. Cultures involving the spores of one capsule were easily handled by these methods. Unopened, undamaged capsules were always used in culture work. The risk of cross contamination between different capsules was thus much reduced.

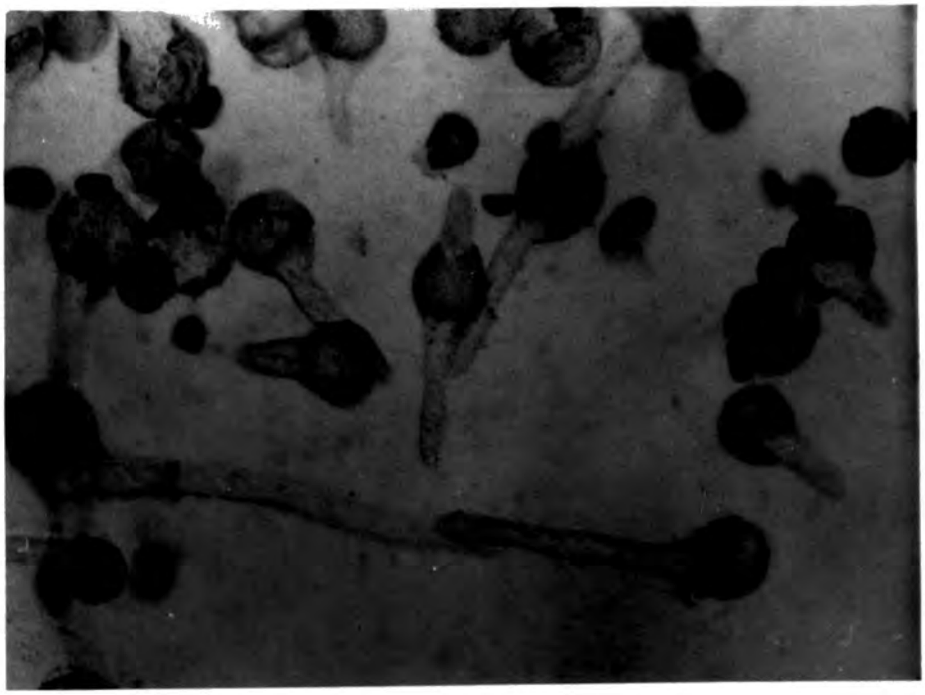


Fig.37 Spore germination in D.scoparium (popn.300).

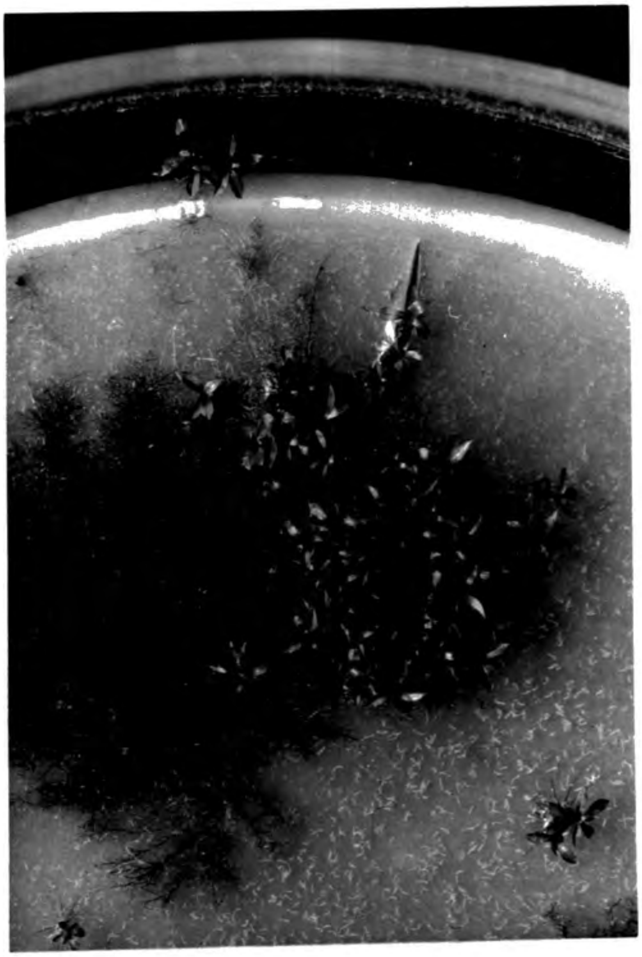


Fig. 38 Protonemata, D.scoparium(popn.402) and Funaria hygrometrica.

Some observations were made with material grown in Knop's solution, and the same basic formula (as for plates) was used, omitting the agar.

Cultures from gametophytic parts of the plants were started with well washed material. Some difficulty was found with algae and nematodes.

(b) Germination of the spore.

The course of germination and the growth of protonema and buds, throughout one experiment, are recorded in Table 6. 5.

Immediately prior to germination the spores are swollen and dark green, in marked contrast to the brown infertile spores often found in the same capsule. In most cases one filament only is produced on germination; occasionally two can be found, the second appearing closely after the first, (fig. 37). All filaments at this stage are richly chlorophyllous, with transverse walls. It is interesting to compare this with the observations of Case & Meyer (1950) on Physcomitrium turbinatum, where 5 types of germination pattern were described. Two types of filament were found;

rhizoid - ± colourless filament, negatively phototropic, slender.

chloromena - broad, richly chlorophyllous, positively phototropic.

Germination type.

A. Chloronematous filament only produced.

B. Rhizoid and chloronema simultaneously.

C. Rhizoid filament first to appear, followed by chloronema.

D. Chloronema first, later rhizoid.

E. Rhizoid only.

80% of nearly 1000 spores were of type C. germination.

The tropisms were not examined in Dicranum but the morphology of all the filaments produced, at an early stage in germination, were of the chloronema type. No rhizoidal filaments were seen.

All spores did not germinate simultaneously; a small number remained in a swollen dark green condition, after considerable growth of filaments had occurred from other spores.

Dicranum species are dioecious, with male plants smaller than the female. If sex is genetically determined, as a result of meiosis, half the spores should be male and half female. The cultures of spores were carefully examined for segregation. None was observed, in any culture, either in the size of the cells of separate filaments or in growth rate, within the spores of one capsule. This even applied to D. majus, where the size difference of male and female is so marked. Further comments on the determination of sex will follow below.

(c) Further growth of the protonema.

Very similar protonemal stages were produced by all four species; it was found impossible to determine the species of a particular culture with absolute certainty.

Table 6. 5 shows the time intervals involved in the growth of branches on the primary filaments, and the eventual production of buds. It is interesting to note that it takes c. 5 months for small shoots to appear on the protonema. This is in marked contrast to *Funaria hygrometrica*, (Van Andel (1955)), which can produce buds in 2 months from cultures started in November or January, and in only 3 weeks in spring cultures.

The actual structure of the protonema will now be examined in more detail. The continued development of the protonema was carefully followed. The production of the first branches occurred in about 35 days, from young filaments, richly chlorophyllous with transverse cross walls. In older cultures the original filaments became brown-walled lost much of their chlorophyll and commonly had oblique walls. Septa at the tip of these same filaments however were transverse and had much chlorophyll. The character of the older parts of the filament therefore had some of the features of the rhizoid described by Case and Meyer (1950) see above. In this case its development was due to a process of ageing of the chloronema and not to the production of two distinct filament types on germination.

It has been found on examination of the cultures that the protonema is far from being a simple weft of filaments over the surface of the agar. Frequently a luxuriant erect system of protonemal branches was produced and also green filaments penetrated down into the agar. For the most

TABLE 6. 5.

GROWTH OF PROTONEMATA ON AGAR.[1]

	D. scoparium	*D. majus*	*D. fuscescens*	*D. bonjeanii*
(i) Germination first observed	9 days	9 days	9 days	9 days
(ii) First branching	35 days	35 days	c. 40[2]	35
(iii) Walls of young filaments	Transverse	Transverse	Transverse	Transverse
(iv) Walls of older filaments	Oblique	Oblique	Oblique	Oblique
(v) Protracted germination	+	+	+	-
(vi) Spiral growth in protonemal filaments	+	+	+	+
(vii) Buds formed	+[3]	+[3]	+[3]	+[3]

[1] Knop's Agar plates at 17°C.

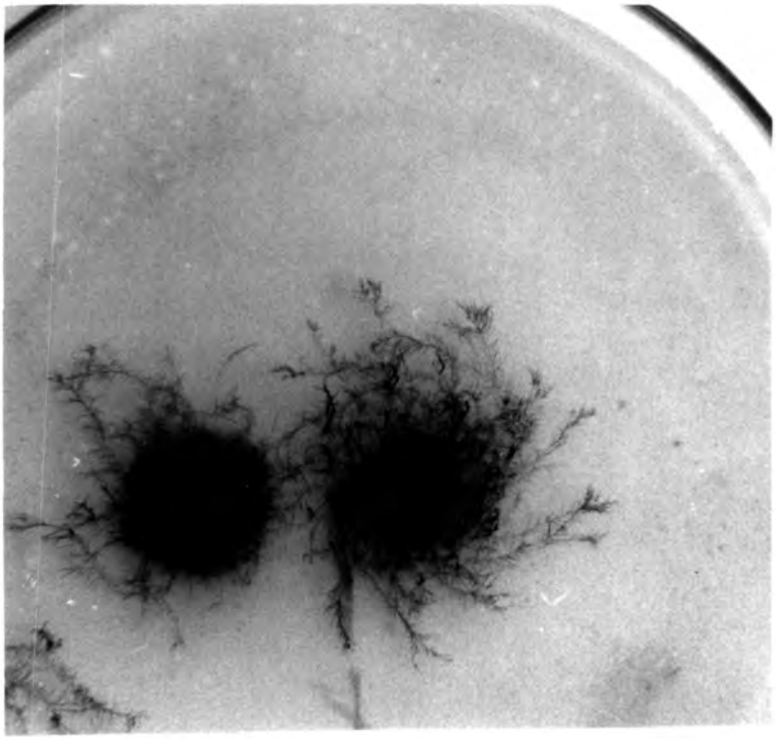
[2] Experiment in progress over Christmas period.

[3] First date of development not noted. Small shoots formed in 5 months.

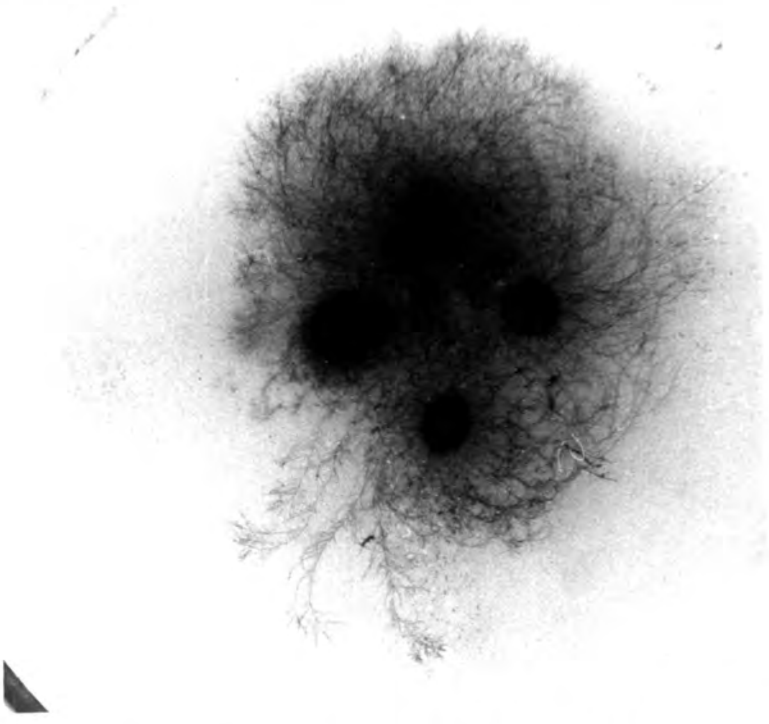
part the brown main filaments, from the first formed chloronema were found on the agar surface. The erect system has been described by Allsopp and Mitra (1956) for several Bryales. Buds were eventually produced at the margin of the protonema and also near the centre of the inoculum. No fairy ring effect was found as occurs in *Tortula muralis* and other species, where bud formation is restricted to a zone of protonema near the advancing front.

Sironval (1947) working with *Funaria hygrometrica* has suggested that protonemal growth is not a continuous process but that an abrupt change is involved from the chloronema to a caulonema stage. The latter is characterised by having more branches and oblique cross-walls. Sironval reports that the chloronema died in his cultures and was replaced by the caulonema, which eventually produced buds. It is doubtful whether these observations indicate the usual course of development. It is possible that his culture conditions were unfavourable in some way and that he was observing abnormal behaviour. Allsopp and Mitra (1956) and Van Andel (1955) have shown that the process can be a continuous one, chloronema and caulonema being growth phases of the same protonema. The results with *Dicranum* bear out the more recent work. No dying of the protonema was seen and the characters of chloronema and caulonema appear in all the protonemal cultures, the characters of the caulonema being found as stated above on the more mature filaments.

Observations of the growth form of the *Dicranum* protonema have shown that the surface filaments do not grow out in a straight line from the point of inoculation but that spiral growth is shown (see below page 175).



a. D.scoparium (369) and D.bonjeanii(485).



b. D.scoparium(369),D.bonjeanii(485),D.fuscescens(374),D.majus(37I).

Fig.39 Interaction of Dicranum protonemata.(Popn. numbers in brackets).

(d) Interaction of protonemata.

A series of agar cultures were set up to investigate the effect of growing different species in juxtaposition. The first series involved established cultures of *Dicranum* protonema and inoculations of the quick growing species *Funaria hygrometrica*. As can be seen in Fig. 38 *Funaria* grows without inhibition. This is an interesting result as Gorton and Eakin (1957) state that in cultures of *Tortella caespitosa* an inhibitor accumulated, which prevented the growth of freshly inoculated spores. It is possible that their culture conditions were responsible for the phenomenon and that inhibition is not the general case; or that the *Dicranum/Funaria* combination does not show the effect.

Another experiment on the effect of growing different protonemata, of several species, on one agar plate, was also started. Spores were used as inocula. (See Fig. 39). The combinations used were those likely to be involved in nature; *D. scoparium*, *fuscescens* and *majus*, and *D. scoparium* and *D. bonjeanii*. Here again the growth of all the species was uninhibited and the protonema of the various species grew freely together.

(e) Secondary protonema.

Secondary protonema is that which is produced from vegetative parts by regeneration. It is well known that various organs can produce protonema. Gemmell (1953) describes the regeneration of detached leaves of *Atrichum undulatum*, De La Rue (1929) the formation of secondary protonema in many American mosses (including *D. scoparium*), from leaves, setae etc., and Ainsworth (1956) the formation of new plants from leafy fragments of *Mnium cuspidatum*. Still further organs recorded as producing protonema under certain circumstances, are calyptrae, paraphyses, antheridia, archegonia, (Wettstein (in De La Rue)).

As *Dicranum* species often occur in habitats where fruiting specimens are not present, it was thought that vegetative reproduction was probably most important in the reproductive biology of the species. Table 6. 6 gives the results of an experiment on the % regeneration of detached leaves placed in distilled water and detached leaves on sterile soil cultures. The percentage regeneration in many cases is very high 87% (424), in others low 2% (422). Gemmell in his work on *Atrichum undulatum* pointed out that the age of the leaves is an important factor in regeneration. Older leaves tend to lose the ability to regenerate. This could probably account for the variation in the figures in Table 6. 6. It is clear that vegetative reproduction must be important in some habitats, especially where clumps of *Dicranum* are likely to be scattered by the wind. A figure of 2% could be highly significant in these species, as there are such large numbers of leaves per tuft.

The regeneration details on soil are interesting. In three species protonema was produced, but not in *D. fuscescens*. It was found that the protonema was not very competitive under the growing conditions employed. *Funaria* and *Leptobryum* were invaders. In several cases detached leaves produced new shoots directly, and this form of regeneration is likely to be important.

TABLE 6. 6.

VEGETATIVE REPRODUCTION IN DICRANUM[1].

	Total no. leaves	% regenerating after 12 weeks[1]	Regeneration on soil after 12 weeks
Dicranum scoparium			
228	82	40	+
355	65	72	
361	68	3	+
369 ♂	84	11	+
422	41	2	-
486 (D♂) ♀ pts	92	4	+
486 (L♂) ♀ pts.	65	40	+
D. majus			
371	104	69	+
424	85	87	
D. fuscescens			
374	114	63	-
381	89	21	
D. bonjeanii			
354	143	2	+
322	99	16	+
485	49	63	+

[1] Submerged in distilled water, frequently shaken. Cultures in lighted window XI-1960 to II-1961.

TABLE 6. 7.

REGENERATION FROM THE SETAE AND CALYPTRAE OF YOUNG SPOROPHYTES OF D. SCOPARIUM[1]. (STARTED 25/1/60).

C. = Calyptra
S. = Seta

PLATE NO.	TREATMENT		REGENERATION	
			4-3-60	10-6-60
1	5 setae cut off below calyptra	C.	-	+ 3/5
	5 calyptrae + internal tissue	S.	-	-
2	as 1.	C.	-	+ 2/5
		S.	-	-
3	5 whole calyptrae	C.	-	+ 4/5
	5 whole setae	S.	-	-
4	as 3	C.	+	+ 5/5 + buds
		S.	-	-
5	5 chopped calyptrae	C.	+	+ 1/5
	5 chopped setae	S.	-	-
6	as 5	C.	-	+ 4/6
		S.	-	+ 1/5
7	5 whole sporophytes + calyptrae	C.+	-	2/5 calyptra tissue
		S.		

([1] Expt. on Knop's agar using popn. 355 *D. scoparium*. Sporophytes collected in Nov. and brought on in lab.)

Fig. 40 D.fuscescens (popn.357).

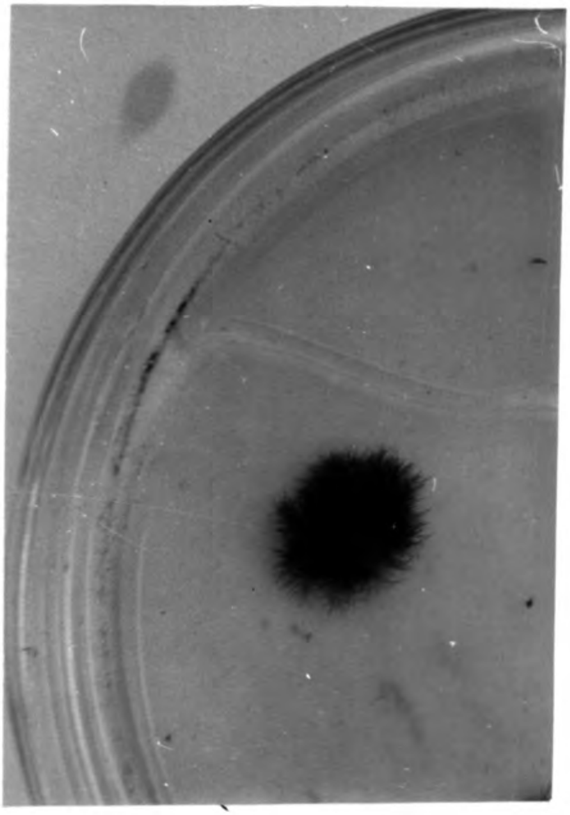


Fig. 4I D.majus (popn.37I).

Fig.42 D.scoparium (popn.40I).

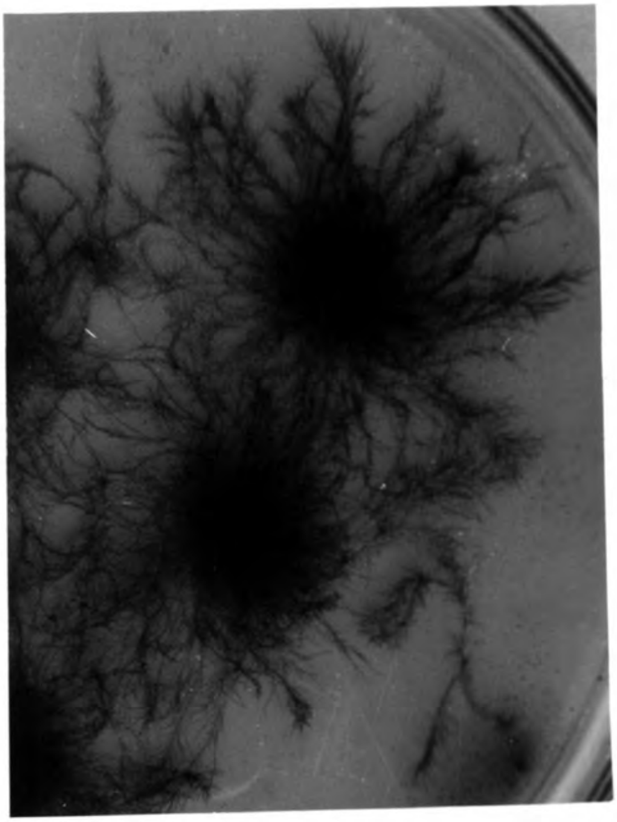


Fig.43 D.scoparium (popn.370).

GROWTH OF PRIMARY PROTONEMA ON AGAR.

Other regeneration experiments were carried out using calyptrae, and sporophytes, (Table 6. 7). It was found that detached and fragmented calyptrae commonly produced protonema. Young as well as old calyptrae could be induced to show the phenomenon. Of dried calyptrae (of D. scoparium (355), one year old), one regenerated on Knop's agar. It is likely that this method of vegetative reproduction could be of importance, especially as the calyptra must fall before the spores are dispersed.

In one case a seta produced a protonema, (Table 6. 7). The tissue involved is diploid, as distinct from the calyptra, which is haploid. Diploid protonema was presumably produced from the fragments of seta. It did not appear to differ in vegetative characters from the haploid protonema. As can be seen from the results, the formation of this protonema is not common.

(f) Spiral growth of protonema.

Table 6. 8 shows the types of spiral growth found in secondary protonema growing on agar. Similar spiral growths were found on primary protonemal filaments. Figs. 40 - 43 show the appearance of such spirals. The different growth patterns involve;

A. the direction of spiral, or its absence,

B. the concentration or diffusion of the protonema.

Not enough work has been done to make more than a few observations. In D. fuscescens (357), protonema commonly showed extreme spiral growth with concentration of the protonema. D. majus (390), was variable but some cultures had a very concentrated growth; some of the D. scoparium had diffuse growth, others more concentrated (e.g. 401 and 370 respectively). (Examples in brackets.)

Observations on secondary protonema are interesting in that filaments regenerated from male and female plants may show different directions of spiral, see Table 6. 8, e.g. 369 male and female. The direction of spiral was maintained in subcultures.

It is interesting to compare these data with those of Köfler (1959). She has produced the first important work on the subject, working with Funaria hygrometrica protonema. Her results indicate that protonema from different regions of Europe may have distinct appearances, though great care had to be exercised in maintaining exactly the same culture conditions. It may be that the differences in D. scoparium growth patterns may be equally as distinctive as the other morphological characters. Köfler records that spiralization in D. scoparium was shown in a figure produced by Gause (1931) in Köfler, but it was not referred to in the text. Other species showing spiral growth are; Phascum curvicollum, Janzen (1912), Leptobryum pyriforme, Pringsheim E. & O. (1935), and Bryum argenteum, Köfler (1959). Cultures of Polytrichum did not show the phenomenon Köfler (1959).

Observations of spiralization in primary protonema suggest that segregation for direction of spiral may occur, as opposite types appear to be found in the same culture of spores. More work involving single spore cultures is essential.

TABLE 6. 8.

PROTONEMAL STRUCTURE IN DICRANUM SPECIES. (STARTED 9-8-60).

Species	Protonemal Growth 16-IX-60	Spiral Growth 8-X-60
Dicranum scoparium		
486 D ♂	+	S
♀	+	S & A
486 L ♂	+	A
♀	+	A
355 L ♂	+	A
♀	+	C & S
369 L ♂	+	A[1]
♀	+	C[1]
Dicranum majus		
371 ♂	+	C
♀	+	C
364 ♂	+	S
♀	+	C
Dicranum bonjeanii		
485 ♂	+	A & S
♀	+	C
Dicranum fuscescens		
373 ♂	+	A
♀	+	A

S = spreading radially

C = clockwise

A = anti-clockwise

[1] Growth direction maintained on sub culturing.

Finally observations on regenerated protonema, from male and female stocks, have shown no differences in culture attributable to differences in sex. Dwarf males of D. scoparium and D. majus produced protonema exactly like that of their respective female plants. Sex differentiation thus probably occurs at a later stage of development.

4. THE GAMETOPHYTE.

(a) Development.

No data are available on the time taken for plants to develop from the protonemal to an adult sexually reproducing stage. If the spores are shed in the autumn, it may be possible for dwarf males to develop antheridial heads in the Spring. The growth of protonema under culture conditions does not reach the stage of bud production until c. 5 months after germination and it is doubtful if large males could be developed in such a short space of time. As pointed out previously, the spores are retained in the capsule until the early months of the year following meiosis and in this case it seems likely that sexually mature plants could not develop until the year after shedding of the spores.

(b) Reproduction.

The formation of sex organs on mature plants takes place in the Spring. Several field observations on the dates at which antheridial heads could be found in fully developed condition have been collected. No observations on the female organs have been carried out. As can be seen from Table 6. 9, antheridial heads are present in populations very early in the year. In D. scoparium (450) they were definitely present

TABLE 6. 9.

PRESENCE OF MALE HEADS IN POPULATIONS.

	Date	Locality
D. scoparium		
329	27-4-59	Hawkshead.
355	15-7-59+	
361	28-5-59*	Bellingham, Northumberland.
	19-6-59*	
362	2-8-60	Bellingham, Northumberland.
369	16-6-60	Dipton Burn, Northumberland.
	16-7-59+	
370	26-9-60	Dipton Burn, Northumberland.
	29-8-59*	
401	5-8-59	Isle of Skye
450	20-4-60	Dolgelley, Mid Wales.
D. majus		
364	9-8-60	Bellingham, Northumberland.
D. fuscescens		
332	27-5-59*	Ullswater.
373/4	16-6-60	Dipton Burn, Northumberland.
D. bonjeanii		
485	21-6-60	Aberdeenshire.

* Antherozoids active.

\+ Empty hyaline antheridia.

before the capsules had undergone meiosis. Not many data are available on the activity of the antherozoids but considerable variation between separate tufts has been found. In sunny habitats antherozoids are found earlier than in shaded ones.

(c) Geographical distribution.

The geographical distribution of fruiting is most interesting. Maps 7-10 have been prepared showing the fruiting in the various Vice-Counties. (A single record has resulted in the shading of the whole Vice-County.) The data are not very numerous, but several features emerge. The area in which fruiting occurs is much less, in all four species, than that occupied by the non fruiting forms. This is particularly the case in D. bonjeanii, which is represented by only a few localities, marked individually on the map; most of these are very old records.

It is interesting to note that D. fuscescens cfr. is restricted to upland areas in Scotland, N. England and Wales. D. majus cfr. occurs in similar areas but with several S. England stations. D. scoparium shows the widest fruiting distribution, montane regions and many Southern and Midland Counties being represented.

No clear cut answer to the problem of the limited fruiting area can be given but it seems likely that the tolerance of the male plants is involved. Capsules are almost always found where male plants are growing and I have never seen male plants in a Vice-County in which sporophytes are not recorded. If the distribution of the males is limiting, it is not at all clear which environmental factors are important. Fruiting tends to occur in Oceanic conditions and it may be that the males are less widely tolerant than the females. Chance must play an important part in the distribution of capsules within a fruiting area. Many potentially fertile tufts probably remain sterile merely because the male plants are not present.

An interesting parallel case of restricted fruiting is found in the literature. Bedford (1938) records that the fruiting of Climaceum dendroides, which is dioecious, probably depends entirely on the distribution of the male plants. Transplant experiments showed that non-fruiting clumps could produce capsules if male plants were added.

(d) The structure of fruiting tufts.

Often male clumps of D. scoparium and D. fuscescens are found separately and many presumed female tufts are also found. In fruiting clumps the males are usually in a group, not scattered as single shoots through the female plants. As is recorded in Chapter II dwarf males have been recorded in D. majus and D. scoparium. They are present in the tomentum of the female plants, just below the perichaetial heads. In 486, D. scoparium, up to 13 male plants were found on a single female plant; and in 364, D. majus, a single female plant had 17 males. In D. bonjeanii dwarf, intermediate and large male plants were found, and again the dwarfs were present in the tomentum of the female plants.

(e) Dwarf males.

Various literature records show agreement with the observations on dwarf males recorded above. E.g. Warnstorf (1906), 'Oft finden sich aber auch überaus winzige, nur unter der Lupe wahrnehmbare, Knospenförmige ♂ Pl., Zwergmannchen, in Kolonien in Rhizoidenfilz der fruchtenden Stämmchen in der Nähe des Perichaetiums'.

The presence of dwarf and large males in *D. scoparium*, 486, raises the question of the nature of the dwarfness. Woesler (1935) working with *Leucobryum glaucum*, which has smaller males than females, concluded that smallness was due to nutritional factors. When dwarf males were cultured many sizes of male plants could be obtained in the offspring produced. Ernst-Schwartzenbach (1944) make similar speculation concerning *D. scoparium* and *D. undulatum*, after investigating sexual dimorphism in *Macromitrium*.

(f) Development of sporophyte.

Few observations are available on the fertilisation of the archegonium. In 355, *D. scoparium* several archegonia appear to be fertilised and one probably suppresses the development of the others. Occasionally disety is found, as in 355. In *D. majus* polysety is the normal condition of many plants. Sowter (1948) has counted large numbers of capsules and reports the following findings.

Number of setae per perichaetium	1	2	3	4	5	6
Number of specimens, aggregate of specimens from several localities.	97	112	69	18	-	1
		Total 297				

TABLE 6. 10.

DEVELOPMENT OF SPOROPHYTES.

		D. fuscescens	D. scoparium	D. majus
Spring 1959		Fertilisation?		
			Fertilisation?	Fertilisation?
Autumn 1959		Seta elongation		
Winter 1959-60		Capsule swelling		
Spring 1960	March	Start of meiosis	Seta elongation	
	April			Seta elongation
	May			
	June		Start of meiosis	
	July			Meiosis
Autumn and Winter 1960 to Apring 1961		Shedding of spores in all 3 species		

Development of the sporophyte from fertilisation to spore dispersal in British material probably takes 16–23 months. These figures are derived from the data given in previous sections. The figures given for *D. scoparium* by Lackner (1939), for East Prussia, are very similar – 15–21 months. This extremely long period of development is probably one cause of spore infertility. Environmental and nutritional factors have a long period in which to produce an effect on the spores.

The development of the sporophytes has been summarised in Table 6. 10. The actual timing given may vary from year to year, and in different localities. Meiosis invariably starts earlier in *D. fuscescens* however with the other three species later. Seta elongation in *D. fuscescens* is in the autumn, whereas in *D. scoparium* and *D. majus* this does not occur until the spring.

(g) Do hybrids occur in natural populations?

It was thought early in the investigations that hybridization might be the cause of some of the variation found within the species. Hybrids are recorded in the literature on mosses. Nicholson (1932) lists hybrids involving *Weissia*, *Funaria*, *Physcomitrium* and *Trichostomum*. Others are recorded by Wettstein (1932). More recently Smarda (1952) reported the hybrid *Physcomitrella patens* x *Physcomitrium eurystomum*, and Khanna (1960) has investigated the hybrid *Weissia crispa* x *W. exserta*. In Nyholm (1958) hybridization is the explanation given for some of the puzzling *Bryum* taxa.

Very commonly *D. scoparium*, *D. fuscescens* and *D. majus* can be found fruiting in the same wood and at Dipton Burn, Northumberland, the

TABLE 6. 11.

CROSSES ATTEMPTED BETWEEN *DICRANUM* SPECIES.

	♀				♂		
	SPECIES	POPN. NO.	NO. PLANTS		SPECIES	POPN. NO.	NO. PLANTS
A.	*D. fuscescens*	374	10	x 1 attempt	*D. bonjeanii*	485	4
B.	*D. scoparium*	370	10	x 3 attempts	*D. bonjeanii*	485	4
C.	*D. majus*	371	10	x 2 attempts	*D. bonjeanii*	485	4
D.	*D. fuscescens*	374	10	x 1 attempt	*D. scoparium*	369	5
E.	*D. majus*	371	10	x 2 attempts	*D. scoparium*	369	5
F.	*D. scoparium*	370	10	x 1 attempt	*D. scoparium*	369	5

CONTROL POTS. NO ♂'s PRESENT

355♀, 10; 357♀, 10; 374♀, 10; 371♀, 10; 370♀, 10;

sporophytes of mixed tufts were carefully studied. Tufts containing D. fuscescens and D. scoparium, and D. scoparium and D. majus were found; D. fuscescens and D. majus mixtures were not recorded. Each sporophyte was carefully examined under a binocular microscope and its characters tabulated, using the criteria given in chapter I. No capsules were discovered which had mixtures of "species characters". Always they fitted exactly one of the species in the mixed tuft. One or two sporophytes, which were at first thought to be possible hybrids, had suffered injury to their tissues during development. E.g. a partially broken seta appeared to affect the development of the capsule. Thus a thorough survey failed to find any hybrid capsules.

Another line of approach was also tried. Artificial hybridization was attempted. Pots of female plants were made up, of the stocks shown in Table 6. 11. They were collected in late March and early April before fertilisation was thought to have taken place. To each pot male plants were added; several intra-population crosses were also included. Control pots were also set up to check that fertilisation had not occurred before the material was collected. The pots, which were kept in a cold frame, were regularly flooded to permit the dehiscence of the antheridia. They were examined at intervals and finally sampled in the late-Spring of 1961. No sporophytes of any description were produced. This applied too to the controls and intra-population crosses. It is clear from the results that, in the controls, fertilisation had not taken place, or that the developing sporophytes died. It is also clear that the techniques were at fault as even the intra-population crosses did not succeed.

The conclusions from these two sets of observations, are that hybrids are either not produced in the field or that they are extremely infrequent and that fertilisation and development of the capsules are more sensitive processes than was allowed for in the design of the experiments.

5. CONCLUSIONS.

Most of the conclusions to individual sections are included under the appropriate heading, but several of the features are worth emphasising.

Concerning reproduction; the spore infertility, capsule mortality, and the considerable time factor involved in the production of spores, are very important in consideration of the relative importance of vegetative reproduction. *Dicranum* species, especially *D. bonjeanii*, are probably exclusively propagated by regeneration of the vegetative parts in some habitats. This is likely to be very important at altitudes above the fruiting zone, where wind dispersal of leaf and stem fragments must be common.

The slow growth of the protonema is also a feature to be emphasised. Its remarkable resistance to drying out probably gives it ecological advantage in extreme habitat conditions. Thus, in one experiment, dried agar medium, which had had a culture of *D. scoparium* on its surface, was laid on a fresh agar surface. New out-growths of filaments occurred rapidly. In humid greenhouse conditions however, *Dicranum* protonema is not competitive.

Of considerable interest is the three dimensional nature of the protonema. Further study of spiralisation and tropisms of the various filaments may prove most rewarding. The protonemal phase of the life cycle does not appear morphologically different in the four species and there appears to be no sex differentiation.

Another problem examined which needs further investigation is that of the tolerance of the male plants of *Dicranums*, with particular reference to fruiting distribution.

Finally it would appear that hybrids between *Dicranum* species are either extremely rare or absent.

CHAPTER VII.

DISCUSSION.

Three vantage points will be taken in a survey of the whole of the results of this work.

1. Consideration of the populations as members of the Genus Dicranum.

The chromosome counts given in Tables 5. 1 and 5. 2 are strong evidence that there is an aneuploid series in this section of the genus, within three of the species different haploid numbers are recorded. Lewis (1961) points out that some of the variation in recorded numbers may be due to faulty technique or difficulties in identification. This possibility cannot be entirely discounted, but as most of the counts are recent there is perhaps little cause to suspect error. It is not known whether all the variation recorded for a given species occurs within a single region, such as the British Isles; my own results, Table 5. 2, indicate some variation in number.

It is extremely interesting to try and work out the cytological situation as it occurs in natural populations. The possibility exists that some of the variation may be transitory. One stable chromosome level may produce occasional variant capsules, which show chromosome imbalance in SMC meiosis, giving rise to infertile spores or perhaps sterile plants. Another possibility is that the adult sexually reproducing gametophyte may vary in chromosome number, populations say with $n = 10$, 11 or 12 chromosomes being equally viable. In the first case the aneuploidy observed may only reflect the variation in number around a stable value, in the second a true aneuploid series is involved. As most of the records are from single localities, widely scattered in the northern hemisphere, it is impossible to make any firm statement on the distribution or permanence of the variants. Clearly more work is required to find out the cytological variation within populations, and especially to prepare mitotic plates, with the object of discovering the chromosome numbers of mature plants. A suggestion by Lewis (1961) seems important in considering variation in number. Breakage of the chromosomes may occur and differing numbers may not reflect differences in genetic material. This point too requires more investigation.

Having pointed out the necessity for more data, it is clear that enough are available to suggest that the taxonomy of the species may have to be modified. Within three of the species, (there are not enough data for D. bonjeanii), variation in haploid number is recorded and if it could be shown that the variants are viable and can reproduce themselves sexually, the important question of species limits is raised. Are the four species, as at present described, aggregates of closely related species and would they show infertility if crosses between different cytotypes could be made in experimental culture? For instance, would American D. fuscescens $n = 12$ be interfertile with British material $n = 10$?

With these ideas in mind any evidence of hybridity within populations has been carefully noted. Different cytotypes, from one taxonomic species, could occur together and if sporophytes were successfully produced univalents and multivalents would probably occur at meiosis, resulting in reduced spore fertility. The meiotic plates of many populations of Dicranum have been studied and it can be stated that they provide no clear evidence of hybridity. A few possible multivalent associations have been described and occasional lagging bivalents and univalents have been seen. From his work on Pleurozium schreberi, Vaarama (1954) makes it clear that occasional multivalents and other cytological pecularities can occur in capsules otherwise behaving normally. Dicranum studies have shown that spore fertility is extremely low in some cases and this is a feature of hybrid material. Such enormous variation however is shown between the capsules of a single population that it is not at all clear whether the variation is entirely genotypic or whether differences in the environment are important. No hybrids have been suspected from the taxonomic studies and attempts at crossing stocks of male and female plants from different populations failed.

It is interesting to examine the relationship between the cytological results and the morphology of the plants. The variation in chromosome number does not always correspond with morphological discontinuities, e.g. D. fuscescens, populations with $n = 10$ and $n = 10 + 1$ small chromosome appear to be closely similar. In D. scoparium there is some evidence that populations 481 and 228, both with large heavily serrated leaves, both have $n = 12 + 1$. The cytology of 228 is not however easy to interpret, 481 is very clearly $n = 12 + 1$. D. majus appears to be very constant in its morphology and populations with small chromosomes do not seem to differ from populations lacking them. As more data become available it may be found that the morphological differences between different cytological types are small but constant. It seems a feature of mosses, (and is well known in higher plants), that the intra-specific cytological variation may occur within what appears to be a single variable species. The following are good examples, (details from Wylie (1957)), *Fissidens taxifolius* = 5, 9, 12; *Tortula muralis* n = c. 48, 50 ± 2, 55 ± 1, 60, 66, 40 ± 2; *Weissia contraversa* n = 13, 14; and *Ctenidium molluscum* n = 7, 10.

Of particular interest is the rarity of polyploidy in *Dicranum*. It has been described for *D. fuscescens*, Anderson and Crum (1959), and a polyploid sector was discovered in British material of this species. In many moss genera polyploidy appears to be an important factor e.g. *Mnium*, *Atrichum* etc. Wylie (1957). During these studies an attempt was made to produce protonema from seta tissue, and thus obtain a protonemal culture of unreduced chromosome number. Marchals (1911) report that such protonemata can be obtained from some species. In my experiments only one fragment of seta regenerated protonema. De La Rue (1929) and Wettstein (in De La Rue) both failed to produce regenerating setae in *Dicranum*. The difficulty of obtaining aposporous plants may reflect the rarity in the field of polyploid material, although a figure of one percent success in regeneration for *Dicranum* would seem a high value. (One fragment out of 35 regenerated protonema in the experiment quoted on page 174). Anderson and Crum (1959) in reporting on the cytology of *D. fuscescens* in Canada discuss an interesting phenomenon. Tetraploid plants of *D. fuscescens* were clearly dioecious. Since the sporophyte is genetically bisexual, plants produced by apospory should also be bisexual. Perhaps some other means than apospory was involved in their production.

The dioecious condition of Dicranum species has been mentioned above and it is of especial importance in discussing variation. In monoecious species cytological and genetical variants are able to reproduce by selfing, providing that the offspring are "genetically" possible. In a dioecious species however the most common occurrence will be a chromosomal or genetic change in one of the sexes. If the change is of great magnitude there is the possibility that crossing may fail, due to chromosome or genetic imbalance. If it is a small change in one sex, it is interesting to note that this will be placed in different genetic background, depending upon the cross. This will especially apply if a clone of the variant becomes established in a large fruiting population.

Finally the status of small chromosomes must be raised. They have been described in at least 12 moss genera and often appear to be constant members of the chromosome complement, e.g. in Sphagnum species where $n = 19 + 2$ is the most frequent number, see Wylie (1957). More work is essential to find out whether plants with these small chromosomes predominate in natural populations, or are of rare occurrence, and also to investigate the origin and division of small chromosomes.

TABLE 7. 1.

DESCRIPTION OF DICRANUM SPECIES, INCORPORATING NEW DATA.

D. SCOPARIUM.

Tufts $\frac{3}{4}$" - $2\frac{1}{2}$" (1.5 - 6 cms), leaves up to 1 cm long, extreme leaf types falcato-secund and erecto-patent, with all intermediates[1]. Serrated at leaf margin and back of nerve, sometimes undulate[1], *cells in upper part of leaf porose*, nerve subulate, with nerve reaching extreme tip in dry communities, apex wider with nerve ending below tip under moist conditions, *nerve* $\frac{1}{8} - \frac{1}{13}$[2] *of maximum leaf width*, seta solitary (rarely disety), *red*, *capsule arcuate, not striate, exannulate*. Leaf section - *4 lamellae and lamina cells quadrate*. ♂ plants variable in size, often slightly smaller (in leaf length and width) than ♀, or dwarf with leaves c. .6 mm long, serrated or entire; or dwarfs and intermediate sized ♂s .6 - 3.0 mm in leaf length. Dwarfs in tomentum.

var. *spadiceum*: entire leaved form of two types, phenotypically and genotypically determined, entire leaved plants in lowland popns. and as occasional leaves in serrated popns. Var. rejected.

var. *recurvatum*: leaf stance modified in culture, no evidence that falcato-secund varieties constant. Probably habitat modification. Variety rejected.

var. *paludosum*: undulation in habitat modification, variety not distinct on other characters also? Variety rejected.

var. orthophyllum: form fitting this description indistinguishable after culture from other forms of D. scoparium. No evidence on range of variation possible in straight-leaved Dicranum populations. They may not all be able to produce falcato-secund leaves. More details required in this variety.

Notes. [1] Experimental evidence suggests plasticity related to relative humidity.

[2] Data for herbarium and cultivated material combined, excluding some ♂ data.

D. BONJEANII.

Tufts $\frac{3}{4}$" - $2\frac{1}{2}$" (1.5 - 6 cm), leaves up to 1 cm erecto-patent, rarely curved[1], with serrated leaf margins, back of nerve faintly toothed or smooth, upper leaf cells porose, nerve 1/16 - 1/20 of maximum leaf width, nerve vanishing below acute apex (to obtuse[2]). Seta solitary, yellow above, red below, bearing striated slightly curved capsules. Capsules exannulate. Male plants[3], variable in size on female tomentum and leaves, leaf size .8 mm - 2.3 mm in length, serrated and rarely undulate, fruiting very rarely.

var. juniperinum: no data from experiments.

var. calcareum: habitat-modification, not constant in culture.

var. rugifolium: undulation variable in all samples; evidence suggests that relative humidity important. Many populations produced rugose leaves in culture.

forma falcato: erecto-patent leaves produced from one population of falcato-secund D. bonjeanii. Habitat modification.

Notes. [1] Feature not constant in culture.

[2] Under high relative humidity.

[3] From one population.

D. MAJUS.

Tufts 1½" - 2¾" (4 - 7 cm), leaves very long usually all over 9 mm long, falcato-secund at apex[1], lower leaves variable stance in moist habitats, serrulate leaf margin and back of nerve, with porose cells in upper leaf, non-undulate[2], nerve 1/11 - 1/14 of maximum leaf width, leaf aristate with nerve reaching apex, polysetous with pale seta. Capsule scarcely striate, cernuous with a long beak, exannulate. Lamina cells rectangular in cross sections of leaves. ♂ plants in female tomentum, usually just below perichaetia, leaf length c .3 - .5 mm long, entire or slightly serrate.

Notes. [1] Maintained under relative humidity extremely high.

[2] Except under special culture conditions, see Chapter IV.

D. FUSCESCENS.

Tufts ½" - 1¼" (1 - 2.5 cm), leaves up to 1 cm long, subsecund, falcate, crowded and falcato-secund[1], leaf apex aristate, serrulate, non-undulate[2], with non-porose upper leaf cells, nerve toothed at back, reaching apex of leaf. Seta solitary, dull, yellow, bearing striated, arcuate, annulate capsules. Nerve 1/3 - 1/6 of maximum leaf width. Male plants[3], smaller than ♀ (in leaf length and width).

var. congestum: not enough data for this variety.

var. falcifolium: more data required, some forms ± constant in culture.

Notes. [1] In some populations falcato-secund leaves constantly produced in culture.

[2] Lower lamina undulate in extremely moist conditions.

[3] One population only.

2. Consideration of the populations at the species level.

Bearing in mind the possibility that further cytological work may modify the taxonomic picture, the evidence presented in the chapters above, indicates that the populations fall into four species. Subsequent work may show that each of these is a group of species but the present state of knowledge is summarised in Table 7. 1. In this the key characters, which have shown themselves constant in culture, are underlined.

As has already been stated in another context, hybrids between the four species have not so far been detected, and attempts to synthesise them in the laboratories have failed.

The discussion of the results of the culture experiments, Chapter IV, indicates that they have been of great value in interpreting the variation. Table 4. 10 records the stable and plastic characters. It is clear from these results and literature records of the work of Buch (1936, 1953), Lodge (1958), and others that the variation in other species might be easier to understand if simple cultures were used, as well as orthodox taxonomic procedures. Buch's work in particular shows how difficult it is to prejudge, which characters are genotypically fixed, and which are plastic. He has shown that Scapania undulata and S. dentata must be regarded as two very dissimilar habitat modifications of the same taxon and that Calypogeia neesiana and C. meylanii are distinct, even though the differences between them are apparently very slight. These two conclusions could not be confidently defended on purely herbarium studies.

The sections of this thesis concerned with the statistical study of populations have shed a good deal of light on such problems as serration of the leaves. Without actual counting, judgment of the serration of a population would be impossible. One major point to be raised in studies of this kind is the enormous labour involved in measuring even dimensions of leaves. A trial run, to find out the difficulties, is most useful. Literature accounts by Greig-Smith (1954) on Lejeunia and Lodge (1958) on Drepanocladus indicate as has been found in this study, that statistical information is invaluable.

The concluding remarks of Chapter II indicate that the four species are most interesting ecologically. The range of habitats, in which

Dicranum species are found, is especially noteworthy. *D. scoparium* creates some difficulties as it occurs in the habitats of the other three species. From my experience *D. bonjeanii* appears to be ecologically separated from *D. fuscescens* and *D. majus*, but this may not be true over its whole range. Studies by Persson (1961) have shown that all four species occur in fen communities in Lappmark, Sweden. It is clearly unwise to make more than the general comments such as are contained in Table 2. 9.

In Chapter I the division of the genus *Dicranum* by Nyholm (1953), into several sections including *Dicrana scoparia* and *Dicrana fuscentia*, was summarised. In some ways *D. fuscescens* is clearly distinct from the other three species, in its upper areolation and sporophyte characters but no clear evidence has been discovered which would confirm or dismiss this classification. Division of the genus based on crossing experiments, to expose the limits of gene flow and hybridization are a very distant prospect indeed.

3. Consideration of the populations at the intra-specific level.

The results obtained from culture experiments have proved extremely instructive in interpreting the variation, (see Table 4. 10 with comments on the intra-specific taxa). Evidence has been put forward, Chapter IV, that the relative humidity of the atmosphere around the tuft is important in determining the leaf stance, undulation and probably in *D. scoparium* and *D. bonjeanii*, the angle of the leaf apex. It is clear that in natural conditions variation in microclimate, especially in water relations, is found over short distances. Variation, in the characters mentioned, is common, and some understanding of why differences occur in the same tuft can be appreciated. For instance *D. bonjeanii* from south-facing dry slopes may be non-undulate, while on north facing grassland in damp conditions it may be markedly undulate. In *D. scoparium* zonation of growth is often found; there is a zone of short erecto-patent leaves with a terminal head of leaves, the uppermost of which are falcato-secund. This clearly indicates the prevailing humidity conditions at different periods of growth, the xeromorphic leaves at the apex marking a point of interruption of growth, the lower leaves being produced in rapid succession in the moist winter months.

Table 4. 10 shows the conclusions reached in Chapters III and IV concerning the falcato-secund varieties of *Dicranum*. Most of these have not proved constant in culture; others produced falcato-secund apical leaves in pot cultures but it was not possible to tell, by inspection of the original gatherings, which would be constant and which variable. These remarks apply to *D. scoparium* and *D. bonjeanii*. The data for *D. fuscescens* are not conclusive; even in polythene cultures some leaves remained falcato-secund, probably indicating genotypic control. Judgment is reserved on the variation in *D. fuscescens*; *Dicranum scoparium* var. *recurvatum* and *D. bonjeanii* forma *falcata* are rejected on the evidence available. Undulate varieties of *D. scoparium* and *D. majus* are treated as habitat modifications, as is the variety *rugifolium* of *D. bonjeanii*.

The environment used does not permit orthophyllous varieties of *D. scoparium* and *D. bonjeanii* to be investigated to see if they are constant. It is not known whether they would produce falcato-secund leaves in the appropriate humidity.

Evidence from ecological observation and culture experiments suggests that different species are affected by different ranges of relative humidity. *D. scoparium* appears to require a higher relative humidity than *D. bonjeanii*, for the production of undulate leaves; and *D. majus* a higher relative humidity still to develop erecto-patent undulate leaves. This difference in sensitivity may be due to differences in leaf structure, most likely in the structure and rigidity of the nerve.

The results for undulation and leaf stance clearly indicate phenotypic plasticity. Those for serration suggest that some genetic control is found in *D. scoparium*. Entire leaved forms, it has been discovered, are of two types; one constantly produces non-serrated leaves in culture, the other produces serrated leaves. One shows genotypic control, the other phenotypic plasticity. The evidence from ecological studies and careful taxonomic examination suggests that entire leaved forms can be found, in *D. scoparium*, where the exposure of the habitat is marked, e.g. on dunes and rocks at low altitudes and as well as at high elevations. As exposure increases gradually in some areas a cline for mean serration values may be present, intermediate serration types being found between populations either heavily toothed (lowland communities) or entire (montane vegetation). A cline was suspected from early studies, but the result of culturing plants shows that it is of complicated form, and the modified populations may arise in different ways. It is likely that the vegetatively reproducing fragments which reach high altitudes could easily arise from lowland populations, which in such circumstances will produce entire leaves by phenotypic plasticity or fail to survive. In addition, selection probably operates on the spores produced in montane woodland etc. and blown to higher altitudes; these may give rise to new populations genotypically distinct from those in the lowlands. As the spore fertility is variable in D. scoparium populations, vegetative reproduction is likely to be very important in these upland communities. Clines in the variation of other mosses are suspected. Richards (pers. comm.) suggests that Dicranum scottianum var. anglicum (northern subsp.) and var. canariense (southern and more serrated subsp.) may be exhibiting clinal variation for serration. The question of the possible functions of the teeth are quite obscure.

The taxonomic value of the entire-leaved varieties described for D. scoparium, on the evidence given above, seems to be negligible. So much plasticity is shown by the various forms of this species that even though some non-serrated forms remain constant in cultivation there is no way of detecting those populations which are plastic for the character. One population of Dicranum fuscescens with entire leaves proved plastic for leaf serration, and this is evidence that var. congestum may not be of taxonomic value. More data are required on this variety.

Of particular interest, in the study of the ecology of the Dicranums, has been the discovery that some populations of D. scoparium from basic soils did not grow in the mildly acid soil cultures. This suggests that the comments of some ecologists on the tolerance shown by D. scoparium may bear no relation to the tolerance of a particular population. E.g. Amann (1928) states that D. scoparium is indifferent to soil reaction. The results obtained in this work suggest that certain populations are very sensitive to soil reaction. The particular factor involved may be pH or mineral balance. Clearly more work is essential to see if ecotypes are present within the species.

Problems of the reproductive biology of Dicranum species have proved most interesting. Particularly consideration has been paid to the dwarf males of D. scoparium, D. bonjeanii and D. majus. Taking the evidence of the various sizes of males found at Warkworth, popn. 355, and at Kirkton, popn. 485, and the increase in leaf size in apparent male plants in culture (see Chapter IV), it would appear that sizes of male plants may be determined by nutritional factors in D. scoparium and D. bonjeanii. It is not yet known however whether dwarf males eventually develop into large male plants. The constancy in the size of dwarf males in D. majus is noteworthy; no variation in size has been discovered. Polysety is clearly a reproductive advantage in D. majus, as the distribution of antherozoids within the tuft may not be very widespread.

The distribution of dwarf male populations of D. scoparium is not at all clear. Five populations are known; one from Cornwall, one from Northumberland and three from Scotland. These are all from the wetter regions of Britain but there are not enough records to permit generalisation. It is very difficult to collect data from herbarium material on this point, as it involves breaking up moistened tufts of the plants. This is not permitted in National collections. Populations with dwarf males are at a selective advantage in comparison with large male tufts. Dwarf males mature quicker and permit earlier reproduction in a new clump of moss. Comment by Nyholm (1954) suggests that large males of the group *Dicrana scoparia* are relatively infrequent in Fennoscandia and dwarf males are commonly found. This suggests that the quick maturing males are a selective advantage in Northern and Western parts of Europe. More complete details of the biology of *Dicranum* males are essential to understand their distribution.

Also important in considering reproduction in *Dicranum* are the problems associated with fruiting. The absence of males in many parts of the country is obviously of great importance. Not much evidence is available but it would appear that male plants are physiologically less adaptable than the female plants. In montane communities,where fruiting is abundant they are restricted to woodlands and lower rocks and ledges. Wann (1925) studying *Marchantia* found that the female plants were more sensitive, as regards production of sex organs, than male plants. In *Dicranum* probably the reverse situation is found. The problems of *D. bonjeanii* seem more difficult to understand, as only a few recent records of fruiting can be found (see map 10); perhaps drainage or burning has reduced the number of fruiting stations in recent times. In all the species a more detailed knowledge of fruiting distribution outside Britain would be most useful.

Vegetative reproduction appears to be important in all the *Dicranum* species, especially *D. bonjeanii*. Many other dioecious species in Britain are very rare in fruit, e.g. *Campylopus* species, and some British mosses are unknown in fruit e.g. *Rhytidium rugosum* and *Atrichum crispum*. A great deal more research is needed to understand the reproductive biology of the *Dicranum* group, and in bryophytes as a whole.

More too is needed in relation to problems of sex determination. Evidence is presented that distinct sex chromosomes cannot be detected in meiotic plates, and that a spore size histogram does not show a bimodal curve, such as would suggest size differences in the spores of the different sexes. Protonemal cultures might have been expected to show that dwarf male protonema, obtained by regeneration of leaf fragments, was of different size to the female protonema. This did not prove to be the case.

One interesting point concerns the dioecious condition of *Dicranum* species. It is extremely difficult to prove that this is in fact the reproductive state of the species, and that the sex organs arise from different unconnected shoots. In regenerating protonema from detached leaves of *D. scoparium* (popn. 369), it was found that the spiral growth patterns of male and female plants were different. On subculturing this feature was constant and thus appears to be genetically determined. This is excellent evidence that the species is dioecious.

In concluding this discussion and the results of the *Dicranum* studies, it is clear that many problems are posed. But a good deal of the morphological variation of the four species is now better understood, and its genotypic components are beginning to come to light. The difficulties of naming intra-specific varieties are very apparent; continuous variation patterns with clear extremes and many intermediates obviously are not amenable to simple classification.

New experiments, to try and understand the variation in more detail, are suggested in plenty. Most productive will probably be further attempts at understanding the cytological backcloth to the group, and to find out whether each species is in fact an aggregate species. Mitotic studies are essential for these problems and new techniques will have to be devised. Data on the reproductive features of the group would also be extremely useful, especially from artificial hybridization experiments, if the technical problems can be overcome. In the ecological sphere, problems of fruiting distribution and soil tolerances are most likely to yield interesting results.

In introducing this thesis the hope was expressed that experimental taxonomic approaches would help to elucidate problems of the variation in mosses. It is clear that such approaches, using simple culture experiments, statistical surveys of difficult criteria, and cytological investigations, have been and will continue to be of value.

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Notes on Maps.

I. Maps I-3, and 4-6 from Census Cat~~o~~alogue of British Mosses, J.B.Duncan (I926),Berwick; with additions from Trans.B.B.S.

2. Maps 7-I0, from:-

Boswell herbarium,Oxford.

Duncan herbarium, Hancock Museum, Newcastle-Upon-Tyne.

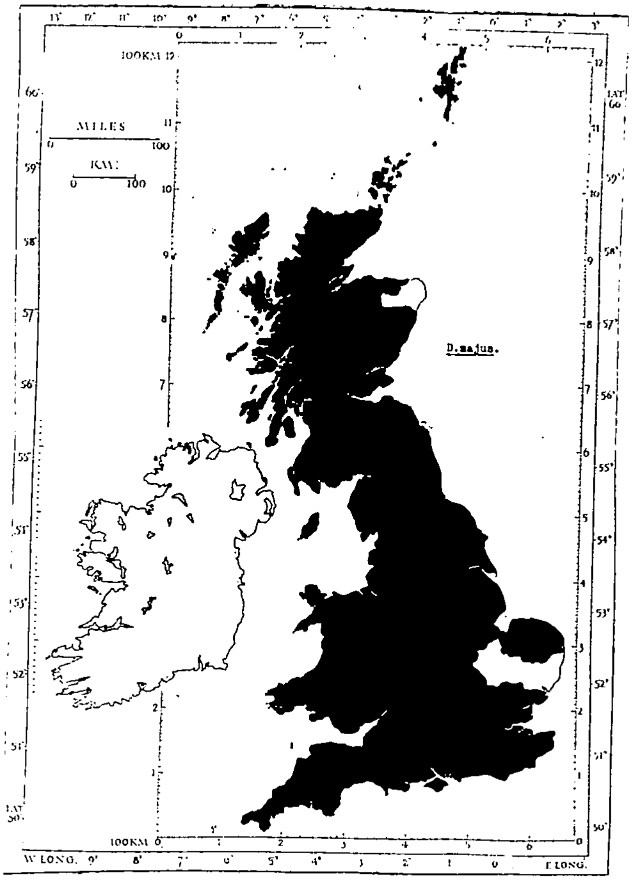
Glasgow University herbarium.

Cambridge Botany School herbarium.

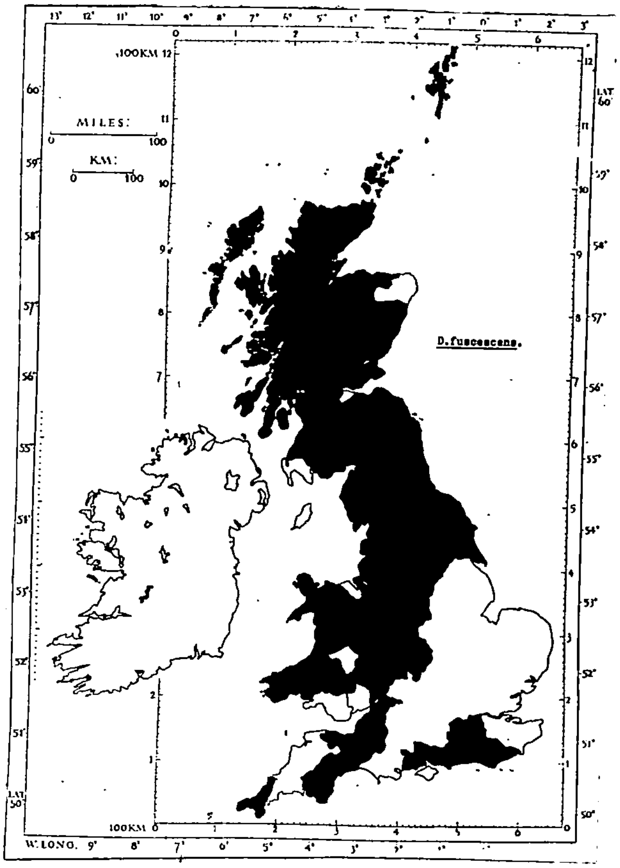
Nat.Hist.Museum.

Specimens and records from Dr.A.C.Crundwell,Mr.E.C.Wallace, Dr.C.D.Pigott, and my own field records.

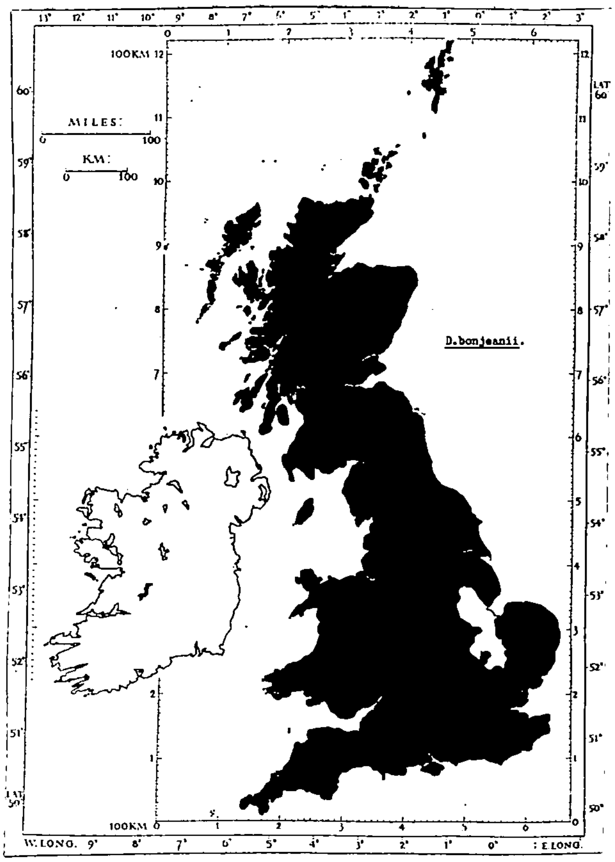
A single record of fruiting has resulted in the blocking in of a Vice-County.



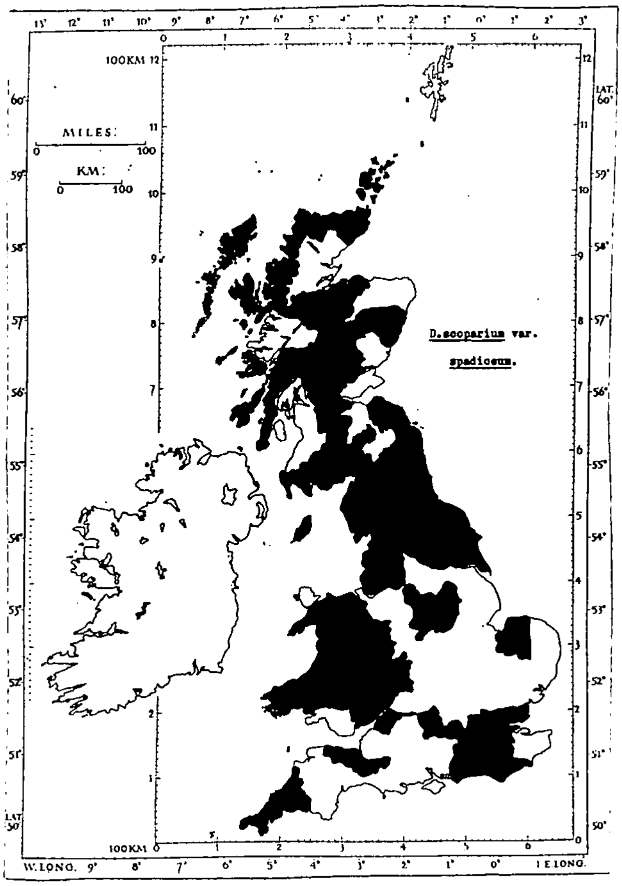
Map. I.



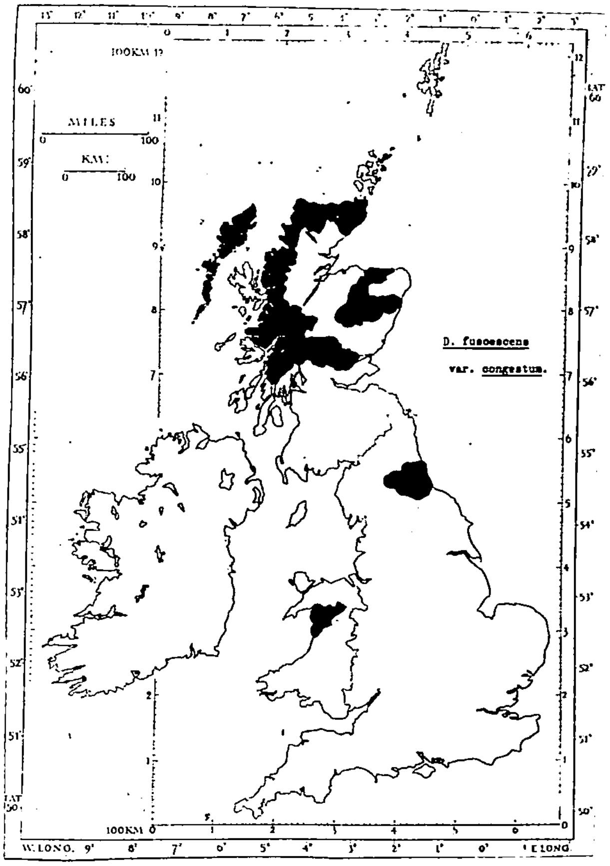
Map. 2.



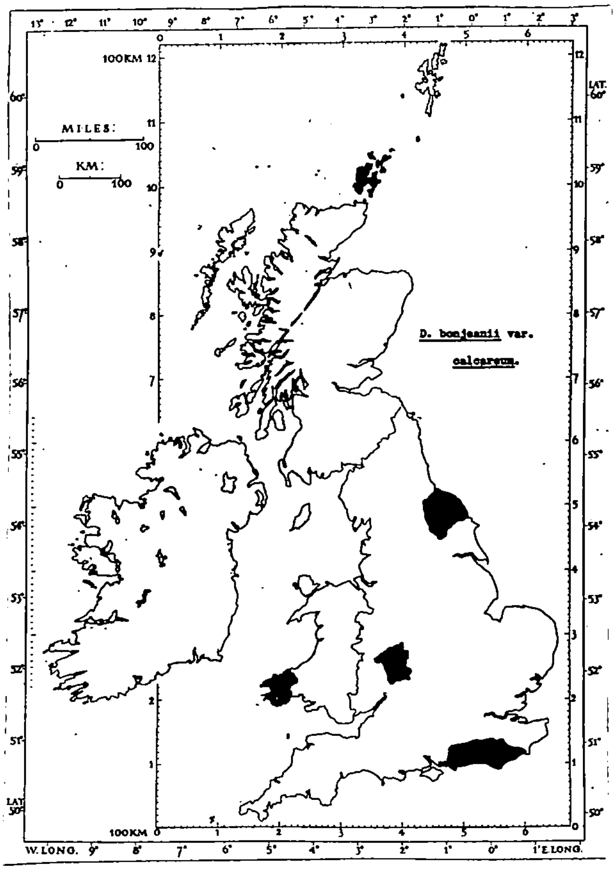
Map. 3.



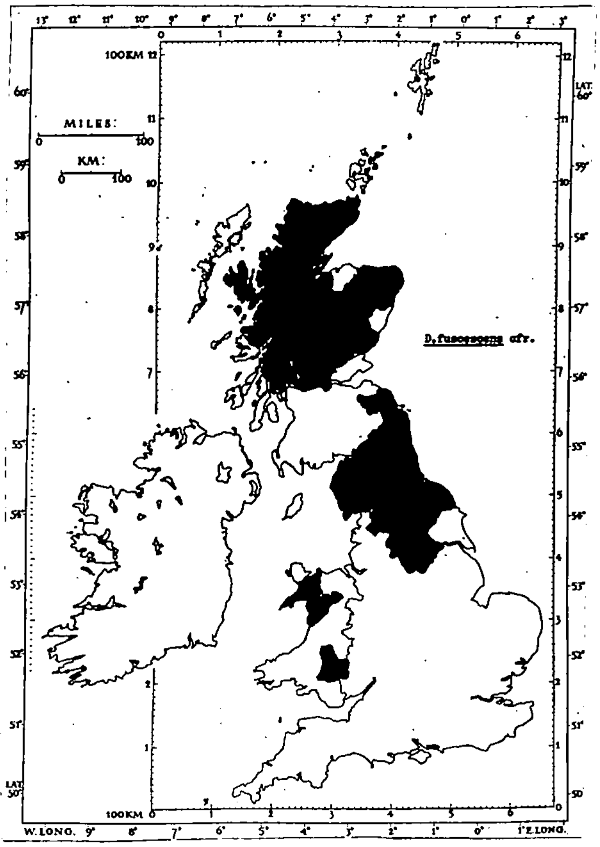
Map. 4.



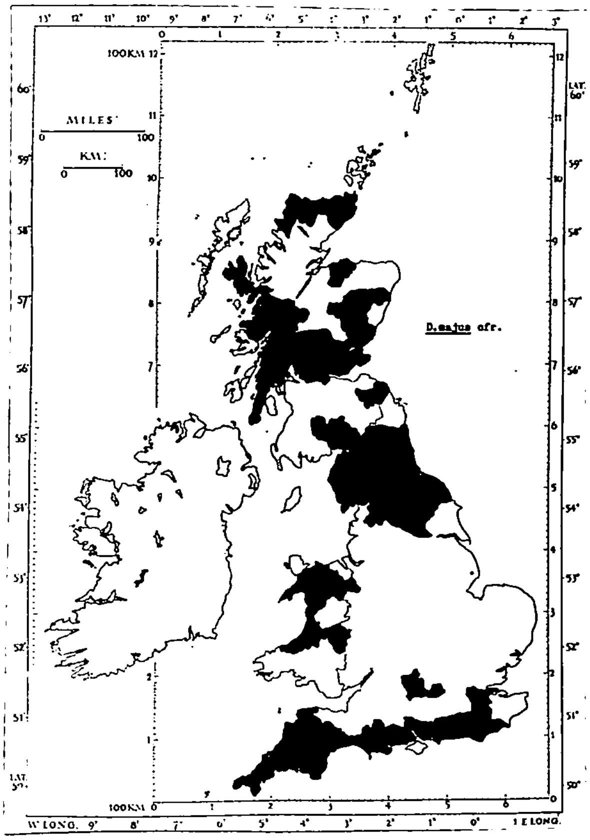
Map. 5.



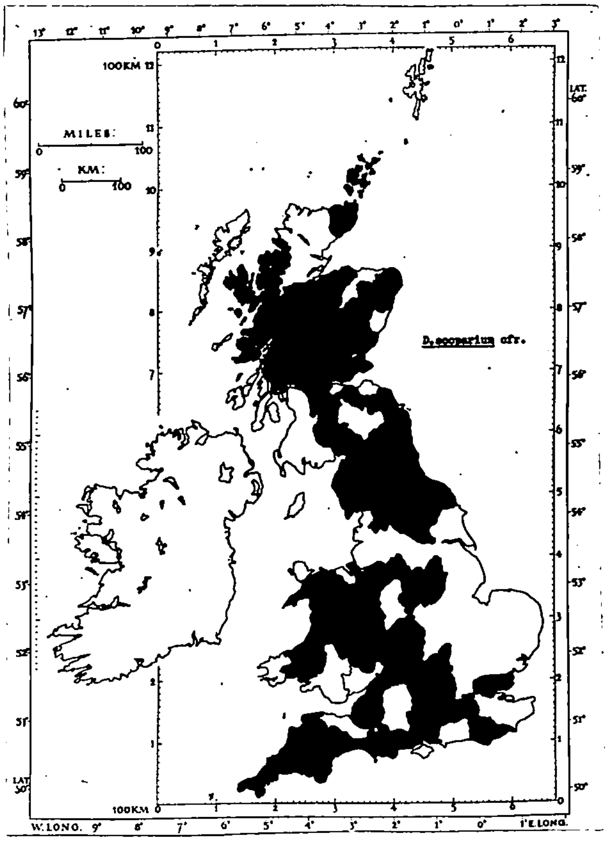
Map. 6.



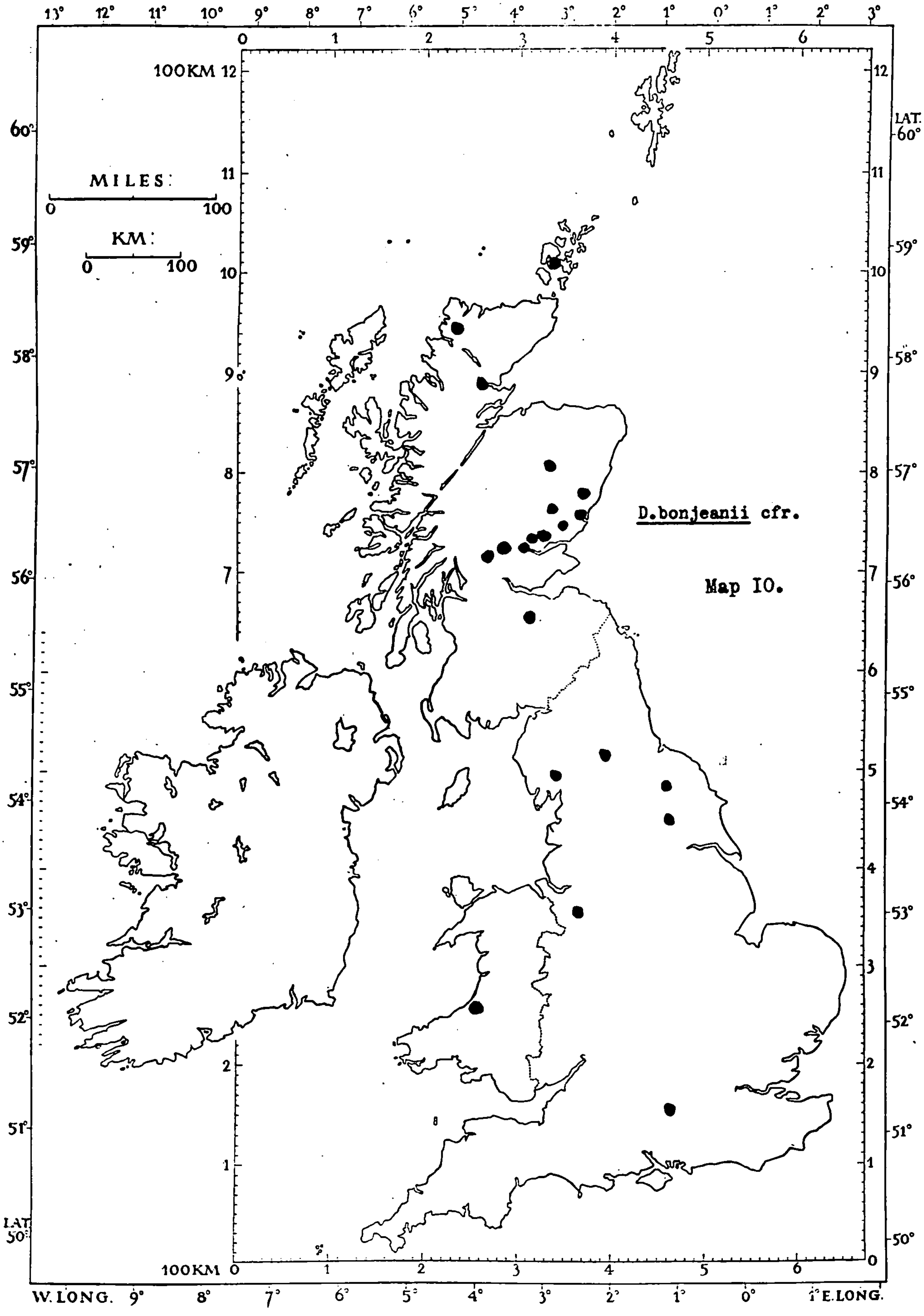
Map. 7.



Map. 8.



Map. 9.



D.bonjeanii cfr.

Map IO.