STUDIES IN THE CYTOTAXONOMY OF THE BRITISH SPECIES OF THE GENUS ATRICHUM.

by

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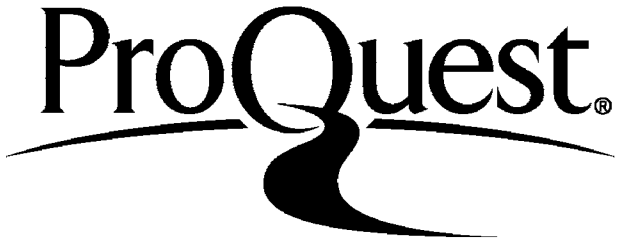

ABSTRACT.

In order to define the present status of the genus *Atrichum* in Britain, data available from various floras and other publications are examined. Also literature relating to the cytology of the bryophytes is reviewed.

Herbarium and living specimens are examined, the latter both in the field and under controlled conditions, to establish the range of variation in each species and to determine whether this is of genetic or environmental origin. Finnish and British material of *A.tenellum* are compared and two new races of *A.undulatum*, with distinct morphology, are described.

Cytological investigation shows that *A.crispum*, *A.angustatum* and *A.tenellum* are all present as N=7 races in Britain. *A.undulatum* occurs mainly as the N=21 race with sporadic aneuploid specimens, but diploid (N=14) races, of very local distribution, also occur.

The use of certain characters for species identification is discussed in the light of the results obtained in the investigation and the cytological basis of sex expression in the genus is discussed with particular reference to *A.undulatum*. Finally the species and races of *Atrichum* in Britain are described.

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INTRODUCTION.

An examination of the available herbarium specimens revealed a great diversity of form in each of the British species of *Atrichum*. It was therefore decided to make a morphological and cytological examination of such members of the genus as occurred in the southern parts of England and Wales, in order to discover whether this range was determined genetically or by environmental conditions. It was hoped to find reliable characters which would define exactly the species and varieties.

CHAPTER I.

REVIEW OF THE LITERATURE RELATING TO THE PRESENT STATUS OF THE GENUS ATRICHUM IN BRITAIN.

A member of the genus Atrichum was first referred to by Dillenius in his 'Historia Muscorum' (1741). The plant was described as:-'Bryum Juniperi,foliis rugosis, capsulis rectioribus.', and has since been identified with Atrichum angustatum.

The genus was mentioned by Hooker and Wilson (Muscologia Britannica 1818), who denied the validity of the division of the Polytrichum into Polytrichum and Atrichum, as proposed by Ehrhart and Mohr, and followed the classification of Wahlenberg in which there was no such division. Thus Polytrichum undulatum i.e.Atrichum undulatum was described as having 'Leaves lanceolate, undulate, their margins plane, denticulated, their nerve winged, capsule cylindric, curved, lid subulate. Stem 1-2 inches high, leaves thin and delicate in structure (unlike the rest of the genus)crisped when dry.'

In 1855 Wilson published his 'Bryologia Britannica', retaining Hooker's name on the title page. In this work a full description of the genus Atrichum, as distinct from Polytrichum, was given, three species being described.

A.undulatum P.Beauv. had 'Upper leaves crowded, long, lingulate-lanceolate, undulated at the margin, sharply denticulated, capsule cylindrical, curved, lid with a long beak.' Two varieties of this

species were described. The first, A.undulatum var γ attenuatum had 'Leaves narrower, more flaccid, more crisped when dry, nerve with a narrower lamella, capsule more slender.' The second, A.undulatum var β abbreviatum had 'A shorter fruit stalk, capsule, and peristome than the type.' A.undulatum was said to grow in grassy, shady places; the variety attenuatum in North America only; the variety abbreviatum in bare shady places. Fruiting was said to occur during October and November.

Of A.angustatum.Brid. it was stated 'It is not yet certain if this species is found in Britain. Mr Mitten has collected plants from Hurstpierpoint which are comparable with the type specimens of Schimper.'

A.tenellum.Br. and Schimper. was described as 'A smaller species, dioecious, short cernuous capsule with a large peristome.' No reference was made to the occurrence of this species in Britain.

Berkeley in his 'Handbook of British Mosses' (1863) added nothing to Wilson's description of A.undulatum and described neither of the varieties . However, he gave a description of A.angustatum which he found to be 'Dioecious, stem shorter, leaves narrower, more densely reticulate, less hispid beneath (than A.undulatum) lamellae numerous, sporangium narrow.' A note added that Schimper had examined the plants from Hurstpierpoint and confirmed that they were A.angustatum.

A.tenellum was given a fuller description being 'Dioecious, stem short, simple, leaves oblong-lanceolate, scarcely undulated

even beneath, margin toothed beyond the middle, nerve slightly lamellate, sporangium subcernuous, obovate or oblong, veil obscurely hairy above, peristome large. On muddy places or clay. Fruit autumn.' Wilson was stated to be the collector of the British material.

In Braithwaite's 'British Moss Flora'(1881-87), the generic name was changed to Catherinea, the authority given being Bridel. A full description of British C.angustata Brid. was given for the first time and a locality in Perthshire, as well as one in Sussex, was given as a place of collection. The plants were 'Dioecious, gregarious or laxly tufted, resembling C.undulata, but smaller and more slender and of a more obscure or reddish tinge. Stems about 1 inch high, simple,erect, leaves crowded, linear lanceolate, shorter and firmer than in C.undulata , less undulated, erecto-patent, more crisped when dry, less spinulose at the back, more densely and minutely aerolate, apex somewhat obtuse, margin reflexed below, very narrowly bordered and serrate in the upper part only, lamellae 5-7, much higher and occupying most of the apex of the leaf, in section 4-6 small, rounded cells, capsule on a purple seta, erect or a little inclined, straight or sub-arcuate, narrowly cylindric, purple red, calyptra very narrow, spinulose at the point, lid dark purple, glossy with a short beak, teeth of peristome narrower. Male plants in separate tufts with cup shaped inner bracts, broadly obovate with the nerve thickened at the apex. Fruit November-January. Much more frequent in America than in Europe. Hurstpierpoint 1846. Perthshire 1864.'

C.undulata Web. and Mohr. was fully described and certain details of the life cycle were given. The plant was 'Paroecious or polyoecious, gregarious in light green patches, rhizome much branched, roots twisted to form a cable.' A note added that Schimper found fruit on a first year stem, not preceded by antheridial formation. A variety C.undulata var β minor Web. and Mohr. was described as 'Short leaves crowded, shorter, less undulated, capsule suberect, ovate-oblong, unequal on a shorter pedicel . In bare stony places, not common.'

C.tenella Rohl. was said to occur in Europe. Three specimens examined by Braithwaite were renamed C.undulata var β minor. A description of the species from foreign material was given in which the plant was described as 'Dioecious, stem ½-1 inch, leaves oblong-lanceolate, scarcely undulate, dull green, capsule cylindric oblong, about half the length of C.undulata , inclined, lid rather conic, tumid, rufescent, nearly straight, pale, beak rather shorter than the capsule.'

C.crispa James. was described from British material collected by Wilson and described by him, apparently in manuscript only, as C.laxifolia and C.tortifolia. Fruit of this species was said to occur only in America.

In 1888 Vaizey published details of plants collected at Broxbourne Hertfordshire, in 1886, and thought to be comparable with the Norwegian specimens of C.anomala Bryhn. The plants bore up to four sporogonia in lateral as well as in terminal position, of which the latter was not invariably the youngest. The Norwegian specimens had been

described by Bryhn as autoecious but three arrangements of sex organs were found in the Broxbourne material. Firstly plants were found bearing archegonia or young sporophytes but no antheridia, and were described as dioecious. Secondly antheridia were found in the axils of some leaves and archegonia in the axils of others on the same plant, and these were said to be autoecious. Thirdly antheridia and archegonia were formed in the axils of the same leaves and so gave rise to synoecious perichaetia. Vaizey observed that the plants resembled C.undulata except for the unusual number of sporophytes formed on each plant. Since the specific name C.anomala had been previously used to describe a different plant from that of Bryhn, Vaizey suggested that the Norwegian and Broxbourne plants should be known as C.lateralis Vaizey.

The moss flora now in general use in Britain is Dixon and Jameson's 'Student's Handbook of British Mosses.' Three editions were published in 1896, 1904, and 1924 respectively. In the 1896 edition only three species of Catherinea were decribed i.e. C.undulata Web and Mohr., C.angustata Brid., and C.crispa James.

C.undulata had 'Stems erect 1-2 inches high, leaves scale-like below, strongly transversely undulate with a distinct margin, sharply spinose for the greater part of the length, lower surface of the lamina beset with spines in transverse rows on the crests of the undulations, 3-6 lamellae, in section each of 3-5 cells, inflorescence paroecious, the male flowers terminating the first

year stem, the axis of which is subsequently prolonged and next year produces a terminal female flower. Seta 1-1¼ inches long, capsule strongly arcuate and inclined with a subulate lid almost as long as the capsule.' Of the two varieties of C.undulata described, C.undulata varβ minor had 'Stem short, leaves less undulated, capsule shorter, suberect, unequal, on a shorter seta. In drier stony places.' C.undulata var γ Haussknechtii Dixon (Catherinea Haussknechtii Broth., Atrichum Haussknechtii Jur. and Milde.) was said to 'Resemble C.undulata very closely, but more slender, ½-1 inch high, the leaves somewhat more shortly and obtusely pointed, the spines on the back smaller. Inflorescence terminal, paroecious or synoecious, antheridia central, surrounded by a row of archegonia. Two or more capsules produced from the same perichaetium. Subsequently the axis is produced so that the fruit stalks appear lateral, and a new inflorescence and fruit may be formed at the fresh apex the following year. Capsule narrowly cylindric, suberect, hardly curved. Very rare. Broxbourne, Vaizey.' Dixon added that the plants were given a provisional varietal status only, since he had not examined the specimens collected by Vaizey i.e. C.lateralis Vaizey.

C.angustata was described as resembling 'Small forms of C.undulata , leaves obtuse, less undulate, with smaller aerolation, the margin serrate only in the upper half, lamellae 5-7, in section 5-8 cells, dioecious, capsule nearly erect and only slightly arcuate or almost straight, narrower in proportion to its length than in C.undulata.'

C.crispa was said to grow in 'Tufts, stems 2-4 inches, leaves distant, large,hardly at all undulate, border dentate from near the base, lamellae very low and indistinct, 1-4, frequently interrupted and vanishing in the lower half of the leaf, in section 1-3 large cells .' The aerolation was 'Larger than in the previous species.'(i.e. C.undulata) and the plants were 'Dioecious, although only male and sterile plants have been found in Britain, growing on the sides and beds of rocky streams in grass and sand.' A variety C.crispa var densifolia Lindb. was said to grow at Oakmere, Cheshire. This plant was dwarf and had 'Leaves crowded, broader and more elliptical, patulous.'

Dixon considered that all the British specimens named C.tenella which he had examined were in fact C.undulata varβ minor .The true C.tenella was 'Dioecious, of a deep green colour, with shorter, hardly undulated leaves, with fewer lamellae and a more inclined capsule.'

The 1904 and 1924 editions of the Handbook differed from each other only in the mention of the variety C.angustata varβ rhystophylla (C.M.) Dixon in the 1924 edition. They both differed from the earlier edition in that measurements of leaf size and cell size were given in the key for the identification of species and also in the descriptions of the species. Also a full description of C.tenella as a British species was included. Under the description of C.undulata in the 1924 edition was added 'Leaves 2-3 lines long, cells of leaf and lamellae 18-22u in diameter.' Of the variety C.undulata varγ Haussknechtii Dixon stated that it was better considered a sport than a true

variety, especially since the form of the inflorescence was such an unstable character in this species. Under C.angustata was added the information 'Leaf cells and cells of the lamellae 12-14u in diameter.' The variety C.angustata varβ rhystophylla differed from the species in having 'Leaves strongly undulate, sharply toothed both at margin and back. Kent, Sussex, CoDown.' Dixon was in doubt as to the validity of this variety and said that it was connected to C.angustata by plants of intermediate character. C.crispa was stated to have 'Leaf cells 25-45u in diameter.' The full description of C.tenella was as follows 'Resembling C.undulata varβ minor, in loose tufts ½-1 inch high, upper leaves oblong-lanceolate or lanceolate, 1½-2 lines long, scarcely undulate, with few or no spines at the back, lamellae 2-4, each of 3-6 cells, leaf cells 18-27u in diameter. Dioecious, seta short, less than 1 inch, capsule very short, obovate or oblong. On sandy or clayey ground, very rare. Bedgbury, Kent.' In a note Dixon compared it with C.undulata varβ minor, the difference lying in the dioecious nature of C.tenella.

Warnstorf (1914), in a paper on the distribution of bryophytes in Russia, included a note on the composition of the perichaetium in C.undulata and C.Haussknechtii (Jur and Milde,) Brotherus. He had found plants of C.undulata in which either archegonia or antheridia were found in the perichaetium. In such plants cross fertilization would probably take place even if subsequent growth of the axis produced a second perichaetium containing organs of the opposite sex. Paroecious plants were also found in which both kinds of sex organs

were formed on the same stem but were separated by development of the shoot. Some plants had terminal antheridia with older archegonia borne below on the stem. In this arrangement cross fertilization could take place more easily than self fertilization. If fertilization did occur, and a scarcity of sporophytes suggested that it was a rare occurrence, the capsule appeared to be lateral in origin. In the more normal paroecious plants, however, the archegonia were borne above the antheridia and the sporophyte appeared to be terminal. Thus purely female and purely male perichaetia occurred in C.undulata, as well as perichaetia containing both male and female organs. In C.Haussknechtii the perichaetium was apparently synoecious, the archegonia and antheridia developing simultaneously in the axils of the leaves. In these perichaetia the archegonia tended to lie towards the periphery of the group. In such an arrangement self fertilization could easily take place. Plants were found however, with purely female perichaetia. Usually several sporophytes were formed in a single perichaetium and subsequent growth of the axis made them appear lateral. Single sporophytes which appeared terminal were also observed. Warnstorf concluded that plants of C.undulata and C.Haussknechtii could not be separated on perichaetal characters or leaf morphology alone. The only constant difference lay in the diameter of the spores, that of C.undulata being 16-24u and that of C.Haussknechtii 8-15u.

Herzog (1926) stated that, in Europe, C.Haussknechtii supplanted C.undulata on the southern slopes of the Transsilvanian Alps and that in the Northern range it was one of the dominant mosses of the

bryophyte flora. C.tenella was found only on the Atlantic coast of Europe in a restricted range, and C.crispa only in Britain and North America.

The decision of the International Botanical Congress that bryophyte nomenclature should use as a starting point Hedwig's 'Species Muscorum'(1801) or Linnaeus's'Species Plantarum' (1753) for true mosses and Sphagna respectively, has resulted in the genus Catherinea now being known as Atrichum P.Beauv.

In the 'Annotated List of British Mosses'(1950) compiled by Richards and Wallace, the following species of Atrichum are listed.

1). A.crispum (James) Sull.

2). A.undulatum (Hedw.)P.Beauv.

β minus (Lam.and D.C.) Web.and Mohr.

γ haussknechtii (Jur.and Milde.) Frye.

3). A.angustatum (Brid.)B.and S.

β rhystophyllum (C.M.) Richards and Wallace.comb.nov.

4). A.tenellum (Rohl) B.and S.

The most recent work on the genus in Britain has been carried out by Rose (1950). His paper was concerned mainly with A.undulatum and A.angustatum , but A.tenellum was also mentioned. Leaves of A.undulatum usually had five or six lamellae, rarely seven, while those of A.angustatum usually had five, but occasionally four or six. The capsules of the latter were often as arcuate as those of A.undulatum but were always smaller and more slender. The leaf cells of A.angustatum

were 10-18u and the spores 11.3u in diameter, while the leaf cells of A.undulatum were 18-25u and the spores 21.7u. These results were based on very small samples. Plants collected by Rose from Combwell Wood Kent, were identified by Crossland as A.undulatum var β minus . The gametophytes were about the size of those of A.angustatum but agreed structurally with A.undulatum , while the capsules resembled A.undulatum in form but were rather smaller. Leaf cells were of the same size range as A.undulatum but the average spore diameter was only 13.3u, and many of the spores were dead and shrivelled. A hypothesis that the plants originated from 'stunted female gametophytes of A.undulatum being fertilized by male plants of A.angustatum' was advanced in this paper. Of A.tenellum , collected in Kent, Rose stated 'The leaves were broad, ovate and scarcely undulate, with 2-4 lamellae and few weak spines on the lamina.' A relationship between A.tenellum and A.crispum was suggested.

Lowry (1954) after examining American specimens of the genus Atrichum , stated that the species differred only quantitatively from each other. A.cripsum had 'Stems up to 5cms, upper leaves oval-oblong to lanceolate-oblong, less than 5mms long and 1mm wide, smooth or slightly undulate, lamina not toothed at the back, margin serrate to half of the length, teeth single or double, leaf cells 20-25u in diameter, lamellae 0-3, 1-3 cells high. Plants unisexual, spores 16-20u in diameter.' He considered A.angustatum and A.xanthopelmum to be the same species the latter merely having papillose cell walls. A.angustatum had 'Stems up to 5cms rarely

branched, upper leaves 4-5mms long, 0.6.-0.75mms wide, undulate with teeth on the back of the undulations, leaf cells 10-15u in diameter, lamellae 4-7, 7-9 cells high. Plants unisexual, spores 10-14u in diameter.' These characteristics were stated by Lowry to be the same as those of the Japanese material examined by Kurita (1937). Of two races of A.undulatum, one (N=7) was unisexual and the other (N=14) bisexual. They were indistinguishable morphologically and his description was as follows 'Plants up to 8cms rarely branched, upper leaves 5-9mms long, 1.0-1.3mms wide, undulate with teeth on the backs of the undulations, margin serrate almost from the base, most of the teeth double, leaf cells 18-40u in diameter, lamellae 2-6, 2-6 cells high. Plants bisexual(N=14) or unisexual (N=7). Spores 9-23u in diameter.' A.undulatum varβ minus was dismissed as a depauperate form of the species, not a true variety, and Frye quoted in support of this view. A.Selwyni was not examined but from data obtained from other publications Lowry supposed it to be a unisexual race of A.undulatum.

It is interesting to note that although A.crispum and A.angustatum both showed a range of 5u in cell size and 4u in spore size, the N=14 and N=7 specimens of A.undulatum examined by Lowry showed a range of 22u in cell size and 14u in spore size. Lowry however, did not comment on this fact.

The following descriptions of the species are compiled from the data already given.

A.crispum(James) Sull.

Height up to 10cms, upper leaves distant, oblong lanceolate,

up to 5mms long and 1mm wide, hardly undulate, no spines on the lamina, margin dentate from near the base, lamellae 0-5, 1-3 cells high, often interrupted, leaf cells 20-45u in diameter. Plants dioecious, only male and sterile plants so far found in Britain. Fertile material found in America. Capsules erect, spores 16-20u in diameter. On the sides and beds of rocky streams.

A.crispum var β densifolium Lindb.

Plants shorter than those of A.crispum, leaves crowded, broader and more elliptical. Found at Oakmere, Cheshire.

A.angustatum(Brid.) B.and S.

Plants up to 3cms in height, rarely branched, upper leaves 4-5mms long, 0.60-0.75mms wide, leaves scarcely undulate (except in American and Japanese material) with spines on the back of the lamina, lamellae 4-7, 7-9cells high, leaf cells 10-18u in diameter. Plants dioecious, capsule erect or suberect, narrow in proportion to its length. Spores 10-14u in diameter. Found on sandy or clayey soil in woods.

A.angustatum var β rhystophyllum(C.M) Richards and Wallace.

Leaves undulate, sharply toothed at the back and margin.

A.tenellum (Rohl) B.and S.

Plants up to 2.5cms in height, upper leaves 4mms long not undulate, few spines on the lamina, margin serrate, lamellae 2-4, 3-6 cells high. Leaf cells 18-27u in diameter. Plants dioecious. Capsule small, obovate, slightly inclined. Found on damp, sandy or clayey soil,

A.undulatum.(Hedw.)P.Beauv.

Plants up to 8cms in height, upper leaves 5-9mms long, margin serrate, lamellae 2-7,2-6 cells high. Leaf cells 18-25u in diameter in British material, 18-40u in American material. Inflorescence autoecious but often apparently dioecious in British plants, subject to much variation. American plants monoecious or dioecious depending on whether they are the N=14 or N=7 race. Capsule strongly arcuate, spores 16-24u in diameter in British material, 9-23u in American material.

A.undulatum varβ minus.(Lam. and D.C) Web.and Mohr.

Plants smaller in every way than the species.

A.undulatum varγ haussknechtii (Jur.and Milde)Frye.

Plants up to 2.5cms in height, slender, leaves resembling those of A.undulatum but with small spines on the lamina. Plants monoecious, perichaetium synoecious or paroecious, capsules resembling A.undulatum, spore diameter 8-15u. Occurring in Europe in mountainous districts.

CHAPTER II.

REVIEW OF THE LITERATURE RELATING TO THE CYTOLOGY OF THE BRYOPHYTES.

Earlier cytological investigations of bryophytes dealt mainly with liverworts. This has been especially true with regard to meiotic phenomena, although Varaama has recently investigated meiosis in mosses in great detail.

Allen (1917, 1919) working on Sphaerocarpos, was the first to describe the difference in morphology of the chromosome complements of the male and female plants. He found a single exceptionally small chromosome in the male set and a single exceptionally large chromosome in the female set and identified these as Y and X chromosomes respectively.

Heitz(1928) investigated many bryophytes with regard to the occurrence of heteropycnotic material in the nucleus, and observed that the sex chromosomes, wherever identified, showed strong heteropycnosis and remained as staining granules in the resting nucleus. In Pellia epiphylla , which is monoecious, the large symmetrical fifth chromosome was heteropycnotic for most of its length, while in the variety Pellia epiphylla var bivalans two such chromosomes were visible. In Pellia Neesiana this heteropycnotic chromosome was the sex chromosome, symmetrical in the female but not in the male. Only one moss, Ceratadon purpureus , had sex chromosomes, although one or more heteropycnotic chromosomes were present in several others. In the Polytrichales, Polytrichum commune, P.piliferum and Pogonatum urnigerum had seven chromosomes, of which one was

heteropycnotic, Polytrichum gracile twelve to fourteen chromosomes of which two were heteropycnotic, and Catherinea undulata twenty to twenty two of which three were heteropycnotic. Previously(1927) N=14-16 had been recorded for C.undulata.

In Japan, Shimotomai and Koyama (1932) investigated the chromosome numbers of several mosses and found that Pogonatum contortum, P.inflexum and Polytrichum formosum all had N=7.

Jachimsky (1935) repeated the work of Heitz and enlarged it in certain respects. He was able to identify sex chromosomes in Ceratadon purpureus, where both were larger than the autosomes, and in Mnium punctatum where both were smaller than the autosomes. He also described heteropycnotic chromosomes in Mnium hornum, Bryum argenteum and B.capillare . He was unable to find sex chromosomes in Barbula unguiculata, Bryum caespiticium and Pogonatum aloides.

Kurita (1937) investigated the chromosomes of several mosses and confirmed that the sex chromosomes, where distinguishable from the autosomes by their size or shape, were always heteropycnotic. A count of N=7 was given for A.angustatum.

No further cytological work on mosses was described until 1943 when Heitz published a note on the correlation of polyploidy and classification in the European species of Mnium. However during the period 1930-40 many papers were published on the cytology of the hepatics. From these works it appears that aneuploidy is a rare occurrence in hepatics. The only naturally occurring example, Pallavicinia Lyellii, was found (Wolcott 1940) as N=8 and N=9 races.

These numbers were due to irregular meiosis in the capsules. Polyploid forms, however occur more frequently. Heitz (1928) reported N=14-15 for Riccia fluitans while Tatuno (1941) found N=8. The latter also found that Dumortiera hirsuta occurred as haploid, diploid and triploid races in Japan, each having a separate restricted range.

The occurrence of these polyploid races has been explained in various ways. Spontaneous doubling of the chromosome number may take place in somatic cells of the gametophyte (Mackay 1937) or in the sporophyte (Knapp 1936). Only in Calobryum rotundifolium however, has an analysis of meiosis, prior to dyad formation, been made. Tatuno (1935) found that after the first meiotic division a restitution nucleus was formed which then divided to form two daughter nuclei, each of which was included in a spore. Marchal (1911) found that regeneration of sporophytic tissue often gave rise to a protonema which had a diploid chromosome number. Plants arising from such a protonema were diploid and showed a reduced fertility. This sterility was overcome in a diploid clone of Bryum caespiticium (Wettstein 1937, 1940, 1942.) where, after many generations the 'gigas' characters were lost and normal fertility restored. Wettstein also found that if the haploid plants were dioecious, then the regenerated diploid plants were less irregular in sex expression. It is of interest to note that Allen (1935) stated that regeneration of sporophytic tissue did not take place in the Polytrichales.

Turning to more recent work, Lowry investigated the occurrence of polyploidy in the American species of the genus Mnium. He found

that the group of Mniums with no teeth on the border of the leaf had a chromosome number based on seven. The double and single toothed Mniums all had a basic chromosome number of six, and the spindle attachment was subterminal or terminal in the double toothed group but could not be distinguished in the single toothed group. Mnium Menziesii had N=5 and so was distinct from both groups. For this reason Lowry considered that it would be better to reclassify it in Leucolepis. In the double toothed group he found that Mn. orthorhynchum and Mn.marginatum, which were dioecious and synoecious respectively, had N=6 and N=12. There were 2587 cells per mm^2 in the leaf of Mn.orthorhynchum and only 2349 per mm^2 in Mn.marginatum. These facts combined with field observations, suggested that the plants were a polyploid pair, of which Mn.marginatum was the autodiploid of Mn.orthorhynchum. Similarly, dioecious Mn.cuspidatum and synoecious Mn.cuspidatum, dioecious Mn.affine and synoecious Mn.medium all appeared to be haploid and diploid members of such polyploid pairs. Indeed Andrews had earlier considered Mn.punctatum and Mn.pseudopunctatum to be forms of the same species. Included in the same paper is a record of N=7 for A.angustatum and N=14 for A.undulatum.

Varaama (1953),working on Finnish mosses, found that the chromosome number in A.tenellum was N=14.

Yano (1951, 1953), working in Japan, investigated the form of the sex chromosomes in species of Polytrichum and found that N=7 in five dioecious species. The sex chromosomes were represented

by the largest chromosome of each set and were heteropycnotic, but no difference could be seen between the X and Y chromosomes. In P.yezoenense, which was monoecious, there were fourteen chromosomes of which two were heteropycnotic; these he identified as sex chromosomes.

Tatuno (1953, 1954) also working on the Polytrichales, published a count of N=7 for Japanese material of A.angustatum . In both sexes he found N=7= 1H(V) +3V +2J +1m(h), the H chromosome being the large sex chromosome. No morphological difference between the X and Y chromosomes occurred. He found that in his material of A.undulatum there were twenty one chromosomes and that two X and one Y chromosomes were present in the gametophyte cells. Plants of A.undulatum var β minus had a chromosome count of N=7.

Lowry (1954) examined certain species of Atrichum occurring in America. A.crispum was strictly dioecious with seven chromosomes in the gametophyte, of which four were long (4.2-6.2u) and three short (2.5-3.4u). A.angustatum and A.xanthopelmum were considered to be two forms of the same species, both having a chromosome count of N=7 of which four chromosomes were long (4.0-6.4u) and three short (2.8-3.5u). Monoecious plants of A.undulatum collected in South Michigan and Tenessee had N=14 but dioecious plants, identical in morphology and occurring only in North Michigan, had N=7. He considered A.Selwyni to be identical with A.undulatum, except that the former is dioecious and the latter usually monoecious, and suggested that A.Selwyni might be a race of A.undulatum with N=7.

He considered that A.crispum, A.angustatum and A.undulatum arose first as an N=7 race which then produced the N=14 race by apospory. The triploid European and Asian races of A.undulatum then arose by hybridization between the N=7 and N=14 races followed by apospory.

CHAPTER III.

METHODS OF INVESTIGATION.

1). Morphological.

Herbarium material was obtained through the courtesy of the Keeper of Botany at the British Museum (Natural History.).

The average height of plants of a single collection was found by measuring twenty plants at random except where otherwise stated in the text. The leaf dimensions were found by averaging the maximum lengths and widths of five of the largest leaves from each of these plants. Herbarium specimens were measured by means of a scale reading to0.02cms. These same leaves were used to find the average number of lamellae on the nerve, spines on the lamina and cells per mm^2 of leaf surface. The number of cells was calculated from counts of cells per 0.08sq mms for A.crispum, 0.04 sq mms for A.tenellum and A.undulatum and, because of the small size of the cells, 0.02 sq mms for A.angustatum . If possible the arrangement of the sex organs was ascertained. Whenever possible the dimensions of twenty sporophytes were measured as well as the angle between the seta and a line drawn perpendicularly through the mouth of the capsule. The average diameter of the ripe spores was found by measuring 200 soaked spores from each capsule.

2).Cytological.

Material was collected and grown for at least a week under warm, damp conditions, prior to fixation . This treatment resulted in an increased rate of mitotic division. The divisions occurred mainly at night or in the early morning and even at these times the number of dividing cells was small. Various reagents were used to macerate the material but none separated the cells from one another while leaving the staining capacity of the nuclei unchanged. To obtain clear mitotic stages in which the number of chromosomes could be counted with some certainty, it was necessary to embed the fixed material in paraffin wax, section the apices and perichaetia at right angles to the young leaves, and stain the resulting sections. Fixation was carried out using Karpechenko's modification of Nawashins solution, and staining was by the Crystal Violet- Chromic Acid technique.

For the examination of the resting nuclei of many plants, it was sufficient to fix material in 1-3 acetic-alcohol for two hours and stain in a saturated solution of aceto-orcein.

To obtain meiotic figures, spore mother cells were squashed into aceto-orcein which both fixed and stained them. The contrast between cytoplasm and chromosomes in poorly staining material was increased by heating the preparations to just below the boiling point of the stain. These mounts were examined, drawn and, wherever possible, photographed, before being made permanent in Euparal Vert.

CHAPTER IV.

EXAMINATION OF THE SPECIES OF ATRICHUM OCCURRING IN BRITAIN.

I. *Atrichum crispum*(James) Sull.

(*C.crispa* James)

Atrichum crispum var β *densifolia* Lindb.

1). Examination of herbarium specimens.

Three collections contained in Dixon's herbarium were examined and the data obtained are summarized below. Plants in all collections bore many intercalary antheridial perichaetia. The plants from Halifax bore neither capsules nor archegonia but those from Tenessee and Long Island were abundantly fertile. No arcuate capsules were found and the spores in the ripe capsules were regularly shaped and green in colour.

Table 1. Gametophyte.

Collection	Height cms	Leaf size cms	Lamellae	Spines	Cells/mm^2
Long Island Grout 1903	2.8	.62x.20	1	0	920
Tenessee Sharp 1935	2.1	.70x.20	0	0	1200
Halifax Brown 1935	2.8	.64x.20	0	0	900

Sporophyte.

Collection	Seta cms	Capsule cms	∠with seta	Spore diameter u
Long Island	1.2	.28x.10	180°	18
Tenessee	1.1	.20x.10	180°	-

2). Collection of living material.

Plants were collected from the banks of the various shallow streams on Dartmoor; the largest collection was made from the River Dart below Wistman's Wood. A.crispum occurred only in open stretches of the rivers and grew in the grass on the river banks and on the bare peat sides of the streams. No plants were found growing between Holne Chase and Holne Bridge although it had been reported as growing there abundantly.

Material from Oakmere, Cheshire, was collected from the bare peat and sand surfaces surrounding the mere. These plants belonged to the variety A.crispum var β densifolium.

3). Morphology.

An examination of plants of A.crispum and A.crispum varβdensifolium showed that there was a small difference in cell size between the two forms. This was the only constant difference. The length of the leaves of the Devon plants varied from 0.30 to 0.70cms and the length of the leaves of the Cheshire plants from 0.35 to 0.60cms. The lamellae on all the leaves examined were indistinct, rarely running the whole length of the leaf, and varied in number from 0 to 3. All leaves examined were non-undulate and without spines on the back of the lamina. Fifty plants were examined from each collection made and the average cell size in each plant found from readings made on five leaves. There was an average of 850 cells per mm^2 of lamina in the Devon plants and 875 in the Cheshire plants. After cultivation in a cold frame for

ten months, the newly formed leaves on the plants previously examined were indistinguishable from each other (Fig 1). Since under identical experimental conditions the two types of plants reacted similarly, any differences between the plants in the field are probably due to differing environmental conditions.

The plants bore the remains of many perichaetia at the time of collection. In the Devon material proliferation had taken place through the perichaetia and in some cases a second perichaetium had been formed. In the Cheshire plants proliferation had rarely taken place. Under cultivation in a cold frame antheridial perichaetia were formed freely and proliferation took place in both Devon and Cheshire plants. No archegonia were found on the plants growing in the field or under frame conditions.

4). Hybridity with other species.

Motile spermatazoids were obtained from antheridia of A.crispum and attempts were made to fertilize the egg cells of A.angustatum, A.tenellum and A.undulatum (N=21). These were unsuccessful, although female plants of the other species, used as controls in the same pots, were easily fertilized by spermatazoids of their own species.

5). Cytology.

Resting nuclei in the gametophyte contained two conspicuous granules which stained with aceto-orcein. In sections stained with Crystal Violet and washed in clove oil it was apparent that one of these

was in the nucleolus.(Fig 17).At early prophase a precociously condensed V shaped chromosome could be distinguished (Fig 18). At mitotic metaphase seven chromosomes were distinguishable, of which three were J shaped and four V shaped (Fig19). No morphological difference was found between the chromosomes of the Devon and Cheshire plants. All cells examined contained seven chromosomes and no cells were observed with an unusual number of heteropycnotic bodies.

Atrichum angustatum (Brid.) B. and S.

(syn. C.angustata Brid.)

Atrichum angustatum var β rhystophyllum (C.M.) Richards and Wallace.

(syn. C.angustata Brid. var rhystophylla(C.M.)Dix.)

1). Examination of herbarium specimens.

Herbarium specimens from Europe and America were used since Asiatic material presented too wide a range of morphology to make it practical to include it in this work. Five collections included in Dixon's herbarium were used and data are summarized in Table 2.

Table 2. Gametophyte

Collection	Height cms	Leaf size cms	Lamellae	Spines	Cells/mm^2
Tirol Dixon 1904	1.2	.40x.06	6	118	6720
Granada Muma 1925	1.2	.46x.06	7	172	6650
Ohio Newell 1929	3.0	.66x.07	6	80	7100
Pyrenees Husnot	1.3	.40x.07	5	140	6300
New York Chamberlain	1.0	.42x.06	6	146	6350

Sporophyte

Collection	Seta cms	Capsule cms	∠with seta	Spore diameter u
Tirol	1.4	.50x.06	180°	13
Ohio	0.8	.40x.07	170°	13
Pyrenees	2.1	.45x.07	180°	12
New York	1.2	.50x.07	175°	13

Four collections of British material at the British Museum were examined, including the specimens collected by Mitten from Hurstpierpoint. Data are summarized in Table 3.

Table 3. Gametophyte.

Collection	Height cms	Leaf size cms	Lamellae	Spines	Cells/mm^2
Sussex Mitten	2.8	.40x.04	6	102	5650
Perthshire McKinlay 1864	1.3	.40x.05	6	48	6150
Kent Nicholson 1898	2.8	.45x.05	5	74	6970
Surrey Shepherd 1892	0.8	.40x.05	5	93	6930

Sporophyte.

Collection	Seta cms	Capsule cms	∠with seta	Spore diameter. u
Perthshire	1.6	.40x.05	180°	12
Kent	1.3	.40x.06	175°	12

All the specimens examined had non-undulate leaves and all were strictly dioecious.

From these data the following description of A.angustatum may be constructed:-

Plants up to 3cms in height, generally about 1.7cms. Leaves

non-undulate, .40-.46cms long, .04-.07cms wide, 5600-7100 cells per mm^2 of leaf lamina, lamellae 5 or 6, 40-170 spines on the lamina. Dioecious Seta about 1.2cms long, capsule .40-.50cms long and up to .07cms wide, erect or inclined. Spores 12-13u in diameter.

A.angustatum var β rhystophyllum.

There were four collections of this variety in Dixon's herbarium and data concerning these are summarized in Table 4.

Table 4. Gametophyte.

Collection	Height cms	Leaf size cms	Lamellae	Spines	Cells/mm^2
Austria 1900 Loitlesberger	1.4	.45x.04	6	88	6530
Lake Maggiore Nicholson	1.6	.50x.04	6	150	6420
Portugal Dixon 1911	1.3	.50x.04	6	140	6550
Bussaco Dixon 1911	1.6	.70x.05	6	80	6530

Sporophyte.

Collection	Seta cms	Capsule cms	∠with seta	Spore diameter u
Lake Maggiore	2.1	.30x.05	160°	13
Bussaco	1.5	.45x.06	125°	13

Plants bearing undulate leaves were found only in the collections from Bussaco and Austria and even here only a few leaves on each plant showed this character to any extent. In the other collections the leaves were rigid and non-undulate, as in the plants of A.angustatum previously examined. The capsules from Lake Maggiore and Bussaco were unique in that they were arcuate and borne inclined on the setae. Those from Lake Maggiore were also shorter than those of the other collections.

In addition, two Irish collections of A.angustatum var β rhystophyllum were examined. Several of these plants bore undulate leaves which were wider on the average than those of the previous collections. Data are summarized in Table 5.

Table 5.

Collection	Height cms	Leaf size cms	Lamellae	Spines	cells/mm^2
CoDown Lett 1909	1.4	.42x.14	6	62	7520
CoDown Waddel 1910	1.6	.42 x .15	6	48	5920

A comparison of A.angustatum and A.angustatum var β rhystophyllum shows that there is little constant difference between the specimens examined. The plants of the variety have longer leaves than those of the species and specimens from Bussaco, Austria and Ireland bear undulate leaves. This is a character of the variety but it was not found in the other collections. The plants from Bussaco and Lake Maggiore

bear arcuate capsules but this is not a character of A.angustatum var.rhystophyllum.

2). Collection of living material.

A.angustatum was collected from Kent where extensive growth of this species occurs in the Castanea sativa plantations of Sissinghurst and Bedgbury. These populations had a cycle of population size ultimately determined by the coppicing of the Castanea. Coppicing was carried out every nine years and the resulting lack of shade and drying of the clay destroyed all traces of living Atrichum plants for two seasons. After this period of time, isolated plants were found in the rides and the number increased in further years until again reduced by the coppicing. Female plants were found most abundantly on the sides of cart ruts in shady rides. Sporophytes were found growing in damp, shady places; in drier places, such as Bedgbury, few sporophytes were found.

3). Morphology.

The gametophyte.

Seventeen populations of plants of both sexes were collected from Sissinghurst and Bedgbury during May 1950. The size of the leaf cells was determined by examining two leaves from each of fifty plants selected at random from each population. No certain distinction could be made between male and female plants at this time of the year. The distribution of cell size in leaves from plants collected direct

from the field, is shown in the first graph, drawn with a solid line, in Fig 3. The second curve, drawn with a broken line, shows the distribution of cell size in new May formed leaves of these same plants when all had been growing under identical conditions in a cold frame for a year. Although a wide range of cell size occurs when plants grow in the field, the range is reduced when plants are all grown under the same conditions. This range, however, is large when compared with that of a single clone of male plants, grown under the same conditions. The cell size distribution of these plants is shown in Fig 3 with a dotted line. The wide range is interpreted as due to either a difference in cell size between male and female plants included in the first random sample from the seventeen populations, or to a difference in cell size between races of the species.

In order to investigate this problem, leaves of both male and female clones of plants were examined at different times of the year to determine how leaf characters, and especially cell size, vary with the different seasons. The collections examined previously were divided into seventeen male populations and fifteen female populations and these were grown separately under identical conditions in a cold frame. Fifty plants were selected at random from each pot at monthly intervals and leaves formed during that month were examined. Some male plants bore antheridia during June and July and because of the modification of the perichaetal leaves, were not included in the sampling. No constant difference in cell size was found between populations of the same sex during one month, but, as can be seen

from Fig2, there was a striking difference between the cell size of male and female plants during the summer months. The cells formed by the female plants during July and August were so much smaller than those of the male plants (7000-7300 as against 5000 per mm^2 of lamina) that this character could be used to separate the two sexes when they were growing under identical conditions. These results suggest that the cell size distribution shown by the original seventeen populations under cultivation, was due to the difference of cell size of the leaves of the male and female plants.

There was no seasonal change in the number of lamellae borne on the nerve of the leaves. The number varied from four to eight in the plants collected from the field, but after cultivation in a cold frame, five were formed on the new leaves of all plants except one clone from Sissinghurst in which seven were formed. The number of spines on the lamina varied from 90 to 130 and it was not possible to determine the factors affecting their formation.

A search was made for plants approximating to the variety A.angustatum var β rhystophyllum. Although some of the plants collected bore undulate leaves characteristic of this variety, when these plants were grown in a cold frame the new leaves were completely non-undulate. This suggests that the character of undulate leaves in A.angustatum is environmental in origin and that the separation of A.angustatum from A.angustatum var β rhystophyllum on this character alone is invalid.

The sporophyte.

Field collections of mature sporophytes made during October and November showed that there was a variation in the form of the sporophyte. The majority of capsules were erect and slender but a proportion of those collected during November were arcuate. 150 capsules were collected on October 3rd, 173 on October 27th and 180 on November 17th 1951. Measurements were made on these capsules of the variation in the angle between the seta and a line drawn perpendicularly through the mouth of the capsule, and these results are shown graphically in Fig 4. Although there were erect capsules in all collections, there was a higher proportion of arcuate capsules in the November collection than in the others.

An attempt was made to investigate the formation of these arcuate capsules by the use of controlled conditions.

1). 170 plants bearing young sporophytes were collected at random from the field and grown in pots in an unheated greenhouse(15°-22°C) until mature. All the 170 capsules formed on these plants were erect and averaged 0.45cms in length and 0.06cms in width.

2). 20 sporophytes were obtained by crossing clones of plants which had invariably borne erect capsules when grown in an unheated greenhouse. These were matured under conditions of high humidity in an unheated greenhouse. The mature capsules were all erect and averaged 0.46cms in length and 0.06cms in width.

3). 60 sporophytes were obtained by the same method used in 2). and were matured at 15°-22°C under conditions sufficiently dry to

curl the ends of the leaves. The mature capsules were all erect and averaged 0.46cms in length. Their average width, however, was reduced to 0.04cms.

4). 160 capsules were obtained by the methods used in 2) and 3), and were separated into four groups. The plants were grown in pots and each group was subjected to a temperature of 4-8°C for 24, 48, 72 or 120hours when the capsules were immature. It was not possible to know the exact stage of development of each capsule, so that, when whole pots were treated, some capsules were at a slightly different stage of development from the others. This may have influenced the results of this experiment. The degree of bending in these four groups is shown in Fig5. 60% of the capsules treated for only 24 hours were erect and the remaining 40% were only slightly arcuate. 40% of the capsules treated for 48-72 hours were erect and 25% of them strongly arcuate. When the sporophytes were treated for 120 hours, less than 20% of the capsules were erect; 80% were arcuate with a value of θ from 140° to 165° and a few had a value of θ as small as 115°. The erect capsules averaged 0.45cms in length and 0.06cms in width but the arcuate capsules had lengths varying from 0.4 to 0.3cms and widths up to 0.1cms.

These results suggest that the temperature during maturation of the capsules affects their final form in A.angustatum. Capsules matured at temperatures below 8°C are likely to be more arcuate than those matured at higher temperatures. During years when there are early frosts and cold weather, a higher proportion of such arcuate capsules might therefore be expected.

Spores were examined from 200 arcuate and 200 erect capsules collected from the field and an average spore diameter of 13u was found in both types of capsule. Fifty spores from each capsule were sown on Culture media (Beijerinck's agar) under artificial illumination. The cutting off of a cell within the spore or the formation of a protonema by protruberance of the spore wall, was taken as evidence of germination. Under these conditions 85% of the spores from the erect capsules germinated but only 60% of those from arcuate capsules did so,.

Fifty immature capsules were maintained at 4°-8°C for 120 hours and then matured in an unheated greenhouse. 50 spores were measured from each capsule and an average spore diameter of 12 u was found. When these spores were sown on culture medium and illuminated only 37% germinated. Twenty eight dyad and giant spores were found amongst the 2500 examined but none of these germinated under experimental conditions. These results suggest that although the arcuate capsules produced experimentally by treating the sporophytes with low temperatures approximate morphologically to those arcuate capsules occurring in the field, the wild capsules are produced by less damaging conditions since a higher percentage of their spores germinate sucessfully. The occurrence of dyad and giant spores in the experimental capsules makes it likely that similar spores may be formed in the field during years of exceptionally low autumn temperatures.

4). Hybridity with other species of Atrichum.

Female plants of A.angustatum were crossed with A.crispum , A.tenellum, A.undulatum (N=21) and A.undulatum (N=14). Fertilization of the egg by spermatazoids of A.tenellum occurred in three out of four hundred and fifty crosses. A few divisions of the zygote took place and then growth ceased. Spermatazoids of A.undulatum (N=21) also effected fertilization in ten out of four hundred crosses. Six of the sporophytes grew to about 2mms in length and then died; four mature sporophytes were finally formed. The mature capsules were 0.31-0.35cms in length and 0.04cms in diameter. They were completely erect and contained spores which were irregular in shape and did not germinate on culture media. Because of lack of material, it was not possible to make cytological preparations of these hybrid sporophytes.

Spermatazoids of A.angustatum fertilized egg cells of A.tenellum and A.undulatum (N=21). The hybrid sporophytes formed by these crosses are described in detail under the sections relating to the female parent.

5). Cytology.

Resting nuclei of both male and female gametophytes contained one large and two small heteropycnotic bodies, one of which was in the nucleolus. During prophase, the large body increased in size and became a V shaped chromosome, while the small body formed the arm of a J shaped chromosome (Fig 24). In fortyfive specimens seven chromosomes were counted at metaphase, forming a complement of three

J shaped and four V shaped chromosomes. These are illustrated in Fig 25. This number agrees with that found for American and Japanese material by various workers (Kurita 1937, Lowry '50, Tatuno '53). One V shaped chromosome was smaller than the rest but not so small as to correspond to the 'h' chromosome of Tatuno. None of the material examined showed evidence of polyploidy.

Collections of green capsules were made from the field on October 3rd, October 27th and November 17th, 1951. The capsules were immediately fixed and stained and between 1000 and 1500 dividing spore mother cells examined from each capsule. Seven bivalents were formed at meiosis in all capsules and the average diameter of the spore mother cells was 11 u. Less than 0.1% of the dividing spore mother cells in all except one capsule collected from the field during October, contained anaphase bridges and fragments or supernumary nuclei. In the one capsule 6% of the spore mother cells contained such meiotic irregularities. In contrast, 9% of the spore mother cells of capsules collected during November contained anaphase bridges and fragments. Eight giant spore mother cells were also found in one of these capsules.(Table 6). Thus there is an increase in the amount of irregularity of division in spore mother cells of capsules maturing late in the season in the field. This increase occurs at the same time as the increase in the number of arcuate capsules in the field.

On each of the occasions that capsules were collected from the

field, twenty immature sporophytes were also collected and matured in a cold frame and when ripe were fixed and stained. Seven bivalents were formed at meiosis in all these capsules. Less than 0.1% of all the dividing spore mother cells showed any irregularity of division at meiosis.(Table 6). This provides further evidence that the irregularities found in dividing spore mother cells of capsules maturing in the field were of environmental origin.

Table 6 .

Collection		Number of capsules	Number of cells examined	Number of cells with irregularities
Oct 3rd.	Field	23	23,000	19
	Frame	20	5,000	0
Oct 27th	Field	17	17,000	7
		1	1,200	71
	Frame	20	5,000	0
Nov 17th	Field	41	48,600	4471
	Frame	20	5,000	4

9 sporophytes, obtained by experimental fertilizations, were matured under dry conditions. In these capsules 970 of 1800 dividing

spore mother cells contained some form of irregularity at meiosis. The most frequent irregularity was the slow separation of bivalents at first anaphase, resulting in the exclusion of chromosomes and chromosome fragments from the nuclei. If the cytoplasm became furrowed at this stage and cleavage took place, no further division of the nuclei occurred. Dyad spores, containing up to three nuclei, were observed. Capsules containing such a degree of irregularity were not found in the field.

10 sporophytes obtained from experimental fertilizations, were maintained at a temperature of 4°-8°C for 120 hours and then matured in an unheated greenhouse. 191 of 2,000 dividing spore mother cells contained irregularities of meiotic division and 18 giant spore mother cells were found (Fig 39). As far as could be determined, one such giant cell had six or eight bivalents on the metaphase plate at meiosis and since the amount of chromatic material present appeared not to be greater than that in a normally sized cell, it seemed likely that the giant cell was not polyploid. Thus capsules maturing in the field late in the season and capsules matured at a low temperature under controlled conditions, showed a similar degree of meiotic irregularity.

The following results may explain the formation of giant spore mother cells with a normal number of chromosomes in them. Investigations into the development of capsules of Tortula muralis (N=60 and N=26-28) by the present author, have shown that treatment with low temperature

checked the mitotic division of some of the cells of the capsule. Division of the sporogenous tissue occurs more or less simultaneously throughout a capsule in this species so that there is reason to believe that all cells undergo the same number of mitotic divisions prior to meiosis. These divisions are accompanied by little cell enlargement so that cells missing one mitotic division will be larger than those completing the full number. Capsules maturing during low temperatures in the field have more giant spore mother cells than those maturing at higher temperatures. It is not improbable that the formation of giant spore mother cells in the genus Atrichum may be accounted for in the same manner although this was not subjected to experiment.

Atrichum tenellum (Röhl) B.and S.

(syn. C.tenella Röhl.)

1). Examination of herbarium specimens.

Material was obtained from three collections in Dixon's herbarium. These were collected in Norway by Nicholson and Dixon and data concerning these specimens are summarized in Table 6.

Table 6. Gametophyte.

Collection	Height cms	Leaf size cms	Lamellae	Spines	Cells/mm^2
Trojafach 1892	1.0	.55x.08	4	35	2470
Hardanger 1900	0.8	.65x.08	5	64	2310
Vossevangen 1900	0.8	.50x.07	4	24	2360

Some of the leaves on plants from all three collections were undulate. Four lamellae were formed on the nerve of the plants from Trojafach and Vossevangen but the plants from Hardanger bore from three to six lamellae. No antheridia were found on any of the plants although approximately two thirds of the plants bore fertilized archegonia and young sporophytes at the stem apices

Material from seven collections made in Britain was examined and data are summarized in Table 7. No undulate leaves were found on plants of these collections. There were many fertilized archegonia at the stem apices but no antheridia were found. An examination of the contents of the capsules revealed that many of the spores were irregularly

shaped and often occurred in unseparated tetrads.

Table 7. Gametophyte.

Collection	Height cms	Leaf size cms	Lamellae	Spines	Cells/mm^2
Northshire French 1875	0.5	.34x.07	4	6	2310
Goudhurst Nicholson 1898	0.5	.40x.07	4	9	2450
Goudhurst Stirling 1905	0.45	.32x.07	4	8	2750
Glen Nevis Nicholson 1923	0.4	.30x.06	4	0	2520
Ben Lawers McKinlay	1.0	.34x.07	4	0	2350
Lancashire	0.5	.40x.07	4	5	2470
Invernesshire	0.4	.32x.05	4	0	2350

Sporophyte.

Collection	Seta cms	Capsule cms	∠with seta	Spore diameter u
Goudhurst Nicholson 1898	1.4	.15x.08	180°	18
Ben Lawers	0.8	.15x.08	180°	18

A further batch of material which, as far as could be ascertained, was distributed by Schimper in 1865, was examined and data are summarized

in Table 8. The plants had been sent to various interested bryologists and represented three separate collections. Habitat data relating to the third collection was not decipherable.

Table 8 Gametophyte.

Collection	Height cms	Leaf size cms	Lamellae	Spines	Cells/mm^2
Silesia	0.8	.44x.06	4	7	2510
Breslau	0.7	.40x.06	4	10	2520
-	1.8	.52x.07	4	8	2420

Sporophyte.

Collection	Seta cms	Capsule cms	∠with seta	Spore diameter u
Silesia	1.4	.12x.08	180°	17
Breslau	1.0	.12x.08	180°	20
-	1.9	.25x.08	170°	18

No undulate leaves were found on any of the plants and no antheridia were discovered.

Although these German plants were much larger than those collected from Britain, the size of the leaf cells was very similar and few

spines were formed on any of the plants. The Norwegian plants, especially those from Hardanger, bore many spines on the leaf lamina. The capsules on the Silesian and Breslau plants were very similar to the British sporophytes in morphology and also resembled them in the diameter of the spores.

Material was obtained from Professor Varaama which had been collected in Finland in 1950 and which had a chromosome count of N=14. The material consisted of six fertile specimens which had been growing on freshly dug soil in a pine wood near Piikiio. Data are summarized in Table 9.

Table 9 Gametophyte.

Collection	Height cms	Leaf size cms	Lamellae	Spines	Cells/mm^2
Finland Varaama 1950	2.1	.65x.08	4	47	2490
Sporophyte.					
	Seta cms	Capsule cms	∠with seta	Spore diameter u	
"	2.0	.44x.14	110°-140°	-	

The leaves on these plants were faintly undulate. Each plant bore one capsule and the remains of several archegonia but no antheridia. No measurement of spore size was possible since the capsules were immature.

It is of interest to compare these N=14 specimens with the other

plants collected from Britain and Europe. There is little difference in cell size among them but the size of the leaf is regularly smaller in the British and German plants than in the Norwegian plants collected by Dixon and the Finnish plants collected by Varaama. The Norwegian and Finnish plants bear many more spines on the lamina than do the other plants and none of the German or British specimens bear arcuate capsules resembling those of the Finnish plants. These facts suggest that the N=14 plants of Varaama are distinct from the race of A.tenellum found in Britain and central Europe, but may more nearly resemble the race of A.tenellum occurring in Norway.

2). Collection of living material.

Male and female plants were collected from the bed of a dried out pond on Oxshott Common, Surrey. This pond was subject to flooding during the winter months but after 1947 it had become colonized by Betula verrucosa and the annual deposition of leaves had raised the pond floor above flood level. With the drier conditions, A.undulatum and Polytrichum formosum colonized the pond bed from the banks above and replaced the A.tenellum. Plants were also collected from a cutting in a bank at Bedgbury State Forest, Kent. These plants, which were all female, were growing on wet peat overlying clay.

3). Morphology.

The gametophyte.

139 separate collections of five plants were made from the field and these plants used to determine the characters of the species.

The plants varied from 0.3 to 1.4cms in height and bore leaves whose average size was 0.46×0.07 cms. There were four lamellae on the nerve and less than nine spines on the lamina. The percentage distribution of cell size was determined from the leaves and is shown in Fig 6. In 67% of the leaves there were between 2300 and 2500 cells per mm^2 of lamina and in only 4% were there between 2800 and 3000 cells per mm^2. These same plants were cultivated in a cold frame for twelve months and the new leaves examined. A greatly reduced range of cell size was obtained although the average cell size remained the same and this is also shown in Fig 6. These results suggest that the range of cell size occurring in the field may be due to environmental differences. The distribution of cell size in all the leaves of the A.tenellum (N=14) specimens obtained from Varaama is also shown in Fig 6. The average cell size of these plants is little different from that of British A.tenellum plants grown in a cold frame.

All plants of British A.tenellum examined were dioecious. Clones of male and female plants were grown separately for three seasons and only produced either antheridia or archegonia. Male plants were of very rare occurrence in the field. They were less than 0.4cms in height and consisted of either a few modified perichaetal leaves forming an antheridial cup, or of unmodified leaves bearing antheridia in their axils. They were never seen to proliferate through the perichaetium; instead, growth was renewed from the base of the plant. Fertile female plants were of frequent occurrence.

The sporophyte.

The sporophytes collected from the field showed a range in external morphology. Many were borne inclined on the setae but no arcuate capsule was found. 243 mature sporophytes were collected and examined. Their length varied from 0.1 to 0.2cms and their width from 0.06 to 0.08cms. The percentage distribution of capsule length in this collection is shown graphically in Fig 7. 147 plants bearing very young sporophytes were also collected from the field and grown for up to a month in a cold frame until mature. The range of capsule length in these plants was the same as that found in plants maturing in the field but the average capsule length was greater i.e. 0.17cms as against 0.14cms. These 147 plants were then grown for a further season in the cold frame and were crossed with male A.tenellum plants in the laboratory. 73 sporophytes were obtained and matured in the cold frame. The range of size of these capsules was 0.16 to 0.23cms and the average capsule length was 0.21cms (see Fig 7). The larger size of the capsules produced by fertilization in the laboratory may have been due to better growing conditions of both gametophyte and sporophyte in the cold frame. The small size of the capsules, collected immature and matured in a cold frame, may be due to damage suffered by the gametophyte and sporophyte during the transplanting operation.

117 mature capsules collected from the field and 130 capsules grown in a cold frame were used to find the range of spore size. 200 spores were measured from each capsule and the two graphs of spore size distribution are shown in Fig 8. Although the average

spore size is the same for both sets of capsules i.e. 18u, the capsules matured in the field contain spores with a much wider range of spore size. Thus the average spore diameter appears to be very constant within the species but, due to the range in size, many spores must be measured to obtain an accurate result.

Samples of spores from both sets of plants were sown on Beijerinck's agar, soil solution and sterile sand. 50 spores were used from each capsule and grown under artificial illumination. 74% of the spores from capsules matured in the frame germinated within two weeks but only 51% of the spores from the capsules matured in the field did so.

An attempt was made to find which conditions caused the formation of the unusually large and small spores in the wild capsules. Immature sporophytes, obtained by crossing clones of plants in the laboratory, were maintained under conditions of low temperature (4°-8°C) for from 24 to 120 hours. However, capsules were very sensitive to such temperatures and disintegrated before completing their normal development. Under normal field conditions sporophytes would be rarely subject to low temperatures since they develop during the late summer. When 25 immature capsules, produced as above, were matured under conditions such that the tips of the leaves became dry and curled, a range of capsule length was obtained (0.08-0.12cms). The spores in these capsules were irregular in shape and many of the small spores were joined together into tetrads. Judged by their appearance these were dead. The diameter of the green spores averaged 18u but the average diameter of all spores of the capsules was 13u. 50 spores were taken from each

capsule and sown on culture media under artificial illumination. 83% of these spores did not germinate. In Fig9 the distribution of spore size for one capsule is shown graphically accompanied by a graph showing the mortality rate of the different sized spores. All spores smaller than 12u were dead and 50% of those between 12 and 16u in diameter. Many of the spores 26uin diameter were also dead. This result suggests that any lack of moisture during the development of the sporophyte and spores, will result in the formation of many dead and malformed spores. Such conditions may occur when the capsules are maturing in the field during August and September and may have given rise to the high percentage of dead spores observed in the capsules of A.tenellum by several workers.

4). Hybridity with other species.

Female plants of A.tenellum were crossed with male plants of A.crispum, A.angustatum, A.undulatum(N=21) and A.undulatum(N=14). Sucessful fertilization by spermatazoids of A.undulatum(N=21) took place in three out of four hundred crosses, but no sporophytes were formed. Fertilization by spermatazoids of A.angustatum was successful in six out of one hundred and fifty crosses but only two mature sporophytes were formed, the others dying when less than 1mm in length. The two living sporophytes were slow in growth and the capsules were borne on spiral setae. The capsules measured 0.20×0.08cms and 0.22×0.08cms and were completely erect. 30 green spores were obtained from these capsules and averaged 17u in diameter. These were grown on Beijerinck's

agar, in soil solution, and on sand and sterile soil in an unheated greenhouse. Under these conditions they formed protonemal growths which bore groups of thickened cells, but did not form adult plants.

5). Cytology.

Since vegetative male and female plants could not be distinguished from each other, antheridial perichaetia were used to investigate the male gametophyte and archegonial apices to investigate the female gametophyte. In the female plants the resting nucleus contained one large and two small heteropycnotic bodies. During prophase of mitosis the large body differentiated into a large V shaped chromosome (Fig 20). In fourteen male plants all the resting nuclei contained one large and two small heteropycnotic bodies similar to those of the female. In contrast, in three other male plants while most of the nuclei contained three heteropycnotic bodies, the nuclei of some patches of cells in the antheridia contained two large and four small bodies.

All the female plants and the fourteen normal male plants had a chromosome complement of N=7, of which three chromosomes were J shaped and four V shaped (Fig 21). In the male plants with unusual numbers of heteropycnotic bodies, there were twenty seven cells with from ten to fourteen chromosomes in them, besides thirty cells with unusually large amounts of chromatic material (Figs 22,23). All other cells contained the normal number of chromosomes. Thus the formation of polyploid spermatazoids from the abnormal cells of these perichaetia is a possibility.

Green capsules were collected from Surrey and Kent and were immediately fixed and stained. Preparations of meiosis were obtained from 143 of these capsules. In these, seven bivalents were regularly formed at meiosis. 1500 dividing spore mother cells were examined in each capsule and it was found that from 18% to 48% of these contained lagging or excluded chromosomes or cytoplasm dividing at first instead of second metaphase (see Table 10).

Immature sporophytes were also collected from the field and grown in a cold frame. 77 such capsules yielded preparations of meiosis. 1500 dividing spore mother cells were examined in each capsule and from 2% to 8% of these contained meiotic irregularities.(Table 10). This result suggests that the cytological irregularities found in capsules maturing in the field may have been due to environment since the capsules matured in a cold frame had been collected at random from the same populations as the previous 143 plants.

Sporophytes were obtained by crossing clones of A.tenellum in the laboratory and maturing the sporophytes in a cold frame. 15 preparations of meiosis were obtained and seven bivalents were regularly formed in these. Irregularity of division occurred in less than 1% of the spore mother cells. In contrast, up to 60% of the dividing spore mother cells of 10 capsules, obtained by a similar method and matured under conditions of low humidity, contained irregularities of division. These consisted of lagging chromosomes and fragments and the division of the cytoplasm at first instead of second metaphase. This gave rise to spores either lacking a nucleus or containing several nuclei.(Fig 34,35).

These results suggest that the irregular division of the spore mother cells found in the field is not due to hybridity with other species of Atrichum but to environmental effects when the capsules are immature. Such effects may lead to the formation of the unusually small and large dead spores found in capsules in the field.

Table 10

Collection	Matured	Number of capsules with a certain %age irregularity								Total number of capsules
		1%	5%	10%	20%	30%	40%	50%	60%	
Field	Field	-	-	-	14	13	41	75	-	143
Field	Frame	61	16	-	-	-	-	-	-	77
Laboratory	Frame	15	-	-	-	-	-	-	-	15
Laboratory	Low humidity	-	-	-	-	1	-	2	7	10

Atrichum undulatum (Hedw.)P.Beauv.

(syn. C.undulata Web.and Mohr.)

Atrichum undulatum var β minus (Lam.and D.C.) Web. and Mohr.

(syn.C.undulata Web.and Mohr var minor Web.and Mohr.)

Atrichum undulatum var γ haussknechtii (Jur. and Milde.) Frye.

(syn.C.undulata Web.and Mohr var haussknechtii (Jur. and Milde.)

(syn. C.lateralis Vaizey)

1). Examination of herbarium specimens.

Data were obtained from the examination of British specimens and are summarized in Table 11. The height of these specimens varied from 0.8cms to 7.0cms, but within a single collection there was little variation. Leaf length varied from 0.4cms to 1.2cms and there were usually four lamellae on the nerve, although in some collections three, five or six was more frequent. The number of spines on the lamina varied from 6 to 142, the average for all collections being 53. There appeared to be some connection between the number of spines borne on the lamina and the undulate character of the leaves, since no undulate leaves were found with less than 20 spines and leaves with a greater number of spines were undulate unless the leaf cells were both small and thick walled, when the leaves appeared plane. The number of cells per mm^2 of lamina varied from 1750 to 3220 and from all collections the average number was 2540. No correlation could be found between plant height, leaf size and cell size. Seta length varied from 0.3cms to 3.2cms with a mean of 1.4cms The shortest setae (in the collections from Dargle and Shropshire) bore very small, erect capsules; all other capsules were arcuate, from 0.2cms to 0.5cms in length and from 0.08cms to 0.12cms in width. Their mean length was 0.29cms. The angle between the seta and a line drawn at right angles to the mouth of the capsule varied from 100° to 170°, except in the collections from Dargle and Shropshire where the capsules were erect. Apart from the collection from Aberdeen, with spores averaging 27u in diamater, the spore size from all collections varied from 19 to 23u with an average of 21u.

Table 11. Gametophyte.

Collection	Height cms	Leaf size cms	Lamellae	Spines	Cells/mm^2
Cotteral Clough	2.0	.72x.10	4	18	1750
Sutherlandshire Sadler 1827	3.0	.65x.16	2	12	1800
Stoke Wood Dorset 1879	4.5	.70x.12	3	66	2050
Forfarshire (Angus)	7.0	.82x.16	5	28	2120
Winchester Brocus 1852	3.4	.96x.12	3	52	2200
Dennant	2.1	.70x.10	4	28	2200
Cotteral Clough Wilson 1827	1.8	.68x.08	5	64	2250
Bonally Sadler 1855	2.2	.75x.10	5	132	2250
Tunbridge Wells Wilson 1910	2.8	.70x.08	4	50	2300
Aberdeen	3.0	.50x.10	3	18	2350
Radnashire Painter 1899	1.6	.72x.12	6	64	2350
Over Wilson 1826	3.0	.65x.08	4	28	2350
Pentlanos Sadler 1855	1.9	.80 x .10	6	108	2400
Hereford Owen 1909	2.0	1.0x.10	6	84	2410
Breconshire Painter 1900	1.8	.65x.12	5	70	2450

Gametophyte ctd.

Collection	Height cms	Leaf size cms	Lamellae	Spines	Cells/mm^2
Aberdeen Richards 1910	3.6	1.0x.07	6	6	2610
Aberfeldy Black	0.8	.42x.05	4	22	2650
Shropshire Benson 1892	2.9	.82x.10	5	50	2650
Shropshire Benson 1895	2.3	1.2x.07	4	14	2650
Hanwell French 1870	5.5	.80x.14	4	10	2670
Ben Lawers Schenk 1863	4.8	.70x.08	4	46	2670
Cardiganshire Painter 1904	1.9	.60x.10	4	28	2700
Gravesend Pocock	2.4	1.1x.12	4	146	2720
Dorset Wood 1879	4.3	.72 x .08	4	64	2720
Dargle Taylor 1849	3.1	.52x.08	4	54	2770
Flint Richards 1911	1.5	.70x.08	4	88	2800
Penzance Cumon 1862	1.3	.56x.08	5	96	2910
Which Broughton French 1845	1.7	.66x.10	4	100	2950
Douglas Carrol 1874	1.4	.62 x .09	4	68	3100
Caergurle Richards 1907	3.0	.92 x .10	4	72	3320

Table 11 Sporophyte.

Collection	Seta cms	Capsule cms	∠with seta	Spore diameter u
Cotteral Clough	2.3	.40x.10	120°	21
Sutherlandshire	1.1	.25x.08	150°	21
Stoke Wood	2.3	.31x.10	150°	22
Forfarshire	1.3	.30x.12	130°	21
Winchester	1.0	.26x.10	120°	21
Dennant	1.2	.30x.08	150°	21
Cotteral Clough 1827	2.0	.40x.10	100°	20
Bonally	1.8	.35x.10	150°	21
Tunbridge	2.6	.50x.12	120°	20
Aberdeen	1.8	.35x.08	150°	21
Radnashire	1.1	.20x.10	145°	22
Over	2.2	.30x.08	155°	21
Pentlanos	1.2	.30x.08	170°	21
Hereford	2.5	.30x.10	165°	21
Breconshire	1.3	.30x.08	160°	20

Sporophyte ctd.

Collection	Seta cms	Capsule cms	∠with seta	Spore diameter u
Aberdeen 1910	1.0	.25x.10	160°	27
Aberfeldy	0.8	.20x.10	170°	21
Shropshire 1892	2.5	.30x.08	170°	22
Shropshire 1895	0.4	.15x.08	180°	20
Hanwell	2.0	.25x.08	150°	22
Cardigan	1.9	.35 x .10	155°	21
Gravesend	1.9	.30x.08	150°	21
Dorset	3.2	.50x.12	140°	20
Dargle	0.3	.10x.10	180°	-
Flint	1.8	.50x.12	170°	21
Penzance	2.1	.35x.08	155°	19
Which Broughton	1.1	.20x.10	180°	22
Douglas	2.2	.30x.08	145°	21
Caergurle	2.4	.25x.08	135°	19

A.undulatum var γ haussknechtii

The two collections in Dixon's herbarium were from Europe. Data obtained from the collection by Schenk from Czeckoslovakia are summarized in Table 12.

Table 12

Collection	Height cms	Leaf size cms	Lamellae	Spines	Cells/mm^2
Czeckoslovakia Schenk 1915	1.8	.64 x .16	4	244	2440
	Seta cms	Capsule cms	∠with seta	Spore diameter u	
	1.9	.40x.08	180°	13	

Dixon noted of Schenk's collection that 'According to Loeske this variety should have the capsule suberect.In these specimens the capsules are all erect and the plants cannot therefore be of the type.' Since however, the plants had been determined by Loeske, the degree of curvature of the capsule may be considered of little diagnostic importance. The plants of Schenk's collection had a distinctive appearance due to the very broad, undulate leaves. The lamina of these bore numerous, small spines, which were arranged in transverse rows of up to thirteen. The capsules were all borne erect on the setae and contained regularly shaped spores which averaged only 13u in diameter. Investigations of the perichaetium showed that in most cases the archegonia were formed below the antheridia on the stem, and that growth continued after antheridial formation, although plants with terminal archegonia

were also found.

Table 13.

Collection	Height cms	Leaf size cms	Lamellae	Spines	Cells/mm^2
Hallen Lettor 1896	2.2	.48x.08	4	143	2830
	Seta cms	Capsule cms	∠with seta	Spore diameter u	
	2.7	.40x.09	130°	24	

The German plants collected by Lettor (Table 13) bore polysetous perichaetia or ones containing several fertilized archegonia. The archegonia were always borne above the antheridia on the stem. As noted by Warnstorf, this fact alone is insufficient to decide whether the plants are A.undulatum or A.undulatum var γ haussknechtii. The large size of the spores however, suggests that these plants are polysetous specimens of A.undulatum.

Four other European collections of A.undulatum var γ haussknechtii were examined(Table 14). Loitlesberger's collection included plants bearing from one to five setal remains and from one to three ripe capsules in a single perichaetium. Archegonia were never terminal, but there were various arrangements of the sex organs e.g. purely female perichaetia, and ones in which the antheridia and archegonia were borne in the axils of different leaves on the stem and were separated by growth. The gametophyte was not separable from A.undulatum

on any one character, but the form of the sporophyte, resemblingthat of A.angustatum, and the small size of the spores was quite distinctive. The two collections made by Paul consisted of plants bearing young and mature sporophytes. The number of these borne on each plant again varied from one to three, and in all cases there was some proliferation of the stem above the archegonia. The sporophytes were all erect and slender with small spores. In the collections by Kaalaas from Norway there were plants bearing one or two sporophytes and as many as three old setae. In these plants little proliferation beyond the perichaetal group had taken place and the archegonia were always formed below the antheridia. The capsules resembled those of A.angustatum and the spores were small.

Table 14 Gametophyte.

Collection	Height cms	Leaf size cms	Lamellae	Spines	Cells/mm^2
Osterreich Loitlesberger 1903	2.2	.70x.10	4	250	3220
Oberbayern Paul 1902	1.4	.45x.06	5	146	2680
Schliersee Paul 1911	1.6	.60x.08	4	130	2870
Norway Kaalaas	2.4	.70x.14	5	270	3210

Table 14 ctd Sporophyte.

Collection	Seta cms	Capsule cms	∠with seta	Spore diameter u
Osterreich	1.4	.38×.06	180°	12
Oberbayern	1.6	.40×.06	180°	12
Schliersee	1.4	.38×.06	180°	12
Norway	2.0	.36×.06	180°	12

These results suggest that European specimens of A.undulatum var γ haussknechtii can only be distinguished from A.undulatum by the small size of their spores and their slender, erect capsule. The size of the leaf cells is not distinct from that of some specimens of A.undulatum and although the leaves of the variety appear to be more spinous than those of normal A.undulatum, the plants of Lettor with a polysetous inflorescence but a spore size resembling that of A.undulatum, also had highly spinous leaves.

Two collections of A.undulatum var γ haussknechtii from Britain were examined and data are summarized in Table 15.

Table 15.

Collection	Height cms	Leaf size cms	Lamellae	Spines	Cells/mm^2
Buttermere Dixon 1895	2.6	.55x.06	4	60	2370
Walton Wheldon 1898	1.8	.70x.10	5	106	2560
	Seta cms	Capsule cms	∠with seta	Spore diameter u	
	2.1	.28x.08	160°	21	

The specimens collected from Buttermere had been growing in sand in the bed of a stream. They bore several immature sporophytes but since there were no ripe capsules it was not possible to identify them as the species or variety. The plants from Walton bore large arcuate capsules containing large spores, 21u in diameter, and so it is better to regard them as a polysetous form of A.undulatum rather than a species or true variety.

The material collected by Vaizey at Broxbourne, Hertfordshire, and called by him Catherinea lateralis Vaizey, was examined. (Table 16)

Table 16.

Collection	Height cms	Leaf size cms	Lamellae	Spines	Cells/mm^2
Broxbourne Vaizey 1886	2.4	.65x.10	4	98	2630
	Seta cms	Capsule cms	∠with seta	Spore diameter u	
	2.2	.44x.14	140°	22	

The eight Broxbourne plants were large and six bore two capsules and two bore three capsules. Some of the perichaetal groups contained both archegonia and antheridia but lack of material precluded any definite statement on the arrangement of the sex organs. The spores were normally 22u in diameter but occasionally as small as 16u. Thus these plants can be distinguished from European specimens of A.undulatum var γ haussknechtii by sporophyte characters and especially by the much larger spores. It seems better to regard them as a polysetous form of A.undulatum rather than a true species or variety.

A.undulatum var β minus

Three collections of British material of this variety were examined and data are summarized in Table 17.

Table 17. Gametophyte.

Collection	Height cms	Leaf size cms	Lamellae	Spines	Cells/mm^2
Kendal Binstead 1885	0.6	.45x.09	4	10	2130
Hertford Darton 1908	0.9	.60x.10	5	68	2360
Westmorland E.H.K. 1911	1.0	.60x.09	5	74	2280

Sporophyte.

Collection	Seta cms	Capsule cms	∠with seta	Spore diameter u
Westmorland	0.9	.25x.06	165°	21

The plants were much shorter than those of A.undulatum previously examined and those collected by Binstead bore very short leaves. The capsules and setae examined were also smaller than those of normal A.undulatum but the diameter of the spores was the same.

2). Collection of living material.

This species is very widespread and it was possible to collect plants from a variety of habitats in southern England and Wales. Particular search was made for plants showing abnormal sexual characters.

3). Morphology and cytology.

In late autumn plants in the field formed new shoots from their rhizomatous base. These shoots overwintered and in the following spring gave rise to antheridial perichaetia at their apices. Under favourable conditions proliferation of the apex took place through these perichaetia and archegonia were formed after a little growth had taken place. Apical growth of the shoot then ceased. In late spring new shoots arose from the same plant bases and archegonia were formed at the ends of these without the previous formation of antheridia. In the wet Castanea woods of Kent, plants often proliferated from below the archegonial group and caused the sporophytes to appear lateral. These plants were grown in a cold frame and the more normal type of growth, without this proliferation, took place.

A single population in which archegonia but not antheridia

were formed, and two populations in which antheridia alone were formed, were examined. Further investigation of these plants is reported in the section dealing with plants of abnormal sexual character.

3a). Morphology and cytology of normal plants.

The places in which plants were found may be divided into three main types, namely, damp and shady, damp and exposed, dry and exposed. Those plants from dry, exposed places, such as stony hillsides, were short and bore small leaves often with thickened cell walls. Plants from wet, exposed places exhibited the widest range of form, both in plant size and leaf characters. 153 populations were examined from damp, shaded places, 187 from wet exposed places and 147 from dry, exposed places. The variation of cell size and the number of spines borne on the lamina of these plants is shown in Figs 10 and 11. Leaves bearing fewer than 20 spines were found to be non-undulate. After cultivation in a cold frame for a year, the variation in number of cells was very much reduced. A few isolated plants from wet exposed habitats bore leaves with abnormally high numbers of spines on them but were otherwise indistinguishable from the other plants. These results are shown in Figs 12 and 13. Thus plants grown in a cold frame will bear leaves having 2000-2800 cells per mm^2 of lamina.

Observations on 387 populations of sporophytes showed that there was some uniformity of morphology within an isolated group of plants. Exceptionally, malformed capsules or capsules borne several

to a perichaetium, were reduced in size. All capsules were arcuate, the angle between the seta and the line drawn through the mouth of the capsule varying from 120° to 165°, but there was no correlation between the diameter of the capsule and the degree of bending (as in A.angustatum). 387 isolated populations were used to find the distribution of capsule length and 20 capsules were measured from each collection.These results are shown graphically in Fig 14. 100 spores were measured from each capsule and their average size found to be 21u. Up to 70% dead spores were found in some capsules.

Plants of the above populations were grown in a cold frame and the next season were self-fertilized and the resulting sporophytes measured. The variation in capsule length is shown in the second curve on Fig 14. The variation is reduced slightly in plants grown under the same conditions in a cold frame but there is still a wide range of sporophyte size (0.2-0.5cms.) No capsule contained more than 18% dead or malformed spores. The living spores had an average diameter of 21u.

All plants described so far were used for cytological work. The number of heteropycnotic bodies present in the resting nuclei of the gametophyte varied, but generally consisted of three large and three small bodies, the latter occurring in the nucleolus (Fig 28). 23 plants however, had eight such granules (Fig 27) and one population of five plants only five (Fig 26).Mitotic counts of N=21 (Fig 29) were obtained from all these plants. One population of plants of normal

appearance which had motile spermatazoids in the antheridia and fertilized archegonia at the stem apices, had only two heteropycnotic bodies in the resting nucleus and a chromosome number of N=18-19(Fig 30). This was confirmed by investigation of sporophytic tissue.

In thirty three populations from Wales, twenty from Devon and ten from Kent, 21 bivalents were always formed at meiosis. In these plants there was a large range of spore mother cell diameter, the smallest being 15u and the largest normally shaped one 24u in diameter. An irregularly shaped spore mother cell with a diameter of 33u was found in one capsule (Fig 40). In all other populations of plants there was a variation in the number of groups formed at meiosis, even within a single capsule. An analysis of the number of groups at first metaphase in capsules from seven populations is given in Table 16. It can be seen that in these capsules the number of groups was never less than eighteen and never more than twenty three. Some of the larger configurations found were possibly polyvalents, and some of the small ones were certainly univalents since they were round and remained undivided on the equator at anaphase or passed slowly to one pole without dividing.

Figs 41-44 were drawn from a single capsule, collected in Kent, in which twelve out of the two thousand cells examined showed some form of irregularity at meiosis. An analysis of this capsule showed that in three spore mother cells, both second metaphase plates of each cell had 21 configurations on them, suggesting that some regular first metaphase plates with 21 bivalents on them occurred. Irregular

distribution of chromosomes occurred in one cell where there were only 20 chromosomes on one second metaphase plate. A spore mother cell in which three bivalents and an associated group have been left on the equator at anaphase is shown in Fig 43 and a lagging chromosome which has been excluded from the nuclei in Fig 44. Separation at second anaphase was irregular in some cells with the formation of bridges and fragments.

Table 16.

Collection	Number of cells containing certain numbers of chromatic groups at 1st metaphase. (18	19	20	21	22	23 groups)
Wales 3.	2	-	1	19	-	-
Devon 5.	1	-	20	22	-	-
Surrey 9.	-	2	1	8	-	-
Surrey 5.	-	1	1	10	3	-
Surrey 2.	-	2	-	7	1	1
Surrey 27.	-	-	3	5	1	-
Surrey 35.	-	-	1	19	2	1

The aneuploid plants(N=18-19) described on page 73, were monoecious and bore several sporophytes, from one of which a slide showing

meiosis was prepared. The average spore mother cell diameter was 22u and only five of the two thousand cells examined had irregular division at meiosis. In each of nine first metaphase plates from this capsule 19 bivalents were distinguished. A count at second metaphase also showed that 19 chromosomes were present. No bridges or fragments were found at second anaphase and the cleavage of the cytoplasm was regular (Fig 45).

Hybridity with other species of Atrichum.

Shoots of A.undulatum(N=21) which bore archegonia but no antheridia were obtained by removing all shoots bearing antheridia during the spring and culturing the new shoots arising from the old rhizomatous bases under conditions of high humidity. These plants were crossed with A.crispum, A.tenellum, A.angustatum and A.undulatum(N=14). Spermatazoids of A.crispum, A.tenellum and A.undulatum(N=14) were unable to effect fertilization although plants of A.undulatum (N=21), in the same pots as the experimental plants, produced sporophytes when fertilized by A.undulatum(N=21) spermatazoids. Spermatazoids of A.angustatum fertilized egg cells of A.undulatum in three crosses out of three hundred. One mature sporophyte was obtained, the others dying when less than 1mm in length. The capsule was arcuate when still green and measured0.30×0.10cms. The average diameter of the spore mother cells was 18u. Only one meiotic metaphase was clear enough for a chromosome count to be made. On this plate there were fifteen large chromatic groups and two very small bodies(Fig 48). Excluded chromosome fragments or supernumary nuclei occurred in 94 out of 200 cells

which had completed division.

3b). Morphology and cytology of plants showing unusual characters.

I. Plants collected from a pine wood at Oxshott, Surrey, bore unfertilized archegonia at the stem apices at the time of collection (July 1951). The plants averaged 3.2cms in height and bore undulate leaves 0.6cms in length and 0.1cms in width. There were five lamellae on the nerve and 58-76 spines on the lamina, and 2460 cells were formed per mm^2 of leaf lamina. None of these characters altered when the plants were cultivated in a cold frame. During the three seasons that these plants were under cultivation, archegonia were formed at the stem apices but no antheridia were found. The archegonia were normal in appearance and the egg cells were fertilized by spermatazoids of other clones of A.undulatum The resulting sporophytes were arcuate when ripe and averaged 0.36cms in length and 0.08cms in width. Resting nuclei of the gametophytes contained three large and three small heteropycnotic granules and 21 chromosomes were visible at mitosis. Meiosis was regular and 21 bivalents were formed. Thus these plants were normal except for the absence of antheridia.

II. A few plants were collected with A.tenellum from a dried out pond bed at Oxshott. They were small and died under cultivation. The plants were all less than 0.8cms in height and bore leaves 0.45cms in length and 0.1cms in width. The leaves were undulate and bore five lamellae on the nerve and 54-68 spines on the lamina.

There were 2430 cells per mm^2 of leaf surface.No archegonia were found on these plants but antheridia were present in the axils of unmodified leaves.Two large and two small heteropycnotic bodies were present in the resting nuclei of the gametophyte and it was not possible to determine exactly the number of chromosomes at mitosis, which appeared to lie between 16 and 18. Thus these plants were unusual because of the absence of archegonia and the 16-18 chromosomes instead of the normal 21.

III. An isolated group of five plants was found in a pine wood at Wisley Surrey. These appeared distinct from other A.undulatum plants growing in the same wood. The leaves of this population averaged 0.55cms in length and 0.10cms in width. All the leaves were rigid and non-undulate and bore five lamellae and up to 240 small spines arranged in transverse rows of 9-12. Fig 15 compares the number of cells per mm^2 of these latter specimens with that of normal A.undulatum plants growing nearby. The average for the normal A.undulatum plants was 2590 cells per mm^2 and for the unusual plants 4350 cells per mm^2. The plants were monoecious and bore antheridia in the axils of unmodified leaves below the terminal group of archegonia. Three immature sporophytes which were borne singly on the plants, were arcuate. These sporophytes probably arose from fertilization within the group of plants since the specimens were spatially isolated from other specimens of A. undulatum. Resting nuclei of the gametophytes contained two large and two small heteropycnotic bodies. No preparation with a countable metaphase plate was obtained. At meiosis the average diameter of the

spore mother cells was 13u, this being 2u smaller than that of the smallest spore mother cell found in normal A.undulatum capsules. In four out of eight hundred dividing cells round bodies were left on the equator at meiosis. In four metaphase plates 14 bivalents were clearly visible(Fig 46). In all other plates examined the number could not be clearly distinguished but appeared to lie in that region. A single cell occurred with 28 groups but these, from their shape, were assumed to be the halves of recently divided bivalents (Fig 47). In both nuclei of each of two spore mother cells at second metaphase, 14 chromosomes were visible. It is likely from this cytological evidence and from the possibility of clonal fertilization, that the parent gametophytes of the sporophytes both had fourteen chromosomes.

IV. Certain plants, collected from the banks of the River Dart in Devon, formed only antheridia. These were borne in the axils of leaves forming perichaetia, and proliferation through these, combined with the non-decay of the old parts, gave rise to prostrate plants as long as 9cms. All leaves were lax and non-undulate and bore four lamellae and a maximum of nine spines. These characters did not alter under cold frame conditions. Under natural condition in the field the leaves formed during May averaged 0.68cms in length and 0.10cms in width and had 3300-4100 cells per mm^2 of lamina. When cultivated in a cold frame the leaves had 3800 cells per mm^2 . The variation in leaf cell size with season of the year in three plants, one, two , and three years old respectively,is shown graphically in Fig 16. The leaves formed on different plants at the same time of the same year

have a similar cell size. However leaves formed during the same season of different years may have a widely different cell size, even when borne on the same plant. Motile spermatazoids from the antheridia of these plants were unable to effect fertilization of egg cells of any of the other British species of Atrichum . Resting nuclei of the gametophytes had two large and two small heteropycnotic bodies in them. Mitotic figures showed 14 chromosomes, of which six were J shaped and eight V shaped,in all the cells examined.

Atrichum undulatum varβ minus.

Plants were collected which were similar to those described by Rose (1950) as A.undulatum varβminus, and consisted of female plants bearing archegonia and sporophytes, sterile plants and rare male plants. The leaves were lax and non-undulate and these characters did not change under cultivation. There were four lamellae on the nerve and less than eleven spines on the lamina. 2370 cells were formed per mm^2 of leaf lamina. The capsules were erect or inclined, never arcuate, and although up to 100% of the spores in capsules collected from the field were dead, capsules collected when young and matured in a cold frame contained less than 15% dead spores. The male and female plants were grown as separate clones for three seasons and were strictly dioecious. Data are summarized in Table 17.

Table 17.

Collection	Height cms	Leaf size cms	Lamellae	Spines	Cells/mm^2
Goudhurst	1.0	.40x.07	4	9	2370
	Seta cms	Capsule cms	∠with seta	Spore diameter u	
	1.2	.20x.08	180°	18	

The lax, weakly spinous leaves and the small erect capsules are typical of A.tenellum rather than a variety of A.undulatum. The strict dioecy of the plants shows that they cannot be A.undulatum var β minus since this variety is monoecious.

Female plants were crossed with both A.undulatum and A.tenellum. No fertilization occurred with spermatazoids of A.undulatum but spermatazoids of A.tenellum fertilized the egg cells and the resulting sporophytes resembled those of A.tenellum rather than those of A.undulatum This suggests that the plants were in fact specimens of A.tenellum.

Atrichum undulatum var γ haussknechtii.

No plants were collected which resembled the herbarium specimens of this variety, previously examined.

CHAPTER V.

DISCUSSION.

In the first chapter of this work, the data obtained from the various floras were reviewed and the British species of *Atrichum* described on the basis of this information. The characters used in their description will now be discussed.

1). The plane or undulate character of the leaf.

The undulate character of the leaf appears to be most marked when there are many spines arranged on the lamina in distinct transverse rows and when the leaf cells are large and thin walled. Leaves with spines scatterred irregularly over the lamina are plane, as are leaves in which the cells are small and thick walled. Since it has been shown that the number of spines varies with environmental conditions, as does the size of the leaf cells, it is to be expected that different environmental conditions will give rise to leaves with different degrees of undulation. This may explain the occurrence of specimens of *A.angustatum* with undulate leaves and specimens of *A.undulatum* N=21 with plane leaves.

2). The size of the leaf cells.

The size of the leaf cells is distinctive in some species, so that *A.crispum* cannot be confused with *A.angustatum* . Under certain environmental conditions *A.crispum* can be confused with large celled *A.undulatum* and *A.tenellum* , and similarly *A.angustatum* can be confused with small celled *A.undulatum* . *A.undulatum* and *A.tenellum*

cannot be distinguished from each other on the character of cell size.

3). The number of spines on the lamina and the number of lamellae on the nerve.

In all the species studied there is a variation in the number of spines on the lamina and the number of lamellae on the nerve. The number of spines appears to be influenced by many environmental factors.

4). The dioecious or monoecious character of the plants.

The dioecious nature of the three species A.crispum, A.tenellum and A.angustatum is constant in Britain, although A.tenellum may occur as a monoecious race in Finland. This character can be used to separate them from monoecious plants of A.undulatum. However, unisexual races of A.undulatum occur in Britain and may be confused with the normally dioecious species.

5). The morphology of the sporophyte.

The character of the sporophyte appears to be well defined when the capsules of the different species are growing under identical conditions. Under unheated greenhouse conditions A.tenellum capsules are obovate and erect and so cannot be confused with the arcuate capsules of A.undulatum grown under the same conditions. A.undulatum capsules cannot be confused with those of A.angustatum grown in a unheated greenhouse, but under conditions of low temperature A.angustatum capsules may be broad and arcuate and only distinguishable from those of A.undulatum on the size of their spores. Further confusion is caused by the variety A.undulatum var. haussknechtii in

which the capsule is slender and erect and contains small spores, similar to those of A.angustatum.

6).The size of the spores.

The mean size of the living spores is remarkably constant within a species, but the range of size of the spores of a single capsule is large and depends on conditions of temperature and humidity at the time of spore maturation. Thus mean spore size can be used to delimit a species provided that a large number of spores from many capsules is analysed.

The variation which occurs within a species and the relationship between sex expression and cytological status will now be discussed and these results compared with those of foreign workers.

A.crispum.

The separation of British specimens of A.crispum from the other species of Atrichum rests largely on the spineless, non-undulate form of the leaves and the large size of the leaf cells (29-37u) The first two characters are constant in expression but variation in the size of the cells is such that there is an overlap with that of A.undulatum N=21 and A.tenellum. There are usually fewer than four interrupted lamellae on the nerve but small specimens may be confused with A.tenellum which also has plane, large celled leaves with few or no spines and four lamellae. The large antheridial perichaetia of A.crispum serve to distinguish it from A.tenellum where the perichaetia are very small and rare. The unisexual nature of the

British plants of A.crispum has to be inferred since no archegonia have been found on any plant. Experimental work on the variety A.crispum var β densifolium suggests that the variety is only an environmental form of the species. The failure of A.crispum to hybridize with other species of the genus in the laboratory, combined with the restricted habitat of the species, suggests that no hybrids are to be expected in the field. The species in Britain is haploid, with a chromosome complement of N=7= 1H(V) +3J +3V , of which one is a totally heteropycnotic chromosome.

These results agree fairly well with those of Lowry for American material. The chief difference lies in the smaller cells of the American plants (20-25u instead of 29-37u).

A.angustatum.

The separation of British specimens of A.angustatum from the other species of Atrichum can be carried out using both the characters of cell size and spore size. The leaves are usually rigid and non-undulate with many spines and small cells (12-14u), but under certain environmental conditions, undulate leaves may be formed with cells 18u in diameter. In the absence of sporophytes the latter could be confused with small celled forms of A.undulatum and would approximate to the descriptions of A.angustatum var β rhystophyllum. Since no race of A.angustatum has been found in which the undulate character of the leaves is genetically determined, the variety is not considered to

be a true one. Dixon himself noted that the variety intergrades with the true species and so is not distinct. It is interesting to note that Lowry's American specimens of A.angustatum bear undulate leaves composed of cells 12-15u in diameter and that these plants are similar to the Japanese material of Kurita (1937). The dimensions of the sporophyte vary with the temperature of maturation, and although normal capsules are erect and slender and can only be confused with A.undulatum var γ haussknechtii, arcuate capsules are formed at temperatures below 8° C which can be confused with those of A.undulatum. Many arcuate capsules will be formed in the field during years when frosts and cold weather occur early in the autumn. Although the arcuate capsules can be confused with those of A.undulatum, the small size of the spores (11u) in both the erect and arcuate capsules of A.angustatum distinguish them from A.undulatum N=21 where the spores measure 21u. They can however, be confused with A.undulatum var γ haussknechtii where the spores measure 12-13u.

A.angustatum is regularly haploid in Britain, the chromosome complement being N=7= 1H(V) +3V +3J. This differs from that of Japanese material where Tatuno found N=7= 1H(V) +1h +3V +2J. In the British material no 'h' chromosome is present, although there is a small heteropycnotic spot in the nucleolus.

It is possible that A.angustatum may hybridize with A.tenellum in the field, although no evidence for this has yet been obtained. The cross between A.angustatum and A.tenellum made in the laboratory produced capsules containing living spores, but these did not grow into

adult plants. The cross between A.angustatum and A.undulatum produced capsules containing only dead spores. Since sex organs of A.tenellum ripen earlier than those of A.angustatum , there is less possibility of a natural hybrid being formed between these species than between A.angustatum and A.undulatum.

A.tenellum.

The separation of British specimens of A.tenellum from A.angustatum can be carried out using the characters of leaf appearance and spinousness. In British A.tenellum the leaves are non-undulate with few or no spines and the leaf cells are 19-22u in diameter. These cells are of the same size range as those of A.undulatum N=21 so that, in the absence of perichaetia and sporophytes, weakly spinous forms of the latter cannot be distinguished from A.tenellum. Similarly in the absence of antheridial perichaetia, small forms of A.crispum can be confused with A.tenellum . The dioecious nature of the plant has been constant in the British specimens examined, but this may not be so for all European specimens since Finnish plants have N=14 and may possibly be monoecious. The capsules of the British plants are always smaller than those of A.undulatum and A.angustatum and are never arcuate. The large numbers of dead spores usually found in the capsules are due to adverse environmental conditions, probably excessive dryness when the capsules are maturing during the months of August and September. Plants identified by Rose as A.undulatum varβ minus have been shown to belong to A.tenellum.

The British material of A.tenellum is all haploid, with a chromosome complement of N=7 =1H(V) +3V +3J, although the occurrence of aneuploid and polyploid antheridial tissue suggests that this species may give rise to polyploid forms. These have so far not been discovered in Britain. The plants of A.tenellum collected by Varaama from Finland have a chromosome complement of N=14, and differ from the British plants in their large, spinous leaves and strongly arcuate capsules. The cell size of these Finnish plants however, is little different from that of the N=7 British plants and it seems likely that the Finnish specimens are either old polyploids derived from A.tenellum N=7 which have lost all 'gigas' characters, or a reduced race of A.undulatum N=21. Investigations of the hybrids between these different plants are necessary before this point can be settled.

A.tenellum may form hybrid capsules with other species of Atrichum, but this has not been observed in the field. In the laboratory the cross between A.tenellum and A.angustatum produced living green spores. There is little possibility of this cross taking place in the field since the two species rarely grow together and the sex organs are ripe at different times of the year.

A.undulatum

A.undulatum has been found in Britain both as the widely distributed triploid (N=21) race and as two locally distributed diploid (N=14) races. As the diploids occur in very small numbers it is likely that other similar races occur in, as yet undiscovered, situations.

The characters used to delineate A.undulatum are the strongly undulate leaves, the monoecious nature of the plants and the arcuate nature of the capsules. Of these, only the arcuate nature of the capsules is at all constant in expression. The undulate nature of the leaves of the N=21 race varies considerably in the field, as does the number of spines on the lamina. The diameter of the leaf cells varies from 15 to 24u in the field but only from 19 to 22u in an unheated greenhouse. Thus, in the absence of perichaetia and sporophytes, small celled plants of A.undulatum (N=21) can be confused with lax forms of A.angustatum, and spineless forms of A.undulatum (N=21) with A.tenellum. The leaves of the diploid male race of A.undulatum are lax, spineless and non-undulate and the leaf cells average 15u in diameter. Thus young plants of this race can be confused with small celled specimens of A.tenellum. Similarly, the diploid monoecious race of A.undulatum has rigid, spinous, non-undulate leaves with leaf cells 16u in diameter and so resembles A.angustatum.

Antheridial formation may take place before archegonial initiation which may be on a separate branch of the plant, so that the monoecious nature of A.undulatum(N=21) is often not apparent. Some plants of A.undulatum (N=21), although normal vegetatively, are unisexual, and it has been shown that such plants may have the normal complement of chromosomes or may be aneuploids. The monoecious diploid race forms antheridial perichaetia on the stem below the terminal archegonia in the same way as the N=21 race, but the male diploid race forms successive antheridial perichaetia along the stem in the same way as A.crispum. However, it

can be distinguished from the latter by the small size of its leaf cells. The length of the capsules of A.undulatum varies from 0.1 to 0.5cms but all are strongly arcuate. This character can be used to distinguish A.undulatum from normal A.angustatum but not from forms where the capsule has matured at low temperatures. The spore size of 21u however, will always distinguish A.undulatum N=21 from A.angustatum whose spores measure 11u. The undulate capsule also distinguishes A.undulatum from British forms of A.tenellum but not from A.tenellum N=14 as found in Finland. The spore mother cell diameter of the monoecious diploid race of A.undulatum suggests that the spore diameter of this plant will be only 15u so that plants of this race could be confused with some specimens of A.angustatum and A.undulatum var γ haussknechtii.

A.undulatum var β minus is defined as a plant much smaller in all parts than A.undulatum with less undulate leaves but otherwise resembling the species. The monoecious diploid race of A.undulatum in which the leaves are shorter and non-undulate and the leaf cells small could be such a variety. Even so, it would be better to discontinue the use of the variety βminus, especially as the wide environmental variation found in the species causes confusion when the variety is defined on quantitative morphological data alone. Plants are better defined on cytological data accompanied by a description of their morphology.

A.undulatum var γ haussknechtii has not been found in Britain. The character of the perichaetium is unstable in A.undulatum and the peculiar form of the inflorescence often found in this variety may be

considered as relatively unimportant. Spore size however, is a very constant character and the small spores of the European specimens of A.undulatum var γhaussknechtii (12-13u in diameter) distinguish them from A.undulatum N=21 as found in Britain. This small spore size combined with the form of the capsule, which resembles that of A.angustatum, suggest that this variety may be a diploid race of A.undulatum .Catherinea lateralis Vaizey, is only a polysetous form of A.undulatum.

A.undulatum occurs in Britain mainly as the N=21 race with sporadic aneuploid plants, and as two N=14 races. Tatuno found that Japanese material of A.undulatum had N=21 and A.undulatum var β minus N=7. So far, all N=7 species of Atrichum and Polytrichum have been dioecious, and it may be inferred that his N=7 plants were similar. His diagnosis of these plants as the variety βminus may therefore be questioned in that this variety is monoecious. In A.undulatum N=21 he identified three sex chromosomes of which two V shaped chromosomes were X and one J shaped one a Y. It has not been possible to identify the sex chromosomes with any definite shape of chromosome in the British material, but there appears to be variation in the number of X and Y chromosomes present. If sex differentiation is of the XY type, then A.undulatum N=21 with three sex chromosomes, will be monoecious with a tendency to express one sex more strongly than the other. This will depend on whether (3A +2X +1Y) or (3A +1X +2Y) chromosomes are present in the nucleus. In the case of the N=19 plants of A.undulatum (page 73) one heteropycnotic chromosome, a sex chromosome,

was missing, but both male and female sex characters were expressed as in normal N=21 plants. Thus these plants may have had both an X and a Y chromosome. Other plants with N=16-18 (page 76) and also with one sex chromosome missing, expressed only male characters and so may have had two Y chromosomes. Similarly the monoecious diploid race (page77) may have had (2A +X +Y) and the male diploid race (page 78) (2A +2Y) chromosomes. The plants which were purely female (page 76) and which had three sex chromosomes, may have had (3A +3X). Spores with different distributions of sex chromosomes might arise from irregular meiotic division and give rise to plants with various sex characters. In dioecious species of Atrichum X and Y chromosomes pair together at meiosis and separate regularly. In tetraploid Grimmia Muhlenbeckii (Varaama 1949) X and Y chromosomes continue to pair together even in the presence of a homologous partner. In N=21 A.undulatum with four X and two Y, or four Y and two X chromosomes in the spore mother cells, such pairing would lead to irregularities including the formation of trivalents and univalents. Experimental evidence for the formation of univalents has been found. Since the size of the chromosomes is small and the number of pairing segments available limited, it is not surprising that the formation of trivalents has not been observed.

It is possible that A.undulatum may hybridize with both A.tenellum and A.angustatum in the field but no evidence for this has been obtained. A.tenellum could be crossed with A.undulatum N=21 in the laboratory but no sporophytes matured. A.undulatum could be crossed

in both directions with A.angustatum and cytological evidence suggests that a few viable spores might be formed.

CHAPTER VI.

CONCLUSIONS.

The genus *Atrichum* exists in Britain as four distinct species. Of these, the species *A.crispum* and *A.angustatum* show no evidence of distinct intra-specific races. *A.tenellum*, although only found so far as the N=7 race in Britain, occurs as the N=14 race in Finland and differs morphologically from the British form. *A.undulatum* occurs mainly as the N=21 race with very occasional aneuploid plants, and also as two distinct N=14 races which occupy very restricted habitats. The variety *A.undulatum* varβ *minus* would best be deleted from the floras owing to insufficient character definition. The diploid races can then be described under their distinct chromosome numbers and left un-named, since it is probable that many more such races may be found with various diagnostic features. The variety *A.undulatum* varγ *haussknechtii* should be retained in the floras since it may occur in some mountainous districts and, at present, its cytological status is unknown.

The following key for the separation of the British species of *Atrichum*, based on data derived from the present investigation coupled with a study of the relevant literature, may now be attempted:-

1). Leaf cells 29-37 u - - - - - - - - - - - - crispum.
Leaf cells 12-27u - - - - - - - - - - - - - 2.

2). Capsule short, obovate, erect or inclined - - - tenellum.
Capsule long, erect , or long, arcuate - - - - 3.

3). Leaf cells 12-15u, N=7. - - - - - - - - - - angustatum.
Leaf cells 15-22u, N=14 or N=21 - - - - - - undulatum.

This work indicates that these species are defined as follows:-

Atrichum crispum (James) Sull.

Plants 0.6-2.5cms in height. Leaves oblong lanceolate, not undulate, leaf cells 29-37u, no spines on the lamina, lamellae 0-4 weak and interrupted. Dioecious, male perichaetia formed frequently, female plants not found in Britain. Growing on the banks of shallow streams in exposed places. N=7.

Atrichum angustatum (Brid) B. and S.

Plants 1.5-2.5cms in height. Leaves lanceolate, plane or slightly undulate, leaf cells 12-15u, 90-160 spines formed on the lamina in regular rows, lamellae 4-8, usually 5. Dioecious. Capsules normally erect, slender, under certain conditions arcuate, broader. Spore diameter 13u . Growing on acid clays in damp places. N=7.

Atrichum tenellum. (Röhl) B.and S.

Plants 0.6-2.5 cms in height. Leaves oblong lanceolate, non-undulate, leaf cells 18-27u in diameter, less than 17 spines on the lamina, lamellae usually 4. Dioecious , male perichaetia small and rare. Capsule small obovate, erect or inclined . Spore diameter 18u Growing on acid peaty soil in damp places. N=7 .

Atrichum undulatum (Hedw.)P.Beauv.

1). N=21. Plants 1.2-10.0cms in height. Leaves lanceolate, varying from plane to strongly undulate, leaf cells 18-22u in diameter, 0-170 spines on the lamina in regular rows, lamellae 4-7, usually5. Monoecious or rarely unisexual. Capsule arcuate. Spore diameter 21u. Growing on soil in woods and heaths.

2).N=14 Plants 2.5cms in height. Leaves lanceolate, non-undulate leaf cells 15-18u in diameter, 100-240 spines on the lamina in regular rows, lamellae 5. Monoecious Capsules arcuate. Spore diameter probably 15u. Growing on soil in a pine wood, Oxshott, Surrey.

3). N=14, Plants up to 10.0cms in height,prostrate. Leaves lanceolate lax and non-undulate, leaf cells 15-18u in diameter, 0-9 spines on the lamina, lamellae 5. Unisexual, only male plants known. Growing on the banks of the River Dart above Holne Bridge.

4). var haussknechtii . Gametophyte similar to A.undulatum N=21 but having terminal antheridia surrounded by archegonia. Monoecious. Capsule slender erect or inclined,often several borne in one

perichaetium. Spore diameter 13u.Not known to occur in Britain.

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BIBLIOGRAPHY.

ALLEN,C. 1935. Bot. Rev. 1 :269-291

1945. Bot. Rev. 11 : 260-287

BERKELEY,M.J. 1863.Handbook of the British Mosses. (London.)

BRAITHWAITE,R. 1880. British Moss Flora.(London.)

DARLINGTON,C.D. 1932. Recent Advances in Cytology. (London.)

DIXON,H.N. and JAMESON,H.C. 1896, 1906, 1924. The Student's Handbook of British Mosses. (Eastbourne.)

GROUT,A.J. 1928-40. Moss Flora of North America. (Vermont.)

HEDWIG,J. 1801. Species Muscorum. (Paris.)

HEITZ,E. 1926. Z.Bot. 18 : 625

1927.Abh.naturw. Ver.Hamburg. 21 : 48-58

1928. Jb. wiss. Bot. 69 : 762-818

1942. Arch. Julius Klaus-Stift.Vererb.Forsch 27 : 444-448

HERZOG,T. 1926. Geographie der Moose. (Jena.)

HOOKER,W.J. and TAYLOR,T. 1818. Muscologia Britannica. (London)

JACHIMSKY,H. 1935. Jb. wiss. Bot. 81 : 203-238

KURITA,M. 1937. Z. indukt. Abstamm.u. Vererblehre. 74 : 24-29

LINNAEUS, 1753. Species Plantarum.

LORBEER, 1934. J. wiss. Bot. 80

LOWRY,R.J. 1948. Mem. Torrey. Bot. Cl. 20.no2: 1-42

1954. Am.J.Bot. 41 : 410-414

MACKAY,E. 1937. Bot. Gaz. 99 : 377-386

MARCHALL, E et Em. 1907-11. Bull.Roy.Acad.de.Belge. 1-3.

KNAPP,E. 1936. Ber. dtsch. bot. Ges. 54: 346-361

RICHARDS,P. and WALLACE,E. 1950. Trans. Brit. Bryol. Soc. Vol 1.Pt4.

ROSE,F. 1951. Trans. Brit. Bryol. Soc. Vol1. Pt5:481-484

SHIMOTOMAI,N. and KIMURA,K. 1934. Bot. Mag. Tokyo. 48:629-635

1936. Z.indukt.Abstamm.u.Vererbl. 12:307-312

and KOYAMA,Y. 1932.J.Sci.Hiroshima.Univ. B.2:95-101

TATUNO,S. 1935. Bot. Mag.Tokyo. 49:892-898

1938. Bot.Mag. Tokyo. 52:434-441

1951. La.Kromosomo. 8:306-310

1945. Bot. Mag. Tokyo.66: 152-154

and YANO,K. 1953. Cytologia. Tokyo. 18:36-42

VAIZEY, 1888. Ann.Bot. 2:69-74

VARAAMA,A. 1949. Portug.acta. biol.(A);47-78

1950.a.Nature.London.165

b.Bot.Notiser:239-256

1953.a.Bryologist.56:169-177

b.Hereditas.Lund.39:305-316

1954.Arch.Soc.zool.-bot.fenn.Vanamo.28:1-57

WARNSTORF, 1914. Hedwigia. 54:156-158

WETTSTEIN,F.von. 1923.Biol.Zbl. 43:71-82

1924.Z.indukt.Abstamm.u.Vererbl. 33:253-257

1925.Bibliogr.genet. 1:1-38

1937.Z.indukt.Abstamm.u.Vererbl. 74:34-53

1940.Ber.dtsch.bot.Ges.58:374-358

WETTSTEIN, F. von. und STRAUB, J. 1942. Z. indukt. Abstamm. Vererbl. 80: 271-280

WILSON, W. 1855. Bryologia Bryologica. (London.)

WOLCOTT, 1940. Science. 91: 573

YANO, K. 1951. Bot. Mag. Tokyo. 64: 234-237

1952. Bot. Mag. Tokyo. 65: 195-198

1953. a. Bot. Mag. Tokyo. 66: 43-48

b. Bot. Mag. Tokyo. 66: 197-202

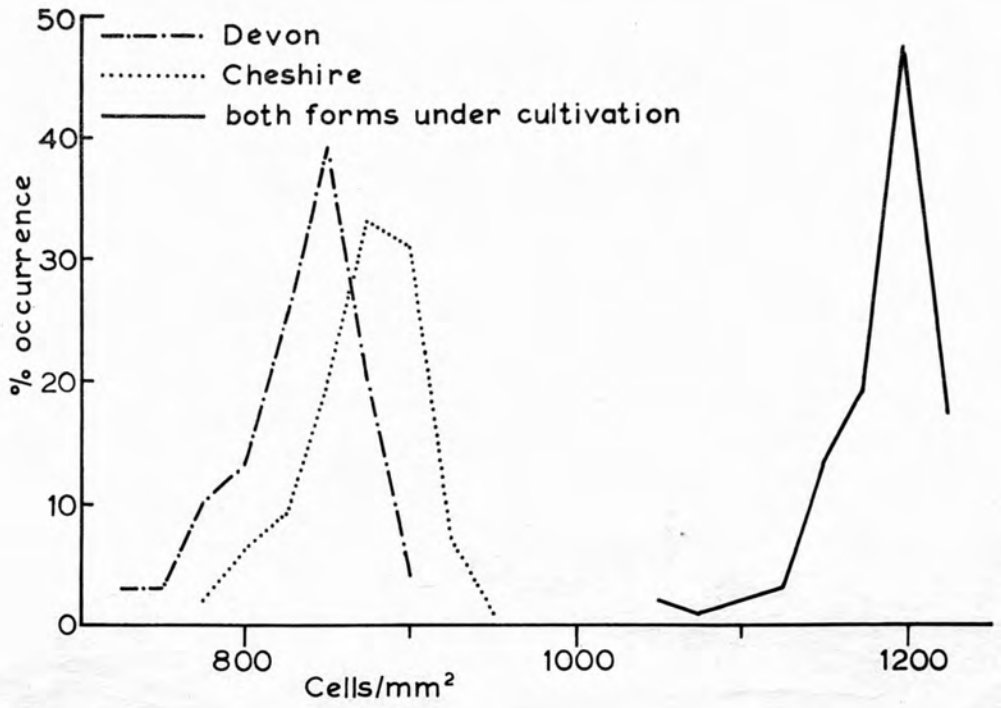


Fig 1. A.crispum. Variation in the number of cells/mm^2 in two forms of the species from the field and variation after the plants had been growing under identical conditions in a cold frame. 5 populations from Devon and 1 from Cheshire examined. (see page 26.)

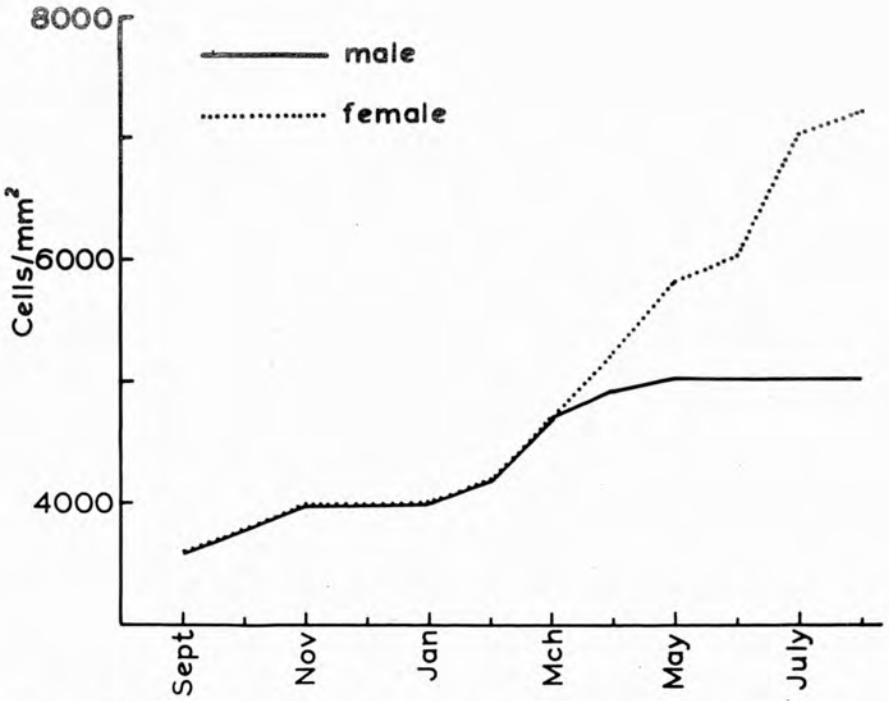


Fig 2. A.angustatum. Variation in cells/mm^2 during one year, in male and female plants in the field. 1200 measurements made on both male and female plants. (see page 34.)

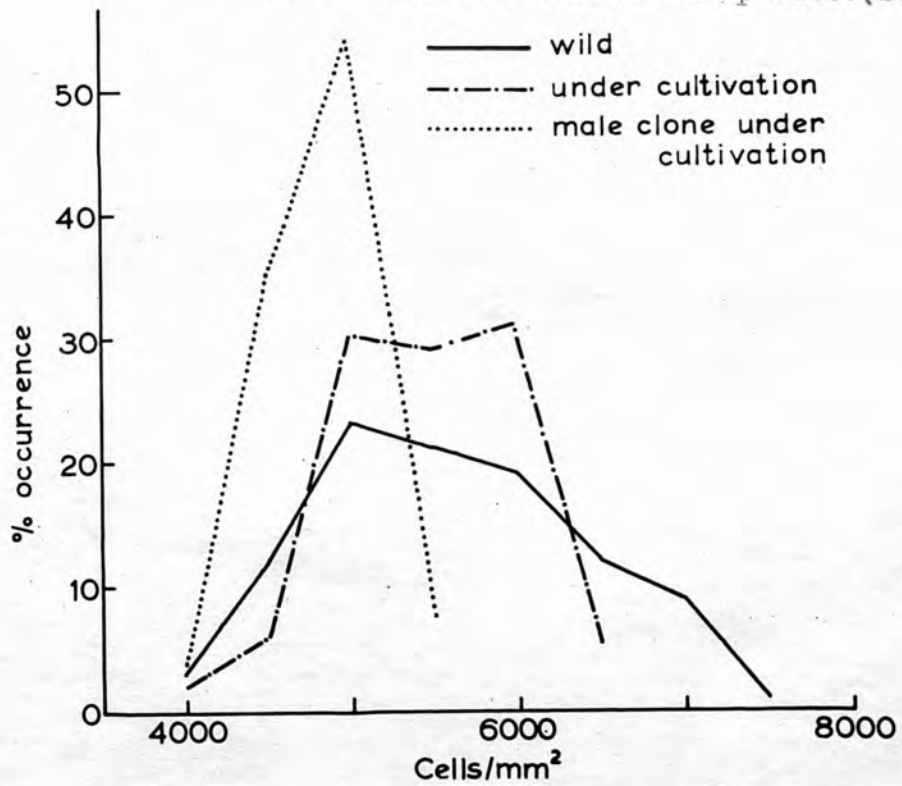


Fig 3. A.angustatum. Variation in cells/ mm^2 in May formed leaves. 1700 measurements on plants from the field, 170 measurements on plants under cultivation and 50 on male clone.

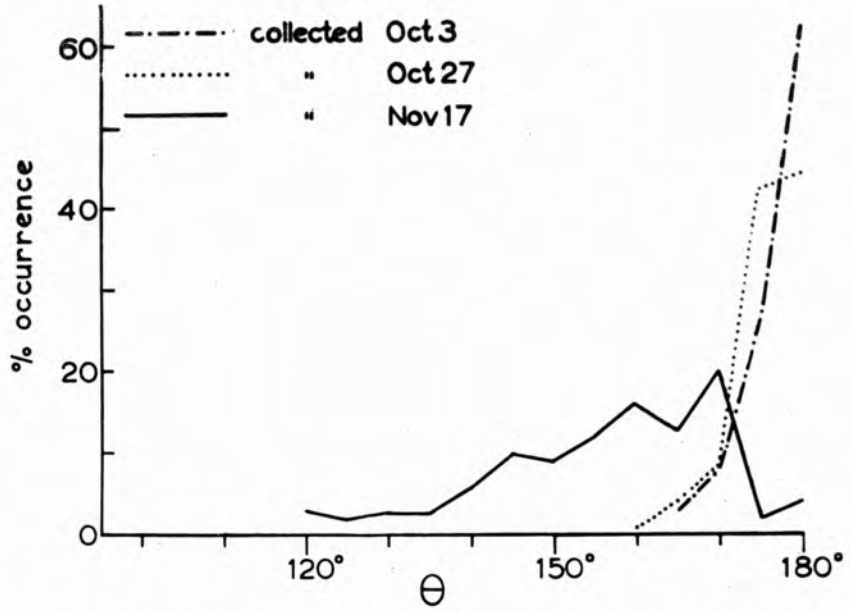


Fig 4. A.angustatum. Variation in the angle of inclination Θ of capsules in a single population sampled on three successive dates. 150 capsules measured on Oct 3rd, 173 on Oct 27th and 180 on Nov 17th. (see page 37.)

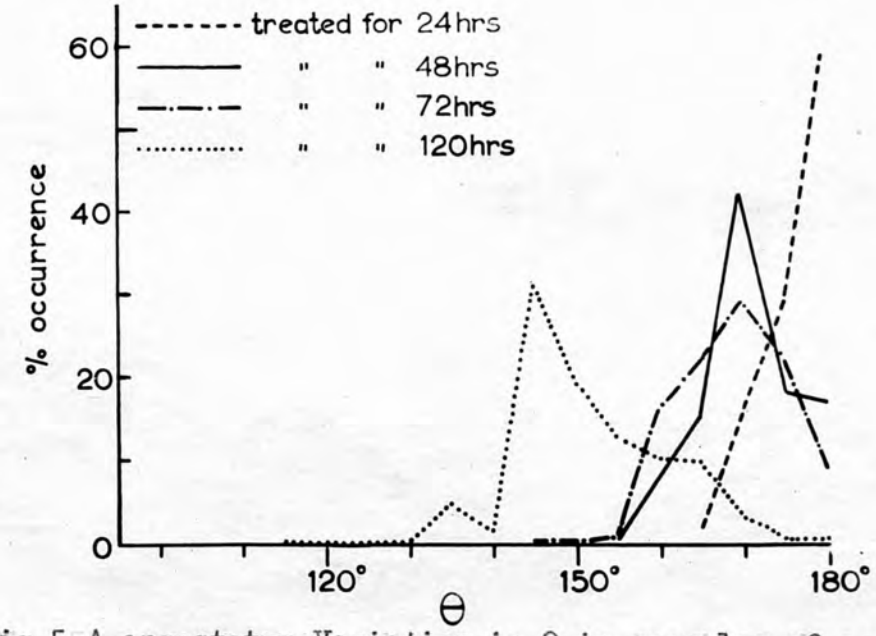


Fig 5. A.angustatum. Variation in Θ in capsules of a single population maintained at 4°-8° C for various periods. 40 capsules measured at each treatment. (see page 38.)

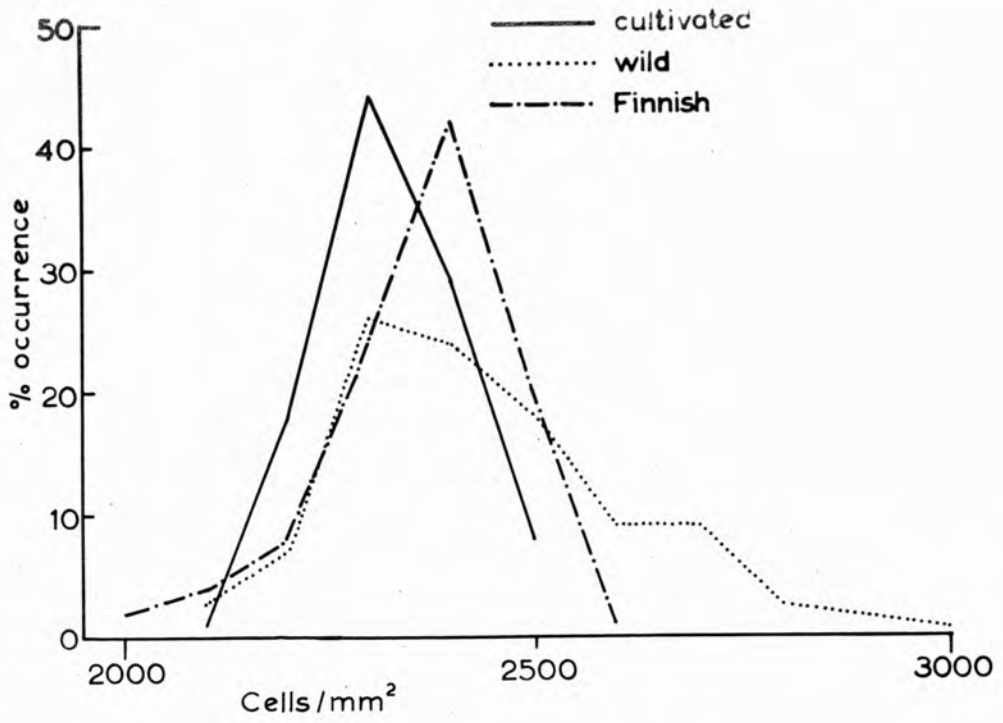


Fig 6. A.tenellum. Variation in cells/mm^2 in May formed leaves of wild plants(1390 measurements), the same after cultivation in a cold frame(695 measurements), and variation in cells/mm^2 in Finnish, N=14, plants(50 measurements.)

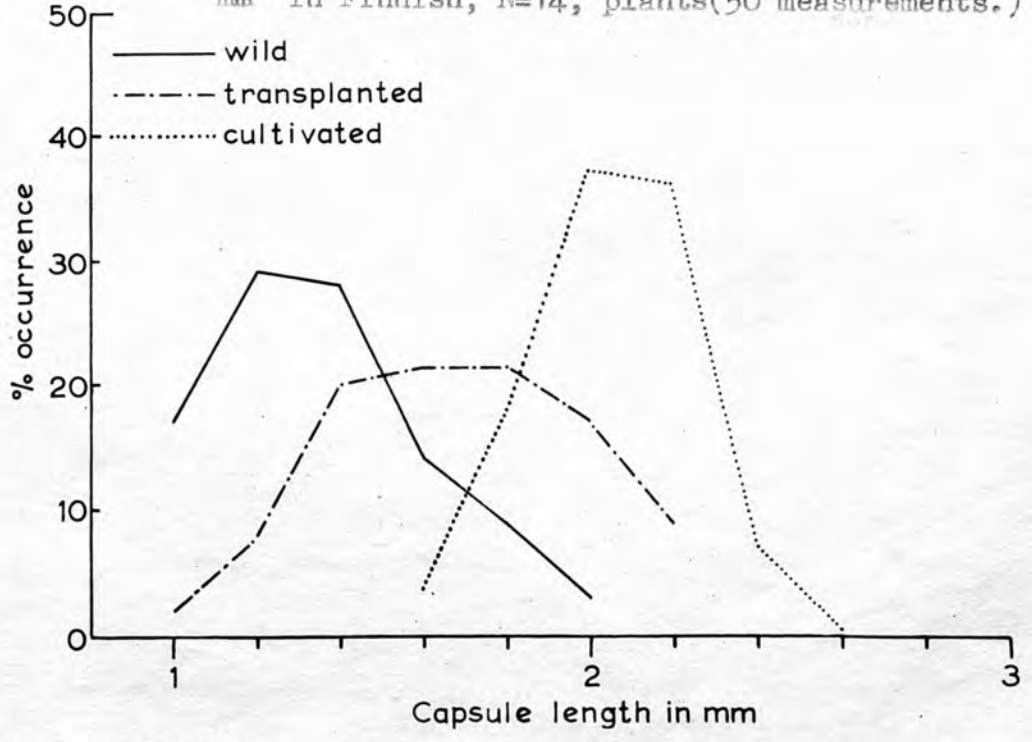


Fig 7. A.tenellum. Variation in capsule length in 243 wild, 147 transplanted and 73 cultivated plants.(see page 52.)

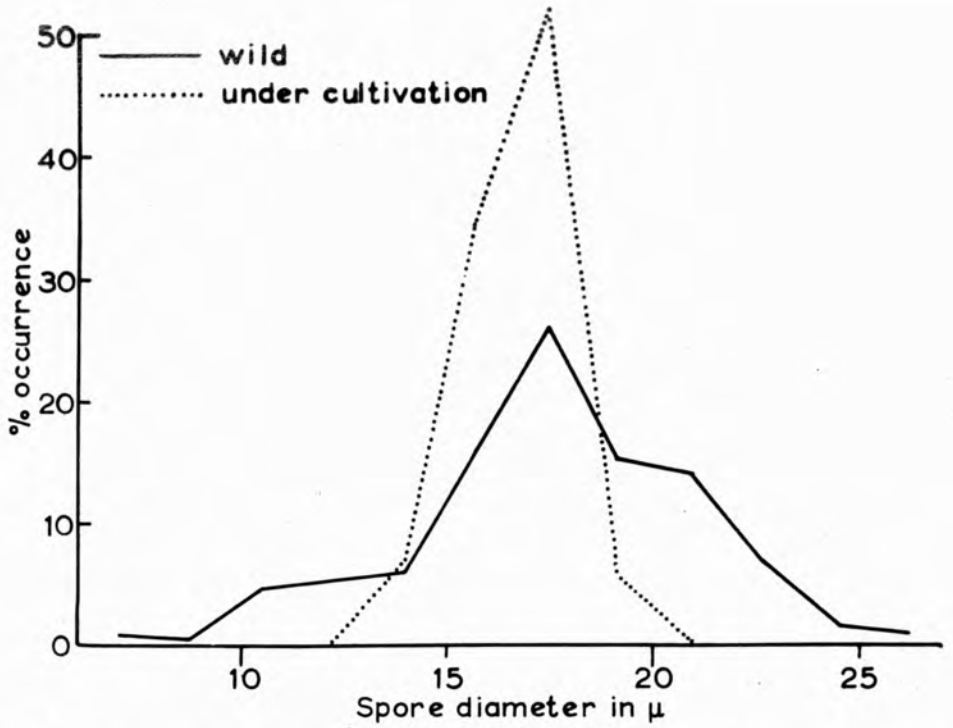


Fig 8. A.tenellum. Variation in spore diameter in 117 wild capsules and 130 capsules grown in a cold frame. 200 spores measured from each capsule. (see page 52.)

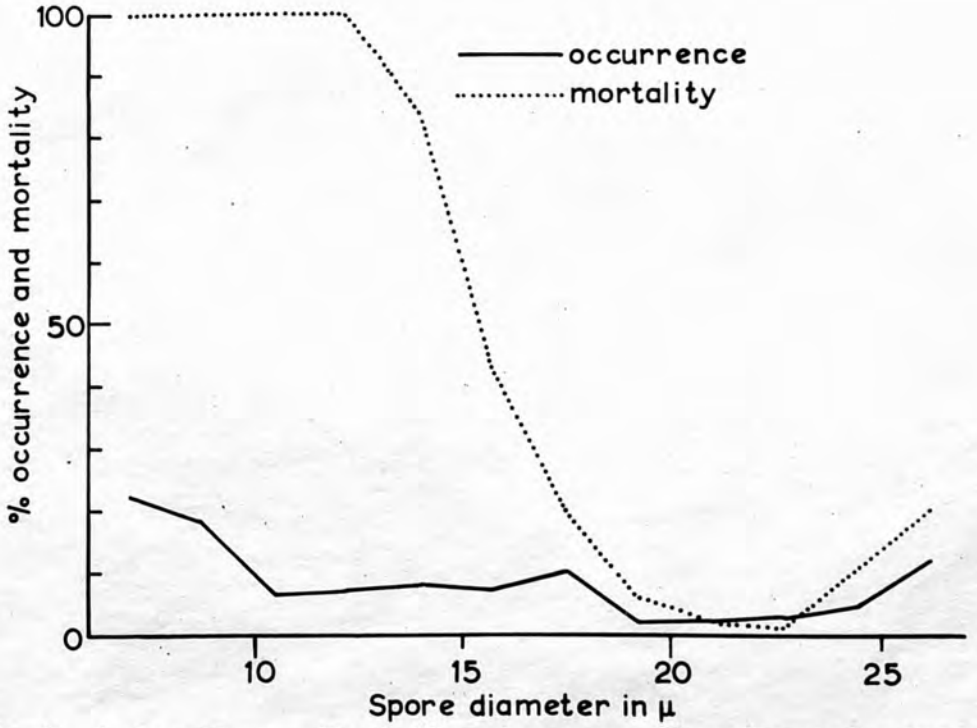


Fig 9. A.tenellum. Variation in spore diameter and percentage mortality of the different sized spores in a single capsule matured under dry conditions. 500 spores examined. (see page 54.)

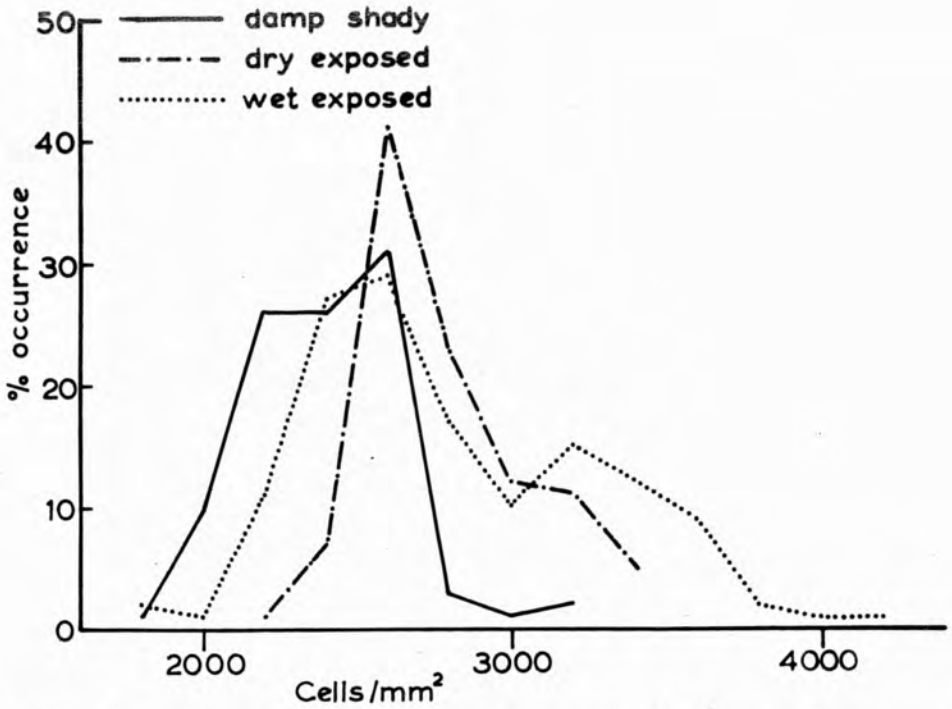


Fig 10. A.undulatum. Variation in cells/mm^2 in 153 populations collected from damp, shady places, in 147 populations from dry, exposed places and 187 populations from wet, exposed places.

(see page 71.)

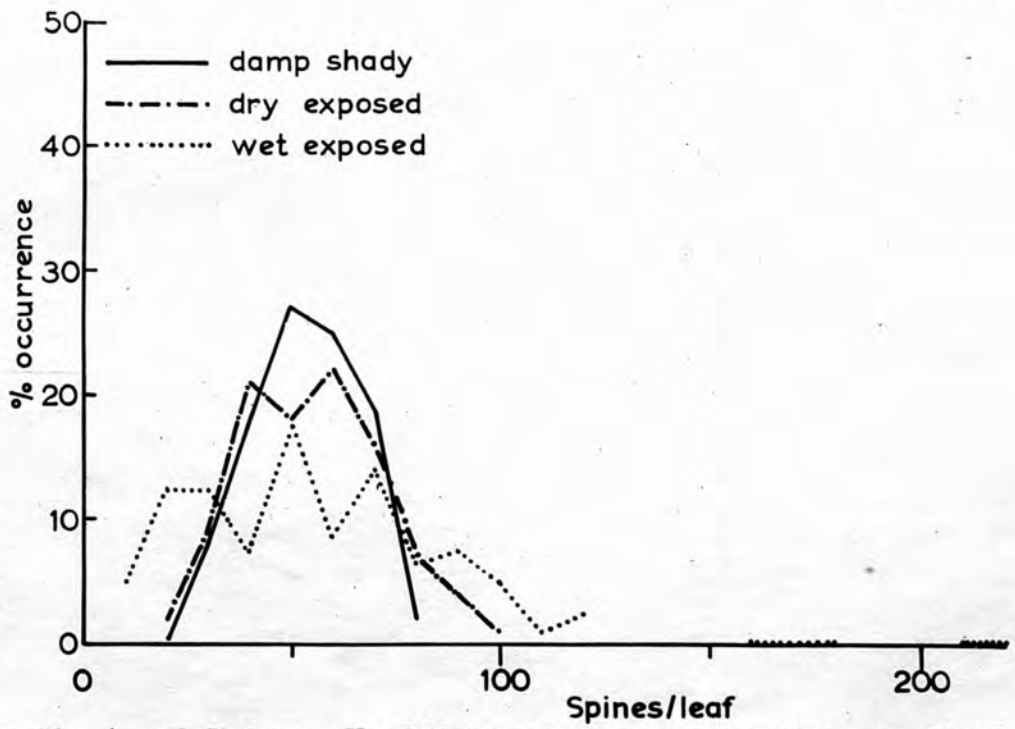


Fig 11. A.undulatum. Variation in number of spines on the lamina in plants collected from the three types of places listed above. (see page 71.)

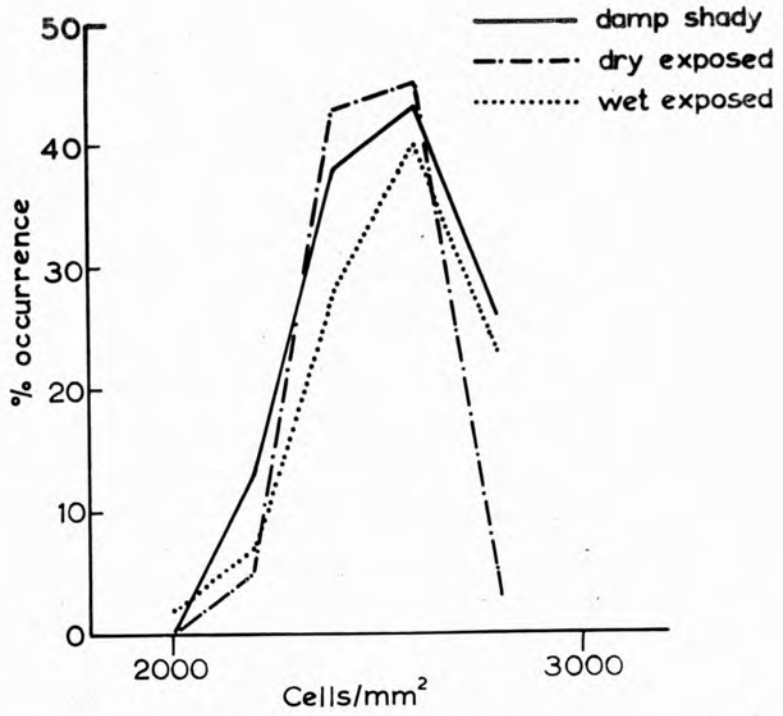


Fig 12. A.undulatum. Variation in cells /mm^2 in 153 populations from damp, shady places, 147 from dry, exposed places and 187 from wet, exposed places when grown in a cold frame. (see page 71.)

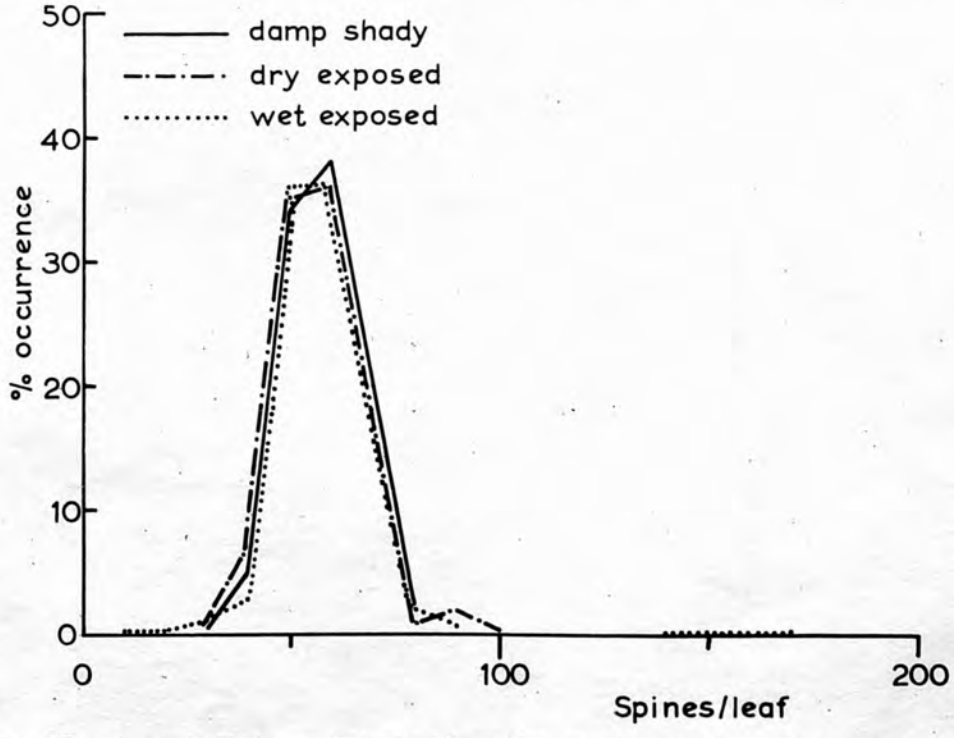


Fig 13. A.undulatum. Variation in number of spines on the lamina in the plants listed above when grown in a cold frame. (see page 71.)

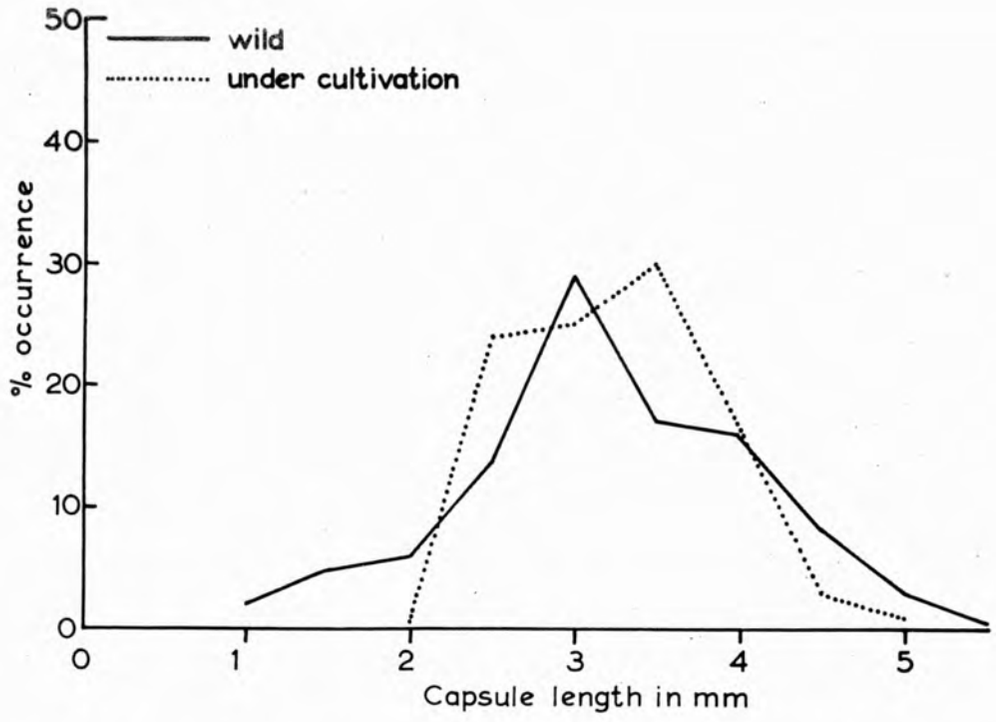


Fig 14. A.undulatum. Variation in capsule length in 387 populations collected from the field, and the same populations after growth in a cold frame.(see page 72.)

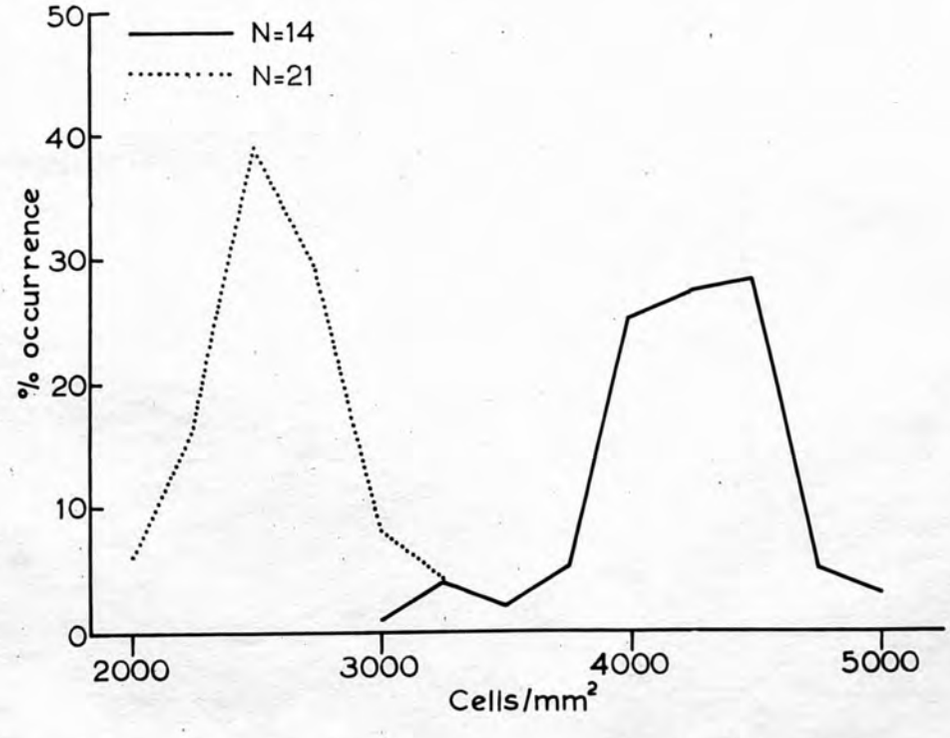


Fig 15. A.undulatum.Variation in cells /mm^2 in N=21 monoecious plants and N=14 monoecious plants growing near to each other. 180 and 100 measurements respectively.(see page 77.)

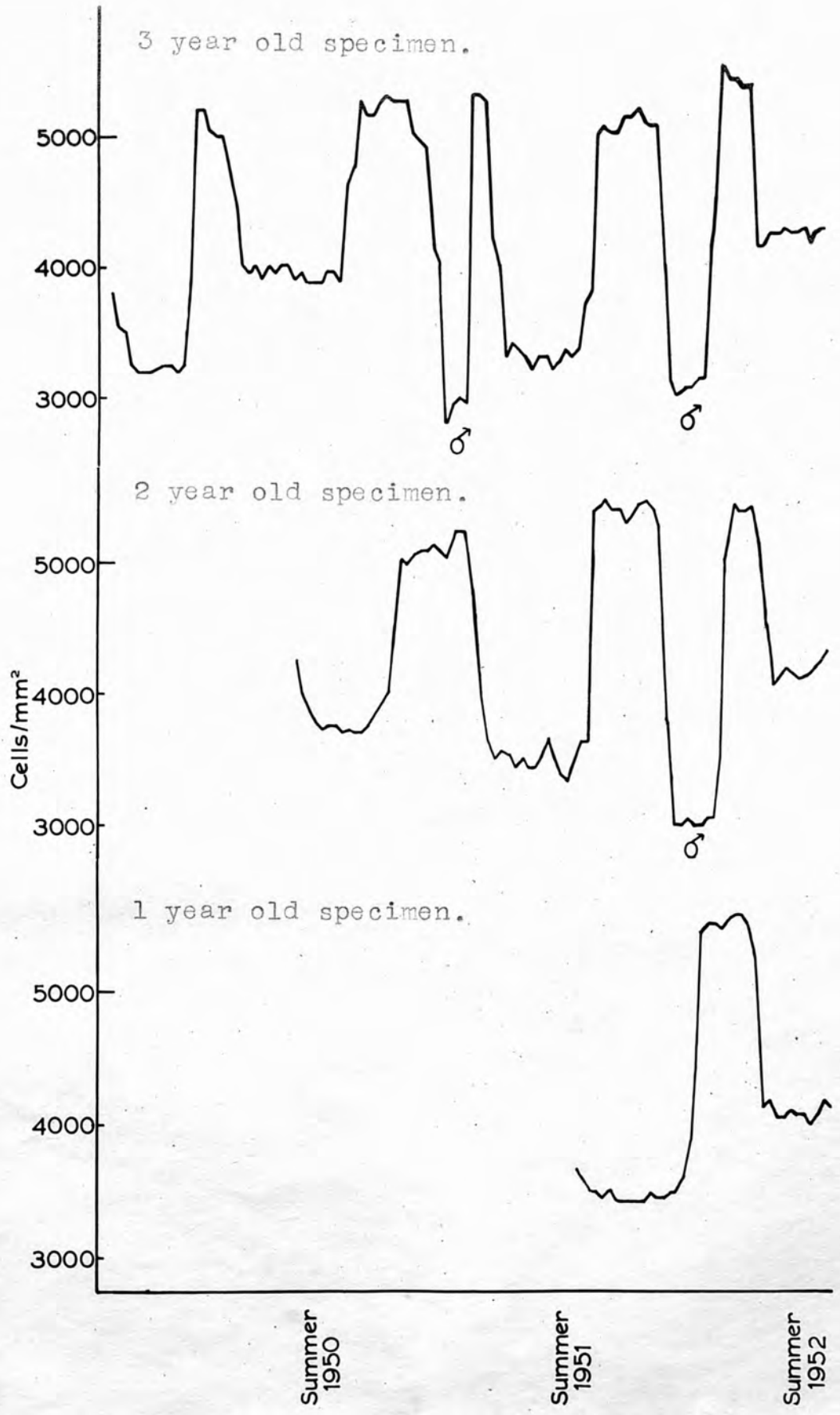
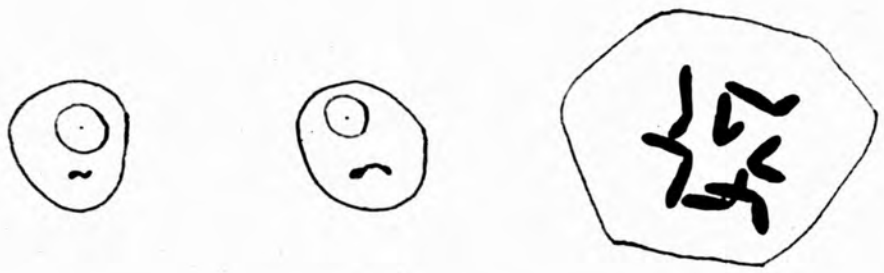
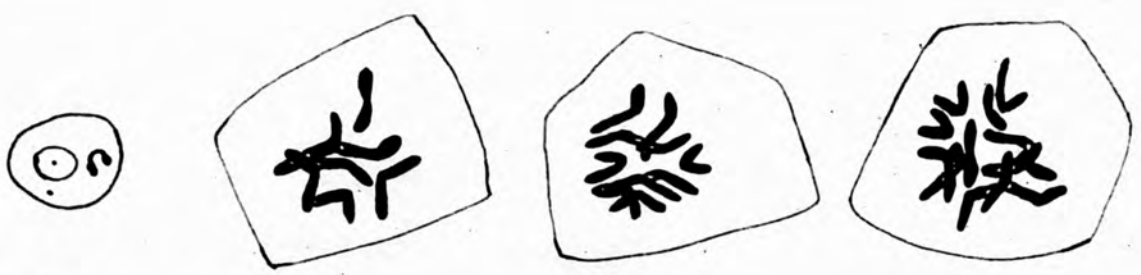


Fig 16. A.undulatum (N=14 male race.) Variation in cells /mm^2 in leaves of three plants from the same population in the field. 34 leaves examined each season. (see page 78.)



17 18 19

Figs17-19 . A.crispum. 17 and 18, resting nuclei. 19, gametophyte metaphase N-7.



20 21 22 23

Figs20-23. A.tenellum. 20 , resting nucleus. 21, gametophyte metaphase N-7. 22 and 23, aneuploid gametophyte metaphase N-10, N-14.

24 25

Figs24-25 . A.angustatum. 24 , resting nucleus 25 , gametophyte metaphase N-7.

All drawings X 3200

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Figs26-28. A.undulatum. 26, 27 and 28, resting nuclei.

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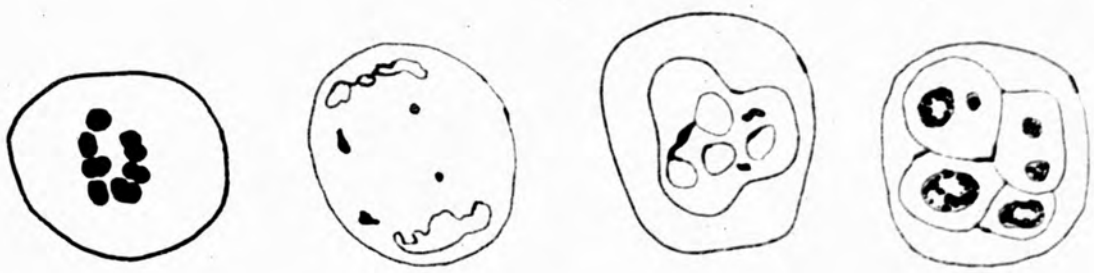
30.

31

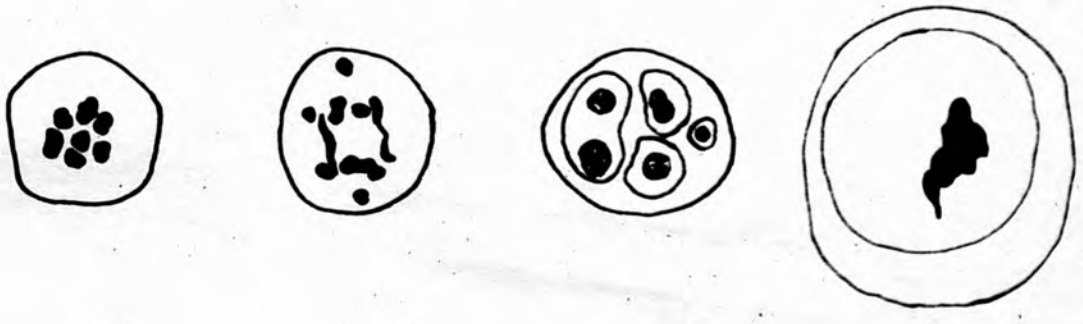
Figs29-31. A.undulatum. 29, 30 and 31, gametophyte metaphases N-21, N-19, N-14.

All drawings X 3200



32 33 34 35

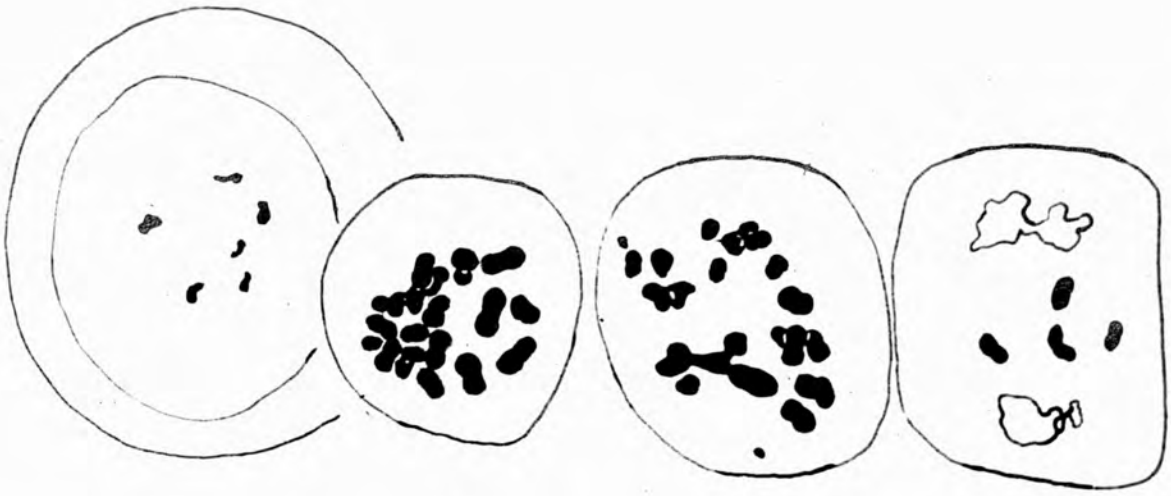
Figs32-35 A.tenellum. 32,meiotic metaphase. N-7. 33,anaphase 34 and 35,spore formation.



36 37 38 39.

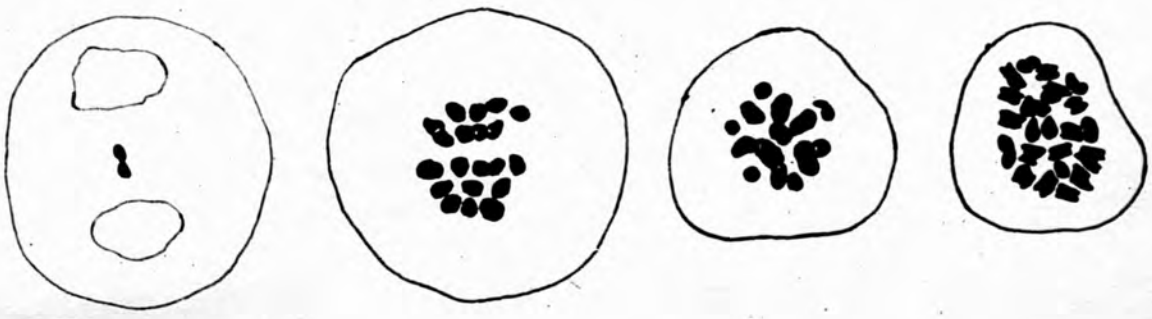
Figs36-39. A.angustatum. 36 ,meiotic metaphase N-7. ,anaphase 38 ,spore formation. 39,giant spore mother cell.

All drawings X 2200



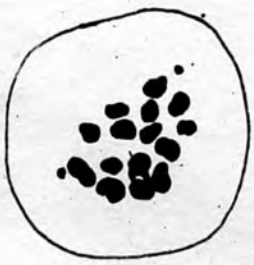
40 41 42 43

Figs40-43 A.undulatum.40,giant spore mother cell.41 and 42 meiotic metaphase.43, anaphase.



44 45 46 47

Figs44-47 .A.undulatum.44,telophase.45,meiotic metaphase N-19 46,meiotic metaphase N-14.47,anaphase N-14.



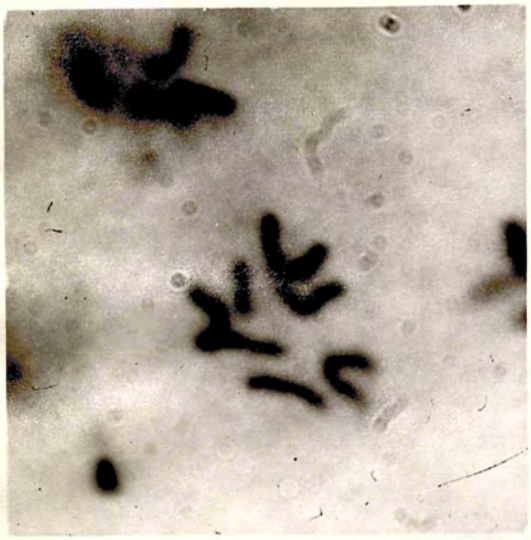
48

Fig48 A.undulatum X A.angustatum. meiotic metaphase.

All drawings X 2200

LIST OF PLATES.

Plates I - IV.



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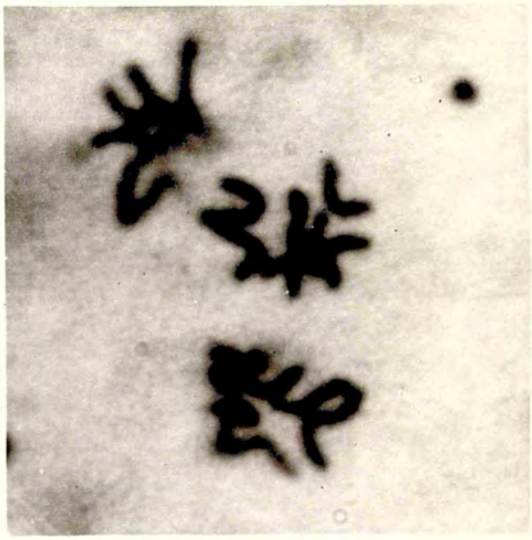
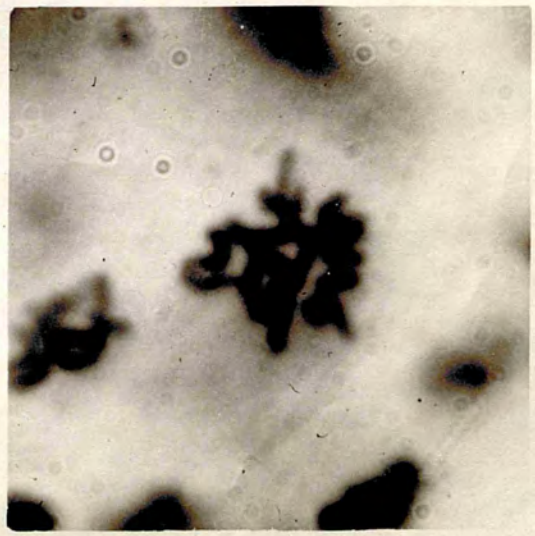


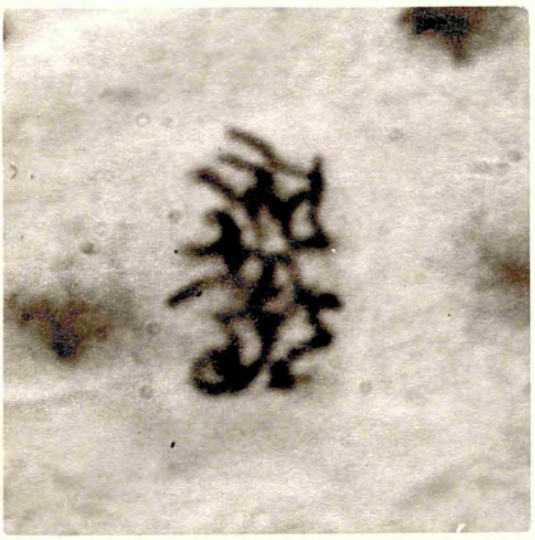
II

III



IV

Plates V - VIII.



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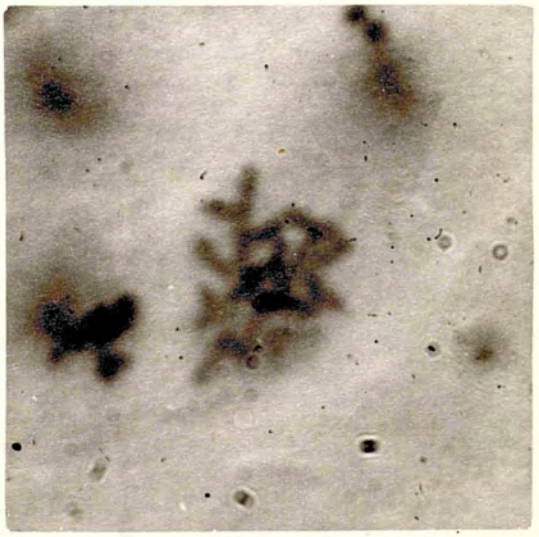

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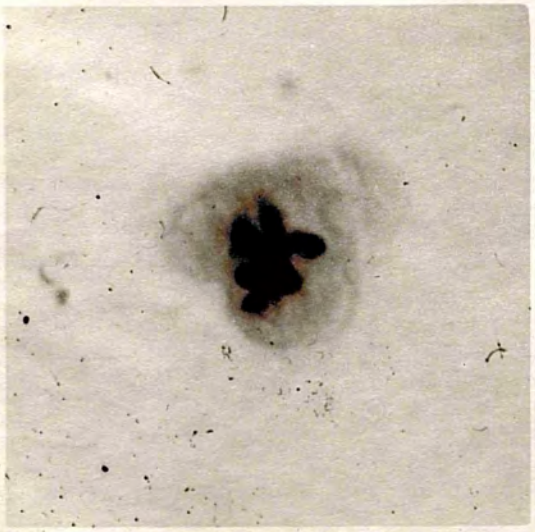
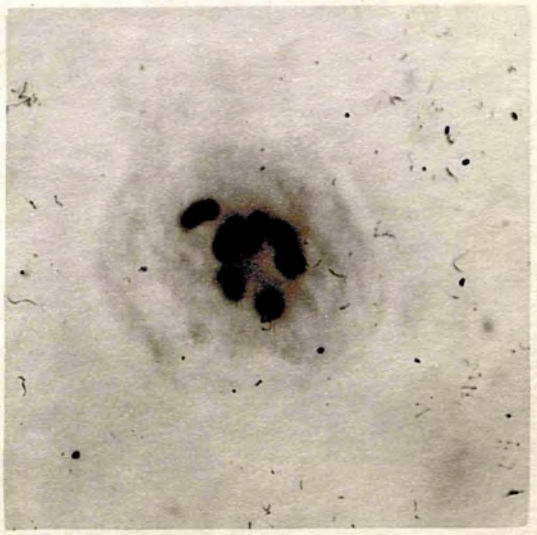
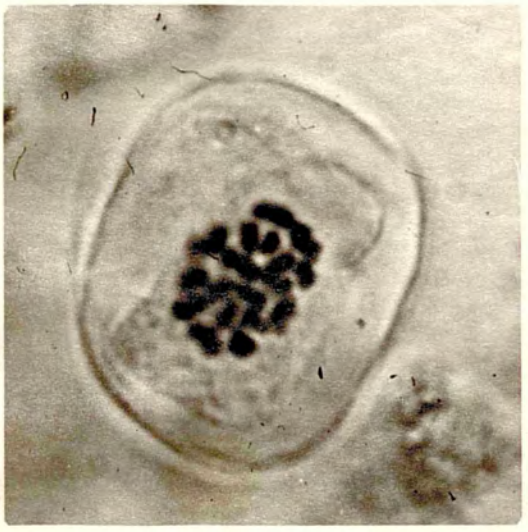


VII

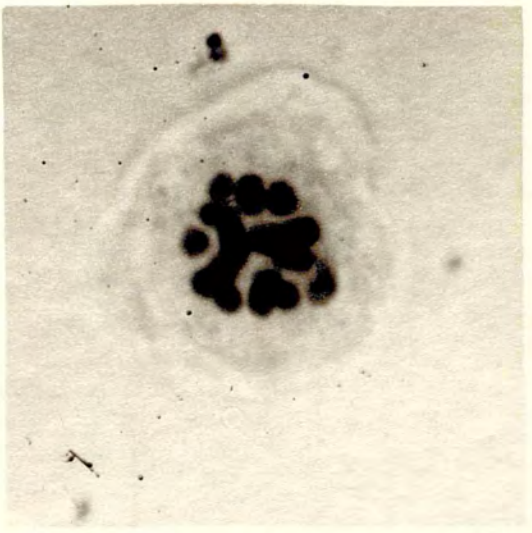


VIII

Plates IX - XII.



IX



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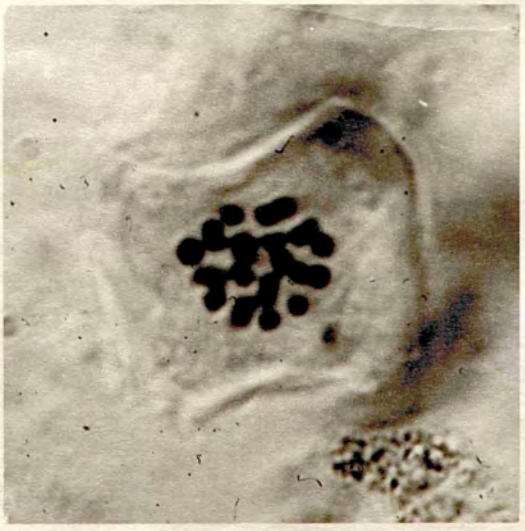
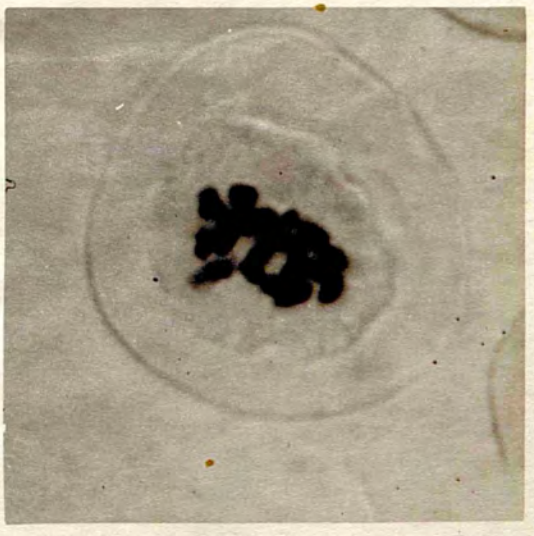


XI



XII