UNIVERSITY OF COLORADO STUDIES

SERIES IN BIOLOGY

NO. 26

UNIVERSITY OF COLORADO PRESS
BOULDER, COLORADO
JULY, 1967

A CYTOLOGICAL INVESTIGATION OF THE MOSSES OF THE ROCKY MOUNTAINS[1]

KULDIP R. KHANNA*

The area under discussion in this paper includes the Rocky Mountains in the United States from Glacier National Park, Montana, to the Elk Mountains of Gunnison County, Colorado. The moss flora of this region is diverse and is comprised of arctic, Northern Rocky Mountain (Canadian) and Pacific elements as well as by a number of southern and eastern species. The mosses of this region have not received any cytological attention earlier, although a number of species growing here have been studied from other areas, particularly from the North (Steere, 1954; Anderson and Crum, 1958; Vaarama, 1950) and Pacific West (Steere et al. 1954; Ireland, 1965). The purposes of this study have been to gather

[1] The support of this study by the National Science Foundation (Grant GB-1537), and by the Committee on Coordination of Research, University of Colorado, is gratefully acknowledged. I am indebted to Dr. John Marr, Director of the Institute of Alpine and Arctic Research, University of Colorado, and Dr. Robert K. Enders, Director of the Rocky Mountain Biological Laboratory, Gothic, for kindly providing facilities in their institutes during a part of the summers of 1964 and 1965, respectively. The chief park naturalists of Yellowstone National Park and Glacier National Park granted permission to collect mosses during the summer of 1964. The spore examination of the various collections of *Grimmia affinis* was made possible through the courtesy of University of Colorado Museum, the New York Botanical Garden, Farlow Herbarium of Harvard University, and Dr. Seville Flowers, University of Utah. A number of discussions with Prof. William A. Weber, particularly on taxonomic matters have been very helpful. For this, and for placing at my disposal the use of the rich facilities of the University of Colorado Museum, I wish to extend him my sincere thanks. Lastly, it is a pleasure to acknowledge the help and encouragement received from Dr. Antero Vaarama, visiting professor in the Department of Biology during the first year of this investigation.

*Department of Biology, University of Colorado, Boulder.
Present address: National Botanic Gardens, Lucknow, India.

cytological information about the uninvestigated species growing in the Southern Rocky Mountains and to get a broader appreciation of the cytological relationships and variability of the previously known ones. Being the first cytological study of the mosses of this area, it makes no claim of being more than a broad survey. However, several problems of significance have come to light during the course of investigation for which explanations have been suggested whenever possible, and the need for further study on these problems has been pointed out.

MATERIAL AND METHODS

The material for all the species was collected personally by the writer. The place of origin for each species is given individually. The cytology of all the species was studied from meiosis. The sporogones were fixed in 1:3 acetic-alcohol for 48 hours and then stored in 70 percent alcohol under refrigeration. Exceptions to this general procedure are: *Ceratodon purpureus* (from Rocky Mountain National Park), *Tortula mucronifolia, Leptobryum pryri-forme* and *Isopterygium pulchellum.* These species were studied without any fixation because the material was available only a short distance away from the laboratory. As pointed out earlier (Khanna, 1960a), it is easier to work out the cytology when the material is fresh. The squashes were made in acetocarmine. The slides were made permanent in Per-mount following the technique already described (Khanna, *loc. cit.*). The voucher specimens have been deposited in University of Colorado Herbarium. Magnification of all camera lucida drawings and photographs is approximately X2,000 unless otherwise indicated.

OBSERVATIONS

POLYTRICHACEAE

Polytrichum alpinum var. *brevifolium.* (R.Br.) Brid.

This species is very common at high altitudes in the Rocky Mountains and was investigated from two localities. The first population was studied from sub-alpine tundra at 7,000 ft. between Logan Pass and Hidden Lake, Glacier National Park, Montana. All the investigated plants show n = 7 (Fig. 1) and thus conform to the basic number of the family *Polytrichaceae.* The six bivalents are regularly oriented at meiosis while the seventh one is slightly precocious at M1. The first meiotic division is normal. During the second division 3 - 4 percent of the tetrads are organized with two nuclei included in a single spore and leaving its opposite counterpart empty (Plate III - 3 to 6). This is due to the failure of spindle organization or excessive shortening of distance between the two poles of the spindle in one of the 'equational' divisions. Ultimately, the nuclei in the spore may fuse to give rise to a single large nucleus. Cytokinesis in such cases usually proceeds normally, as it does in the rest, and the resulting spores from this tetrad have the constitution n = 7, 7, 14, 0. Rarely, when only a triad results, they have the constitution of n = 7, 7, 14. The diploid spores are bigger than

the rest (Plate III:-6) and in spite of the variation in size in both types the diploid spores are easy to identify. Such giant spores were found with a frequency of 1-3 percent in all the mature sporogones of this population.

The second population of *Polytrichum alpinum* var. *brevifolium* was studied from alpine tundra at 11,500 feet, close to Niwot Ridge, Colorado. Except for slightly longer leaves, this population is indistinguishable from the first population. Cytological observations revealed this to be a diploid with n = 14. While it is hard to demonstrate the origin of this race without undertaking considerable experimentation, the morphology of this race is highly suggestive of its close relationship with the first one and it seems quite likely that the diploid race has arisen from a diploid spore of the type mentioned above. The fact that the diploid has a regular meiosis and shows no apparent difference in spore or cell size from the haploid is not unexpected. A gradual reversion in size, getting close to the original haploid, is known to have occurred in several auto-diploids of mosses (see Khanna, 1960b). Furthermore, the distribution of the plants of the two sexes of the diploid is very interesting. The population seems predominantly dioicous comprised of pure male or pure female patches. Normally, however, a diploid race should be monoicous (Heitz, 1942; Mehra and Khanna, 1961). This fact gives further support to the above mentioned manner of origin of the diploid race. As the diploid spores of the haploid race are the result of fusion of two nuclei with identical constitution (being the product of the same equational division), they must carry identical chromosomes of the same sex. The diploid produced in this way has to be unisexual in contrast to the diploids arising by sporophytic apospory and containing chromosomes of both the sexes. The formation of purely male or purely female patches of this species around Niwot Ridge is obviously the result of vegetative reproduction. Further breeding within the population would definitely produce monoicous spores but their germination and development will depend upon their ability to compete with the already established individuals of the species. A study of the relative distribution of the dioicous and monoicous (if present) individuals in the diploid race as well as the relative distribution of the two cytological races in the Rocky Mountains should be very interesting.

Polytrichum alpinum has received considerable cytological attention earlier but not the variety *brevifolium*. Kurita (1937) and Yano (1957) reported n = 7 in this species. Steere (1954) reported n = 7 in variety *septentrionale* and Khanna (1964) reported n = 14 in the variety *arcticum*. Frye (in Grout, 1937) has used only quantitative characters such as the length of leaves and the length and thickness of the urn for differentiating the various toothed varieties of *P. alpinum*. Both the variation in size and ploidy in this species show that polyploidy has played a considerable evolutionary role within this species.

Atrichum undulatum (Hedw.) Beauv.

The material was found near the beginning of Sperry Glacier Trail starting from Lake McDonald, Glacier National Park, Montana. The chromosome number is n = 7 (Fig. 2). Earlier, this species is known in haploid (Tatuno, 1953;

Lowry, 1954), diploid (Heitz, 1926; Lowry, 1954a), and triploid (Heitz, 1928; Kurita, 1937; Tatuno, 1953; Lewis, 1957) races. All these races have a wide geographic distribution. The genus *Atrichum* has the highest frequency as well as grade of polyploidy among the genera of Polytrichaceae investigated thus far.

Polytrichadelphus lyallii Mitt.

This species was studied from the southeast side of Long Lake, Colorado. The chromosome number of n = 7 (Fig. 3) is in conformity with the earlier reports from the North (Anderson and Crum, 1958). On the basis of three populations known so far cytologically this species seems to be uniform, a feature much to be expected in *Polytrichaceae.*

DITRICHACEAE

Distichium inclinatum Hedw.

The material for this species was studied from Gothic Natural Area, Gothic, Colorado. The chromosome number is n = 13 with one large heterochromatic bivalent (Fig. 4). Following the existing terminology for this bivalent (Yano, 1957; Mehra and Khanna, 1961) it will be called H bivalent in the present article and the small heterochromatic bivalent will be called h bivalent.

The previous reports on the cytology of this genus are from Alaska. Steere (1954) reported n = 14 and n = 42 in *D. capillaceum* and *D. hageni* respectively. Steere (*loc. cit.*) expressed the hope that "It will be of considerable interest to determine the chromosome number of another American member of the genus, *D. inclinatum*, from which *D. hageni* probably originated, since further evidence of relationship may well be given by chromosome number and morphology." The present findings give little cytological support to the relationship between *D. hageni* and *D. inclinatum.*

Ceratodon purpureus (Hedw.) Brid.

The chromosome number of this thoroughly investigated species is n = 13 (Fig. 5) from the Rocky Mountains as well. The H chromosome is very large and perhaps has the largest relative size (in comparison to other members of the complement) in mosses.

DICRANACEAE

Dicranum strictum Schleich.

This species has a wide range of occurrence in the Rocky Mountains going as far down as Southern Colorado. Although a large number of populations of this species were examined, it was possible to get the chromosome counts only for the population from Long Canyon, Colorado. Twelve bivalents were observed (Plate I-1) out of which a large bivalent H and a small one h showed early disjunction. However, they attained normal condensation by M1 and but for disjunction and size they were indistinguishable from the rest. The large bivalent

was almost invariably disjoined precociously in all the spore mother cells examined while the smaller one had comparatively a much lower frequency of precocious disjunction.

This species has also been studied by Anderson and Crum (1958) from the Canadian Rockies. Their observations differ from the present one. The precocious bivalents H and h have not been observed in the Canadian material but two very small bivalents have been described which were not observed in the present material. The behavior of these small bivalents as described by Anderson and Crum and their absence in the present material suggest that they are accessory in nature.

Dicranum scoparium Hedw.

This weedy species is very abundant in the Rocky Mountain area and the material was collected from a large number of populations from Montana down to New Mexico. However, only three populations, two from Yellowstone National Park and one from Rocky Mountain National Park yielded cytological results. The Rocky Mountain Park population came from the southern bank of Big Thompson River close to Hayden Gorge. Twelve bivalents (Fig. 6) were observed in this population and the meiosis was perfectly normal. Vaarama (1950) reported a ring-shaped bivalent in the complement with precocious disjunction. This bivalent was observed in the present material as well. In several sporogones it gave a clear indication of being heterochromatic. It is an H bivalent. The report of $n = 12$ in this species is in accord with the findings of other workers.

Meiosis in both the Yellowstone Park populations coming from west of Blacksand Basin (Plate IV - 1 to 6) and Tower Falls was highly disturbed. It was not the clumping of the chromosomes but the asynapsis which was the predominant feature although general clumping and agglutination did occur. The population from west of Blacksand Basin was more abnormal than that of Tower Falls in having 6 - 8 univalents occurring frequently before M1 while in the latter population no more than 4 univalents were observed at this stage. These counts of univalents exclude the halves of the H bivalent which are always precociously disjoined by M1. A cytological analysis of one of the sporogones of the Blacksand Basin population is given in Table I.

The number of the univalents is so random in the different mother cells that it is difficult to point to any definite trend. For the same reason it appears that the abnormalities observed are due to seasonal effects rather than to hybridization even though this species is quite variable. The absence of odd numbers of univalents at M1 and their presence during A1 and T1 suggest that their movement to the poles is irregular. While some of the univalents move to the poles, the others divide at random at or off of the equator. This is followed by abnormal cytokinesis and abnormal spores.

An examination of herbarium sheets of *Dicranum scoparium* for spore characteristics revealed tremendous variation in the size of the spores produced by the same capsule. This was observed particularly in a large number of North

TABLE I. The occurrence of univalents in a sporogone of an abnormal population of *Dicranum scoparium*.

M1											
Number of univalents	0	1	2	3	4	5	6	7	8	9	10
Number of mother cells in which observed.	2	0	4	0	7	0	7	0	6	0	1

Late A1 or Early T1									
Number of univalents	1	2	3	4	5	6	7	8	9
Number of mother cells in which observed.	4	6	9	10	2	4	1	0	1
The division of the univalents in the mother cell.	ND 1D 1 3	ND 2D 1 5	1D 2D 3D 1 3 5	2D 3D 4D 1 4 5	1D 3D 1 1	ND 3D 5D 1 1 2	7D 1		1D 1

(ND=no univalent dividing, 1D=one univalent dividing, 2D=two univalents dividing, etc.)

American populations. The spores of two such populations are pictured in Plate IV - 8 and 10. Because of the great disparity in the size of the male and the female plants in this species the occurrence of heterospory is much to be expected. Although this question must at present be left open, it appears that the differences observed in the spore size in the present populations are not due to heterospory. There are two reasons for making this statement: First, in all cases the smaller spores appear much shrivelled and wrinkled which points more to their deficit genetic constitution than to their male character. Second, the spore nuclei, which were studied by staining with acetocarmine also showed a variation in size which was relative to the size of the spores. The larger spores usually contained larger nuclei. Since there are no heteromorphic sex chromosomes in this species, the difference in the size of the nuclei must be due to abnormal meiosis.

Dicranoweisia crispula (Hedw.) Lindb.

The material was studied from Many Parks Curve, Rocky Mountain National Park, Colorado, in March 1964 and the observations were repeated in 1965 from Gothic and Cottonwood Pass, both in south central Colorado. In all cases 14 bivalents were counted unmistakably (Plate I-2, Fig. 7). It is much easier to obtain well spread plates in this species as compared to the other members of the family Dicranaceae and due to almost complete lack of stickiness, the counting is considerably facilitated.

The above observations differ strongly from the earlier counts on this species according to which the chromosome number is n = 11 (Steere, Anderson and Bryan, 1954; Anderson and Crum, 1958). If the reports by these authors are correct, then there must exist two distinct cytological races in this species.

Oncophorus virens Hedw.

The material was studied from Fourth of July Camp Ground, Colorado. Fourteen bivalents have been observed (Fig. 8). Three of these bivalents are heterochromatic, the two being among the larger and one among the smaller members of the complement. The larger heterochromatic bivalents are characterized by peripheral location and occasional precocious disjunction at M1. The latter feature was also observed by Anderson and Crum (*loc. cit.*) in the Canadian material of this species. The present meiotic studies are in conformity with mitotic karyotype studies of this genus by Yano (1957) both with regard to the number of the chromosomes and the number of the hetero-chromosomes. The monoicous nature of the species is quite expected because of the presence of two large heterochromatic bivalents (Khanna, 1964).

O. polycarpus (Hedw.) Brid var. *strumiferus* (Hedw.) Grout

The material for this species was collected from a stream bank in Gothic Natural Area. The chromosome number is n = 14 (Fig. 9) with one h bivalent clearly distinguishable. This species receives cytological investigation for the first time.

POTTIACEAE

Gymnostomum calcareum Nees and Hornsch.

The material for this species was studied from Lake McDonald Creek at the beginning of Lake John Trail, Glacier National Park, Montana. The chromosome number is n = 13 (Fig. 10). The only previous count of this species is from the Himalayas where it is also n = 13 (Khanna, 1960a). The large H bivalent characteristic of the Himalayan material was observed in the Glacier National Park population as well. The occurrence of this subtropical species so far north with remarkable uniformity of chromosome number is very interesting.

Didymodon recurvirostris (Hedw.) Jenn.

The material was investigated from Gothic Natural Area, Gunnison National Forest, Colorado. The chromosome number is n = 13 with heterochromatic H and h bivalents characteristic of Pottiaceae (Plate I-3, Fig. 11).

The same chromosome number for this species has been reported from Alaska (Steere, 1954) and the Canadian Rockies (Anderson and Crum, 1958) and in both cases the large H bivalent has been observed.

Tortula mucronifolia Schwaegr.

The material was studied from Gothic, Colorado. The chromosome number is n = 26 (Fig. 12) with two large bivalents. The smaller h bivalents, although expected to occur in the present material, could not be located with certainty.

The present report differs from all the previous counts on this species. Steere (1954) reported n = 30 from Alaska while Anderson and Crum (1958) report n = 12 and 24 from two different Canadian populations. It appears that *T. mucronifolia* too, like other species of the genus *Tortula, e.g., T. princeps* and *T. muralis*, is a highly variable species cytologically.

Trichostomum cylindricum (Bruch) C. Muell.

The material for this species was collected near Tower Falls, Yellowstone National Park. The chromosome number is n = 13 with one very large bivalent which is the H bivalent (Plate I-4). The smaller heterochromatic bivalent h could not be located in the complement. To the best of the knowledge of the writer this is the only chromosome record of this species.

Desmatodon latifolius (Hedw.) Brid.

Three populations of this essentially arctic-alpine species have been studied. These populations are from Garden Wall, Glacier National Park, Montana, timberline area of the Institute of Alpine and Arctic Research, University of Colorado, and Cottonwood Pass, Colorado. In all three populations n = 28 (Fig. 13-15) was observed out of which two of the bivalents are very small and show a behavior described for the h bivalents of mosses (Khanna, 1960a, Mehra and Khanna, 1961). The population from Gothic gave good evidence of the presence of two H bivalents which could not be spotted in the northern popu-

lations. Considering the previous chromosome reports on this genus, i.e., n = 26 in the present species (Anderson and Crum, 1958) and n = 13 in *D. hendersonii* (Steere, Anderson and Bryan, 1954) it appears that the small heterochromatic chromosomes observed by the writer might be accessories but their occurrence with remarkable uniformity in such widely spaced populations would suggest that they are a definite part and parcel of the genetic makeup of the species.

Phascum cuspidatum Hedw. var. *americanum* Ren. and Card.

This species was studied from Steamboat Mountain, Lyons, Colorado. Twenty-six bivalents (Fig. 16) were observed and out of this two large H bivalents could be clearly differentiated while only one h was observable.

The chromosome number observed in the present material is in accordance with the reports from Tennessee (Bryan, 1956) and one population from California (Steere et al, 1954) but differs from other California population which has n = 28 + 1-2 m. No accessory chromosomes have been observed in the present population.

GRIMMIACEAE

Grimmia alpicola Hedw.

The material for this monoicous species was collected from boulders in and around Big Thompson River west of Hayden Gorge, Rocky Mountain National Park. The chromosome number was found to be n = 13 (Fig. 17). It was not difficult to find well spread plates and there was no problem with regard to counting the number of the chromosomes. Three bivalents were observed to show precocious disjunction as a rule.

This species has also been investigated by Anderson and Crum (loc. cit.) who report that four bivalents show precocious disjunction. In the present material, however, only three or sometimes a lesser number of bivalents were observed to show this phenomenon. It is likely that there are several races with regard to the distribution of heterochromatin in this species.

G. apocarpa Hedw.

This species was studied from the west side of Summit Lake and Jackson Creek, Colorado. In both cases it was growing over boulders and adjoining soil. The chromosome number for both populations was observed to be n = 13 (Fig. 18). This is in conformity with the chromosome number reported for this species from California (Steere et al, 1954) and France (Ho, 1956) but is different from the number reported from other localities. Vaarama (1953) has reported n = 12 for this species from Finland. Anderson and Crum (1958) have reported n = 14 in this species from Canadian Rockies. In the present material although no H or h bivalents could be detected, one of the bivalents was observed to show frequent precocious disjunction.

Grimmia alpicola and *G. apocarpa* have been placed by several authors in a separate genus *Schistidium* on the basis of morphological characters. The cytological evidence does not give support to this view. The writer agrees with Anderson and Crum (*loc. cit.*) that *Schistidium* should not be given a rank greater than a subgenus within the genus *Grimmia.*

G. elatior B.S.G.

The chromosome number for this species was studied from the Royal Gorge of Como Creek, Colorado. First observations were made during the summer of 1964 and they were repeated again during the summer of 1965. From the observations of both these years it was possible to establish the chromosome number of this species to be n = 13 (Fig. 19). However, the course of meiosis during the two years was very different. Meiosis was normal during the second year while during the first it was greatly disturbed.

The meiotic abnormalities were of the type of asynapsis, occasional failure of spindle formation and irregular cytokinesis. The degree of asynapsis was variable. The number of univalents observed at M1 ranged from 2 - 14. While 2-6 univalents can be expected in the normal complement of the Grimmias due to the earlier disjunction of the heterochromatic chromosomes, a larger number is certainly abnormal. The common number of the univalents observed was 8 - 12 (Fig. 20). The behavior of the univalents is similar to what has been observed in many other organisms. They behave in either of the following two ways: 1. They may move to the opposite poles quite early during the first division and may constitute nuclei there while the bivalents are still lagging at the equator. 2. The bivalents divide first and the chromosomes constituting them move on to the poles while the univalents stay at or around the equator as laggards and may not be included in the anaphase nuclei (Fig. 21). They ultimately constitute nuclei at this place (Fig. 22). The univalents may also be scattered over the spindle at random without any definite arrangement or movement towards the poles. This results in the formation of micronuclei of various sizes upon completion of meiosis.

In comparison to the asynaptic abnormalities spindle abnormalities were only slight. In most cases there was disorientation of the bipolar axis of the spindle which according to Östergren (1950) is the weakest type of spindle abnormality. The formation of additional smaller spindles which results in asynaptic plants (Vaarama, 1949) was totally absent.

Cytokinesis was severely affected. The irregularities of cytokinesis (Figs. 22 and 23) seemed to bear no correlation with the movement or the distribution of the chromosomes in the cell. It was not always the case that the larger nuclei were included in a larger bit of cytoplasm and the smaller ones in the smaller. A large percentage of enucleate spores were also produced.

The difference in the behavior of the same population in the two years seems to be related with the fluctuation of temperature and atmospheric humidity. The Front Range was relatively much drier during the summer of 1964 as

compared to that of 1965. It is most likely that the meiotic abnormalities were caused by the dry summer of 1964.

G. affinis Hornsch.

This is one of the abundantly fruiting species of the genus *Grimmia.* Its small compact cushions of various shades between olive and greyish green are common on rocky slopes and talus at higher altitudes in North America. Although a large number of populations was sampled from the Rocky Mountains, cytological investigation was possible on only two of them. The population from the Rocky Mountain National Park showed regular meiosis except for slight disturbances in cytokinesis at the end of the meiotic division. The tetrads were almost regular. Thirteen bivalents were counted with 2 H and one h among them. The population from Yellowstone National Park, although having the same chromosome number and morphology as described for the first population, showed very interesting abnormalities with regard to spindle formation and cytokinesis. The exact location of this population is about a mile north from Tower Falls, along the Loop Road of Yellowstone Park. As material at the right stage was plentiful, it was possible to note that the range of meiotic abnormalities from one sporogone to another was considerable. While some of the sporogones seemed to be barely affected, others showed a total clumping of the chromosomes and complete spindle inactivation. One sporogone containing spore mother cells at different meiotic stages exhibited all types of meiotic abnormalities. This will be described in detail as the representative type.

The earlier stages of meiosis give little or no indication of chromosome clumping which showed up in subsequent stages. This is perhaps explained by the recent studies of Taylor (1959), Hotta and Stern (1963), and Kemp (1964), all of whom have shown that even though the early stages of meiosis, leptotene and pachytene, are most vulnerable with regard to protein and RNA synthesis, the effects of disturbances caused at these stages do not show up profoundly until later in the division. In fact, in most sporogones in this study diakinesis with complete pairing and no clumping was observed and, therefore, was a perfectly suited stage for making chromosome counts as is the case in other mosses. It is only after this stage that the chromosomes become clumped and the defective organization of the spindle becomes apparent.

The data concerning the various kinds of spindle abnormalities are presented in Table II and Plate II-1 to 12. It is clear from the table that the majority of spindle disturbances fall in the category of either disturbed bipolar or monopolar types. There are many transitional types between the two kinds of spindles in which the shortening of the normal distance between the two poles (Plate 2-4) is observed to a varying degree. It seems that some kind of a process of telescoping is involved where the two poles of the spindle ultimately coalesce into one another. In the process, however, certain other irregularities such as the partial tripolar (Plate II-7), tripolar (Plate 2-8), multipolar and apolar spindles also show up. The number of such cases is relatively small and, perhaps they represent divergent

intermediate steps in the process of degeneration of spindle from bipolar to monopolar or apolar types. The present results, thus, correspond more with c-mitosis in onion root tips observed by Levan (1938) or with the effects of various

TABLE II. The occurrence of various kinds of spindle abnormalities in *G. affinis*.

Type of spindle	Number of spore mother cells in which observed.
Normal Bipolar	5
Disturbed Bipolar	40
Comprised of following sub-types	
a. dislocation of the two poles	
b. shortening of the distance between the two poles	
c. unequal development of the two poles	
Multipolar	15
Comprised of following sub-types	
a. partial tripolar	
b. complete tripolar	
c. multipolar	
Monopolar	93
Comprised of following sub-types	
a. circular	
b. star-shaped	
c. budding out a number of smaller spindles	
Apolar	10
The chromosome distribution following no definite pattern.	
Total number of cells examined	163

spindle inhibitory drugs described by Östergren (1950) where the spindle degenerates from bipolar to monopolar or apolar types through the intermediate steps of multipolar spindles, rather than with the cases of independently behaving split spindles observed by Vaarama (1949) in *Ribes nigrum* and divergent spindles observed by Darlington and Thomas (1937) and Clark (1940).

The monopolar spindle itself may appear circular or star-shaped (Plate II-1) or it may bud out into a number of smaller spindles (Plate II-2) which ultimately result in small micronuclei around the main nucleus (Plate II-3). The "star metaphases" have been observed in a number of organisms under the influence of drugs (Östergren, 1950). Finally, the spindle is completely disorganized giving rise to an apolar structure with chromatin irregularly distributed without any definite pattern.

The second division, if it takes place, is apparently 'equational,' but the number, size, and location of the ultimate nuclei have already been determined during the first division. It is, however, doubtful that even the largest tetrad nuclei carry a fully functional amount of genetic material.

Even the severest chromosome clumping or spindle abnormalities seldom suppress cytokinesis completely, so that a monad as the end result of meiosis is only of a rare occurrence. However, these abnormalities do lead to a highly disturbed and irregular cytokinesis. During normal cell division, cytokinesis always occurs with respect to the orientation of the spindle, so that the two are

related phenomena. This relationship seems rather delicate and may be easily upset by a number of factors. In *Weissia exserta*, an amphidiploid, it was observed by the writer (Khanna, 1960c) that while the two genomes presented no pairing problems, they did not synchronize enough to bring about a regular cytokinesis. This resulted in four regular nuclei at the end of meiosis, but the spores were very irregular in size and some of them were enucleate. In the present case also cytokinesis does not proceed in harmony with the spindle and thus irregular and enucleate spores result (Plate II-11 and 12). The cause here seems to be either a gene mutation or unfavorable weather at the time of meiosis or both. A similar result may also be obtained through the action of drugs (Hotta and Stern, 1963; Kemp, 1964). That it is not always true that spindle formation and cytokinesis are independent is shown, amongst others, by the work of Levan (1938). He observed that in c-mitosis of root tips of *Allium cepa* the multipolar spindle in giant cells resulted in their division into a large number of smaller cells each including a single nucleus. The explanation for such cases might be in a lesser cytoplasmic disturbance in these cases or in an inherent relationship between spindle orientation and cell wall formation.

The Spores: The range of spore abnormalities like the meiotic abnormalities was also considerable in the Yellowstone population. However, the majority of the mature sporogones show more than 50 percent degenerate spores (Plate III-2). To determine the geographic extent of such abnormalities, 60 herbarium collections of this species were examined from North America. Some of the collections proved inadequate for the purpose of the present study because they either bore no sporogones at all or the sporogones were so young that the spores within them had not matured. It is important that the young spores, as they tend to wrinkle irreparably with the loss of water under herbarium storage, should be discarded from the calculations of the present type. Otherwise, they are likely to show more abnormalities than are actually present. In the present case, therefore, only the fully mature sporogones were considered. All the dots on the map (Fig. 28) are on the basis of these collections. Furthermore, only completely empty and shrivelled spores were considered abnormal. It may be pointed out that while studying these collections, several cases were observed which showed different percentages of shrivelled spores in the same package of material. A notable example of this type is the material collected by Viereck from Mt. McKinley National Park, Alaska. In this respect it is similar to the population from Yellowstone National Park.

Specimens cited on the map: ALASKA: Bering Strait District, *Johnson, Viereck and Melchoir*, July 5, 1959 (COLO); Okpilak River, *Shushan and Thompson*, August 4, 1956 (COLO); Mt. McKinley National Park, *Viereck*, July 10, 1958 (COLO) (two results represented from the same population); *Weber and Viereck*, July 23, 1956 (COLO); *Viereck*, July 10, 1956 (FH); CANADIAN EASTERN ARCTIC: Southampton Island, *Polunin*, August 22, 1936 (FH); BRITISH COLUMBIA: near Fort Nelson, *Correll*, July 18, 1943 (COLO); MANITOBA: Norway House, *Scoggan*, June 19, 1949 (COLO); QUEBEC:

58°.5 N and 72°.40 W, *Marr*, August 9-18, 1948 (FH); WYOMING: Yellowstone National Park, *Khanna*, August 2, 1964 (COLO); Sheep Mountain, *Goodding*, September 2, 1903 (FH); near Centennial, *Conard*, August 10, 1953 (COLO); COLORADO: Fort Collins, *Hermann*, August 11, 1961 (COLO); Rocky Mountain National Park, *Sayre*, June 16, 1935 (COLO); *Khanna*, September 24, 1963 (COLO); *Weber*, May 30, 1956 (COLO); base of Green Mountain, *Weber*, February 24, 1949 (COLO); Rampart Range, *Flowers*, August 22, 1964 (UT); Cebolla Creek Camp Grounds, *Weber*, July 29, 1964 (COLO); ARIZONA: Chiricahua Mountains, *Weber and Shushan*, April 18, 1957 (NY); NEW MEXICO: Las Vegas, *Arsene*, May, 1927 (FH); TEXAS: Mt. Livermore, Hinkley, August 6, 1939 (NY); NEW YORK: Avalanche Lakes, *Peck* (NY). The abbreviation of herbarium names is according to Lanjouw and Stafleu (1959).

ENCALYPTACEAE

Encalypta vulgaris Hedw. var. *mutica* Brid.

This species was studied from Lyons and Gregory Canyon, Colorado. In both the populations 14 bivalents were observed out of which 13 bivalents are large and one is small (Fig. 24). The behavior of the latter was of the nature of an h bivalent. In this respect, this species simulates *E. alpina* which also has the same constitution, *i.e.*, n = 14 (13 + h) (Steere, 1954), rather than its own Californian population which has only 13 bivalents with the h bivalent missing (Steere et al, 1954).

The genus *Encalypta* provides another example where the presence of the h chromosome is a variable feature. In addition to the cases of *E. vulgaris* var. *mutica* (both California and Colorado populations) and *E. aplina* cited above, a single h bivalent has been observed to be present in polyploid *E. procera* (n = 27 + h) and absent in another polyploid species, *E. rhabdocarpa* (n = 26). Both polyploid species were studied from Alaska by Steere (1954). Although the h bivalent occurs with a great deal of uniformity in most mosses, it seems to be of less importance in some cases than in others. As pointed out earlier by the writer (Khanna, 1960a) the cases where the h bivalent fluctuates in different population may easily be representatives of a transitional stage between the two basic numbers.

BRYACEAE

Bryum pallescens Schleich.

The material for this species was studied from Garden Wall and Logan Pass, Glacier National Park, Montana. Eleven bivalents were counted in both populations (Fig. 25). The heterochromatic bivalents could not be identified. This species receives cytological attention for the first time.

Pohlia longicolla (Sw.) Lindb.

The material was studied from Summit Lake, Colorado. Eleven bivalents

were observed (Fig. 26) out of which 2-3 are precocious. No H or h bivalents could be identified with certainty.

The earlier count on this species is from Japan by Yano (1957) who has observed 22 bivalents.

Leptobryum pyriforme (L.) Schimp.

The material for this species was studied from Gothic, Colorado. The chromosome number is n = 20 (Fig. 27). It was not possible to identify the heterochromatic bivalents. Anderson and Crum (*loc. cit.*) report the same number of chromosomes for this species from the Canadian Rockies.

BARTRAMIACEAE

Philonotis americana Dismier

The material was studied from a wet aspen grove near the junction of the Institute of Alpine and Arctic Research Road and Rainbow Lakes Road, Colorado. The chromosome number is n = 6 (Plate I-5). No H or h bivalents could be detected. This species receives cytological attention for the first time.

P. fontana (Hedw.) Brid.

The material for this cosmopolitan species was studied from the west side of Garden Wall, Glacier National Park, Montana and Gothic Natural Area, Colorado. The chromosome number is n = 6 (Fig. 29).

Previously, this species has been studied from Finland (Vaarama, 1953), Ireland (Vaarama, 1956) and Canada (Anderson and Crum, 1958). All these authors report the same chromosome number of n = 6. The genus *Philonotis* is very uniform cytologically.

Bartramia ithyphylla Brid.

The material for this species was studied from Gothic, Colorado. Twelve bivalents were observed with two large H and two small h chromosomes (Fig. 30). The chromosome number of the species is the same as reported from the North. Steere (1954) and Vaarama (1950) worked on this species from Alaska and Finland respectively and in both cases n = 12 was reported.

B. breviseta Lindb.

This species was studied from Summit Lake, Colorado. Six bivalents were observed in a number of sporogones (Plate I-6). Both the H and h bivalents are conspicuous at M1 though they could be detected at other stages as well. Their behavior is typical of the heterochromatic bivalents described earlier. This species receives cytological attention for the first time.

The present discovery of n = 6, the lowest chromosome number in the genus *Bartramia* necessitates a review of the species of this genus with higher chromosome number. Vaarama (1950), Steere (1954) and Lowry (1954b) have suggested that the basic number for the genus might be 4. Then, the species with

n = 8 and n = 12 are diploid and triploid respectively. Lowry (loc. cit.) advanced an explanation for the origin of n = 8 in *B. pomiformis* taking into consideration both the karyotype and the meiotic studies. In the light of the general pattern of karyotype in mosses, it was pointed out by the writer (Khanna, 1960a) that this explanation was untenable and a suggestion was made that a related genus, *Philonotis* might be looked for an explanation of the basic number of some of the species of the genus *Bartramia.* In the same communication it was stated "It is quite likely that 6 may be the basic number of some of the species of the genus *Bartrama* as well, of which *B. ithyphylla* has so far been investigated and is diploid." The chromosome number of *B. brevista* as well as its close relationship with *B. ithyphylla* which is discussed below, fully justifies the above hypothesis. The question of their origin of basic number 8, however, remains unanswered. Nor is it possible at present to correlate the two basic numbers, 8 and 6, with each other or to attempt a generic subdivision on this basis as too few species have so far been investigated to permit this.

Like the 8 chromosome species, *i.e., B. pomiformis* and *B. subpellucida, B. breviseta* is monoicous and thus along with them and a number of other mosses pointed out earlier (Mehra and Khanna, 1961) is an exception to the general rule that the mosses with one large heterochromatic bivalent H are dioicous.

A comparative morphological study of *B. breviseta* and *B. ithyphylla* reveals that the two are related. The structure of the various plant parts is essentially similar in the two cases but all the organs in *B. breviseta* are very dimunitive as is clear from Fig. 35. This dimunition is sometimes reflected in the cell size as well. The cells of the leaf lamina of *B. breviseta* are considerably smaller than those of *B. ithyphylla* although this difference is less marked in the basal cells. The spores of *B. ithyphylla* and *B. breviseta* are not very different from each other in size. Because of the essential similarity between these two taxa they have been occasionally treated together. *B. breviseta* has often been considered a variety of *B. ithyphylla* (see Van Der Wijk, 1959; Nyholm, 1956). The difference in size between these two taxa is well marked making them very distinct from each other in the field. There is a strong barrier to crossability between them due to the difference in the level of ploidy. The treatment of the two as separate species is fully justifiable on both morphological and cytological grounds.

Although the relationship between *B. ithyphylla* and *B. breviseta* is undoubted, the degree or type of relationship is difficult to interpret. The haploid chromosome number of *B. breviseta*, its diminutive organ and cell size as well as the observation by Vaarama (1950) of the occurrence of a quadrivalent which probably represents two H bivalents would suggest that *B. ithyphylla* might be an autodiploid from *B. breviseta.* However, the general lack of multivalent formation in *B. ithyphylla*, which could also be attributed to its well-established nature (see Khanna, 1960b), would tend to withdraw support from the autodiploid interpretation of this species. The question has to be left open for a future investigation.

Plagiopus oederi (Gunn.) Limpr.

This species was studied from the wet quartzite cliffs near Emerald Lake, Gothic, Colorado. Seven bivalents were observed in several sporogones (Fig. 31). The heterochromatic bivalents could not be identified with certainty. The present report confirms the only earlier count on this species and genus which is from the State of Washington (Ireland, 1965). The occurrence of taxa with n = 7 in the family Bartramiaceae is interesting after the report of the basic numbers 6 and 8 in this family.

SPLACHNACEAE

Tayloria acuminata Hornsch.

This species was also studied from the area of Emerald Lake, Gothic, Colorado. Thirty bivalents (Fig. 32) were observed in it without doubt. This is the first chromosome count on this genus. This high chromosome number is definitely polyploid but since it is the only count available on the genus *Tayloria*, the basic chromosome number cannot be decided with certainty. From the other members of this family which show chromosome numbers such as 8, 9, 10 and 19 (Wylie, 1957; Khanna, 1963) it appears that in all probability the basic chromosomic number for the genus *Tayloria* is 10.

ORTHOTRICHACEAE

Amphidium lapponicum (Hedw.) Schimp.

The material for this species was studied from south of Emerald Lake, Gothic, Colorado. The chromosome number is n = 16 with 4 bivalents having the size and behavior of small heterochromatic bivalents, h (Fig. 33). The chromosome number is in accord with the earlier reports on this species from Finland (Vaarama, 1950) and Canadian Rockies (Anderson and Crum, 1958). Although the latter authors make no mention of the small heteochromatic bivalents in this species, Vaarama notes three such bivalents. The present report of 4 small heterochromatic bivalents in this species makes it probable that one bivalent may be variable with regard to heteropycnosis in different races of this species.

BRACHYTHECIACEAE

Eurhynchium strigosum (Hoffm.) Br. & Sch.

The material was studied from boulders along Lake John Trail, Glacier National Park, Montana. The chromosome number is n = 10 (Plate I-7). This includes five large and five small bivalents. Among the larger group there is a heterochromatic bivalent whose behavior is very irregular. Occasionally this bivalent gives the impression of being heteromorphic but this feature could not be established even after a study of large numbers of cells. The irregular behavior of the H bivalent is due to the different condensation of the various chromatids sometimes belonging even to the same chromosome (Fig. 34). The dioicous to pseudomonoicous nature of this species (Grout, 1928) could be due to

the occasional irregular separation of the various components constituting this bivalent. In the smaller group also there is the h bivalent characterized by occasional precocious disjunction and light staining but its behavior is not as irregular as that of H.

AMBLYSTEGIACEAE

Amblystegium juratzkanum Schimp.

The material was studied from Pelican Creek, Yellowstone National Park. The habitat in this case deserves special mention because this is one of the few species of mosses where the chromosome number has been related with the habitat (Vaarama, 1956). The present site of collection was under the edge of the creek bank, on wet sandy soil which is frequently inundated with the rise of the water level in the creek. The chromosome number as observed from several sporogones is n = 20 (Fig. 36). There is a distinct h bivalent.

This species is very closely related to *A. serpens*, from which it is distinguished in having widely spaced leaves and oblong to rectangular basal cells. The latter character is so much variable that Grout (1903) states "I have seen leaves with one side having cells of *serpens* and the other of *juratzkanum*." A similar situation has been noted by the present investigator as well. Anderson and Al-Aish (1963) state that the distinctions between these two species are not always evident. It has been decided, therefore, to treat them together in the present discussion. *A. serpens* is one of the widely studied taxa of mosses with regard to polyploidy and intraspecific chromosome races. Marchal and Marchal, Wettstein, and Hofer have reported n = 12 in the wild plants of *A. serpens* (Wylie, 1957). The same chromosome number has been confirmed for *A. juratzkanum* by Anderson and Al-Aish (1963) but Steere et al (*loc. cit.*) have reported n = 13 in this species from California. By examining the figures of the latter authors the writer feels that the population from Golden Gate also has 12 bivalents which have been interpreted as 13 because of the disjunction of one of the bivalents. The haploid race seems uniform with regard to its chromosome number both in North America and Europe.

The polyploids have evolved into several cytological races which seem to have taken place by loss of varying numbers of chomosomes from what probably was a diploid complement. Races of *A. serpens* with n = 22 have been reported from Finland and California (Vaarama, 1950, 1953) and with n = 19 and 20 from various populations from England (Vaarama, 1956). Vaarama observes in the latter case that all the eight populations which had n = 20 came from wet habitats while all the three which had n = 19 came from drier habitats. On this basis Vaarama suggested that there might be a correlation between the habitat and the number of chromosomes. The present study adds support to this hypothesis.

Hygrohypnum eugyrium (Br. and Sch.) Loeske

The material for this species was studied from the banks of a small creek

west of Mammoth Hot Springs, Yellowstone National Park. The chromosome number is n = 11 with one clearly identified h bivalent (Plate I-8).

H. ochraceum (Turn.) Loeske

The material for this species was studied from two populations, Fourth of July Campground, Colorado and Sprague Creek, one and a half miles below Sperry Glacier Chalet, Glacier National Park, Montana. In both cases the chromosome number is n = 11 (Fig. 37) with the configurations of the bivalents exactly similar to *H. eugyrium.*

H. dilatatum (Wils.) Loeske

The material for this species was studied from Lower Akaiyan Lake between Sperry Glacier Chalet and Sperry Glacier, Glacier National Park, Montana. The chromosome number is n = 11 with the configuration of the various bivalents similar to the ones described for the other two species of *Hygrohypnum.*

Plagiothecium denticulatum (L.) Br. and Sch.

The material was collected from wet boulders south of Emerald Lake, Gothic, Colorado. Eleven bivalents were observed (Fig. 38) in a number of sporogones. Both the H and the h bivalents could be identified in many mother cells. The present report is in accord with the report of n = 11 in this species from Finland (Vaarama, 1950) and England (Vaarama, 1956) but differ from the reports of n = 10 in this very species from Finland (Vaarama, 1950) and Japan (Yano, 1957). Considering 10 as the probable basic number of this species, the occurrence of n = 20 in this species from the Southern Appalachians (Anderson and Bryan, 1958) and Quebec (Al-Aish and Anderson, 1960) is not unexpected but the report of n = 25 from the Canadian Rockies (Anderson and Crum, 1958) is difficult to interpret.

Drepanocladus uncinatus (Hedw.) Warnst.

The material was collected from wet boulders near Lake John, Glacier National Park, Montana. The chromosome number is n = 12 (Fig. 39). Three bivalents show a tendency towards earlier disjunction. The heterochromatic bivalents could not be identified with certainty. The chromosome number is in accord with the findings of Vaarama (1950) and Steere (1954).

D. exannulatus (Guemb.) Warnst.

The material for this species was studied from the west side of Garden Wall, Glacier National Park, Montana. The chromosome number is n = 12 (Fig. 40). The same chromosome number for this species has been reported from Finland by Vaarama (1953). The h bivalent described as special bivalent by Vaarama (*loc. cit.*) was observed in the present case as well. In addition to the h bivalent 2-3 other bivalents were observed to be precocious in the present material. This tendency to precocious disjunction has not been reported from the Finnish material.

D. aduncus (Hedw.) Warnst.

The material for this species was studied from Ohio Pass, Gunnison National Forest, Colorado. The chromosome number is the same as in the other two species, i.e., n = 12 (Fig. 41). One h bivalent was noted but the H bivalent could not be identified.

The chromosome number of this species is being reported for the first time.

Isopterygium pulchellum (Hedw.) Jaeg.

The material was studied from south of Emerald Lake, Gunnison National Forest, Colorado. The chromosome number is n = 11 with both H and h bivalents (Fig. 42). The same chromosome number as well as the H and h bivalents have also been reported for this species from the Canadian Rockies (Anderson and Crum, 1958).

FONTINALACEAE

Fontinalis neomexicana Sull. and Lesq. See item 42, table III.

The material for this species was studied from the Royal Gorge of Como Creek, near the Institute of Alpine and Arctic Research, University of Colorado. The chromosome number is n = 10 (Plate I-9). The bivalents can be divided into two distinct groups, i.e., five large and five small. This species receives cytological attention for the first time.

SUMMARY AND CONCLUSIONS

Chromosome counts obtained for various mosses from the Rocky Mountains have been summarized in Table III. Out of 42 species investigated, the counts of 14 are reported for the first time. These mosses are: *Polytrichum alpinum* var. *brevifolium*, *Distichium inclinatum*, *Oncophorus polycarpus* var. *strumiferus*, *Trichostomum clylindricum*, *Grimmia elatior*, *Bryum pallescens*, *Philonotis americana*, *Bartramia breviseta*, *Tayloria acuminata*, *Hygrohypnum eugyrium*, *H. ochraceum*, *H. dilatatum*, *Drepanocladus aduncus*, and *Fontinalis neomexicana*. It is interesting that n = 6 has been discovered in a species of *Bartramia*, *i.e.*, *B. breviseta*, as was predicted earlier by the author. This is the new report of the basic number for the genus *Bartramia* and on this basis a closely related species *B. ithyphylla* is to be interpreted as a diploid and not as a triploid as has been done by several workers. The report of n = 30 in *Tayloria acuminata* is the first chromosome count on the genus *Tayloria*. *Tayloria acuminata* is undoubtedly a polyploid and by comparison with other numbers of Splachnaceae (see Wylie, 1957 and Khanna, 1964) there is good probability that the basic chromosome number for the genus *Tayloria* may be 10. The present study also establishes the basic chromosome number for the genus *Fontinalis* to be 10. The only other study on the cytology of this genus is by Heitz (1928) whose report on the chromosome number is ambiguous. Heitz reported n = ca.8 in *F. antipyretica*. The occurrence of n = 10 in *Dichelyma falcatum* (Vaarama, 1950), the only other member of Fontinalaceae investigated, would suggest that the basic number for this family is 10.

A feature which has been observed to be common in the mosses of the Southern Rocky Mountains is the occasional departure of the chromosome number from the previous reports. This, perhaps, indicates the occurrence of different geographical races for these species. These races may be due to different grades of ploidy, variation in the number of h bivalents, or the variation in the number of the normal members of the complement. Examples of the plyploid races are: *Pohlia longicolla* which is haploid in the Rockies but is diploid in Japan, and *Amblystegium juratzkanum* which has n = 13 (12) from California and n = 20 from the Rockies. Variation due to h bivalent or due perhaps to the accessory chromosomes is much more common. Examples for this are: *Dicranus strictum* (with the presence of two accessory chromosomes in the Canadian Rockies and their lack in the Southern Rockies); *Desmatodon latifolius* (with the presence of two accessory chromosomes in the American material and their lack

TABLE III. Summary of observations

S. No.	Name of the species	Source	Meiotic chromosome number	University of Colorado herbarium number	Figure number
	POLYTRICHACEAE				
1.	Polytrichum alpinum Hedw. var. brevifolium (R.Br.) Brid.	Glacier National Park, Montana	7	B - 14914	1
		Scientific Reserve, University of Colorado	14	B - 14915	--
2.	Atrichum undulatum (Hedw.) Beauv.	Glacier National Park, Montana	7	B - 14916	2
3.	Polytrichadelphus lyallii Mitt.	Long Lake, Colorado	7	B - 14917	3
	DITRICHACEAE				
4.	*Distichium inclinatum Hedw.	Gothic, Colorado	13	B - 15327	4
5.	Ceratodon purpureus (Hedw.) Brid.	Gothic, Colorado	13	B - 15326	5
		Rocky Mountain National Park, Colorado	13	B - 14920	
	DICRANACEAE				
6.	Dicranum strictum schleich.	Long Canyon, Colorado	12	B - 14918	Plate I-1
7.	D. scoparium Hedw.	Rocky Mountain National Park	12	B - 14924	Fig. 6
		Yellowstone National Park		B - 14922	
		Yellowstone National Park		B - 14923	
8.	Dicranoweisia crispula (Hedw.) Lindb.	Rocky Mountain National Park	14	B - 14919	Plate I-2
		Cottonwood Pass, Colorado	14	B - 15329	7
		Gothic, Colorado	14	B - 15330	--
9.	*Onchophorus virens Hedw.	Fourth of July Camp Ground, Colorado	14	B - 14921	8
10.	O. polycarpus (Hedw.) Brid. var. strumiferus (Hedw.) Grout	Gothic, Colorado	14	B - 15331	9

TABLE III. Summary of observations

S. No.	Name of the species	Source	Meiotic chromosome number	University of Colorado herbarium number	Figure number
	POTTIACEAE				
11.	Gymnostomum calcareum Nees and Hornsch.	Glacier National Park	13	B - 14949	10
12.	Didymodon recurvirostris (Hedw.) Jenn.	Gothic, Colorado	13	B - 15334 11	Plate 1-3
13.	*Tortula mucronifolia Schwaegr.	Gothic, Colorado	26	B - 15332	12
14.	Trichostomum cylindericum (Bruch) C. Muell.	Yellowstone National Park	13	B - 14932	Plate 1-4
15.	Desmatodon latifolius (Hedw.) Brid.	University of Colorado Scientific Reserve, Colorado.	28	B - 14930	13
		Glacier National Park	28	B - 14931	14
		Cottonwood Pass, Colorado	28	B - 15333	15
16.	Phascum cuspidatum Hedw. var. americanum Ren. and Card.	Lyons, Colorado	26	B - 14933	16
	GRIMMIACEAE				
17.	Grimmia alpicola Hedw.	Rocky Mountain National Park	13	B - 14925	17
18.	G. apocarpa Hedw.	Summit Lake, Colorado	13	B - 14926	18
		Jackson Creek, Colorado	13	B - 14927	--
19.	*G. elatior B.S.G.	"Little Royal Gorge" of Como Creek, Colorado	13	B - 14928	19
20.	G. affinis Hornsch.	Yellowstone National Park	13	B - 14929	
	ENCALYPTACEAE				
21.	Encalypta vulgaris Hedw. var. mutica Brid.	Lyons, Colorado	14	B - 14934	24
	BRYACEAE				
22.	Bryum pallescens Schleich.	Glacier National Park, Montana	22	B - 15349	25
23.	Pohlia longicolla (Sw.) Lindb.	Summit Lake, Colorado	11	B - 15344	26
24.	Leptobryum pyriforme (L.) Schimp.	Gothic, Colorado	20	B - 15337	27
	BARTRAMIACEAE				
25.	*Philonotis americana Dismier	Near the Scientific Reserve of University of Colorado, Colorado	6	B - 14938	Plate 1-5
26.	P. fontana (Hedw.) Brid.	Glacier National Park	6	B - 14937	29
		Gothic, Colorado	6	B - 15340	

TABLE III. Summary of observations

S. No.	Name of the species	Source	Meiotic chromosome number	University of Colorado herbarium number	Figure number
27.	*Bartramia breviseta Lindb.	Summit Lake, Colorado	6	B - 14936	Plate 1-6
28.	B. ithyphylla Brid.	Gothic, Colorado	12	B - 15338	30
29.	Plagiopus oederi (Gunn.) Limpr.	Gothic, Colorado	7	B - 15339	31
	SPLACHNACEAE				
30.	*Tayloria acuminata Hornsch.	Gothic, Colorado	30	B - 15336	32
	ORTHOTRICHACEAE				
31.	Amphidium lapponicum (Hedw.) Schimp.	Gothic, Colorado	16	B - 15335	33
	BRACHYTHECIACEAE				
32.	Eurhynchium strigosum (Hoffm.) Br. and Sch.	Montana, USA	10	B - 14950	Plate 1-7
	AMBLYSTEGIACEAE				
33.	Amblystegium juratzkanum Schimp.	Yellowstone National Park	20	B - 14942	Fig. 36
34.	*Hygrohypnum eugyrium (Br. & Sch.) Loeske	Yellowstone National Park	11	B - 14943	Plate 1-8
35.	*H. ochraceum (Turn.) Loeske	Fourth of July Camp Ground, Colorado	11	B - 14944	37
		Glacier National Park	11	B - 14946	--
36.	H. dilatatum (Wils.) Loeske	Glacier National Park	11	B - 14946	--
37.	Plagiothecium denticulatum (L.) Br. & Sch.	Gothic, Colorado	11	B - 15343	38
38.	Drepanocladus uncinatus (Hedw.) Warnst.	Glacier National Park	12	B - 14940	39
		Ohio Pass, Colorado	12	B - 15341	
39.	*D. exannulatus (Guemb.) Warnst.	Glacier National Park	12	B - 14941	40
40.	D. aduncus (Hedw.) Warnst.	Gothic, Colorado	12	B - 15342	41
41.	Isopterygium pulchellum (Hedw.)-Jaeq.	South of Emerald Lake. Gunnison National Forest, Colorado.	11	B - 15346	42
	FONTINALACEAE				
42.	*Fontinalis neomexicana Sull. and Lesq.	"Little Royal Gorge" of Como Creek, Colorado	10	B - 14948	Plate 1-9

*Species are reported cytologically for the first time.

in the Canadian material) and *Encalypta vulgaris* (with one h bivalent in the Rocky Mountain material and its lack in the Californian material). Races in which no definite chromosomes can be specified on the basis of morphology have been found in *Dicranoweisia crispula*, *Grimmia apocarpa* and *Plagiothecium denticulatum*.

Polyploidy has been found in 14 percent of the species investigated. In none of them has the level of ploidy been found to be beyond triploid (hexaploid according to the terminology used for flowering plants). The diploid species are: *Polytrichum alpinum* var. *brevifolium*, *Tortula mucronifolia*, *Desmatodon latifolius*, *Phascum cuspidatum*, *Leptobryum pyriforme*, *Bartramia ithyphylla* and *Amblystegium juratzkanum*. The only probable triploid species is *Tayloria acuminata*. The number of species investigated is, however, so small that it can hardly be considered to give a true picture of the amount of polyploidy present in the mosses of the Southern Rocky Mountain Region.

Meiotic abnormalities in the form of spindle breakdown and abnormal cytokinesis have been observed in *Grimmia affinis*. These features were further accompanied by asynapsis in *Grimmia elatior* and *Dicranum scoparium*. The abnormalities in *Grimmia affinis* and *Dicranum scoparium* are spread over a wide geographic range. A study of the reasons for such abnormalities should be very interesting but no correlation between meiotic abnormalities and geographic distribution could be established for these species. In *Grimmia elatior*, however, it was possible to say that the abnormalities were due to seasonal effects among which temperature and humidity during the growing seasons were the major factors.

LITERATURE CITED

AL-AISH, M. and L. E. ANDERSON. 1960. Chromosome numbers in some mosses from Quebec. Canadian Jour. Bot. 38: 335-341.

ANDERSON, L. E. and M. AL-AISH. 1963. Chromosome numbers of some mosses from North America. The Bryologist 66: 165-178.

———— and V. S. BRYAN. 1958. Chromosome numbers in mosses of Eastern North America, Jour. Elisha Mitchell Sci. Soc. 74: 163-199.

———— and H. CRUM. 1959. Cytotaxonomic studies on mosses of the Canadian Rocky Mountains. National Museum of Canada Bull. 160: 1-89.

BRYAN, V. S. 1956. Cytological and taxonomic studies of some species of *Astomum*, *Acaulon* and *Phascum*. The Bryologist. 59: 118-129.

CLARK, F. J. 1940. Cytogenetic studies of divergent meiotic spindle formation in *Zea mays*. Amer. Jour. Bot. 27: 547-559.

DARLINGTON, C. D. and P. T. THOMAS. 1937. The breakdown of cell division in a *Festuca—Lolium* derivative. Ann Bot. (n.s.) 1: 747-761.

GROUT, A. J. 1903. Mosses with a hand lens and microscope. New York.

————. 1928-39. Moss flora of North America north of Mexico, Vol. 3. Newfane, Vt.

HEITZ, E. 1926. Der Nachweis der Chromosomen. Zeitschr. f. Bot. 18. 625-681.

————. 1928. Das Heterochromatin der Moose I. Jahrb. f. Wiss. Bot. 69: 762-818.

————. 1942. Über die Beziehung zwischen Polyploidie und Gemischtgeschlechtlichkeit bei Moosen. Arch. Klaus-Stift. Vererb. Forsch. 20: 119-125.

HO, P. H. 1950. Etude de la mitose et specialement du megachromocentre chez quelques muscinées. Rev. Gen. Bot. 63: 1-44.

HOTTA, Y. and H. STERN. 1963. Inhibition of protein synthesis during meiosis and its bearing on intracellular regulation. Jour. Cell Biol. 16: 259-279.

IRELAND, R. E. 1965. Cytotaxonomic studies of mosses of Washington and Idaho. The Bryologist 68: 72-85.

KEMP, L. 1964. The effects of inhibitors of RNA and protein synthesis on cytological development during meiosis. Chromosoma 15: 652-665.

KHANNA, K. R. 1960a. Cytological studies on some Himalayan mosses. Caryologia 13: 559-618.

————. 1960b. The haploid and the spontaneous diploid race in *Octoblepharum albidum* Hedw. Cytologia 25: 334-341.

———. 1960c. Studies in natural hybridization in the genus *Weisia*. The Bryologist 63: 1-16.

———. 1964. Cytology of some mosses from the Adirondack Mountains. The Bryologist 67: 343-350.

KURITA, M. 1937. Geschlechtschromosomen und Chromosomenzahlen bei einigen Laubmoosen. Zeitsch. Indukt. Abstamm. Vereb. 74: 24- 29.

LANJOUW, J. and F. A. STAFLEU. 1959. Index Herbariorum. Part 1. The Herbaria of the World. Regnum Vegetabile. Vol. 15.

LEVAN, A. 1938. The effect of colchicine on mitoses in *Allium*. Hereditas 24: 471-486.

LEWIS, K. R. 1957. Squash techniques in the cytological investigations of mosses. Trans. Brit. Bryological Soc. 3: 279-284.

LOWRY, R. J. 1954a. Chromosome numbers and relationships in the genus *Atrichum* in North America. Amer. Jour. Bot. 41: 410-414.

———. 1954b. The chromosome number and chromosome morphology of *Bartramia pomiformis*. The Bryologist 57: 1-5.

MEHRA, P. N. and K. R. KHANNA, 1961. Recent cytological investigations in mosses. Res. Bull. Punjab Univ. (n.s.) 12: 1-29.

NYHOLM, E. 1956. Illustrated Moss Flora of Fennoscandia. Lund.

ÖSTERGREN, G. 1950. Cytological standards for the quantitative estimation of spindle disturbances. Hereditas 36: 371-382.

STEERE, W. C. 1954. Chromosome number and behavior in arctic mosses. Bot. Gaz. 116: 93-133.

———, L. E. ANDERSON and V. S. BRYAN. 1954. Chromosome studies of California mosses. Mem. Torrey Bot. Club 20(4): 1-75.

TATUNIO, S. 1953. Geschlechtschromosomen und Polyploidie von *Catharinea*. Bot. Mag. Tokyo. 66: 150-154.

TAYLOR, J. H. 1959. Autoradiographic studies of nucleic acids and proteins during meiosis in *Lillum longiflorum*. Amer. Jour. Bot. 46: 477-484.

VAARAMA, A. 1949. Spindle abnormalities and variation in chromosome number in *Ribes nigrum*. Hereditas 35: 136-162.

———. 1950. Studies on chromosome numbers and certain meiotic features of several Finnish moss species. Bot. Notiser pp. 239-256.

———. 1953. Some chromosome numbers of California and Finnish moss species. The Bryologist 56: 169-177.

———. 1956. A contribution to the cytology of some mosses of the British Isles. Irish Naturalist Jour. 12: 1-11.

VAN DER WIJK, R. (ed.). 1959. Index Muscorum Vol. 1. Utrecht.

WYLIE, A. P. 1957. The chromosome numbers of mosses. Trans. Brit. Bryol. Soc. 3: 260-278.

YANO, K. 1957. Cytological studies in Japanese mosses. Mem. Takada Branch, Niigata Univ. 1: 129-158.

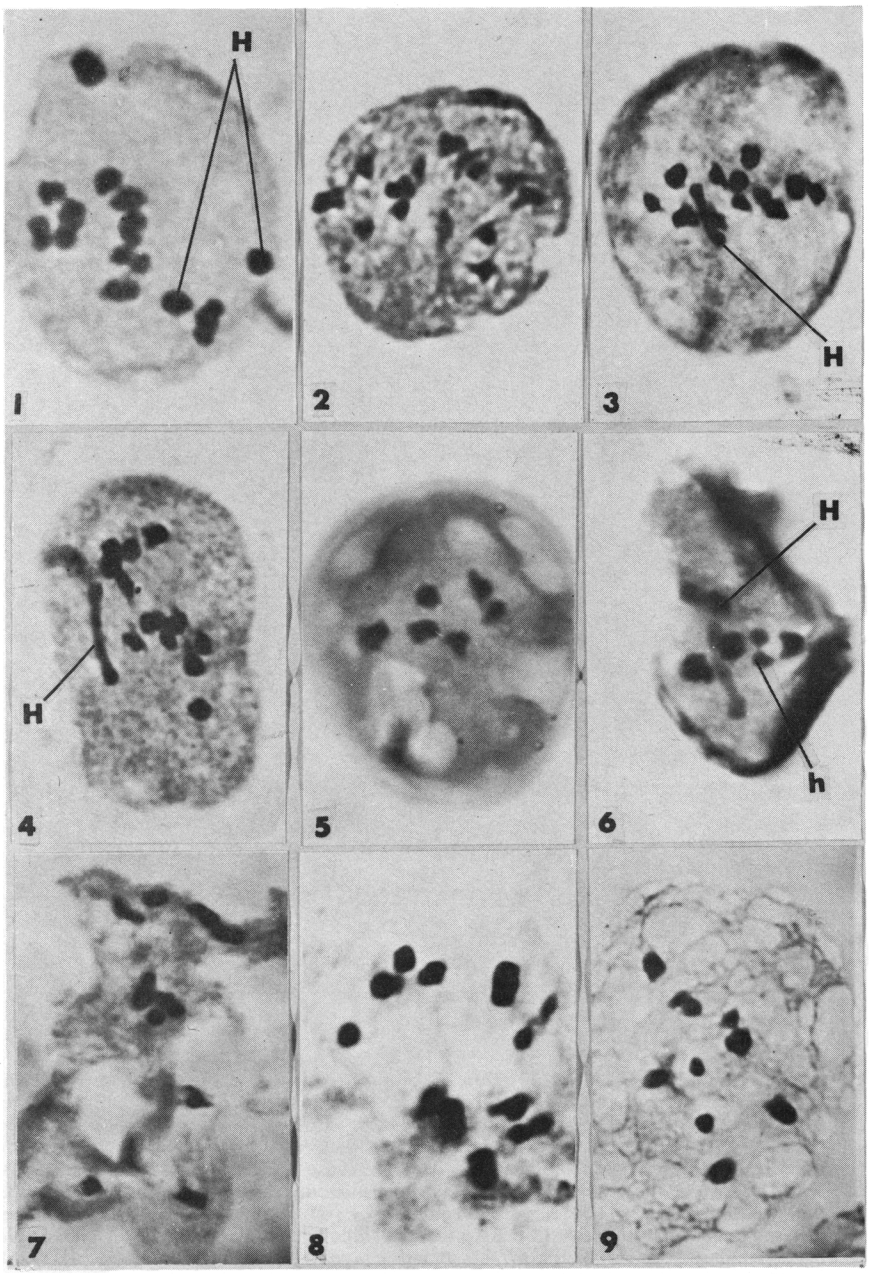


PLATE I. (1) *Dicranum strictum*, n = 12. (2) *Dicranoweisia crispula*, n = 14. (3) *Didymodon recurvirostris*, n = 13. (4) *Trichostomum cylindricum*, n = 13. (5) *Philonotis americana*, n = 6. (6) *Bartramia breviseta*, n = 6. Note the elongated H bivalent and a precocious h bivalent. (7) *Eurhynchium strigosum*, n = 10. (8) *Hygrohypnum eugyrium*, n = 11. (9) *Fontinalis neomexicana*, n = 10.

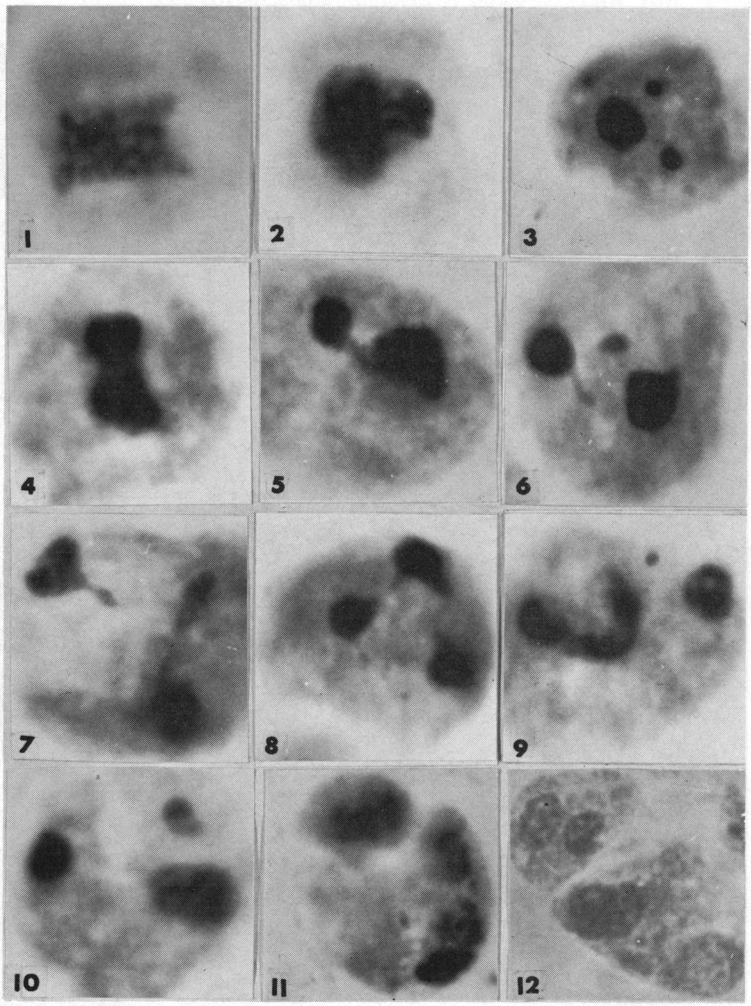


PLATE II. (1-12) Spindle abnormalities in *Grimmia affinis* Hornsch. (1) The chromatin material entering interphase after a prolonged M1. The four radiations into which the chromatin has flowed depict the position of the arms of the star-shaped monopolar spindle. (2) The chromation following the budding of the monopolar spindle to the right and in the direction of the plane parallel to the surface of the photograph. (3) Small portion of the chromatin cut out as three micronuclei around the main nucleus as the process shown in (2) has been completed. (4) Bipolar spindle with shortened distance between the poles. (5) Asymmetrical bipolar spindle resulting in an unequal distribution of the chromatin to the two poles. (6) The laggards, caused probably by stickiness in the chromatin, at the end of AI in an otherwise fairly normal bipolar spindle. (7), (8) Partial tripolar and tripolar spindle, respectively. (9), (10) The unequal size and irregular orientation of the tetrad nuclei at the end of meiosis. (11) and (12) Cytokinesis. Note the difference in the shape of the spore mother cells in (11) and (12), the lack of relationship between the distribution of the tetrad nuclei and wall formation, and the cutting out of the enucleate pieces of cytoplasm which will result in empty, enucleate and degenerate spores.

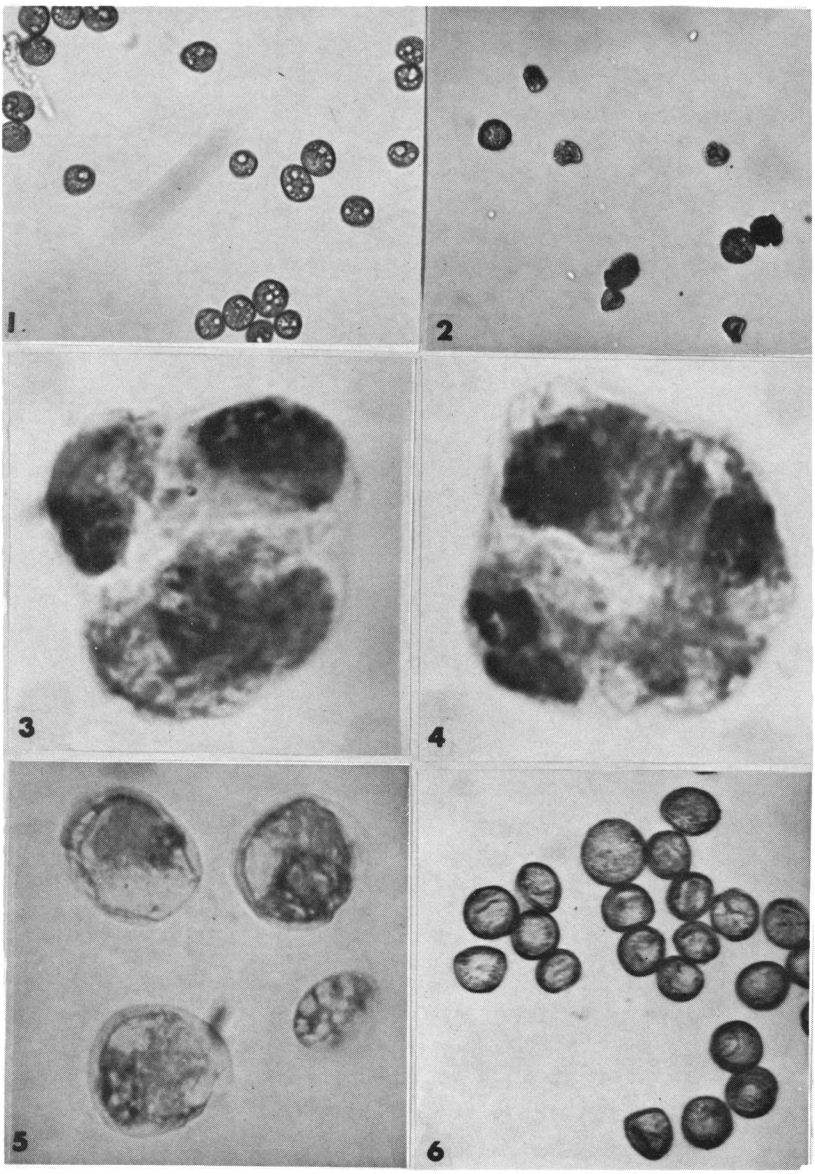


PLATE III. *Girmmia affinis*. (1) Normal spores from a population near Boulder, Colorado. (2) Abnormal spores from the Yellowstone National Park populations. *Polytrichum alpinum* var. *brevifolium*. 1 and 2, X400. (3) A tetrad with two nuclei included in the bottom spore. (4) An abnormal tetrad with two nuclei included in the top spore and its counterpart empty. (5) Four spores arising out of a tetrad. The spore at the right hand top corner has a double nucleus and its counterpart at the right hand bottom corner is enucleate. (6) A giant spore (at 12 o'clock), possibly a diploid, among the normal ones X500.

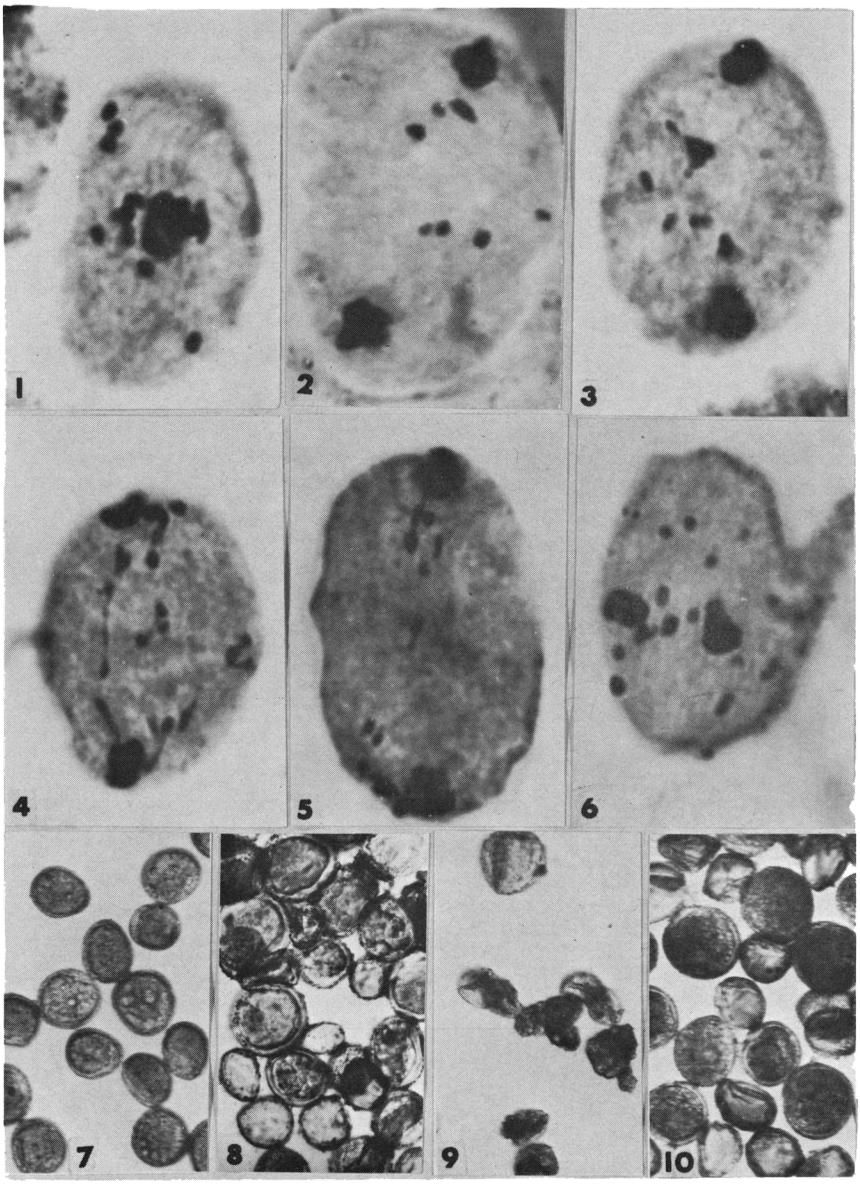
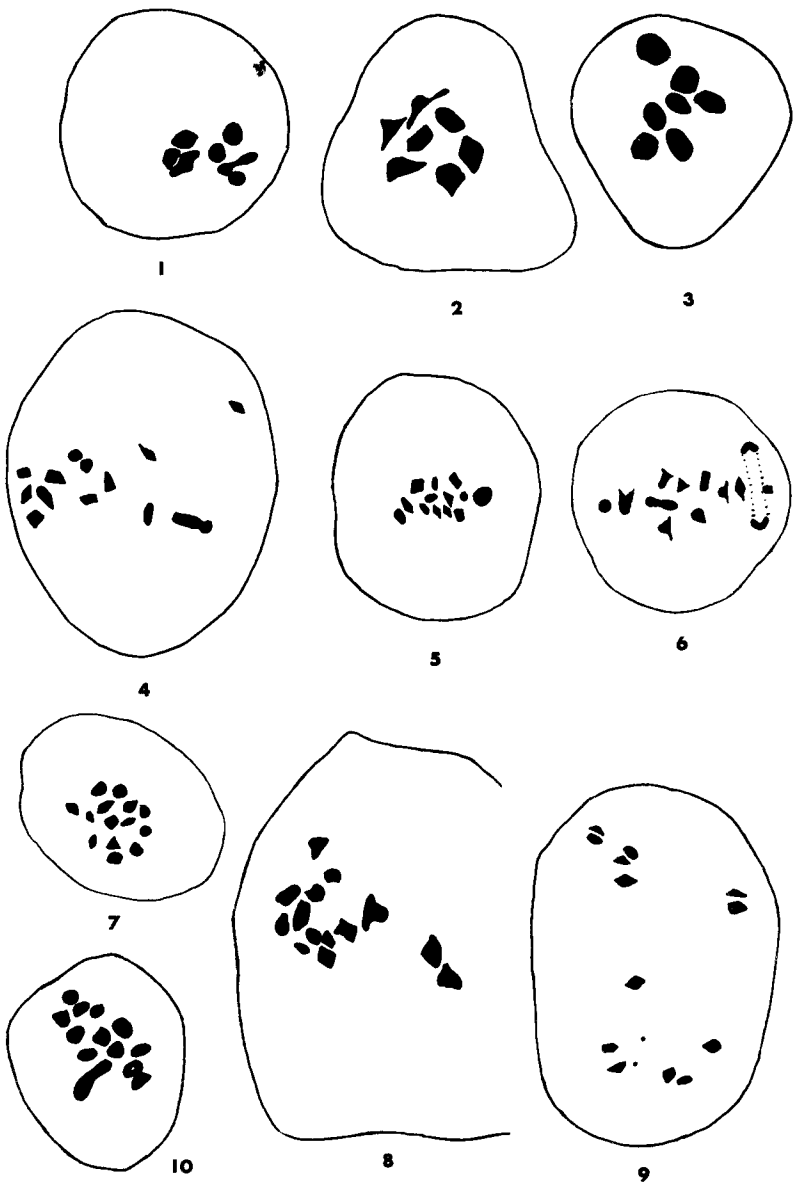
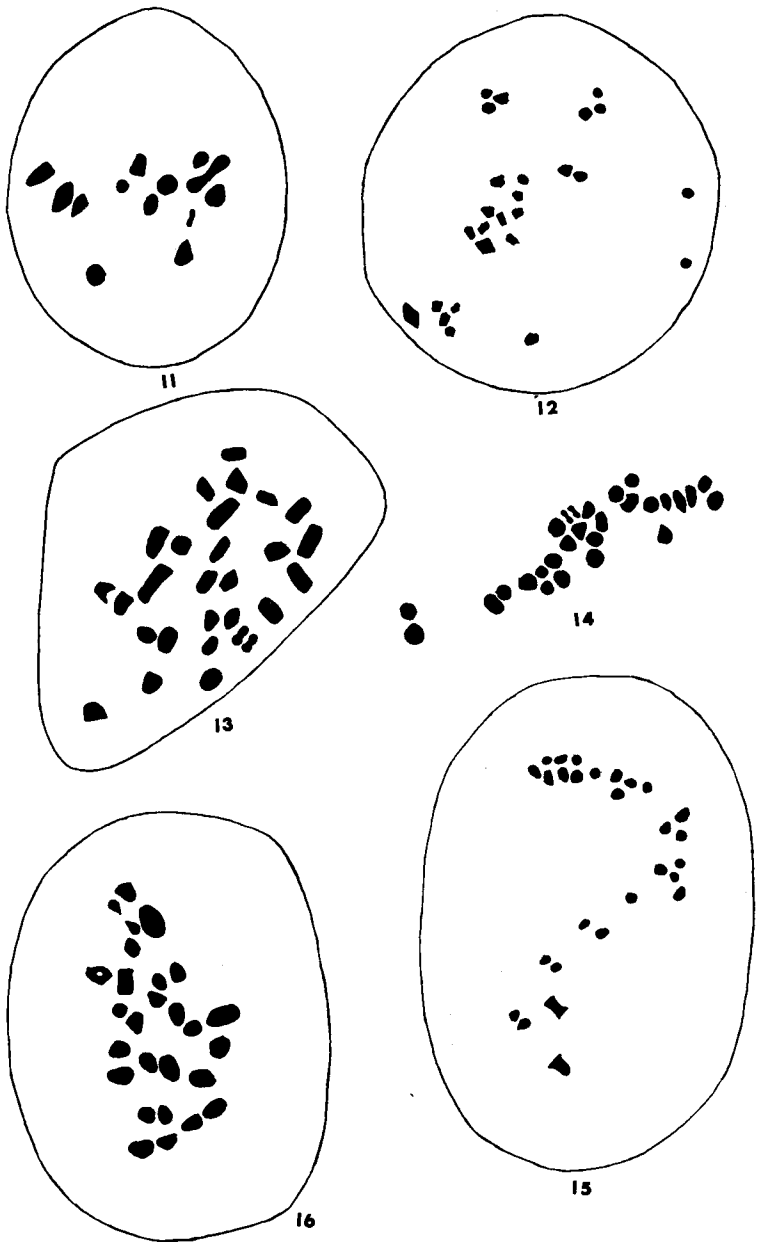


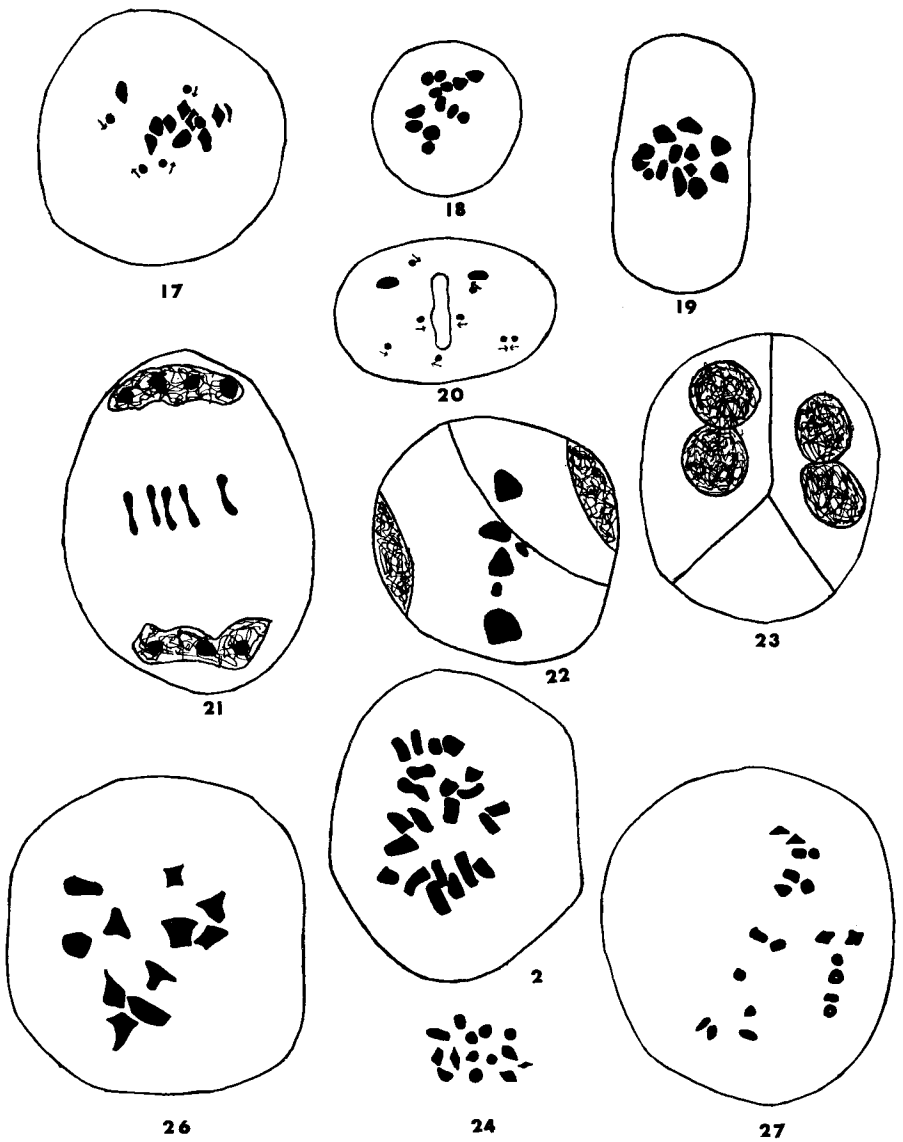
PLATE IV. (1-10) *Dicranum scoparium*. (1) Six univalents at M1. This does not include the precocious H bivalent. (2), (3), (4), (5), (6) Varying number of laggards and division of univalents after A1. (7) Normal spores of a population from New York (B-12450, Colo). (8) Abnormal spores of a population from North Carolina (B-7155, Colo). (9) Abnormal spores of a population from Black Sand Basin, Yellowstone National Park (B-14923, Colo). This population has been studied cytologically. (10) Abnormal spores of a population from British Columbia (B-10967, Colo). 7-10, X500.



FIGURES 1-10. (1) *Polytrichum alpinum* var. *brevifolium*, n = 7. (2) *Atrichum undulatum*, n = 7. (3) *Polytrichadelphus lyallii*, n = 7. (4) *Distichium inclinatum*, n = 13 with H bivalent between three and four o'clock. (5) *Ceratodon purpureus*, n = 13. (6) *Dicranum scoparium*, n = 12. The H bivalent is precociously disjoined. (7) *Dicranowiesia crispula*, n = 14. (8) *Oncophorus virens*, n = 14. The h bivalent is not conspicuous. (9) *O. polycarpus* var. *strumiferus*, n = 14. The h bivalent is precociously disjoined between six and seven o'clock. (10) *Gymnostomum calcareum*, n = 13.



FIGURES 11-16. (11) *Didymodon recurvirostris*, n = 13. Both h and H bivalents are conspicuous. (12) *Tortula mucronifolia*, n = 26. Note two H bivalents. (13), (14), (15) three different populations of *Desmatodon latifolius*, n = 28. (16) *Phascum cuspidatum*, n = 26. Two H bivalents are conspicuous while only one h bivalent is conspicuous by its precocious disjunction.



FIGURES 17-27. (17) *Grimmia alpicola*, n = 13. Two H bivalents which are smaller than the usual size of the H bivalents are precociously disjoined. (18) *G. apocarpa*, n = 13. (19), (20), (21), (22), (23), *G. elatior*, n = 13. (20) precocious disjunction of the bivalents at M1. (21) laggards at T1. (22) abnormal cytokinesis. (23) tetrad formation. (24) *Encalypta vulgaris var. mutica*, n = 14. (25) *Bryum pallescens*, n = 11. (26) *Pohlia longicolla*, n = 11. (27) *Leptobryum pyriforme*, n = 20.

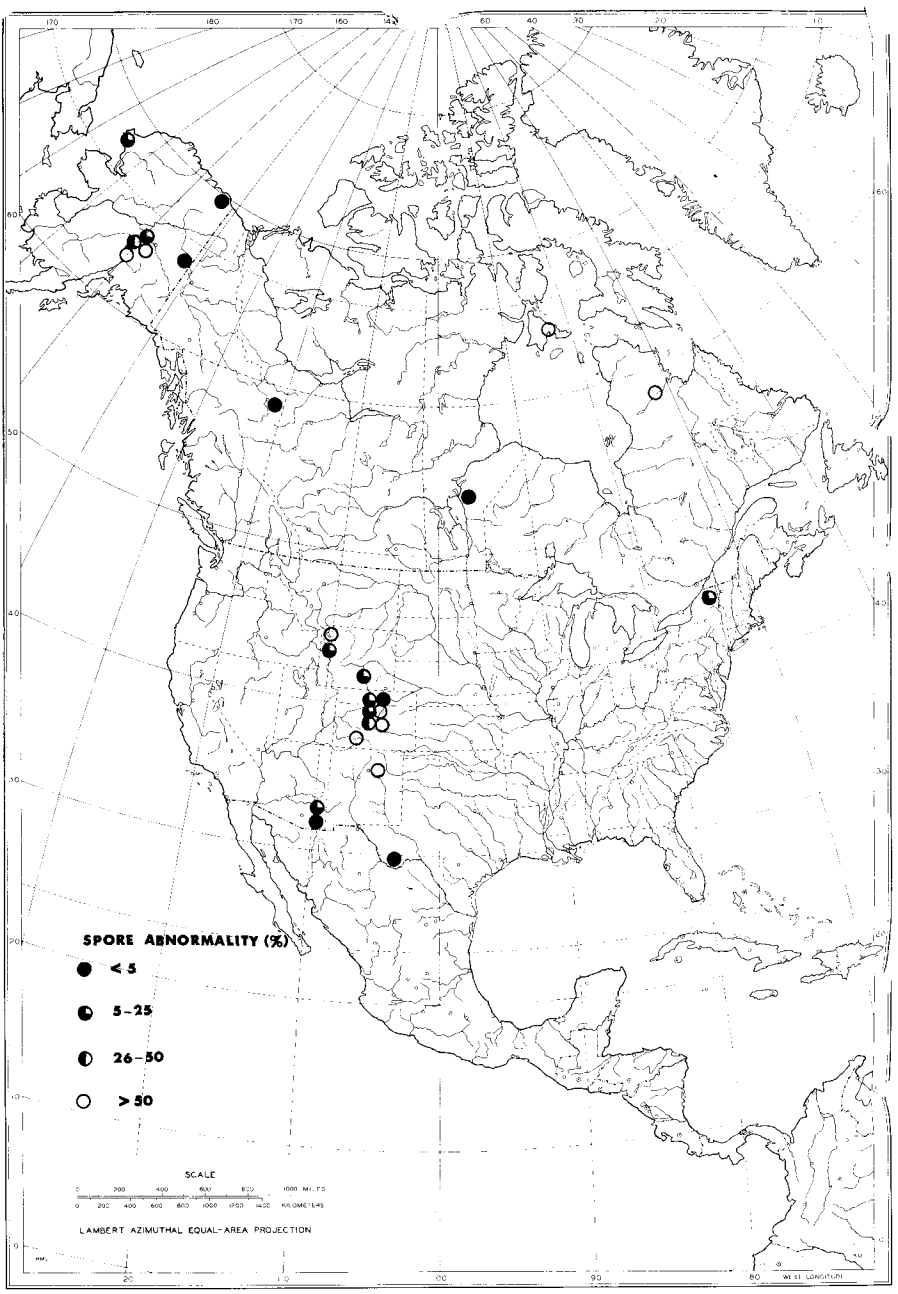
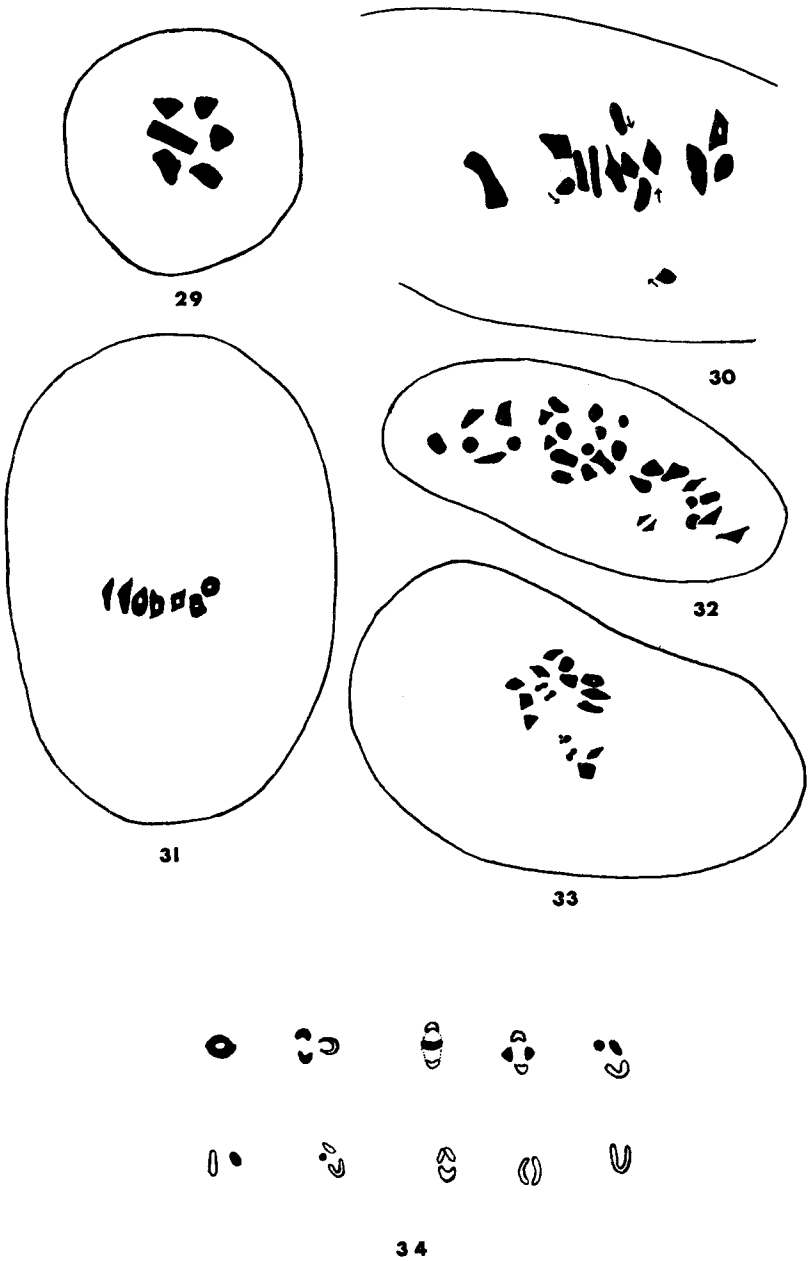


FIGURE 28. Distribution of normal and abnormal spore types in *Grimmia affinis* in North America. The base map belongs to Goode series, University of Chicago.



FIGURES 29-34. (29) *Philonotis fontana*, n = 6. (30) *Bartramia ithyphylla*, n = 12. (31) *Plagiopus oederi*, n = 7. (32) *Tayloria acuminata*, n = 30. (33) *Amphidium lapponicum*, n = 16. (34) *Eurhynchium strigosum*. The erratic behavior of H bivalent at M1. The unshaded portions show negative heteropycnosis.

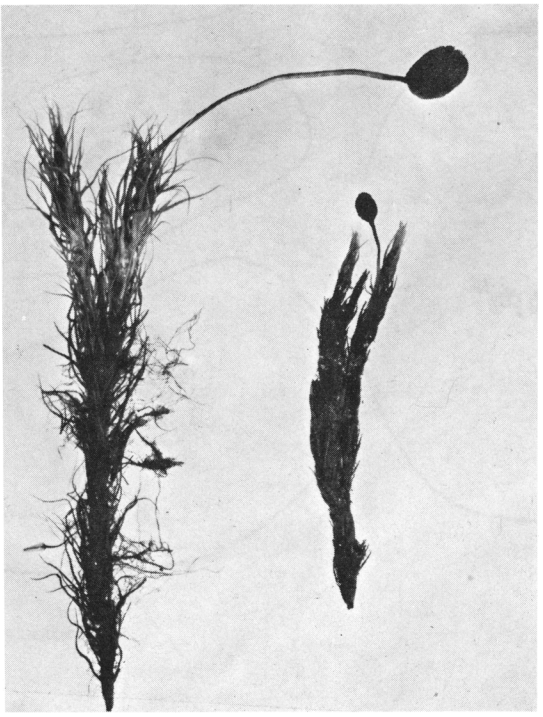
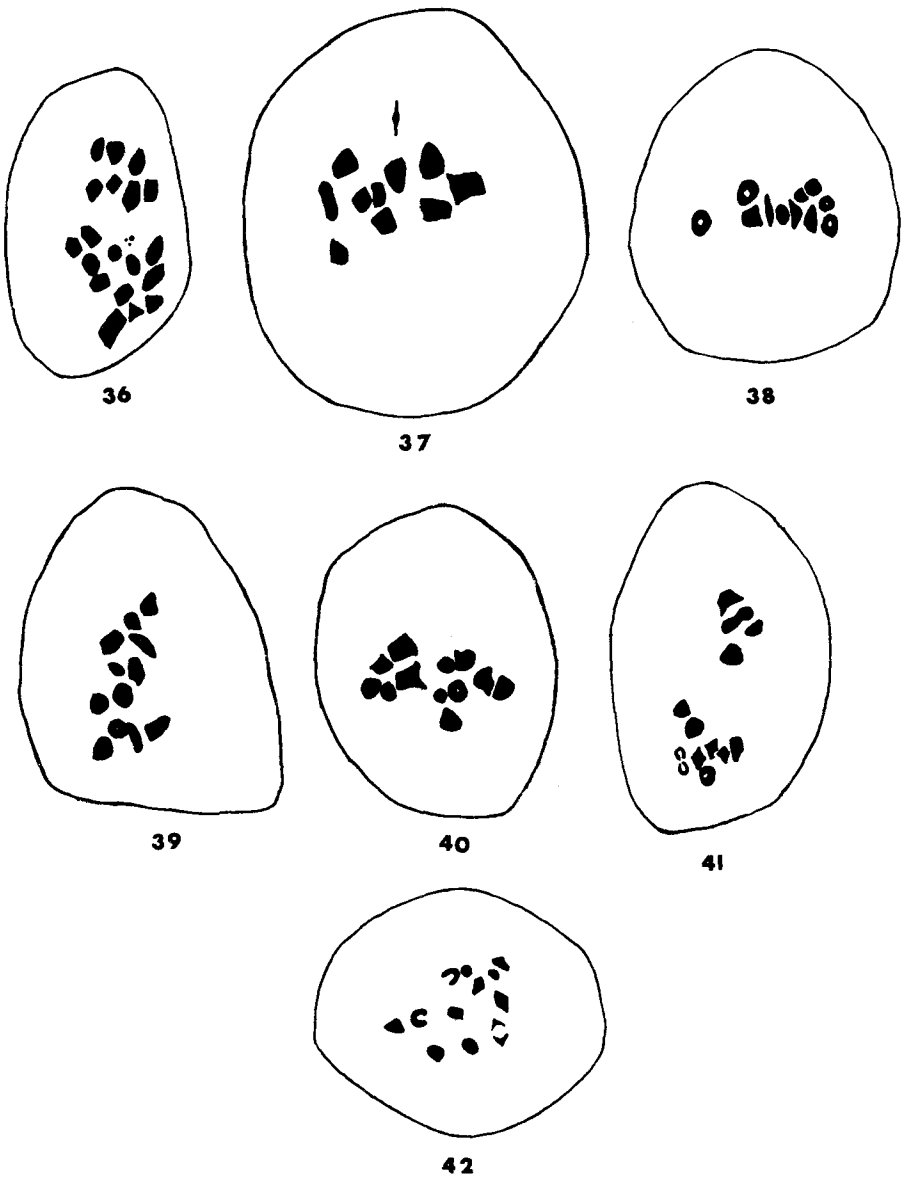


FIGURE 35. A morphological comparison of *Bartramia ithyphylla* (left) and *B. breviseta* (right) (X6).



FIGURES 36-42. (36) *Amblystegium juratzkanum*, n = 20. (37) *Hygrophypnum ochraceum*, n = 11. (38) *Plagiothecium denticulatum*, n = 11. (39) *Drepanocladus uncinatus*, n = 12. (40) *D. exannulatus*, n = 12. (41) *Drepanocladus aduncus*, n = 12. (42) *Isopterygium pulchellum*, n = 11.