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CONTENTS

STUDIES IN SPERMATOGENESIS AND APOGAMY IN FERNS.

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During recent years, the interest in the cytology of the ferns has developed along two main lines—the study of the male cells, for which the ferns are very favorable, and the study of apogamy, a field in which ferns also offer excellent opportunities for the investigation of the important cytological questions involved.

The literature relating to the structure and development of the motile male cells is very extensive and has been frequently summarized in recent years. I shall here review only the papers most closely related to my own studies.

The early work was done with the aim of determining whether the entire cell or only the nucleus entered into the formation of the antherozoid. At the close of the eighties it was fairly well established that the spiral body of the antherozoid was formed from the nucleus and that the cilia and the vesicle were derived from the cytoplasm. The question of the presence of a cytoplasmic envelope about the spiral nucleus was still under debate.

Guiguard (43) in 1889 studied the metamorphosis of the mother cell into a spiral antherozoid in *Chara, Pellia, Sphagnum,* and *Angiopteris.* In *Angiopteris,* the large nucleus moves to one side of the cell and elongates into a crescent lying against the surface of the cell. The nucleole disappears and the chromatin becomes dense and homogeneous. The cilia originate from a special hyaline layer on the surface of the cell. The nucleus now elongates further, becoming transformed to a spiral band. Guiguard remains in doubt whether a cytoplasmic envelope encloses the nucleus of the mature antherozoid.

In the same year, Belajeff also describes the formation of the antherozoid in *Pteris, Gymnogramme* and *Aneimia.* The antherozoid mother cell first develops a hook-shaped projection of the cytoplasm which becomes the anterior end of the antherozoid. Belajeff believes that the spiral form results from a folding in of the surface of the cell while the nucleus becomes stretched into a shorter parallel spiral. Belajeff describes the origin of the cilia from the outer surface of the spiral band.

Strasburger in 1892 (84) discusses the formation of motile cells in algae and in ferns. At this time, Strasburger inclined toward a belief in the general occurrence of centrosomes in plants. In the much-elongated, spiral, motile cells of ferns he finds the nuclear matter in the thicker posterior coils and kinoplasm in the slender anterior coils from which the cilia grow. In the antherozoid of ***Marsilia,*** the spiral consists of eleven coils, ten of which are slender and nearly uniform in diameter. From the last of these ten coils arise the cilia. The eleventh coil is larger and in its hollow lies the vesicle. Strasburger believes that in this case the nuclear material is to be found in the heavy posterior coil, that the kinetic center is at the anterior end and that the numerous intermediate coils consist of kinoplasm.

Belajeff in 1894 (11) studied the development of antherozoids in *Chara.* He did not succeed in finding centrosomes in the nuclear divisions in the antheridial filaments. Within the antherozoid mother cell the nucleus assumes a lateral position. A deeply staining thread is seen in contact with the nucleus at one end and extending along the plasma-membrane for some distance. This thread Belajeff thinks may have been derived from an "attraction-sphere." The cytoplasm on the opposite side of the nucleus pushes out into a slender curved horn—this is the posterior end of the antherozoid. The cytoplasm now shrinks in about the elongating anterior thread so that the thread comes to lie in a pointed projection on the cell surface. From this projection, two long cilia grow out. Further development consists in the elongation of both the nucleus and the enclosing cytoplasm of the large central mass. The result is a long spiral cell consisting of a thin spiral sac of protoplasm containing the deeply staining thread in the anterior end, the elongated nucleus in the central coils and plasma in the posterior coil.

Belajeff follows this account by several short papers in 1897 (12, 13, 14). He had not yet found centrosomes in the divisions preceding the formation of the antherozoid, but in the young antherozoid mother cell of a fern (genus not mentioned) he saw a rounded deep-staining body in the plasma and was able to trace it in its elongation into a spiral band lying along the convex side of the nuclear spiral. In Equisetum, he established the origin of the cilia from this thread.

During the same year (1897) Hirase and Ikeno (53 and 54) reported their notable discovery of motile male cells in Gymnosperms. The antherozoid is top-shaped and a spiral band on the conical surface of the cell bears numerous short cilia throughout its length.

Later in the same year (1897) Webber (92, 93) reported the discovery of similar antherozoids in *Zamia.* In the generative cell, before the last division, two centrosome-like bodies surrounded by very pronounced asters are found in the cytoplasm on opposite sides of the nucleus. During the ensuing division, the asters about these bodies disappear, and they break up into fragments which later unite to form a band which at the end of the division moves out to the cell surface and there grows into a spiral band of several successively narrower coils, just beneath the plasma membrane. From this band, the cilia arise as delicate projections even before it reaches the surface of the cell. Webber concludes (94, 95) that this cilium producing body is not homologous with the centrosome and he proposes to call it a "blepharoplast."

In 1898, Ikeno (55, 56) describes further the development of the antherozoids in *Cycas.* The chief difference between his account and that of Webber for *Zamia* is that in *Cycas* the cilia-bearing band while young is attached to a beak on the nucleus. Ikeno considers the term "blepharoplast" unnecessary and believes the body in question to be a centrosome.

Belajeff (15) in the light of these discoveries in the Gymnosperms, finds two rounded bodies in the cytoplasm on opposite sides of each nucleus before the last division in the antheridial sac in *Gymnogramme*. After the division, he finds one of these granules in each cell. He did not succeed in finding them during the division and so cannot consider it proved that they are centrosomes.

Shaw (83) in 1898, working on the antheridial sacs of *Marsilia,* finds at the end of the third from the last division a tiny granule on the polar side of each daughter nucleus. This granule which he calls the "blepharoplastoid" grows during the resting stage of the cell and divides during the prophase of the next division. The resulting pair of granules migrate in the cytoplasm to the equatorial plane and there disintegrate. At the same time, there forms near each pole another granule, the true blepharoplast. This persists through the resting stage and divides just before the last nuclear division. The two granules so formed migrate to opposite ends of the cell and stay near the poles during the last division. After this division, the blepharoplast grows, fragments, and then stretches out into a band along the surface of the nucleus. The band and nucleus migrate to the surface of the cell so that the band lies close to the plasma membrane. Here nucleus and blepharoplast elongate together into a spiral within the still rounded cell. The nucleus forms three or four coils and the blepharoplast extends beyond it at both ends.

In the same year, 1898, Belajeff (17, 18) working also on the antheridia of *Marsilia* finds centrosomes present in all stages of nuclear division and concludes that we should assume that centrosomes exist in every cell but are not always stainable.

Thom (89) working on the formation of the antherozoids of *Adiantum* and *Aspidium* claims that the nucleus moves to one side of the cell, leaving a nucleole behind which stays there while the nucleus elongates to form one coil. At this stage the nucleole becomes attached to the anterior end of the coil where later the cilia are inserted.

Webber (96, 97) still working on *Zamia* finds that the blepharoplasts originate in the cytoplasm of the generative cell as tiny granules with two or three fibres radiating from them. When first seen they were some distance from the nucleus. He reaffirms his earlier statement that the blepharoplast is not a centrosome.

Ikeno (57, 59) claims that in *Marchantia,* centrosomes are to be found at the spindle poles during several divisions preceding the formation of the antherozoid but that the centrosome comes at each division from within the nucleus. The centrosome is conspicuous during the last division and at its close migrates to a corner of the cell and elongates against the plasma membrane. Two cilia grow from it. A body which Ikeno calls the "Nebenkern" appears after the last division and disappears soon after. The nucleus comes to lie connected with the elongating centrosome. The whole cell and the nucleus and centrosome within it now elongate to a spiral of one or two coils.

Yamanouchi 1908 (102) finds in *Nephrodium molle* that the blepharoplasts first appear as well defined spheres in the cytoplasm on opposite sides of the cell just prior to the last division in the antheridial sac. The blepharoplasts remain near the spindle poles during the last division. Then the blepharoplast applies itself to the nuclear membrane and elongates together with the nucleus to a spiral. In the mature antherozoid, the blepharoplast runs two-thirds of the length of the spiral and cilia spring from its whole surface.

The widespread occurrence of Apogamy in ferns together with the fundamental problems involved have led to considerable investigation in this field. The earlier studies by Farlow, De Bary and others were models of accuracy and careful work and the observations of these authors have been almost wholly confirmed by more recent students.

Farlow (35) discovered in 1874 that prothallia of *Pteris cretica* produce sporophytes directly by vegetative growth. According to his description, the prothallia bear numerous antheridial sacs but no archegones. A projecting mass of cells forms on the ventral side of the prothallium a few cells back from the apical notch. There is no definite boundary between the cells of the prothallium and those of the outgrowth. Farlow describes tracheids extending back from this cell mass into the vegetative tissues of the prothallium. The first leaf grows out on the anterior side of this projection. Then the first root forms and after this the stem apex is organized on the upper side of the base of the first leaf. The three organs, leaf, root and stem form successively, and there is no foot.

Apogamy has since been found in many different groups of ferns and the list of these is still being increased.

In 1878 De Bary (5) gave a more detailed account of the "Farlow shoots" in *Pteris cretica.* De Bary describes the apogamous outgrowth as beginning as a group of three or four cells just back of the marginal meristem at the apical notch. A mass of cells is formed by growth and division and at the apex of this mass an apical cell is differentiated and through its activities the first leaf develops. In the rounded angle between the upper surface of the leaf base and the prothallium a shallow protuberance—the stem Anlage—is formed. It soon becomes clothed with hairs and later a second leaf forms. The boundary between gametophytic and sporophytic tissue is obscure. The vascular bundle runs down the leaf stalk and into the prothallial tissue. Ventral to the vascular bundle, and usually near the first leaf insertion, a root is formed endogenously which pushes out and grows down into the ground. The root may form in the prothallium considerably below the leaf insertion when the vascular bundle reaches that far.

De Bary found that with the formation of the sporophyte the prothallium ceases growth. In case no sporophyte is produced on a prothallium it gives rise to secondary or adventive prothallia. Occasionally a sporophyte forms on a secondary prothallium.

In addition to the "normal" Farlow shoots, various anomalies are found. There may be two "first" leaves with a stem Anlage between them. The first two roots may appear simultaneously. There may be two apogamous outgrowths, one on the dorsal and one on the ventral surface of the prothallium. The leaf may be as usual while the stem Anlage is on the dorsal side of the prothallium. When the sporophyte aborts, a vascular bundle may form running the length of the prothallium. A "middle lobe" may grow out from the apical meristem. Transitions are found between middle lobes and normal first leaves. Some of these have stomata and tracheids.

In addition to this description of *Pteris cretica,* De Bary gives the first account of Apogamy in *Aspidium felix-mas* var. *cristatum* and in *Aspidium falcatum.* The process in essentials is the same as in *Pteris cretica.* In *Aspidium falcatum* archegones are found on twenty-five to thirty per cent of the prothallia but they do not open and they cease to form when the sporophyte develops. The apogamous shoot forms as in *Pteris,* but its surface is sometimes irregular. The root is often very late in forming. There are very few abortive sporophytes in *Aspidium falcatum.* Secondary prothallia sometimes form.

Leitgeb (66) (1885), studied the light reactions of Apogamous fern prothallia. If a prothallium of *Aspidium falcatum* bearing a very young sporophyte is lighted on the ventral side, the sporophyte is suppressed and a new one forms on what has been the dorsal side. In rare cases both survive and they appear to form one sporophyte with its members on both sides of the prothallium. Leitgeb explains some of the anomalies described by de Bary as due to alteration of light relations during the growth of the prothallia.

Bower (20) in 1888 reports a further case of Apogamy accompanied by apospory in *Trichomanes alatum.* Spores are commonly produced in this species but on old fronds that lie on the ground, aposporous prothallia form freely. The gametophyte, which consists of alternating protonema-like filaments and flat one-layered cell masses or ribbons, bears gemmae and antheridial sacs but no archegones. On this prothallium sporophyte buds may form either on the end of a filament or sessile at the margin of a ribbon or on its surface. The transition between the gametophyte and sporophyte tissues is sometimes very gradual. Bower regards apogamy and apospory as merely a simplification of the life cycle and states that "the fact that apogamy and apospory occur on the same plant is a coincidence rather than a point of further importance."

Heim (50) in 1896 describes apogamy in *Doodya caudata.* The prothallia bear archegones and antheridial sacs, and sexual reproduction may take place. When a normal embryo does not form, the tissue about the sex organs grows out into "archegonial projections" or "antheridial projections" as the case may be. On these tissue masses, of which there may be thirty on one prothallium, the sporophyte buds form much as in Pteris cretica. Only a few of those upon one prothallium can survive.

Lang (64) in 1898 made some interesting experiments upon the following ferns:

Scolopendrium vulgare, Nephrodium dilatatum, Nephrodium Oreopteris, Aspidium aculeatum, Aspidium angulare, (two varieties) *Athyrium niponicum, Aspidium frondosum, Polypodium vulgare,* and *Athyrium filix-foemina.* Eight of the nine ferns studied were not known to reproduce in any but the usual way. The prothallia were maintained under conditions which favored vegetative growth but prevented fertilization. In all of the cultures the prothallia sooner or later made attempts, often abortive, at producing sporophytes apogamously.

In *Scolopendrium vulgare,* for example, Lang finds that when fertilization fails to take place, the meristem at the apical notch or the tissue just back of it on the ventral side of the prothallium develops into a massive cylindrical solid outgrowth, radial in structure and often two centimeters long. The interior of this mass may contain only parenchyma or there may be isolated tracheids or even a fairly well organized stele. In some cases there are rhizoids on its lower surface, in others, roots arise endogenously, break through and grow down into the ground. The apex of this cylindrical vegetative outgrowth may grow out into a flattened prothallium returning to the typical gametophyte phase, or on the other hand it may give rise to a sporophytic bud with leaf, stem and root. This cylindrical process bears achegones and antheridial sacs on all sides. If fertilization is allowed to take place a normal embryo can form. If not, the tissue about an archegone forms an "archegonial projection" upon which may be formed a group of sporanges. These sporanges are often ill-formed but in a few cases are perfect, showing stalk, wall and annulus and containing several spores. Gametophytic and sporophytic characters are intimately associated here and the cytological problems presented are certainly very complex.

Woronin (100) in 1907 describes apogamy in *Trichomones Kraussii, Pellia flavens, Notochlaena Eckloniana, N. sinuata* and *Pellaea tenera.* Cultures of *Pellaea flavens* grown in poor light or on poor soil show transitions between gametophyte and sporophyte as mixed as those reported by Lang.

Farmer and Digby (40) in 1907 have described a most remarkable nuclear migration and fusion in the prothallium of an apogamous species of *Lastraea* which they characterize as a vegetative fertilization, and they have traced out the history of the chromosome number in several other abnormal types. Their results may be summarized as follows:

1. *Athyrium felix foemina* var. *clarissima* Jones. In this variety, there are apospory and apogamy. Both the soranges and the archegones are abortive. There is no reduction or doubling of the chromosomes, the number, presumptively the double number, ninety, is maintained unchanged throughout the life history.

2. *Athyrium felix-foemina* var. *clarissima* Bolton. Here we have apospory and parthenogenesis. The sporanges are always sterile. The double number of chromosomes, eighty-four, is present in both gametophyte and sporophyte. In spite of the double chromosome number eggs and antherozoids of normal form occur. The egg, which grows without fertilization to form the embryo, has the double or diploid chromosome number and on this account Farmer and Digby do not regard it as the physiological equivalent of an egg.

3. *Athyrium felix-foemina* var. *uncoglomeratum*—Stansfield. The account of this form is incomplete. Apparently here, too, there is apospory and parthenogenesis. The chromosome number is about one hundred.

4. *Scolopendrium vulgare* var. *crispum Drummondae* is aposporous and parthenogenetic. The counts of chromosomes varied. In the prothallium there were seventy, in the embryo eighty to a hundred. In the normal *Scolopendrium vulgare*

the diploid number is sixty-four. Since this is considerably less than the lowest number found in the abnormal variety, the authors conclude that the latter has at least the diploid number. The variability of the number at different points in the life history is held to be real and not due to errors in counting.

5. *Lastraea* pseudo-mas var. *polydactyla.* The sporophyte produces spores and the prothallia grown from them have sixty-five chromosomes. The prothallia do not bear archegones. Vegetative nuclei from adjacent prothallial cells come together and fuse to form the beginning of the new sporophyte. Several fusion figures are shown. The sporophyte grown from these diploid cells contains one-hundred and thirty chromosomes.

6. *Lastraca pseudo-mas.* var. *cristata apospora.* Here, too, there is apospory and apogamy. The prothallium grows from marginal or superficial cells of the frond. It bears antheridial sacs but no archegones. The sporophyte forms vegetatively on the prothallium. The counts of chromosomes which vary between sixty and seventy-eight at different points in the two generations show in the author's opinion that it is the reduced chromosome number that is present throughout the life history.

Nathansohn (72) concludes that exposure to higher temperatures for a limited time stimulates the development of apogamous embryos from the gametophytes of *Marsilia Drummondi.*

Shaw (82) calculated the percentage of embryos formed from isolated macrospores of *Marsilia Drummondi* and compared this with the percentage formed when macrospores and microspores remained together. The percentage of embryos formed in the first case is considerably lower than in the last.

Strasburger (88) in 1907 made a cytological study of *Marsilia Drummondi* and related species. In the macrosporange Strasburger finds fewer than sixteen spore mother cells. One instance is mentioned where there were only four. This is in marked contrast with the conditions in such species as *M. vestita, M. elata* and *M. hirsuta* in which the invariable number is sixteen. These spore mother cells pass into a synaptic condition perfectly normal in appearance. Subsequent to synapsis, Strasburger observes a lack of uniformity in the appearance of the spore mother cells. Some nuclei are larger and much richer in chromatin content than others. In these denser nuclei thirty-two double chromosomes are found. Upon the spindle they present a fairly close resemblance to heterotypic chromosomes. In the second division thirty-two chromosomes can again be counted at the equatorial plate stage. Other spore mother cells in the same macrosporange remain poor in chromatin content and when they divide, sixteen chromosoms are found on the spindle in both divisions. Here the figures are also characteristic for heterotypic and homoeotypic divisions.

Strasburger believes that in these latter cases there is a true reduction. Concerning the larger mother cells he believes that the synaptic condition from which come the diploid number of chromosomes cannot be considered as a true synapsis since the chromosomes did not fuse or at least did not remain fused. Consequently he concludes that the first division in this case is homoeotypic in nature and the second division is an added one without homologue in other reduction divisions.

The result of this varied behavior of the spore mother cells is that we have spores of two sorts—diploid and haploid.

He holds further that the diploid macrospore develops into a gametophyte normal in appearance except that the neck of the archegone remains closed and the canal cells do not die. Thirty-two chomosomes are preesnt during the divisions in the growth of this gametophyte. The diploid and haploid chromosome number in other species of Marsilia are thirty-two and sixteen respectively.

The micro gametophyte of *Marsilia Drummondi* does not develop normally. No antherozoids were seen. The egg develops directly into the embryo without fertilization. Since the egg possessed the diploid chromosome number, Strasburger does not regard it as a true sex cell and in accord with this view the form of reproduction found here is called apogamy and not parthenogenesis. Thirty-two chromosomes appear in the vegetative divisions of the sporophyte so formed.

Yamanonchi (104) in 1908 studied apogamy in *Nephrodium molle*. When conditions for fertilization are supplied, this species reproduces normally. The diploid and haploid chromosome numbers are one hundred and thirty-two, and sixty-six rspectively. If cultures of prothallia are placed in strong light and watered from below, fertilization is prevented and apogamous outgrowths form instead. These sporophytes develop from a single surface cell of the prothallium and the chromosome number remains sixty-six. Here, then, is a second case (*Lastraea pseudo-mas* being the first) in which the chromosome number present in the gametophyte persists during the development of the sporophyte.

I have studied the development of the antherozoids in *Adiantum* and *Aspidium falcatum* and the apogamous development of the latter species, Prothallia of *Adiantum Capillus-Veneris* were purchased. The prothallia of *Aspidium* were grown in pots of red clay. The pots were covered with bell jars or were kept in a Wardian case and surrounded by *Sphagnum* or moist sand. The prothallia were not watered from above. The moisture in the sand or *Sphagnum* provided the clay with a uniform supply. Material for sectioning was fixed in the different Flemming's solutions. The solution of medium strength gave the best results. The sections were stained in the triple stain or in Heidenhain's iron-haematoxylin.

The material for sporogenesis in *A. falcatum* was taken from vigorous green house plants. Flemming's medium solution, picro-formol solution, and a mixture of one-half glacial acetic acid and one-half absolute alcohol were used for fixing. Sections were stained in Flemming's triple stain or with Heidenhain's iron-haematoxylin.

THE DEVELOPMENT OF ANTHEROZOIDS IN ADIANTUM CAPILLUS-VENERIS AND ASPIDIUM FALCATUM.

The dome-shaped mother cell from which the antheridial sac arises has a volume nearly equal to that of the entire sac, just after nuclear and cell division is completed. At the end of this period of active division there ensues a considerable period of growth during which the diameter of each antherid (or antherozoid mother cell) is nearly doubled.

One would naturally expect under such circumstances to find a typical resting nucleus in the growing cell. Yet a true resting condition of the nucleus with finely divided chromatin and large nucleoles, such as is found between divisions in the eight or sixteen cell stage of the sac for example, (Cf. fig. 27 of *Aspidium falcatum)* or in the adjacent vegetative tissue of the prothallium, was not found at this stage. After the dispirem of the last division, the chromatin passes into a very heavy network, exceedingly dense and compact at first, but becoming looser and more open as the cell and nucleus grow. (Fig. 1–5.) The chromatin strands throughout are thick and approximately uniform in diameter. The appearance at first glance all through this period is strongly suggestive of a spirem. Only by careful study can it be determined that there are real anastomoses and not mere crossings of the strands of chromatin. This net-work is distributed uniformly throughout the nucleus.

The relatively small size of the nucleoles at this stage is also notable. The conspicuously large nucleoles found in each resting nucleus in the earlier stages of development of the antheridial sac, are represented here by two small nucleoles, easily overlooked, the time of whose appearance and disappearance is doubtful.

Figures one to three show a stage in which the cells have begun to round up leaving intercellular spaces at their angles. The nucleus is somewhat irregular, conforming roughly to the general shape of the cell. As noted, it is completely filled by a dense close network of chromatin. No nucleoles have been observed at this stage.

About half way between the nuclear membrane and the cell wall, is the blepharoplast. It stains bright red with safranin and is constantly present at this stage. It is not at this time a definite well-rounded granule. It is large, more or less transparent, irregular in outline, with ill-defined boundaries, the peripheral parts shading off gradually into the surrounding cytoplasm. No aster could be brought out by any method of fixing or staining which was tried. The blepharoplast may be comma-shaped (fig. 2) or more irregular (fig. 1). Sometimes there seem to be several darkly staining portions embedded in a less stained ground mass (fig. 3).

The position of the blepharoplast bears no fixed relation to the shape of the nucleus but the latter is often slightly flattened just beneath it. The different cells in a sac are not oriented alike—the blepharoplast being on one side in one cell—another in another.

A slightly later stage is shown in figure four. Small nucleoles have formed in the nucleus. The exact time of the appearance of the nucleole is not easily determined. These nuclei stain densely and the nucleoles are never conspicuous at any time.

The blepharoplast here has become a denser rounded mass, smaller and more sharply stained than before.

Figure five shows a still later stage in which there is a marked increase in the size of the cell and nucleus. The strands of the nuclear net are heavy and uniform in diameter as before. This nucleus showed no nucleoles although at the stage represented they are generally present. Of the other nuclei in the same sac, some had two small nucleoles, others one, and a number like the one drawn had none. There was a lack of uniformity in the blepharoplasts in this sac. Several were still densely staining spheres. Others had elongated into a short, very narrow band, lying parallel to the surface of the nucleus but not in contact with it.

A later stage is represented in figures six to nine. The cell has reached its mature size. The nucleus is still in the center of the cell. Some of the nuclei contain two nucleoles—others one. The meshes of the nuclear net are greatly increased in size, making the structure comparatively easy to examine. The cytoplasm has become vacuolated.

The blepharoplast is here a band, tapering gradually to a point at one end, and coming more abruptly to a point at the other. This band lies across the nucleus, keeping parallel to the nuclear membrane and at a small distance from it, except at the narrower, thinner end which projects out into the cytoplasm. This is probably to become the anterior end of the antherozoid. Figures six and nine show profile views and eight shows a surface view of the blepharoplast. Figure seven shows a section through the same nucleus shown in surface view in figure eight. It is plain on comparing the blepharoplasts of this and the earlier stages that it has grown materially in mass.

Shortly after this the cells round up, separating from each other. The intercellular spaces are filled with a slimy substance that stains strongly with orange G. The nucleus moves to one side of the rounded cell so that the blepharoplast comes to lie near the plasma membrane. The nucleus increases in volume during this change in position and rounds out so that the blepharoplast and the nuclear membrane below it, run parallel to the plasma membrane. The meshes of the nuclear net increase in size and the small nucleoles disappear. The blepharoplast meanwhile continues to grow along the surface of the nucleus until it forms a broad band running half of the way around the nucleus and then out into the cytoplasm at one end, forming a curved, pointed beak at the anterior end.

The fact that the cells in a sac are not oriented alike gives opportunity for studying them from all points of view. Figures ten to twelve show median sections through the cell in three planes which intersect each other at right angles. Figures ten and eleven are longitudinal sections through the nucleus at right angles to each other and figure twelve is a cross section. The nucleus is slightly elongated, rounded at the posterior end and drawn out to a short conical beak along the inner surface of the blepharoplast, at the anterior end. The blepharoplast, as may be seen from the different sections (figures 10–12) forms a broad band along the outer convex side of the nucleus, curving around the tip of the nuclear beak and projecting on into the cytoplasm at the anterior end. It is broadest in the middle (figure 12) and narrower towards the ends (*a* and *b* figure 11).

The nucleus now pushes out at the posterior end forming a short conical projection (figure 13). The blepharoplast runs clear to its tip but does not extend beyond the nucleus as it does at the anterior end. The anterior end of the nucleus has meanwhile become longer and slenderer so that the entire nucleus forms over three-fourths of a circle.

At this stage a slow, gradual shrinking of the cytoplasm begins. Along the middle of the blepharoplast (figure 13) the plasma membrane has drawn in against it. This shrinkage is more pronounced in figures fourteen and fifteen where the plasma membrane is in contact with the blepharoplast throughout.

Just after the stage represented in figure thirteen, the nucleus also begins to decrease in volume. The network of chromatin becomes more dense, the threads forming the meshes becoming shorter and thicker. Apparently an extrusion of nuclear sap takes place along the inner side of the nucleus, resulting in the formation of a series of large vacuoles in the cytoplasm on the concave side of the nuclear membrane (figure 15). The irregular, somewhat angular contour of the inner side of the nucleus as drawn in figure thirteen is changed to the smooth curve that is shown in figure fifteen.

In figure fourteen, the position of the nucleus corresponds to that in figure eleven and the stage represented is intermediate between that of figures thirteen and fifteen. The curvature of the nucleus was followed in making this drawing. The blepharoplast which is in the form of a broad band around the convex side of the nucleus, is represented in cross section twice, once at each end of the drawing of the nucleus (figure 14, a and b). There is, as can frequently be seen in this and later stages, a distinct space between the nuclear membrane and the blepharoplast. The cross section of the blepharoplast is unequal in thickness and somewhat ragged in outline. From this time on, the band is often wider than the nucleus—projecting beyond the borders of the nuclear spiral. The nucleus at this stage forms about one coil of a counter-clockwise spiral as seen under the microscope.

In figures sixteen to eighteen, are shown three cells in different positions, in which the spiral is a coil and a half in length. In figure sixteen, the anterior end is uppermost and in the drawing the plane of the nuclear coil is followed down and around to the posterior tip. Other views of the same stage are given in the next two drawings (figures 17, 18). Both are side views of the nuclear coil corresponding to that shown in figure fourteen. With the elongation of the nucleus and blepharoplast, a curved horn-shaped projection of the cell is formed which will be the anterior end of the antherozoid (figure 16). The bulk of the cytoplasm lies back of the middle of the spiral and bulges out beyond the posterior coil of the nucleus (to the right in figure seventeen and to the left in figure eighteen).

Figure nineteen shows a longitudinal section through the cell somewhat above the median plane at a stage when the nucleus forms about two turns of a spiral. Four portions of the coil appear at a, b, c and d respectively. The anterior end is below. Figure twenty shows the coil with its posterior end uppermost. The anterior part which would lie under the portion drawn, is not represented.

From these drawings (drawn to the same scale as those preceding) it is seen that a marked contraction has taken place in both nucleus and cytoplasm. The larger nuclear coil has only three-fourths its former diameter. The hollow of the same coil, however, is as large as before. This decrease in the volume of the nucleus is accompanied by a contraction of the chromatin network into a coarse reticulum containing heavy aggregations of chromatin irregularly connected.

The blepharoplast bears the same relation to the nucleus as before.

The cytoplasm has undergone an even greater alteration than the nucleus. The cytoplasmic mass has no longer a bulging convex outline. At the posterior end (figure 20) the cytoplasm has drawn back into the hollow of the spiral. At the anterior end also there are changes. The shrinking in of the cytoplasm and the pushing forward of the anterior end have continued.

The mother cell wall, already vague and somewhat disintegrated in the preceding stages, is here nearly obliterated, and the intercellular slime is encroaching upon the space between it and the developing antherozoid. The cell wall is omitted in later drawings.

The further development consists in the condensation of the chromatin into an apparently homogeneous mass and the elongation of the antherozoid to form a rapidly narrowing spiral about which the cytoplasm shrinks to form a close fitting sheath.

A stage in this process in which the nucleus forms between two and one-half and three coils, is shown in figure twenty-one *a*. The shape of the last coil and a half is almost the same as in the two-coil stage (figure 20). The anterior part forms an additional turn of comparatively small diameter.

Nothing remains visible of the structure of the nuclear contents. With the increasing homogeneity of the nucleus, the blepharoplast becomes more difficult to distinguish. In figure twenty-two, there is no line of demarcation between the portion of the spiral composed of blepharoplast alone, i. e. the beak, and that which also contains the nucleus. The two portions form a smooth curve and the stain is uniform, red or gray, according to whether the triple stain or the iron-haematoxylin is used. In the triple stain, however, when the preparation has been deeply stained in the blue, the blepharoplast can still be discerned as a purple line bordering the red of the nucleus (figure 23).

The changes in the cytoplasm are not marked. The bulk of it lies as before in the hollow of the large posterior coil. Its form can be seen in figure twenty-one *b* which represents twenty-one *a* with the last half turn removed. A coil near the anterior end (figure 22) shows the cytoplasm drawing in about the nucleus. The cytoplasm forms a spiral following that of the nucleus, very bulky in the hollow of the large posterior coil but growing more and more slender toward the anterior end. The posterior end of this spiral has the same shape in ripe antherozoids so long as they are still in the sac.

The origin of the cilia is not clear in my preparation. As the mature antherozoids become active the cilia are seen as a coil of threads about the anterior end (figure 24). They are fastened to the coil along the tip, curve outwards, then run back in a spiral following the nucleus. In figure 25 a portion of the cilia are shown free throughout their length and are directed forward, still loosely coiled.

The development of the antherozoid in *Aspidium falcatum* is essentially similar to that of *Adiantum*. As will be described below, the antherozoids of this species never function, since the sporophyte of *Aspidium falcatum* is always formed apogamously. The disuse of the motile male cells in this species has not, however, been accompanied by their degeneration.

Antheridial sacs are formed abundantly upon the prothallia. They are found chiefly along the middle, but scattered sacs are often seen on either side and may be even marginal.

Figure twenty-six represents an anaphase stage in the first division of the central cell of an antheridial sac. It has the usual shape of such central cells; the basal side is conical; the distal side nearly hemispherical. The cytoplasm is dense, containing few vacuoles. The karyokinetic figure occupies a relatively small part of the central portion of the cell. The spindle is broad-poled. The chromosomes are long, slender rods. About one-third of the total number in each of the two groups is repreesnted in the drawing. There are several darker staining granules scattered in the cytoplasm whose nature has not been determined, but neither in this nor in later divisions in the antheridial sac up to the sixteen celled stage has anything been seen which could be called a centrosome or blepharoplast. The last division in the sac was not found.

A resting cell of the eight-celled stage in the antheridial sac is shown in figure twenty-seven. It is drawn on a much larger scale (2700 diameters) than figure twenty-six (1950 diameters). The cell drawn in figure twenty-seven resembles closely the corresponding stage in Adiantum. Cells at this period are commonly but not always long and narrow. The convex surface of the cell drawn, was applied closely to the inside of the wall of the antheridial sac. The other sides were flattened, fitting against the neighboring cells in the sac. The cytoplasm is loose, containing large vacuoles. The nucleus is elongated, following roughly the contour of the cell. The chromatin is in a very finely divided condition and the reticulum consists partly of granules of various shapes and partly of fine branching threads. There are several large conspicuous spherical nucleoles, three of which are shown in the drawing.

In figure twenty-eight, which represents an antherid at the time of the beginning of the elongation of the blepharoplast, the conditions are very different. The cell (drawn to the same scale as figure twenty-seven) is much smaller. No nucleoles are present. The chromatin is in the form of a heavy branching net-work composed of uniform threads.

The blepharoplast lies close to the nuclear membrane but as a rule not in contact with it. It is a short, thick, more or less conical mass. In figure twenty-eight, a section is shown through the thick end of the blepharoplast. In figure twenty-nine is given a section through the same blepharoplast at its thinner, narrower end. Figure thirty shows a side view of another blepharoplast at the same stage. The nucleus is often indented just under the blepharoplast.

As the metamorphosis progresses, a nuclear beak forms under the elongating blepharoplast. The beginning of this process is seen in figure thirty-one. The section cuts through the blepharoplast obliquely. There is a distinct angle in the contour of the nucleus, probably representing a ridge or projection under the anterior end of the blepharoplast. Nucleus and blepharoplast are not yet in contact.

In a slightly later stage, the nuclear projection lies in contact with the middle portion of the blepharoplast (figure 32). The nucleus at this stage is still in the center of the well-rounded cell. The anterior end of the blepharoplast forms a short beak (a) beyond the nucleus, then runs back for some distance in contact with it. The posterior third of the blepharoplast is not at this stage in contact with the nuclear membrane. It extends out through the cytoplasm and its posterior tip is in contact with the plasma membrane.

In figure thirty-three, we have a cross section of the blepharoplast at a slightly later stage. The section cuts through behind the nuclear projection, as may be seen from the fact that the nucleus and blepharoplast are not in contact. The condition of the chromatin has changed but little since the stage in figure twenty-eight. The network is perhaps more open.

The blepharoplast and nucleus now push out forming a slender half coil, lying just below the plasma membrane. In this projection the blepharoplast extends somewhat farther forward than the nucleus. The larger part of the nucleus still forms a rounded mass as shown in figure thirty-four. Figures thirty-four and thirty-five are drawn on a smaller scale (1950 diameters) than the rest of this series. At the right in figure thirty-four is a surface view of the slender beak—at the left, a cross section of the main nuclear mass.

Occasionally at this stage, and more and more frequently in later stages, little masses coloring dark blue in the triple stain are seen scattered in the cytoplasm. Several of these are present in figure thirty-four.

Figure thirty-five represents a somewhat later stage than the preceding. The blepharoplast appears at two points in the section, once at its widest place where it lies in contact with the nucleus and again below where the plane of the drawing passes through its anterior end.

About this time, the posterior end of the nucleus also begins to grow out into a slender curved projection. Both anterior and posterior extremities of the nucleus continue to grow for some time. At this time, too, the cytoplasm begins to decrease in volume, shrinking in about the nucleus.

Figure thirty-six shows a stage in which one and a half turns of the spiral have been formed. This stage corresponds to the one in Adiantum represented in figure sixteen. In both, the blepharoplast runs the full length of the nuclear spiral and in both, the anterior end has pushed out forming a projection of the cell-body. In both, the greater mass of cytoplasm is at the posterior end.

The later stages of the development of the antherozoids in *Aspidium* resemble in the main, those of *Adiantum*. In one respect, however, the older antherozoids are unlike those of *Adiantum*. The cytoplasm contains numerous rounded granules which stain dark blue. These are probably starch grains. Figure thirty-seven shows the posterior part of a nearly mature antherozoid. The cytoplasm contains a large number of these starch granules. They vary considerably in size and shape. These granules are still present in the cytoplasm of the mature antherozoids. Similar starch granules have been noted by various authors for other ferns.

Living prothallia were mounted in a drop of water and watched under the microscope. The mature antherozoids were observed as they were liberated and swarmed about actively in the water.

No signs of degeneration have been detected in the antherozoids of *Aspidium.* So far as can be seen, either from a cytological study of the development or from observation of the living antherozoids, the male cells here are perfectly normal.

THE FORMATION OF THE APOGAMOUS SPOROPHYTE IN ASPIDIUM FALCATUM.

The spores of this species germinate a few days after sowing. The short filament coming from the spore broadens at the apex and is divided into a narrow plate of cells. An apical notch is soon developed and the prothallium assumes the usual heart shape. The prothallium is never more than three cells thick excepting perhaps at the margin of a large apogamous outgrowth. Glandular hairs are found along the margin and on the dorsal surface.

Antheridial sacs, as has been described above, are developed in large numbers on nearly all of the prothallia. De Bary found archegones on twenty-five to thirty per cent of the prothallia of *Aspidium falcatum.* In my material, grown under the conditions described, archegones are of much less frequent occurrence.

The apogamous outgrowths usually form when the prothallia are five or six months old. The time of their appearance varies considerably, however. In several cases a very young sporophyte was found upon a large prothallium eleven months old. A great majority of the prothallia produce sporophytes sooner or later.

The position of the outgrowth is on the ventral side a few cells back from the apical notch. Since the prothallium is only two cells thick at this place, the outgrowth is certainly superficial and may be of epidermal origin. The origin of this outgrowth has not been traced back to the first cell divisions, but figure thirty-eight shows a median section through an early stage in its formation. The little projecting mass of tissue, though but two or three times the size of one of the adjacent prothallial cells, consists of twenty-five or thirty cells. The well-defined surface layer of this compact mass is composed of small irregular cells. In the interior of this mass, repeated tangential divisions have resulted in several layers of still smaller tabular cells. No apical cell can be distinguished at this stage. The limits of the sporophytic tissue are well defined.

As this compact mass of embryonic tissue grows larger, the contrast in size between its cells and the adjacent prothallial cells becomes less marked. It is still possible to determine the limits of the sporophytic tissue, however, when the outgrowth is large enough to be seen with the hand lens. (Figures 39 and 40.)

The prothallium is now three cells thick for a short distance back of the sporophyte. The tangentially placed walls in the mass are still conspicuous, bounding the flat cells which extend in rows radially from the center of the mass to its outer surface. (Figure 39.) At a still later stage, as shown in figure forty, the arrangement of the cells is somewhat more irregular. Cell differentiation has begun at this stage. There is a series of fully formed tracheids in the interior of the mass and the chromatophores of the outer layer of cells contain good sized starch grains.

In its further growth, an apical cell is differentiated at the outer anterior angle of the young sporophyte. This by growth and division gives rise to the first leaf. In the hollow between the base of this leaf and the prothallium the apex of the stem is organized. The first root arises endogenously and pushes backward from a point near the base of the first leaf. Figure forty-one shows a somewhat oblique section of a sporophyte in which the root (r) is just breaking through the tissues. The young incurved leaf (l) protects the stem apex (s) which lies near its base. A strand of vascular tissues runs from the leaf tip back toward the root. The section is slightly oblique and the missing part of the vascular strand is found in adjacent sections. The leaf and stem of the young sporophyte are covered with glandular hairs of the same form as those found upon the prothallium.

The prothallium may live for a considerable time after the sporophyte has formed upon it. Apical growth, however, ceases and the cells at the base of the apical notch grow to full size. The expansion of these cells makes the notch shallower and pushes the lobes farther apart. Even after the prothallium stops growing, it may remain fresh and green until the sporophyte borne upon it has five or six leaves and as many roots.

The appearance upon a prothallium of an isolated member of the sporophyte, as a leaf or a root (so common in some apogamous ferns) is, so far as I have observed, rare in *Aspidium falcatum.* I have but once seen a leaf growing directly from the prothallium with no sign of stem apex or root. I have never seen an isolated root nor have I ever seen tracheids in the tissue of a prothallium which was producing no sporophyte. The mixtures of gametophytic and sporophytic characters which have been described by Lang and others for *Scolopendrium vulgare* and other ferns I have not found in *Aspidium falcatum.*

A certain percentage of the prothallia are slow to produce sporophytes or fail altogether to produce them. In these prothallia, the same growth phenomena are to be observed which are seen in old prothallia of normal ferns when an embryo is not formed. These prothallia of *Aspidium falcatum* continue growing for months and attain a length of two or three centimeters. The growth may be apical, the prothallium becoming gradually narrower and thinner as it increases in length until it ends in a narrow one-layered strap of cells. Usually in this case the apical notch becomes very shallow and may even disappear. These conditions are doubtless due to unfavorable environment.

Ordinarily, however, in prothallia producing no sporophyte, the growth is more irregular. Even in the prothallia described above, there is some marginal growth, resulting in notched edges and in more or less folding of the whole prothallium. Usually apical growth ceases entirely and marginal growth becomes more pronounced. Sometimes the two lobes grow out into broad straps. Sometimes growth begins at various points along the margin, the outgrowths varying greatly in width. An outgrowth may begin as a filament and then broaden into a strap, or it may continue as a filament and branch, much in the fashion of the prothallium of *Trichomanes* as described by Bower and others. All of these adventitious prothallia bear rhizoids and glandular hairs and antheridial sacs. In one case I saw a filament thirty-five cells long with a side branch three cells long. Scattered along its length were nine antheridial sacs. No indication of a sporophyte has been observed on any of these secondary prothallia.

CELL AND NUCLEAR FUSION IN THE SPORANGE OF ASPIDIUM FALCATUM.

In the light of Farmer's and Digby's discovery of nuclear migration and fusion in the tissue of the prothallia from which the young sporophyte arises in *Lastraea pseudo-mas* var. *polydactyla,* the possibility of the existence in other apogamous ferns of vegetative fusions replacing normal fertilization, must be especially considered. In *Aspidium falcatum* I find a substitution fusion in the sporanges. The sixteen spore mother cells fuse in pairs to form eight much larger cells which then undergo the reduction division.

The development of the sporanges and sporogenesis proceeds normally up to the point at which fusion takes place. In the first eight-celled stage the spore sac is small. The cells of the two-layered tapetum are still intact. They are fitted closely to each other and occupy their original position. The nuclei of the tapetal cells are dense and stain heavily but the cells do not show marked signs of degeneration. The eight cells of the sporogenous tissue are angular and pressed closely against each other, leaving no intercellular spaces. The equatorial plate stage of the division of these eight cells is shown in figure forty-two. The cell was one of eight which were passing simultaneously through the last division before the formation of the spore mother cells. The cells at this stage are still angular, fitting closely to each other and to the walls of the inner layer of tapetal cells. The cell walls, if present, are very thin and delicate. The cytoplasm here is dense and the vacuoles are small. The chromosomes are relatively large and form a very compact group. The spindle is as in the other tissues broad-poled. Slightly over a third of the chromosomes are represented in the drawing.

As a result of this division, sixteen spore mother cells are formed. The cells were carefully counted. Camera lucida sketches were made of successive sections of a sporange and these sketches were carefully studied and compared and the number of cells thus determined. The result was invariably sixteen.

These sixteen young spore-mother cells are normal in appearance. (Figure 43.) As a rule they are angular and nearly isodiametric, but a few are more elongated. The cell wall, if present, is very thin. The cytoplasm is dense and is free from darkly staining granules. The nucleus is rounded and is ordinarily at the center of the cell. The chromatin forms a loose reticulum consisting of small aggregations connected by delicate strands. The amount of nucleolar material varies greatly. In some nuclei there are three or four good-sized nucleoles.

In the next stage we find that the sixteen spore mother cells are fusing in pairs. The fusion figures are numerous and unmistakable, and as the cells are large and easily fixed and stained, the process can be followed in detail. The drawings of these fusion stages are all made on the same scale. They are magnified nineteen hundred and fifty diameters.

A stage showing the earliest indications of fusion is represented in figure forty-four. In this instance, the nuclei are nowhere in actual contact, but the cells are united along one side. The chromatin is in the form of fine, uniform, much convoluted threads. There are several nucleoles in each nucleus. On each nucleus there is a slender pointed projection extending to the plasma membrane. Each of these projections contains a loop of the spirem. The projection on the one nucleus is exactly opposite the one on the other but the plasma membranes of the two cells are not quite in contact at this place. The surfaces of the nuclei are smooth and rounded except at the points where these beaks protrude.

A slightly later stage is shown in figure forty-five. The cells are united along one side but are still distinct through more than half of the surface of contact between them. The two cells are rounded except along the edges of the surface of contact. A broad lobe from one nucleus extends into the other cell and lies in contact with its nucleus. It is doubtful whether there is yet actual continuity between the two nuclear cavities. The chromatin here is distinctly reticulate. There are a few uniform threads of chromatin—but there is also a real meshwork with small aggregations of chromatin at the angles.

It is plain from figures forty-four and forty-five that the chromatin is not always at the same stage at the time of fusion. In figure forty-four the chromatin is in practically the spirem stage. In figure forty-five it is in the earlier stage of the reticulum. The beginning of fusion is not dependent upon any particular condition of the chromatin.

Further, the sixteen cells, although formed at the same time, do not always fuse simultaneously. In the spore sac from which figure forty-four is drawn, in the case of one or two pairs of cells the fusion was fairly well advanced; in some others it was about half completed; and in the one drawn it was just beginning. In all of the nuclei in this spore sac the chromatin is in nearly the same condition, consisting of fine threads of uniform diameter. In general, however, the reticulate condition of the chromatin predominates in the earlier stage of fusion and the spirem is more common in the later stages.

In figure forty-six, we have a slightly more advanced stage of fusion. The nuclear cavities are in communication and the cytoplasm of the two cells is almost completely fused, although along the left hand side of the figure the cytoplasmic masses are not yet in contact. The chromatin is reticulate and no nucleoles are present.

It is noteworthy that although the stage of fusion in figure forty-six is somewhat more advanced, the fusion cell appears to be distinctly smaller than in either of the two preceding figures. As noted above, the drawings are all made on the same scale. This difference in size is probably due to the fact that the time when fusion begins, varies, and the spore mother cells are growing both before and after fusion. The fusion may take place early, in which case as in figure forty-six, the fusion cell is small. On the other hand, the fusion may be delayed until the cells are half grown. The fact that the stage when fusion begins, varies both in different spore sacs, and to some extent in the same spore sac, accounts in part for the abundance of these stages in sections through the young sori.

In figure forty-seven, the cytoplasm of the two cells is shown completely united. It is to be noted, however, that at the middle of the right hand side, where the union is most recent, the line of union is still traceable by the openness of the cytoplasmic mesh-work and the large vacuoles. In the nuclei the fused region is much broader than in figure forty-six and the chromatin reticulum of the two is continuous. No nucleoles were present in this case.

Figure forty-eight represents the type of fusion figure encountered most frequently. I have recorded not less than forty like it. Some of these are smaller than the one drawn and a few are larger. The condition of the chromatin varies in the different cases from that of a reticulum to that of a well-defined spirem. In all cases, the nucleus has the characteristic kidney shape, and the cytoplasm of the two cells is completely fused around the convex side of the fusion nucleus, but remains separate almost to the nuclear membrane on the concave side.

Just why the cells and nuclei should fuse and round out more quickly on one side than on the other is hard to understand, but in the majority of cases the fusion plainly occurs in this fashion. These figures are not oriented in any particular way in the sporange. In some, the convex side of the nucleus is turned toward the sporange wall, while in others the concave open side is turned outward.

Figure forty-nine represents a more unusual type of fusion. The cell here is almost full grown. The cytoplasm of the two is completely fused. Neither the contour of the cell nor the appearance of the cytoplasm gives any evidence that a fusion has occurred. The nucleus on the other hand still shows clearly its double nature. In fusing, the two component nuclei evidently came to lie side by side and flattened against each other.

Although there is a broad connection between the two, each nucleus has retained to a large extent its individual contour. The zone where the two nuclear membranes are in contact is marked by a deep furrow. A number of the fine strands of chromatin run through from one nuclear cavity to the other. There is a dense tangle of threads between the two. Many of the chromatin strands in the nucleus at the right, run radially inward toward the opening, suggesting perhaps the idea of motion toward the chromatin of the other nucleus. In a half dozen places the chromatin threads are already paired for a short distance.

In figure fifty, we have another characteristic fusion figure. Here, as in figure forty-eight the fusion in the nuclei is the more advanced. A rather deep furrow still partially separates the two masses of cytoplasm. The plasma membranes of the two cells are continuous but at the plane of junction of the nuclei a furrow extends in almost to the nuclear membrane. The fusion nucleus is well rounded. A protruding ridge in the outline along the upper side is the only remaining evidence of fusion so far as form is concerned. Within the nucleus the strands of the spirem run more or less continually from one end of the nucleus to the other. Here, too, in a few places the chromatin threads are paired. Two or three small nucleoles are present.

That the fusion is always in pairs and that all the sixteen mother cells fuse in the above described fashion is further established by the number of sporogenous cells in the spore sac before and after the fusion process.

The stage during which sixteen spore mother cells are present in the spore sac is apparently short. The fusion stages are next found abundantly. The growth of the cells continues during fusion and when the spore mother cells reach their full size and round up, only eight are to be found in a sporange.

This second eight-celled stage is markedly different from the first eight-celled stage described above. The spore sac has now increased greatly in size. The tapetal cells are shrunken and crushed and often out of place. The spore mother cells are more or less rounded up and separate from each other. The nucleus of the spore mother cell is much larger in proportion to the volume of the cell than it was in the cells of the first eight-celled stage.

In a few cases not all of the cells fuse. In the spore sac from which the cell in figure fifty-one was drawn, there were nine separate cells. Seven of the cells were like the one drawn. The other two, which were lying at a little distance from each other, were smaller. Each had considerably less than half the volume of one of the larger cells. The ratio of the diameters of the smaller and larger cells is about 2:3. In this case, fourteen of the sixteen cells apparently fused by pairs. The other two, either because they were too far apart, or for some other reason, remained separate. Two cases of this sort have been recorded. A third case of a similar nature was studied. Here ten cells were were found in a spore sac, six of which were large and four were small.

The cells after fusion proceed directly to the heterotypic division. Several counts were made at the time of the very conspicuous synaptic stage and here, too, there are only eight cells in a sporange. Eight cells go through the double division and eight tetards are formed. Spore counts were made from fresh material. The sporange was mounted under the microscope and crushed and the spores counted. The number of spores is frequently fewer than thirty-two but never exceeds that number. The evidence from all these data is conclusive that the sixteen young spore mother cells fuse by pairs to form eight cells.

THE REDUCTION DIVISIONS.

After the fusion, the eight diploid cells at once enter upon the prophases of the reduction divisions.

In figure fifty-one, we have a cell in which fusion is complete. The chromatin is still reticulated in certain regions but the spirem is appearing also. The volume of the nucleus is larger in proportion to the size of the cell than it has been in any preceding stage. There are relatively large, clear spaces between the chromatin strands. So far as the chromatin development is concerned, this is really an earlier stage than those given in figures forty-nine and fifty. The latter are really entering upon the special presynaptic stage, while in figure fifty-one there is no evidence of this.

Soon after this time, the cells become more uniform in appearance. The larger ones round out and become spherical, lying free from each other in the cavity of the full-grown spore sac. The smaller ones in which fusion is complete, grow, becoming spherical as they increase in size, and the chromatin gradually assumes the appearance found in larger cells.

Figure fifty-two shows a thin section through a cell during this growth. There has been a decided increase in volume since the stage shown in figure fifty-one and the angular outline has changed to a well rounded form. The cell is nearly spherical. The nucleus has also increased somewhat. Nearly all of the chromatin is in the form of delicate threads, suggesting the leptoneme spirem. There are still chromatin aggregations, however, especially in the immediate neighborhood of the nucleoles.

Shortly after this, the chromatin draws off to one side of the nucleus forming a dense mass having about one-half the diameter of the nuclear cavity. Spore sacs containing nuclei in synapsis are seen freqeuntly, and usually all the cells in the spore sac are in the same stage. These masses are not oriented in any particular manner in the sporange. In some of the cells the mass is on the side away from the peripheny of the sporange, in others it is on the side nearest it. While the cell is in synapsis the layer of cytoplasm is always thinner on the side of the cell adjacent to the mass of chromatin than it is elsewhere. In cells which have been very lightly stained, the structure of the synaptic mass can be made out. No nucleole is found at this stage. The chromatin thread of which the mass is made is markedly crinkled, and winds irregularly in and out. The thread cannot be seen to be double at this time and the two strands have probably fused.

At this stage also there are occasionally cell-fusion stages to be found. In one case, a sporange was found containing seven large spherical cells in the synaptic stage. The eighth cell (figure fifty-three) had the form of two spheres slightly flattened against each other. The two nearly spherical nuclear cavities are connected by a rather narrow region of fusion. In each of the two nuclear cavities there is a dense mass of chromatin threads, and a dense series of similar threads runs from one mass to the other. The two synaptic masses of chromatin are equal in size (the plane of the drawing passes tangentially through the left hand mass) and resemble very closely the synaptic masses in the other cells in the sporange. Double cells with a somewhat broader opening between them have been seen in even later stages, containing normal heterotypic chromosomes.

After synapsis, which apparently lasts a considerable time, the chromatin again spreands out through the large nuclear cavity. A stage in this loosening of the knot is seen in figure fifty-four. A rather thick section through the cell is represented, and shows the enormous length of thread that is present at this time. No attempt was made to follow the thread through its intricate windings. The thread is everywhere uniform in diameter and can nowhere be seen to be double. Here, as in synapsis, the layer of cytoplasm on the side of the cell nearest the chromatin knot is very thin.

As the spirem spreads through the nuclear cavity, the nucleus regains its central position in the cell. In figure fifty-five we have the large nucleus centrally placed. The spirem, which is now nearly uniformly distributed, consists of long, fine threads that wind in and out irregularly through the large nuclear cavity and are everywhere double. Sometimes the two strands lie parallel, sometimes they are twisted upon each other, but there are always two. The course of one of these double strands can often be traced, irregularly bending and looping, half way across the nucleus.

Segmentation now occurs and the chromosomes are at first long and slender but soon shorten and thicken. In the stage represented in figure fifty-six, the length of a chromosome exceeds the diameter of the nucleus. The chromosome is easily seen to be double. Later, as the chromosomes shorten they appear as pairs of thick rods uniformly distributed through the nuclear cavity. Sixty-nine chromosomes were counted in a nucleus at this stage. This is practically the same number which is found throughout the gametophyte and the vegetative life of the sporophyte as will be described below. As noted, each of these chromosomes is double, as is regularly the case in diakinesis.

At about this stage, kinoplasmic fibres appear in the cytoplasm. They are at first few and scattered. Later, they become more numerous and collect into bundles forming a multipolar spindle.

The chromosomes meanwhile have shortened into irregular lumps, each composed of two very short, thick rods twisted about each other. The appearance of these heterotypic chromosomes is very different from the long slender rods in the vegetative mitoses.

The nuclear membrane now breaks down and the multipolar spindle becomes bipolar. It may remain multipolar, but sometimes at least becomes strictly bipolar as in the one drawn (figure fifty-seven). During the formation of the spindle, the chromosomes which have hitherto been scattered through the large nuclear cavity, come to lie in the equatorial region of the spindle. The equatorial plate is frequently irregular in outline and forms sometimes a curved surface so that the chromosomes do not lie in the same plane.

As the halves of these double chromosomes are pulled apart, the halves themselves become double. In several cases in figure fifty-seven the daughter chromosomes are seen to consist of two thin parallel rods whose united bulk would about equal one-half of the heavy heterotypic chromosome.

When the chromosomes are drawn back to the poles, the daughter nuclei are partially reorganized but no cell division takes place.

In the homoeotypic division which soon follows, the two spindle axes may be placed parallel to each other, or they may lie at right angles. In other cases one is oblique to the other. An example of the last named case is represented in figure fifty-eight. Extending between the two spindles is a thick plate of rather dense cytoplasm. The cytoplasm of the remainder of the cell is much less dense. The spindles themselves are usually broadpoled and the chromosomes are short and thick.

At the close of the second division the daughter nuclei are formed and the chromatin goes into the form of a reticulum. Central spindles are then formed connecting all four muclei in preparation for cell plate formation. Figure fifty-nine shows a stage in this process. Only two of the four nuclei lie in the plane of the drawing. The volume of all four taken together is considerably less than that of the fusion nucleus before division. These four nuclei are irregular and angular in outline. The rather scanty chromatin is in the form of a loose irregular network. At this stage numerous fibres are seen running radially from almost the entire surface of every nucleus. The only side of each nucleus that is free from fibres is that lying toward the mother cell-wall. This space between the nuclei and the mother cell wall is filled with vacuolated cytoplasm. Many of the fibres can be followed through their entire length from one nucleus to the other. They are uniformly distributed throughout the space between the nuclei. In the middle plane between each pair of nuclei, thickenings in the fibres are formed. They do not as yet touch each other and are still placed a little irregularly. This is the beginning of cell-plate formation.

With the formation of the cell plates, the spore mother cell is divided simultaneously into four approximately equal cells. Figure sixty represents a section through a tetrad of young spores. Only three of the four spores lie within the plane of the drawing, and the middle one of the three is not seen in median section. The four cells lie loosely connected—spaces appearing between them. Each young spore is a somewhat elongated cell whose surfaces of contact with the other spores are still flat but whose free surface is convex. The nucleus also is elongated following more or less the contour of the mother cell. The chromatin is more conspicuous than it was in the stage shown in figure fifty-nine and forms a dense reticulum in which there are comparatively large aggregations.

As mentioned before, the number of spores formed in a spore sac never exceeds thirty-two. Eight spore tetrads is the maximum. Not infrequently, twenty-eight spores are found, indicating the abortion at some stage in the development, of one of the spore mother cells. There are sometimes even fewer. Cases in which one pair of spore mother cells fail to fuse may account for some of the cases in which twenty-eight spores have been found in a sporange. There is no evidence that the unpaired cells can undergo a double division to form spores. Cases of incomplete fusion such as those already described may also explain reductions of the final spore number.

The question as to the number of chromosomes in the nuclei of the sporophyte of apogamous ferns as contrasted with those in which normal fertilization occurs, has attracted much attention in recent years, and in the light of the facts as to the fusion of the spore mother cells above described it becomes especially important for *Aspidium falcatum.* In my sections of prothallia, I have not found division figures common. Figure twenty-six shows a characteristic division figure in the young antheridial sac as described above. It represents an early anaphase in the first division. About one-third of the total number of chromosomes are represented in the drawing. The chromosome number is so large and the chromosomes are so massed together that a single counting cannot be depended upon to give trustworthy results. The difficulties in the way of arriving at an exact determination of the number of chromosomes in any particular division are very great. I have followed the plan of making at least three separate counts for each division figure. The three numbers so obtained varied from each other within a range of five or six. It is an average of the three counts in each case which I have taken as representing the nearest possible approximation to the actual number.

The two chromosome groups in the diaster of a vegetative division in the prothallium when counted in this manner showed respectively *62* and *61* daughter chromosomes. The three countings of the first figure gave *61, 62,* and *63;* for the second *63, 60, 60.* Four equatorial plates from an antheridial sac counted in the same way showed respectively *61, 63, 58* and *60* chromosomes. The three countings from which in each case these figures were derived were respectively *59, 63, 60; 62, 64, 63; 60, 55, 59;* and *60, 61, 58.* The average for all of these countings is *60*, which it seems probable is slightly below the number of chromosomes characteristic of the prothallium in this species. The higher numbers were obtained in spindles where the chromosomes were spread out to the best advantage for counting. It is probable that sixty-two or sixty-three is more nearly correct than the average of the six numbers.

The chromosome number in the dividing nucleus of the young sporophyte was determined in the same way. In sections through the young apogamous outgrowth, division figures are comparatively abundant. An equatorial plate stage is shown in figure sixty-one. It was taken from a point near the newly formed stem apex. Here, too, as in the division figures in the gametophyte, the spindle is broad-poled. The denser part of the cytoplasm is massed about the poles of the spindle. Toward the periphery of the cell there is a much greater proportion of cell sap. The slender chromosomes, a few of which show the longitudinal split, are apparently attached by one end at the equator of the spindle. The free ends may extend toward the poles or radially outward. They hide from view the greater part of the spindle fibres. About a third of the total number of chromosomes are represented in the figure.

The counting of the chromosomes was done as before, each number given representing the average of three counts for the same nucleus. The division figures from which counts were made were from different parts of the young sporophyte. The majority were in the central mass of tissue near the base of the stem apex; some came from the apical region of the young leaf. The numbers obtained in the individual countings were *63, 64,*—ave. *63; —, —, —* ave. *64; 63, 69,*—average *66; 59, 59, 63,*—average *60; 56, 58, 59,* average, *58; 58, 61, 58,*—ave. *59; 58, 60, 59,*—average *59; 62, 66, 64,*—ave. *64;* and *61, 65, 62,*—average *63.* The average of the means so obtained is *62.*

The greater variation in the numbers here is probably due to inaccuracies in counting and does not prove irregularity in the chromatin content of the nuclei.

To make certain that the same chromosome number persists throughout the life of the sporophyte, sections were made of the young spore sac and the chromosome number in dividing nuclei counted in the same way. Division figures are easily obtained. Figure forty-two which was earlier described, shows an equatorial plate stage. The numbers obtained in the individual countings in the young sporophyte were *61, 63, 64,*—ave. *63; 66, 63, 66,*—average *65; 61, 64, 64,* average *63.* The total average here is *64.*

The evidence is conclusive from all the above countings that the chromosome numbers from the nuclei of the prothallium, young sporophyte and sporange are approximately the same. The number characteristic of all these stages may then be said with considerable certainty to be between *60* and *65.*

Whether it is the original gametophyte number which persists through the sporophyte or whether it is the diploid sporophyte number which persists through the gametophyte is a question of considerable difficulty.

General Discussion.

Belajeff has described especially the transformation of the nucleus into a spiral form, but the change in form of the cell as a whole, the question as to the persistence of the plasma membrane, etc., are much less clearly worked out.

In the antherozoid of the Gymnosperm the cytoplasm remains as a more or less rounded mass enclosing a large spherical nucleus. Here there can be no doubt that the entire cell is present in the mature antherozoid and that the plasma membrane is still intact. According to Belajeff, it is also intact in *Chara.* In *Adiantum* as described above, the plasma membrane forms an unbroken covering of the antherozoid. Here, however, as is usual in ferns, the bulk of the cytoplasm is at the posterior end. It is found there very early in the process of transformation and remains there as the spiral is developed. The plasma membrane apparently shrinks in about the spiral nucleus throughout its whole extent.

Ikeno, as noted above, concludes from his observations on

Cycas and *Marchantia* that the centrosome forms within the nucleus before the last division and then moves out through the nuclear membrane into the cytoplasm. Yamanonchi, though non-committal, considers this as a possibility in *Nephrodium molle.* Thom, whose work like my own was largely on *Adiantum,* inclines to the belief that the nucleus of the antherozoid mother cell in moving to the side of the cell leaves one of its large nucleoles behind in the center of the cell and that this nucleole later becomes attached to the anterior end of the nucleus and becomes the blepharoplast.

My preparations do not support either of these views. The figure that Thom gives (fig. 27) of the stage before the appearance of the blepharoplast corresponds very closely to what I find in the sixteen-celled stage of the sac. I do not find large nucleoles and finely divided chromatin in nuclei after the last division. I find the blepharoplast present in the cytoplasm before the appearance of the antherid nucleole and continuously present in all succeeding stages. The blepharoplast certainly does not originate as a nucleole.

Although the nucleole as such does not move out into the cytoplasm and become the blepharoplast, the possibility is of course not excluded that the material for the growth of the blepharoplast is derived from the nucleus. Strasburger holds this view. In the swarm-spores of *Oedogonium,* Strasburger finds that the hyaline disk about which the cilia grow, forms only when the nucleus is in contact with it. In antherozoids, too, the nucleus and blepharoplast are closely associated. These facts suggest to Strasburger that the source of material for the origin and growth of the blepharoplast lies within the nucleus and may perhaps be found in the nucleoles.

This, of course, cannot be regarded as proved, still, the contact of two organs while one increases in size suggests that the one is furnishing material for the growth of the other. The blepharoplast which is seen in the young antherid cell certainly increases in volume many fold during its development. Still, the nucleoles found in the nucleus of the growing mother cell are far too small to supply sufficient material for all this growth.

There may be more material of the same sort in solution in the nucleus, but not all of the substances used in the growth of the blepharoplast can have been derived from the recognizable nucleolar material of the antherozoid mother cell.

The question as to the relations of the blepharoplast and centrosome is still an open one. There is considerable evidence that the animal centrosome is a permanent structure of the cell. The plant blepharoplast as it appears in Archegoniates and seed plants is apparently not permanent. It is present during a few divisions or perhaps only one. There can be no question that after considerable growth and various transformations, the blepharoplast becomes the structure from which the cilia are developed. In this it conforms entirely to the behavior of the centrosome in animal spermatogenesis. It seems probable that the animal centrosome and the blepharoplast are closely related in their essential nature, to the spindle and astral fibres and may both be classed under the category of kinoplasmic substances. As our knowledge of the various activities of kinoplasm and of the equally varied forms which it can assume, increases, it perhaps becomes less surprising that a kinoplasmic organ, similar in form and function to the centrosome can be formed de novo for a special function.

In connection with the old question as to the effects of use and disuse upon the persistence of a structure, it is interesting to note that the majority of the apogamous ferns, including *Aspidium falcatum,* still produce normal antherozoids. Yet so far as can be judged, apogamy is here an old and well established process. Winkler find equal persistence in apogamous seed plants.

The occurrence of substitution fusions in plants that have become apogamous is a fact of fundamental importance for the interpretation of sexual phenomena. Such cases are apparently not uncommon among the fungi but the case reported by Farmer and Digby for Lastraea pseudo-mas var. polydactyla is the only one hitherto reported for the apogamous ferns. There can be no question that as described above, sixteen spore mother cells are formed in the spore sac of *Aspidium falcatum* and that these sixteen cells fuse in pairs to form eight. The nuclei of these eight cells fuse at once and immediately enter upon the prophases of the heterotypic division. Synapsis and the reduction divisions are normal in every respect. Thirty-two spores are formed. The number of chromosomes, sixty to sixty-five, persists through both the gametophytic and sporophytic generations.

Whether this is the original haploid or diploid number is not at once evident. I am inclined to the view that it is the haploid number and that in the evolution of *Aspidium falcatum,* apogamy appeared before the fusion of the spore mother cells in the spore sac. The fern may have existed for some time with no nuclear or cell fusion or reduction divisions of any sort before by further and perhaps correlated variation the fusion of the spore mother cells appeared. This seems to me the more probable view but the possibility exists that the fusion of the spore mother cell appeared first and then led to the immediate suppression of the normal fertilization. In this case the number of chromosomes found at present in both the sporophyte and gametophyte would be of course the diploid number.

There can be no doubt that the chromosome number in both gametophyte and sporophyte is the same in this case as shown from the counts described. The nuclei of the prothallium and of the sporophyte which is produced vegetatively upon it, contain sixty to sixty-five.

Winkler (99) classifies the cases of apogamy under two heads, (1) somatic apogamy and (2) generative apogamy. Under somatic apogamy are included all cases of apogamy in which the double number of chromosomes runs through both gametophyte and sporophyte. Under generative apogamy are included the few known instances in which the reduced chromosome number persists through the sporophyte. On this basis *Aspidium falcatum* would be classified as a case of generative apogamy.

In discussing generative apogamy Winkler suggests the possibility that a case might be found in which a haploid gametophyte would produce a sporophyte without change of chromosome number and that later in the growth a nuclear fusion would make good the sporophyte number. In the case of Aspidium the fusion comes at the close of the sporophyte, showing that it is not necessary for the development of the sporophytic characters.

Two other cases of generative apogamy have been discovered in which, as in *Aspidium,* it is claimed that the haploid chromosome number is continued through the sporophyte. *Lastraea pseudo-mas* var. *cristata* apospora is reported by Farmer and Digby. As previously noted, this form is aposporous as well as apogamous. The variety is not known to produce spores and no reduction divisions have been discovered. The only evidence at present which shows that it is the haploid and not the diploid chromosome number that is present, is the size of that number. The counts for *Lastaea* vary between sixty and seventy-eight. Another variety of the same species has sixty-six as the gametophyte number and double that in the sporophyte. Among ferns in general sixty and seventy are common gametophyte numbers. Such being the case the presumption is in favor of Farmer's and Digby's assumption that it is the haploid number which runs through the whole life-history.

The second case in which it is claimed that the reduced chromosome number is maintained unchanged in the development of the sporophyte is that of *Nephrodium molle* described by Yamanonchi. Here there is no question about its being the haploid chromosome number, since the species is reported as also reproducing normally in which case the haploid number, sixty-six, is doubled to one hundred and thirty-two at the origin of the sporophyte and reduced to sixty-six once more at spore formation. No description is given by Yamanonchi of the process of spore formation in these apogamously produced sporophytes. They may possibly resemble *Aspidium* in showing a fusion of spore mother cells.

The reverse case, in which the gametophyte has the sporophyte number, i. e., somatic apogamy, is reported more commonly. Among the instances noted are the macrogametophytes of *Antennaria alpina, Thalictrum purpurascens, Taraxacum officinale, Wikstroemia indica,* and several species of *Eualchimilla* and *Hieracium* among the Phanerogams. In all these cases, however, the macrogametophyte is reduced to a few cells and its morphological characters are not very complex. Among the ferns, *Athyrium felix-foemina* varieties *clarissima* and *unco-glomeratum* and *Scolopendrium vulgare* var. *crispum Drummondae* are reported to have a gametophyte with the diploid number. With few exceptions these gametophytes have normal form.

It seems to be fairly well established that a gametophyte can be normal in all morphological details and have the double chromosome number, and that a sporophyte can be quite as normal and have the reduced chromosome number. Under these conditions, the view held by Strasburger that a gametophyte with the double number of chromosomes must be regarded as sporophytic tissue, is no longer tenable. To call the large plant of *Aspidium falcatum* with its stem and roots, and its fronds bearing numerous spore sacs, a gametophyte because it has the haploid number of chromosomes, involves the neglect of too many important and conspicuous characters both physiological and morphological.

We can, in my opinion, no longer maintain that the chromosome number as such, determines the morphological characters of the gametophyte and sporophyte We are forced to the conclusion that the morphological characters may be in certain cases independent of the chromosome number. This view is accepted by Farmer and Digby, Winkler and others.

In *Marsilia Drummondi* as noted above, the same chromosome number appears in the gametophyte and the somatic cells of the sporophyte and again in the majority of the reduction division figures in the spore sac. Strasburger also found that there were fewer than sixteen spore mother cells in a spore sac at the time of reduction. Correlated with this condition, some of these spore mother cells were found to be larger than others and to contain a larger amount of chromatin. It seems to me possible from these facts that a fusion of the spore mother cells in *Marsilia Drummondi* similar to that which I have found in *Aspidium falcatum* may occur. In full accord with this is Strasburger's statement: "Im allgemeinen konnte man darauf rechnen, diploiden Makrosporen in einem Sporocarp um so häufiger gu begegnen, je geringer die Zahl der Sporenmutter Zellen war, die man in den Makrosporangium angelegt sah." The observation that there were fewer than sixteen spore mother cells at the time when the reduction division begins, is at least suggestive.

Against the possibility of such a fusion in *Marsilia* is the fact that the smaller spore mother cells which were poor in chromatin content also undergo reduction divisions, according to Strasburger. It would certainly be hard to believe that cells already possessing the reduced number of chromosomes could carry out regular reduction divisions. Possibly these cells correspond to the cells remaining unfused in the sporange of *Aspidium,* but they seem to have been of more frequent occurrence in *Marsilia* than I have found them in *Aspidium.*

On the second hypothesis suggested as to the origin of the condition in *Aspidium falcatum,* i. e., that the fusion in the spore sac arose before the fern had become apogamous, the reduction divisions of unfused cells might of course be expected. In this case the difficulty Strasburger feels in the assumption of a sporophyte with the haploid number of chromosomes would also be obviated. I am, however, of the opinion as argued above, that in *Aspidium falcatum* it is the haploid number which appears in both generations.

The finding of a fusion of vegetative nuclei at the beginning of the sporophyte in the prothallium of *Lastraea* as described by Farmer and Digby, combined with the above described discovery of a fusion of vegetative nuclei in so unexpected a place as the young sporange in *Aspidium falcatum* emphasizes still more strongly the fundamental significance of cell and nuclear fusion for the maintenance of the life cycle. In these cases, at least, when the normal sexual fusion has disappeared it is replaced by a substitute fusion either at the same or some other stage in the ontogeny. The facts already ascertained show the need of careful search for similar fusions in such plants as are now supposed to be continually apogamous.

This work was done under the supervision of Dr. R. A. Harper, to whom I am indebted for many valuable suggestions and criticisms.

Summary.

1. In *Adiantum,* the antherozoid mother cell has a dense nucleus containing a heavy chromatin network, and a large irregular blepharoplast in the cytoplasm. Cell and nucleus grow, the blepharoplast elongates into a band running half way around the nucleus and out into the cytoplasm. Nncleus and blepharoplast move to one side of the cell and elongate together into a spiral. As the elongation of the nucleus and blepharoplast progress, the cytoplasm shrinks in to form a close fitting sheath. The cilia are attached near the anterior end of the blepharoplast and tend at first to extend backward about the spiral.

2. In *Aspidium falcatum,* the antherozoids develop normally, are set free and swim about actively although they do not function.

3. The young apogamous sporophyte of *Aspidium falcatum* forms by a vegetative outgrowth from the median region of the prothallium. There is no vegetative fusion of nuclei at this stage.

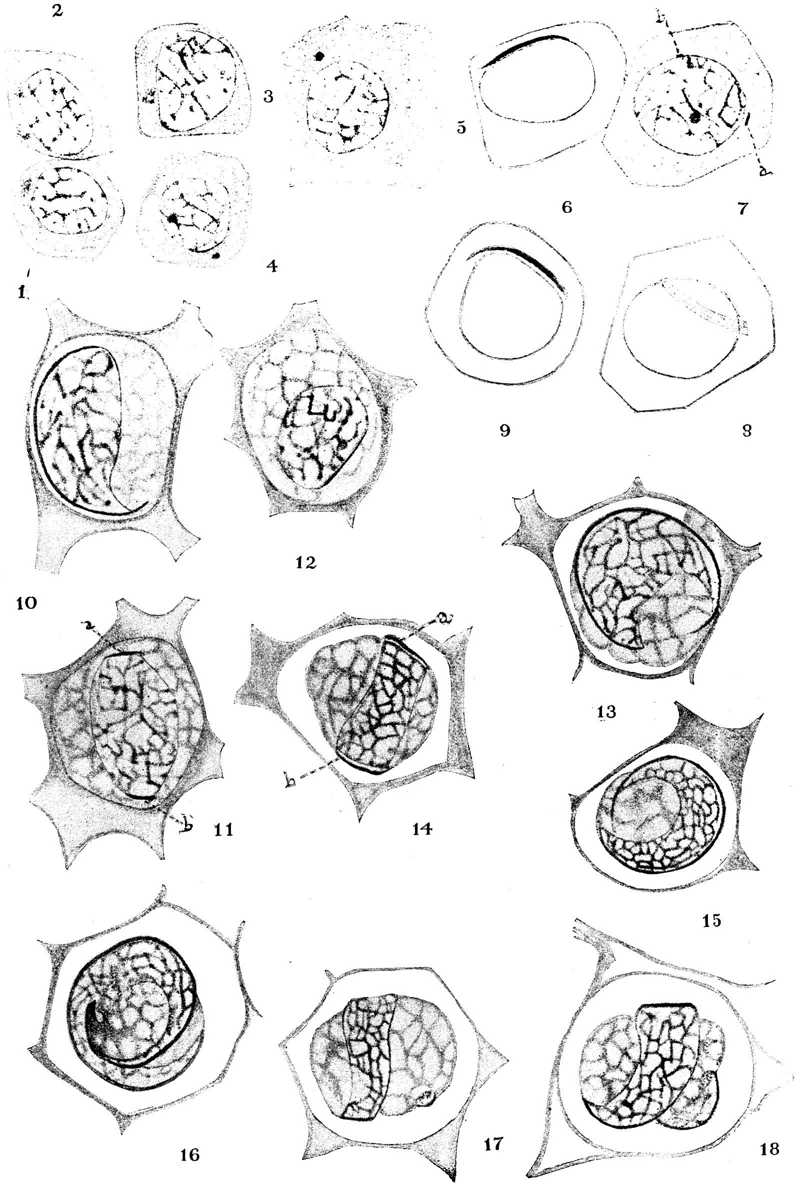
4. In the prothallium of *Aspidium falcatum* the nuclei have from sixty to sixty-five chromosomes.

5. In the nuclei of the young sporophyte sixty to sixty-five chromosomes are also present. This number is maintained unchanged throughout the growth of the sporophyte as is shown by counting in the divisions in the young sporange. The "haploid sporophyte" so formed is normal in all morphological respects.

6. Sixteen sporemother cells are formed as in other ferns. These sixteen cells fuse by pairs to form eight cells which then enter directly upon the reduction divisions.

7. Eight cells are found in the spore sac in synapsis, in post-synapsis and throughout the divisions.

8. A maximum of thirty-two spores is found in the mature spore-sac.



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Description of Plates.

The drawings were made with a camera lucida. Figures 1–25 are magnified 2250 diameters. Figures 26, 34, 35 and 42–61 are magnified 1950 diameters. Figures 27–33 and 36–37 are magnified 2700 diameters and 38–41 are 162 diameters.

The drawings are arranged in regular sequence on the plates except number 38 to 41 which are omitted in plate 3 and placed by themselves on plate 4.

Plate 1—*Adiantum Capillus-Veneris.*

1. Young antherid. Small. Nucleus containing heavy chromatin network—no nucleole. Blepharoplast large and irregular.

2. Same stage. Blepharoplast comma-shaped.

3. Same stage. Blepharoplast showing dense granules.

4. Later. Nucleole present. Blepharoplast more sharply bounded.

5. Later. Cell larger. Blepharoplast spherical, dense.

6. Blepharoplast elongated to a band parallel to the surface of the nucleus. Nucleus in center of cell.

7. Same stage. Nucleole present. Nuclear net more open. Blepharoplast cut twice at *a* and *b*.

8. Same cell as 7. Surface view of blepharoplast.

9. Same stage. Corresponds to 6. Space between blepharoplast and nuclear membrane.

10. Older. Cell rounded. Nucleus larger and at the side of the cell. Nucleus somewhat elongated, having formed an anterior beak. Blepharoplast seen in edge view. It extends along the whole convex outer surface of the nucleus and on into the cytoplasm at the anterior end.

11. Same stage. Longitudinal section at right angles to 10. Width of blepharoplast seen at two points—*a* and *b*.

12. Same stage. Median cross section showing the width of the blepharoplast.

13. Later. Nucleus forms three-fourths of a coil. Nucleus

here has its maximum volume. The anterior nuclear projection is longer and the posterior projection is forming.

14. The cytoplasm has contracted away from the wall. The middle half coil of the nucleus is shown. An edge view of the blepharoplast is seen at each end of nucleus.

15. The nucleus forms one coil. Nucleus is shrinking—the hollow of the coil is larger. Blepharoplast is shown along the convex side.

16. One and a half turns of the spiral. The anterior end of the coil is elongating. The cell shows a projection, the anterior end of the antherozoid.

17. Same stage. Side view. Narrow half coil near anterior end. Section through posterior tip of nucleus and blepharoplast.

18. About the same stage. Showing the broad posterior end of the nucleus. The narrow anterior end of the cell comes up from below on the right.

Plate 2.

Figures 19–25. *Adiantum Capillus-Veneris.*

Figures 26–31. *Aspidium falcatum.*

19. Two coil stage. Longitudinal section through cell. Posterior end upward. Nucleus has become condensed to a thick band. The cytoplasm is also contracting.

20. Same stage. Posterior portion of spiral shown. The cytoplasm has drawn back into the hollow of the posterior coil.

21. Two and a half coil stage. Chromatin homogeneous. *a.* Complete. *b.* Last half coil omitted to show retraction of the cytoplasm between last coil and the one next to it.

22. A single coil from the middle of the antherozoid. The cytoplasm now forms a heavy spiral.

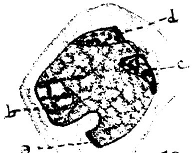
23. Later. Posterior coil and a half. Cytoplasm same.

24. Mature antherozoid. Cytoplasm forming posterior vesicle. Cilia conspicuous near anterior end.

25. Same. Some cilia directed forwards.

26. Division of central cell in antheridial sac. Spindle broad poled. No centrosome.

PLATE II



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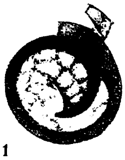

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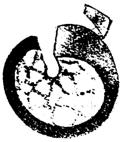

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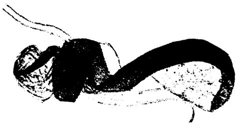

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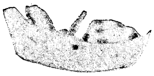

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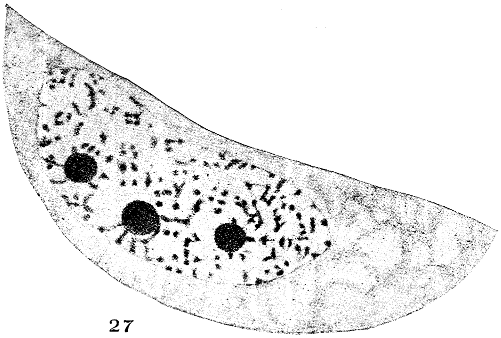

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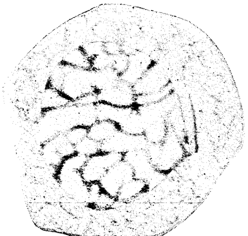

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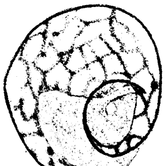

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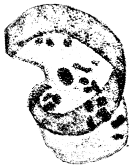

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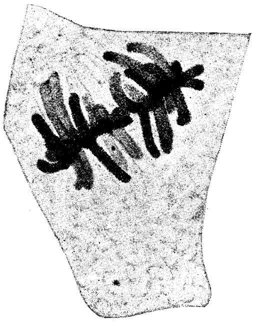

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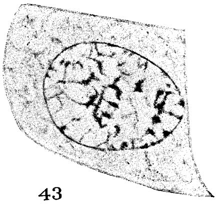

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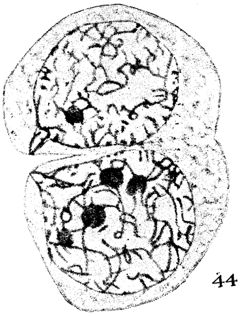

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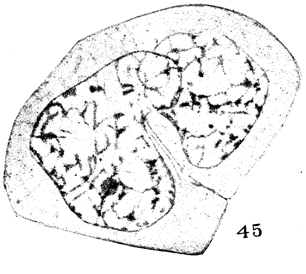

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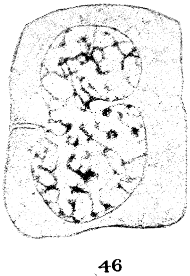

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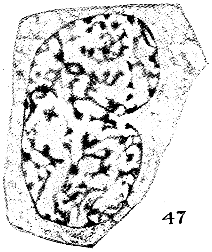

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27. Resting cell at eight cell stage. Nucleus contains large nucleoles and finely divided chromatin.

28. Antherid. Shows section through thick end of blepharoplast.

29. Same cell. Shows section of same blepharoplast at smaller end.

30. Same stage. Surface view of blepharoplast

31. Blepharoplast elongating. Cut obliquely. Projection on the nucleus below the blepharoplast.

Plate 3.

Figures 32–37. Development of antherzoid in *Aspidium falcatum.*

Figures 42–47. Nuclear fusion in spore-soc of *Aspidium falcatum.*

32. Blepharoplast elongated further. Nucleus touches middle region of blepharoplast.

33. Cross section, somewhat oblique, at the same stage, showing projection.

34. Shows long anterior beak.

35. Median cross section through nucleus. Blepharoplast on outer side. Anterior projection below.

36. One and a half coil stage. Anterior and posterior projections slender. Bulk of nucleus in the center. The cell shows a pointed projection containing the anterior end of the blepharoplast.

37. Posterior coil from nearly mature antherozoid. Starch grains in the cytoplasm.

42. One of the eight equatorial plate stages in a spore-sac.

43. One of the sixteen young spore mother cells. Cell small and angular.

44. Beginning of fusion of spore mother cells. Cytoplasm of the two cells fused at the right. Projection on each nucleus extends toward the other.

45. A broad lobe of one nucleus extends over to the other nucleus. Cytoplasm is still separate through more than half of the surface of contact between the two cells.

46. The two nuclear cavities are continuous.

47. Cytoplasm completely fused. The fusion nucleus kidney-shaped.

Plate 4.

Figures 38–41. *Aspidium falcatum.*

38. Median longitudinal section of young apogamous outgrowth.

39. Older sporophyte showing radial rows of cells. Vascular tissue present.

40. Still older. The boundary between gametophytic and sporophytic tissues obscure.

41. Sporophyte has developed the first leaf (l). The first root (r) is just breaking through. *s* is the newly organized stem apex.

Plate 5.

Aspidium falcatum.

48. Fusion nucleus kidney shaped. Cytoplasm is not fused on the concave side of the nucleus.

49. Cytoplasm fused. Nucleus still shows its double nature. Chromatin threads show pairing.

50. Furrow remains in the cytoplasm at the plane of fusion. Chromatin threads show pairing.

51. Fusion just completed.

52. Older. Cell rounded. Occasional paired threads.

53. Incomplete fusion. Synapsis. A dense tangle of threads in each nuclear cavity. Similar threads run from one mass to the other.

54. Early post-synapsis. Nucleus eccentric. The tangle of threads is loosening. Threads very long, uniform in diameter and can not be seen to be double.

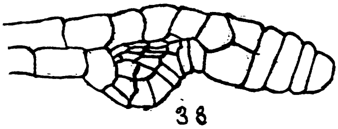
55. Nucleus central. Slender double threads.

56. Segmentation. Double chromosomes. Spirem thicker.

57. Equatorial plate of heterotypic division.

58. Equatorial plate of homoeotypic division.

59. Central spindles after the last division.



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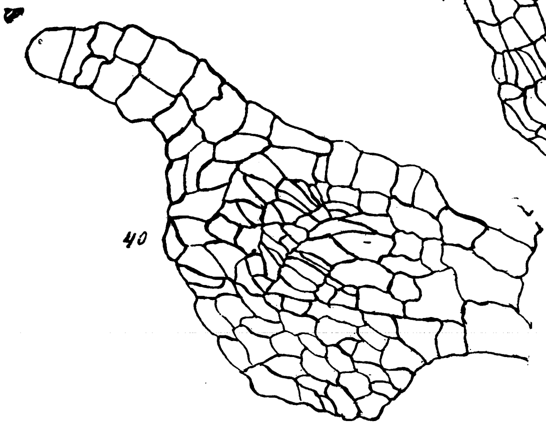

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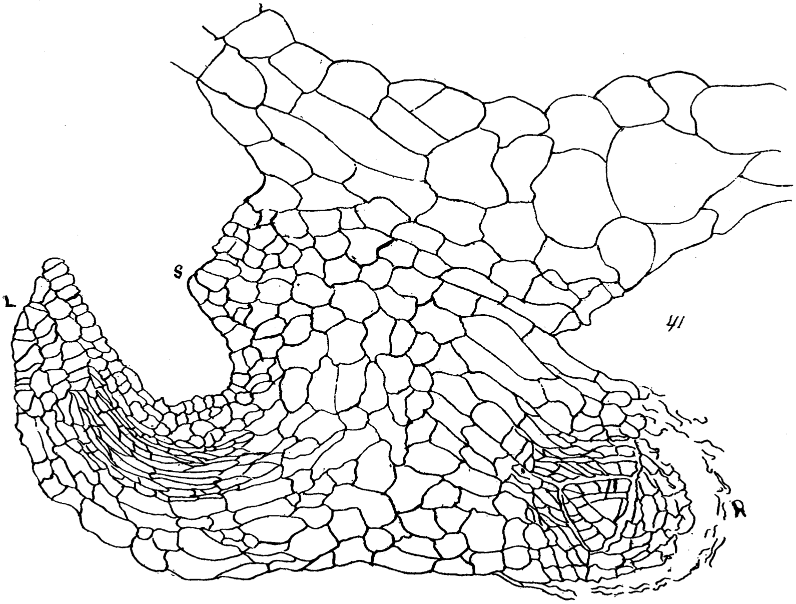

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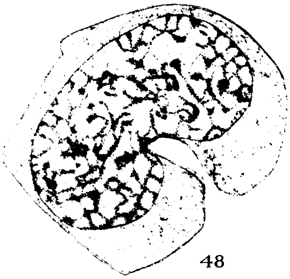
ALLEN, R. F.:—

ADIANTUM AND ASPIDIUM

COCKAYNE, BOSTON



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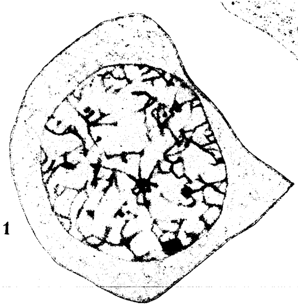

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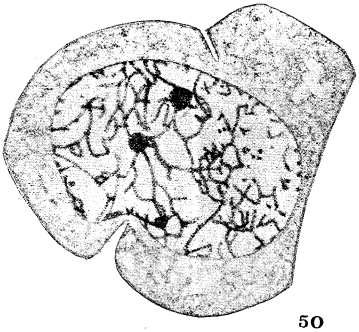

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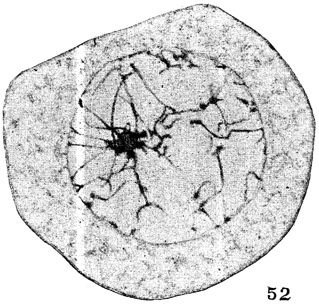

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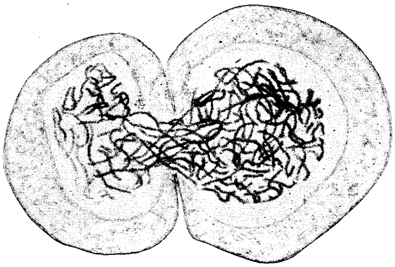

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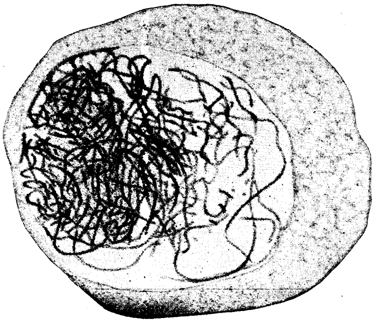

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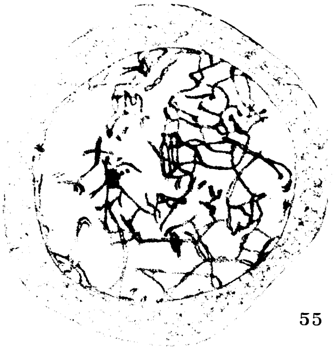
ALLEN, R. F.: —

ADIANTUM AND ASPIDIUM

COCKAYNE, BOSTON



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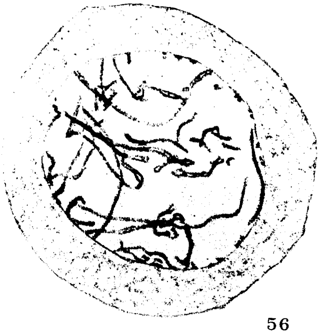

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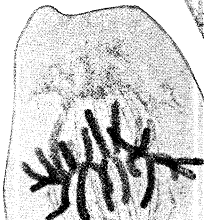

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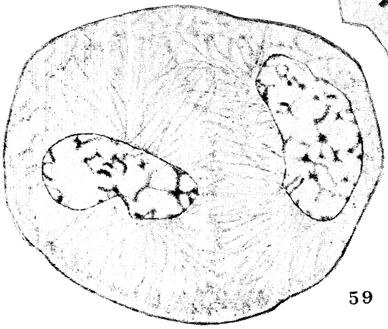

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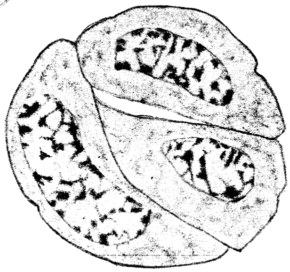

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ALLEN, R. F.:—

ADIANTUM AND ASPIDIUM

COCKAYNE, BOSTON

60. Section through tetrad of young spores.

61. Equatorial plate from young apogamous outgrowth near stem apex.

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University of Wisconsin,
December 23, 1909.

THE GRASSES OF MILWAUKEE COUNTY, WISCONSIN.

BY CHARLES T. AND BEIRNE B. BRUES.

Milwaukee County includes an area of about 180 square miles in the southeastern part of Wisconsin, and is adjacent to Lake Michigan along its entire eastern boundary. All of the county is covered by glacial drift and presents the moderately undulating surface characteristic of such drift deposits. Lake Michigan is about 580 feet above mean sea-level, and along the lake the shore rises in most places abruptly in the form of bluffs from 60 to 120 feet high. From these westward, the undulations assume a more or less parallel direction, defining slight ridges with a north and south trend, until in the western part of the county elevations of from 220 to 260 feet above the lake are attained. No large rivers traverse the county, although there are several streams of considerable size which empty their waters into the lake. The most important of these is the Milwaukee river which enters the county on the north, and due to the position of the previously mentioned ridges, follows a southward course only from one to three miles removed from the lake shore, finally turning abruptly eastward near the center of the city of Milwaukee where it reaches Lake Michigan. The next in size, known as the Menomonee river, enters the county at the northwest corner and flows south and east through Wauwatosa into the Milwaukee river about three-fourths of a mile from its mouth. In the southern part of the city of Milwaukee is a third stream, the Kinnickinnic river, scarcely over five miles in length, which enters the lake with the Milwaukee river; and finally in the extreme southeastern part of the county, another small stream, Oak creek, flows into the lake. There are no lakes within the county, except two or three very small ones in the southwestern part, although there is much marshy land scattered throughout the area. Most of this is not contiguous to the larger streams, and much of it is being drained for commercial reasons. A considerable part of the county is wooded, almost entirely by deciduous trees, although much land has been cleared for farming purposes. There are also small patches tending toward prairie formation in the southwestern part. One other small locality in the northern part of the county, along the Milwaukee river south of Whitefish Bay also supports several typical prairie forms like *Panicum virgatum* and *Spartina Michauxiana.* In the region to the south of Bay View, there are a few small open sandy places, and beaches of very limited extent occur sporadically along the shore of Lake Michigan. Railroads enter the county from the west, and these have afforded paths for the ingress of several typically western species which appear to have established themselves within the county.

From its geographical position, the region under consideration lies close to the northern limit of the upper austral zone as defined by Merriam,[1] and therefore, besides a predominance of the species characteristic of this zone, affords a congenial environment for many forms belonging to the adjoining more northern transition zone.

The present list is based on collections made during three seasons and a part of a fourth, and while quite likely not complete, undoubtedly includes the great majority of species occurring within the county. In all, 101 species and varieties are listed, which include a number of cultivated forms that occur regularly and actually form a part of the present flora. The grasses of Milwaukee county have been previously enumerated twice in connection with general lists of the flowering plants of this region, first by Wheeler[2] in a short paper which gives also considerable general matter pertaining to the county; and later by Russel,[3] but as little attention has hitherto been

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[1] Bull. U. S. Biol. Surv. No. 10. (1898.)

[2] Proc. Nat. Hist. Soc. Wisconsin, 1888, pp. 187–189.

[3] Bull. Wisconsin Nat. Hist. Soc. vol. 5, pp. 172–175. (1907.)

paid to the grasses of the county, these lists are necessarily incomplete with regard to this group.

With the exception of a single one, all the species which we have collected appear to be described, although the range of a number is somewhat extended by the present records. The following are the more important of these:

Panicum tennesseense Ashe.
Setaria verticillata (L.) Beauv.
Leersia oryzoides (L.) Sw.
Sporobolus compressus (Torr.) Kunth.
Calamagrostis Macouniana Vasey.
Sphenopholis nitida (Spreng.) Scrib.
Trisetum melicoides (Michx.) Vasey.
Cynosurus cristatus L.
Poa trivialis L.
Glyceria pallida (Torr.) Trin.
Bromus breviaristatus (Hook.) Buck.
Bromus ciliatus laeviglumis Scrib.
Agropyron Gmelini Scrib. & Smith.
Elymus Macounii Vasey.

The nomenclature and sequence used is essentially that adopted in Robinson and Fernald's seventh edition of Gray's manual (1907) with a few changes, particularly in respect to species listed by them as varieties or synonyms, although a number of species are included which do not appear in the manual. The references cited after each species are in nearly all cases only those which contain descriptive matter or figures. Thus, B. & B. Ill. Fl. refers to Britton and Brown's Illustrated Flora of the Northern United States, Vol. 1 (1896); B. & B. Man. to the later manual of these authors; Beal, 2 to the second volume of Beal's Grasses of North America (1896); Hack. trans. to the translation by Scribner (1896) of Hackel's article on Gramineae which appeared originally as a part of Engler and Prantl's "Die Natürlichen Pflantzenfamilien;" and Bull. Agrost. to the various bulletins of the division of Agrostology of the U. S. Department of Agriculture.

No species are included of which we have not seen authentic specimens from the county, but we have been able to add a few to those collected by ourselves from a study of specimens contained in the herbarium of the Milwaukee Public Museum.

On account of the draining of marshes, clearing of woodlands for farming purposes, and the building up of villages and towns, many of the grasses hitherto found are disappearing, and in their place the railroads and other sources are bringing in new species. This probably accounts for our own failure to find a number of the species previously recorded which have no doubt now disappeared entirely.

KEY TO THE SUBFAMILIES AND TRIBES.

1. Spikelets one, rarely two flowered; when two flowered the terminal flower perfect, the lower staminate or neuter; rhachilla articulated below the glumes; spikelets more or less dorsally compressed..........................Subfamily PANICOIDEAE. 2.
Spikelets one to many flowered, the rudimentary floret if present usually uppermost; rhachilla usually articulated above the glumes which are persistent on the pedicel or rhachis after the fall of the florets; when 2-many flowered a distinct internode of the rhachilla separates the florets and is articulated below them; spikelets more or less laterally compressed...Subfamily POACOIDEAE. 3.
2. Spikelets in pairs or threes on the usually articulate rhachis of a spike-like raceme; one sessile and fertile, the other pedicelled and perfect, staminate, neuter or rudimentary...Tribe ANDROPOGONEAE.
Spikelets all perfect, in racemes or panicles; glumes membranous, unequal; first usually small, sometimes obsolete; fertile lemma and palea indurated, firmly clasped together enclosing the free grain, almost always awnless...............Tribe PANICEAE.
3. Spikelets upon pedicels, in panicles, spike-like panicles, or racemes, not in rows..4.
Spikelets arranged in two rows......................................7.
4. Spikelets with but one perfect flower which is terminal except in *Ammophila* and certain species of *Calamagrostis*..............5.
Spikelets with two or more perfect flowers. (The lower one staminate in *Arrhenatherum*)..6.
5. Glumes one or none............................Tribe ORYZEAE.
Glumes four, (Only two in *Savastana*, but the pair above bear only staminate flowers) palea one-nerved.....Tribe PHALARIDEAE.
Glumes two, palea two-nerved.............Tribe AGROSTIDEAE.
6. Lemmas generally shorter than the glumes, usually with a bent awn on the back..........................Tribe AVENEAE.
Lemmas generally longer than the glumes, unawned or with a straight awn from the apex..............Tribe FESTUCEAE.
7. Spikelets forning a one-sided spike or raceme...Tribe CHLORIDEAE.
Spikelets in opposite rows forming an equilateral spike...Tribe HORDEAE.

KEY TO THE GENERA.

Subfamily PANICOIDEAE.

Tribe ANDROPOGONEAE.

Inflorescence composed of spike-like silky racemes...ANDROPOGON.
Infloresence paniculate; spikelets silky................SORGHUM.

Tribe PANICEAE.

1. Spikelets without an involucre of bristles.......................2.
   Spikelets with an involucre of bristles.........................4.
2. Lemma leathery, indurated, with hyaline margins, not inrolled; spikelets lanceolate, forming slender spike-like racemes......... .... DIGITARIA.
   Lemma chartaceous, indurated, margins inrolled, not hyaline.....3.
3. Glumes and lemmas awnless..........................PANICUM.
   Sterile lemma awned or pointed, inflorescence a panicle of crowded one-sided racemes............................ ECHINOCHLOA.
4. Involucre consisting of one to many persistent bristles; spikelets in a dense cylindrical spike-like panicle...........SETARIA.
   Involucre consisting of two spine-bearing valves forming a bur. .... CENCHRUS.

Subfamily POACOIDEAE..

Tribe ORYZEAE.

1. Spikelets unisexual, unlike in appearance...............ZIZANIA.
   Spikelets consisting of perfect flowers..................LEERSIA.

Tribe PHALARIDEAE.

1. Third and fourth glumes small and empty or rudimentary.......... .... PHALARIS.
   Third and fourth glumes enclosing staminate flowers............ .... HIEROCHLOE.

Tribe AGROSTIDEAE.

1. Lemma indurated at maturity.................................2.
   Lemma membranous ....3.
2. Spikelet awnless, no callus..........................MILIUM.
   Spikelets with a terminal awn, callus at the base..........STIPA.
3. Lemma awned from the tip or mucronate, closely infolding the grain...4.
   Lemma awnless or dorsally awned, loosely embracing the grain..5.
4. Rhachilla not prolonged behind the palea; lemma pointed or awned. .... MUHLENBERGIA.
   Rhachilla prolonged into a bristle behind the palea; lemma long awned.................................. BRACHYELYTRUM.
5. Glumes conspicuously compressed, carinate; spikelets in dense spike-like panicles..6.
   Glumes not conspicuously compressed; spikelets in open or narrow panicles..7.

6. Spikelets readily deciduous at maturity; lemma awned below the middle.......... ....ALOPECURUS.
   Spikelets not deciduous; lemma awnless...............PHLEUM.
7. Lemma one, rarely three-nerved, awnless; pericarp readily separating from the grain..........SPOROBOLUS.
   Lemma three to five-nerved, awned or awnless; pericarp adherent to the grain..........8.
8. Florets sessile; stamens three..........9.
   Florets plainly stalked; stamen one..........CINNA.
9. Rhachilla not prolonged behind the palea..........AGROSTIS.
   Rhachilla prolonged behind the palea into a bristle..........10.
10. Panicle loose or contracted, callus and prolonged rhachilla with long hairs..........CALAMAGROSTIS.
   Panicle dense, spike-like, callus and prolonged rhachilla with short hairs..........AMMOPHILA.

Tribe AVENEAE.

1. Spikelets articulated below the glumes, falling entire or with glumes and lowest floret together; florets usually awnless.... .........SPHENOPHOLIS.
   Articulation above the glumes; glumes not falling off with the spikelets; awns present..........2.
2. Awns dorsal dorsal, not flattened..........3.
   Awns from between the teeth of the bidentate apex of the lemma, flattened and twisted..........DANTHONIA.
3. Spikelets two to several-flowered, lowest floret perfect..........4.
   Spikelet two-flowered, lower floret staminate, long-awned, upper perfect and usually awnless..........ARRHENATHERUM.
4. Spikelets less than one centimeter long, grain free from the palea. ....5.
   Spikelet more than 1 cm. long; grain adherent to the palea. ....AVENA.
5. Lemma keeled, bidentate, awns arising from above the middle. ....TRISETUM.
   Lemma convex, awn arising at or below the middle.......... ....DESCHAMPSIA.

Tribe CHLORIDEAE.

Spikelets one flowered, all alike; rhachilla articulated below the narrow, unequal glumes..........SPARTINA.

Tribe FESTUCEAE.

1. Rhachilla with long hairs enveloping the lemma; tall aquatic grasses..........PHRAGMITES.
   Rhachilla and lemma naked or hairy; hairs much shorter than the lemma..........2.
2. Spikelets of two forms, the fertile 1-3 flowered, surrounded by the sterile consisting of many pectinate scales..........CYNOSURUS.
   Spikelets all alike..........3.
3. Lemmas 1-3 nerved, all with perfect flowers, or the upper staminate or empty..........ERAGROSTIS.
   Lemmas 5-many nerved, each with a perfect flower, or the uppermost sometimes aborted..........4.
4. Scales more or less strongly compressed or keeled..........5.
   Scales rounded on the back, at least below..........6.

5. Lemmas herbaceous, awn-pointed; spikelets collected in one-sided clusters...DACTYLIS.
   Lemmas scarious margined; rhachilla glabrous; lemmas mostly webby at the base..POA.
6. Stigmas placed at or near the apex of the ovary.................7.
   Stigmas plainly arising below the apex of the ovary; spikelets large, usually drooping; scales generally awned............BROMUS.
7. Lemma obtuse or subacute and scarious at the apex, usually toothed..8.
   Lemma acute, pointed or awned at the apex, not webby...FESTUCA.
8. Lemma plainly 5–7 nerved; styles present............GLYCERIA.

Tribe HORDEAE.

1. Spikelets solitary at each notch of the rhachis.................2.
   Spikelets 2-6 at each notch of the rhachis.......................5.
2. Lemma with its convex dorsal surface turned toward the rhachis. ....LOLIUM.
   Spikelets with their lateral aspect turned toward the rhachis.....3.
3. Lemma with a distinct callus which is limited by a furrow at the base, falling off at maturity with a single grain which is grown to the palea..AGROPYRON.
   Lemma without a callus, persistent at maturity; grain free......4.
4. Glumes subulate, 1-nerved..................................SECALE.
   Glumes ovate, 3-many nerved.........................TRITICUM.
5. Spikelets 1-flowered, or with only the vestige of a second...HORDEUM.
   Spikelets two-many flowered......................................6.
6. Glumes a little smaller than the lemmas (in one species the glumes more reduced in a part of the spikelets).............ELYMUS.
   Glumes very small or none..........................HYSTRIX

Andropogon L.

Andropogon furcatus Muhl. Willd. Sp. Pl. 4, 919. (1806) B. & B. Ill. Fl. p. 102; Beal, 2, p. 55 *(provincialis);* Bull. Agrost., 7, f. 14 *(provincialis);* Bull. Agrost., 20, f. 13; Gray, 7th, p. 94.

There is a single specimen of this species bearing the label "Bay View, Sept. 4" in the herbarium of the Milwaukee Public Museum. We have not found it in the county although it is quite abundant to the southward in Racine County.

Sorghum halepense (L.) Pers. Sp. Pl. 1047. (1753.) var. technicum. B. & B. Ill. Fl. p. 104; Hack. trans. p. 59; Gray, 7th, p. 95.

The occurrence of a single specimen of this species has been brought to our attention. It was found in a yard, within the City of Milwaukee, under conditions which suggest that it sprouted from seed dropped by passing birds.

Digitaria Scop.

1. Pedicels terete; first glume obsolete; spikelets scarcely over 2 mm. long...*D. humifusa.*
   Pedicels sharply angled; first glume present, minute; spikelets over 2 mm. long.....................................*D. sanguinalis.*

Digitaria humifusa Pers. Syn. 1; 85. (1805.) B. & B. Ill. Fl. p. 111 *(linearis);* Beal, 2, p. 110; *(lineare);* Bull. Agrost. 7, f. 37; Gray, 7th, p. 95.

There is a specimen of this species from Milwaukee County in the Milwaukee Public Museum.

Digitaria sanguinalis (L) Scop. Sp. Pl. 57. (1753.) B. & B. Ill. Fl. p. 111; Beal, 2, p. 110; Bull. Agrost. 17, f. 339; B. & B. Man. p. 77; Gray, 7th, p. 96.

This naturalized European species is extremely common in waste land within or close to the City of Milwaukee.

Panicum L.

1. Annuals ....2.
   Perennials ....3.
2. Panicle erect, spikelets not over 2½ mm. long..........*P. capillare.*
   Panicle drooping, spikelets 5 mm. long..............*P. miliaceum.*
3. Basal leaves similar to the culm leaves; not forming a winter rosette; culms usually simple, unbranched..........*P. virgatum.*
   Basal leaves usually distinctly different from the culm leaves, forming a winter rosette; culms usually much branched late in the season ....4.
4. Leaves about 3 cm. wide; spikelets 3½ mm. long......*P. latifolium.*
   Leaves less than 1 cm. wide; spikelets less than 2 mm. long..*P. tennesseense.*

Pancum capillare L. Sp. Pl: 58 (1753). B. & B. Ill. Fl., p. 123; Beal, 2, p. 129; Bull. Agrost., 17, f. 350; B. & B. Man., p. 81: Gray, 7th, p. 103.

Abundant along country roads and waste places throughout the county.

Panicum miliaceum L. Sp. Pl. 58 (1753). B. & B. Ill. Fl., p. 123; Beal, 2, p. 125; Hackel, trans., p. 76, f. 77; B. & B. Man., p. 82; Gray. 7th, p. 104.

Near the Rolling Mills in Bay View, July 19, 1908.

Panicum virgatum L. Sp. Pl. 59 (1753). B. & B. Ill. Fl., p. 122; Beal, 2, p. 123. Bull. Agrost., 7, f. 54. B. & B. Man., p. 82; Gray, 7th, p. 104.

Along the Milwaukee River near the Cement Mills.

Panicum tennesseense Ashe. B. & B Ill. Fl., p. 120 *(nitidum pars.);* B. & B. Man, p. 85 *(nitidum pars);* Gray, 7th, p. 110.

On dry, rocky hillsides along the Milwaukee River opposite the Cement Mills.

Panicum latifolium L. Sp. Pl. 58 (1753). B. & B. Ill. Fl., p. 117 *(macrocarpon);* Bull. Agrost., 17, f. 396; B. & B. Man., p. 88; *(macrocarpon);* Gray, 7th, p. 117.

On summit of lake bluffs at Bay View; Mitchell's Woods and New Coeln.

Echinochloa Beauv.

Echinochloa crusgalli (L.) Beauv. Sp. Pl. 56 (1753). B. & B. Ill. Fl., p. 113 *(Panicum);* Beal, 2, p. 119; Bull. Agrost. 7, f. 64; B. & B. Man., p. 78; Gray, 7th, p. 117.

Setaria Beauv.

1. Setae at base of each spikelet 5 or more..................*S. glauca.*
   Setae at base of each spikelet 1-3..............................2.
2. Setae downwardly barbed..............................*S. verticillata.*
   Setae upwardly barbed..3.
3. Spikelets 2 mm. long; panicle 2-8 cm. long, 1 cm. or less thick..*S. viridis.*
   Spikelets 3 mm. long; panicle 5-10 cm. long, about 1 cm. in diameter. ....*S. italica,* var. *germanica.*

Setaria glauca (L.) Beauv. Sp. Pl. 56 (1753). B. & B. Ill. Fl., p. 126 *(Ixophorus);* Beal, 2, p. 155 *(Chamaeraphis);* Bull. Agrost. 17, f. 401; Bull. Agrost. 21, p. 9 *(Chaetochloa);* B. & B. Man., p. 89 *(Chaetochloa);* Gray, 7th, p. 118.

Common in sandy and waste places. We have collected it at West County Line, New Coeln, Mitchell's Woods, McKinley Park and Bay View during the latter part of July and August.

Setaria verticillata (L.) Beauv. Sp. Pl. Ed. 2. 82 (1762). B. & B. Ill. Fl. p. 126 *(Ixophorus);* Beal, 2, p. 151 *(Chamaeraphis);* Bull. Agrost., 21, p. 16 *(Chaetochloa);* Bull Agrost., 17, fig. 403; B. & B. Man., p. 89 *(Chaetochloa);* Gray, 7th, p. 118.

Much less common than the preceding. It was collected near the rolling mills in Bay View and at the foot of the lake bluffs in McKinley Park.

Setaria viridis (L) Beauv. Sp. Pl. Ed. 2, 83 (1762). B. & B. Ill. Fl. p. 126 *(Ixophorus);* Beal, 2, p. 157 *(Chamaeraphis ;* Bull. Agrost. 21, p. 19 *(Chaetochloa);* Bull. Agrost, 7, fig. 65; B. & B. Man., p. 90 *(Chaetochloa);* Gray, 7th, p. 118.

Exceedingly common and widely distributed, although rare in the northern part of the county.

Setaria italica (L.) Beauv. var. germanica (Mill.) Richter. Mill. Gard. Dict. Ed. 8, p. 1. (1768.) Bull. Agrost 21, p. 21; Bull. Agrost 7, fig. 68; Gray, 7th, p. 119.

This species was found in McKinley Park where it had evidently escaped from cultivation.

Cenchrus L.

Cenchrus carolinianus L. Sp. Pl. 1050. (1753). B. & B. Ill. Fl. p. 127 *(tribuloides);* Beal, 2, p. 161 *(tribuloides);* Bull. Agrost, 7, fig. 69 *(tribuloides);* B. & B. Man., p. 90 *(tribuloides);* Gray 7th, p. 119.

Occurs quite commonly in sandy localities in Bay View and also along the lake beach of Jones Island, but apparantly never extends into the northern part of the county.

Zizania (Gronov.) L.

Zizania palustris L. Mant, 2, 295. (1771.) B. & B. Ill. Fl. p. 128 *(aquatica pars);* Beal, 2, p. 173 *(aquatica pars);* Bull. Agrost, 17, p. 113 *(aquatica pars);* Gray, 7th, p. 120; Hitchcock, Cont. U. S. Nat. Herb, 12, p. 124.

There are specimens in the herbarium of the Milwaukee Public Museum bearing the label "*Zizania aquatica*, Milwaukee and Clinton Roads," and it has been recorded as common in the Menomonee valley by Russel ('07) but is apparently becoming extinct in the county although very abundant along the inland lakes.

Leersia Sw.

1. Spikelets 2½–3 mm. long, panicle simple, its branches usually rigid. .... *L. virginica.*
Spikelets 4–5 mm. long, panicle diffusely branched, its branches usually lax.................................... *L. oryzoides.*

Leersia oryzoides (L.) Sw. Sp. Pl. 55. (1753). B. & B. Ill. Fl. p. 129 *(Homalocenchrus);* Beal, 2, p. 178 *(Homalocenchrus);* Bull. Agrost, 7, fig. 76 *(Homalocenchrus);* B. & B. Man., p. 91 *(Homalocenchrus);* Gray, 7th, p. 120.

Occurs along the Milwaukee river in the extreme northern part of the county.

Leersia virginica Willd. Sp. Pl. 1, 325. (1797.) B. & B. Ill. Fl. p. 129 *(Homalocenchrus);* Beal, 2, p. 178 *(Homalocenchrus);* Bull. Agrost, 7, fig. 77 *(Homalocenchrus);* B. & B. Man., p. 91 *(Homalocenchrus);* Gray, 7th, p. 120.

This species occurs in Mitchell's Woods, New Coeln, western part of Wauwatosa.

PHALARIS L.

1. Panicle very dense, spike-like; glumes wing-keeled...*P. canariensis.*
Panicle branched; glumes not winged on the back...*P. arundinacea.*

PHALARIS CANARIENSIS L. Sp. Pl. 54. (1753.) B. & B. Ill. Fl. p. 131; Beal, 2, p. 182; B. & B. Man. p. 92; Gray, 7th, p. 121.

Bay View, near the rolling mills.

PHALARIS ARUNDINACEA L. Sp. Pl. 55. (1753.) B. & B. Ill. Fl. p. 130; Beal, 2, p. 183; Bull. Agrost. 17, fig. 411; B. & B. Man., p. 92; Gray, 7th, p. 121.

Found on Howell's Road one and one-half miles north of New Coeln according to a specimen in the Milwaukee Public Museum. We have not seen it in the county although the variety *picta* is often seen in gardens.

HIEROCHLOE. (Gmel.) R. B.

HIEROCHLOE ODORATA (L.) Scribn. Sp. Pl. 1048. (1753.) B. & B. Ill. Fl. p. 132 *(Savastana);* Beal, 2, 186 *(Savastana);* Bull. Agrost. fig. 83 *(Savastana);* Gray, 7th, p. 122.

Occurs in the early spring in swampy places in Mitchell's woods and Wauwatosa.

MILIUM (Tourn.) L.

MILIUM EFFUSUM L. Sp. Pl. 61. (1753.) B. & B. Ill. Fl. p. 141; Beal, 2, p. 234; Bull. Agrost, 20 fig. 42; B. & B. Man., p. 98; Gray, 7th, p. 122.

Mitchell's woods, growing in damp, shady places.

ORYZOPSIS Michx.

ORYZOPSIS ASPERIFOLIA Michx. Fl. Bor. Am. 1, 51. (1803.) B. & B. Ill. Fl. p. 140; Beal, 2, p. 225; Bull. Agrost, 7, fig. 93; Gray, 7th, p. 123.

"East of New Coeln," represented in the herbarium of the Milwaukee Public Museum.

STIPA L.

STIPA SPARTEA Trin. Mem. Acad. St. Petersb. 6, 1:82. (1831.) B. & B. Ill. Fl. p. 139; Beal, 2, p. 215; Bull. Agrost. 7, fig. 89; Bull. Agrost. 20, p. 62; Gray, 7th, p. 124.

"Bay View?" There is a specimen in the herbarium of the Public Museum in Milwaukee bearing this label.

MUHLENBERGIA Schreb.

MUHLENBERGIA SYLVATICA Torr. Flor. U. S. 1, 87. (1824.) *Agrostis diffusa* Muhl. Gram. 64. (1817.) B. & B. Ill. Fl. p. 143; Beal, 2, p. 248; Bull. Agrost. 20, fig. 43; B. & B. Man., p. 100; Gray, 7th, p. 127.

Found growing along the shore of the Milwaukee River near the Cement mills and on the Menomonee River in Wauwatosa.

BRACHYELYTRUM Beauv.

BRACHYELYTRUM ERECTUM (Schreb.) Beauv. Agrost. 39. (1812.) *Muhlenbergia erecta* Schreb. Beschr. Gräs. 2, 139. (1772–9.) B. & B. Ill. Fl. p. 146; Beal, 2, p. 269; Bull. Agrost. 20, p. 66; Bull. Agrost. 7, fig. 112; Gray, 7th, p. 128.

Represented in the Milwaukee Public Museum by a specimen from "City limits, between Howell's and Chicago Road."

PHLEUM L.

PHLEUM PRATENSE L. Sp. Pl. 59. (1753.) B. & B. Ill. Fl. p. 147; Beal, 2, p. 276; Bull. Agrost, 20, fig. 47; B. & B. Man. p. 102; Gray, 7th, p. 128.

Common throughout the county in open places and along roads.

ALOPECURUS L.

ALOPECURUS GENICULATUS L. Sp. Pl. 60. (1753.) var. ARISTULATUS Torr. Fl. U. S. 1, 97. (1824.) B. & B. Ill. Fl. p. 149; Beal, 2, 280; Bull. Agrost. 7, fig. 115 *(fulvus)*; B. & B. Man. p. 103; Gray, 7th, p. 129.

Found in Bay View near the Rolling Mills and further southward, and also at Whitefish Bay.

SPOROBOLUS R. Br.

1. Pedicels equalling or shorter than the spikelets; first glume about half as long as the second.....................*S. cryptandrus*.
   Pedicels at least twice the length of the spikelets; first glume about equalling the second...........................*S. compressus*.

SPOROBOLUS CRYPTANDRUS (Torr.) Gray. Ann. Lyc. N. Y. 1, p. 151. (1824.) B. & B. Ill. Fl. p. 155; Beal, 2, p. 304; Bull. Agrost. 17, fig. 456; B. & B. Man. p. 106; Gray, 7th, p. 131.

Collected at Bay View near the Rolling Mills, and also along the lake shore in the same region.

SPOROBOLUS COMPRESSUS (Torr.) Kunth. Cat. Pl. N. Y. 91. (1819.) B. & B. Ill. Fl. p. 156; Beal, 2, p. 297; Bull. Agrost. 7, fig. 125; B. & B. Man. p. 107 *(torreyanus)*; Gray, 7th, p. 131.

Mitchell's woods.

AGROSTIS L.

AGROSTIS ALBA L. Sp. Pl. 63. (1753.) B. & B. Ill. Fl. p. 159; Beal, 2, p. 332; Bull. Agrost. 20, fig. 58; Bull. Agrost. 17, fig. 483; B. & B. Man. p. 109; Gray, 7th, p. 132.

Common throughout the county in open places both in high, dry situations and in swampy meadows.

CALAMAGROSTIS Adans.

1. Spikelets 2 mm. in length..........................*C. macouniana*.
   Spikelets 3-3.5 mm. in length.........................*C. canadensis*.

CALAMAGROSTIS MACOUNIANA Vasey. Coult. Bot. Gaz, 10, p. 297. (1885.) B. & B. Ill. Fl. p. 163; Beal, 2, p, 343; Bull. Agrost. 11, p. 31; Bull. Agrost. 17, fig. 492; B. & B. Man. p. 113.

Mitchell's woods and Milwaukee River near the Holton St. viaduct. The specimens apparently belong to the Missouri form of the species.

CALAMAGROSTIS CANADENSIS (Michx.) Beauv. Fl. Bor. Am. 1, p. 73. (1803.) B. & B. Ill. Fl. p. 163; Beal, 2, p. 350; Bull. Agrost. 11, p. 28; B. & B. Man p. 112; Gray, 7th, p. 135.

Common throughout the county in swampy meadows, often in dense patches.

AMMOPHILA Host.

AMMOPHILA ARENARIA (L.) Link. Sp. Pl. 82. (1753.) B. & B. Ill. Fl. p. 166; Beal, 2, p. 354; Bull. Agrost. 7, figs. 149 & 265; Bull. Agrost. 20, fig. 61; B. & B. Man. p. 114; Gray, 7th, p. 136.

Found along the sandy beach of Lake Michigan on Jones Island.

CINNA L.

CINNA ARUNDINACEA L. Sp. Pl. 5. (1753.) B. & B. Ill. Fl. p. 158; Beal, 2, p. 318; Bull. Agrost. 7, fig. 134; Bull. Agrost. 20, fig. 57; B. & B. Man. p. 108; Gray, 7th, p. 136.

Mitchell's woods and Wauwatosa, growing in wet, rather open woods.

SPHENOPHOLIS Scribn.

1. Panicle narrow, densely flowered; second glume as broad as long. .... *S. obtusata.*
   Panicle lax, more or less spreading, at least in flower ....2.
2. Glumes subequal; second broadly obovate, obtuse; florets obtuse, the second scabrous .... *S. nitida.*
   Glumes unequal; first shorter than the narrowly obovate second one; florets mostly acute, glabrous .... *S. pallens.*

SPHENOPHOLIS OBTUSATA (Michx.) Scribn. Fl. Bor. Am. 1, p. 62. (1803.) B. & B. Ill. Fl. p. 192 *(Eatonia);* Beal, 2 p. 492 *(Eatonia);* Bull. Agrost. 7, fig. 252 *(Eatonia);* B. & B. Man. p. 132 *(Eatonia);* Gray, 7th, p. 138.

Occurs in Wauwatosa.

SPHENOPHOLIS NITIDA (Spreng.) Scribn. Fl. Hal. Mant. 1, p. 22. (1807.) B. & B. Ill. Fl. p. 193 *(Eatonia);* Beal, 2, p. 492 *(Eatonia dudleyi);* Bull. Agrost. 7, fig. 253 *(Eatonia);* B. & B. Man. p. 132 *(Eatonia);* Gray, 7th, p. 138.

Whitefish Bay.

SPHENOPHOLIS PALLENS (Spreng.) Scribn. B. & B. Ill. Fl. p. 193 *(Eatonia pennsylvanica);* Beal, 2, p. 493 *(Eatonia pennsylvanica);* Bull. Agrost. 7, fig. 251 *(Eatonia pennsylvanica);* B. & B. Man. p. 132 *(Eatonia pennsylvanica);* Gray, 7th, p. 138.

Common in shady places in Mitchell's woods, along the banks of the Milwaukee River and at Wauwatosa.

DESCHAMPSIA Beauv.

DESCHAMPSIA CAEPITOSA (L.) Beauy.. Sp. Pl. 64. (1753.) B. & B. Ill. Fl. p. 169; Beal, 2, p. 368; B. & B. Man. p. 116; Gray, 7th, p. 140.

Milwaukee River, near the Cement Mills and below the Humboldt Street bridge.

AVENA (Tourn.) L.

1. Lemma with a long bent and twisted awn .... *A. fatua.*
   Lemma awnless or with a straight awn .... *A. sativa.*

AVENA FATUA L. Sp. Pl. 80. (1753.) B. & B. Ill. Fl. p. 173; Beal, 2, p. 384; Bull. Agrost. 17, fig. 499; Hack. trans. pp. 121–122; B. & B. Man. p. 118; Gray, 7th, p. 141.

Found west of Bay View, but is apparently rare in our region.

AVENA SATIVA L. Sp. Pl. 79. (1753.) Beal, 2, p. 385; Hack. trans., p. 121; Gray, 7th, p. 141.

Common everywhere along country roads and city streets.

ARRHENATHERUM Beauv.

ARRHENATHERUM ELATIUS (L.) Beauv. Sp. Pl. 79. (1753.) B. & B. Ill. Fl. p. 173; Beal, 2, p. 387; Bull. Agrost. 7, fig. 167; B. & B. Man. p. 118; Gray, 7th, p. 141.

Hawley Road in the Menomonee Valley in Wauwatosa and in the city near McKinley Park.

DANTHONIA DC.

DANTHONIA SPICATA (L.) Beauv. Sp. Pl. 80. (1753.) B. & B. Ill. Fl. p. 174; Beal, 2, p. 391; Bull. Agrost. 7, fig. 168; B. & B. Man., p. 119; Gray, 7th, p. 142.

Whitefish bay; locally common in open, dry places.

TRISETUM Pers.

TRISETUM MELICOIDES (Michx.) Vasey. var. MAJUS (Gray) Hitch. Ann. Bot. Soc. Canada, 1, p. 57. (1861.) B. & B. Ill. Fl. p. 210 *(Graphephorum);* Beal, 2, p. 562 *(Graphephorum);* B. & B. Man., p. 142 *(Graphephorum);* Gray, 7th, p. 139.

Whitefish Bay.

SPARTINA Schreb.

SPARTINA MICHAUXIANA Hitch. Cont. U. S. Nat. Herb. 12, p. 153. (1908.) B. & B. Ill. Fl. p. 175 *(cynosuroides);* Beal, 2, p. 397 *(cynosuroides);* Bull. Agrost. 9, p. 6 *(cynosuroides)* Bull. Agrost. 7, fig. 173 *(cynosuroides);* B. & B. Man., 120 *(cynosuroides);* Gray, 7th, p. 142.

Along the Milwaukee River to the northward from the Humboldt Street bridge and also in Bay View.

PHRAGMITES Trin.

PHRAGMITES COMMUNIS Trin. Fund. Agrost. 134. (1820.) B. & B. Ill. Fl. p. 184 *(P. Phragmites);* Beal, 2, p. 460 *(P. Phragmites);* Bull. Agrost. 7, fig. 229; B. & B. Man., p. 126 *(P. Phragmites);* Gray, 7th, p. 148.

Jones Island, growing in swampy places near slips tributary to the lake.

ERAGROSTIS Beauv.

1. Culms creeping; plants polygamous.................. *E. hypnoides.*
   Culms erect; ascendant or decumbent; flowers perfect...........2.
2. Spikelets 2–5 flowered, 2–3 mm. long.................. *E. capillaris.*
   Spikelets 5–many flowered, 5 mm. or more long..................3.
3. Spikelets not over 1.5 mm. wide.......................... *E. Purshii.*
   Spikelets 2–3 mm. wide..4.
4. Lemmas densely imbricated; rhachilla joints and base of lemma hidden.................................... *E. megastachya.*
   Lemmas rather loosely imbricated; rhachilla joints or base of lemma visible.. *E. minor.*

ERAGROSTIS HYPNOIDES (Lam.) BSP. Tabl. Encycl. 1, p. 185. (1791.) B. & B. Ill. Fl. p. 192; Beal, 2, p. 477; Bull. Agrost. 7, fig. 245; Gray, 7th, p. 150.

"Near Forest Home." Represented in the Milwaukee Public Museum.

ERAGROSTIS CAPILLARIS (L.) Nees. Sp. Pl. 68. (1753.) B. & B. Ill. Fl. p. 188; Beal, 2, p. 481; Bull. Agrost. 17, fig. 514; Gray. 7th, p. 150.

Represented by specimens in the Milwaukee Public Museum from New Coeln.

ERAGROSTIS PILOSA (L.) Beauv. var. PURSHII Schrad. Linnæa 12, p. 451. (1838.) B. & B. Ill. Fl. p. 189; Beal, 2, p. 487; Bull. Agrost. 17, fig. 241; B. & B. Man., p. 130; Gray, 7th, p. 150.

West of the Rolling Mills in Bay View.

ERAGROSTIS MEGASTACHYA (Koeler) Link. B. & B. Ill. Fl. p. 189 *(major);* Beal, 2, p. 486 *(major);* Bull. Agrost. 17, fig. 511 *(major);* Gray, 7th, p. 150.

Within the limits of the city of Milwaukee, growing in the courtyard of the Public Museum.

ERAGROSTIS MINOR Host. Fl. Austr. 1, p. 135. (1827.) B. & B. Ill. Fl. p. 189 *(E. Eragrostis)*; Beal, 2, p. 482 *(E. Eragrostis)*; B. & B. Man., p. 130 *(E. Eragrostis)*; Gray, 7th, p. 150.

Occurs in the Bay View region and also with the preceeding species.

DACTYLIS L.

DACTYLIS GLOMERATA L. Sp. Pl. 71. (1753.) B. & B. Ill. Fl. p. 200; Beal, 2, p. 523; Bull. Agrost. 7, fig. 269; Bull. Agrost. 20, fig. 114; B. & B. Man., p. 136; Gray, 7th, p. 154.

Common throughout the county and also in the city. One of our most conspicuous grasses, noticeable on account of the light color of its foliage.

CYNOSURUS L.

CYNOSURUS CRISTATUS L. Sp. Pl. 72. (1753.) B. & B. Ill. Fl. p. 200; Beal, 2, p. 524; Bull. Agrost. 7, fig. 255; Bull. Agrost. 20, fig. 115; B. & B. Man., p. 126; Gray, 7th, p. 154.

Growing on lawns near Lake Park, where it had doubtless been introduced with commercial grass seed.

POA L.

1. Annual...*P. annua.*
   Perennials..2.
2. Culms strongly flattened, oval in cross-section........*P. compressa.*
   Culms terete, or but slightly flattened............................3.
3. Panicle lax, the branches long, slender, naked half their length; usually widely spreading...4.
   Panicle branches rough, erect or ascending...........*P. nemoralis.*
4. Pedicels commonly shorter than the spikelets.......................5.
   Pedicels commonly equalling or longer than the spikelets...*P. debilis.*
5. Lemma obscurely nerved; spikelet about 4 mm. long.....*P. triflora.*
   Lemma prominently nerved..6.
6. Lateral nerves silky pubescent; spikelets 4–5 mm. long..*P. pratensis.*
   Lateral nerves naked; spikelets about 3 mm. long......*P. trivialis.*

POA ANNUA L. Sp. Pl. 68. (1753.) B. & B. Ill. Fl. p. 201; Beal, 2, p. 530; Bull. Agrost. 17, fig. 533; B. & B. Man., p. 138; Gray, 7th, p. 155.

Seen in the Lake Park region, but not common.

POA COMPRESSA L. Sp. Pl. 69. (1753.) B. & B. Ill. Fl. p. 202; Beal, p. 546; Bull. Agrost. 17, fig. 544; B. & B. Man., p. 141; Gray, 7th, p. 155.

Very common in all parts of the county, especially along roadsides and in waste ground.

POA NEMORALIS L. Sp. Pl. 69. (1753.) B. & B. Ill. Fl. p. 205; Beal, 2, p. 552; Bull. Agrost. 17, fig. 546; B. & B. Man. p. 139; Gray, 7th, p. 156.

Woods along the Milwaukee River, south of the Cement Mills.

POA DEBILIS Torr. Fl. N. Y. 2, p. 459. (1843.) B. & B. Ill. Fl. p. 206; Beal, 2, p. 539; Bull. Agrost. 17, fig. 535; B. & B. Man. p. 139; Gray, 7th, p. 157.

Found in the Menomonee Valley near the Sixth Street viaduct.

POA TRIFLORA Gilib. Exercit. Phyt. 2, p. 531. (1792.) B. & B. Ill. Fl. p. 205 *(flava)*; Beal, 2, p. 550 *(flava)*; B. & B. Man. p. 139 *(flava)*; Gray, 7th, p. 156.

Common and widely distributed throughout the county, growing in damp meadows and along streams.

POA PRATENSIS L. Sp. Pl. 67. (1753.) B. & B. Ill. Fl. p. 204; Beal, 2, p. 543; Bull. Agrost. 7, fig. 273; Bull. Agrost. 20, fig. 117; B. & B. Man., p. 139; Gray, 7th, p. 156.

Common, especially in dry, open fields, but not so abundant in the less thickly settled parts of the county.

POA TRIVIALIS L. Sp. Pl. 67. (1753.) B. & B. Ill. Fl. p. 204; Beal, 2, p. 541; Bull. Agrost. 17, fig. 539; B. & B. Man., p. 139; Gray, 7th, p. 157.

Whitefish bay.

GLYCERIA R. Br.

1. Spikelets 2–7 mm. long, ovate or oblong........................2.
   Spikelets 1.5–2 cm. long, compressed, cylindric, subsessile or nearly so..*G. septentrionalis.*
2. Panicle contracted, or narrow, 1.5–3 dm. long........*G. Torreyana.*
   Panicle open, lax; spikelets not over 2.5 mm. wide; lemmas strongly nerved ....3.
3. Second glume 1 mm. long..............................*G. nervata.*
   Second glume 2–2.5 mm. long....................................4.
4. Panicle ample, many flowered, 2 dm. or more long.......*G. grandis.*
   Panicle narrow, few flowered, rarely 1.5 dm. long........*G. pallida.*

GLYCERIA SEPTENTRIONALIS Hitchc. B. & B. Ill. Fl. p. 213. (*Panicularia fluitans*); Beal, 2, p. 569 (*P. fluitans*); Bull. Agrost. 7, fig. 285 (*P. fluitans*); B. & B. Man. p. 144 (*P. fluitans*); Gray, 7th, p. 159.

Lindwurm and New Coeln.

GLYCERIA TORREYANA (Spreng.) Hitch. B. & B. Ill. Fl. p. 212 (*Panicularia elongata*); Beal, 2, p. 565 (*P. elongata*); Bull. Agrost. 7, fig. 282 (*P. elongata*); B. & B. Man p. 143; Gray, 7th, p. 158.

Occurs in Mitchell's Woods.

GLYCERIA NERVATA (Willd.) Trin. Sp. Pl. 1, p. 389. (1797.) B. & B. Ill. Fl. p. 212 (*Panicularia*); Beal, 2, p. 567 (*Panicularia*); Bull. Agrost. 7, fig. 281 (*Panicularia*); B. & B. Man. p. 144 (*Panicularia*); Gray, 7th, p. 159.

Common throughout the county along streams and in swampy land.

GLYCERIA GRANDIS Wats. Gray, Man. ed. 6, p. 667 (1890). B. & B. Ill. Fl. p. 212 (*Panicularia Americana*); Beal, 2, p. 568 (*P. Americana*); Bull. Agrost. 7, figs. 280, 281 (*P. Americana*); B. & B. Man. p. 144 (*P. Americana*); Gray, 7th, p. 159.

Milwaukee River near the Humboldt Street bridge; Wauwatosa; swamp in Bay View, and swamp at head of ravine in Lake Park.

GLYCERIA PALLIDA (Torr.) Trin. Cat. N. Y. 91. (1819.) B. & B. Ill. Fl. p. 213 (*Panicularia*); Beal, 2, p. 566 (*Panicularia*); Bull. Agrost. 7, fig. 283 (*Panicularia*); B. & B. Man. p. 144 (*Panicularia*); Gray, 7th, p. 159.

Collected at Whitefish Bay.

PUCCINELLIA Parl.

PUCCINELLIA AIROIDES (Nutt.) Wats. & Coult. Gen. 1, p. 68. (1818.) B. & B. Ill. Fl. p. 215; B. & B. Man. p. 145; Gray, 7th, p. 160.

We have collected at Wauwatosa specimens which evidently belong to this species.

FESTUCA L.

1. Annuals; stamens usually one; leaves 2 mm. wide or less.......... ....*F. octoflora.*
   Perennials, stamens 3; leaves 4 mm. wide or more, flat..........2.
2. Lemmas 5–7 mm. long; spikelets 5–10 flowered..........*F. elatior.*
   Lemmas 4 mm. long or less; spikelets 3–6 flowered......*F. nutans.*

Festuca octoflora Walt. Fl. Car. 81. (1788.) B. & B. Ill. Fl. p. 216; Beal, 2, p. 586; Bull. Agrost. 17, fig. 580: B. & B. Man. p. 146; Gray, 7th, p. 161.

Whitefish Bay.

Festuca elatior L. Sp. Pl. 75. (1753.) B. & B. Ill. Fl. p. 217; Beal, 2, p. 591; Bull. Agrost. 20, fig. 124. B. & B. Man. p. 147; Gray, 7th, p. 162.

Common everywhere in open places.

Festuca nutans Spreng. Fl. Hal. Mant. 34. (1807.) B. & B. Ill. Fl. p. 218; Beal, 2, p. 588; B. & B. Man. p. 147; Gray, 7th, p. 162.

Western part of Bay View.

Bromus L.

1. Lemma with pubescence about equally distributed over the dorsal surface ....2.
   Lemma with pubescence conspicuously unevenly distributed over the dorsal surface, longest and densest on the margins or base or both..5.
   Lemma smooth or scabrous..7.
2. Panicle narrow, lower branches not over 10 cm. long..*B. breviaristatus.*
   Panicle rather broad, some of the lower branches over 10 cm. long..3.
3. Lower glume more or less distinctly 3 nerved...........*B. Kalmii.*
   Lower glume 1 nerved, acute..4.
4. Sheaths densely soft, pilose pubescent, longer than the internodes. ....*B. incanus.*
   Sheaths sparsely pilose pubescent, or nearly smooth, shorter than the internodes ....*B. purgans.*
5. Panicle rather broad, loose and drooping; awn less than 3 mm. long or absent..6.
   Panicle rather narrow and erect, or not conspicuously drooping; awn 3–5 mm. long..*B. ciliatus.*
6. Lower glume 1 nerved; spikelets 2–2.5 cm. long.........*B. inermis.*
   Lower glume 3 nerved; spikelets 3–4.5 cm. long......*B. inopinatus.*
7. Margins of lemmas strongly involute in fruit..........*B. secalinus.*
   Perennials, sheaths usually pubescent; lemmas not involute in fruit................................*B. ciliatus lœviglumis.*

Bromus breviaristatus (Hook.) Buckl. Fl. Bor. Am. 2, p. 253. (1840.) B. & B. Ill. Fl. p. 223; Beal, 2, p. 623; Bull. Agrost, 23, p. 53 *(marginatus)*; B. & B. Man. p. 151.

In Wauwatosa and along the Milwaukee River near the Humboldt Street bridge. These records extend the eastern range of the species.

Bromus Kalmii Gray. Man. ed. 1, p. 600. (1848.) B. & B. Ill. Fl. p. 221; Beal, 2, p. 624; Bull. Agrost. 17, fig. 584; Bull. Agrost. 23, p. 34; B. & B. Man. p. 150: Gray, 7th, p. 164.

Whitefish Bay, Fox Point, and along the Milwaukee River near the Humboldt Street bridge.

Bromus incanus (Shear) Hitch. Bull. Agrost. 23, p. 41. (1900.) Gray, 7th, p. 164.

Mitchell's Woods and Wauwatosa.

Bromus purgans L. Sp. Pl. 76. (1753.) B. & B. Ill. Fl. p. 219 *(ciliatus pars)*; Beal, 2, p. 619 *(ciliatus pars)*; Bull. Agrost. 23, p. 39; B. & B. Man. p. 149 *(ciliatus pars)*; Gray, p. 164.

Fox Point, at the Cement Mills.

Bromus inermis Leyss. Fl. Hal. 16. (1761.) Beal, 2, p. 612; Bull. Agrost. 7, fig. 290; Bull. Agrost. 23, p. 47; B. & B. Man. p. 149.

Menomonee Valley, along the railroad tracks near 34th street, where it has been undoubtedly introduced from the west.

BROMUS INOPINATUS sp. nov.

An erect perennial, 9.5–10.5 dm. high. Culms smooth, slightly pubescent just below the nodes; stout at the base. Sheaths smooth, ligule 1 mm. or less. Leaves linear lanceolate, 5–10 mm. wide, 2–2.5 dm. long; smooth above, and slightly scabrous below. Panicle dense, rather diffuse, spreading; 1.7–2.5 dm. long; lower branches 10–14 cm. long. Spikelets 3–4.5 cm. long, mostly 3.5–4; subcylindrical, 3 mm. wide and but slightly flattened before flowering; later spreading and flattened, 6–10 mm. wide; florets distinctly separating. Spikelets 8–14 flowered, the usual number being 12. First glume 7–8 mm. long, distinctly 3 nerved; lateral nerves nearly reaching the apex; subacute, puberulent, the median nerve delicately hispid. Second glume 9–10 mm. long, 3 nerved; subacute and not much broader than the first; faintly hispid on the keel. Lemmas 12–14 mm. long; those near the apex of the spikelets becoming shorter; shining, with short, very sparse pubescence near the base, extending almost to the middle on the lateral nerves; 7 nerved. Awn 1–2 mm. long, sometimes obsolete; palea nearly equalling the lemma, faintly pubescent along the nerves. Joints of the rhachilla covered with thick silky pubescence.

Described from specimens collected within the limits of the city of Milwaukee, in the Lake Park region. Some were found growing at the foot of the bluffs along the shore of Lake Michigan near McKinley Park, and others nearby in an open field at the head of the bluffs.

In general appearance this form resembles *inermis* Leyss. very closely, but in characters might be confounded most easily with *pumpellianus* Scribner. It differs from this form, however, by the almost entire absence of pubescence on the lemmas; narrower, longer, more flowered spikelets; distinctly 3 nerved lower glume; and longer leaves, which are scabrous below; also by its larger panicles, with longer lower branches. From *inermis* it may be distinguished by its much larger size, longer spikelets, large number of florets, and 3 nerved lower glume. On close examination of the specimens of the genus *Bromus* contained in the Gray Herbarium at Cambridge, no exotic forms were found which resemble the present species. There are several specimens of *pumpellianus* from the western United States in the same collection of quite similar habitus, differing structurally, however, as previously set forth.

BROMUS CILIATUS L. Sp. Pl. 76. (1753.) B. & B. Ill. Fl. p. 219; Beal, 2 p. 618; Bull. Agrost. 17, fig. 583; Bull. Agrost. 23, p. 31; B. & B. Man. p. 149; Gray, 7th, p. 164.

Menomonee Valley in Wauwatosa; Lake Park Region, and at New Coeln.

BROMUS CILIATUS var. LAEVIGLUMIS Scrib. Bull. Agrost. 23, p. 32. (1900.)

Wauwatosa, and Milwaukee River near the Port Washington Road.

BROMUS SECALINUS L. Sp. Pl. 76. (1753.) B. & B. Ill. Fl. p. 222; Beal, 2, p. 625; Bull. Agrost. 7, fig. 291; Bull. Agrost. 23, p. 16; B. & B. Man. p. 150; Gray, 7th, p. 163.

City Street near McKinley Park; New Coeln; southwestern Bay View, and also sparingly in other localities.

LOLIUM L.

1. First glume shorter than the spikelet....................*L. perenne.*
First glume equalling or extending beyond the lemmas.............
....*L. temulentum.*

LOLIUM PERENNE L. Sp. Pl. (1753.) B. & B. Ill. Fl. p. 225; Beal, 2, p. 629; Bull. Agrost. 7, fig. 295; B. & B. Man. p. 152; Gray, 7th, p. 165.

Along lake shore bluffs, Lake Park region, and generally in county near farms.

Lolium temulentum L. Sp. Pl. 83. (1753.) B. & B. Ill. Fl. p. 225; Beal, 2, p. 630; Bull. Agrost. 17, fig. 587; B. & B. Man. p. 152; Gray, 7th, p. 165.

Menomonee Valley near sixth street viaduct.

Agropyron J. Gaertn.

1. Culms tufted, no creeping rootstocks............................2.
   Culms solitary or few, erect from creeping rootstocks.............4.
2. Basal culm leaves shorter than the upper..............*A. Gmelini.*
   Basal culm leaves longer than the upper..........................3.
3. Lemmas long-awned, the awn about twice the length of the lemma.. ....*A. caninum.*
   Lemmas awnless, or short awned...................*A. tenerum.*
4. Spikelets compressed, ovate, acute, diverging............*A. Smithii.*
   Spikelets narrow, subcompressed, or subcylindrical, acute or obtuse.. ....5.
5. Leaves scabrous on both sides; joints of rhachilla minutely scabrous ....*A. pseudorepens.*
   Leaves glabrous below, scabrous or sparsely hirsute on the nerves above; joints of rhachilla smooth...........................6.
6. Leaves sparsely hirsute along the nerves above; spike more elongate...*A. repens.*
   Leaves hirsute above; spike crowded..........*A. repens* var. *agreste.*

Agropyron Gmelini Scrib. & Smith. Bull. Agrost. 4, p. 30. (1897.) Bull. Agrost. 17, fig. 601: B. & B. Man. p. 154.

Wauwatosa, in places along the railroad tracks in the Menomonee Valley.

Agropyron caninum (L.) Beauv. Sp. Pl. 86. (1753.) B. & B. Ill. Fl. p. 228; Bull. Agrost. 4, p. 29; Beal, 2, p. 639; B. & B. Man. p. 153; Gray, 7th, p. 167.

Western part of Bay View; Whitefish Bay; Milwaukee River near Humboldt Street bridge.

Agropyron tenerum Vasey. Coult. Bot. Gaz. 10, p. 258. (1885.) B. & B. Ill. Fl. p. 227; Beal, 2, p. 637; Bull. Agrost. 17, fig. 593; B. & B. Man. p. 153; Gray, 7th, p. 167.

Bay View.

Agropyron Smithii Ryd. Mem. N. Y. Bot. Gard. 1, p. 60. (1900.) Bull. Agrost. 4, p. 33 *(spicatum)*; Bull. Agrost. 17, fig. 594 *(occidentale)*; B. & B. Man. p. 154 *(spicatum)*; Gray, 7th, p. 166.

In most parts of the county. Specimens from the Menomonee Valley at 30th street are of the form with two spikelets at each node of the rhachis.

Agropyron pseudorepens Scrib. & Smith. Bull. Agrost. 4, p. 34. (1897). Gray, 7th, p. 167 *(tenerum pars).*

Menomonee Valley at 30th street, and near the Rolling Mills in Bay View.

Agropyron repens (L.) Beauv. Sp. Pl. 86. (1753.) B. & B. Ill. Fl. p. 226; Bull. Agrost. 4, p. 35; Beal, 2, p. 636; Bull. Agrost. 7, fig. 298; B. & B. Man. p. 154; Gray, 7th, p. 166.

Common everywhere except in wooded areas, and escaping in many places from cultivated fields.

Agropyron repens var. agreste Anders. Bull. Agrost. 4, p. 36; Bull. Agrost. 7, fig. 298.

Lake Park region and in Bay View.

Triticum L.

1. Spikes long, more or less loose, somewhat dorsally compressed...... ....*T. sativum vulgare.*
   Spikes short, dense, distinctly 4-sided......*T. sativum compactum.*

Triticum sativum vulgare Vill. Hist. Pl. Dauph. 2, p. 153. Hack., trans. p. 183; Beal, 2, p. 642.

Escaped from cultivation in various places. Both the awned and awnless forms occur.

Triticum sativum compactum Host. Hack., trans. p. 184.

This has also escaped from cultivation in various parts of the county.

HORDEUM L.

Secale cereale L. Sp. Pl. 84. (1753.) Hack., trans. p. 177; Beal, 2, p. 640.

Occasionally found throughout the county.

HORDEUM L.

1. Only the middle spikelet of each cluster of three fertile; spike about as wide as long, readily separating at maturity......*H. jubatum.*
   All spikelets fertile, therefore six rows of fruit.................2.
2. All six rows of fruit distinctly separated....*H. sativum hexastichon.*
   Only the middle rows distinctly separated, the side rows overlapping ....3.
3. Lemma awned ....*H. sativum vulgare.*
   Lemmas each with a peculiar 3-branched horn........................ ....*H. sativum vulgare,* form *trifurcatum.*

Hordeum jubatum L. Sp. Pl. 85. (1753). B. & B. Ill. Fl. p. 229; Beal, 2, p. 644; Bull. Agrost. 17, p. 603; B. & B. Man. p. 165; Gray, 7th, p. 167.

In open fields and waste places, especially in the southern part of the county.

Hordeum sativum hexastichon L. Sp. Pl. 85. (1753.) Hack., trans. p. 189; Beal, 2, p. 647.

Occurs rarely, escaped from cultivation.

Hordeum sativum vulgare L. Sp. Pl. 85. (1753.) Hack., trans. p. 190.

Escaped from cultivation in various places throughout the county.

Hordeum sativum vulgare form **trifurcatum** Jacq. Bull. Bot. Soc. France, 1:187. (1854.) Hack., trans. p. 190.

West of the Rolling Mills in Bay View.

ELYMUS L.

1. Glumes as long as the florets, or nearly so..........................2.
   Glumes reduced to short awns...7.
2. Spikelets spreading ....3.
   Spikelets appressed to the rhachis...................................6.
3. Glumes awl-shaped.....................................*E. striatus.*
   Glumes narrowly lanceolate...4.
4. Glumes indurated below, spike erect.................*E. virginicus.*
   Glumes not indurated below, spike nodding............................5.
5. Lemma hirsute ....*E. canadensis.*
   Lema minutely scabrous............................*E. brachystachys.*
6. Spikelets in pairs...................................*E. glaucus.*
   Spikelets mostly solitary...........................*E. Macounii.*
7. Awn-like glumes of varying size in each spike....*E. diversiglumis.*

Elymus striatus Willd. Sp. Pl. 1, p. 470. 1797). B. & B. Ill. Fl. p. 230; Beal, 2, p. 655; Bul. Agrost. 17, fig. 611; B. & B. Man. p. 156; Gray, 7th, p. 169.

Wauwatosa, Mitchell"s Woods and Menomonee Valley at 30th Street.

ELYMUS VIRGINICUS L. Sp. Pl. 84. (1753). B. & B. Ill. Fl. p. 230; Beal, 2, p. 653; Bull. Agrost. 17, fig. 612; B. & B. Man. p. 166; Gray, 7th, p. 169.

Menomonee Valley in Wauwatosa, and shore of Lake Michigan near Lake Park.

ELYMUS CANADENSIS L. Sp. Pl. 83. (1753). B. & B. Ill. Fl. p. 231; p.169.

Quite common, especially along the lake shore and the Milwaukee River.

ELYMUS BRACHYSTACHYS Scrib. & Ball. Bull. Agrost. 24, p. 47. B. & B. Man. p. 1064; Gray, 7th, p. 169.

Menomonee Valley in Wauwatosa, and in Mitchell's Woods.

ELYMUS GLAUCUS Buckl. Proc. Acad. Philadelphia, p. 99. (1862). B. & B. Ill. Fl. p. 231; B. & B. Man. p. 157; Gray, 7th, p. 170.

Mitchell's Woods.

ELYMUS MACOUNII Vasey. Bull. Torr. Club, 13, p. 119. (1886). B. B. Ill. Fl. p. 231; Beal, 2, p. 653; Bull. Agrost. 17, fig. 614; B. & B. Man. p. 157; Gray, 7th, p. 170.

Bay View.

ELYMUS DIVERSIGLUMIS Scrib. & Ball. Bull. Agrost. 24, p. 48. (1900). Gray, 7th, p. 170.

Ravine in Lake Park; South Milwaukee, and Mitchell's Woods.

HYSTRIX Moench.

HYSTRIX PATULA Moench. Meth. 295. (1794). B. & B. Ill. Fl. p. 233. *(H. Hystrix)*; Beal, 2, p. 656 *(Asprella hystrix* ; Bull. Agrost. 7, fig. 302; B. & B. Man. p. 158 *(H. Hystrix)*; Gray, 7th, p. 171.

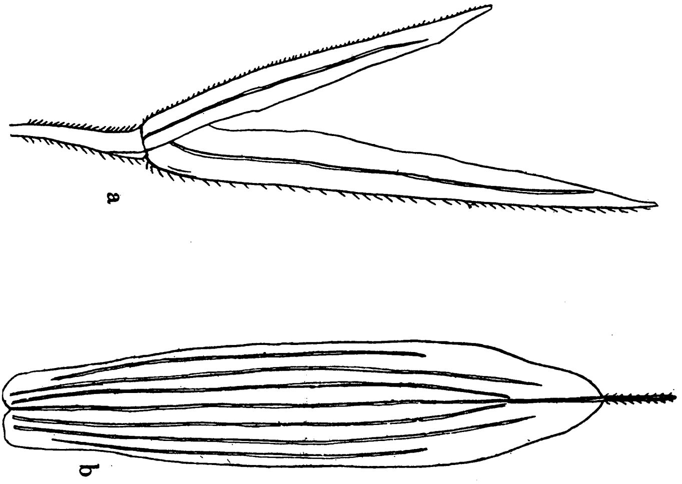
Common in most parts of the country.

APPENDIX.

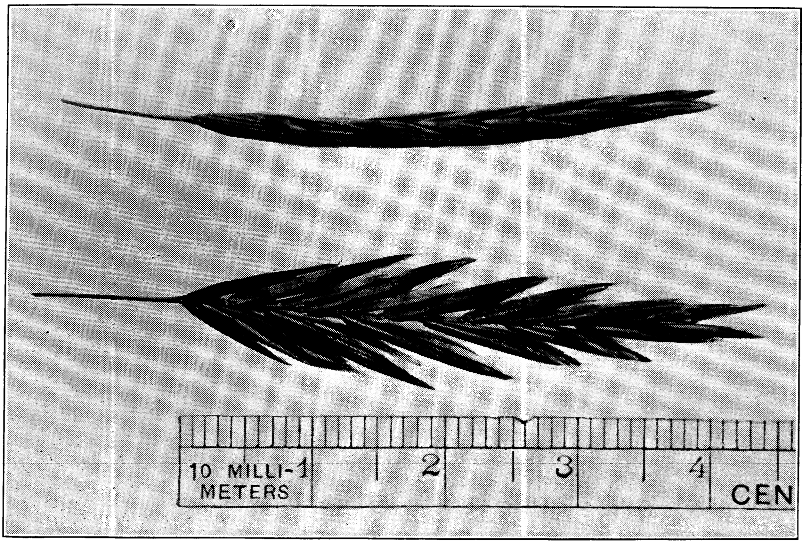
The following additional species have been listed by Russel (Bull. Wisconsin Natural History Soc. Vol. 5, pp. 172–175 (1907), but we have neither collected them, nor are they represented in the herbarium of the Milwaukee Public Museum by specimens from Milwaukee County.

Andropogon scoparius Michx.
Panicum dichotomum L.
Muhlenbergia mexicana (L.) Trin.
Agrostis perennans (Walt.) Tuckerm.
Agrostis hyemalis (Walt) BSP.
Melica striata (Michx.) Hitch.
Poa glauca Vahl.
Festuca ovina, var, *duriuscula* (L.) Koch.
Bromus hordeaceus L.
Elymus arenarius L.

Jamaica Plain, Mass.
January 30, 1910.

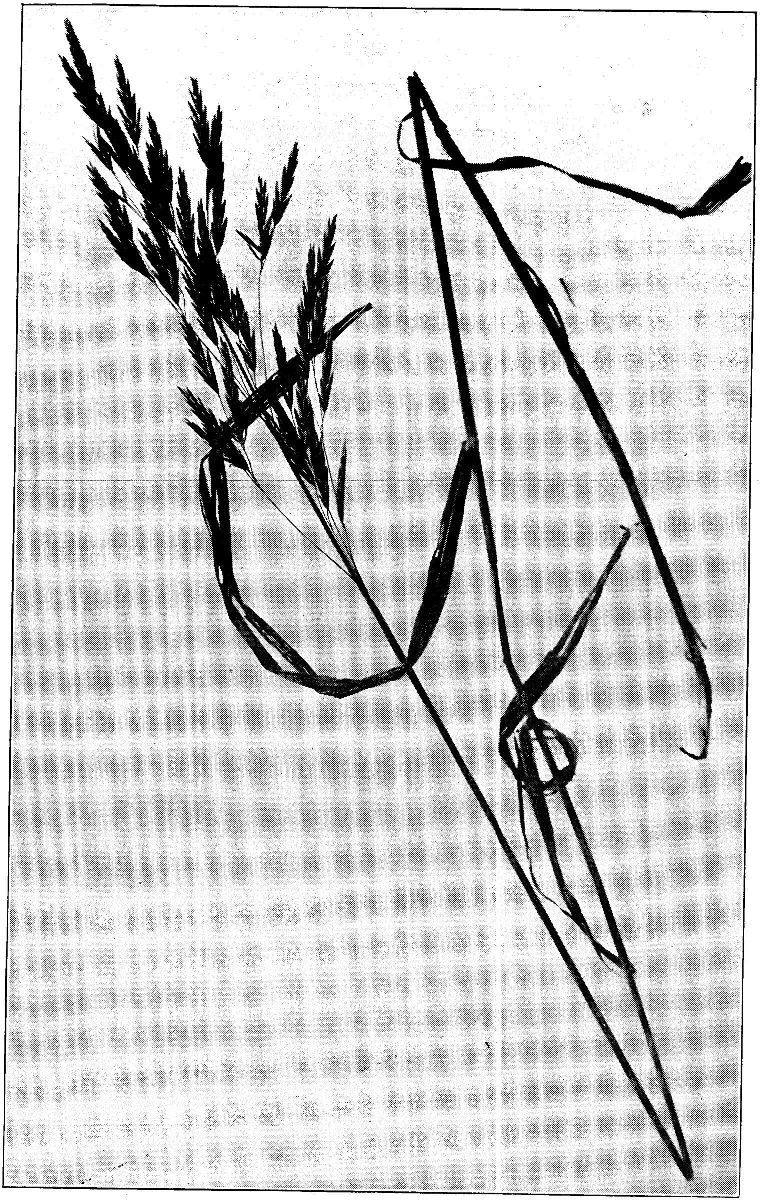


A. GLUMES; B LEMMA



SPIKELETS BEFORE AND AFTER FLOWERING

BROMUS INOPINATUS SP. NOV.



BROMUS INOPINATUS SP. NOV.

PLATE IX

BROMUS INOPINATUS SP. NOV., NATURAL GROWTH