

Sex Determination in *Mnium hornum*.

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With Plate XX.

THE method of sex determination in dioecious plants has recently been the subject of a number of investigations, and, amongst these, those published by Él. and Ém. Marchal on the Apospory and Sexuality of the Mosses have created very considerable interest.

In a paper which appeared in 1906 (9), these investigators showed experimentally that, in the case of dioecious mosses, the spores produced in a single sporogonium are heterogeneous as regards their sexual characters; the spores are unisexual, the male giving rise to protonemata which bear exclusively male axes while the female produce protonemata which develop female axes only. They also proved that the protonema obtained vegetatively from the gametophyte always retains the sex of the parent plant. In protonemata produced either from spores or vegetatively from the gametophyte the sex is constant, and is not affected by external conditions.

In 1907 (10), a further paper was published dealing with the sexual characters of protonemata produced aposporously from the sporophyte of dioecious mosses. It was discovered that such protonemata always gave rise to a certain proportion of hermaphrodite axes, and it was presumed that no meiotic phase had taken place prior to the production of these individuals. The writer therefore concluded that, in the normal life-history of these mosses, the sex of the spores is determined at the reduction division immediately preceding their formation.

A third contribution appeared in 1909 (11), and in this the writers showed that, although the plants produced aposporously develop sexual organs, these are sterile and no sporogonia are produced. In this paper the discovery of organs of mixed sex is recorded in plants of *Bryum caespitium* and *Mnium hornum* which had been produced aposporously. The authors emphasized the fact that up to that time no mixed organs had ever been described in dioecious mosses; Hy (7) had previously observed similar organs in *Atrichum undulatum* and Holferty (6) in *Mnium cuspidatum*, but both these species are monoecious.

Organs of mixed sex had, however, been noted in two dioecious mosses previously to 1909. Lindberg in 1879 (8) described and figured such organs in *Brachythecium erythrorrhizon*. This moss is described as monoecious in the 'Bryologia Europaea' (4, 14), but Lindberg, after the examination of numerous specimens, concluded that this species is really dioecious. The mixed organs were discovered in heads* situated on stems which also bore normal female inflorescences; some of the organs resembled antheridia and others archegonia, while a complete series of intermediate forms were also present. Bergevin in 1902 (1) discovered and figured similar structures in *Plagiothecium sylvaticum*, an undoubtedly dioecious species; among the examples described, some are monoecious, some synoecious, and organs showing all stages of transition between antheridia and archegonia are found; no sections of these organs were made. A similar instance has been discovered in *Mnium hornum* by the present writer.

The axis which bore the organs of mixed sex had the appearance of a male individual and was collected in Kent in the spring of 1911, with a number of others which, as far as they were examined, all bore normal antheridia. The specimen was preserved in Flemming's weak fluid, and was examined by means of longitudinal sections. A considerable number of normal antheridia are borne in the head, and the majority of these contain almost mature spermatozoids; no normal archegonia are present.

Unfortunately the whole of the sections were not retained, but in those kept fourteen organs of mixed sex were discovered. These show almost all transitions in structure between archegonia and antheridia. The organs represented in Pl. XX, Figs. 1, 2, 3, 4 resemble the normal female organ in form, consisting of a venter and elongated neck. The walls of the venter are, in most cases, only one cell in thickness, and thus differ from those of the normal archegonium; traces of a double wall are however seen in the organ represented in Fig. 4. The neck canal-cells have in many cases divided by walls parallel to the axis of the organ, and the resulting cells resemble spermatogenic cells; this is particularly the case in Fig. 1. It is, however, difficult to definitely ascertain the nature of these cells as, in most cases, they appear to have undergone partial degeneration; it seems evident that the organs under consideration possess archegonial characters, in so far that a ferment is produced by the neck-cells which acts upon the cells present in the canal and brings about their partial conversion into mucilaginous material. It is improbable that the condition of the cells in question is due to imperfect fixation as spermatogenic cells in neighbouring normal antheridia are well preserved. In the organ shown in Fig. 3 two cells are present in the venter, each containing a deeply-staining nucleus of medium size and somewhat scanty cytoplasm. It is probable that the upper of these represents the ventral canal-cell, and the lower the ovum. Similar cells are

found in the younger archegonium represented in Fig. 1. In the organ shown in Fig. 2 two naked cells are present in the venter, and the canal only contains a small quantity of mucilaginous material. In this case it appears probable that the contents of the neck have been ejected, leaving the ovum and ventral canal-cell in the cavity of the venter; unfortunately the upper part of this organ had been destroyed during manipulation. Although it is doubtful whether fertilization could have taken place in the structures represented in Figs. 1 and 3, there appears to be no reason why one of the cells present in the venter of the organ shown in Fig. 2 should not have functioned as an ovum. In Fig. 4 three cells are apparently present in the venter.

The organ shown in Fig. 5 has the general form and appearance of an antheridium, but differs in being longer and narrower than the normal organ. The upper part contains numerous spermatids, while in the central part of the lower portion two cells are present which bear a close resemblance to an ovum and ventral canal-cell, both in appearance and position. The spermatids closely resemble those found in the normal antheridia, and little or no production of mucilaginous material appears to have taken place. The organs previously described may perhaps be looked upon as modified archegonia, but that shown in Fig. 5 is obviously bisexual.

It has been already pointed out that É. and Ém. Marchal have discovered organs of mixed sex in aposporously produced plants of *Mnium hornum*, and it might be urged that the organs just described were borne on an individual which had been aposporously produced. It has been shown by Brizi (3) that capsules of *Funaria hygrometrica* can give rise to protone-mata while still attached to the living moss plant, and it is not improbable that apospory may sometimes take place in nature. É. and Ém. Marchal (12) have shown that a plant produced in this way would possess the diploid number of chromosomes. An examination of the normal antheridia was therefore made, and this led to the discovery of one in which divisions of the spermatogenic cells were taking place. The dividing cells are in the condition of late prophase, and there is little difficulty in determining the number of chromosomes (Figs. 6, 7, and 8). A number of counts were made, and in all cases six chromosomes were present. As it has been previously shown (18, 19) that this is the haploid number for *Mnium hornum*, it is evident that the plant in question did not have an aposporous origin.

In view of the discovery of organs of both sexes on a single axis of *Mnium hornum*, a further examination of the results obtained by É. and Ém. Marchal is rendered necessary. According to these investigators there is an absolute separation of the sexes at the reduction division. The unisexual character is retained throughout the haploid phase, and the reunion of the sex determinants is brought about by fertilization. 'La réduction chromatique . . . est, à coup sûr, la cause déterminante de la disjonction sexuelle. Le caractère unisexué de la spore conserve rigou-

reusement à travers tout la phase haploïdique. . . . L'acte de la fécondation réunit à nouveau dans l'œuf les deux déterminants sexuels' (10, p. 766). In an aposporously produced individual it was assumed that no previous reduction had taken place, and in a later paper (12) the correctness of this assumption is demonstrated, for it is shown that the gametophyte of an aposporously produced moss contains the $2n$ number of chromosomes. In the absence of meiosis such an individual, according to the theory, will be necessarily bisexual, and proof that this is actually the case is brought forward by means of numerous cultures (10).

The proportion of bisexual axes in such cultures is, however, unexpectedly small. In the case of *Bryum caespitium*, out of 1,738 axes examined, 1,579 or 90.8% were found to be male, 154 or 8.8% bisexual, and 5 or 0.28% female. During the third month of the production of sexual organs the proportion of bisexual axes rose to 11.2% (10, p. 782). *Mnium hornum* and *Bryum argenteum* gave almost similar results.

If there is an absolute separation of sex determinants at the reduction division as suggested by É. and Ém. Marchal, it would be expected that at least a very large proportion of the axes formed on aposporously produced protonemata would bear both male and female organs. The results just quoted show, however, that this is not the case, and a further explanation must evidently be sought for to account for the great preponderance of male individuals. It is evident that the proportion is not affected by external conditions for, in cultures of dioecious mosses produced from spores, carried out by the same investigators (9) under similar cultural conditions, the numbers of male and female individuals were approximately equal; variations in light intensity, heat, and nutritive conditions had no appreciable effect on the proportions of the sexes.

É. and Ém. Marchal assume that the unisexuality of the plants in the aposporously produced cultures is only apparent, and that it hides a potential hermaphroditism. Evidence for this is brought forward by showing that, in the second aposporous generation, i.e. in plants borne on protonemata normally produced from the leaves of the first aposporous generation, a small number of synoecious axes is always found, and this proportion is approximately constant whatever the sexual condition of the parent plant.

The production of protonemata from various parts of the gametophyte may be looked upon as a special form of vegetative reproduction, and it would be expected that such protonemata would produce axes of similar sex to that of the parent. This, indeed, has been shown to be the case by É. and Ém. Marchal in normally produced individuals (9). In the case of *Bryum caespitium*, however, a protonema derived from an aposporously produced synoecious axis gave rise to twenty-two axes, of which eighteen or 81.8% were male and four or 18.2% bisexual. Male and female axes gave

similar results. It is noteworthy that the percentage of bisexual axes produced has no relation to the sexual condition of the parent; the protonema derived from a bisexual individual does not produce a larger number of bisexual axes than one produced from a male or female plant; in all cases a large proportion of male axes are produced.

Several instances of the occurrence of hermaphrodite axes in various dioecious mosses have been mentioned above, and these render it questionable whether the proportion of bisexual individuals in the aposporous generations is really higher than that occurring in normal plants. If, as the result of further research, it is established that the increased proportion does exist, the possibility that it is brought about by the disturbance in the metabolic processes caused by the abnormal number of chromosomes present in each cell must be considered. It has been shown by É. and Ém. Marchal (11) that the presence of the diploid number of chromosomes results in the increased size of the organs, cells, and nuclei of the aposporously produced plants, and it appears to be possible that it has also had a disturbing influence on the sexual condition of the individuals.

Strasburger (15) in discussing the results obtained by É. and Ém. Marchal points out that the work of Philibert is of importance. Philibert (13) found that in *Homalothecium fallax*, *Camptothecium lutescens*, and *Fissidens bryoides* protonemata derived from dying leaves and lower parts of the female plants produced small male plants. These mosses are normally dioecious, but it is obvious that in these cases no complete sex separation can have taken place. The peculiar distribution of sexual organs in *Mnium cinclidioides* described by Milde in 1865 (12a) must also be considered here. This species is normally dioecious, but in certain apparently sterile axes Milde found small bud-like structures each containing antheridia and archegonia. In this case also sex separation must therefore be incomplete.

If the conclusions of É. and Ém. Marchal are accepted, it must necessarily follow that in the Musci each kind of gamete bears only the potentialities of its own sex. There is, however, no direct evidence that this is the case in the Bryophyta. No instances of apogamy are at present known in this group, and investigations as to the sexual condition of particular species are very few in number. Apart from the work of É. and Ém. Marchal no researches of this kind have been carried out in the Musci. Among the Hepaticae *Sphaerocarpus* has, however, been the subject of a somewhat similar investigation. Strasburger (16) quotes the results obtained by Ch. Douin, who examined the sexual condition of the plants arising from the four spores of each tetrad in two species of this genus. In both *S. terrestris* and *S. californicus* the spores of each tetrad remain in contact, and the resulting plants are in consequence found in groups of four. Eighty-one of these groups were examined, and in sixty-four of these two male and two female plants were found; in thirteen cases

no conclusion could be arrived at on account of the failure of germination of some of the spores; in four groups the results did not agree with the supposition that two male and two female spores were present in the tetrad. Strasburger accepts this as proof that sex separation takes place at the division of the spore mother-cells, and results in the formation of two male and two female spores. Blakeslee (2) has investigated the sexual condition of the spores in *Marchantia polymorpha* and *Fegatella conica*, and finds that in each of these species the spores from any one capsule give rise to both male and female plants.

It is interesting to note that variations in the sexual condition of normally dioecious species have been discovered in the Hepaticae as well as in the Musci. In *Preissia commutata* the occurrence of an androgynous receptacle has been described by Townsend (17), and such organs are not infrequently found in this species. The investigations on the Hepaticae which have just been described are of the type of that of Él. and Ém. Marchal on the Musci, and do not bring forward any direct evidence as to the sexual condition of the gametes.

Investigations carried out on other groups are more numerous in number, but it is questionable how far the results obtained are applicable to the Bryophyta.

Strasburger fully discussed the question of sex determination in 1909 (16), and concluded that in plants generally each kind of gamete bears only the tendency of its own particular sex, i. e. maleness is confined to the spermatozoid, and femaleness to the ovum. Correns (5), on the other hand, concludes that in the higher plants and animals the germ-cells of one sex are homogametic, while those of the other are heterogametic; he considers that it is probable that the homogametic germ-cells agree in sexual tendency with the sex producing them, while of the heterogametic germ-cells half bear the tendency of one sex and half of the other. It appears, therefore, that considerable difference of opinion exists on this point, and that the evidence is not by any means conclusive.

The results obtained by Él. and Ém. Marchal in their experiments with the Musci are of great interest, and emphasize the necessity for further research. In view, however, of the occurrence of mixed organs in an axis of *Mnium hornum* which has been just described, and the similar cases previously noted by investigators in other mosses, together with the work of Philibert and Milde, these results cannot be accepted as conclusive of the place and method of sex determination in this group; further research is necessary before a definite statement on this subject can be made.

The supposition that sex determination takes place at some fixed stage in the life-history of the plant, and that it is brought about by the separation of chromosomes, obviously leads to many difficulties. It is therefore suggested that sex is determined by certain metabolic processes

which are spread over a considerable number of cell generations, and which, as a general rule, are unaffected by external conditions. It is possible that these processes are initiated at a certain stage in the life-history, but it is unlikely that they depend on the separation of actual protoplasmic masses at any particular cell-division. If this view is accepted, variations from the normal sexual condition of a species may be explained by assuming the presence of some unusual factor which has interrupted the normal course of metabolism. No adequate explanation of such sexual abnormalities has been given by the upholders of the theory of sexual determination by the separation of determinants at some particular division. If, however, the view outlined above is accepted, the explanation of such cases becomes very considerably simplified.

In conclusion, it may be pointed out that the majority of investigations on the subject of sex determination have been carried out on animals. The conclusions so arrived at cannot be justly extended to plants, which differ fundamentally from animals in the possession of a definite alternation of generations in their life-history. The fact that in animals meiosis always corresponds with the gametogenic divisions, while this is rarely or perhaps never the case in plants, renders comparison of the two groups very difficult.

Similar investigations on plants have almost all been confined to Angiosperms, in which the alternation does not result in sharply distinguished generations. It is probable that further research of a similar nature carried out on the Bryophyta and Pteridophyta, in which the generations are always distinct and, in the latter group, usually lead an independent existence, would give valuable results.

SUMMARY.

1. An axis of *Mnium hornum* is described, bearing normal antheridia, bisexual organs, and modified archegonia.

2. The spermatogenic cells of the normal antheridia possess six chromosomes and, since this is the normal gametophytic number, the plant in question cannot have been produced aposporously.

3. The results obtained by É. and Ém. Marchal are discussed, and it is suggested that sex determination is not bound up with meiosis, but is brought about by metabolic processes which operate in the organism over a considerable part of its life-history.

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EXPLANATION OF PLATE XX.

Illustrating Dr. Wilson's paper on Sex Determination in *Mnium hornum*.

All the figures were drawn with the camera lucida, Figs. 1-4 under a 2 mm. apochr. hom. imm. Zeiss N. A. 1.40 with comp. oc. 4, $\times 500$; Fig. 5 under a D achrom. Zeiss with comp. oc. 4, $\times 220$; Figs. 6, 7, and 8 under a 2 mm. apochr. hom. imm. Zeiss N. A. 1.40 with comp. oc. 18, $\times 2250$.

All the figures refer to *Mnium hornum*.

Fig. 1. A young modified archegonium, showing division of the neck canal-cells.

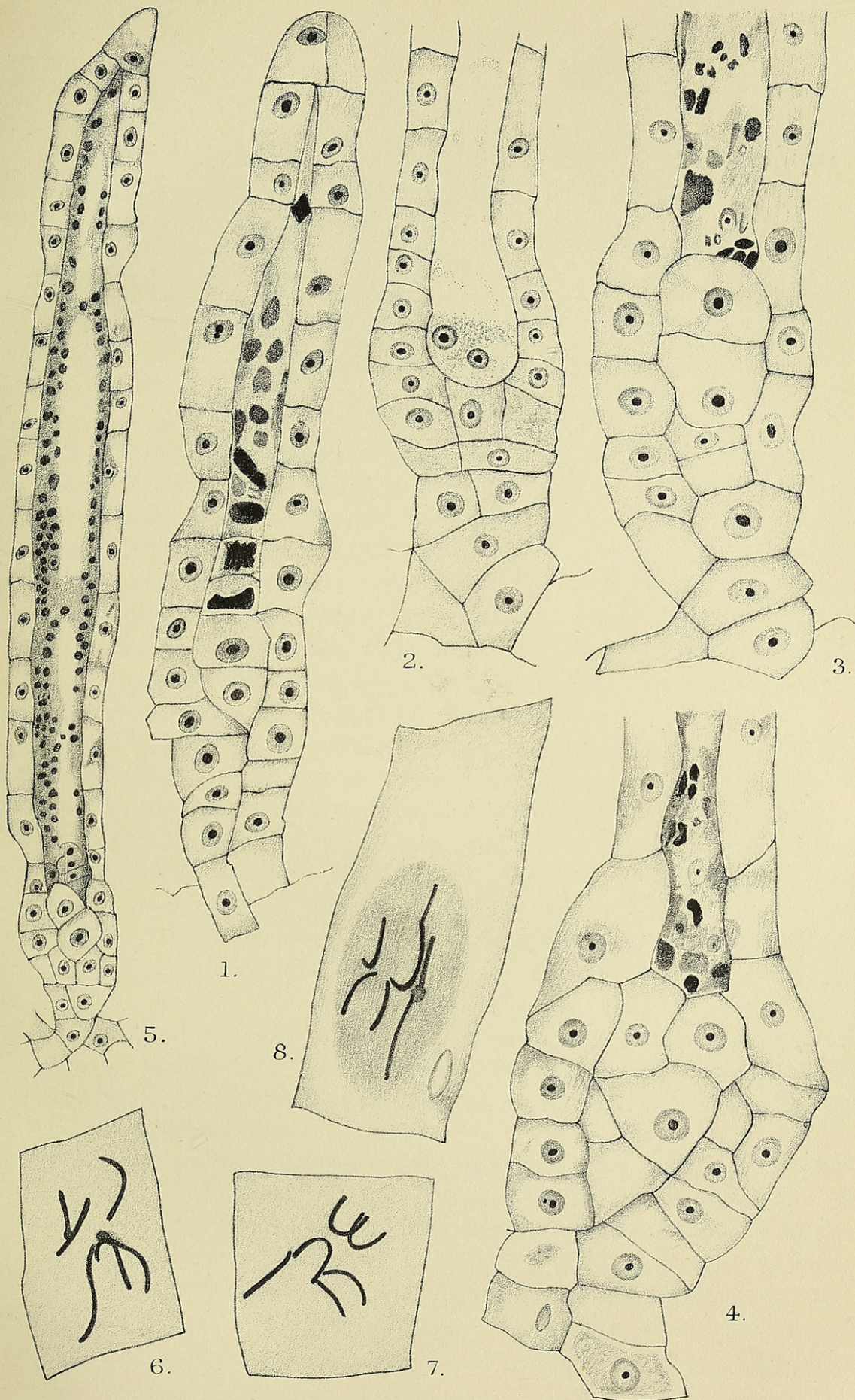
Fig. 2. A mature modified archegonium in which the contents of the neck have been ejected; the naked cells in the venter are probably the ovum and ventral canal-cell.

Fig. 3. A modified archegonium, showing spermatogenic cells (?) in the neck-canal.

Fig. 4. A modified archegonium, showing spermatogenic cells (?) in the neck-canal.

Fig. 5. A bisexual organ, showing spermatids in the upper part and an ovum (?) and ventral canal-cell (?) in the lower part.

Figs. 6-8. Spermatogenic cells from a normal antheridium in late prophase of division, each showing six chromosomes. A chloroplast is seen in the right-hand lower corner of the cell shown in Fig. 8.



M.W. del.

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WILSON — *MNIUM HORNUM*.



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