On Androgynous Receptacles in Marchantia.

BY

E. M. CUTTING, M.A., F.L.S.

Assistant, University of London, University College, and Lecturer on Biology, St. Thomas's Hospital Medical School, London.

With five Figures in the Text.

IN some material of *Marchantia* which had been collected for class-work, a number of archegoniophores were found which differed considerably from those of *Marchantia polymorpha*, the stalk ending in a well-marked disc bearing a variable number (6–12) of short lobes, and it was observed that some of these archegoniophores bore on the lower surface a prominent outgrowth (Figs. 1, 2, and 3) rather suggestive of an antheridial lobe.

A few hand sections were cut of one of these abnormal receptacles, and it was at once noticed that antheridia were borne in great abundance on the apparently under side of the outgrowth. There were also indications of the presence of archegonia in other parts of the sections. The material was not examined any further by means of hand sections, but the microtome sections which were afterwards cut from this and other of these abnormal receptacles have shown that archegonia are also present on them.

The material had been originally obtained from Mr. Williams, of Avery Hill, Eltham, from whom I learnt that the species was *Marchantia palmata*; that he had obtained the original specimens from the Chelsea Physic Gardens, and that the receptacles with the disc shape, already shortly described, were commonly formed on some of the plants, and on others archegoniophores similar to those of *Marchantia polymorpha*, but more robust and with longer stalks. He also said that the plants had, unfortunately, all died, but he kindly placed at my disposal all that remained of the material, which had been preserved in alcohol. There was, unfortunately, very little of this and it was in a fragmentary condition; so that it was seldom possible to trace more than one inflorescence to any individual thallus: indeed I have only been able to do this in the case of the antheridiophores and of the ordinary 'polymorpha' type of archegoniophores. All of the 'disc'-type of receptacles were unattached.

[Annals of Botany, Vol. XXIV. No. XCIV. April, 1910.]

There were present two kinds of archegoniophore, the disc-type with short processes, and the 'polymorpha' type with long processes; and two kinds of antheridiophore—one with only a slightly crenate edge and equal lobes, and one that was asymmetric and in which the lobes were free for the greater part of their length. In the last mentioned the number of lobes varied greatly.

A microscopic examination of the thallus and gametophores revealed the fact that at least three different types of pore were present in the material, and this fact, as well as the presence of different types of gametophores, makes it more than probable that two or more species had somehow got mixed.

I intended to try to get a further supply from Chelsea in the hope that more androgynous receptacles might be found, and that experiments might be tried in order to find the factors that regulate the appearance of this condition in this species, and to find out whether it can be inherited. As both Schiffner (17) and Stephani (18) regard *Marchantia palmata* and *Marchantia emarginata* as synonyms, and as two very characteristic species under these names are grown at Chelsea, both of these were collected during this year: neither of them, however, showed the androgynous condition. The *Marchantia palmata* formed archegoniophores like those with the long processes found in the Avery Hill material, but no disc-shaped ones. The *M. emarginata* formed very few gametophores during the year and none that I had were adult, but Mr. Hales, the Curator of the Gardens, informs me that the adult shape is in the form of a disc similar to that of the androgynous receptacles described above.

Mr. Gepp, of the Natural History Museum, has very kindly shown me the Herbarium specimens of *M. palmata* and *M. emarginata.* They seem very similar and both are evidently very variable, but neither of them resembles either the Chelsea specimens or my own: nor does Stephani's description of *M. palmata* (syn. *M. emarginata*) agree with either the Chelsea specimens or my material. The latter, unfortunately, is in too fragmentary a condition for the separation of the constituent species and the determination of the specific name of the androgynous specimens.

As I have failed to find any androgynous gametophores on the Chelsea specimens, and as the androgynous material at my disposal was insufficient for the determination of the species, it was determined to publish the results that have so far been obtained.

The disciform receptacle has a wide, slightly concave upper surface, and its margin is produced into 6–12 short, blunt protuberances which at times show indications of a slight apical depression (Figs. 1, 2, and 3). Between two of the protuberances on each receptacle is a very deep cut reaching in some cases almost to the centre of the disc-like upper surface. This cut indicates the first dichotomy of the shoot which gave rise to the

inflorescence, and the organ is rendered bilaterally symmetrical on account of it. On the under surface is to be found a dense mass of rhizoids, &c., and amongst these are often to be seen a number of sporogonia, thus showing that the archegonia are fertile. On some of these gametophores there are one or more irregular masses of tissue attached by a short stalk to the under surface (Fig. 5). The stalk quickly widens out from above downwards, and ends in an almost flat downwardly-directed disc of irregular shape and slightly crenate outline (Figs. 1 and 2). The disc, when looked at from below, is seen to resemble a lobe or a few lobes of the antheridiophore, and the surface, which is directed downwards,

FIG. 1. Side view of androgynous receptacle of *Marchantia* sp., showing a male outgrowth. ×*circa* 2.

FIG. 2. Under surface of an androgynous receptacle, showing two male outgrowths one of which has branched. ×*circa* 2.

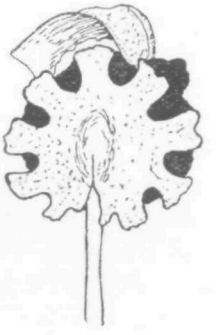

FIG. 3. An androgynous receptacle, view from above. ×*circa* 2·5.

is covered with minute punctations which, from a comparison with the sections, are evidently caused by the presence of antheridia. As many as three such masses have been noticed on some of these abnormal gametophores.

A macroscopic examination does not show whether these antheridia-bearing lobes correspond to any definite lobe of the hermaphrodite receptacle or not. Sections, however, show very clearly that they are formed as outgrowths from a portion of the under surface of a female branch. In cases so examined it was found that archegonia were present at the base of the stalk of the outgrowth. This is clearly shown in Fig. 4. Here on the right hand we have a male outgrowth, and at the base an archegonium is shown, and a little to the right of this the involucre of the branch. The other sections in the series had other archegonia in a similar position; one only is put in the drawing for the sake of clearness. It would not be unlikely for the entire archegonia-bearing portion of a branch to grow out into a protuberance, but no such case

has been seen. In the *Marchantia* here described we have, therefore, a male outgrowth from one or more branches that have not only been formed in the manner characteristic of female branches, but which also bear archegonia. The outgrowth, as has been mentioned above, may form only one branch (Fig. 1), or it may divide again to form an asymmetric branch-system; as many as three branches have been seen in one such outgrowth.

The structure of the antheridia and of the branch which bears them is perfectly normal, with the usual amphigastria and rhizoids. One very remarkable feature, however, was noticed. Although the gametophores

FIG. 4. Longitudinal section through an androgynous receptacle, showing hermaphrodite branch on right side. ♀ = archegonia, ♂ = antheridia, *s* = stalk, and *i* = involucre. × 15. Semidiagrammatic.

were provided with a long stalk and gave other evidence of being fairly adult, the majority of the antheridia had not yet discharged their contents. In the older parts of the male outgrowths empty antheridia were found, so that the fact that the majority were full evidently was not caused by their not having the power of opening. It seems, on the other hand, to suggest that the male outgrowth was formed secondarily as a kind of proliferation, and is not a mere replacement of the normally female branch. This point will be discussed later.

Only about half of the disc-shaped gametophores bore male outgrowths, but the latter easily fall off, and it is certain that many have lost them. It is probable, however, that some few of them were purely female, as no sign of a broken surface was seen on them.

The other type of female receptacle and the two types of antheridiophore have already been shortly described. They are perfectly normal in structure, and a detailed account of them is not given because it is certain that the material contained at least two species and it is impossible to separate them. It is probable, however, that the asymmetric type of antheridiophore belongs to the same species as does the disc-shaped

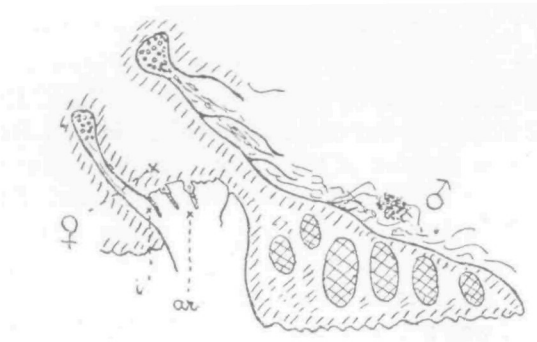

FIG. 5. Hermaphrodite branch from a gametophore. *i* = involucre, *ar* = archegonia, ♀ part, and ♂ = male part. × 15. Diagrammatic.

gametophore; the male outgrowth of the latter much resembling the lobes of the former.

HISTORICAL.

The first record of androgynous gametophores in the Marchantiaceae seems to have been made by Taylor (20), who in 1834 writes of them as occurring in *Dumortiera irrigua* (*Hygropyla irrigua*, Tayl.). In 1836 he writes of *D. irrigua* (*Hygropila*, Tayl.) in Mackay's Flora Hiberniae (21), 'The fructification is commonly dioecious, sometimes monoecious, and not rarely androgynous as observed in *Marchantia androgyna*.' This last-mentioned plant is now known as *Preissia commutata*. In his paper 'De Marchantieis' (20), published two years previously, an account is given of *Marchantia androgyna* (*Preissia commutata*), but this peculiarity is not mentioned. Since then androgynous receptacles of *Preissia commutata* have been found and described by Goebel (9), Leitgeb (12), and Miss Townsend (22).

Goebel found that the front portion of the fructification bore antheridia on the upper surface and the back portion archegonia on the lower surface. He compared the androgynous condition to the state of affairs noted by him (8) in *Isoetes lacustris*, where a vegetative bud was found in the position in which a sporangium usually occurs. He does not think that the androgynous receptacle need necessarily be explained as a reversion to a primitive, monoecious arrangement of the sexual organs.

Leitgeb (12) confirms Goebel's results, and also points out that the organ has four rays as usual, and that two of these are male, two female. He also grew plants which were producing androgynous fructifications, and in the following year another crop of androgynous receptacles was formed—an extremely interesting observation, the significance of which will be discussed later. Leitgeb also mentions that Schmidel and Bischoff have observed androgynous Preissias. He holds the opinion that the androgynous condition is caused by the sexual differentiation being delayed until the formation of the branches which bear the sexual organs instead of taking place in the vegetative portion of the thallus. He gives some interesting facts concerning the distribution of male and female gametophores in *Reboulia* in support of this view. In this genus the male and female receptacles bear a relationship to each other similar to that of the male and female branches on the *Preissia* androgynous gametophores. Mention is also made of the relationship of the gametophores to the ordinary vegetative branches in *Marchantia.*

Miss Townsend was not aware of the work already done on *Preissia commutata.* She expresses the opinion that the gametophore of the androgynous *Preissia* was primarily an archegoniophore, and it is to be presumed that she therefore thinks the development of the antheridia on the structure to be secondary. She does not record any correlation between the lobes and their sex. The gradual development of complexity in the arrangement of the sexual organs in the Marchantiales is described, and the question whether the hermaphrodite condition recorded in *Preissia* is to be regarded merely as abnormal or as a reversion to an earlier type is discussed. It is suggested that the latter is the more likely explanation, and the different arrangements of the gametophores in the *Vaucherias* are brought forward in support of this theory.

Ernst in 1907 published a preliminary note (6) on androgynous receptacles in *Dumortiera velutina*, Schiffn., and *D. trichocephala*, (Hook.) N. ab E., and in 1908 a very full and interesting paper (7), entitled 'Untersuchungen über Entwicklung, Bau und Verteilung der Infloreszenzen von *Dumortiera*'. Androgynous receptacles would seem to be very common in these species, and were found abundantly in specimens gathered from many different localities. The nature of the disturbance of the usual arrangement in these cases is very much more complicated than in the case of *Preissia*, the proportion of the female to the male portion varying within wide limits. As in *Preissia*, the antheridia are borne on the upper surface, and the whole of the branch is male. Pure male and female gametophores are very commonly found on thalli which bear androgynous receptacles.

Discussion.

The androgynous specimens of *Marchantia* described above differ from any androgynous fructifications yet described, in that the male portion not only arises from a branch after this branch has been definitely differentiated as female and has grown with the configuration of such and with a portion of its morphologically upper surface turned downwards, so that the morphologically upper surface of the male outgrowth is likewise turned downwards, but also is capable of continuing its growth and giving rise to a series of branches, resembling, in general outline, the arrangement seen in the asymmetric antheridiophores of some of the Marchantias, e. g. in *M. chenopoda.* In this respect it resembles a proliferation[1] of the tissues of the female branch rather than a replacement of it, and this suggestion is made even more likely when we remember that archegonia are usually, if not always, formed before the female branch gives rise to the male outgrowth. The distribution and number of the male outgrowths is irregular, agreeing in this respect with *Dumortiera* rather than with *Preissia.*

Leitgeb was of opinion that the androgynous nature of his *Preissia* receptacles was due to a delaying of the sexual differentiation; granting this, the reason for the delay still remains to be discovered. The fact that a clump of thalli, probably derived from one or a few thalli by vegetative reproduction, was found by Leitgeb bearing androgynous receptacles, and that individual thalli selected from these continued to bear such in abundance the following year, strongly suggests that their formation does not depend on external conditions, but on the inherent nature of the thallus. Ernst reports that *Dumortiera* may bear male, female, and androgynous receptacles in any combinations,[2] but this does not negative the view given above, more especially as *Preissia* itself is often monoecious. It must also be remembered that in some of the monoecious species amongst the Marchantiales the male and female gametophores are borne quite close to each other, and yet androgynous receptacles have not been recorded in them.

In the absence of living plants of the androgynous *Marchantia* it is not possible to decide whether the condition in this species is governed by external or internal factors. It is very interesting, however, to find a bisexual species in a genus which has always been regarded as strictly dioecious.

The experiments of Kny, in which the gemmae of *Marchantia*

[1] Similar vegetative proliferations have been noticed by Lindberg (13) in archegoniophores of *Dumortiera*, by Leitgeb (12) in those of *Dumortiera* and *Marchantia*, and by Okamura (16) in the antheridiophores of *M. cuneiloba* and *M. geminata.*

[2] I cannot find whether this is so in *Preissia* or not, but as it is often monoecious it would seem that this is very likely to be so.

polymorpha on germination always gave rise to thalli of the same sex as the parent plant, are quoted by Blakeslee (3) in support of his view that the sexual tendencies are separated at spore-formation in this species, and the experiments of Strasburger (19) on *Sphaerocarpus*, in which two female plants and two male plants came from each tetrad, point more strongly to a similar conclusion in this case. Also the experiments of E. and E. Marchal (14 and 15), in which regenerated portions of the gametophytes of certain dioecious mosses always gave rise to plants of the same sex as the experimental plants and a regenerated stalk of a sporogonium to monoecious plants, seem to prove this for certain of the mosses also. Both Harper (11) and Strasburger (19) have pointed out that this coincidence between sexual differentiation and the reduction-division is by no means a general one, so that even in the same genus the sexual differentiation may take place at different points in the life-history.

In the higher plants the gametophyte is always unisexual, but the sporophyte often bears both mega- and microspores, and the sex of the plants arising from these is determined even before spore-formation. The interesting case of *Salix*, which is usually dioecious, but occasionally monoecious, shows that plants usually forming only one kind of spore—and this giving rise only to one kind of gametophyte—are capable, under certain unknown conditions, of forming both, and thus giving rise to both gametophytes. The power of forming both of these kinds of spore—and through them both kinds of gametophyte—was present in the plant, but the formation of one kind of spore was inhibited by some factor or factors.

A similar case is to be seen in *Lychnis dioica*, in which the ordinary plants are strictly 'dioecious'. The macrosporangiate form, when attacked by a smut fungus, forms microsporangia as a result of a stimulus caused by the fungus. A similar result has never been obtained by artificial stimulation, so that without the fungus we should not have known that the 'female' plants possessed the power of forming anthers. On several ordinary bisexual fern-prothallia we can inhibit the formation of either or both of the sexual organs, and the gametophyte of *Equisetum*, usually described as unisexual, can be made to bear either antheridia or archegonia or both by altering the external conditions (10). In many other cases it is possible that the plant contains the factors necessary for the formation of both sexual organs, but that one of these factors is obscured by some other internal or external condition. The case of *Lychnis* suggests that this factor, even if an external one, may be difficult to find or even to imitate when found. From this point of view it may be seen that many plants regarded as strictly unisexual may yet contain the factor necessary for the formation of the other sex.

Any underlying phenomena that may exist in the inheritance of sex can only be arrived at by thoroughly investigating each separate case of sex-inheritance. The efforts to get at a general theory of the subject

have often been premature, and it is certain, as has been pointed out by Bateson (1 and 2), that the results obtained in one field of observation often differ from those in others. It may also be, as he has suggested, that the inheritance of sex is differently arranged in different species.

UNIVERSITY COLLEGE, LONDON,
December, 1909.

REFERENCES.

1. BATESON, W.: Mendel's Principles of Heredity. Cambridge, 1909.
2. ————: Heredity and Variation in Modern Lights: Darwin and Modern Science. Cambridge Press, 1909.
3. BLAKESLEE, A. F.: Differentiation of Sex in Thallus, Gametophyte, and Sporophyte. Bot. Gaz., xlii, 1906, p. 161.
4. ————: The Nature and Significance of the Sexual Differentiation in Plants. Science, vol. xxv, No. 636, March 8, 1907.
5. ————: Sexual Condition in *Fegatella*. Bot. Gaz., xlvi, 1908, p. 384.
6. ERNST, A.: Über androgyne Infloreszenzen bei *Dumortiera*. Berichte d. d. bot. Ges., Jahrg. 1907, Bd. xxv, Heft 8, p. 455.
7. ————: Untersuchungen über Entwicklung, Bau und Verteilung der Infloreszenzen von *Dumortiera*. Annales du Jard. bot. de Buitenzorg, 2nd series, vol. vii, 1908, p. 153.
8. GOEBEL, K.: Über Sprossbildung auf *Isoetes*-Blättern. Bot. Zeit., xxxvii, 1879.
9. ————: Über die Verzweigung dorsiventraler Sprosse. Arb. des Bot. Instit. in Würzburg, 1880, Bd. ii, Heft 3, p. 353.
10. ————: Organography of Plants (English Trans.). Oxford, vol. ii, 1905.
11. HARPER, R. A.: Sex-determining Factors in Plants. Science, vol. xxv, No. 636, March 8, 1907.
12. LEITGEB, H.: Untersuchungen über die Lebermoose. Graz, 1874–82. vi. Die Marchantiaceen, 1881.
13. LINDBERG, S. O.: Hepaticae in Hibernia mense Julii 1873 lectae. Helsingfors. Acta Soc. Scient. Fennicae, x, 1875, p. 468.
14. MARCHAL, E. and E.: Recherches expérimentales sur la sexualité des spores chez les mousses dioïques. Mém. couronnés Classe des Sci. Ac. Roy. de Belgique, vii, 1907.
15. ————: Aposporie et sexualité chez les mousses. Bull. de l'Ac. Roy. de Belgique, vii, 1907.
16. OKAMURA, S.: Contributions to the Study of Japanese Bryophyta: ii. On the Regeneration of the Antheridial Receptacle of *Marchantia*. Bot. Mag., vol. xxii, No. 256, May, 1908.
17. SCHIFFNER, V.: Die Hepaticae der Flora von Buitenzorg. Leiden, 1900.
18. STEPHANI, F.: Species Hepaticarum. Bull. de l'Herb. Boissier, t. vii, 1899.
19. STRASBURGER, E.: Zeitpunkt der Bestimmung des Geschlechts, Apogamie, Parthenogenesis und Reduktionsteilung. Hist. Beit., Heft vii, 1909.
20. TAYLOR, TH.: De Marchantieis. Trans. Linn. Soc., xvii, 1834, p. 375.
21. ————: Mackay's Flora Hiberniae, ii, 1836, p. 54.
22. TOWNSEND, A. A.: An hermaphrodite Gametophore in *Preissia commutata*. Bot. Gaz., Dec., 1899.