The Monoecism of *Funaria hygrometrica*, Sibth.¹

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With Four Figures in the Text.

THE published statements regarding the distribution of the male and female flowers in *Funaria hygrometrica* are contradictory, this species being described as monoecious in bryological works, while dioecism is attributed to it in various botanical textbooks. In view of the conflicting nature of the different descriptions, Dr. D. H. Scott, F.R.S., suggested to me that I should make an examination of this species, his attention having been drawn to the subject by Prof. Charles Stewart, F.R.S., who informed him that the plant was monoecious.

In the first place a few references to literature may be made. Sachs², Van Tieghem³, and Goebel⁴ refer to *Funaria hygrometrica* as an example of a dioecious species, in which the male organs are on smaller plants of shorter duration. Campbell⁵ states that '*Funaria* is strictly dioecious,' and adds that the 'male plants either grow separately or more or less mixed with the females.' In agreement with Campbell, Scott⁶ describes *Funaria* as dioecious, the male plants as of fair size, and the female plants as very small. Bower and Gwynne-Vaughan⁷ describe the sexual organs as occurring on distinct plants. Thus the works quoted above agree as to the dioecious character of the species.

¹ From the Jodrell Laboratory, Royal Botanic Gardens, Kew.

² Sachs, Text-Book of Botany, 2nd Eng. ed. (1882), p. 370.

³ Van Tieghem, Traité de Botanique, 2nd ed. (1891), p. 1350.

⁴ Goebel, Outlines of Classification, Eng. ed. (1887), p. 174, and Die Muscineen, Schenk's Handbuch, 2. Bd. (1882), p. 375.

⁵ Campbell, Mosses and Ferns, 2nd ed. (1905), p. 195.

⁶ Scott, Structural Botany, Part II, 4th ed. (1904), p. 132 et seq.

⁷ Bower and Gwynne-Vaughan, Practical Botany for Beginners (1905), p. 211.

Bruch and Schimper¹ state that the primary stem is terminated by a male flower, and that it subsequently gives rise to fertile [female] branches. Wilson² describes the stem as 'at first simple, terminated by a barren [male] discoid flower; subsequently branched, the branches bearing terminal fertile flowers.' Lesquereux and James³ give the flowers as monoecious and terminal, the male on the primary stems, the fertile on the innovations. Sullivant⁴ and Brotherus⁵ also describe the male flowers as terminal, and the female as borne on innovations. Limpricht⁶ describes *F. hygrometrica* as monoecious, but does not mention the relative position of the male and female organs. According to Braithwaite⁷ the plant is autoicous [monoecious], and the male inflorescence terminal on a short basal branch, and Dixon and Jameson's⁸ description is similar: (*Funaria*) 'Autoicous in all the British species, male flower discoid, terminal on a lateral branch.' We see then that in all these bryological works *F. hygrometrica* is described as monoecious, though different opinions are given as to whether the male or the female flower is terminal on the primary axis.

As it seemed possible that the divergent statements on the distribution of the sexes might be due to local differences, plants from several localities were examined, but no evidence confirming this view was obtained. The specimens were collected in the following places: Royal Botanic Gardens, Kew, Richmond (Surrey), Seaford (Sussex), Wye (Kent), and near York. The material from York was supplied by the British Botanical Association, Holgate, York, and was accompanied by a letter from Dr. A. H. Burt, in which the writer mentions that 'of the several thousand hitherto examined during the past few years, by far the larger majority of antheridia-bearing plants had young female branches attached to them. I am indebted to Mr. E. S. Salmon, F.L.S., for the material from Wye.

In a sod of *F. hygrometrica* it is often no easy matter to separate the individual plants, owing to the interwoven growth of the rhizoids borne by the stems. In tearing the rhizoids apart, one is liable to break the connexion between a stem and its branch. Out of 102 specimens I was able to determine that seventy-seven were monoecious, the male and female axes being clearly attached to one another. In sixty-five of these it was evident

¹ Bruch and Schimper, *Bryologia europaea*, vol. iii (1836-51). *Funaria* is described as agreeing with *Physcomitrium*, in which the position of the male and female flowers is described.

² Wilson, *Bryologia Britannica* (1855), p. 268.

³ Lesquereux and James, *Manual of the Mosses of North America* (1884), pp. 200 and 199. Details are given for *Entosthodon*, and *Funaria* is described as similar.

⁴ Sullivant, *Icones Muscorum* (1864), p. 87.

⁵ Brotherus, in Engler and Prantl, 1. Teil, 3. Abt. (1903), p. 521.

⁶ Limpricht, *Die Laubmoose Deutschlands*, in Rabenhorst's *Kryptogamenflora*, vol. iv, 2. Abt. (1895), p. 199.

⁷ Braithwaite, *The British Moss-Flora*, vol. ii (1888-95), p. 136.

⁸ Dixon and Jameson, *The Student's Handbook of British Mosses*, 2nd ed. (1904), p. 300.

that the female axis was a branch of the male. We will return to these numbers later, after first describing two or three typical specimens.

When a plant, consisting of a male and female axis, has been isolated, it is often the case that the rhizoids form such a dense weft on some portions of the stem that the relation of the two axes to one another cannot be determined until the greater number of the rhizoids have been dissected away. Fig. 1 is a drawing of a plant prepared in this way, several rhizoids being also omitted for the sake of clearness. The long straight stem is the male axis bearing a terminal discoid male flower (σ^7), in which the antheridia were found to be brown and withered. The branch on the right ends in the female flower (φ), which contained one nearly

FIG. 1. ($\times 6$).

FIG. 2. ($\times 6$).

mature archegonium, as well as two or three others with brown necks. In this specimen it is fairly evident that the female axis has been produced as a branch of the male stem. In many cases, especially in older plants, the main axis may become bent in such a way that the female branch appears at first sight to belong to the primary stem, and the male flower to be on a lateral branch, but the removal of the rhizoids makes the matter clear. The base of the female branch is usually tuberously swollen, and ends in a short free downward prolongation bearing a large number of rhizoids.

A plant somewhat older than the last specimen is shown in Fig. 2. Here the female branch (φ) is inserted at a lower level, and a young

sporogonium (sp.) has been produced by the female flower, the leaves of which now overtop those of the male inflorescence. An older specimen, bearing a nearly mature sporogonium, is shown in Fig. 3, in which the rhizoids have been entirely omitted. The only essential difference from the two preceding cases is that the insertion of the female branch is nearer the base of the male axis.

FIG. 3. (× 6).

We have so far relied on the external appearance for determining which is the parent axis, but naturally it was necessary to supplement this by other data. In sections cut through the two axes in the region of attachment, the structure gave evidence of the lateral origin of the female branch. The central conducting strand in the male stem has a straight or even course. That of the female branch, when traced downwards into the tuberos base, comes to consist of several large, and a few small elongated elements, which in the region of attachment run obliquely across towards the central strand of

FIG. 4. (× 95).

the male axis, some of the elements terminating nearly, but not quite, in contact with it. A transverse section through the united axes is shown in Fig. 4. The female branch (♀) is considerably the larger of the two, and its central strand is cut obliquely, as it is beginning to curve across towards the male axis. The free base of the female branch consists of large-celled parenchyma, and contains no conducting

tissue. The tissues in the female branch become mature later than those of the male branch at a corresponding level. Further evidence on the same point is given by the fact that male plants bearing young branches (with no sexual organs) were found, but no female plants showing the same character.

To return to the records of the examination of plants; as stated above, seventy-seven specimens out of 102 were proved to be monoecious. We will now inquire into the figures obtained as affecting the proportional number of plants in which the female axis is a branch of the male. This was found to be the case in sixty-five cases. Of the remaining thirty-seven most, at any rate, are not to be regarded as necessarily exceptions to this mode of growth. Firstly, in seven specimens the male and female axes were proved to be attached to one another, but no record was made as to which was the parent stem. This was because, when the first few plants were examined, it was thought that the monoecism or dioecism was the only point in dispute. Next there were five plants in which the two axes were attached to one another quite basally, so that it could not be seen which was the primary stem and which the branch. It may be mentioned here that the level of insertion probably has some relation to the crowding of the moss-plants and the conditions as to dampness. In three cases a male and female axis were closely associated, but attachment was not proved. It is quite likely that the two axes may have been accidentally torn apart in preparing the specimen. Six examples were found of a female branch attached to a stem, on which no sexual organs could be found. In these cases, however, the parent stem showed signs of having been injured at the apex, hence it is quite possible that a male flower may have been present previous to the injury. Four other specimens showed a male stem bearing a lateral branch, on which there were no sexual organs. Judging by the external appearance, these are probably to be interpreted as examples of a female branch borne on a male stem, but too young to show archegonia. Twelve plants remain, viz. three male stems with no branches, and nine female axes apparently unattached. As the female branch develops late, it is possible that the three male plants would have subsequently given rise to female branches.

From what has been said in recording the last thirty-seven cases, it is seen that all except the nine free female plants should be disregarded as clearly inconclusive¹ on the question as to whether female axes are ever produced otherwise than as branches of male stems.

As regards the nine female stems, it may be that they were accidentally detached from male stems in separating them from the sod. When examining the last batch of plants (twenty-two in number) it occurred to me that

¹ The proportional number of inconclusive specimens would have been greater if tufts had been specially chosen in which basal attachment was common or young male plants numerous.

by cutting sections of any apparently free female stems it might be possible to obtain evidence of previous attachment to another axis, if the female stem had been formed as a branch. Among this series only one independent female stem was found, and this certainly had a scar in its basal region suggesting a broken attachment. Hence the nine apparently free female stems all come under suspicion, especially as most of them were among the earlier plants examined, when less care was taken in separating the specimens; consequently one may say that the female axis is produced as a branch of the male in the majority of cases, perhaps in all.

No certain case was observed of a female stem producing a male branch. Male plants remaining unbranched may perhaps occur, but as far as these observations go they must be relatively rare.

We have restricted our view to the relation of the female branch to the male stem bearing it, but branching may be carried further. Thus a plant was observed in which the male axis had given off a male branch, which in its turn had produced a female branch. A few other specimens were probably similar, but the primary axis was partly decayed, so that the presence of antheridia on it could not be determined. Evidence of branching carried to a higher order was obtained, and one or two cases of the production of more than one branch on a single male axis were also seen.

We may observe that the production of the female axis as a branch, of rather late origin, on the male stem appears often to lead to the maturing of the archegonia at a time when the antheridia of the same plant are empty and withered, so that cross-fertilization occurs.

One phaenological record regarding *F. hygrometrica* made by Grimme¹ in Germany may be quoted as agreeing well with the formation of the female axis as a branch of the male: 'numerous male flowers with almost mature, yellowish-brown (and also green) antheridia. One female inflorescence with immature archegonia.'

The result of the present observations is to confirm the statements of Bruch and Schimper, Wilson and other bryologists, and agrees with the observations of Dr. A. H. Burtt. The distinct contrary statements made in different textbooks are at first sight difficult to understand, but the explanation is probably as follows. In certain cases numbers of distinct male plants can no doubt be found, most, if not all of these being young specimens which have not yet produced female branches. This gives a first impression of dioecism. Again, when obtaining a specimen for examination, if one pulls a female branch on the edge of a tuft of plants, it will often come away, leaving the primary male axis behind. If greater care be exercised and a clump of two or three plants be put on a glass slide for separation under a dissecting microscope, the slight difficulty in tearing apart a male and female axis may easily be attributed to the

¹ Grimme, Ueber die Blüthezeit deutscher Laubmoose, &c., Hedwigia, 1903, p. 38.

resistance of the rhizoids, which invest the region of attachment. In both cases, when the female branch has been separated, it appears like an independent plant on account of its rounded base (which bears a tuft of rhizoids), the scar being lateral, above the base, and hidden by rhizoids. Also, when the female plant is old, the male stem sometimes begins to decay away, and it is probable that from this cause actually free female branches may be found. The statement of Sachs, Goebel and Van Tieghem, that the male organs are on smaller plants of shorter duration, probably refers to this and to the fact that the female branches in most cases ultimately overtop the male. Campbell¹ states that the male plants are about one cm. in height, but that the archegonia are formed while the female plant is still very small—a few millimeters in height. Substituting 'axis' for 'plant,' this is true especially in those cases in which the female branch is inserted near the top of the male stem (see Fig. 1 of the present paper).

SUMMARY.

Funaria hygrometrica is as a rule monoecious, and, where the point could be determined, the female stem was a branch of the male. The male axis bears a terminal male flower, and produces a lateral branch (innovation), which forms a terminal female flower. The female branch may be inserted at different levels, sometimes high up, sometimes basally; it usually has a tuberous base bearing a tuft of rhizoids, and, if torn away, appears like an independent plant. In the region of attachment the conducting strand of the female branch terminates nearly in contact with that of the male stem. The male axis bearing the female branch may, in its turn, be a branch of another male stem. Dioecism, if it occurs, is comparatively rare.

ADDENDUM.—I am indebted to Mr. H. N. Dixon, F.L.S., for a further supply of *Funaria hygrometrica*, which he kindly collected for me at Collyweston, Northants. The material was from an oolitic limestone-quarry. The rhizoids were numerous, and held a large amount of fine limestone soil, hence examination of the specimens was difficult.

Twenty plants examined included: fourteen in which the female axis was clearly a branch of the male stem; four in which the two axes were attached to one another basally; one female branch attached to a decayed stem; and one female axis apparently unattached. Thus the results obtained are confirmatory of those given above. Some of this material showed rather prolific branching, similar to that described on p. 298.

¹ Campbell, loc. cit.

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