Sphagna, their Habitats, Adaptations, and Associates.¹

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With five Figures in the Text.

INTRODUCTION.

THE familiar names of bog-moss, turf-moss, and peat-moss indicate the general habitats of the different species of *Sphagnum*, since they are all found in places where peat is present, and in most cases where the ground is wet and has that yielding character which is associated with the word boggy. The degree of bogginess varies greatly; in some cases the *Sphagnum* layer conceals a treacherous depth, in others a firm substratum is quickly reached. In exceptional cases peat is absent or almost so, but if not present in the particular spot where the *Sphagnum* actually grows can be found in the near vicinity. *Sphagnum inundatum*, *S. subnitens*, *S. recurvum*, and other species are sometimes found on the sides of furrows cut by streamlets, or in other spots where the immediate presence of peat is not apparent, but usually little search is necessary to establish the presence of peat in the neighbourhood. One of the most striking cases of this kind noticed by the author occurs by the side of a sloping hard-metalled road on the Blackdown Hills in Somersetshire. *S. pulchrum* is present in fair quantity and seems to obtain its supply of water from the inconstant drainage after rain; the district, however, is turfy and further search reveals the presence of patches of *S. recurvum* which are constantly moist and have a somewhat peaty substratum. Sphagna sometimes occur on moist rock-ledges which have little or no peaty covering. This very rarely happens in lowland or even in upland districts, but is not uncommon on sheltered alpine or subalpine ledges, where the moisture from the clouds forms no inconsiderable part of the water-supply. As concrete instances of this habitat noticed by the author the following may be given: *S. acutifolium* on moist rock-ledges, altitude 3,500 feet, Ben Doran, Argyllshire; *S. molluscum*, with a similar habitat on the same mountain, but at a lower elevation (2,500 feet) and in company with *Scapania ornithopodioides*.

When the water is squeezed out of these tufts of *Sphagnum* it is found to be more or less acid; the peat derived from its decay seems to retain this

¹ This paper forms part of a thesis for the degree of Doctor of Science, London.

acidic character, and when the catchment area for an urban water-supply is coincident, special means have to be adopted to prevent the so-called 'humic acids' from attacking the lead pipes. Much research work has been done on this acidity of *Sphagnum* and a great deal of literature deals with it.¹ This acidic nature of *Sphagna* has a great effect on their habitats and distribution, and the main purpose of this article is to attempt to correlate their morphological with their ecological characters.

The distribution in regard to altitude is more affected by human agency than through any discrimination by the species themselves. Many of our low-lying 'mosses' have been drained, the reclaimer has extended

FIG. 1. Sketch-map of Somerset to show the distribution of *Sphagna*.

The areas where *Sphagna* have been found are shaded; dotted lines represent the contour-line of 700 feet, the continuous lines indicate the contour-line of 1,000 feet. A few towns are indicated by crosses.

the land available for agricultural purposes, and in England *Sphagneta* are seldom found below the altitude where it is economically possible for the farmer to bring the land into cultivation. This altitude varies according to many other influencing factors, but generally is about 700 feet. Some of our lowland *Sphagneta* which still exist owe their survival to the excellent cover for game which is afforded by associated plants such as *Betula*, *Myrica*, and *Molinia*. The accompanying map of Somerset (Fig. 1) shows the altitudinal distribution of *Sphagnum* and illustrates how it is seldom

¹ See Skene: The Acidity of *Sphagnum* and its Relation to Chalk and Mineral Salts. Ann. of Bot., January, 1915.

found below 700 feet in this agricultural county. The only places below 700 feet where *Sphagna* are found are on the flanks of the hills, a *Myrica* heath near Chard, an Old Red Sandstone area near Bristol, and isolated areas on the peat-moor of Central Somerset. The *Sphagnum* occurring at the lowest elevation (50 feet) is *S. subnitens* (= *S. plumulosum*), and this species is also present near the summit of Dunkery Beacon, the highest (1,700 feet) hill in Somerset. The distribution of the different species growing in the county has also been worked out, but the altitudinal range is too limited and human interference has been too prominent for any useful result to be attained by more detailed and specific mapping of the data available. The map, however, clearly shows the preference of *Sphagnum* for non-calcareous areas. In the hilly Mendip region of East Somerset it only grows in a few isolated areas where inliers of Old Red Sandstone occur, whilst on the surrounding Carboniferous Limestone it is entirely absent. The central peat-moor (Sedgemoor) is chiefly on a substratum of Jurassic calcareous beds with alluvial clays and a few recent marine beds, and it is only in the uncultivated areas where the calcareous character is neutralized that *Sphagnum* occurs, and such patches are isolated and rare. All the other *Sphagnum* regions are underlain by siliceous and argillaceous rocks, especially those of the Devonian and Old Red Sandstone system. The geological distribution of Somerset Sphagneta may be summarized as follows:

Devonian:—The hilly region to the west of the county, including Exmoor, the Brendons, and the Quantocks.

Old Red Sandstone:—Isolated areas on the Mendip hills and a small patch west of Bristol.

Lower and Mid-Lias argillaceous beds:—Small areas on Chard Common and on the Blackdown hills.

Kimeridge and Oxford Clays of the Oolite:—Small and isolated areas on the eastern boundary.

Greensand:—Portions of the Blackdown hills.

Detailed maps of some uncultivated or semi-cultivated portion of Scotland would probably lead to good results as regards the range in altitude of the different species, but at present sufficient data for such maps are not available, though there is some evidence that species such as *S. acutifolium*, *S. fuscum*, *S. rubellum*, *S. Lindbergii*, *S. Girgensohnii*, and *S. papillosum* should be considered as plants of elevated moorlands, whilst such species as *S. fimbriatum* and *S. Warnstorffii* are normally plants of low elevations. In Somerset *S. rubellum* and *S. papillosum* occur at an altitude of 320 feet, and *S. Girgensohnii* is found at 600 feet, and similar (and even more striking) exceptions are known in other counties.

Little definite information can be given as to the specific endurance of sub-halophytic conditions. None of the *Sphagna* appears to have any tolerance of such habitats; they very rarely occur on sand-dunes, and abhor

salt-marsh associations. *S. subnitens* grows sparingly on the dunes near Southport; *S. imbricatum* is said to prefer wet heaths and bogs near the coast, but the author has found it more common in inland regions, in one case preserved in peat cuttings on the Pennines in a district where the living plant is now extinct. Experimental work with culture solutions has shown that the effect of high concentration of salts is variable according to the salt and the species employed, and that a concentration useful to most plants generally acts injuriously.

PROTECTIVE DEVICES.

Sphagnum is often regarded as a pronounced hydrophyte, but any bryologist who carefully studies its structure and compares it with that of other Mosses must be struck by the presence of a number of characters which in other plants would be considered as of a xerophytic nature, enabling the plant to endure periods of drought. Such characters as compactness of habit, imbrication of the leaves, concave leaves with hooded or inrolled apical portions, formation of capillary chambers along which water passes, papillosity of the cell-membrane, intermixture of dead empty cells with living chlorophyllous ones, and presence of reservoirs for the storage of water, are usually accounted xerophytic devices in other Mosses, and all these characters are shown by species of *Sphagnum*.

Imbrication of the branch-leaves to a greater or less extent is of general occurrence in the Sphagna, being entirely absent only in species which are usually found submerged (e. g. *S. cuspidatum*, Fig. 4, A) or in shaded moist situations (e. g. *S. squarrosum*). In some plants of drier moorlands, e. g. *S. compactum* (Fig. 5, W), *S. cymbifolium* var. *congestum*, *S. papillosum* var. *confertum*, the imbrication is very pronounced; in fact it is a general rule that the drier the habitat the closer is the imbrication. *S. subnitens* (Fig. 2, A) in other respects has a similar structure to *S. quinquefarium*, but the latter usually grows in drier places, and has its leaves more closely imbricated.

The branch-leaves of nearly all species are more or less concave, but generally the most pronounced hydrophytic member of a group of allied species has the leaves least concave. In the Cuspidata group, *S. cuspidatum* has a much flatter leaf (Fig. 4, B) and a wetter habitat than *S. pulchrum* (Fig. 4, F); similarly in the Subsecunda section, *S. obesum* (Fig. 5, R) may be compared with *S. subsecundum* (Fig. 3, K). The leaves, it may be noted, are usually larger or longer in the more aquatic species.

Inrolling of the branch-leaf is another character which is general for the Sphagna. The lateral margins of the upper half of the leaf become incurved so that two small chambers are formed (Fig. 2, G), or the incurving may be so pronounced that a tube results (Fig. 4, F). In some Sphagna the inrolling is little shown, but the leaf is very concave and is cucullate, i. e. its

apex is curved over so as to form a hood (Fig. 5, I). This cucullate leaf is a distinctive character of the *Cymbifolia* section (*S. cymbifolium*, *S. papillosum*, *S. medium*, *S. imbricatum*), but is slightly shown in members of other groups, e.g. *S. rubellum* (Fig. 3, E).

FIG. 2. *Sphagnum subnitens*, R. and W. A. Diagrammatic sketch of the fertile plant, $\times \frac{1}{2}$. B. Portion of the plant showing two fascicles or groups of branches, $\times 3$; the stem-leaves are numbered to show the $\frac{2}{5}$ arrangement, leaves 2 and 5 being on the other side of the stem. The leaves 3 and 4 are usually nearer together than they are shown in the figure. C. Stem-leaf, $\times 17$, indicating the border of narrow cells becoming broader below. D. Stem-leaf, $\times 17$, showing undulations and the margin inrolled at apex. E. Cells from the middle of the stem-leaf, $\times 210$. Chl. Chlorophyllous cell with chlorophyll granules. Hy. Hyaline or empty cell which is usually divided by oblique septa. F. Cells from the margin of the stem-leaf, $\times 210$. G. Branch-leaves, $\times 17$. H. Outer surface of branch-leaf showing fibres and pores, $\times 210$. I. Inner surface of branch-leaf, $\times 210$. Chl. Chloroplastids. J. Portion of section of branch-leaf showing two hyaline and one chlorophyllous cell, $\times 210$.

The formation of capillary chambers along which water may pass is general in the genus. The branches are in fascicles (Fig. 2, A), their number varies in different species, and what is more important, they vary in position, some being stronger than others so that they occupy more patent positions. The weaker branches are often closely appressed to the stem and so form

FIG. 3. (See description on opposite page.)

fine channels along which water passes by capillary action. In most species there are two or three divergent and one or two pendent branches (Fig. 2, B). In the two allied plants *S. cuspidatum* and *S. recurvum*, the former is a plant with a more characteristic aquatic environment, and this is reflected in the almost complete absence of pendent branches, especially in the wholly-immersed variety *plumosum* (Fig. 4, A), whilst the stem of *S. recurvum* is concealed by them, two or three of the four or five fascicled branches being pendent (Fig. 5, A). *S. squarrosum*, which, as its name implies, has squarrose leaves, often grows in shaded places, but when growing in open places has, like *S. recurvum*, two or three pendent branches which enable water to be drawn up from the constantly moist substratum. In the usually immersed *S. riparium* the pendent branches are scarce or absent, and in *S. obesum*, the most aquatic member of the Subsecunda group, they are wanting.

The intermixture in the branch-leaf of empty hyaline cells with those containing protoplasm and chlorophyll is a generic character. The hyaline cells are provided with small openings or pores, strengthening fibres prevent collapse, and generally they are much wider than the alternating chlorophyllous cells. They are regarded as water-reservoirs with a special aptitude for obtaining a quick and copious supply of water, and there is no reason to doubt this explanation of their presence, but the relative orientation of the two kinds of cells, though constant for a particular species, is variable in the genus, and in some cases is suggestive of a protective device against undue loss of water from the living cells. It is also significant that in some submerged species, varieties, and forms, the hyaline cells are reduced or are replaced by chlorophyllous ones. In the submerged species, *S. obesum* and *S. riparium*, many of the cells, which are structurally hyaline, contain chlorophyll, and in a submerged form of *S. imbricatum* (form *degenerans*) the chlorophyllous cells are so much broadened that the hyaline cells sometimes seem to be absent.

FIG. 3. *Sphagnum subnitens*. A. Portion of transverse section of stem, $\times 100$. B. Surface view of two of the external cells of the stem, $\times 100$. C. Perichaetial leaf, $\times 16$. D. Perichaetial leaf indicating the border of narrow cells, $\times 16$. In the middle of the leaf the hyaline and chlorophyllous cells are distinct; in the lower part they are indistinctly differentiated; in the upper part the cells are smaller, relatively broader, and not differentiated. The hyaline cells have no fibres or pores and are one—or more—septate. F. Branch, bearing antheridia in the middle portion, $\times 10$. G. Leaf and antheridium, $\times 32$. M. Three spores, $\times 400$. The upper shows the papillose surface, the two lower show the triradiate marks.

S. rubellum. E. Branch-leaf, $\times 30$.

S. inundatum. H. Stem-leaf with auricles, $\times 30$. I. A few cells from the auricles showing incomplete or weak fibres, $\times 200$.

S. rufescens. J. Transverse section of stem, $\times 100$.

S. subsecundum. K. Branch-leaf, $\times 30$. O. Section of branch-leaf, $\times 400$, showing two hyaline and two chlorophyllous cells.

S. cymbifolium. N. Surface view of two of the outer cells of the stem showing fibres and pores, $\times 400$.

S. papillosum. P. Transverse section of branch-leaf, $\times 400$. The outer surface is uppermost in the figure.

All the leaves are figured as viewed from the inner surface.

FIG. 4. *Sphagnum cuspidatum* var. *plumosum*. A. Portion of the plant showing a fascicle of branches, $\times 5$. The positions of two other fascicles are indicated. B. Branch-leaf, $\times 23$. C. Cells of the branch-leaf viewed from the outer surface, $\times 300$. D. Cells viewed from the inner surface, $\times 300$. E. Transverse section of branch-leaf, $\times 300$.

S. pulchrum. F. Branch-leaf, $\times 23$; apical portion forming a tube, $\times 45$. G. Transverse section of branch-leaf, $\times 300$.

S. compactum. H. Branch-leaf, $\times 23$. I. Transverse section of branch-leaf, $\times 300$.

S. medium. J. Branch-leaf, $\times 23$. K. Cells as seen from inner surface of branch-leaf, $\times 300$. L. Cells from outer surface, $\times 300$. M. Transverse section of branch-leaf, $\times 300$.

All the leaves (unless otherwise stated) are figured as seen from the inner surface. The incurved portions of the leaves are shaded. In a figure of a leaf-section the outer surface is placed uppermost.

FIG. 5. *Sphagnum recurvum*. A. Portion of plant showing a fascicle of branches, three other fascicles being indicated. The figure is somewhat diagrammatic, since the pendent branches have been separated from each other and from the stem, whilst those from the other fascicles have been removed, $\times 4$. B. Transverse section of stem, $\times 60$. C. Transverse section of branch-leaf, $\times 240$.

S. amblyphyllum (= *S. recurvum* var. *amblyphyllum*). D. Outer portion of branch, showing the layer of retort cells and one layer of cortical cells, $\times 80$. All the leaves have been removed.

S. molluscum. E. Outer portion of branch, showing large retort cells and smaller cortical cells, $\times 80$.

S. inundatum. F. Branch-leaf, $\times 18$. G. Cells of branch-leaf as seen from the inner surface, $\times 240$. H. Cells of branch-leaf from the outer surface, $\times 240$.

S. cymbifolium. I. Branch-leaf, $\times 18$. J. Cells from inner surface, $\times 240$. K. Cells from outer surface, $\times 240$. The chlorophyllous cells are almost concealed by the hyaline cells, the walls of which appear to be thick, this appearance being due to the nearness of the two walls, whilst the darker contents of the chlorophyllous cells just show between. L. Transverse section of branch-leaf, $\times 240$. M. Transverse section of stem, $\times 60$. N. Portion of stem-section showing one hyaline cell and part of the stereom cylinder, $\times 240$. Chloroplasts are present in some of the cells.

S. imbricatum. O. Transverse section of branch-leaf, $\times 240$.

S. cuspidatum. P. Transverse section of stem, $\times 60$.

S. obesum. R. Branch-leaf, $\times 18$. T. Cells of branch-leaf viewed from inner surface, $\times 240$. U. Transverse section of branch-leaf, $\times 240$, showing four chlorophyllous and three hyaline cells.

S. compactum. W. Branch showing imbrication of leaves, $\times 7$.

S. rufescens. X. Cells of branch-leaf viewed from inner surface, $\times 240$. Y. Cells from outer surface, $\times 240$.

All the leaves are figured as seen from the inner surface. The incurved portions of the leaves are shaded. In a figure of a leaf-section the outer surface is placed uppermost.

The orientation of the two kinds of cells, their relative sizes, shapes, and porosity, will be discussed in a more detailed manner later.

Papillosity of the cell-wall (Fig. 3, P) is a character met with in few species (*S. papillosum*, *S. imbricatum*). In *S. medium*, *S. squarrosum*, *S. teres*, and *S. Wulfianum* papillae are sometimes met with, but they are scarce or very minute. In some varieties of *S. papillosum*, which are generally plants of wetter situations than the type, the papillae are absent (var. *leve*) or very minute and only met with in some of the leaves (var. *subleve*). *S. imbricatum* has longer papillae (Fig. 5, O), but has not a drier habitat; in some other respects (e.g. greater width of chlorophyllous cell in respect to the hyaline one) its structure is more hydrophytic. Its variety *affine* has its cell-walls devoid of excrescences and is found in more constantly wet places.

Many examples of chambers for the storage of water have been mentioned; in addition the outer layers of the cells in stem, the spaces between the stem-leaves and the stem, the swollen auricular cells at the basal angles of the stem-leaves, the retort cells of the branches, and the spaces between the imbricated and concave leaves often serve for storing water. Some of these will be referred to with more detail later on.

Many *Sphagna* have a compact or tufted habit which is more pronounced in plants of drier moorlands, e.g. *S. compactum*, *S. cymbifolium* var. *congestum*.

REASONS FOR PROTECTIVE DEVICES.

It is difficult to reconcile the general watery habitat of *Sphagnum* with the presence of characters which, in other Mosses, act as xerophytic devices, and, as is evident from the comparison of different kinds of *Sphagnum*, also tend to act as protective devices with them. This tendency, however, is not always manifest; inconsistencies and anomalies are apparent if we attempt to make a comparative correlation of the structure of the plants and the wetness of their habitats. A species which is often found in a moist place, where it may be exposed to temporary dryness, is also found in a bog pool where wetness is permanent or almost so; a species showing many of the foregoing devices may occur in an almost constant pool, whilst another with fewer or less prominent devices is in a temporary water-basin, so that one is almost tempted to conclude that there is no correlation, and that the species of *Sphagnum* have wide ranges of habitat. Careful field-work, however, shows that there is some selective power, some species favouring very wet, and others moist habitats; but still there must be other factors influencing the distribution besides the degree of wetness, and the most important of these is the acidity of the solution.

It seems highly probable from recent work that *Sphagna* produce acids owing to the adsorption of the base by some substance of a colloidal nature present in the cell-walls, the amount of acid liberated being

a character which is fairly constant for a particular species under similar conditions. Owing to this method the plant is able to obtain its mineral food from very dilute solutions, and the author has long held the view that it can only grow well after fresh water has been supplied.¹ It may be submerged in water that is useless for the due discharge of its physiological functions since it is too acid in character and not available owing to its high osmotic activity; it is only when the solution is considerably weakened (as after rain) that the plant resumes its normal growth, the death and decay of the cells in the lower portions of the plant being largely due to the inability of the cells to use the water after it has become strong in 'humic' substances by concentration during a period of dryness.

Sphagnum seldom occurs in standing pools and stagnation of the water eventually kills it. It may occur in deep bogs, but the cells which are normally active are those towards the surface, and therefore in a position to profit more directly by the influx of dilute solutions. The normal habitat of many species, e. g. *S. cymbifolium*, *S. papillosum*, *S. acutifolium*, is on the margins of bogs, or in other places where an influx of fresh water is readily perceived by them. *Sphagnum* is a plant which has rapid growth in suitable conditions, and if very dilute solutions supply the mineral and nitrogenous substances necessary for metabolic processes, a large amount of these solutions will be required, and it is possible that

- (1) the solution is absorbed by the plant and the redundant water got rid of (a) by excessive transpiration from the chlorophyllous cells, or (b) by evaporation from the hyaline cells;
- (2) there is a special method whereby a colloidal substance present in the cell-wall adsorbs the base of the mineral salt.

When the plant relies mainly on the latter method the surrounding water becomes acid and may so interfere with endosmosis that sufficient water for physiological purposes is not available, and so devices protective against loss of water may occur. The structure of the plant is such that available water is quickly taken in by the hyaline cells, and passage of water up or down the surface of the plant is facilitated. For example, in *S. cymbifolium*, the hyaline cells with pores on their outer surfaces will quickly absorb the water during or after rain, whilst the pendent branches preserve a watery communication for diffusion of the mineral salts to the cells and of the liberated acids from the cells.

This special method does not exclude the more normal methods of obtaining mineral substances, is possessed by all *Sphagna* to some extent, and in most species appears to be the chief method. We can roughly place the species in three groups:

¹ Goebel, in *Organography of Plants*, has a note on the habitat of *Sphagnum*. He says, 'Sphagna chiefly live upon rain-water; they grow in places where the water only contains a small amount of mineral substances necessary for their nourishment, so that a profuse water-evaporation is necessary'.

1. Species which obtain their mineral substances from the water in which they live, have no excessive transpiration or evaporation, but supplement their income by the special method. They are usually plants of slow growth completely immersed in water. Their acidic value is low and their structure is the nearest to the phylogenetically primitive form. *S. obesum* is the best example of this group, but some other members of the Subsecunda section approximate to it.
2. Species which obtain their mineral substances by excessive transpiration of the redundant water from the exposed chlorophyllous cells, and also add to their income by the special method. They are plants of constantly moist situations, have a good supply of pendent branches for the passage of water to the exposed portions (Fig. 5, A), their acidic value is usually low and their chlorophyllous cells have been displaced to the outer sides of the leaves. *S. recurvum* and *S. amblyphyllum* belong to this group, whilst some other allied species closely approximate to it. *S. squarrosum* is better placed with this group, though in some respects it approaches the next.
3. Species which usually obtain most of their mineral substances by adsorption of the base and liberation of the acid. They are plants of variable habitat, their acidic values are usually high, and their structure is greatly modified. The most definite members of this group belong to the Acutifolia (e.g. *S. rubellum*) and Cymbifolia (e.g. *S. medium*) sections. They may sometimes be partially immersed in acidic water, whilst at other times they are much exposed, so that devices protective against dryness are adopted, these devices being chiefly for the purposes of facilitating intake and passage of water rather than against loss of water.

Some species have varieties which may be more appropriately placed in another group; thus the variety *imbricatum* of *S. squarrosum* is nearer to the third than to the second group, in which the type may be placed.

The species of the third group obtain their mineral salts from very dilute solutions formed after rain, those of the first group from the dilute solutions in which they live (the solids in siliceous streams are often less than 0.1 gm. per litre), whilst the second would usually be able to obtain a rather stronger solution. The following results were obtained on evaporating the water squeezed out from the tufts of *Sphagnum*:

<i>Species.</i>	<i>Group.</i>	<i>Habitat of Example tested.</i>	<i>Solid in Grm. per Litre.</i>
<i>S. cymbifolium</i>	3	Moist hollow of heath	0.05
<i>S. cymbifolium</i>	3	Damp hollow of heath	0.09
<i>S. Girgensohnii</i>	3	Moist places of heath	0.07
<i>S. rufescens</i>	1	Stream side just above the water, a constantly wet place	0.11
<i>S. subnitens</i> , mixed with a little <i>S. cymbifolium</i>	3	Stream side, but some distance above the water	0.08
<i>S. amblyphyllum</i>	2	Wet place on heath, a constantly moist place	0.13

FURTHER CHARACTERS IMPORTANT IN RELATION
TO WATER-SUPPLY.

Besides the characters previously mentioned there are others which are worth considering in relation to the water-supply :

1. *The relative positions, shapes, and sizes of the chlorophyllous and hyaline cells*, particularly of the branch leaves. (a) In *S. subsecundum* and its allies the two kinds of cells are almost rectangular in shape ; the chlorophyllous cell is medianly placed between the contiguous hyaline cells, and is more or less exposed on both the inner and outer surfaces of the leaf (Fig. 3, K ; Fig. 5, V), so that the only protection afforded to it by the hyaline cells is due to the fact that the thickness (antero-posterior diameter) of the hyaline cell is greater than that of the barrel-shaped chlorophyllous one and so to some extent overlaps it, the surface of the latter being less than the average area of a cross-section. The species of this section are founded on differences between the characters of the upper branch leaves ; the lower branches are usually immersed in water, have less distinctive characters, their chlorophyllous cells are wide, more or less rectangular, and little overlapped by the hyaline cells. In *S. obesum*, the most hydrophytic member, there is often little difference in size, shape, and position of the two kinds of cells (Fig. 5, V).

The median position of the chlorophyllous cell is also found in *S. papillosum* (Fig. 3, P) and *S. medium* (Fig. 4, K, L, M), plants of higher acidity and drier situations, but the chlorophyllous cell is more enclosed by the hyaline, and other methods (e. g. imbricated and cucullate leaves) for retaining or obtaining water are more prominent in these plants.

(b) In *S. cuspidatum* (Fig. 4, E), *S. squarrosum*, and their allies the chlorophyllous cell is triangular to sub-rectangular with its broader end exposed on the outer surface of the leaf. The outer walls of the hyaline cells are slightly convex but afford little shade to the surface of the chlorophyllous cell ; the inner walls are often more convex and overlap the chlorophyllous cells, but little protection against normal desiccation is afforded by this structure, so that practically the only advantage accruing to the living cell by the proximity of the hyaline one is that the latter acts as a reservoir. Under strong desiccating influences evaporation may occur on both the inner and outer surfaces and then the enclosure of the chlorophyllous cell on the inner surface may be beneficial.

S. cuspidatum (Fig. 4, E), with large sub-rectangular chlorophyllous cells free on both surfaces of the leaf, has the most aquatic environment ; *S. pulchrum* (Fig. 4, G), with the cells partially enclosed, has the driest habitat ; whilst *S. recurvum* (Fig. 5, C) and *S. squarrosum* are intermediate both in structure and habitat. *S. compactum* has its chlorophyllous cells

almost median but nearer to the outer surface (Fig. 4, I). Its densely tufted and compact habit, its closely imbricated and slightly cucullate leaves, enable it to grow in drier situations than any of the above, though its var. *squarrosus* with less crowded branches and more or less squarrose leaves has a wetter habitat than the type.

(c) In *S. cymbifolium* (Fig. 5, J, K, L), *S. imbricatum*, *S. fimbriatum*, and the *Acutifolia* group (Fig. 2, J), the chlorophyllous cells are triangular in shape, the base of the triangle being on the inner side of the leaf, whilst the outer walls of the hyaline cells are so convex that they entirely or almost entirely enclose those containing chlorophyll. This arrangement is an excellent device for lowering the illumination and for preventing excessive transpiration, and the *Sphagna* which possess it grow in situations exposed to light and with an inconstant water-supply, or in water which is strongly acid at times. These plants are seldom shaded; if they are, compensating characters such as looser or squarrose leaves (e.g. *S. cymbifolium* var. *squarrosulum*) are shown. As the *Sphagna* with median cells are more primitive in this respect, the displacement to the outer or inner surfaces may be regarded as due to light as well as to water requirements.

The relative sizes of the two kinds of cells must also be considered. The water-supply will be more profuse when the ratio

$$\frac{\text{Volume of hyaline cell}}{\text{Volume of chlorophyllous cell}}$$

becomes greater if we consider cells with similar positions and shapes, and when there is any overlapping of the hyaline cell over the chlorophyllous one, the shading will be greater the narrower the latter is; in *S. obesum* and *S. medium* the chlorophyllous cell is median, but is wider in the former, a plant of wetter habitat (cf. Fig. 5, T, V; and Fig. 4, K, L, M).

The stem-leaves also have variations similar to those of the branch-leaves, though of much less extent (Fig. 2, C, D, E, F). As they are usually concealed by the branch-leaves they have less chlorophyll; there is often little differentiation between the two kinds of cells, pores and fibres are fewer or absent, and in most cases their chief function is to assist the pendent branches in supplying water to the upper parts of the plant. The perichaetial and perigonal leaves are often more primitive in their structure and the differentiation into two kinds of cells is often incomplete (Fig. 3, C, D, F, G).

2. *Position, size, number, and bordering of pores in the hyaline cells*, especially in the leaves of the upper divergent branches.

The hyaline cell usually possesses fibres to maintain its shape, and its membrane is usually perforated to form pores. The usual form of pore is surrounded by a distinct thickened ring of cell-membrane which keeps it open, but non-bordered perforations also occur, especially on the lower portions or the inner surfaces of the leaf. The chief function of these pores

is the rapid intake of water, but they are also of use in promoting a readier diffusion of acids, and in some cases (especially in the Subsecunda section) a considerable amount of evaporation may occur through the pores on the outer surface. Their disposition varies according to the species:

(a) Pores chiefly on the outer surface of the branch leaf.

1. Pores large and few in each cell:—*Cymbifolia* section (Fig. 5, J, K; Fig. 4, K, L). In *S. squarrosum* and *S. teres* the pores are large and few, but the porosity of the inner is similar to that of the outer surface.

2. Pores moderate and few in each cell:—*Acutifolia* section (Fig. 2, H, I), *S. compactum*.

3. Pores small and many in each cell:—*S. subsecundum*, *S. inundatum* (Fig. 5, G, H), *S. rufescens* (Fig. 5, X, Y), *S. auriculatum*. In *S. rufescens* the pores are often numerous on the inner surface as well.

(b) Pores small and many, chiefly on the inner surface of the branch leaf:—*S. crassycladum*, *S. molluscum*. In the former the outer surface shows thickenings (pseudopores), indicating that it has been evolved from an ancestor possessing pores on the outer surface.

(c) Pores absent or few on both surfaces, if present small and usually on the inner surface:—*S. cuspidatum*, *S. riparium*, *S. obesum*, *S. recurvum*, *S. amblyphyllum*, all of which have an abundant water-supply (Fig. 4, C, D; Fig. 5, T).

The pores on the outer surface facilitate the rapid intake of surface water (as after rain), are usually bordered and so kept open. Evaporation of water may occur through them, and will be greater when the pores are numerous and small than when few pores have an equal area. When the leaves are more or less imbricated the pores on the upper exposed portions of the outer surface will be more efficient for obtaining external water, and these places show the most characteristic pore formation. The pores on the inner surface are favourably situated for interchange of substances and for obtaining water from the dilute solution passing along the axis of the plant; they are present though few and scattered in *S. recurvum* and *S. squarrosum* (with large pores), which obtain their main water-supply from below, but are best shown in the upper branches of *S. crassycladum*, a plant which is often immersed or almost immersed in streamlets or pools of fresh water.

The pores on the inner surface of the leaf or on the lower part of the outer surface overlapped by an imbricated lower leaf are usually weakly- or non-bordered, are often larger, and allow ready interchange of substances with the axial water-supply. The absence or paucity of pore formation is correlative with an abundant water-supply.

3. *Large superficial hyaline cells of the stem.* The presence of these may be considered a generic character, as in all species there are one or more cortical layers of large, thin-walled, hyaline cells surrounding a stereom ring of smaller and thicker walled cells and a central core of thin-

walled and fairly large cells. The only cells containing chlorophyll are immediately underneath the superficial hyaline cells. The following types occur :

- (a) The hyaline cells are in two or three layers but are not very distinct from the more internal cells, being only slightly larger and thinner walled:—*S. recurvum* (Fig. 5, B), *S. amblyphyllum*, *S. obtusum*. In *S. riparium*, *S. compactum*, and *S. pulchrum* they are often somewhat distinct, and therefore these plants may be better placed in (c).
- (b) They form one layer of large cells (with few or no pores) clearly differentiated from the stereom cylinder:—*S. subsecundum* and its allies (Fig. 3, J).
- (c) They form two to five layers of large cells clearly differentiated from the stereom cylinder:—*S. acutifolium* and its allies (Fig. 3, A), *S. squarrosum*, *S. teres*, *S. cuspidatum* (Fig. 5, P), *S. molluscum*, *S. cymbifolium* (Fig. 5, M) and its allies. Pores are few or absent (Fig. 3, B) except in the Cymbifolia group, which also have strengthening fibres in the cells (Fig. 3, N).

The plants of the first two types have an abundant water-supply, and have a low acidity, whilst most of the plants of the third type have a high acidity, and at times are exposed to drier conditions. The hyaline cells of the stem and their contained pores have similar functions to those of the leaf. The fibres similarly serve as strengthening bodies which cause the cell to retain its shape so that water may be quickly absorbed. In the leaf the fibres are often weak or absent in parts where there is a constant water-supply. Other things being equal the plants with pores and fibres are more able to withstand exposure.

4. *Other hyaline cells for the storage of water* are present in the retort cells and leaf auricles.

The retort cells are large flask-shaped cells superficially placed on the outside of the hyaline cells of the branch; their necks often curve away from the axis and are perforate at the ends. They vary according to the species, sometimes being absent, and reach their highest development in *S. molluscum* (Fig. 5, E, cf. D).

The basal angles of the stem-leaf are usually occupied by larger hyaline cells, and sometimes these are extended into little outgrowths known as auricles (Fig. 3, H, I). e.g. *S. auriculatum*, *S. inundatum*.

SPOROAGONIAL PLANT.

As the sporogonium is overtopped by the perichaetial leaves till it is almost mature, little further protection is needed by it. The calyptra is small and quickly disappears when the false seta elongates. The sporogonia then soon begin to 'pop' and the spores are scattered. In some species the

spores are shed when the plant is exposed to drier conditions than usual, and this may account for the papillosity of the spores (Fig. 3, M).

ASSOCIATES.

The associates of *Sphagnum* will be dealt with in a later paper.

GENERAL CONCLUSIONS.

Sphagna obtain their mineral salts from very dilute solutions.

They possess a special method of obtaining mineral food by adsorbing the base and liberating the acid.

In order to do this, special devices (which may seem of a xerophytic nature) are adopted to obtain a sufficient quantity of dilute solution, and to get rid of the superfluous acid and water.

These devices vary in different groups of *Sphagnum*. During periods of drought the income of exposed plants is suspended and the xerophytic devices may act as such, keeping the plant in a moist condition till a further supply of dilute solution is available.

Watson, William. 1918. "Sphagna, their habitats, adaptations, and associates." *Annals of botany* 32, 535–551.

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