THE ECOLOGY OF PEATLANDS: TEN MILLENNIA OF FLUID HISTORY

R.S. CLYMO

School of Biological Sciences, Queen Mary and Westfield College
LONDON E1 4NS, UK

This article was written for a book in Finnish that resulted from a Conference *'Aesthetics of Bogs and Peatlands'* held at Ilomantsi, Finland in June 1998. It presents some rough-hewn facts for those who appreciate peatlands but have little technical knowledge about them. I treat the peatland here as if it were a living bicycle: a relatively simple mechanism in which one may easily see that 'this' causes 'that', but which also has the most important property of life - it grows. The account is simplified but, with this limitation, I believe that it is 'true'. There are, of course, many other truths about peatlands that are not in this account. Treat it as a map of some of the main roads only.

The partial failure of decay

Let us approach peatlands obliquely by way of a woodland. The trees take in the gas carbon dioxide(1) from the air in which it occurs at very low concentration. To form a 10-centimetre cube of wood needs the carbon dioxide from the air in a cube of about 20 metres side. The leaves of the tree use the energy from light (the process called photosynthesis) and with it they convert the carbon dioxide into more chemically complex sugars, and these in turn into a cascade of other even more complex molecules including the cellulose and lignin(2) that form the main bulk of the leaves and wood. Leaves die and fall, and so, eventually, do the branches and trunk. On the forest floor a range of small and larger invertebrate animals such as mites and worms chew the fragments, digest what they can and excrete the bulk, thus mechanically reducing the size of the fragments. At the same time a precisely ordered series of fungi and bacteria of differing abilities break the fragments down chemically, reversing the effects of photosynthesis, and returning carbon dioxide to the air. At any one time the forest floor is covered by dead fragments in various stages of decay and decomposition, but eventually almost all the carbon returns to the air.

In peatlands things are different. Their plants 'fix' carbon dioxide by photosynthesis and incorporate it into the plant body in the same sort of way as trees do. But the processes of decay are impeded so that about 10 % of what is fixed does not decay and gradually accumulates as peat. Decade after decade, century after century, millennium after millennium this accumulation continues until today we may find ourselves standing on top of 5-10 metres of peat representing 5000-10000 years of growth.

Peatlands as archives

Throughout that time an impalpable dust of microscopic pollen grains from the surrounding forests and fields has been falling on the surface turning the peatland into a sequential archive: deeper is older. The pollen is exceptionally resistant to decay[3]. Individual grains can be identified under a microscope by the furrows, pores, spines, and plates on their surface. Examples are shown in Figure 1. {EDITOR: Fig. 1 near here.} From these identifications the changing composition of the surrounding forest and farmed land can be reconstructed. Absolute dates can be assigned from measurements of the residual proportion of the naturally occurring radioactive isotope[4] of carbon. The wing covers of beetles, often iridescent, are also preserved and can be used in the same way as pollen. Sometimes the bodies of larger animals (primarily the hair, nails and skin) are at least partially preserved, and even human bodies are occasionally found. A few of these human 'bog bodies' ('Tollund Man', 'Lindow Man') have been of great interest to archaeologists, and to journalists, while a thousand more all over Europe have attracted only local notice.

Why, then, is decay in peatlands so ineffective? That is the thread we must follow. Let us start at the present surface.

Bogs as deserts

Peatlands have a living and growing skin of plants on their surface. Some plants grow only on low hummocks, wine-red or tawny brown; others grow in wet hollows, bright green but softly treacherous. The crucial plants are the bog-mosses, *Sphagnum*, of which there are a dozen common sorts, that thrive on nothing more than air and rainwater or water that has flowed through soil or rock that is very poor in dissolvable plant nutrients. The moss has no roots with which to absorb nutrients, but its leaves are only one cell thick, and it absorbs over the whole of both surfaces. In fact conditions which, for most plants, would represent starvation are much too rich for *Sphagnum* and kill it. Sometimes the *Sphagnum* grows as a raft, held together by the roots and rhizomes of sedges growing with the mosses, and floating over a lake that is rich in solutes. In such cases the rain is sufficiently frequent and abundant to ensure that nutrient-poor rainwater flows downward around the mosses, thus preventing the baleful influence of the lake water beneath reaching the growing part of the mosses at the surface.

Besides living of necessity in undesirable neighbourhoods, *Sphagnum* makes conditions worse by turning the water around it almost as acid as dilute vinegar, using the same process that a water softener uses[5]. These conditions - acid and starved of nutrients - are very restrictive. Few rooted plants can survive: heathers (Ericaceae) on hummocks; cotton 'grasses' (*Eriophorum*) and other sedges such as beaked sedge (*Rhynchospora*) and deer sedge (*Scirpus*) in hollows. All these are set in a matrix of *Sphagnum*.

Of special interest are the insect-catching sundews (*Drosera*) and pitcher plants (*Sarracenia*), evading famine by digesting and absorbing the prey they have captured. These two groups of plants have very similar flower structures, and on these grounds are classified close to each other. It is not surprising that both are also insectivorous but it is extraordinary that the mechanisms are so different. The sundews have handsome, sticky, gland dotted leaves in which insects become stuck, while the pitcher plants rely on elegant modified leaves forming partly water-filled tubes with smooth rims down which insects slide to be drowned.

Even more surprising is that there is another pair of closely related insectivores: the bladderwort (*Utricularia*) and the butterwort (*Pinguicula*). Again the mechanisms are totally different. The bladderwort, which grows in bog pools, has hollow sacks a few millimetres across on submerged stems. Each sack has a hinged trapdoor at one end, and a mechanism that reduces the pressure inside the bladder thus putting the whole structure under stress. A water flea (*Daphnia*) inadvertently moving one of the trigger hairs that project outside around the entrance springs the trapdoor which is sucked inward. The water flea is also sucked in by the rush of water and, as the trapdoor springs back into the closed position the water flea is trapped. By contrast the butterwort mechanism is mundane: the untidy leaf surface is covered by sticky glands into which small animals blunder and from which they are unable to free themselves.

Sundews fed small insects in experiments do indeed grow better than unfed ones, and it seems obvious that the ability to garner extra nutrients in this way should give plants that have developed it an advantage in these peatland deserts: there must be strong selection favouring insectivory in peatlands, and we see here four different solutions to the nutritional problems posed to other plants by *Sphagnum*.

The bog asphodel, *Narthecium ossifragum*, looks like a small iris with beautiful bright yellow flowers. Its specific name means 'fragile bones' and reveals another aspect of starvation, this time of calcium (chemical symbol Ca). In the early part of the year, when other herbage is scarce, sheep graze on peatlands. They pull out the leaves of the cotton grass (*Eriophorum*), known for this reason to English farmers as 'draw moss', and eat the sugary leaf bases. They also eat the early leaves of bog asphodel. Both plants have unusually low concentrations of calcium in their leaves, and the sheep become calcium deficient and liable to break limb bones(6).

The colours of peatland plants are connected with nutrition too, and with temperature. When nitrogen is abundant the leaves of the sundew appear green - caused by the pigment chlorophyll(7) - with only tinges of red, but when starved of nitrogen and prevented from catching insects, the leaves become bright scarlet as a red anthocyanin masks the chlorophyll. *Sphagnum* too has a wide range of colours. The species that live submerged in hollows or pools are usually bright green - chlorophyll again. Species such as *S. magellanicum*, which lives just above the watertable, and *S. capillifolium*, which lives on hummocks, are able to produce a unique red pigment that masks the green chlorophyll. The formation of this red pigment is favoured by temperatures above freezing but below 10 °C, so in the low sun of autumn the carpets of wine-red *Sphagnum* can seem to dazzle with an inner light.

The upward growth process

The processes in the surface are summarised in Figure 2. {EDITOR: Figure 2 NOT yet please! Place is marked later} *Sphagnum* has only one growing point, a dome 1-2 millimetres across at the top of the plant. This dome grows upwards and produces on its surface the humps that develop into branches that in turn produce leaves. The moss plant therefore stretches ever upwards. At first the leaves are green, and the stem, branches and leaves are alive. The leaves photosynthesize and fix carbon dioxide adding to the moss substance. But by the time a few centimetres of new moss has been added above where we started the shade at that level has become so dense that most of the moss dies. It turns straw-colour but keeps its very open structure, like a very porous sponge, so air and water can and do move easily among the dead stems and leaves. Almost nothing eats *Sphagnum* deliberately - the reason is unclear - but in these conditions, with abundant oxygen in the air, fungi attack the dead *Sphagnum* and begin its decay. By woodland standards the rate of 5-20 % each year is rather low, but if it were allowed to continue without interruption all the plants would be reconverted to carbon dioxide eventually. We might have 60 centimetres of rotting moss, but not the ten times greater depth of peat that actually accumulates. So what causes the difference?

The continuing decay is like knocking random bricks out of a wall. For some time the wall stays as a wall though increasingly perforated. Eventually one more brick is removed and the whole structure collapses. This happens to the dead *Sphagnum*, which now occupies perhaps a quarter of the height it began with. When it does collapse all the remaining stem and leaf fragments are pushed closer together. The effect is the same as squashing a sponge: water finds it several hundred times more difficult to move. This change has dramatic consequences, as Figure 2 shows. {EDITOR: Fig. 2 near here.} Water draining from above can no longer flow downwards easily and is diverted sideways. As long as there is more rain than can evaporate then the pores in the peat, as it now is, are refilled with water as soon as they begin to empty. In a dry summer the watertable may sink 30-50 centimetres, but it rises again at the first heavy rains. The higher it rises the easier it is for the water to flow away sideways, so it is self-regulating, never getting much above the average level.

We now have a permanently water-saturated sponge of peat, in which 95 % is water and only 5 % solid[(8)]. Above the watertable oxygen in the air moves about easily by mass-flow ('breezes'), but below it the oxygen moves down through the water mainly by diffusion[(9)], which is ten thousand times slower than diffusion in air. Bacteria just below the water level use up the oxygen faster than it can be replaced by diffusion, so the whole mass of peat below contains no dissolved oxygen - it is anoxic[(10)] as Figure 2 shows. The fungi require oxygen and so do many bacteria: none of them can function and most cannot survive any longer. The decay, of which they were the causes, stops.

These oxygen-requiring microorganisms are replaced by other sorts that operate without oxygen and continue the decay, producing methane[(11)] instead of carbon dioxide[(12)]. In a layer a few centimetres thick the rate of methane production is as high[(13)] as was that of carbon dioxide. The rate of methane production and consequent decay soon drops, however, so that the rate of decay becomes no more than a few thousandths of the rate that it was in oxygen. Most of the plant material that survived to be engulfed by the watertable (rising to the level where the dead plants collapsed) now has a much greater 'life' expectancy. It is the waterlogging and the consequent anoxia and change to much slower anaerobic bacterial processes that results in the accumulation of peat. The peat also acts as a thermal insulator, much as expanded polystyrene blocks do for a house. The further down into the peat the smaller the temperature variations become: at 5 metres deep the fluctuation throughout the year may be only 2 degrees Celsius. Dark, water-saturated, anoxic and nearly isothermal are the monotonously uniform conditions in which the decay bacteria live.

We see, then, that peat accumulation is not a passive process: it depends on the continuing addition of sufficient rain, and the continuing activity of bacteria that consume oxygen faster than it can diffuse down.

In this waterlogged world then, held together by a surface skin and containing barely 5 % of solid matter, decay almost stops. Every year another centimetre of moss is added to the surface and, as a result of decay and collapse, 90 % of that is lost so that about 1 millimetre of peat is added each year. The entombed dead plants accumulate, layer on layer, millennium after millennium. They preserve with them the evidence of the climate and plants of their own time. The giant semi-fluid drops of peatland, like enormous over-ripe cheeses, can be ten kilometres across and ten metres deep. When we carefully pick our way across them we may indeed be walking on 10 000 years of viscous history.

Hummocks and hollows

The majority of peatlands have hummocks and hollows, each with its own distinctive species of *Sphagnum* and associated rooted plants. In hollows we find species such as *Sphagnum cuspidatum*, dark green in Spring, robust, and with a shaggy outline. With it grow a variety of sedges all with grass-like leaves. These leaves live for a year or so, but they provide no sort of permanent structure. Hummocks are quite different. The densely packed, small but tough, *Sphagnum fuscum* forms a matrix in which grow woody ericaceous shrubs. When growing on mineral soil these shrubs have a limited life of perhaps 30-100 years. But on peatlands the *Sphagnum* grows up around the stems creating humid conditions that encourage the stems to produce new roots. This rejuvenates the shrub which then grows on upwards. The *Sphagnum* is also encouraged to elongate by the shade of the shrub - a near universal response of plants in shade. Moss and shrub thus encourage each other upwards, forming a hummock, and making the shrub potentially immortal.

We know from the identifiable remains of the plants in the peat that hummocks tend to remain as hummocks for thousands of years, and hollows do likewise. But why does the hummock not get further and further above the hollow? As it gets taller so there is an increasing depth of peat below it in the hummock and that peat is odic and decays relatively fast, as Figure 3 shows. {EDITOR: Fig. 3 near here} Eventually this loss over an increasing depth comes to balance the greater gains of the moss and shrub association on the surface[14]. The hummocks behave like small dogs on a lead, straining ahead of their slow-moving owner - the hollows - as far as they can. If the owner speeds up the dogs immediately rush to the limit of the lead re-establishing their distance in front of their owner. If the owner slows down the dogs are forced to do so too. Hummocks and hollows are a self-regulating pair, just as the water level itself is.

The uses of peatlands

Peatlands had many traditional uses. The frequent discovery of 'bog butter' suggests that peatlands served as primitive refrigerators. The number of human burials, often in circumstances suggesting capital punishment or sacrifice, also suggests deliberate use. William King (1685), giving the fourth of six reasons for draining Irish bogs, writes that '[the bogs] are a shelter and refuge to *Torys*, and *Thieves*, who can hardly live without them.' The traditional fear of peatlands, mostly fuelled by ignorance, gave powerful protection to those who were bold or necessitous enough to test these beliefs experimentally.

A few of the modern users of peatlands are content to accept the peatland as it is: cloudberry and bilberry pickers, and the occasional scientist, are examples. Most walkers avoid crossing wet and unstable ground. Ornithologists and artists with pencil, brush or camera may be attracted but most stay at a 'landscape' distance unless there is a wooden walkway. Most of these users are concerned to avoid damaging or changing the peatland.

Others see the peatland as a 'resource' to be bent to their own ends with unavoidable changes. The first, and essential, inclination of farmers and foresters is to drain the peatland. Engineers of roads and railways are happiest to remove the peat or, if that is not possible, will lay their constructions on piles of brushwood on top of it. Most destructive of all are those who mine the peat for fuel or horticulture. The argument that 'as much new peat is forming in numerous other untouched peatlands in the same region as is being mined in this one' seems specious. This one, with its archive, is gone for ever. Nevertheless there are strong economic arguments for *some* mining, and there are growing concerns among the exploiting companies about the brown wastes that result during the process and especially about some form of rehabilitation afterwards.

A wider view: the sorts of peatland

The account I have given applies strictly to an unforested rainwater-dependent bog. There are many other sorts of peatland. The most important factor, common to all, is waterlogging for all or most of the year, with the consequent anoxic conditions, slow decay, and accumulation of organic peat. The circumstances that enforce waterlogging differ however.

Nutritional state is the second most important factor. If the peatland *surface* is dependent on rainwater, or on water that has flowed through soil or rocks ('groundwater') but with few dissolvable nutrients, then *Sphagnum* is the usual dominant, forming peat by the processes already described. The underlying water may be nutrient-rich, but rainfall must be sufficiently high and frequent to ensure that water flow *through the surface* is almost always downward.

Peatlands whose surface is rainwater-dependent are 'bogs' (the technical use of the term) while those dependent on groundwater are 'fens'[(15)]. If the groundwater is rich in nutrients there will be no *Sphagnum* but a great variety of rooted sedges, herbs, and brown mosses can flourish: often more than 30 species in a metre square. The process of peat accumulation is much the same as in a bog but the constancy of supply of groundwater is more important than collapse of plant structure in maintaining waterlogging. The groundwater may, however, be so nutritionally poor that *Sphagnum* and its associates can flourish. Such a peatland is technically a fen because of its surface dependence on groundwater, but its plants may be scarcely distinguishable from those found in a bog. In practice therefore it may sometimes be difficult to decide whether a particular peatland is bog or fen.

The third important factor is how the peatland has formed. There are two main ways. A lake may be gradually filled in - the process of *terrestrialisation* - passing through being a fen and then, as the peat rises above the height at which it can be flooded occasionally by groundwater, becoming a bog, whose surface is dependent on rainwater and becomes colonised by *Sphagnum*. The watertable now rises in a dome above the regional watertable and is maintained so by rain in excess of both evaporation and very slow drainage through the peat. Excess water, and there must be some excess, runs off sideways through the porous surface.

The second main way a peatland forms is directly on mineral soil. This requires either or both a fairly constantly damp climate and an existing peatland that can extend outwards. This process is *paludification.*

Ecologists have taken some of the common words for watery places - mostly English, German, Finnish and Swedish - and have restricted their use for technical purposes. A summary of these specialist uses is in Table 1. {EDITOR: Table 1 near here}

Acid *Sphagnum*-dominated bog, more alkaline fen, and swamp with permanent standing water are the three main types of peatland; peatlands and marsh together constitute mire; while 'wetland' is a very much broader term including shallow lakes and stream sides with very different ecological features. Those who use 'wetland' usually have these permanent shallow water systems in mind, often with an ornithological bias, and then go on to ignore the much greater area of peatlands.

Thumbnail sketches of some of the main sorts of peatland, in the strict sense, follow.

Fen

The range from nutritionally rich and strongly alkaline to poor and mildly acidic is 'extreme rich', 'rich' and 'poor' fen. The water source is usually some sort of spring(s) or seepage(s) ensuring a fairly constant supply. The terms parallel the species richness too. At one extreme there may be a hundred species of sedges, herbs and brown mosses in a hectare; at the other only a few tens, and resembling a bog in the abundance of *Sphagnum*. Small fens are often heavily grazed and this keeps them open and species-rich. Others support willow bushes and trees. Such woodlands are called *fen carr*.

Schwingmoor

A German word. The extreme form of terrestrialisation. A small lake fills a hole, sometimes shallow but often perhaps 15-20 metres deep where a block of ice was stranded at the end of the last glaciation. A floating mat of sedges grows out from the sides of the lake toward the middle forming a raft, supported by the interlaced roots and underground stems of the plants, and moving up and down as the lake level does. If the rainfall is sufficient this raft may be invaded by *Sphagnum*, followed by its associates and even by pine trees. The underlying lake water may be nutritionally rich but as long as the rain ensures downward water movement the *Sphagnum* is chemically insulated from the lake below and thrives. The raft thickens and spreads, eventually occluding the central pool that is all that can now be seen of the lake. From time to time, when the raft has become 1-2 metres thick, slabs of peat fall from its bottom. One may stand on the surface, flex ones knees, and see waves travelling out across the vegetation surface. But beware! Schwingmoor is the only type of peatland that is really dangerous[16].

Schwingmoor is instructive, and exotic, but it occupies only small areas.

Blanket bog

The (opposite) extreme example of terrestrialisation. Dominated by *Sphagnum* and its associates, forming in a very wet climate. Best developed at the southern tip of South America, Newfoundland, Ireland and Scotland especially in its far north. The sea spray is sometimes sufficient to support species such as black bog rush (*Schoenus nigricans*) usually found only in fens. The peat is usually 1-3 metres deep and blankets the whole countryside on slopes as much as 20 °. On such slopes it is unstable and there are frequent reports of 'bog bursts' or 'bog slides' usually resulting from exceptionally heavy rain. The break usually occurs at the top of a slope and the whole mass of peat slides downhill, often on an underlying lubricating bed of glacial clay.

Raised bog

English equivalent of the original German 'Hochmoor'. Rainwater dependent, with a domed cross section, perhaps 5-10 metres of peat at the deepest point and half to several kilometres across. Dominated by *Sphagnum* and its associated sedges and dwarf shrubs. Usually with patterns of concentric permanent pools and intervening hummocks around the highest point, but hummocks and seasonally wet hollows further from the highest point. Water from surrounding hills is diverted around the edges of the raised bog and gives a marginal 'lagg' fen. Raised bogs often developed initially by terrestrialisation through fen to bog, but may now be spreading by paludification. In very wet climates (continental west coasts) they may have developed by terrestrialisation from the beginning and be difficult to distinguish from blanket bog. In Fennoscandinavia from south to north, and in North America from east to west, a series of sorts of raised bogs is found: plateau (large flat tops); concentric (highest point near the centre, usually formed on a horizontal or saucer-shaped base); eccentric (highest point near one edge, often near the top of an underlying gently sloping base).

Aapamire

Finnish origin and abundant there and in Sweden and adjacent Russia. Occurring to the north of the raised bogs in Fennoscandinavia. From the air one sees 'strings' separated by large flat 'flark's, also called 'rimpi'. On the ground it becomes clear that the flarks are fens, fed by groundwater, filled with a barely stable mat of sedges and specialised species of *Sphagnum.* The strings are hummock ridges, dependent on rainwater and are therefore linear bogs. The strings run parallel to the contours and are thus athwart the water flow: an implausible fact that still defies adequate explanation. The steeper the slope, the closer the strings are to one another.

North American mires

The peatlands occupying the bed of the former Lake Agassiz in Minnesota and those around James Bay are enormous. They consist of sedge and brown moss covered fen 'water tracks' up to several kilometres across and longer than wide. Dotted among these are raised, tear-shaped, forested 'ovoid islands' up to a few hundred metres across and rather longer than broad, oriented with their long axis parallel to the water flow. On either side of the water tracks are 'raised bogs' usually forested. The peat shows that there have been historical reversals of sequence rarely found in European mires: fen has been replaced by bog in both areas, but in North America bog has often then been replaced by fen, and that in turn by bog again. In Europe one usually finds that the rock underlying a mire is practically impermeable to water. But the giant North American mires have formed on the bed of what were enormous lakes in glacial times and the water circulation continues into the old lake sediment. An increase in rainfall on a ridge 50 km away may result much later in an increased upwelling of nutrient-rich water at a particular spot that has been raised bog, but must now change to fen vegetation as nutrients break though to the surface again. In Minnesota where evaporation is high and rainfall relatively low raised bog is particularly liable to such reversals.

Conclusion

These then are the peatland essentials: waterlogging; the source of water - its amount, reliability and nutrient content; the resulting presence or absence of *Sphagnum* - determining the other plants that can grow with it; only partial decay of the plants with consequent accumulation of peat and an archive of pollen and other organic remains spanning as much as 10 metres in depth and 10 millennia in time. Great variety in detail but unifying mechanisms controlling water level and the persistence of bog hummocks and hollows. In all the largest natural landscape engineering enterprise that we know.

Bibliography and References

Most of the publications that follow are written for the general reader, and assume little or no formal scientific education.

Anonymous 1984. *Peat Dictionary.* International Peat Society, Helsinki. [Technical peatland and peat-users dictionary with equivalents in Russian, English, German, Finnish and Swedish and a separate index in each language.]

Brothwell D. 1986. *The Bogman and the Archaeology of People.* British Museum Publications, London. [Lindow Man.]

Clymo R.S. (1987) The ecology of peatlands. *Science Progress, Oxford* 71: 593-614. [For the general scientific reader.]

Glob P.V. 1969. *The Bog People. Iron Age Man Preserved.* Faber and Faber, London. [Tollund Man.]

Godwin H. 1981. *The Archives of the Peat Bogs.* Cambridge University Press, Cambridge. [Botany, ecology and archaeology of peatlands.]

Kerr W.A. (1905) *Peat and its products.* Begg, Kennedy and Elder, Glasgow. [Peat getting and its uses.]

King W. 1685. Of the bogs and loughs of Ireland. *Philosophical Transactions of the Royal Society of London* 15: 948-960.

Moore P.D. and Bellamy D.J. *Peatlands.* Elek Science, London. [Rather out of date but the only simple scientific account.]

Rennie R. 1807, 1810. *Essays on the Natural History and Origin of Peat Moss. Vol.1 1807; Vol. 2 1810.* George Ramsay, Edinburgh. [Early account of the types and uses of peatlands for agriculture.]

Vasander H. (ed) 1996. *Peatlands in Finland.* Finnish Peatland Society, Helsinki. [Ecology, uses, and conservation.]

Wright H.E Jr, Coffin B.A. and Aaseng N.E. (eds) 1992. *The Patterned Peatlands of Minnesota.* University of Minnesota Press, Minneapolis. [General account of the ecology, geology, and archaeology of one of the giant North American peatlands.]

Notes

(1) Carbon dioxide has one carbon atom linked strongly to two oxygen atoms: the chemical formula is CO_2, with 'C' indicating carbon, 'O' indicating oxygen, and the subscript the number of oxygen atoms. Carbon dioxide is a gas at ordinary temperatures, and water will dissolve about an equal volume of CO_2. In air one molecule in every 2500 is carbon dioxide. Most of the rest in decreasing abundance are nitrogen (80 %), oxygen (20 %), water vapour (variable), and argon (1 %).

(2) *Cellulose* is composed of simple sugar molecules linked in a long chain - an example of a polymer. It forms the main part of the flexible structures in plants and confers toughness. *Lignin* is a series of complex molecules containing rings of six carbon atoms (called aromatic rings) with side chains attached. It is deposited among the cellulose polymers and makes the structure more rigid and strong.

(3) A small piece of peat teased out in water will usually display abundant remains of *Sphagnum* leaves, which may be identified and from which the surface type may be inferred.

Pollen grains (and the spores of fungi) can be separated from the peat by boiling it for quarter of an hour with strong caustic alkali which dissolves most of the peat but leaves the pollen unchanged. The pollen can be sifted (or centrifuged) to separate it from the solution. It is washed several times with water to remove the alkali. A tiny amount of the sediment is mixed on a microscope slide with a warm jelly containing a red dye that is absorbed selectively by the pollen grains. A very thin flat cover glass is put on top, spreading the pollen suspension out. When the jelly cools the cover glass is firmly stuck to the slide. After a few days the pollen has turned bright pink and individual grains can be identified under the microscope. Figure 1 shows examples. The process is highly skilled and tedious. It is usual to identify and count at least 150-200 grains on each slide for routine purposes, and several thousand for special ones.

(4) The common form of carbon atom weighs almost exactly 12 times as much as a hydrogen atom. But there is a much rarer form that weighs 14 times as much as the hydrogen atom. These forms with different weights are called *isotopes* and are represented as ^{12}C and ^{14}C, the presuperscripts indicating the isotope. The ^{14}C is formed in the upper atmosphere when an energetic particle from outside the Earth hits a nitrogen atom. The ^{14}C is incorporated into carbon dioxide and some of that is fixed in plants by photosynthesis. The ^{14}C is weakly

radioactive, about half the atoms formed disintegrating back into nitrogen in the first 5800 years, half of what is left (i.e. a quarter of the original) in the next 5800 years, and so on. After, say, 4 'half-lives' we have ½ x ½ x ½ x ½ ≈ 6 % of the original ^{14}C left. The rate of addition of new ^{14}C in the upper atmosphere is balanced by the later loss by radioactive decay, wherever the ^{14}C has got to, so the proportion of ^{14}C:^{12}C in newly formed plant matter stays fairly constant. From then onward in dead plant matter it decreases as the ^{14}C disintegrates, and from the proportion left we can infer the age. If in a piece of peat it is half what it starts at then the peat formed about 5800 years ago; if it is only a quarter then the peat is 11600 years old, and so on.

(5) The process used in water softening, and that causes the water around *Sphagnum* to become acid, is called *cation exchange*. Solutes carrying a positive electrical charge are called cations. An example is the sodium ion: Na^+ (Na for the Latin 'natrium' by which name sodium was once known). Negatively charged ions are anions, for example chloride Cl^-. The number and sign of charges is shown as a superscript. A water softener consists of an aggregate of large insoluble negatively charged molecules whose charges are initially matched with an equal number of Na^+ from the common salt, Na^+Cl^-, with which the softener was charged. The hardness of water is caused by dissolved calcium ions, Ca^{++} or Ca^{2+}, each carrying two positive charges. As water passes through the softener the Ca^{++} ions compete with the Na^+ for the fixed negatively charged sites, and most succeed and are retained there. The water emerges with less Ca^{2+} and equivalently more Na^+ than when it entered. *Sphagnum* behaves like this too except that the plant forms its exchange sites as long polymers of acids derived from sugars, with which it makes part of its walls. These tethered anions are formed with associated acid hydrogen ions, H^+, as the counter ions. These H^+ are then displaced by the low concentrations of other cations in rainwater. The displaced H^+ are what makes the water acid.

(6) An interesting example of two common questions. First, is illness caused by a 'deficiency' or by a 'poison' i.e. by something negative or something positive? Secondly, is the plant the 'cause' or is it simply associated with something else that is itself the cause. This is the distinction between causal '*regression*' and mere associative '*correlation*', probably with some underlying common cause. The strong human tendency to assume that a correlation is a regression contributes powerfully to survival, even when it is incorrect as it often is, and is the usual basis for that unfairly maligned response: prejudice or prior expectation.

(7) Plants contain many groups of pigments. Within any one group the differences are relatively small, between groups they are large. A single pigment molecule typically contains tens to hundreds of atoms. The green *chlorophylls* have four pyrroles (a ring of four carbons and one nitrogen) linked in a super-ring, and are involved in the conversion of light energy to chemical bond energy - the primary step in photosynthesis. Rather surprisingly their chemical structure is similar to the red blood pigment haemoglobin. The yellow or orange *carotenes* are ancillaries in photosynthesis. The *anthocyanins*, red when acid and blue when alkaline, and the yellow *xanthophylls* are flower pigments that may serve to attract pollinators. The dark red to violet *sphagnorubins* are unique to *Sphagnum*. Their function, if they have one, is not known.

(8) The average concentration of solids in peat is about the same as that of solids in milk. Yet one can walk on a peatland. Partly this is because of the surface mat of plant roots and rhizomes (under-surface stems), which form a dense weft in the 20 centimetres or so below the surface. But the peat below has greater strength than milk too, as a result of the separate

plant structures, especially the fibres, that have not yet decayed. Take a small piece of peat and tease it out in a saucer of water to see how abundant these fibres are. Some of the cotton grass fibres resist decay so well that they can be separated, spun, and woven into a textile.

(9) Matter moves in two main ways: *diffusion* and *mass flow*. Diffusion is like an aimless crowd that starts in a compact mass. Every individual (molecule) moves and is buffeted randomly by others. As time passes a few favoured individuals that, by chance, have had fewer or less diverting collisions, have moved a long way. Most, however, have found movement in one direction countered by later collisions, so they remain concentrated near the original centre of the crowd. Mass flow, by contrast, is like having the crowd on a train. An external force moves the whole mass collectively in the same direction (probably with small scale diffusion inside the train). Diffusion is unavoidable in a fluid and is an effective mechanism for moving molecules over distances up to perhaps a tenth of a millimetre. But to move large amounts quickly over bigger distances needs mass flow, and that requires conduits and external forces.

(10) Where there is no free molecular oxygen (O_2), i.e. oxygen not combined in some bigger molecule, the *conditions* are 'anoxic'; where there is molecular oxygen conditions are 'oxic'. Bacteria whose *life processes* can operate without molecular oxygen are said to be 'anaerobic' while the processes of those that use molecular oxygen are 'aerobic'. The molecular bases are very different. Some bacteria are able to operate in either mode, switching between one and the other as conditions change. They are 'facultative'. Those that can work in only one mode are 'obligate'.

(11) Methane consists of a carbon atom with four hydrogen atoms strongly bound to it: so the chemical formula is CH_4. At ordinary temperatures methane is a gas. Water will dissolve about 4 % by volume of methane (and about 100 % of carbon dioxide). A methane molecule in the atmosphere absorbs about 20 times the energy that a carbon dioxide molecule does, and is thus a more potent contributor to climate warming. Peatlands lock away carbon dioxide as peat (reducing the warming potential) but return some of the carbon dioxide as methane (increasing the potential). It is unclear whether the balance of these opposing processes is to warming or cooling.

(12) In anoxic conditions the oxygen-containing *oxidised* form of carbon, CO_2, is replaced by the hydrogen-containing *reduced* form CH_4. There are other similar changes. Sulphur which was present as sulphate, SO_4^{2-}, now appears (Figure 2) as the gas hydrogen sulphide, H_2S and gives the smell of rotten eggs easily noticeable as one walks in the wetter parts of a bog.

(13) Some of this methane escapes. It may be the cause of the light occasionally seen on moonless nights on bogs, variously know as 'will o' the wisp', 'ignis fatuus', 'foolish (or fool's) fire' and 'Jack o'lantern'. I have yet to meet an eyewitness of this light. How methane might be ignited is a matter for speculation: we know that piles of milled peat stored on the bog surface can ignite spontaneously but the peat in the piles is much drier than it was in its native state. Jack o' lantern stories as well as the superficial surface instability and unplumbed depths of peatland pools, contribute to the suspicion with which peatlands have traditionally been viewed.

(14) At this point the system is controlled by *negative feedback*. Deviations from the *set point* create forces that are so directed that they tend to return the system to the set point.

(15) Bogs, dependent on rainwater for their nutrients, are termed *ombrotrophic* (Greek 'rainstorm-fed'); fens are *minerotrophic*. Rainwater, including snow, hail and other forms of precipitation, is sometimes termed *meteoric* water (Greek 'atmosphere') while groundwater is *telluric* (Greek 'Earth').

(16) Conan Doyle describes the Great Grimpen Mire on Dartmoor into which Sherlock Holmes pursues the evil Stapledon, owner of the Hound of the Baskervilles, and himself an unacknowledged Baskerville. '[The] path zigzagged ... amongst those green scummed pits and foul quagmires which barred the way. Lush slimy water-plants sent an odour of decay and a heavy miasmatic vapour into our faces, while a false step plunged us more than once thigh-deep into the dark quivering mire, which shook for yards in soft undulations around our feet. Its tenacious grip plucked at our heels as we walked, and when we sank into it it was as if some malignant hand was tugging us down into those obscene depths, so grim and purposeful was the clutch in which it held us.'

Foxtor Mires on Dartmoor best fits the location in the story. It is not a schwingmoor and is barely a metre deep in most places. But schwingmoor is the only type of peatland that deserves the sense of real danger that Conan Doyle's description evokes.

TABLE 1.

Sediment type	Water source	Summer water level	Name	Composite peatland	Wider term - - - - - - - >		
	Rain[C]	At or below the surface	*BOG*[E]	Aapamire[F] Agassiz[G]	|	|	|
Mainly peat[A]	Ground-water[D]	At or below the surface	*FEN*[E]		*PEAT-LAND*[E]	*MIRE*[E]	|
	Ground-water[D]	Above the surface	*SWAMP*[E]		|	|	*WET-LAND*[E]
Mainly mineral[B]	Ground-water[D]	At or below the surface	*MARSH*[E]			|	|

[A] Organic matter most of which burns, leaving little behind.
[B] Inorganic matter most of which will not burn, and remains if put in a fire.
[C] *Meteoric* water including snow, hail etc.
[D] *Telluric* water that has flowed through rock or soil or both.
[E] The seven names in capital italic have restricted meanings in ecology.
[F] See text for brief description.
[G] Enormous North American peatland complex; see text for brief description.

CAPTIONS TO FIGURES

Figure 1. Examples of pollen (left) and *Sphagnum* (bogmoss) leaves found in peat.

At the top left: tree pollen, in order of immigration. Birch (*Betula*), pine (*Pinus*) with two 'sacs', oak (*Quercus*); elm (*Ulmus*), alder (*Alnus*) with five pores; linden (*Tilia*), hornbeam (*Carpinus*), beech (*Fagus*) with three furrows. At the middle left: two sedges from hollows and two dwarf shrubs from hummocks. Cotton grass (*Eriophorum*), beaked sedge (*Rhynchospora*); ling (*Calluna*), heather (*Erica tetralix*). These pairs are very similar and are separable only on details of the surface sculpturing that are not visible at this magnification. At the bottom left: a grass crop plant and a weed of cultivation. Rye (*Secale cereale*), plantain (*Plantago*). Crop grass pollen is usually bigger than its wild ancestors.

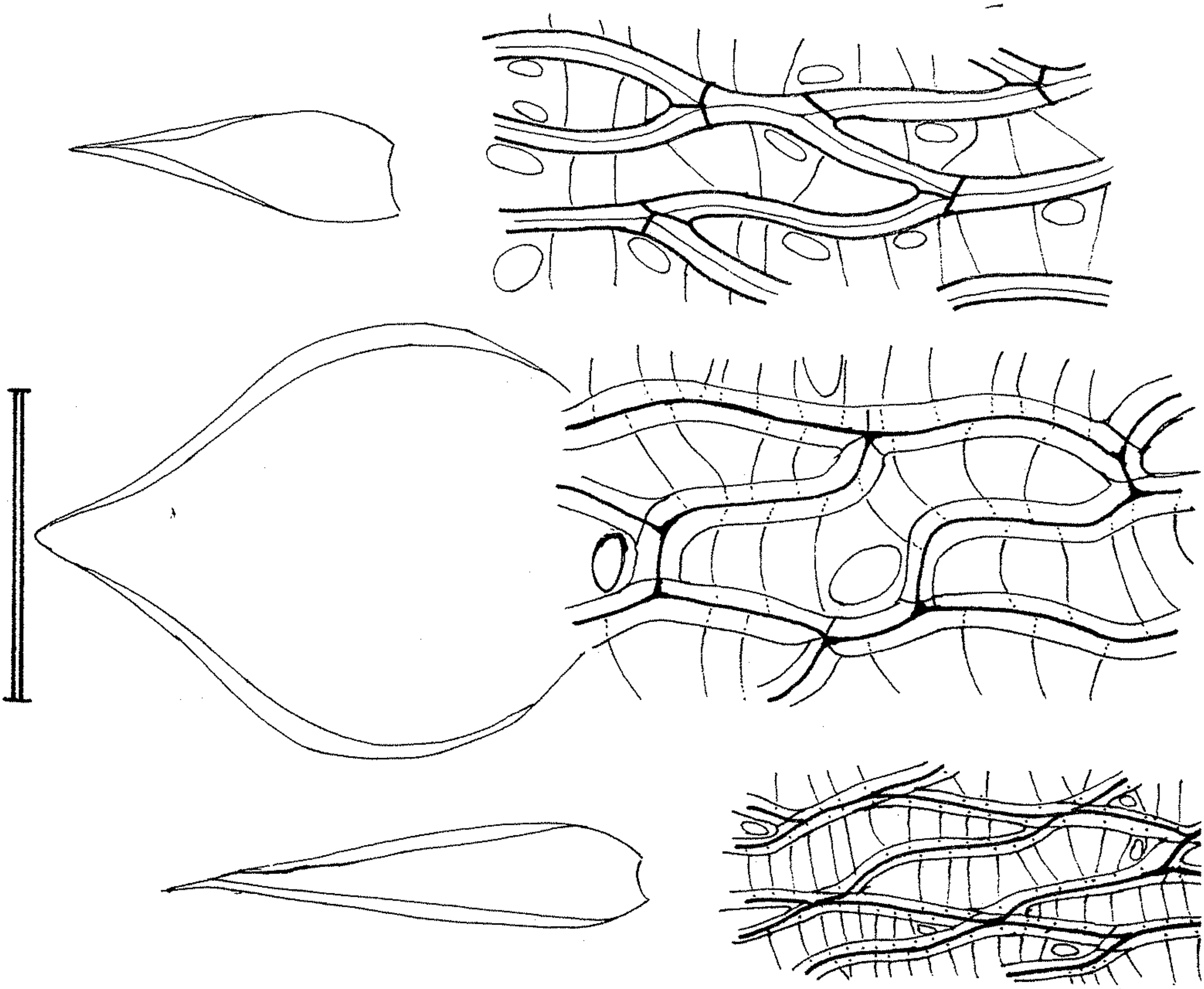
At the bottom right: details of cells in the leaf of *Sphagnum* species of hollow, lawn and hummock. *Sphagnum cuspidatum*, *Sphagnum magellanicum*, *Sphagnum fuscum*. Cells are of two kinds. Thin sinuous live chlorophyll-containing cells appear as three parallel lines. In cross section these cells are triangular or pointed ovoid. The outer two lines show the maximum width; the centre line shows the narrowest part of the cell. The left leaf has the point of the triangle upwards; the right leaf has it downwards, and the centre leaf has pointed ovoid live cells. The larger sinuous cells are dead and empty of contents. They have hoops of thickening shown by thin lines, and pores in the walls shown as ovoids.

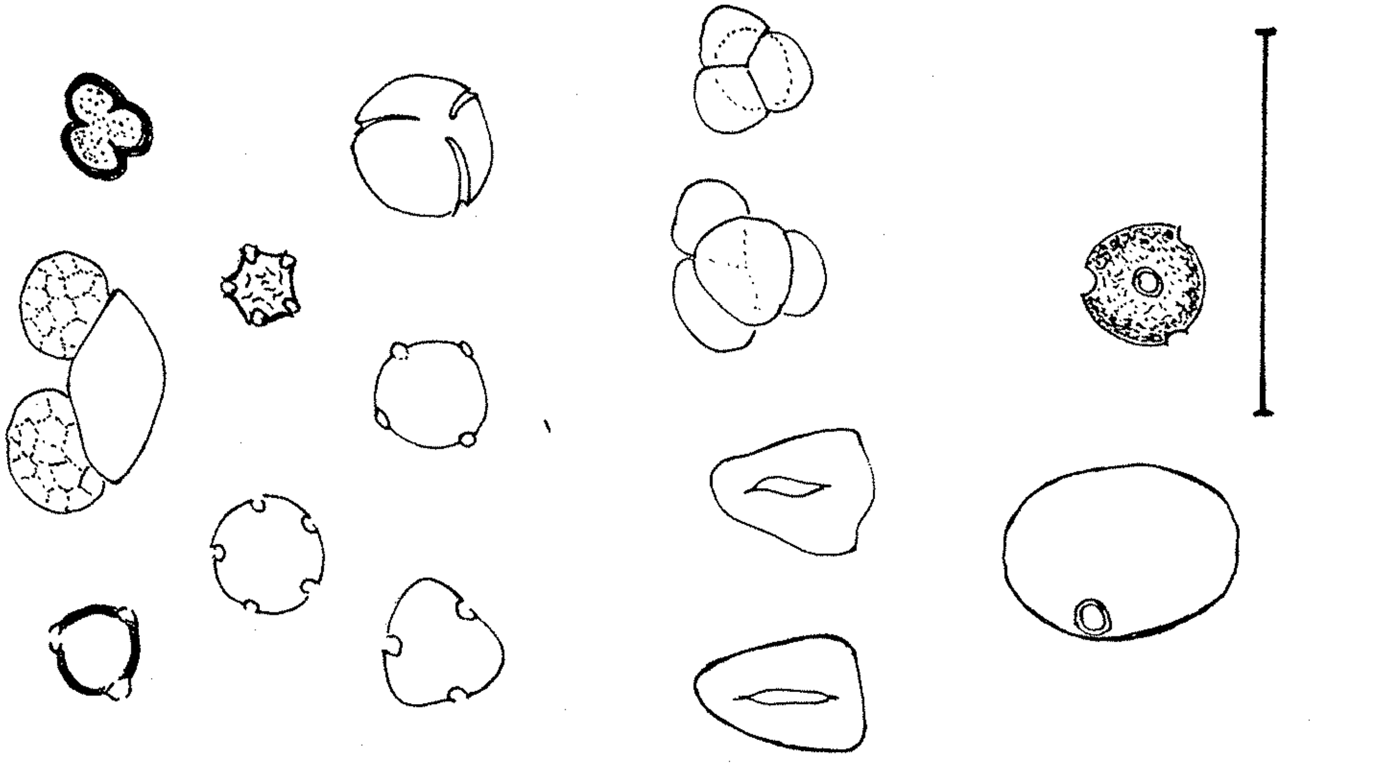
All pollen and *Sphagnum* leaf cells at the same magnification - the bar indicates 1/10 millimetre.

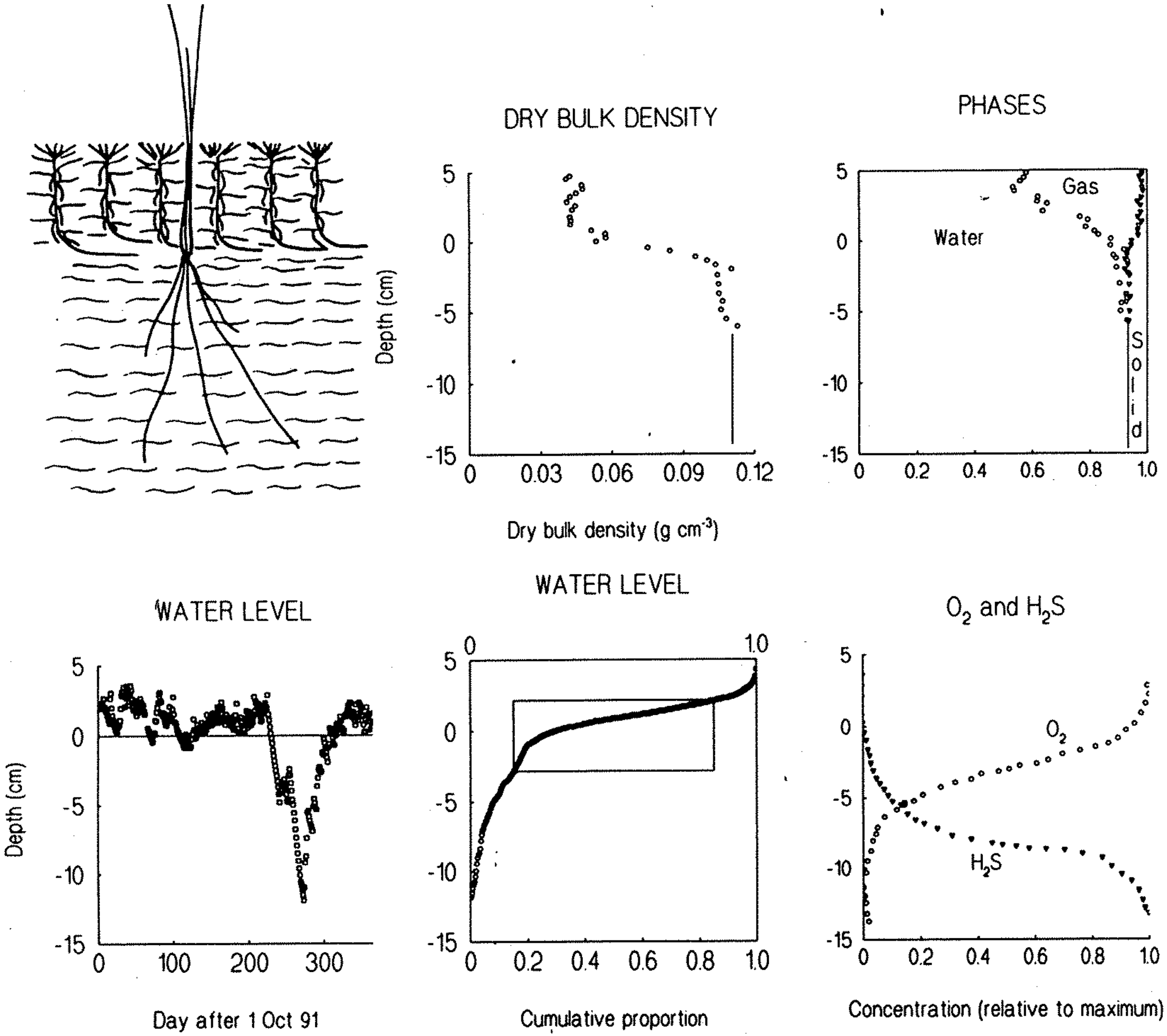
At the top right: leaves of the same three *Sphagnum* species magnified ten times less than the pollen and cells - the bar indicates 1 millimetre.

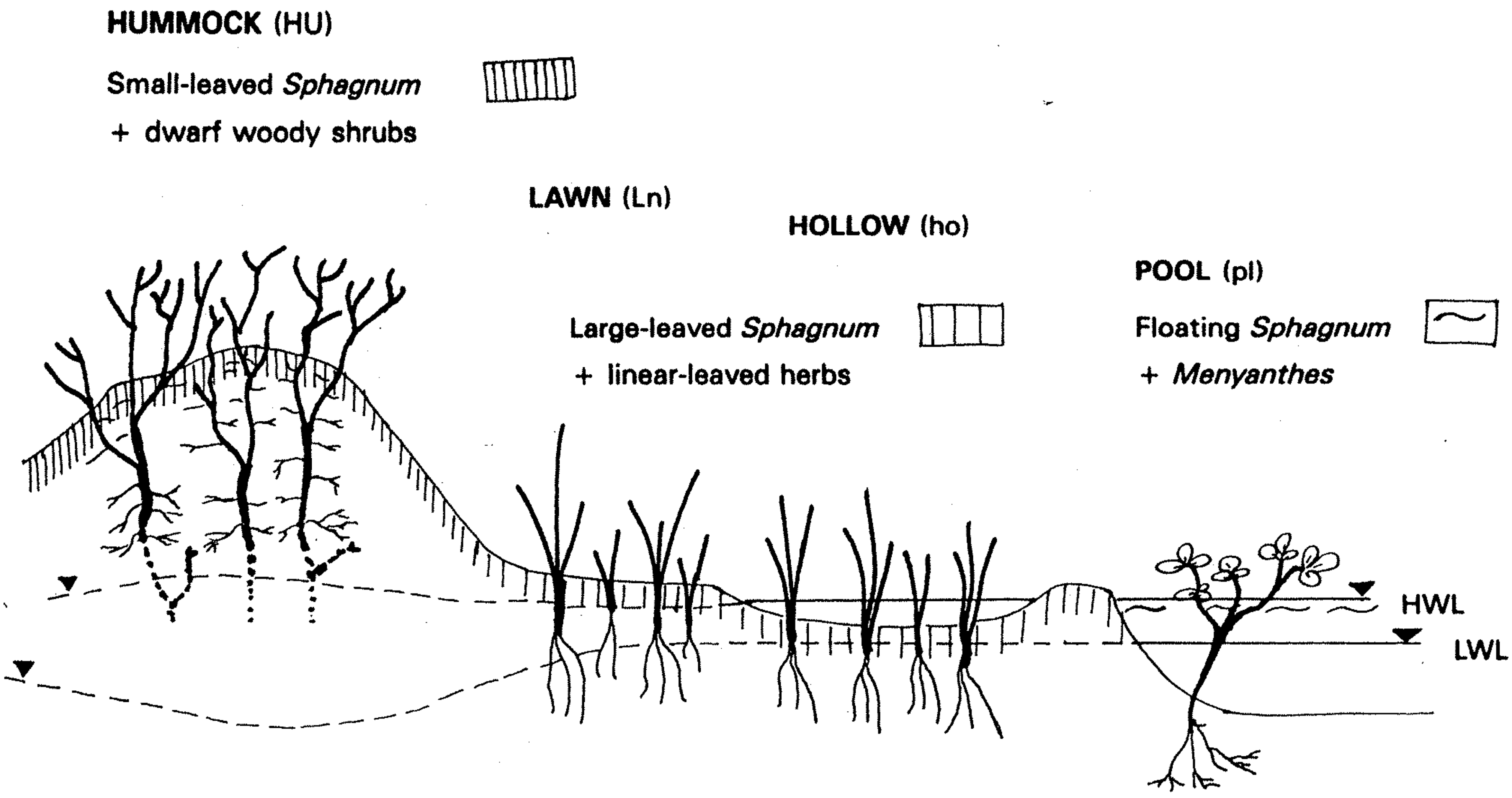
Figure 2. Processes in the surface of a bog. Collpse of structure, following aerobic decay, causes bulk density (the amount of plant matter in a given volume) to increase. This impedes water flow downward, leads to anoxia, and then to decay so slow that peat accumulates. The bottom left graph shows how the water level drops in summer. Next to it the box round 15-85 % of the time, including 70 %, on the cumulative height of the water level shows that the water level is within plus or minus 3 centimetres of the mean for 70 % of the time.

Figure 3. Processes in a hummock and hollow. The hummock fixes carbon faster than the hollow because of the support the woody shrubs give to the *Sphagnum*, and the mutual stimulus that the woody shrubs and *Sphagnum* give each other. But as the hummock rises above the hollow the depth of peat in which relatively rapid aerobic decay occurs also increases, until the difference between the (greater) rate of fixation and the (now also greater) total rate of loss by decay is the same as that in the hollow.






DRY BULK DENSITY
PHASES
Depth (cm)
Dry bulk density (g cm-3)
Gas
Water
Solid
WATER LEVEL
WATER LEVEL
O2 and H2S
Depth (cm)
Day after 1 Oct 91
Cumulative proportion
O2
H2S
Concentration (relative to maximum)
5
0
-5
-10
-15
0
0.03
0.06
0.09
0.12
0.2
0.4
0.6
0.8
1.0
100
200
300


HUMMOCK (HU)
Small-leaved Sphagnum
+ dwarf woody shrubs
LAWN (Ln)
HOLLOW (ho)
Large-leaved Sphagnum
+ linear-leaved herbs
POOL (pl)
Floating Sphagnum
+ Menyanthes
HWL
LWL