

rare (unknown in Britain), but locally frequent in some arctic localities; spores yellow, lightly papillose to almost smooth, 27–31 μm diameter.

HABITAT: In wet, oligotrophic to slightly mesotrophic areas. It forms cushions or carpets in the wetter parts of open, ombrotrophic *Sphagnum*/dwarf shrub mires, either as the major *Sphagnum* species, or in association with *S. majus*, *S. fuscum* or *S. cuspidatum* in the wetter parts, or with *S. papillosum* or *S. magellanicum* in the somewhat drier parts. Vascular plants associated with these lawns may include *Erica tetralix*, *Eriophorum angustifolium*, *Carex limosa*, *C. pauciflora* or *Scheuchzeria palustris*. In the north, it may also be associated with *S. lindbergii*, particularly between dwarf shrub tussocks.

DISTRIBUTION: Circumpolar in northern Europe, northern Asia, North America and Greenland. In Europe, it is mainly a lowland species (although reaching 1250 m in northern Sweden), with northern and somewhat continental tendencies. It is present in most of Scandinavia, except the south-west, and extends as far south as the Alps, but becomes increasingly rare in the sub-alpine zones. Rare and scattered in north-east Britain.

Sphagnum balticum is rather like a brown version of *S. angustifolium* or weak plants of *S. annulatum*, and in many ways seems to form a connecting link between these species. *S. angustifolium* is a paler plant (never deep brown), with non-fibrillose stem leaves and mostly indistinct stem cortex. However, some plants of *S. balticum* from central Europe are structurally very close to *S. angustifolium*. *S. annulatum* is usually distinctly larger, has some pores on or near the hyaline cell mid-line (abaxial side), and lacks the large apical resorption gaps in the lower lateral cells of the spreading branch leaves and the pendent branch leaves. *S. annulatum* has not been found in Britain, but in northern Europe it may occur in the same areas as *S. balticum*. It is generally unsafe to rely solely on field identifications in regions where both species occur.

Sphagnum fuscum (Acutifolia) could be mistaken for this species, in the field, by beginners, but can be separated easily by its dark stems, thin-textured, larger stem leaves, and strongly dimorphic branches. There is no possibility of confusion under the microscope.

32. SPHAGNUM ANNULATUM

Sphagnum annulatum Warnst. (Bot. Zbl., 76, 422, 1898)

PLANTS: Medium-sized to small, rather lax to more or less compact; yellow-brown to brown, rarely green (resembling a robust *S. balticum* or a weak *S. jensenii*). **Fascicles:** Distant or rather close set, slightly dimorphic; of 3, occasionally 4, tapered branches; stronger branches 8.0–14.0 mm long. **Stem:** 0.4–0.8 mm diameter; cortex distinct, 2–3 layers of rather narrow cells with distinctly thickened walls; internal cylinder yellowish. **Branch anatomy:** Retort cells distinct, mainly in linear groups of 2–3, slightly protuberant at apertures; internal cylinder yellowish to pale brown. **Stem leaves:** Erect-spreading; 1.0–1.2 mm long, triangular-ovate, concave; apices broadly rounded-obtuse, eroded; border expanded below into wide areas of prosenchymatous tissue. Hyaline cells below apex more or less strongly fibrillose (leaves indistinguishable from those of *S. balticum*). **Branch leaves:** 5-ranked or not, moderately large, 1.5–2.0 \times 0.8 mm on stronger branches, broadly lanceolate. Leaves of pendent branches (in more dimorphic fascicles) smaller, ovate to ovate-lanceolate in lower third of branch, 0.8–1.2 mm long. **Hyaline cells:** Rather small in upper mid-leaf, 70–90 \times 11.0–15.0 μm on abaxial surface, 12.0–20.0 μm on adaxial. Abaxial surface variable but mostly with some pores and pseudopores on, or near, the commissures and usually with one or a few ringed and/or unringed pores in, or near, the cell mid-line (these pores not as numerous, or in regular rows, as in *S. jensenii*, although, in some lower lateral cells, they may be in interrupted rows). Adaxial surface often without true pores, or pores few (rarely more than 4 per cell), sometimes with numerous pseudopores along the commissures and, particularly, adjacent to the lateral angles; unringed, circular pores, when present, seldom larger than 5.0 μm diameter. Hyaline cells of pendent branch leaves with slightly larger pores, otherwise identical to those of the spreading branch leaves, normally lacking large, apical resorption gaps on the abaxial surface. **Leaf TS:** Hyaline cells almost plane on both surfaces. Photosynthetic cells oval-triangular with more or less oval lumina and distinctly thickened abaxial walls; mostly distinctly, but shallowly, enclosed on the adaxial surface. **Fertile plants:** Probably dioecious, but no fertile material seen.

HABITAT: Like the closely related *S. jensenii*, this is a species of wet, unshaded, mesotrophic habitats, though it tends to be more aquatic and is more or less confined to areas of open, moving water, eg soaks and ditches within minerotrophic mires. Its most common associate is *S. jensenii*, though it may also be found in *S. majus*.

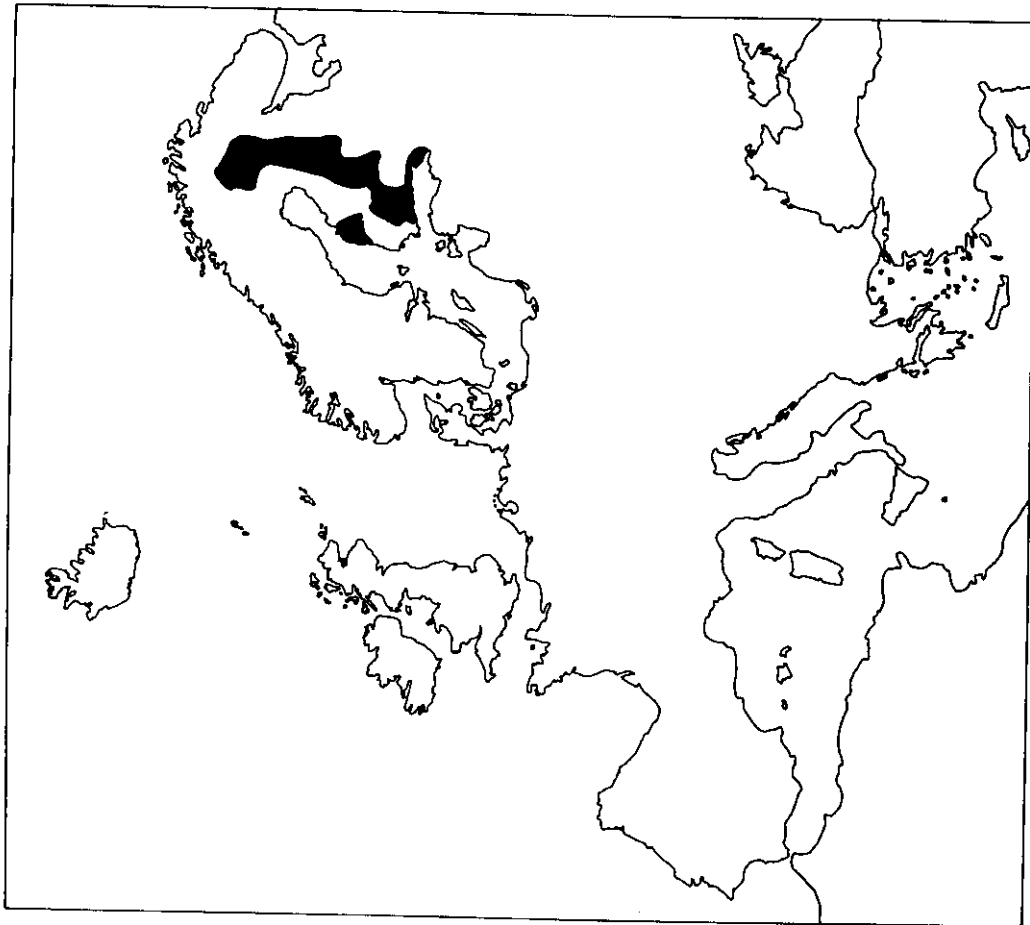


Figure 68. Distribution of *S. annulatum*

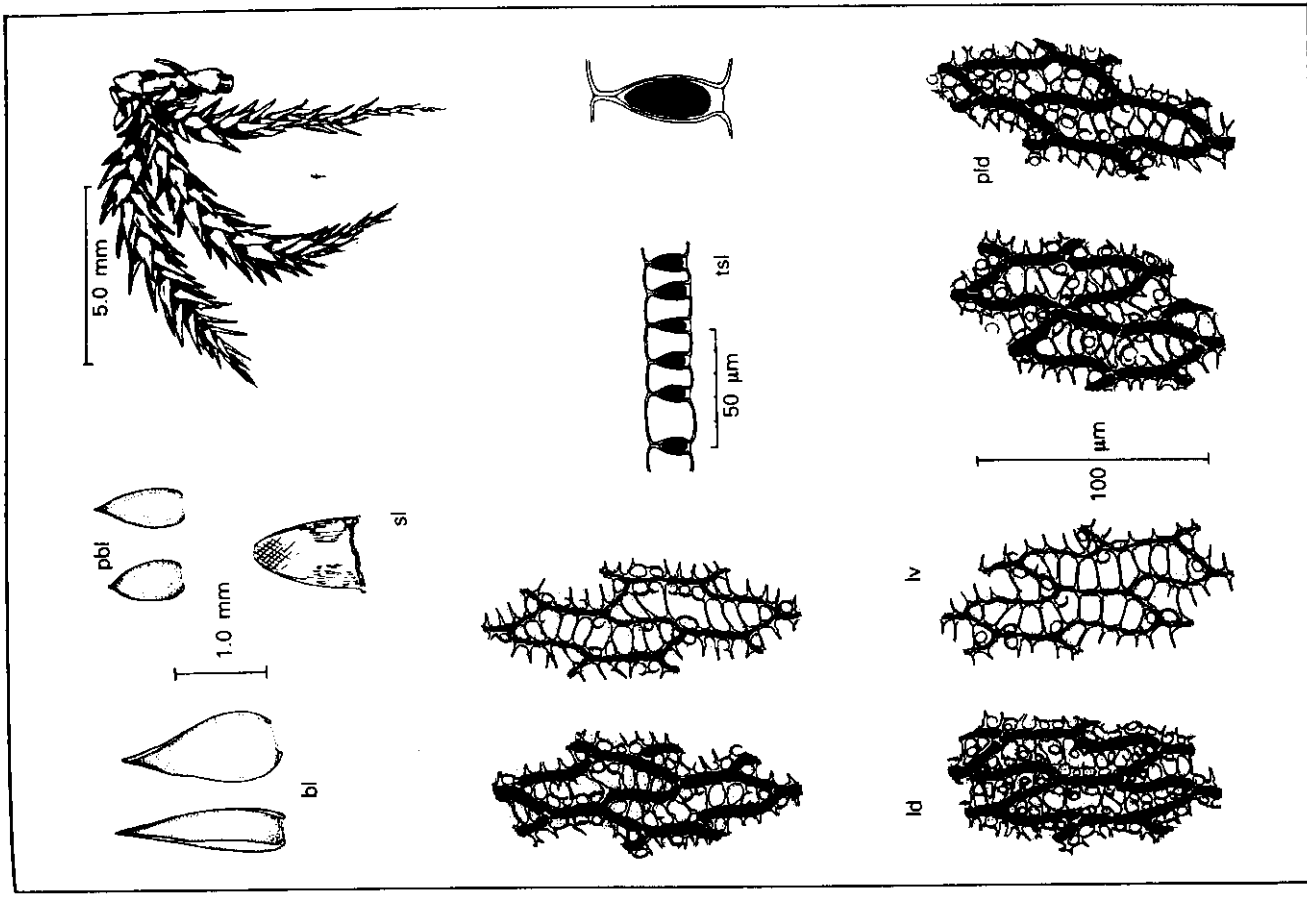


Figure 69. *Sphagnum annulatum*

DISTRIBUTION: Discontinuously circumboreal, being found in parts of northern Fennoscandia and USSR, and in north-eastern Canada (Ontario and Labrador).

There has been a great deal of confusion about the identity and status of *S. annulatum*, especially in its relationship to *S. jensenii* and, in North America, *S. mendocinum* Sull. It has been treated as a variety of *S. jensenii* (or *vice versa*) by many authorities. We follow the nomenclature of Isoviita (1966). As here interpreted, *S. annulatum* is intermediate between *S. jensenii* and *S. balticum*. The geographical ranges and ecological preferences of these 2 species and of *S. majus* are similar, and possibly *S. annulatum* is of hybrid origin.

We have been unable to find fertile material from Europe, the only putative fruiting plant from the British Museum herbarium being a misidentified *S. majus* mixed with sterile *S. jensenii*.

In the field, *S. annulatum* resembles a weak *S. jensenii* or a rather robust *S. balticum*, but can really only be identified with certainty on the microscopic characters of the branch leaf pores. The absence or paucity of adaxial pores and the lack of large, apical resorption gaps distinguish *S. annulatum* from *S. balticum*. *S. jensenii* has minute pores, either in the cell mid-line or partially in two rows, one either side of the mid-line, and none, or very few, along the commissures.

In a recent appraisal of *S. annulatum* and its relatives, Flatberg (1988c) has proposed a different demarcation between this species and *S. jensenii* from that presented above. In effect, he dismisses *S. annulatum*, as typified in the sense of Lindberg (1899) and understood by us in this treatment, as an aberrant plant that does not deserve taxonomic recognition. Instead, he redefines the species to include the later-described *S. propinquum* Lindb. ex Warnst., which has hitherto been regarded by most authors as synonymous with *S. jensenii*. The characters which separate the 2 taxa are concisely presented in the key (Flatberg 1988c, p.349) thus:

Capitulum glossy chestnut-brown to sometimes (in spring fen vegetation) dark red-brown; outer branches of the capitulum, and the divergent branches below the capitulum, distinctly arcuato-decurved in their distal part; leaves of the divergent branches markedly concave and distinctly smaller near the proximal end than the middle part of the branches; terminal bud of the capitulum conspicuous, usually of about equal length or only slightly shorter than the inner branches, and always visible.*S. annulatum*

Capitulum dull yellowish brown to brown, outer branches of the capitulum, and divergent branches below the capitulum not distinctly arcuato-decurved in their distal part; leaves of the divergent branches not markedly concave and not distinctly smaller near the proximal end than in the middle part of the branches; terminal bud of the capitulum moderately large, exceeded in length by the inner branches, and sometimes concealed by them.*S. jensenii*

According to Flatberg (1988c), *S. annulatum* is predominantly a species which prefers somewhat richer, less wet sites than the oligotrophic to weakly minerotrophic mires preferred by *S. jensenii*. Their geographical ranges are largely coincident, but *S. annulatum* shows more pronounced arctic-alpine tendencies.

33. SPHAGNUM JENSENII

Sphagnum jensenii Lindb. (Acta Soc. Fauna Flora fenn., 18, 13, 1899)

PLANTS: Medium-sized to robust rather lax, sometimes rigid; brown, green-brown or yellow-brown, rarely all green. **Fascicles:** Distant or close set, not, or slightly, dimorphic; of 3-4 branches; spreading branches 2, short or much elongated (8.0-20.0 mm), often appearing stout; pendent branches weaker and attenuated distally, or almost as vigorous as spreading and scarcely differing (if 4 branches, then one usually intermediate in attitude and form between the 2 spreading and the weakest pendent branch). **Stem:** Rather thin, 0.4-0.7 mm diameter; cortex developed but not conspicuous, sometimes indistinct, in TS of 2-4 layers of rather narrow cells with distinctly thickened walls; internal cylinder yellowish. **Branch anatomy:** Retort cells distinct, mainly in linear groups of 3, slightly protuberant at apertures; internal cylinder relatively thick, yellowish to pale brown. **Stem leaves:** Mainly erect-spreading; 1.0-1.3 x 1.0 mm, oval-triangular, concave; apices rounded-obtuse; border strong, expanded below. Hyaline cells below leaf apex on abaxial side strongly fibrillose, lacking pores, or with an occasional small and inconspicuous pore; adaxial surface with or without scattered complete fibrils, cell wall almost completely resorbed, but with numerous, strongly ringed, small pores or pseudopores, often in short series along the commissures. **Branch leaves:** Large, mostly over 2.0 mm long, erect-spreading, more or less 5-ranked, lanceolate. Leaves of pendent branches (where distinct) broadly lanceolate, 1.3-1.8 mm long in basal third of branch. Hyaline cells: Long, 11.0-20.0 x 100-150 µm. Abaxial surface with frequent to abundant

small, ringed and unringed pores in one or 2 rows in, or on either side of, the cell mid-line; with no, or only an occasional, pore or pseudopore on or near the commissures. Adaxial surface (at least in cells from the lower lateral parts of the leaf, usually throughout the leaf) with small pores more or less identical to those on the abaxial surface. Hyaline cells of pendent branch leaves similar to those of spreading branch leaves. **Leaf TS:** Hyaline cells almost plane on both surfaces. Photosynthetic cells triangular-oval with oval lumina and, usually, strongly thickened abaxial walls; mostly shallowly enclosed on adaxial surface. **Fertile plants:** Dioecious. No fertile material seen by the authors.

HABITAT: In open, wet, mesotrophic mires, usually partly submerged in pools or in hollows subject to seasonal flooding; a typical habitat is in the elongated pools, or 'flarks' of aapa fens (string bogs). It prefers open habitats without shade, and either forms mats of rather prostrate individuals or occurs in association with, most commonly, *S. majus*, though it may also be found with *S. riparium*, *S. lindbergii* or *S. annulatum*. Other associates may include *Drepanocladus exannulatus*, *Carex limosa* and *Menyanthes trifoliata*.

DISTRIBUTION: Circumpolar in the boreal and sub-arctic regions, but extending as far south as the Rocky Mountains of Wyoming (at an altitude of over 3000 m) and Honshu, Japan. In Europe, it is distinctly northern-continental and is found throughout much of northern and central Scandinavia, in northern USSR as far as west Siberia, in northern Poland and, reportedly, as an isolated population in the Ukraine.

The pores of *S. jensenii* are much more clearly defined than those of *S. obtusum* and occur throughout the leaf. In depauperate specimens, the pores may be less numerous, and it is not always possible to separate such plants from *S. annulatum* (assuming them to be distinct species). *S. majus* has similar pores, but these are usually larger and confined to the abaxial leaf surface. *S. majus* can also be distinguished by its leaf section, which shows the photosynthetic cells exposed on the adaxial leaf surface, not enclosed as in *S. jensenii*.

The close relationship between *S. jensenii* and *S. annulatum* is discussed in the notes under the latter species. In North America, the position is further complicated by the occurrence of another, apparently closely related, taxon, *S. mendocinum* Sull.

34. SPHAGNUM MAJUS

Sphagnum majus (Russ.) C. Jens. (Festskr. Bot. Kjøb. halvhundrede-
daarsf., 106, 1890)
S. duseunii Warnst. (Hedwigia, 29, 214, 1890)

PLANTS: Semi-rigid to very lax (resembling robust forms of *S. cuspidatum* or lax *S. jensenii*); nearly always at least partly brown, and often the whole plant brown, green only in shade. **Fascicles:** Of 3–4, often vigorous, branches (15.0–20.0 mm or more) which are at most only slightly dimorphic (though varying in vigour). **Stem:** 0.6–0.8 mm diameter, pale yellow-green; cortex moderately distinct, of 2–3 layers of enlarged hyaline cells with slightly thickened walls; internal cylinder well developed, yellow. **Branch anatomy:** Retort cells in linear pairs, distinct, slightly protuberant at apertures; internal cylinder greenish yellow to faintly brown. **Stem leaves:** Hanging or spreading, often loosely appressed to stem; triangular-ovate, concave; apices rounded-obtuse, eroded across the tips; border strong, expanded below into, usually large, patches of prosenchymatous tissue; hyaline cells near apex strongly fibrillose on abaxial surface; adaxial surface almost completely resorbed, but with numerous, rather irregular, thick-ringed pores or pseudopores along the commissures, sometimes with occasional intact fibrils, especially towards cell ends (stem leaves like those of *S. jensenii*). **Branch leaves:** Lanceolate to linear-lanceolate (distal leaves somewhat reduced and linear), often curved and secund; 2.0–2.8 mm long on the more vigorous branches; mostly obscurely 5-ranked. **Hyaline cells:** Long, 100–220 x 13.0–22.0 µm in upper mid-leaf; abaxial surface with numerous (rarely few) medium-sized mainly unringed (never strongly ringed) pores (ca 5.0 µm diameter), more or less scattered over the surface, or in one or 2 irregular rows; adaxial surface without pores or with few (usually 1–3 at most) rather large, unringed pores. **Leaf TS:** Hyaline cells almost plane on abaxial face, shallowly convex on adaxial. Photosynthetic cells trapezoid, moderately thick-walled, with oval triangular lumina; reaching, and often appreciably exposed on, adaxial leaf surface, but with wider exposure on abaxial surface. **Fertile plants:** Dioecious. Antheridial bracts brown; shorter and proportionately wider than branch leaves. Inner perichaetial bracts spatulate; about 4.5 mm long; apices broad and rounded, tissue near apex strongly fibrillose, in lower third of bract more or less uniformly prosenchymatous. Capsules occasional; spores pale, coarsely papillose, 33–35 µm diameter.

HABITAT: An extremely hydrophilous species, submerged in pools or forming carpets in very wet parts of open, oligotrophic to weakly mesotrophic mires. Its range overlaps with those of *S. cuspidatum* and *S. jensenii*, and it

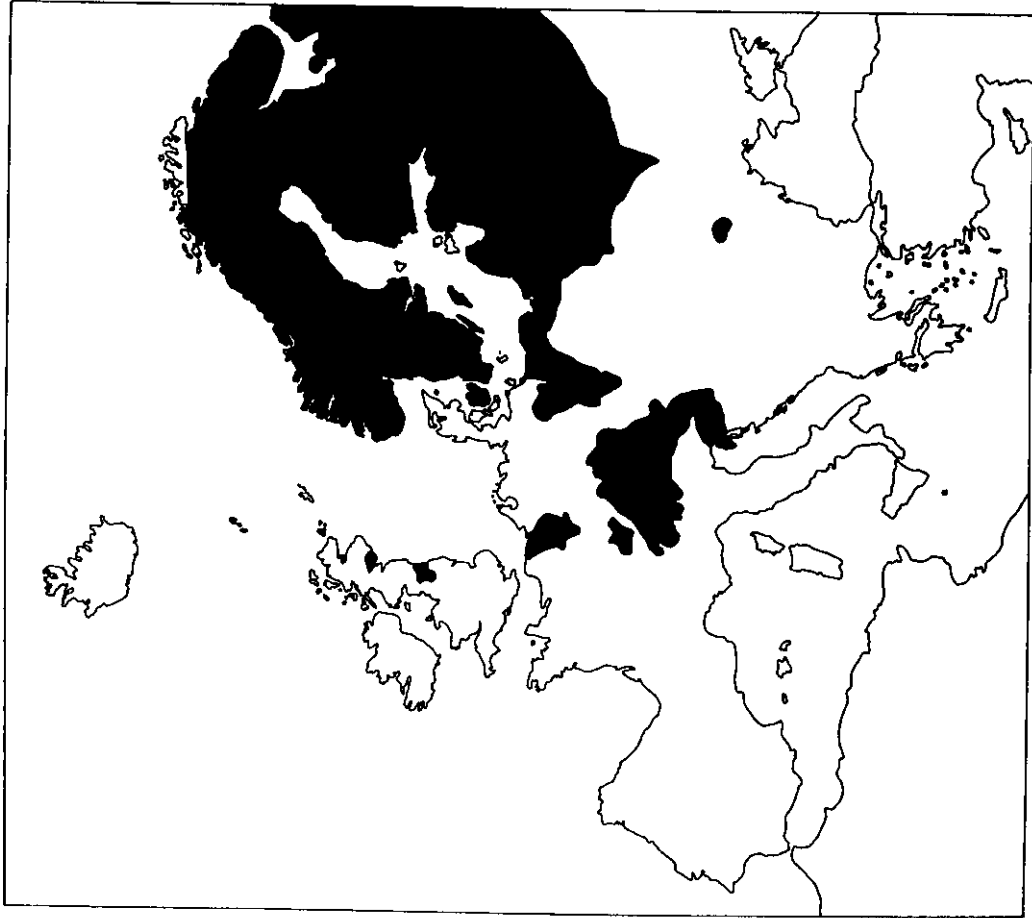


Figure 72. Distribution of *S. majus*

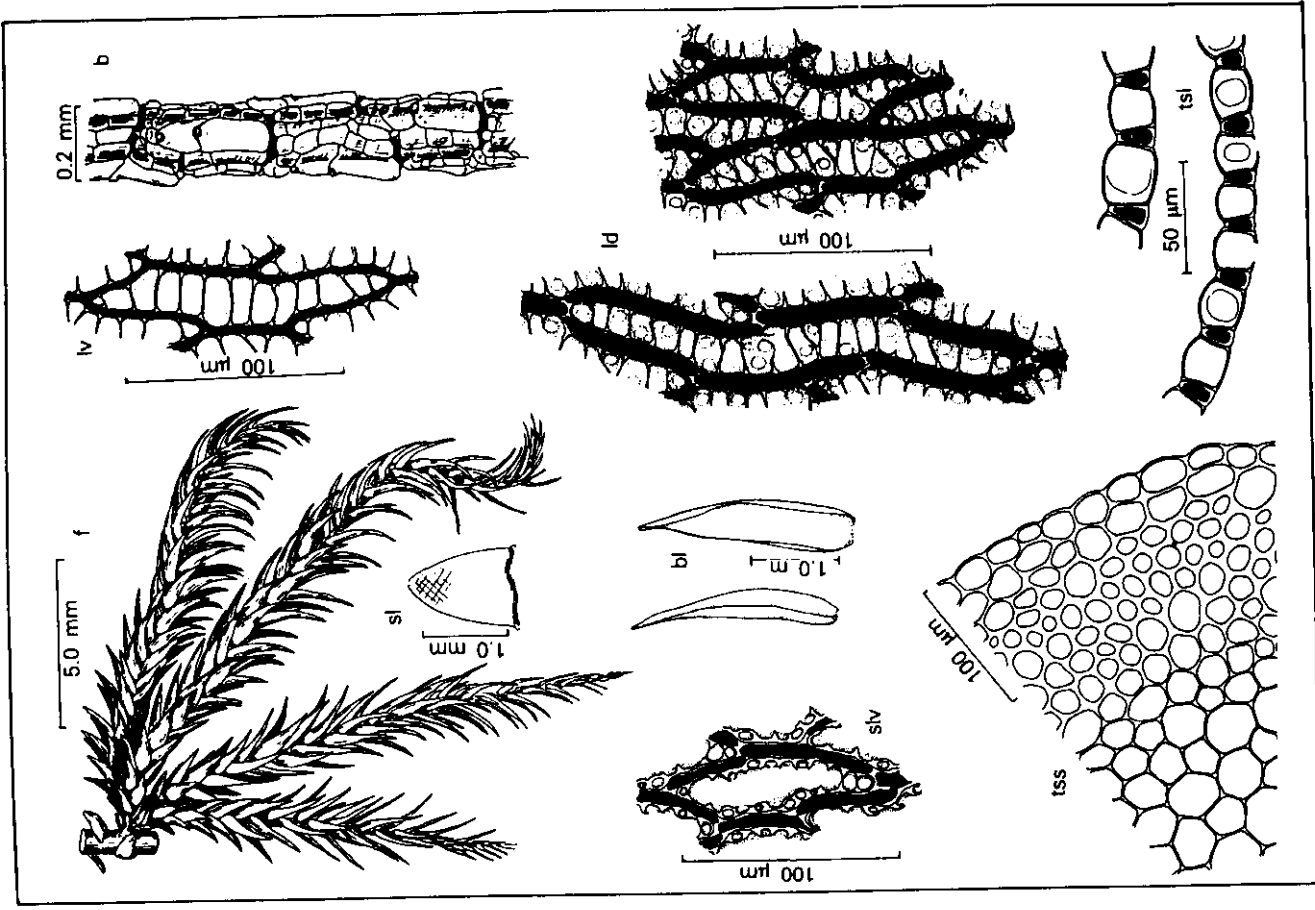


Figure 73. *Sphagnum majus*

may be found in association with either of these species, or forming monospecific carpets beneath scattered sedges, *Eriophorum angustifolium* or *Scheuchzeria palustris*. It may be found in ombrotrophic bogs, and in the north it may replace *S. cuspidatum* even in distinctly oligotrophic pools, or in those with a limited amount of mineral water influence.

DISTRIBUTION: Circumpolar in the boreal and sub-arctic zones of Europe, northern Asia and eastern North America, but rare in western North America. The European distribution is somewhat continental, though it is more oceanic in North America: the species is common through most of Fennoscandia but decreases in frequency towards the south and west. It extends to the Vosges and the Alps, but is rare above the sub-alpine zone. It is found in 2 localities in north-east Britain.

With its rather elongated branch leaves and lax habit, *S. majus* bears a superficial resemblance to *S. cuspidatum*, a resemblance enhanced further in weaker or shade forms. However, the two species are not closely related, *S. majus* belonging to the species group that contains *S. jensenii*, *S. annulatum* and *S. balticum*. *S. cuspidatum* has narrower, more widely truncate branch leaves and lacks the abaxial pores of *S. majus*. Lax forms of *S. jensenii* can be identified by the smaller pores which usually extend to the adaxial as well as the abaxial leaf surface, and by the adaxially enclosed photosynthetic cells.

35. SPHAGNUM PULCHRUM

Sphagnum pulchrum (Braithw.) Warnst. (*Bot. Zbl.*, **82**, 42, 1900)

S. intermedium var. *pulchrum* Braithw. (*Sphag. Eur. N. Am.*, **81**, 1880)

PLANTS: Medium-sized to rather robust, often growing in wide carpets or smaller mats; yellow or yellow-brown to chestnut. (Of similar appearance to *S. lindbergii*, but with a different range, or to a less slender, more shaggy *S. recurvum*.) **Fascicles:** Rather close set, rarely distant; of 4 slightly to (usually) rather strongly dimorphic branches; spreading branches 2, relatively short (10.0–13.0 mm, rarely over 15.0 mm long) and thick, shortly tapered; pendent branches 2, weaker and often shorter, mostly less than 12.0 mm long. **Stem:** 0.5–0.9 mm diameter; cortex distinct, 2–3 layers of enlarged cells with slightly thickened walls; at least the outer layer of cortex with some brown pigment; internal cylinder well developed, brown to yellow-brown, rarely pale, green. **Branch anatomy:** Retort cells distinct, in linear pairs, the lower with relatively strong protuberant apertures; internal cylinder yellowish to brown. **Stem leaves:** Hanging or spreading; small, 0.8–1.0 mm long and about the same width; more or less equilateral ovate-triangular; apices rounded-obtuse, but mostly appearing mucronate due to inrolling of leaf margins; border strong, expanded below into large, almost confluent, patches of prosenchymatous tissue. Hyaline cells in upper half of leaf, or less, weakly fibrillose on the abaxial surface, occasionally without fibrils; adaxial surfaces partially to completely resorbed. **Branch leaves:** Erect-spreading, uniformly and conspicuously 5-ranked, densely arranged and branches appearing prismatic; 1.4–1.8 x 0.6–0.9 mm; broadly lanceolate, widest at, or just below, mid-leaf, often shallowly inrolled above. Pendent branch leaves small (in dimorphic forms), 0.9–1.1 x 0.5 mm, ovate, concave. **Hyaline cells:** In upper mid-leaf 100–150 x 13.0–18.0(–20.0) µm abaxially, up to 25.0 µm adaxially. Abaxial surface sometimes without pores, usually with resorption gaps in the apical angles and often 1(–2) pores (6.0–9.0 µm diameter) in the upper lateral angles; lateral angles with or without pseudopores. Adaxial surface with medium-sized (ca 8.0 µm) unringed pores, mainly adjacent to cell angles. Hyaline cells of pendent branch leaves proportionately shorter, but otherwise similar to those of spreading branches. **Leaf TS:** Hyaline cells plane on abaxial surface, shallowly convex on adaxial. Photosynthetic cells equilateral, or shortly isosceles, triangular, with wide abaxial exposure but deeply enclosed on adaxial surface (the fused walls of the hyaline cells on either side more or less equalling in length the height of the photosynthetic cell). **Fertile plants:** Dioecious. Antheridial branches rather inconspicuous, especially in brown plants; antheridial bracts orange-brown. Inner perichaetial bracts large, 4.5 mm long, ovate; apices broadly rounded-obtuse, often minutely retuse;

upper hyaline cells intact, lacking fibrils, or a few cells with irregular fibrils; hyaline cells differentiated to below mid-bract; basal tissue more or less uniformly prosenchymatous. Capsules very rare (a single capsule seen on British material); spores yellow-brown, slightly papillose, ca 28.0 μm diameter.

HABITAT: As loose mats or dense carpets in wet oligotrophic mires. Occasionally, it may be submerged in shallow pools. In north-western Britain and Ireland, it may form extensive carpets on ombrotrophic peatlands, but further east it is increasingly confined to oligotrophic sites with a throughflow of water (eg valley mires of Dorset in southern England) or the margins of soakways or pools within the mire expanse. Although forming pure mats or carpets in many locations, it may also be mixed with other *Sphagnum* species (eg *S. papillosum*, *S. magellanicum*, *S. tenellum*) and leafy hepatics, as well as associated with scattered individuals of such vascular plants as *Rhynchospora alba*, *Drosera rotundifolia*, *D. intermedia*, *Andromeda polifolia*, *Erica tetralix* and *Narthecium ossifragum*.

DISTRIBUTION: A lowland, sub-oceanic species of north-west Europe, eastern Asia (Japan and Kamchatka) and eastern North America. It has a scattered distribution through the north-western parts of Europe, extending as far east as south-central Finland and the Baltic coast of Russia, and south as far as the Black Forest, although it is also recorded from the Ukraine. In Britain, it has a disjunct distribution in western areas from Dorset, through west Wales and north-west England, to Galloway, Argyll and Skye. It also occurs in parts of western Ireland.

Sphagnum recurvum is the most likely species to be confused with *S. pulchrum*. In the field, the shorter, relatively fatter branches, tapering fairly sharply both towards the insertion and the distal end, together with the wider set of the leaves on the branch and the dark stem, should distinguish *S. pulchrum*. The branch leaf outline is also different, being widest near the middle of the leaf in *S. pulchrum* and widest a little above the insertion to about a third of the leaf length in *S. recurvum*, whilst under the microscope the more shortly triangular and more deeply immersed photosynthetic cells characterize *S. pulchrum*. The dark stem of *S. pulchrum* separates it from forms of *S. jensenii* with distinctly 5-ranked branch leaves, and the triangular stem leaf outline contrasts with the more or less rectangular stem leaf with a tattered apex found in *S. lindbergii*, but, in any case, field confusion should be no real problem as the geographical ranges of these 2 species are very different from that of the oceanic, western to somewhat south-western *S. pulchrum*.

36. SPHAGNUM LINDBERGII

Sphagnum lindbergii Schimp. ex Lindb. (Öfvers. K. VetenskAkad. Förh., 14, 126. 1857)

PLANTS: Robust and usually tall (somewhat resembling *S. pulchrum*, but with longer branches); brown, often growing in extensive light to dark brown mats. **Fascicles:** Of 4(-5) more or less dimorphic branches; spreading branches 2, (10.0-)15.0-25.0 mm long, prismatic, strong; pendent branches 2(-3), weaker and usually slightly shorter than spreading. **Stem:** Rigid; 0.6-0.8 mm diameter; dark brown to almost black, except in etiolated plants; cortex well developed and distinct, of 3-4 layers of inflated thin-walled cells; internal cylinder dark brown, thick, of strongly thickened cells. **Branch anatomy:** Retort cells variable in length; in linear pairs or threes or, often, in clusters 2-3 cells wide and 2-3 cells long; internal cylinder brown. **Stem leaves:** Hanging and appressed to stems; large, 1.3-1.6 x 0.9-1.5 mm, rectangular to broadly spatulate; apices wide, truncate, conspicuously fimbriate; border inconspicuous above, merging below mid-leaf into large areas of prosenchymatous tissue. Hyaline cells much enlarged in upper mid-leaf, without fibrils, rarely with a few fibrils below; broadly rhomboid near apex; both surfaces resorbed in upper part of leaf. **Branch leaves:** Densely imbricated in 5 ranks; 1.6-2.0(-3.5) x 0.7 mm; broadly lanceolate, in submerged plants sometimes lanceolate to linear-lanceolate; with a minute spur at either side of insertion (formed by projection of the lowest hyaline cells); border 3-5 cells wide. Pendent branch leaves ovate to ovate-lanceolate, the lower about 1.0 mm long. **Hyaline cells:** In upper mid-leaf 80-150 μm long x 10.0-15.0 μm on abaxial surface, 18.0-25.0 μm adaxially; in lower lateral areas of leaf, up to 200 μm long or more. Abaxial surface mostly without pores, except for a small resorption gap in the apical angle, usually with a few pseudopores in one or more lateral angles; cells in lower lateral parts of leaf usually with 1-4 circular pores adjacent to cell angles. Adaxial surface with 5-8 rather small, 3.0-5.0 μm diameter, unringed pores mainly near the cell angles. Hyaline cells of pendent branch leaves similar to those of the spreading branches. **Leaf TS:** Hyaline cells plane on the abaxial surface, shallowly convex on the adaxial. Photosynthetic cells ovate-triangular to somewhat ovate-trapezoid, with oval lumina and strongly thickened abaxial walls; moderately widely exposed on the abaxial surface, enclosed to varying degrees on the adaxial. **Fertile plants:** Dioecious or autoecious. Antheridial branches similar to sterile branches. Perichaetial bracts large; lower bracts ovate, entire, the middle and upper ones fimbriate like the stem leaves. Inner bracts with 3 types of tissue: near base, lax; in mid-bract, thick-walled, prosenchymatous; near apex, differentiated, with enlarged, non-fibrillose

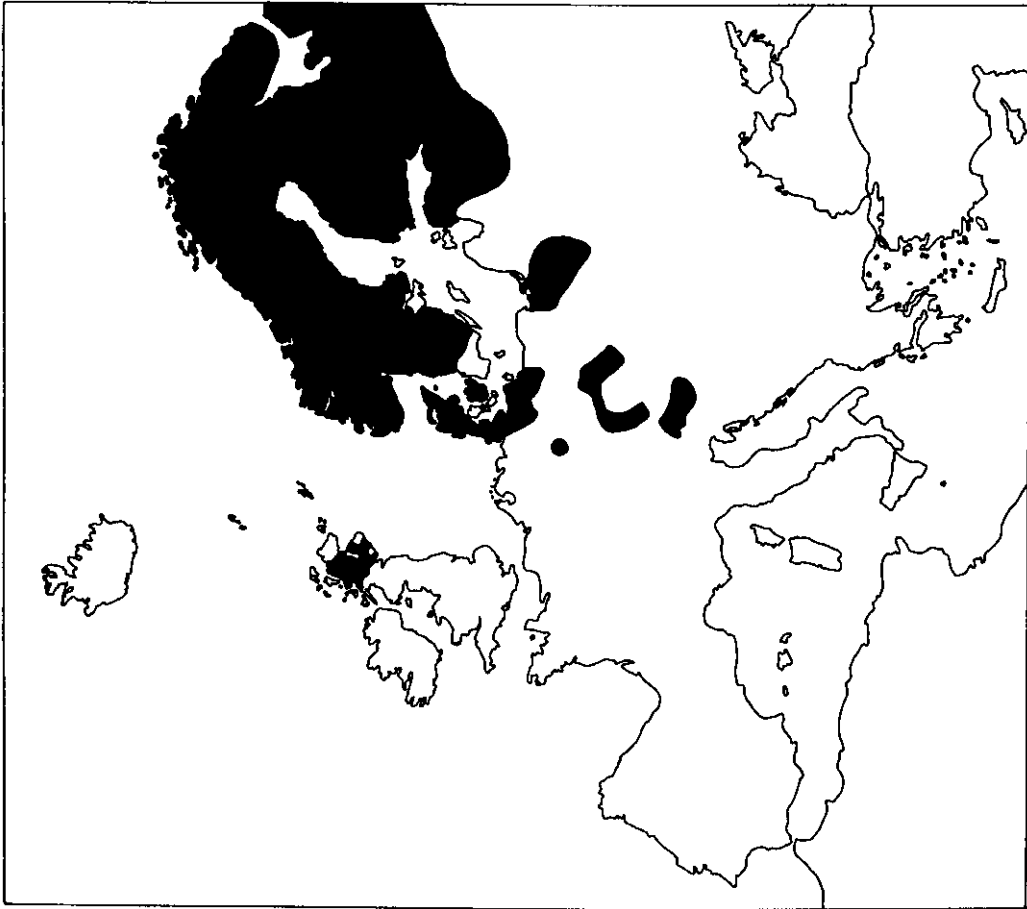


Figure 76. Distribution of *S. lindbergii*

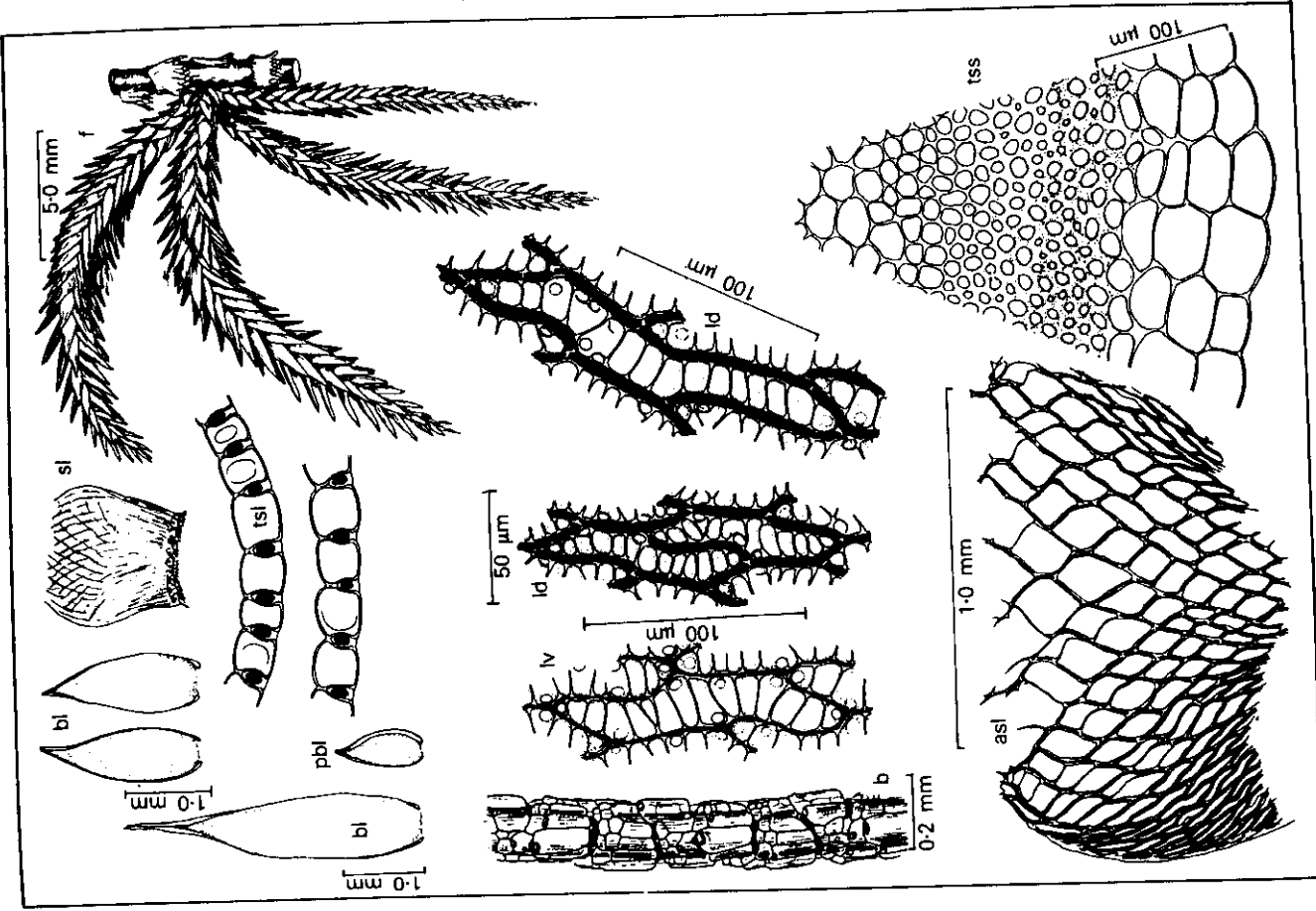


Figure 77. *Sphagnum lindbergii*

