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Bryoecology of the Appalachian Spruce-Fir Zone

Daniel Howard Norris
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To the Graduate Council:

I am submitting herewith a dissertation written by Daniel Howard Norris entitled "Bryoecology of the Appalachian Spruce-Fir Zone." I have examined the final electronic copy of this dissertation for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, with a major in Botany.

A. J. Sharp, Major Professor

We have read this dissertation and recommend its acceptance:

F. H. Norris, James T. Tanner, T. S. Osborne

Accepted for the Council:

Carolyn R. Hodges

Vice Provost and Dean of the Graduate School

(Original signatures are on file with official student records.)

August 10, 1964

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Accepted for the Council:

Hilton A. Smith
Dean of the Graduate School

BRYOECOLOGY OF THE APPALACHIAN SPRUCE-FIR ZONE

A Dissertation
Presented to
the Graduate Council of
The University of Tennessee

In Partial Fulfillment
of the Requirements for the Degree
Doctor of Philosophy

by
Daniel Howard Norris

August 1964

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I. INTRODUCTION

Ecological investigation of an area ordinarily follows a certain course. First explorations attempt to discover the nature of the flora, and ecological information is incidental to the habitat notes of collected species. Later, general qualitative observations appear regarding the vegetation of particular habitats. Only after this is a quantitative study using quadrats or other sampling techniques begun, and this quantitative work lays the foundation for future autecological, ecosystem and productivity work. Traditionally the above course is followed first by workers in vascular plant ecology, and studies of cryptograms are seldom as far advanced as that of the spermatophytes.

The vascular vegetation of the southern Appalachians is well known, due to the important works of Cain (1935), Whittaker (1956), and others. Studies in the spruce-fir zone of the Great Smoky Mountains National Park are exceptionally complete (Cain, 1935; Crandall, 1958; Schofield, 1960). The knowledge of the bryoecology of the boreal coniferous zone is not, however, so adequate. Sharp (1939) has provided an excellent bryophyte flora of eastern Tennessee, and Cain and Sharp (1938) did important exploratory work in which many of the bryophyte communities recognized in this study were described.

The present report is based upon researches made on the bryophyte communities of the major substrates in the spruce-fir zone of the southern Appalachians. It attempts to deal not only with the vegetational composition of each community but also with a description of the frequency of that bryophyte community in the plant association as a whole. The studies were made from 1958 to 1963 during all months of the year, but primarily in summer and fall. Most of the work was done in the Great Smoky Mountains National Park, but excursions were also made to most of the other mountainous areas in North Carolina and Tennessee which have a forest dominated by boreal conifers. The spruce-fir forest of the Adirondacks of New York was also visited for comparative studies. In the Smokies every area of spruce and fir accessible by trail was seen at least once. The region on Forney Ridge between Mt. Kephart and Silers Bald, and the Mt. LeConte area were most intensively studied because of their easy accessibility. Figure 1, adapted from Crandall (1957), illustrates the location of spruce and fir in the Great Smoky Mountains National Park and maps the location of some of the places mentioned in this paper.

The data obtained in this study have laid a foundation for more intensive examination of particular communities, using objective methods of classifying and quantifying vegetation instead of the very subjective ones here used.

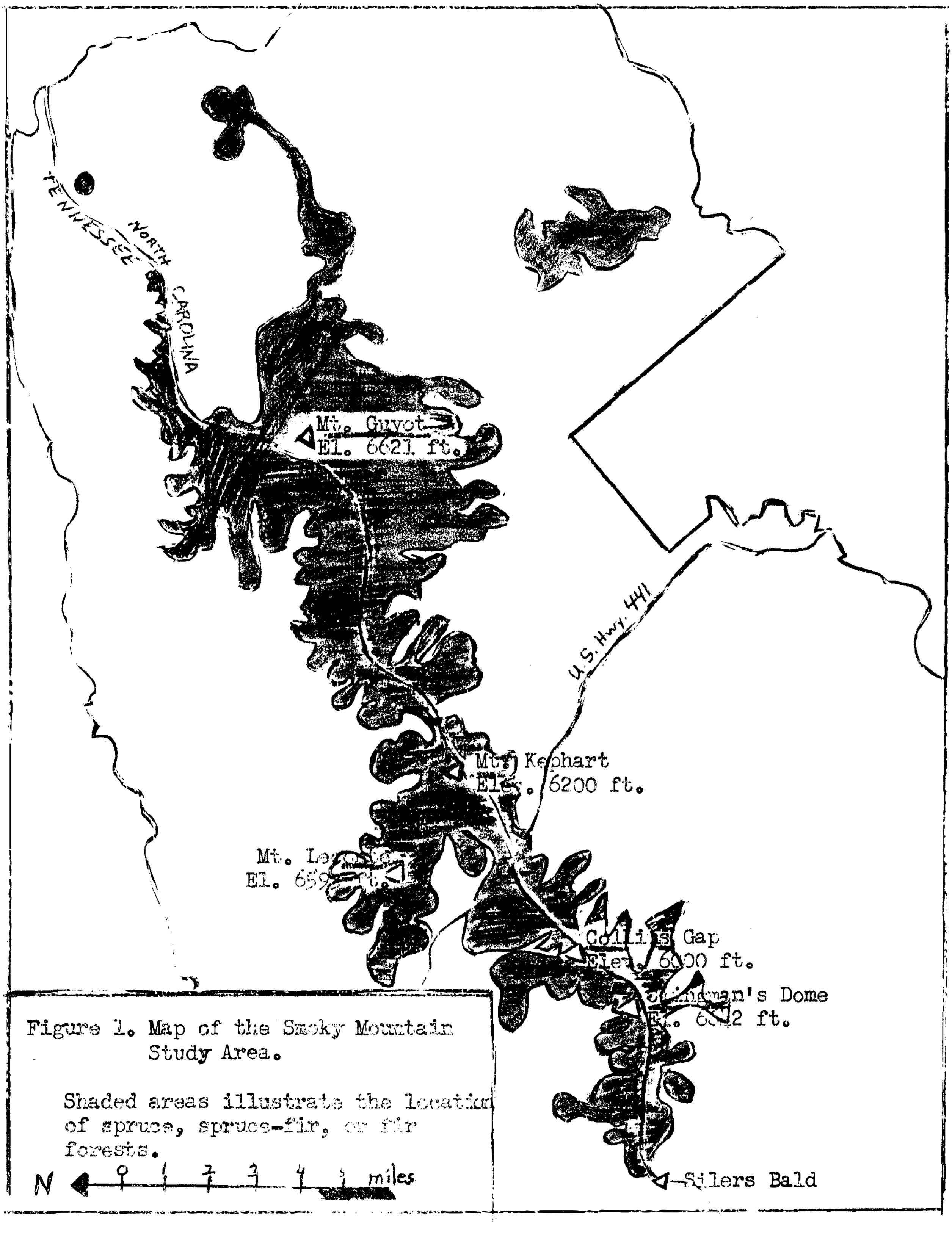

Figure 1. Map of the Smoky Mountain Study Area.

Shaded areas illustrate the location of spruce, spruce-fir, or fir forests.

II. METHODS

Bryoecological studies have, in the past, been devoted primarily to single substrates, and large works giving an overall picture of the qualitative and quantitative distribution on all substrata within the confines of a higher plant community are absent. This work, therefore, requires new methods--some eclectic and some original. Most of the possible substratal habitats have been individually studied by bryoecologists--tree limbs (Hale, 1955); tree trunks (Iwatsuki, 1960; Barkman, 1958); rotten logs (Peck, 1954); rock outcrops (Redfearn, 1960; Foote, 1963) and ground cover (many workers in vascular plant ecology). Tree bases have been considered by Cain and Sharp (1938) by the use of a trunk diagram, but no study of tree-base bryophytes includes the more rapid method of estimating coverage on defined quadrats. In the present study the latter method has seemed necessary because of the importance of extensive data replication in statistical studies on many habitats.

Bryophyte coverage was estimated on all substrates on plots of a single size-4 square decimeters. This was an arbitrary figure chosen so that the size of the plot would fit into most of the environmental niches where sampling was to be conducted. This constancy of plot size is necessary for certain statistical comparisons; and so, those niches that fell short of the required plot size were dealt with by aggregating the data from several similar and spatially adjacent areas whose collective area equalled that of the standard bryophyte quadrat. This alteration of method, though undesirable, was considered better than the alternative of reducing the size of the sample area.

Bryophyte coverage was estimated in increments of ten per cent and the presence of species of lesser than ten per cent coverage was merely noted. The estimation of cover of bryophytes of differing life form was often difficult. Brophytes may show lower coverage when desiccated than when hydrated, and pleurocarpous bryophytes closely appressed to their substrate may form a uniform reticulate pattern difficult to estimate. The cover percentage of the more abundant species was estimated in the field, but the species listing of the others was done in the laboratory from a complete collection of all the bryophytic material occurring within the confines of each quadrat.

The lack of instrumental measurements of the microenvironments of the niches occupied by the various bryophytes made it necessary to use subjective terms of environmental description. These are listed and defined in Appendix A under the separate headings of "Intensity of Light," "Soil Depth," and "Water Availability." Substratal habitats of importance are defined in Appendix A under the headings of "Epilithic Habitats" and "Epiphytic Habitats."

In accord with the attempt to understand the bryophyte communitities in relation to the entire plant association, most of the study was conducted on large study blocks of defined size (100 square meters) within which a variable number of standard bryophyte quadrats were systematically placed. Each of the 120 major study blocks was located so as closely to approximate the vascular plant vegetational composition of one of the fourteen site types described by Crandall (1958) in the southern Appalachian spruce-fir forest. These fourteen site types are listed in

Appendix A and the number of major study blocks located in each site type is also there stated. On the field data sheets the location of each block was recorded along with slope direction and degree. The percentage cover of the deciduous and evergreen trees was separately estimated and general observations were set down regarding the local topography. Ecologically significant features such as seepages, gravel screes, and boulder fields were also listed.

Vascular plants were sampled on plots laid out within the confines of the major study block. On the entire large block all trees more than one inch dbh. were tabulated and their circumferences recorded. Shrubs and transgressives were recorded by species and stems were counted on two 10 x 1 meter plots set at right angles to one another on adjacent margins of the major block. Woody stems less than one foot in height were considered as "reproduction" and not recorded, and shrubs branched above the ground were counted as a single stem. On each of the four corners of the major study block were located the quadrats for the coverage estimates of superior and of inferior herbs and for the stem enumeration of woody plant reproduction. Ground cover of bryophytes was estimated on four standard bryophyte plots located within the herbaceous plant quadrats at each of the corners of the major study block. Unless attachment to the soil was apparent, plants fallen from the tree canopy were ignored, as was the bryophyte flora of fallen twigs and of chips of shale.

Within the major (100 square meter) block, epiphytic bryophyte sampling was done on ten trees (fewer if the plot had a smaller number) by locating bryophyte quadrats of the standard size--one on the north side at breast height, one on the south side at breast height, one on the root flare, and one on the bridge (dark area in space between roots and soil), if present.

Six rotten logs, stumps, or dead standing trees (spars) were examined in the major study block, or, if necessary, in contiguous and similar portions of the forest stand. Three pairs of bryophyte plots were used per log and the two members of each pair were located, one on top of the log and one on the shaded side near the soil line. Logs less than ten feet long had only two pairs of plots and a few logs were so short as to warrant only a single pair. Stumps were sampled on the flare and on the bridge, and spars were sampled like the living trees. Special habitat data recorded for each log included their size, degree of decay (see Appendix A) and the per cent of deciduous and evergreen tree coverage. Logs laid parallel to the slope contours were distinguished from those lying across contours and, for each plot pair on each log, mention was made as to whether the log was at that point in contact with the ground. The cut faces of logs sawn by trail-clearing crews were sampled for their somewhat unusual bryophyte vegetation.

Because major rock outcrops seldom occurred within a large study block, the examination of epilithic bryophytes was conducted within the spruce-fir zone on areas not included in any major study block. Quadrats were so located as to assure uniformity of habitat within the limits of the ecological parameters used in the study. These habitat notes included the sixteen "Epilithic Habitats" listed in Appendix A as well as information on slope degree and direction, forest site type, type of rock and geographic location. Amount of light, water, and soil was recorded according to scales listed in Appendix A.

The data obtained by the several types of quadrat studies were coded and placed on McBee Keysort cards and were arranged into a number of bryophyte communities or "unions" by the method of Goodall (1953). This consists in sorting groups of cards, each representing a quadrat, in such a way as to minimize the number of significantly associated species pairs. Significance of association is judged by the Chi square method on a two by two table for each possible species pair. This method of objective classification of vegetation was considered appropriate because preliminary investigations indicated a closer correlation with habitat between plots of similar species composition than between plots of similar species dominance.

In addition to the already outlined approaches to this vegetational study, other types of information were obtained. A notebook for general observations was kept at all times in the field. Collections of bryophytes were made whenever it was felt that they would be useful. Species lists of bryophytes from the canopy portion of windfallen spruces and firs were also compiled. The annual increment of growth of *Hylocomium splendens* was studied by the method of Tamm (1950) from forty-eight quadrats scattered at all elevations and in all forest site types. Herbarium studies at The University of Tennessee were combined with the catalogue of this writer's own collections to produce a list of the bryophyte species known from the spruce-fir zone of the southern Appalachians.

In August of 1959, a travel grant from the Sigma Xi-RESA allowed an excursion to the Adirondacks in the region between Mt. Marcy and

Colden Lake in Essex County, New York, (see Figure 2). About five hundred collections were made in the spruce-fir zone of that region and a few log and tree quadrats were used for comparison with the bryophyte communities of the southern Appalachians.

The names of the herbaceous vascular plants are taken from Fernald (1950) and tree names follow Little (1953). Manuals by Grout (1928-1940), Frye and Clark (1937-1947) and Blomquist (1938) were used for bryophyte identification, but some names were changed to suit more modern nomenclatorial and systematic findings. In Appendix B, all bryophyte names used in this paper are available with their authorities. Appendix B also includes a listing of all the unions in which each bryophyte species has been found. Abbreviations used for the unions preface the table of spruce-fir bryophytes.

Collections useful in validating species discussed in this study are deposited in The University of Tennessee Herbarium.

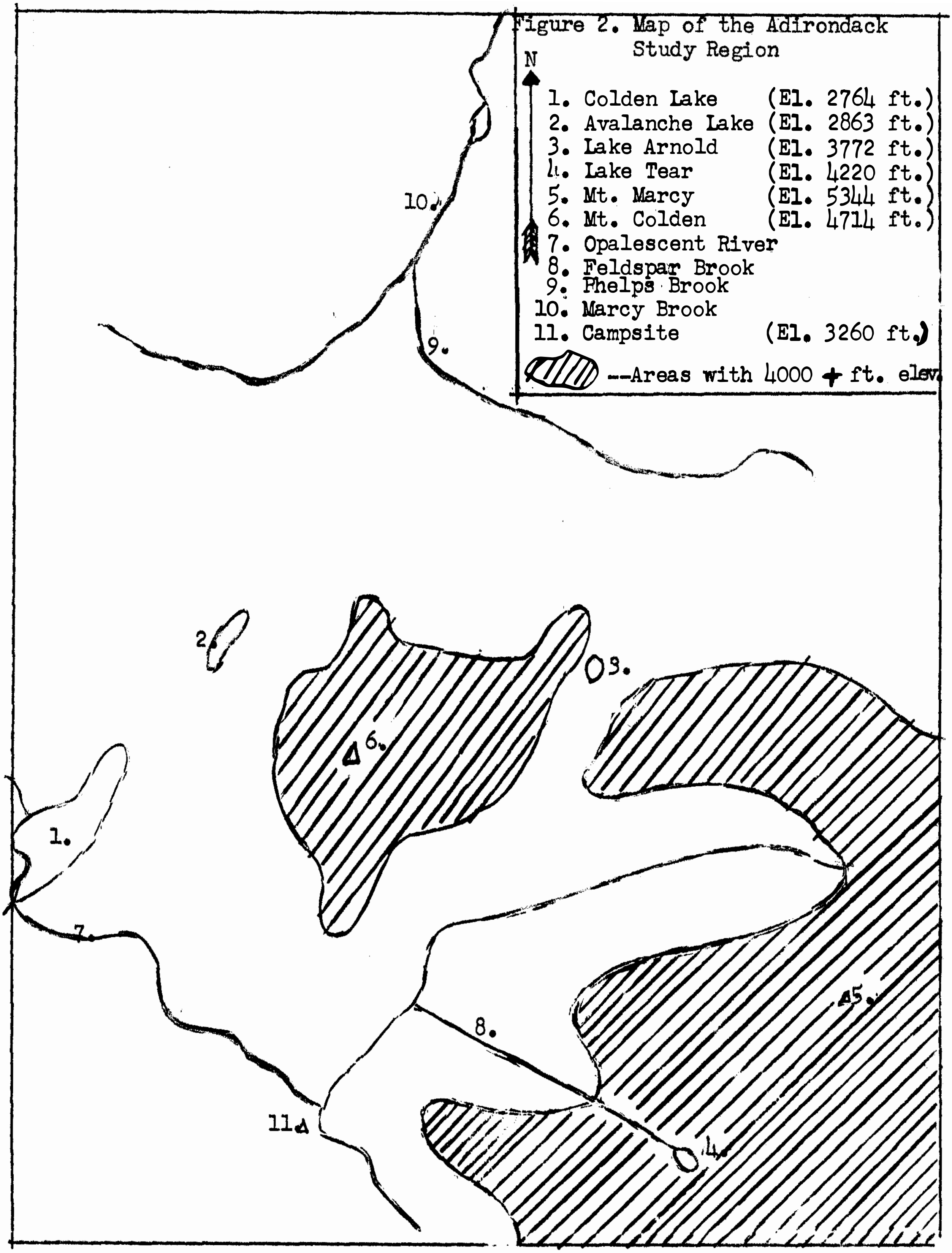

Figure 2. Map of the Adirondack Study Region

III. THE SPRUCE-FIR FOREST OF THE SOUTHERN APPALACHIANS AND ITS FLORISTIC RELATIVES

Forests dominated by red spruce and Fraser fir are usually found wherever the mountain peaks reach heights of 5500 feet or more in the Appalachians of North Carolina, Tennessee, and adjacent areas of Virginia. This forest has been studied by a number of investigators (including Korstian, 1937; Cain, 1935; Crandall, 1958; Schofield, 1960), and its geographic extent and coenological variety are well known. On all peaks inhabited by a boreal forest red spruce occurs, but on several of these areas (White Top, Virginia; Craggies and Mt. Pisgah, North Carolina) there is a complete absence of Fraser fir (Ramseur, 1960). Where present in the Great Smoky Mountains, the spruce-fir forest extends downward to about 5000 feet and isolated stands may be found as low as 4000 feet (Cooley, 1954). Its lower limits are, however, considerably more elevated elsewhere--Blacks of North Carolina (Davis, 1930) and on Roan Mountain (Brown, 1941).

Spruce and fir in the southern Appalachians grows almost exclusively on areas of resistant Cambrian or pre-Cambrian rocks. The soils (Ramsey series) are podsolized to various degrees and sometimes present true podsol profiles (McCracken, et al., 1962). The geological history of the mountain areas is one of almost complete diastrophic inactivity since late Tertiary time.

In the mountains within range of this forest type, relatively cold, snowbound winters and cool summers prevail (Shanks, 1954). The climate resembles that of the main body of the forest in New England, but the southern Appalachians have more precipitation, greater humidity, a longer growing season, and higher minimal winter temperatures (Oosting and Billings, 1951).

The southern Appalachians are not characterized by any true timber-line, but wind-flagging is common on the ridges and peaks of some of the mountains, especially Grandfather Mountain, North Carolina (Harshberger, 1903). The major peaks rising above 6000 feet are characteristically flat-topped and are very moist, apparently due to poor drainage and high humidity. Rock outcrops are usually restricted to the peripheral areas of the peaks and slaty gravel is the most typical material of the summits. All of these high elevation features correspond to those indicated by Denny (1951) to be congeliturbation features. Extensive falling of trees on these high peaks during the winter may be caused by frost-heaving and subsequent wind-fall of those trees with a weakened root system. This writer believes that frost-heaving, by favoring the shorter-lived and more prolific fir over the spruce, may account for the successive up-ward elevational bands of spruce, spruce-fir and fir forests in the mountains of the southern Appalachians.

As already mentioned in Section II, the above three types of forests have been classed by Crandall (1958) into fourteen sub-types based upon the understory vegetation. These subtypes (site-classes) are similar to vegetation groupings found throughout the boreal forest as shown by studies in the Adirondacks (Heimburger, 1934), central Canada (Ilvessalo, 1929); Scandinavia (Cajander, 1949); and Siberia (Sukachev, 1928).

In Table 1, the vascular plant data is presented by forest site type. Cover percentage and slope degree are averaged to the nearest multiple of ten; while other figures represent calculated means. The information differs in no important respect from that in Crandall's publication, because selectivity was exercised in the present study so that the areas examined would be distinctly classed as one of Dr. Crandall's forest sites.

The spruce-fir type is physiognomically distinct from contiguous forest communities, and this distinctiveness modifies and elaborates an already unique environmental complex. Major environmental features important to bryophytes include the low mineral content both of the surface soil and of its seepage water, the conditions of year-round shading typical of the coniferous forest, and the lesser likelihood of bryophyte death by complete blanketing with leaf-litter.

In the northern portion of the Appalachians and on associated mountain systems in New England, forests dominated by spruce and fir are also present. As compared with the southern Appalachian forest, the most striking change is the complete absence of _Abies fraseri_ and its replacement by a phylogenetically (Fernald, 1909) and ecologically similar species: _A. balsamea._ Also _Betula papyrifera_ almost completely replaces _B. alleghaniensis_ in the spruce-fir zone of these northern areas with the latter species now restricted to altitudinally lower zones (Heimburger, 1934).

The red spruce-balsam fir forest in the northeastern United States is primarily coastal, seldom extending more than a hundred miles inland.

Table 1. Vascular Vegetation Data

Crandall's Forest Site Types	Superior Herb Cover (%)	Inferior Herb Cover (%)	Shrubs Stems/10m^2	Basal Area ft^2/Acre	Trees Stems/100m^2	% Fir (Basal Area)	% Fir Stems	Elevation	% North and East-facing Slopes	Slope (°)
F-O-H	20	90	4	159	14	76	94	6200-6600	100	10
F-O-D	90	90	5	189	16	80	96	6400-6600	88	10
F-V-V-D	30	40	28	147	10	58	84	6000-6300	55	20
F-S	30	60	8	136	10	83	91	6300-6600	11	40
F-R	0	30	many	2	2	100	100	6500	0	30
S-F-O-H	10	80	12	206	12	18	58	5400-6000	100	20
S-F-H-V	30	50	17	192	9	42	72	5500-6100	44	20
S-F-V-V-D	90	60	52	222	8	32	72	5900-6300	66	20
S-F-V-V-S	90	10	16	266	8	26	48	6000-6200	22	30
S-F-R	0	10	many	192	7	20	65	5400-6100	55	40
S-H-V	0	40	21	196	8	14	76	4100-5700	33	10
S-V-V-D	50	50	9	304	8	13	72	5200-5700	77	40
S-V-V-L	20	10	8	275	9	5	61	5400-5800	0	30
S-R	10	0	many	268	6	10	39	5000-6000	11	40

Like the forest of the southern Appalachians, its climate may be considered maritime. It is found at elevations of above 3200 feet in its southernmost appearance in the Catskills of New York. Sea-level forests of red spruce and balsam fir extend southward in Maine to Mt. Desert Island (Küchler, 1956) and north into New Brunswick.

Inland mountain ranges in New England on which spruce and fir forests occur include the Presidential Range (Antevs, 1932), the White Mountains (Oosting and Billings, 1951), and the regions around Mt. Katahdin, Maine, (Harvey, 1903). Unlike the southern Appalachians, on most of these ranges, fir forest fringes an alpine timberline.

A high percentage of the shrubs and herbs found abundantly in the southern Appalachians also are commonly found in the red spruce-balsam fir forest of the north (Crandall, 1958; Heimburger, 1934). Others common in the north may be present as isolated relicts in southern localities. These include, for example, the paper birch (Betula papyrifera) present even in the krummholz of the northern mountains (Griggs, 1946), on Spruce Mountain, West Virginia, (Robison, 1950) and the Black Mountains of North Carolina (Harshberger, 1903); Cornus canadensis, regularly present and with wide ecological amplitude in the north but, in the south, occurring on only a few peaks such as Spruce Mountain, West Virginia, (Robison, 1950); and Alnus crispa extending even to the arctic timberline (Porsild, 1939) and present on Roan Mountain (Brown, 1941).

From this discussion, it is apparent that, in the forested area occupied by red spruce, two divisions may be recognized. The present study has been concerned primarily with the southern Fraser fir type but preliminary investigations have also been made in the spruce-fir zone of the Adirondacks. The forest type with which we have been concerned in this work is physiognomically and floristically distinct from all surrounding forests and is derived from the circumpolar boreal forest whose American expression is the white spruce-black spruce woodland of lowland Canada east of the Rockies. The boundaries of the spruce-fir forest are distinct in the southern Appalachians and more diffuse (due to the mixed spruce-hardwoods) in the more northern areas.

IV. BRYOPHYTIC HABITATS IN THE SPRUCE-FIR FOREST

Habitats on Soil

Except on disturbed sites, the ground surface in the southern Appalachian spruce-fir zone is covered by a rather thick mat of humus overlaid with a thin film of unincorporated coniferous leaves and stems and overgrown by bryophytes. Islands of litter of deciduous trees and shrubs interrupt this carpet and produce a corresponding decline in soil bryophyte cover.

Trees, shrubs, and tall herbs all intercept light, but dense layers of shrubs, especially *Rhododendron*, and herbs, especially *Dryopteris*, are most effective. On steep slopes and the crests of ridges at upper elevations, widely-spaced trunks of the firs often allow ground level conditions sometimes even approaching full sun. The differential seasonal effects of deciduous and coniferous shade do not seem significant on the forest floor because of the approximate coincidence in time of the loss of snow cover with the leafing of the hardwoods.

Soil moisture, too, may influence the kind and amount of bryophytes present. Moisture differences are produced by topographic features which result in differential drainage. Nearly level regions with poor drainage are frequently found at the tops of ridges and peaks where slopes are sometimes imperceptible and fallen logs and heavy moss mats may impede whatever slope-induced water movement there is. Areas of seepage vary considerably in the duration of surface water presence and in the erosive force of the water. On the more widely distributed areas of good drainage, some sites show almost constant adequacy of water, while bryophytes on other sites may exhibit drought symptoms within only a few days after rain. Tree fall, erosion, and drainage impediments may expose or allow to accumulate mineral soil and such a substratum will support a moss and liverwort vegetation different from that occurring on the humus.

Exposed clay banks and road cuts often support communities of Pogonatum pennsylvanicum on the less stable soil and Pohlia elongata on the more stable or the humus-impregnated types. Brachythecium plumosum occupies openings in the coniferous forest populated by herbaceous plants and underlain by mineral soil.

Four different unions of bryophytes were recognized from the sample data on soil surfaces. On poorly drained sites the Sphagnum union occurs, while the Atrichum crispum union is abundant on seepages. Polytrichum ohioense occurs occasionally on the well-drained areas of mineral soil usually associated with windfallen trees. Elsewhere Hylocomium splendens is dominant but areas in deep shade and areas under low elevation spruce have very few bryophytes and are considered part of the Hylocomium splendens union only by default.

Habitats on Trees

The configuration of a tree establishes the primary pattern of corticolous bryophyte distribution. The bridge, flare, trunk, and canopy of the tree all have a strikingly different epiphytic vegetation. This zonation is influenced by light, water, and the nature of the substratum.

The sources of water for corticolous communities are flow along the trunk surface ["stem flow" of Voigt (1960)], rain, and condensation; and these factors vary in their relative importance in the various portions of the tree. The amount of "stem flow" on a tree will vary considerably with the branching pattern of the tree. Trees such as fir and birch with ascending main branches may channel more rain water down the trunk than will the spruce whose descending branches shed water from tips. The water shed from spruce branches may support on properly located subordinate trees and shrubs an unusually luxuriant bryophyte cover. Rough, porous bark and epiphytic mats of vegetation absorb considerable quantities of water and may reduce the amount of "stem flow."

Rain may wet the various portions of a tree differentially with the more horizontal surfaces receiving maximum rainfall. For this reason, the basal flare and the limbs in the canopy are struck by rain more frequently than is the trunk. Trunks which lean from the vertical will receive more direct rain than will the more upright stems, and spruces in such a condition have a high cover of *Hypnum reptile* and *Brotherella recurvans* on the upper side of the tree trunk. For rain directly to reach their surfaces, vertical trunks are dependent upon wind, air, trubulence, and canopy splash.

Condensation from fog and subsequent fog drip is probably an important source of moisture to bryophytes of the spruce-fir forest. In the areas of more abundant bryophytes, fog conditions have been observed to be frequent in all the warm months of the year and such conditions have been noted by this writer to restore dry epiphytic mats of bryophytes to an hydration probably sufficient to permit growth. Fogs in the spruce-fir zone appear to be most frequent on ridges and especially on ridge saddles between higher peaks. Frequent ground-level fogs are almost restricted to regions of fairly open tree and shrub canopy, but canopy-level fogs are common even in the more dense forests on ridges.

This openness of fog-belt forests sometimes subjects the bryophytes to high evaporation rates and the frequency and duration of drying conditions is a further important factor in the zonation of the epiphytes. The rate of drying of a site may also be influenced by the nature of the bark of the trees. Bark differs in roughness, in porosity, and in nature of exfoliation (Billings and Drew, 1938); and bryophytes on fir have been observed to become dry less quickly than those on contiguous spruces; birch represents an intermediate condition. This difference between the cited trees appears to be correlated with the greater water availability on fir because of the smooth capillary surfaces provided between the thin scales of exfoliating bark. The large thick plates of spruce bark become loosened from the trunk in a manner which probably does not allow much outward movement of water in the bark. The intermediate position of birch in this regard is apparently due to its quite porous bark, which shows little or no exfoliation plates.

The accumulation of organic materials between the bark and the living bryophyte is another bark factor worthy of mention. Humus collects primarily on the less vertical surfaces and is especially prominent on the bases of trees. The typical tree base union is dominated by Brotherella recurvans and its margins usually coincide with the limits of noticeable humic material.

The nature of the bryophyte colony also may influence its rate of drying. Flat mats appressed to the bark surface, like those of Frullania asagrayana, have been observed to lose water more rapidly than do turfs of upright mosses, and the latter lose water more rapidly than do the hemispherical clumps of mosses which characterize the canopy levels of the trees. An interesting corollary to this observation is the conversion of the turf-forming Paraleucobryum longifolium of the tree trunks to a hemispherical clump-former on the bole and branches on exposed ridge-top trees.

The amount of light received by any one site on the tree is another factor of significance to the zonation of bryophytes. It would appear that this factor is limiting in its influence upon the vegetation of the very dark root bridges of the tree. The trunk of a tree below branch level receives more light than does that above the level of the branches but light may be screened from the trunk by tall shrubs and herbs. Of probable significance to trunk and canopy bryophytes is the difference between the annual duration of shade cast by deciduous and evergreen trees. The upper level trunk and canopy epiphytes remain unprotected by snow cover during all of the year and would be exposed to greater extremes of temperature and more light if located on a deciduous tree in contrast with evergreens. Observations by this writer indicate that growth does occur on these sites in the winter--at least in the sporophyte of Paraleucobryum longifolium; and differential temperature is here conjectured as one factor explaining the location of this species primarily on the evergreen tree, fir.

The size of the tree is of importance in the nature of the basal bryophyte communities. Larger trees are more buttressed, and the humus-correlated Brotherella recurvans mat extends higher on such trees. Ferns and other tall herbs may shade the base of smaller trees, but larger ones have a broad zone free of tall herbs and with correspondingly higher light intensities.

The nature of slopes may be of importance in regulating the amount of light received. Ridges which crown west- or south-facing bluffs may have trees receiving on their trunks and bases almost direct sunlight during much of the day. Trees on steep slopes may be exposed to very dense shade or to quite open conditions depending upon the placement of the canopies--some canopies are staggered and let in much light, while others produce a very dense shade.

The exposure of any site on a tree relative to sun and fog is important in bryophyte distribution. Southerly and westerly exposures receive more sunlight (unless a supertending slope excludes it) and north-westerly or southeasterly exposures may have greater frequency of fog.

The nature of the epiphytic bryophyte community is also a function of the type of tree and is particularly related to the nature of the bark and the type of branching.

Another as yet unmentioned factor is the chemical composition of the bark. Very little evidence has been obtained by this writer with regard to chemical effects. Bazzania trilobata does, however, seem closely associated with spruce, being more abundant on the basal bark of spruce than on any other tree and also unusually frequent on slopes below the logs, stumps, living trees and even the exfoliated bark of spruce. In the absence of any better explanation, this would appear to be a chemical effect.

Five unions of epiphytic bryophytes are recognized in the spruce-fir forest. Root bridges are all occupied by a Plagiothecium laetum union which usually has a very low coverage and resembles the Cephalozia union of log sides. Tree flares are usually populated by the Brotherella recurvans union, but a Bazzania trilobata union is recognized from spruce flares, especially at lower elevations. Ridge forests with open canopies, especially in the fir-Senecio site type, often have a downward extension of the Ulota crispa union of their trunks and therefore this union is occasionally represented in the data on tree flares. Away from areas of unusual exposure, tree trunks regularly show the Frullania asagrayana union. In areas of high bryophyte coverage (on fir) Frullania shares dominance with Paraleucobryum longifolium; while, on spruce trunks, this union is composed of F. asagrayana and Hypnum reptile sparsely distributed on an otherwise bare trunk. The dominance of Cephaloziopsis pearsoni, Leptodontium excelsum, Zygodon viridissimus, or Bazzania nudicaulis is predictable in certain sites, and these sites might have been recognized as distinct unions if more data had been available.

Habitats on Decaying Wood

The primary factor influencing the type of bryophyte community on decaying wood is the degree of decay. Bryophyte communities show a gradual vegetational change from the time of the tree's first falling to the occasion of the log's complete loss of form by decay. Three important events in the decay of logs may be mentioned. These are decortication, softening of the outer woody cylinder, and complete humification.

Decortication is important in removing the bryophytes typical of the living tree and in exposing wood whose chemical and physical properties differ from those of the bark. Decortication takes place by loss of fragments of the bark rather than by the bark's decay. Loss of bark may take place before the falling of a tree (see Figure 3), in which case the outer woody cylinder becomes weathered to a hard water-repellent surface very unsuitable to the growth of most bryophytes; or, it may take place after a tree has fallen and will lay bare a soft, slightly rotted woody cylinder immediately suitable to bryophyte growth.

Subsequent softening of the outer woody cylinder is not uniform--some areas remain hard and relatively undecayed and surround elliptical masses of decayed wood. The decayed areas are most readily colonized by acrocarpus mosses such as Dicranum fuscescens while pleurocarpous mosses such as Brotherella recurvans are first to colonize the harder areas of the logs. The pattern of this interdigitating mat of bryophytes differing in life-form is soon obscured by centrifugal growth of the colonizing individuals.

A log represents a temporary topographic high in the forest floor and is, as a result, usually above the shading effects of the herbaceous plants. Its light relations are, therefore, a product of the nature of the tree and the shrub canopy and of the configuration of the log. A notable feature of the log with regard to light is the existence on its

Figure 3. View of decorticated fir spar showing dry, water-repellent surface and illustrating the lack of bryophytes on such sites. Found on Clingman's Dome, 6600 feet elevation, May, 1964.

sides, near the soil margin, of a very dark area unsuitable to the growth of most bryophytes.

The decaying wood may have a moisture regime and chemical properties different from surrounding soil habitats; this gives a coordinate amount of vegetational distinctiveness to the epixylic bryophytes. As decay progresses, this distinctiveness of the log's vegetation lessens and eventually approaches that of the humus on the forest floor.

Although the epiphytic vegetation of the various species of trees in the spruce-fir zone may differ markedly, this difference is not apparently maintained beyond the decortication stage, and log species does not appear to be an important factor in the bryophyte ecology of the spruce-fir forests.

Of more importance is the position of a log on a slope. Logs which lie perpendicular to the countours of a slope may tend to channel seepage water along them while those lying parallel to the contours may block the flow of water and dam the immediate upslope section of the forest floor against further movement of eroded soil materials.

Many logs lie in such a position that portions of them are above any contact with the soil. Such areas are exposed to the high light intensity and low humidity of microenvironments away from the influence of the soil. The sides of such logs, too, are exposed to neither the low light intensities nor the high humidity of logs in contact with the ground.

Trees which are windthrown turn up a root mass enclosing a large amount of mineral soil which may then drop or be carried on to the upper surface of the log if it points downslope. For this reason, areas lying near the base of windthrown trees may have a bryophyte vegetation different from that of other regions of the log.

Bryophytes on decaying wood usually grow at right angles to the orientation of the vascular elements of the substratum. Because of this, water seeping along internal vascular strands will not directly affect the bryophyte communities. Broken or cut faces of stumps and logs, however, will show a bryophyte flora whose uniqueness is apparently the product of seepage directed along the vascular elements of the dead tree.

Ten unions are recognized on decaying wood. Some bear successional relationships to one another and some occur on sites which are ecologically differentiated. Succession on decaying logs typically begins with the *Frullania asagrayana* union of logs and spars prior to decortication; or with a community of *Nowellia curvifolia* which occurs on logs which were decorticated before falling. *Nowellia* unions too may occur on wood made bare by the shedding of unusually large fragments of bark. The *Brotherella recurvans* union follows either of the above two bryophyte unions and it is made up of numerous species, any of which may, by their growth, become the dominant species in areas as large as the standard bryophyte quadrat. The *Brotherella* union gives way to a *Hylocomium splendens* union on logs of decay class "4" and "5"; and this, by loss of species, soon becomes indistinguishable from the same union of soil.

Special ecological sites on the log support the other major unions. The *Cephalozia* union occurs exclusively on log sides near the soil margin, where it is subject to low light intensity and high humidity. A similar union--*Plagiothecium laetum*--is present on the bridges of the spars and is virtually unchanged in species composition as compared to its representation on living trees. The Cephalozia union is typically developed on decorticated logs of decay class "2" and it gives way in more decayed logs to an aspect in which Tetraphis pellucida is dominant. This succession is gradual and the data from Tetraphis dominated quadrats were not considered to warrant separate union designation. The broken upper faces of stumps also show the Tetraphis facies of the Cephalozia union. The Riccardia palmata union is present on the downslope portions of cut faces of logs. Sphenolobus michauxii forms a union especially abundant at higher elevations and localized on logs which exhibit regular channelling of seepage waters down their length. This occurs on logs, especially at high elevations, which lie perpendicular to the contours of the slope, or in the absence of mineral soil, in seepage pathways across the logs. Sphenolobus, like Nowellia, gives way on logs of decay class "3" to the Brotherella union. On logs of decay class "4" and "5," with mineral accumulation, Polytrichum ohioense is the typical union unless those logs are in very poorly drained sites where the Sphagnum union is dominant on nearly any substratum.

Habitats on Rocks

From the standpoint of bryophyte growth, epilithic sites are the most diverse of the habitats encountered in the present study. Each of the sixteen rock configurations defined in this paper and used in field habitat descriptions were selected for use because of their apparent significance to the growth of bryophytes. Rock configuration is important because it produces differences in the light intensity, the water regime, and the temperature.

The intensity of light on rocks is more variable than that on any other substratum. Bryophytes on rocks in full sun (tops of boulders, faces), receive not only the sun's direct light, but also receive light reflected from the rock surface. At the other extreme, sites with overhanging rocks (cavern ceilings, cavern faces, crannies, incisions, and cracks) cast a more intense shade than do the canopies of plants.

The water regime of epilithic bryophyte habitats is even more complex than their light environment. Lacking a moisture-holding substrate, bryophytes on rocks may be subject to frequent fluctuations between excess and insufficient moisture. Sources of water are of importance as well as amounts and duration of availability; and erosive effects, too, must be considered. The major sources of water for epilithic bryophytes are direct application from streams and drainage channels; seepage from soils lying above the outcrop; seepage from the interior of the rock on which the bryophyte is growing; direct hydration by precipitation; and finally, condensation.

Very few permanent streams lie within the boundaries of the spruce-fir forest, and only the upper reaches of Ramsey Prong and Camp Prong in the Great Smokies were studied. Zonation along permanent streams is related to the duration of water flow over the site and to the erosive effects of the water. Many intermittent streams and drainage channels, as well as "drainages" and "incised drainages" are present in the study area. These water courses seldom show rapid enough movement of the water to effect severe erosion and their courses are so narrow as to have a light environment not too different from that of the surrounding forest. This contrasts with the high light intensities frequently present in the courses of permanent streams. For these reasons, vegetation zonation in drainage channels and intermittent streams is primarily a function of the frequency and duration of presence of surface water; and the frequency and duration of drought conditions. The latter may be a function of the exposure of the habitat while the former is related to the size of the watershed.

The seepage water coming from soils differs from that coming from the rock interior in that the former may be chemically different and of a temperature more closely approaching the ambient air temperature. Water seepage from soils may also be very erratic in amount of flow, being tied closely to the precipitation of the season. The topographic position of sites receiving seepage from rocks is more variable than that of those receiving soil seepage, because the former can be located under an overhanging bluff. This additional possibility of location allows a greater reduction in light intensity and a greater moderation of the temperatures than can characterize the sites receiving soil-water seepage.

Sites receiving direct precipitation are, of course, very much influenced by the intensity and frequency of that precipitation. Those sites which are partially protected by overhanging bluffs and overstory vegetation, may receive only the water from heavy rainfalls or that carried by wind. Other sites receive all or nearly all of the water that falls from above. The intense shade present in caverns is not found in areas which receive rain. Boulder pits present the deepest possible shade in this type of habitat; the temperatures extremes in such pits are more moderate than those of other rock sites subject to precipitation.

The more exposed sites are by reason of their wide range of temperatures more subject to the receipt of large amounts of condensation than are those sites on rocks which are shaded by overhanging bluffs and dense vegetation. Desiccated bryophytes in such exposed localities have been observed to be restored to adequate hydration by condensation. Sites shaded or enclosed by rocks often have apparent constant high humidity and the walls of such enclosures are often constantly damp--- whether by seepage from the enclosing rocks or by condensation from the enclosed air it is difficult to tell. These enclosures differ from the condensation-subject exposed areas in being seldom or never under drought conditions.

This separate treatment of the sources of precipitation is not meant to imply that each bryophyte habitat receives its water from only a single source. Any or all of the stated water sources may be effective in giving moisture to an area, and the water regime is a product of these water sources modified by the dehydrating forces effective in the area.

All of the rocks of the study area are siliceous and of low pH. The only chemical feature appearing worthy of note is the copper or sulfur content (see Schatz, 1955) of some of the phyllites--a feature facilitating the growth of certain "copper mosses" such as *Mielichhoferia mielichhoferiana* and *Merceya ligulata*. The availability of seepage water and the susceptibility to the formation of certain types of rock configuration differ between the several types of rocks in the area. Such differences give to some epilithic bryophyte communities a restriction to certain rock types but the rock types are not by themselves ordinarily effective in the zonation of bryophytes.

Rocks in outcropping areas differ in bryophyte vegetation from those in apparently identical habitats on road cuts. This would appear to be a function of the differing degrees of weathering of the exposed rocks and may result from differences in porosity and roughness of the surface.

Bryophyte communities on rocks are numerous and the number of species available for colonization on rocks is much greater than the number on any other substrate. The one thousand quadrats chosen for the analysis of rock sites were probably inadequate for the distinguishing of all of the unions which appear on rocks.

At least thirteen unions can be recognized in the data from rocks. Three of these are primarily found in stream courses where erosion, silt deposition, inundation, and exposure-induced rapid drying seem to be the most important limiting factors. The Scapania nemorosa union is present in the major water courses and also in regions of constant seepage. In the water courses it occupies areas constantly under water and is bounded near the water line by the Marsupella sphacelata union. This, in turn, is replaced by the Rhacomitrium aciculare union in regions flooded only by high water, and at other times, exposed to drying conditions.

Outside of the stream courses, the normal forest-floor conditions of high humidity and shading prevail. The most xeric conditions are presented by the tops of boulders and the faces of outcrops, and on such areas the Rhacomitrium heterostichum union prevails. With accumulation of soil, this latter union is replaced successively by the Brotherella recurvans union and then by the Hylocomium splendens union--a succession similar to that on rotten logs. On sloping rock surfaces, heavy Hylocomium splendens mats are regularly sloughed off and replaced by a seral union of Lophozia incisa.

On steep slopes, eroded mineral soil may accumulate on tops of boulders, ledges, and bases. Here, Polytrichum ohioense forms a union not easily distinguishable from that of soil and log habitats. Smaller ledges and soil-covered drainages are populated by the Dicranella heteromalla union while the Sphagnum union may occur on ledges where water stagnates or it may occur in drainages of steep cliffs.

In the darker regions formed by cracks, caverns, crannies, recesses, and boulder pits, three unions occur, limited apparently by humidity and seepage. Most of these areas receive no direct precipitation but absorb water under conditions of high humidity or uses the seepage water which usually keeps the rock surface damp. The most widespread of these communities is the Herberta hutchinsiae union found in areas protected from rainfall and subject to frequent drying. Smooth, usually wet rock surfaces such as may occur on north-facing walls of outcrops regularly support the Dicranodontium denudatum union while the rough surfaces of phyllites show a high cover of the Rhabdoweisia denticulata union. This latter union extends to the most shaded of areas which support bryophytes and there includes large quantities of Trichostomum cylindricum and Plagiothecium laetum.

V. BRYOPHYTE GROWTH-FORMS AND ECOLOGY

A system of life forms usable in ecological studies is possible only as knowledge accumulates concerning the ecology and physiology of the plant type (Gimingham and Robertson, 1950). Such knowledge has allowed useful constructions like those of Raunkiaer (1928), but the state of knowledge of bryophytes is so fragmentary that only the more tentative "growth-form" classification, based on physiognomy, is possible. Observations made during the course of the present study have indicated that certain bryophyte growth-forms are strongly correlated with particular habitats, and a tabulation of this ecological correlation should allow the formulation of a scheme of life forms appropriate to statistical examination of floras. The ecological placement of many of the growth-forms will be explained tentatively as primarily related to differences in the abilities of the bryophyte to resist drought and to obtain and retain water. Such explanations should, however, in the future, be subjected to experimental studies to test the statistical inferences.

Bryophytes differ from higher plants in the lack of both a vascular system and true roots. Water movement from the substratum into the plant must therefore depend on conduction on the outside surface of the "stem," a process probably made more effective by the presence of rhizoids, paraphyllia, or appressed leaves. Many acrocarpus mosses with apparent ecological requirements for substratal mositure have some or all of these features. Other bryophytes such as members of the family Polytrichaeceae have a well-developed central strand along which water and minerals may possibly be conducted; and these mosses also appear to grow primarily on moist substrates.

Unlike higher plants, bryophytes have little or no cutinization of their subaerial protions, and water absorption is usually possible over the entire plant surface. Bryophytes occurring in areas of probable high yield of water from condensation are generally more or less papillose and have thick-walled cells, isodiametric in surface view. Such bryophytes (e. g., Ulota crispa) have been observed to be changed from conditions of dryness to conditions of wetness while contiguous plants without such features (Brotherella recurvans) remain dry.

Bryophytes range in color from black (Grimmia) to reddish-brown (Frullania asagrayana), to very light green (Geocalyx graveolens). In general the darker colored bryophytes are exposed to light of higher intensity, while those of lighter color occur in areas of lesser insolation. The pigment producing the darker hues is usually located in the cell wall and may be important in protecting internal cell contents from the more intense rays of the sun; this modification is further elaborated, especially in the Grimmiceae, by piliferous leaftips which may reflect light from the dark-colored desicated bryophyte.

Several features characterize bryophytes of humid areas in deep shade, and each may have certain adaptive significance. Complanate leaf arrangement such as characterizes most liverworts and mosses, as for example Plagiothecium laetum, exposes a maximum photosynthetic surface, but higher evaporation rates restrict this character to sites of infrequent dryness. Plants with large leaf cells have a similar distribution as do those with dissected leaves.

Some bryophytes have specialized cells or groups of cells which allow an increase in rate of absorption and in quantity of water retention; dead porous cells like those of *Leucobryum* and *Sphagnum* or inflated lobules like those of *Frullania* illustrate this quality.

This discussion of features which seem important in any consideration of the ecological classification of bryophytes, has been presented as a prelude to an annotation of the growth-form classification of Barkman (1958). Barkman's system makes a primary distinction between erect and repent bryophytes and this may be related to the increasing difficulties of material translocation which accompany extension of the plant apex away from the substratum. Upright bryophytes are further subdivided into turf-formers and clump-formers, with the low surface-volume ratios of the latter probably resulting in decreased rates of evaporation. Both the turf- and clump-formers are distinguished on the basis of size, with the larger ones presumably requiring more effective means of translocation than do the smaller ones.

The great heterogeneity of Barkman's "*Bryum* type"--a short turf-former--may be rectified by attention to the large size of cells (Bryaceae) of such plants on mesic soil sites; to the darker color (*Andreaea*) of exposed rock types; and to the papillosity (Pottiaceae) of other members on exposed habitats.

Among the tall turf-formers, *Polytrichum* and its allies cover mostly on mineral soil, while members of the Dicranaceae may be found on rocks, trees, and logs, as well as soil. The central strand of the former may be contrasted to the radiculose cloak of many members of the latter family.

The short clump-formers (Grimmia type) may be divided primarily on the basis of color, with the dark-colored Grimmiaceae of exposed habitats on rocks separated from the light-colored Orthotrichaceae of trees, especially in fog-belt regions.

Leucobryum and Sphagnum are the only tall clump-formers in our region, and they share properties such as light green color, and presence of leucocysts. The former, however, is a plant tolerant of fairly dry conditions, while the latter is restricted to regions of almost constant surface water. This ecological difference may be related to the multiple cell thickness of the leaves of Leucobryum and to the lack of any exposure to evaporation from the chlorocyst.

Barkman's division of the repent bryophytes emphasizes the placement of the secondary branches relative to the substratum. This again should affect the ease of material translocation in the plant.

The "Leskea type" has all branches closely appressed to the substratum and it includes plants as diverse as the light-colored, large-celled, dissected-leaved Cephalozia of humid, shaded sites and the dark-colored, Frullania asagrayana with inflated lobules of tree boles and canopies. Brotherella recurvans, when it occurs on tree trunks in the southern Appalachians, may also approach the "Leskea type" growth form and may, on such sites, show unusual appression of the ascending leaves—a condition shared with Leskea.

In many mosses and liverworts, plants may be ascending or repent, in wefts, supported by each other and in contact with the substratum only at their base or along a creeping main stem. This "Hypnum type" may have ascending non-complanate leaves as in Brotherella recurvans, or the leaves may be divergent from the stem in bryophytes of moister sites, such as Sphenolobus michauxii. The color of plants of this growth-form is usually grass-green, but in Marsupella sphacelata, exposed in its habitats to frequent drying, the color may be very dark. Many plants of the Hypnum type growth-form are papillose and frequently have paraphyllia (e.g., Thuidium delicatulum) and these are often characteristic of open woods with moderate exposure. Complanate bryophytes of the Hypnum type growth-form, such as Plagiothecium sylvaticum, may be found in shaded areas subject to infrequent drying.

Vaguely identifiable with the "Leucodon type" of Barkman are the feather mosses of soil habitats in the spruce-fir forest. The definition of this growth-form demands that secondary stems arise from a creeping main stem, but in Hylocomium the stems arise by innovations from the previous year's growth. Hylocomium differs from the Leucodon in having elongate, thin-walled cells, indistinct papillae, and many paraphyllia; these features seem to indicate a greater dependence upon substratal moisture than characterizes Leucodon. In many respects Hylocomium represents a transition between the growth-form with which it is here identified, and the "Isothecium type" which is absent in the spruce-fir zone.

The "Metzgeria type," whether represented by Metzgeria fruticulosa of decaying spots in tree tops or by Riccardia palmata of cut faces of logs, is a type apparently dependent upon substratal moisture, but nevertheless, resistant to prolonged drought.

A growth-form unmentioned by Barkman is the pendant type represented by *Leptodontium excelsum* and *Herberta tenuis.* Both of these plants have isodiametric dark-pigmented cells and closely appressed leaves, and they are indistinguishable on a physiognomic basis.

VI. THE BRYOPHYTE UNIONS

Many recent bryoecologists [see Barkman (1958) and his exhaustive bibliography] have classified bryophyte communities into hierarchies of orders, alliances, and associations. This procedure, analogous to that of the organismal taxonomist, has the advantage of allowing intercontinental comparisons of communities, but it suffers from relying upon the unproven assumption that phylogeny and physiognomy bear a definite relationship to the habitat. The organismal concept of a community also obscures the fact that ecological amplitude of a species is individualistic. Another difficulty involved in the European classification of plant communities into taxonomic hierarchies is related to the large amount of descriptive material which must be accumulated before nomenclature can be established. In the United States so few bryoecological researches have been published that, even were it advisable to classify those communities in hierarchies of relationship, such a task would be impossible with present knowledge. For these reasons, the present section has taken the more noncommital approach of calling a distinct community of bryophytes a "union." Unions derive their names from their most important species or, in the case of unions sharing a dominant, by a prevalent species which distinguishes them.

The descriptions of the unions which will follow are in many places less quantitative than this writer's data might have allowed. Subjective descriptions and indefinite quantifying terms such as "many" or "most" were used to avoid indicating a stronger environmental restriction of certain unions than is allowed by the accuracy of the data.

In this section, unions will be dealt with in alphabetical order of their abbreviations, and a similar order of listing is maintained in the flora presented in Appendix B. The tables which appear in this section list frequency and mean and maximum coverages computed from all quadrats assigned to each union. Choice of species to be included in the tables was determined by demanding a frequency in the union of at least ten per cent.

In the tables, frequency and mean cover are averaged to the nearest ten per cent rather than being calculated to a more precise figure than the data would allow. These computed means are represented by symbols as follows:

0 - 0- 5%	6 - 56-65%
1 - 6-15%	7 - 66-75%
2 - 16-25%	8 - 76-85%
3 - 26-35%	9 - 86-95%
4 - 36-45%	10 - 96-100%
5 - 46-55%	

The symbol "X" was used in the column "Maximum Cover" to signify presence but with coverage less than five per cent.

Habitat factors and other appropriate information which could not easily be included in the tables are presented as a tabular preface to the discussion of each union. The choice of items to be presented for any one union is guided by the demand that a listed factor be significant in the ecological orientation of the union. Coverage data are averaged to the nearest ten per cent and, where three numbers are listed, these represent the extremes and the mean.

In the material which is to follow, the reader should examine the tables and figures accompanying each unit before proceding with the reading of the pertinent text.

The Atrichum crispum Union (Ac) (See Table 2, Figure 4)

Number of times encountered	62
Average bryophyte cover within quadrats	100%
Minimum bryophyte cover in any one quadrat	90%
Proportion of quadrats on east and north-facing slopes	71%
Elevation	5500-6300 ft. (mean--5800)
Tree Canopy Coverage	70-100% (mean--80)
Shrub Stems / 10 m^2	4-26 (mean--11)
Superior Herb Coverage	10-80% (mean--20)
Inferior Herb Coverage	0-80% (mean--20)

Wherever surface mineral soil is present in intermittent seepages and washes, Atrichum crispum is the dominant species. On constantly wet, level to gently sloping areas, Mnium punctatum or its variety, elatum, replaces Atrichum, but this vegetational change is so gradual that these two communities are here considered merely as facies of a single union. More abrupt is the boundary between this union and that of Polytrichum ohioense of well-drained mineral soil, and clear lines of demarcation also define the zone of contact of Atrichum with the Hylocomium splendens union of humic soils and with the waterlogged soil union of Sphagnum spp. Logs and tree bases with a mineral soil cover may support occasional Atrichum crispum-dominated communities, but such sites are few and their vegetation is otherwise distinct from that of soil, and so data from such sites was identified with the Brotherella recurvans union.

The surface materials of the seepages where Atrichum crispum is found typically comprise pebbles and slabs of rock scattered among

Table 2. Atrichum crispum Union

Species	Freq.	Mean Cover	Max. Cover
Atrichum crispum	9	7	10
Polytrichum ohioense	7	1	6
Mnium punctatum	4	1	8
Scapania nemorosa	4	1	3
Brotherella recurvans	4	0	2
Sphagnum quinquefarium	2	1	2
Lepidozia reptans	2	0	1
Bazzania trilobata	1	0	7
Mnium punctatum var. elatum	1	0	6
Hylocomium splendens	1	0	2

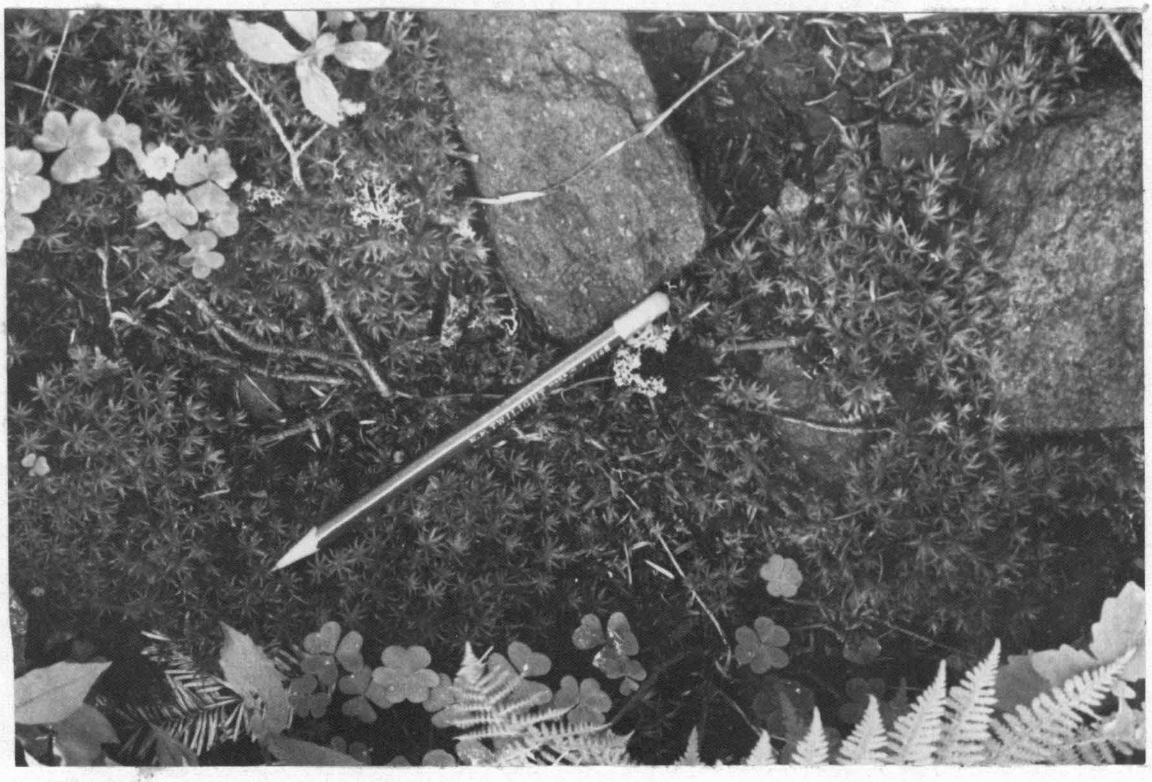

Figure 4. The Atrichum crispum union on steep slope near Clingman's Dome, 6400 feet elevation, May 1964.

finer textured materials (usually sand). On the sand, there is almost a complete cover of Atrichum, but the rocks have large quantities of Scapania nemorosa. In this writer's opinion such areas would probably have been described as a vegetational mosaic of two unions, had the sampling methods been appropriate to the revealing of such a reticulate pattern.

The Atrichum crispum union forms a tall turf, and the dominant moss has a central strand. Intertwining stems of dissected-leaved creeping liverworts of the Leskea-type growth form (Lepidozia reptans) regularly occur among the larger plants, and the borders of this union frequently bear bryophytes customarily found in nearby communities.

An extensive and typical example of the A. crispum union is found in the spruce-fir-Oxalis-Hylocomium stand on the slopes above Mt. Collins shelter near the intersection of the Appalachian and Sugarland trails. This almost level area has large uni-specific mats on sandy mineral soil. Co-occurence with Scapania nemorosa typifies steep slopes such as occur in the fir forests on the west slopes of Mt. Guyot.

The Brotherella recurvans Union (Br) (See Table 3, Figure 5)

Number of times encountered	
on logs	804
on trees	763
on rock	13
Average bryophyte cover within quadrat	100%
Minimum bryophyte cover in any one quadrat	30%
Proportion of epixylic quadrats below 5500 feet	32%

Table 3. Brotherella recurvans Union

Species	All Substrates			All Logs			All Tree Bases		
	Freq.	Mean Cover	Max. Cover	Freq.	Mean Cover	Max. Cover	Freq.	Mean Cover	Max. Cover
Brotherella recurvans	8	5	10	8	4	10	9	5	10
Dicranum fuscescens	7	2	10	8	3	10	6	3	10
Lepidozia reptans	5	0	3	5	0	3	2	0	3
Hylocomium splendens	3	1	5	3	0	4	3	0	5
Hypnum imponens	3	0	8	6	2	8	0	0	0
Bazzania trilobata	2	1	10	3	0	10	5	1	10
Dicranum scoparium	2	0	10	4	0	10	0	0	0
Thuidium delicatulum	2	0	8	2	0	8	1	0	7
Hylocomium brevirostre	2	0	7	1	0	6	2	0	5
Heterophyllium nemorosum	2	0	6	4	0	6	0	0	0
Jamesoniella autumnalis	2	0	2	2	0	2	1	0	1
Blepharostoma trichophyllum	2	0	1	2	0	X	3	0	1
Ptilium crista-castrensis	1	0	5	2	0	5	2	0	2
Sphenolobus michauxii	1	0	5	1	0	4	3	0	5
Polytrichum ohioense	1	0	3	1	0	2	1	0	3
Sphenolobus exsectus	1	0	2	1	0	1	1	0	2
Plagiothecium laetum	1	0	1	1	0	X	1	0	1
Cephalozia spp.	1	0	1	2	0	1	0	0	0
Dicranodontium denudatum	0	0	8	1	0	8	0	0	0
Hypnum reptile	0	0	7	0	0	1	0	0	7
Herberta hutchinsiae	0	0	4	0	0	0	4	0	4
Bazzania nudicaulis	0	0	4	0	0	0	1	0	4
Calliergonella schreberi	0	0	4	1	0	4	0	0	0
Sphagnum spp.	0	0	3	2	0	3	0	0	0
Geocalyx graveolens	0	0	2	2	0	2	0	0	0
Rhytidiadelphus triquetrus	0	0	2	0	0	0	1	0	2
Mnium punctatum	0	0	1	1	0	1	1	0	X
Plagiochila tridenticulata	0	0	1	0	0	X	0	0	1
Scapania nemorosa	0	0	1	0	0	X	0	0	1

Table 3. (Continued)

Species	Logs Below 5500 Feet Freq.	Mean Cover	Max. Cover	Logs Above 5500 Feet Freq.	Mean Cover	Max. Cover
Brotherella recurvans	6	3	10	9	5	10
Dicranum fuscescens	7	2	10	9	3	10
Lepidozia reptans	5	0	3	5	0	3
Hylocomium splendens	1	0	4	4	0	3
Hypnum imponens	6	2	7	6	1	8
Bazzania trilobata	5	2	10	2	0	9
Dicranum scoparium	4	0	10	5	0	8
Thuidium delicatulum	4	0	8	1	0	5
Hylocomium brevirostre	3	1	6	0	0	2
Heterophyllium nemorosum	7	0	6	3	0	5
Jamesoniella autumnalis	2	0	2	3	0	2
Blepharostoma trichophyllum	0	0	X	3	0	X
Ptilium crista-castrensis	0	0	1	3	0	5
Sphenolobus michauxii	0	0	3	2	0	4
Polytrichum ohioense	1	0	2	1	0	1
Sphenolobus exsectus	0	0	X	1	0	1
Plagiothecium laetum	0	0	X	1	0	X
Cephalozia spp.	0	0	1	4	0	X
Dicranodontium denudatum	0	0	X	1	1	8
Calliergonella schreberi	0	0	0	2	0	4
Sphagnum spp.	1	0	2	3	0	3
Geocalyx graveolens	0	0	X	3	0	2
Mnium punctatum	0	0	1	2	0	1

Table 3 (Continued)

Species	Spruce Tree Bases			Fir Tree Bases			Hardwood Tree Bases		
	Freq.	Mean Cover	Max. Cover	Freq.	Mean Cover	Max. Cover	Freq.	Mean Cover	Max. Cover
Brotherella recurvans	7	2	10	10	6	10	8	5	10
Dicranum fuscescens	8	2	10	6	3	9	6	3	8
Hylocomium splendens	3	0	5	3	0	3	2	1	5
Bazzania trilobata	9	3	10	4	0	4	5	1	10
Thuidium delicatulum	5	0	7	0	0	1	1	0	4
Hylocomium brevirostre	5	1	5	1	0	1	7	1	5
Jamesoniella autumnalis	0	0	X	2	0	1	0	0	X
Blepharostoma trichophyllum	0	0	X	4	0	1	2	0	X
Ptilium crista-castrensis	2	0	1	1	0	1	1	0	2
Sphenolobus michauxii	1	0	2	4	0	5	5	0	1
Polytrichum ohioense	2	0	2	1	0	2	3	0	3
Sphenolobus exsectus	0	0	X	2	0	1	0	0	2
Plagiothecium laetum	2	0	1	1	0	X	1	0	1
Hypnum reptile	4	0	7	0	0	X	0	0	X
Herberta hutchinsiae	3	0	4	4	0	3	5	0	2
Bazzania nudicaulis	1	0	X	2	0	4	0	0	4
Rhytidiadelphus triquetrus	0	0	X	1	0	X	1	0	2
Mnium punctatum	0	0	X	1	0	X	0	0	X
Plagiochila tridenticulata	0	0	0	1	0	X	0	0	1
Scapania nemorosa	0	0	1	1	0	X	0	0	X

Figure 5. The Brotherella recurvans union on log of decay class "3" on Clingman's Dome, 6600 feet elevation, June 1964.

Proportion of epiphytic quadrats on spruce	8%
on fir	78%
Proportion of epixylic quadrats on logs of decay class "3"	79%

The *Brotherella recurvans* union is found on logs, trees, and rocks. Many terrestrial quadrats in spruce and spruce-fir forests are dominated by *B. recurvans*, but the total bryophyte cover on such sites is so sparse (usually less than 30%) that a more conservative approach was followed--that of identification with a more typical terrestrial union (*Hylocomium splendens*). On logs, the *B. recurvans* union is intermediate in a successional trend between the *Nowellia curvifolia* union and the *Hylocomium splendens* union. It is bordered by the *Cephalozia* union of the sides of logs and it gives way gradually to the latter union as light diminishes and humidity increases. Except on large, low elevation spruces all tree flares have the *B. recurvans* union. On boulders flush with the surface soil this union lies in an intermediate position between the *Rhacomitrium heterophyllum* union of bare rock and the *Hylocomium splendens* union of soil.

Many species may be dominant in the *Brotherella recurvans* union, and the dominance by any one species is not always easily correlated with habitat. In general, *B. recurvans* shares high cover values with *Dicranum fuscescens*. Large quantities of *Dicranum scoparium* and *Dicranodontium denudatum* may occur on unusually moist logs, while logs subject to high light intensities are ordinarily covered by *Hypnum imponens* (high elevations) and *Thuidium delicatulum* (low elevations). *Bazzania trilobata* and *Hypnum reptile* are frequent on spruce tree bases and the former may dominate logs under such trees; bases of hardwood trees at all elevations often have a high cover of Hylocomium brevirostre.

Two types of life-form characterize the B. recurvans union. One is a typical Hypnum type and the other is a low turf of radicle-clad mosses. Interspersed among either of these types of plant colonies may be a partial layer of complanate liverworts, such as Jamesoniella or of plants with dissected leaves like Blepharostoma trichophyllum and Lepidozia reptans.

The epixylic expression of this union is identical with the Dicranum fuscescens union of Cain and Sharp (1938); while the epiphytic example of the B. recurvans union is called by the same authors the "Brotherella recurvans facies of the Hypnum union."

The Bazzania trilobata Union (Bt) (See Table 4, Figure 6)

Number of times encountered	115
Average bryophyte cover within quadrats	100%
Minimum bryophyte cover in any one quadrat	70%
Proportion of quadrats on spruce	99%
Elevation of quadrats	4100-6000 feet (mean--5400)

Entirely restricted to the flares of large spruces is the Bazzania trilobata union. Its habitats closely resemble those of the tree-base communities of Brotherella recurvans. The reason for the luxuriance of Bazzania on spruce is not clear to this writer. It borders tree trunk communities dominated primarily by Hypnum reptile, and touches upon terrestrial plant communities which are almost devoid of bryophytes.

Table 4. Bazzania trilobata Union

Species	Freq.	Mean Cover	Max. Cover
Bazzania trilobata	10	8	10
Brotherella recurvans	9	1	3
Lepidozia reptans	5	0	1
Hypnum reptile	4	0	5
Hylocomium splendens	3	1	3
Hylocomium brevirostre	3	1	3
Polytrichum ohioense	3	0	1
Herberta hutchinsiae	3	0	1
Thuidium delicatulum	1	0	X

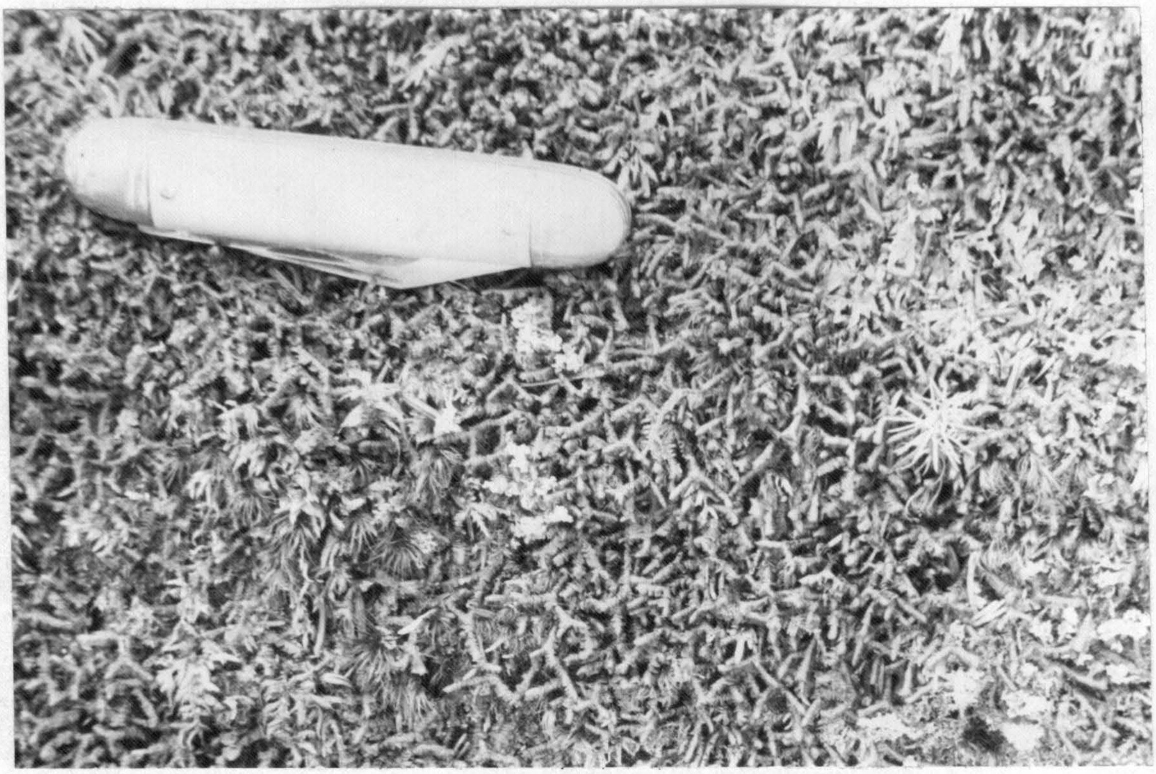

Figure 6. The Bazzania trilobata union on spruce base near Indian Gap, 5200 feet elevation, May 1964.

On tree bridges Bazzania trilobata extends farther into poorly lighted regions than do members of the related Brotherella recurvans union.

Areas dominated by Bazzania trilobata also occur on rocks and on logs, but the associated vegetation on such substrates is too different to warrant identification with the spruce-flare communities. The life-form exhibited by Bazzania trilobata is that of the Hypnum type, but divergent, complanate leaves allow a distinction of this life-form from that exhibited by Brotherella recurvans. In a very large number of cases, a well-developed inferior layer of bryophytes is contributed by a reticulate mass of Lepidozia reptans among the larger plants of Bazzania.

This union is apparently identical with the Bazzania facies of the Hylocomium union recognized by Cain and Sharp (1938).

The Cephalozia Union (Ce) (See Table 5, Figure 7)

Number of times encountered	
on logs of decay class "1" and "2"	489
on logs of decay class "3" and "4" and "5"	816
Maximum bryophyte cover within quadrats	100%
Average bryophyte cover within quadrats	40%
Minimum bryophyte cover within quadrats	0%

The Cephalozia union is found only on the shaded sides of decorticated logs and is bordered by any of the communities of log tops. It is closely related to the Plagiothecium laetum union of tree bridges, but differs in the frequent presence of Tetraphis pellucida and in the greater cover formed by its bryophytes.

Table 5. Cephalozia Union

Species	Decay Class 1-2			Decay Class 3-5		
	Freq.	Mean Cover	Max. Cover	Freq.	Mean Cover	Max. Cover
Cephalozia spp.	8	2	9	6	2	9
Plagiothecium laetum	7	0	3	7	0	5
Tetraphis pellucida	4	1	6	9	3	10
Dicranum fuscescens	4	0	1	5	0	2
Brotherella recurvans	3	0	3	5	0	1
Lepidozia reptans	3	1	7	3	1	10
Bazzania trilobata	1	0	2	4	0	4
Hylocomium splendens	3	0	2	2	0	X
Dicranodontium denudatum	1	0	6	3	0	7
Geocalyx graveolens	1	0	4	1	0	6
Sphenolobus exsectus	2	0	2	0	0	2
Sphenolobus michauxii	1	0	X	1	0	4
Jamesoniella autumnalis	1	0	1	1	0	X
Thuidium delicatulum	0	0	X	1	0	X
Scapania nemorosa	0	0	X	1	0	X
Nowellia curvifolia	1	0	X	0	0	X

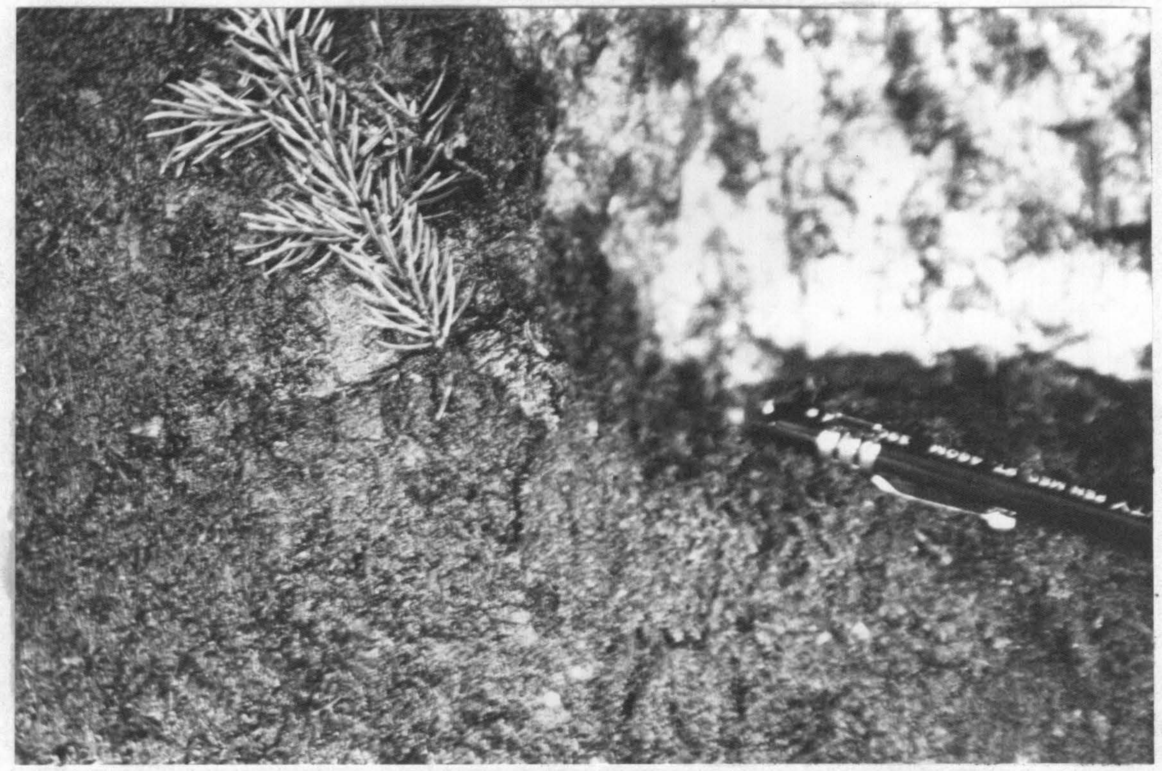

Figure 7. The Tetraphis pellucida facies of the Cephalozia union on log of decay class "4" near Indian Gap, 5200 feet elevation, May, 1964.

Four plants may dominate in the Cephalozia union. Cephalozia spp. is found primarily on logs in early stages of decay and Tetraphis pellucida predominates on more decayed logs; while drier sites and more exposed niches show high coverage of Lepidozia reptans. Moist areas with moderate shading may have as a dominant, Dicranodontium denudatum. Some sites, especially those on logs in later stages of decay, lack bryophytes as a result of continuous sloughing of decayed wood. The absence may also be related to shading by a pendant screen of Brotherella which frequently trails from a luxuriant mat on the log's top.

Most of the Cephalozia plants encountered in this union are depauerate and few have perianths or other features enabling identification. For this reason, this genus was seldom identified to species. The information available, however, indicates that C. bicuspidata is probably the most abundant Cephalozia here.

The Dicranodontium denudatum Union (Dd) (See Table 6, Figure 8)

Number of times encountered	41
Average bryophyte cover within quadrats	100%
Minimum bryophyte cover in any one quadrat	70%
Proportion of quadrats with "very diffuse" or less light	89%
Proportion of quadrats on walls or incisions	78%
Elevation of quadrats	5600-6600 feet (mean 5900)

On moist rocks which are shielded from rainfall, Dicranodontium denudatum is the most frequent dominant. This dominance is interrupted only by the presence of Bazzania denudata, which forms masses pendant

Table 6. *Dicranodontium denudatum* Union

Species	Freq.	Mean Cover	Max. Cover
Dicranodontium denudatum	10	5	10
Herberta hutchinsiae	7	1	3
Bazzania denudata	4	1	10
Thuidium delicatulum	3	1	2
Oncophorus rauei	2	0	4
Tetraphis pellucida	2	0	2
Andreaea rupestris	2	0	1
Paraleucobryum longifolium	1	0	5
Scapania nemorosa	1	0	1
Marsupella emarginata	1	0	X
Radula andicola	1	0	X
Dicranum scoparium	1	0	X
Sematophyllum carolinianum	1	0	X

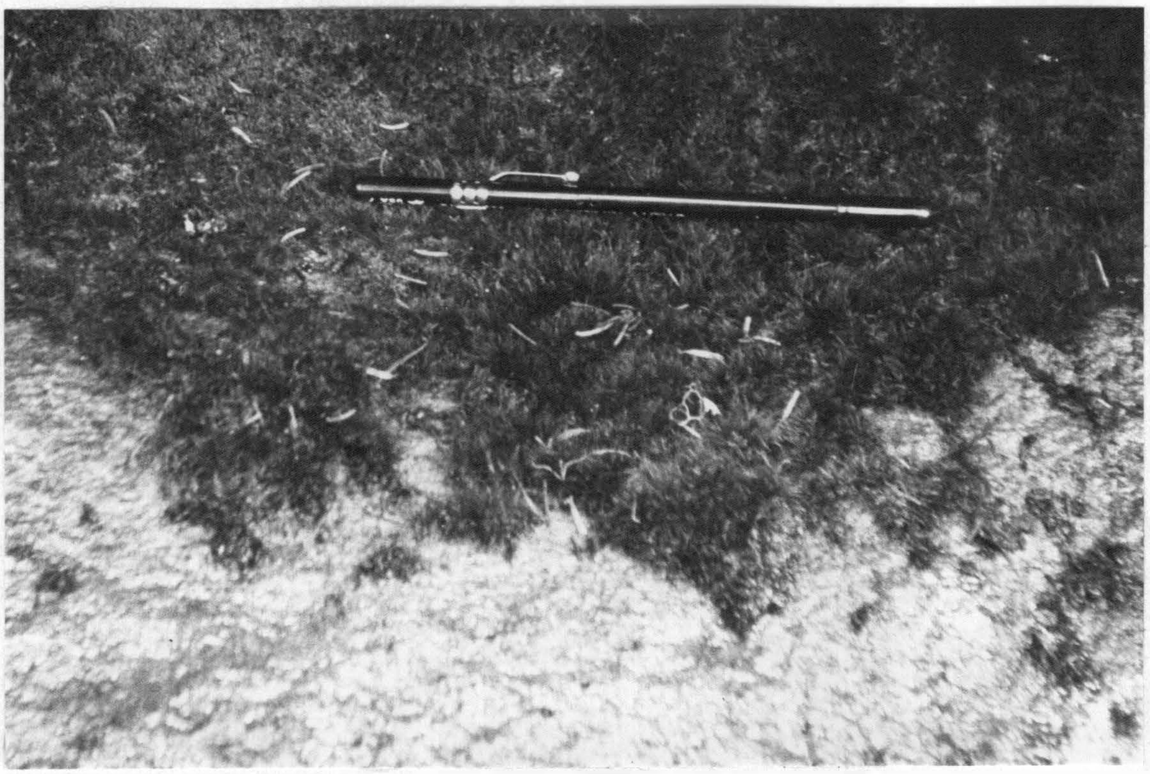

Figure 8. The Dicranodontium denudatum union on rock face below overhang near Mt. Kephart, 5800 feet elevation, July, 1964.

from narrow ledges. This union is bounded by regions receiving direct rainfall, by regions of intense shade (Rhabdoweisia denticulata union); and by areas of frequent drying conditions (Herberta hutchinsiae union).

D. denudatum is also an occasional dominant species of the root bridges of stumps and spars and is there associated primarily with Tetraphis pellucida and identified with the Plagiothecium laetum union. The occasional occurrence of high quantities of D. denudatum in the Brotherella recurvans union of log tops appears correlated with logs whose early decay stages supported the Sphenolobus michauxii union.

The life-form of the D. denudatum union is that of a low turf formed by plants with caducous leaves. Strands of Bazzania denudata are regularly found in this turf and this latter plant too has caducous leaves. The presence of caducous leaves or large gemmae (Tetraphis pellucida) is a feature of possible significance to the composition of a life-form classification. Sharp (1955) states, ". . . species with asexual reproduction may perhaps migrate into areas in which sexual reproduction is inhibited by some extreme." It appears to the present writer that this phytogeographic observation of Sharp may equally be applied to ecological niches presenting extreme environmental conditions.

The Dicranella heteromalla Union (Dh) (See Table 7, Figure 9)

Number of times encountered	25
Average bryophyte cover within quadrats	100%
Minimum bryophyte cover in any one quadrat	100%
Proportion of quadrats with "VDF," "DF," or "RDF" light intensities	80%

Table 7. Dicranella heteromalla Union

Species	Freq.	Mean Cover	Max. Cover
Dicranella heteromalla	7	5	10
Pohlia elongata	5	3	10
Scapania nemorosa	5	0	X
Diplophyllum apiculatum	4	0	2
Microlepidozia sylvatica	3	0	4
Lepidozia reptans	2	0	1
Sphenolobus michauxii	2	0	1
Mnium punctatum	1	1	2
Hypnum fertile	1	0	1
Blepharostoma trichophyllum	1	0	1
Jamesoniella autumnalis	1	0	X
Plagiothecium denticulatum	1	0	X
Trichostomum cylindricum	1	0	X

Figure 9. The Dicranella heteromalla union on vertical north-facing bluff near Mt. Kephart, 5600 feet elevation, July, 1964.

Proportion of quadrats on "ledges," "bases," and "cracks"	64%
Proportions of quadrats with soil depth greater than "1"	88%

Narrow ledges with little or no mineral soil cover have a low turf dominated by Dicranella heteromalla or Pohlia elongata. Pohlia nutans occasionally replaces the latter species in areas of intense shade. Scapania nemorosa regularly occurs on the margins of such unions, and the drainages of such ledges may be covered by Diplophyllum apiculatum or Microlepidozia sylvatica. This union borders upon any of the epilithic bryophyte unions which occur on the surface of diffusely shaded rocks, but it is most abundant in the vicinity of the Rhacomitrium heterostichum union. Its margins are distinct, being set by the limits of the ledge on which it occurs. The only similar community of bryophytes encountered by this writer is that found on rocky trail banks and typically dominated by Dicranella heteromalla.

The Frullania asagrayana Union (Fa) (See Table 8, Figures 10 and 11)

Number of times encountered	1569
Number of quadrats lacking bryophytes	313
Average bryophyte cover within quadrats	70%
Maximum bryophyte cover in any one quadrat	100%
Average cover on fir	90%
Average cover on spruce	20%

The most abundant bryophyte union on tree boles in the spruce-fir zone is that of Frullania asagrayana. This union alsp persists on dead

Table 8. Frullania asagrayana Union

Species	All Trees			Spruce Trees			Fir Trees		
	Freq.	Mean Cover	Max. Cover	Freq.	Mean Cover	Max. Cover	Freq.	Mean Cover	Max. Cover
Frullania asagrayana	8	6	10	5	1	8	9	6	10
Paraleucobryum longifolium	6	1	10	2	1	7	7	3	10
Brotherella recurvans	5	1	5	1	0	5	6	1	3
Herberta hutchinsiae	3	0	10	2	0	4	4	0	10
Sphenolobus exsectus	2	0	4	1	0	1	1	0	1
Hypnum reptile	2	0	2	5	1	2	1	0	X
Bazzania trilobata	1	0	4	2	0	4	1	0	X
Dicranum fuscescens	1	0	3	1	0	3	0	0	X
Ulota crispa	1	0	3	0	0	X	1	0	2
Zygodon viridissimus	1	0	2	0	0	X	1	0	1
Plagiochila tridenticulata	1	0	1	0	0	1	1	0	1
Microlejeunea ulicina	1	0	1	2	0	X	1	0	X
Anomylia cuneifolia	0	0	1	0	0	1	1	0	X

Figure 10. The Frullania asagrayana union on bark of fir near Collins Gap, 6000 feet elevation, June, 1964.

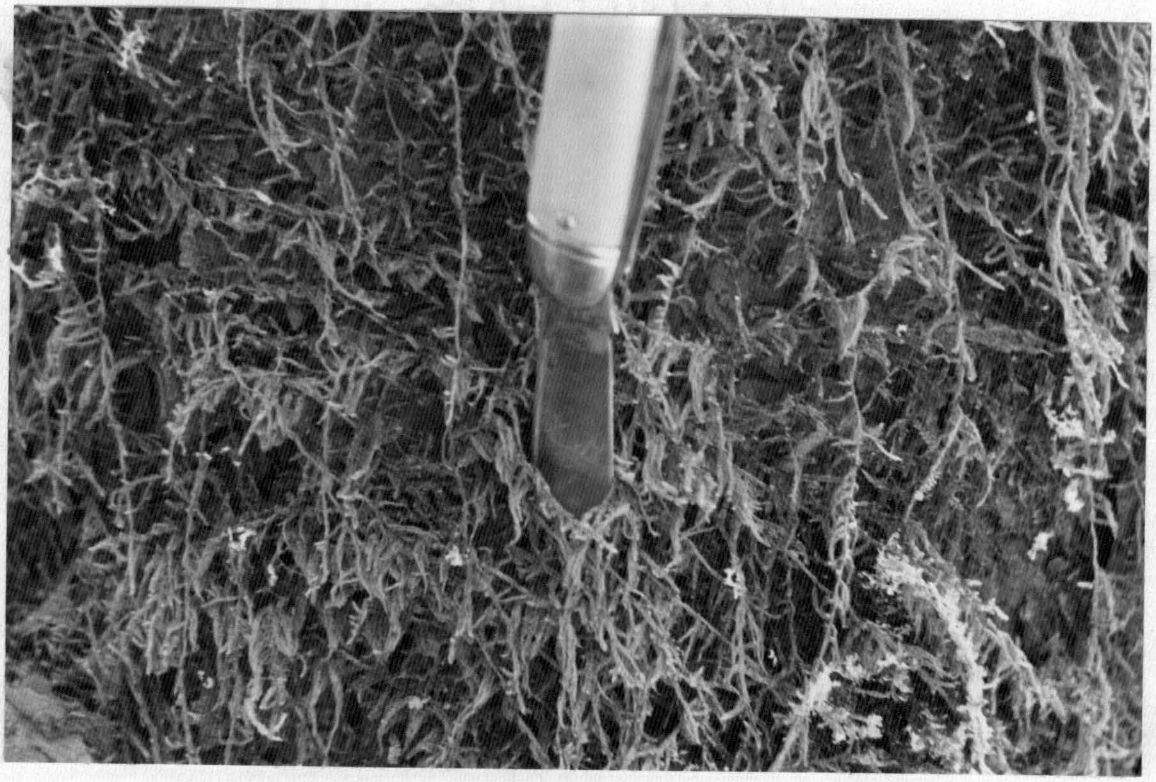

Figure 11. The Frullania asagrayana union overgrown by Hypnum reptile on bark of undecorticated dead fir tree near Indian Gap, 5200 feet elevation, May, 1964.

undecorticated spars where it may for a time grow more luxuriantly than on the living tree. On fallen logs, however, the members of the *Frullania* union gradually decline in vigor and may be completely dead before decortication. The *Ulota crispa* union forms the upper limit of occurrence on trees in areas of high exposure, and the lower margin is set by the *Brotherella recurvans* union of flares.

The composition of the *Frullania* union is influenced, in large part, by the nature of the species of tree. Best development occurs on fir where a tall turf of *Paraleucobryum* and an appressed mat of the dark-colored *Frullania asagrayana* form a growth pattern related to successive cycles which include *Frullania* establishment, *Paraleucobryum* overgrowth, subsequent loss of the latter species by bark-sloughing, and *Frullania* re-establishment.

The *Frullania asagrayana* union on spruce is seldom well developed; mnay quadrats, especially on large trees, are completely free of bryophytes, and most of the others have only scattered strands of *Frullania*, *Paraleucobryum*, and *Hypnum reptile*.

The bark of birch frequently supports *Sphenolobus michauxii*, and branches of *Acer spicatum* are excellent substrates for *Zygodon viridissimus* and *Ulota crispa*.

This union is identical with the "*Frullania* union" of Cain and Sharp (1938).

The *Herberta hutchinsiae* Union (Hh) (See Table 9, Figures 12 and 13)

Number of times encountered	141
Maximum bryophyte cover in any one quadrat	90%

Table 9. Herberta hutchinsiae Union

Species	Freq.	Mean Cover	Max. Cover
Herberta hutchinsiae	8	5	10
Dicranodontium denudatum	7	1	6
Bazzania denudata	4	1	7
Andreaea rupestris	4	0	2
Scapania nemorosa	3	0	1
Thuidium delicatulum	2	0	2
Paraleucobryum longifolium	1	0	9
Oncorphorus rauei	1	0	6
Plagiochila austinii	1	0	4
Bazzania nudicaulis	1	0	1
Pohlia elongata	1	0	1

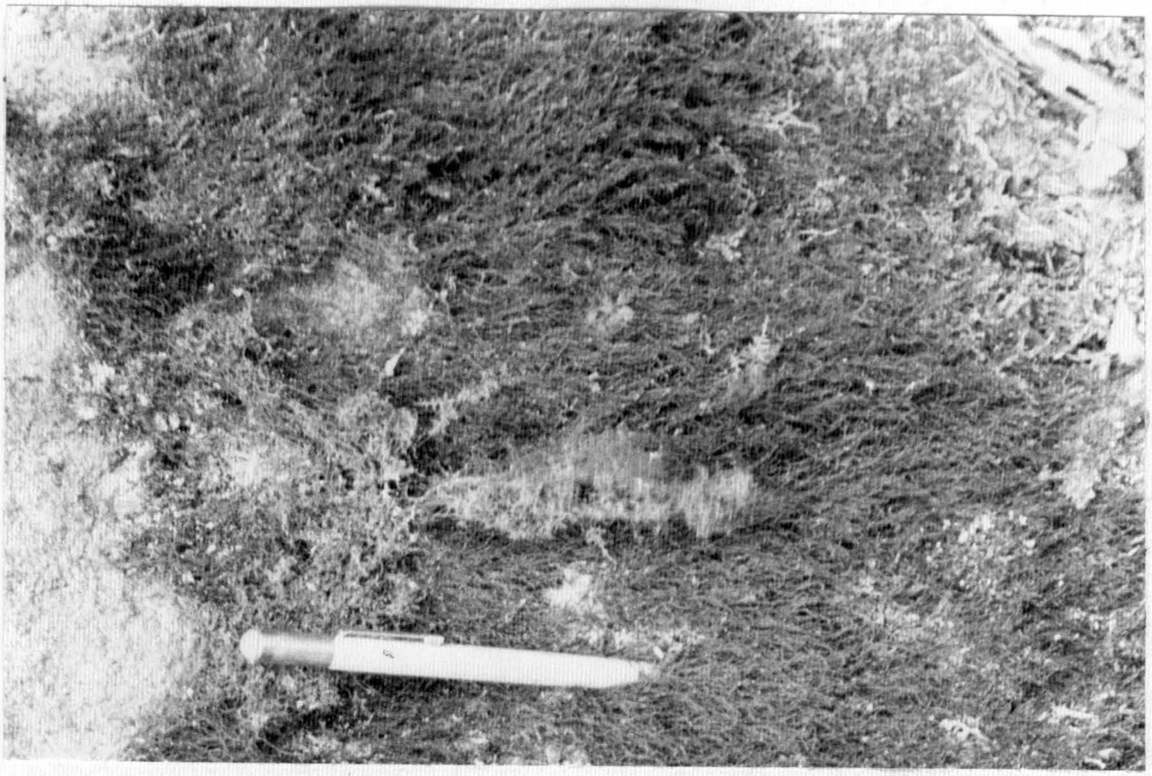

Figure 12. The Herberta hutchinsiae union on ceiling of rock overhang on north-facing bluff near Mt. Collins, 6200 feet elevation, June, 1964.

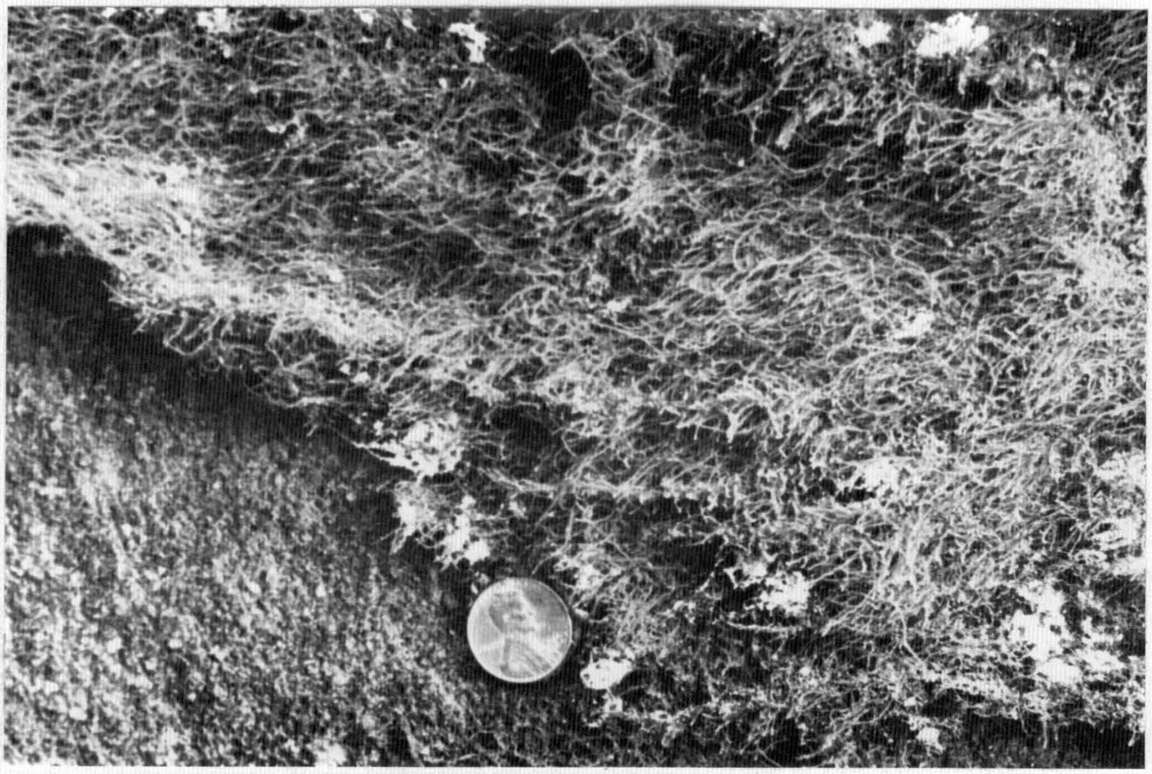

Figure 13. The Herberta hutchinsiae union on rock face below overhang, near Mt. Kephart, 5800 feet elevation, July, 1964.

Average bryophyte cover within quadrats	70%
Minimum bryophyte cover in any one quadrat	60%
Proportion of quadrats on walls or incisions	96%
Proportion of quadrats with "2h" water availability	76%
Proportion of quadrats over 5500 feet elevation	100%

Rocks shielded from rain and subject to occasional drying support large populations of Herberta hutchinsiae. This union grades imperceptibly into the Dicranodontium denudatum union and may be in contact with the constantly moist Rhabdoweisia denticulata union of very dark crannies. Bazzania denudata occurs in pendant masses anchored to narrow ledges just as it does in the Dicranodontium union. Near the top of overhanging rocks occasional direct rainfall is received and there, Andreaea rupestris is frequent, but of low coverage. The cause of the occasional high coverage in this union by Plagiochila austinii, Paraleucobryum longifolium and Oncophorus rauei is unknown to this writer.

Herberta hutchinsiae also is a frequent dominant in fog belts on exposed trees. In such sites, designated in this paper as the Ulota crispa union, Herberta is the dominant species, but subordinate species on rocks are so different from those on trees that the Herberta and the Ulota unions are considered distinct.

The pendant, dark-colored life-form typical of areas of fog and high evaporation rates is predominant in the Herberta hutchinsiae union.

The Hylocomium splendens Union (Hs) (See Table 10, Figures 14, 15, and 16)

Number of times encountered	
on logs	142
on soil	340
on rocks	36

Table 10. Hylocomium splendens Union

Species	All Substrates			Forest Site Types with High Soil Bryophyte Cover			Forest Site Types with Low Soil Bryophyte Cover		
	Freq.	Mean Cover	Max. Cover	Freq.	Mean Cover	Max. Cover	Freq.	Mean Cover	Max. Cover
Hylocomium splendens	8	7	10	9	9	10	6	0	2
Brotherella recurvans	8	1	3	7	0	3	9	1	2
Hylocumium brevirostre	4	0	10	1	0	2	8	0	3
Rhytidiadelphus triquetrus	4	0	8	5	0	8	0	0	X
Dicranum fuscescens	4	0	6	6	0	6	0	0	X
Polytrichum ohioense	4	0	4	4	0	2	0	0	X
Ptilium crista-castrensis	4	0	3	4	0	3	0	0	0
Thuidium delicatulum	3	0	3	2	0	2	4	0	X
Bazzania trilobata	2	0	6	3	0	6	1	0	X
Calliergonella schreberi	1	0	8	1	0	8	0	0	0
Hylocomium umbratum	1	0	5	1	0	5	0	0	0
Dicranum scoparium	1	0	2	1	0	2	0	0	0
Lepidozia reptans	1	0	1	1	0	1	0	0	0

Figure 14. The Hylocomium splendens union on floor of spruce forest near Newfound Gap, 5500 feet elevation, July, 1964.

Figure 15. The Hylocomium brevirostre facies of the H. splendens union on base of birch tree at top of ridge near Collins Gap, 6000 feet elevation, June, 1964.

Figure 16. A typical view of the forest floor in spruce forest near Indian Gap, 5200 feet elevation, June, 1964. (Note the almost total lack of bryophytes and low cover of other plants.)

Maximum coverage in any one quadrat	100%
Average bryophyte cover within quadrats	80%
Minimum coverage in any one quadrat	0%

Terrestrial sites with moderate to good drainage, logs in late stages of decay, and the tops of soil-covered rocks are the normal habitats of the Hylocomium splendens union. On soil, Hylocomium splendens is abundant only in certain forest site types, and it is almost absent from the following:

1. spruce - fir - Viburnum - Vaccinium - Senecio
2. spruce - fir - Rhododendron
3. spruce - Viburnum - Vaccinium - Lycopodium
4. spruce - Rhododendron

The data from the thirty-six terrestrial quadrats in each of the above four types are presented in Table 10 under the heading, "Forest Site Types with Low Soil Bryophyte Cover." All other soil cover quadrats are considered together as originating from high coverage communities.

The major difference between the low cover terrestrial types and those of high cover lies in the absence of Hylocomium splendens from the former, accompanied by a parallel but slight increase of Brotherella recurvans in the former. The filmy mat which covers the leaf litter in low coverage sites is composed of depauperate plants which rarely produce sporophytes. With such sterile and poorly developed plants, it was often difficult to distinguish B. recurvans from B. delicatula.

Four species may dominate in high-coverage Hylocomium splendens unions. A low elevation species found primarily in the vicinity of hardwoods is Hylocomium brevirostre. Rhytidiadelphus triquetrus is especially common on well-drained sites and may be found most frequently on upraised areas such as the erosion control banks of trails. The virtual restriction of Calliergonella schreberi to the Mt. LeConte region will be commented upon in the next section.

The typical life-form exhibited by plants of the Hylocomium splendens union is that which has been identified with the Leucodon type of Barkman (1958), but perhaps should have been separately treated as a "feather moss" consociation. Secondary layers of bryophyte vegetation are not well developed, although the plants of the primary life-form typically present a multistratal vegetational cover.

Cain and Sharp (1938 described this union and used the identical name.

The Lophozia incisa Union (Li) (See Table 11, Figure 17)

Number of times encountered	74
Maximum bryophyte cover in any one quadrat	100%
Average bryophyte cover within quadrats	80%
Minimum bryophyte cover in any one quadrat	30%
Proportion of quadrats with water availability of "3" or more	100%
Proportion of quadrats with "very diffuse" or less light	70%
Proportion of quadrats on "shoulders," "faces," or incisions"	91%

On bare rocks occasionally subject to drying is found the Lophozia incisa union. This is probably a complex of several unions not adequately

Table 11. *Lophozia incisa* Union

Species	Freq.	Mean Cover	Max. Cover
Lophozia incisa	9	5	8
Scapania nemorosa	7	2	4
Mnium punctatum	7	1	4
Atrichum crispum	4	1	3
Plagiothecium sylvaticum	3	1	10
Diplophyllum apiculatum	3	0	2
Sematophyllum marylandicum	1	0	10
Jubula pennyslvanica	1	0	4
Dicranella heteromalla	1	0	3
Pohlia elongata	1	0	1
Bazzania trilobata	1	0	X
Microlepidozia sylvatica	1	0	X
Radula andicola	1	0	X

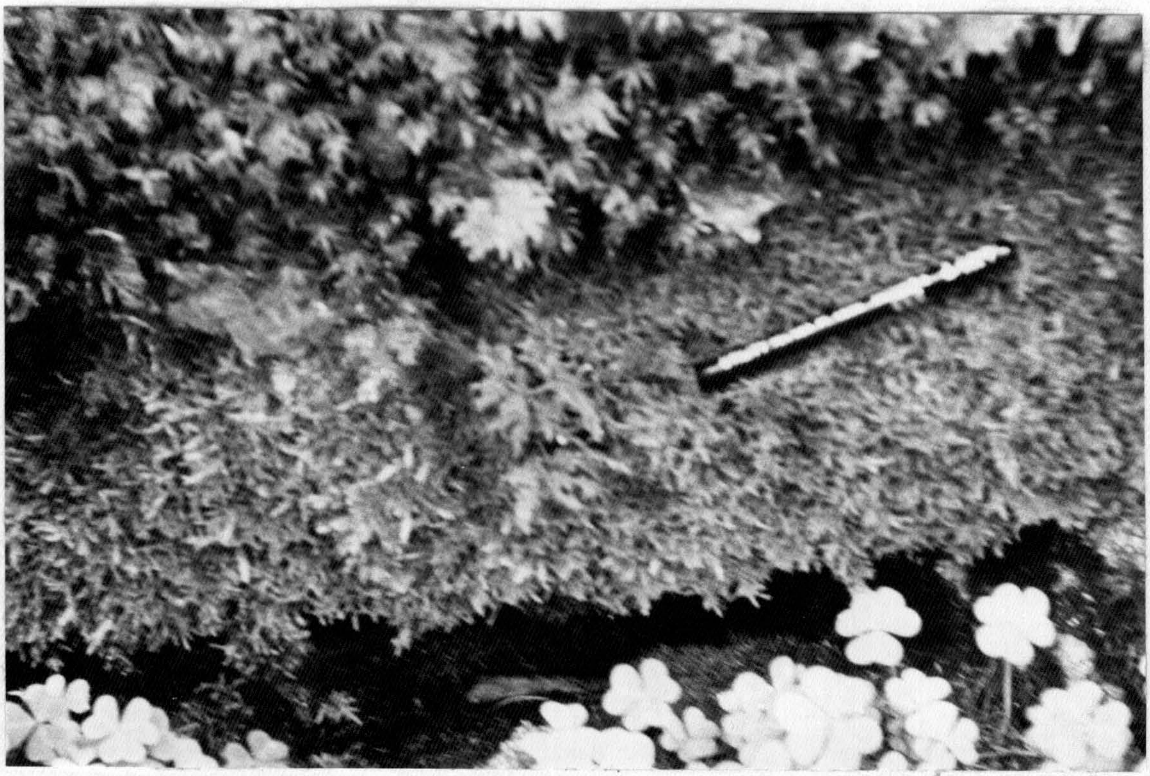

Figure 17. The Sematophyllum marylandicum facies of the Lophozia incisa union in seepage near Mt. Kephart, 6000 feet elevation, July, 1964.

distinguished by this writer's sampling techniques. At least three species may be dominant here, and each of these seldom occurs in the presence of either of the others. Rock faces subject to intermittent seepage have Sematophyllum marylandicum in the areas of moderate shade. More intense shade is correlated with dominance of Plagiothecium sylvaticum. Lophozia incisa is found primarily in moist areas where surface water is seldom visible. It would appear that this community is probably closely related to the Scapania nemorosa union which often borders it in areas of more constant seepage. It may also be found as a successional type on bare rocks from which a Hylocomium splendens mat has fallen, and in this latter case, Cephalozia spp. may be fairly abundant, at least in the early stages of succession.

The life-form characterizing this community is generally that of a Hypnum mat whose plants have divergent or complanate leaves. Sematophyllum marylandicum, however, approaches the appressed-leaved Leskea type.

The Marsupella sphacelata Union (Ms) (See Table 12, Figure 18)

Number of times encountered	27
Maximum bryophyte cover in any one quadrat	100%
Average bryophyte cover within quadrats	90%
Minimum bryophyte cover within quadrats	70%
Proportion quadrats with intensity of light "RDF" or greater	100%
Proportion quadrats subject to occasional submergence	100%

Table 12. Marsupella sphacelata Union

Species	Freq.	Mean Cover	Max. Cover
Marsupella sphacelata	10	6	10
Rhacomitrium aciculare	6	1	4
Scapania nemorosa	6	1	4
Mnium punctatum	3	1	2
Hygrohypnum eugyrium	1	1	6
Brachythecium rivulare	1	0	6
Sematophyllum marylandium	1	0	4
Diplophyllum apiculatum	1	0	1
Radula andicola	1	0	1

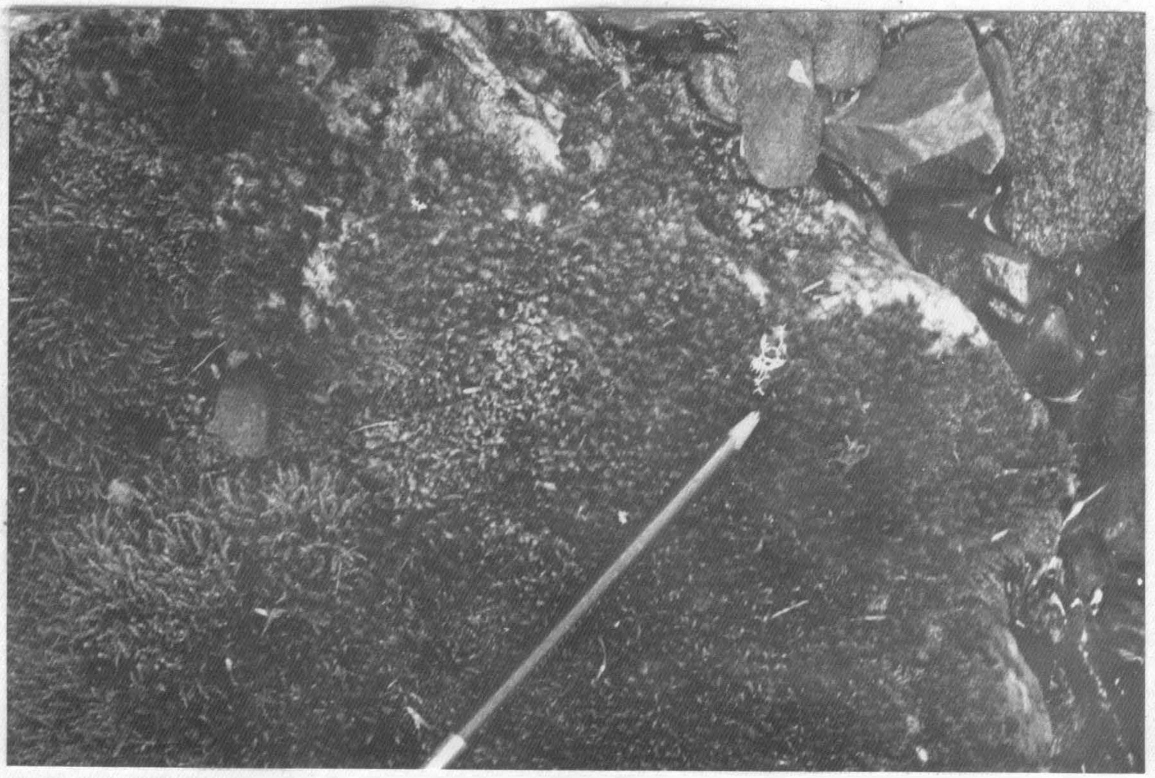

Figure 18. The Marsupella sphacelata union on top of rock in Camp Prong near Indian Gap, 5000 feet elevation, June, 1964.

At or near the water-line on rocks in permanent streams is a dark-colored plant with a Hypnum life-form. Only Marsupella sphacelata ideally composes this union; plants from the Rhacomitrium aciculare union of drier rocks and the Scapania nemorosa union on inundated rocks appear with Marsupella in the data but are transgressives from contiguous unions.

In many respects the physiognomy of the Marsupella sphacelata union resembles that of the Lophozia facies of the Lophozia incisa union. There are also parallels in the ecological position--both unions occur contiguous to more moist areas dominated by Scapania nemorosa.

This union was seen mainly in the upper reaches of Ramsey Prong in the Great Smoky Mountains National Park.

The Nowellia curvifolia Union (Nc) (See Table 13, Figure 19)

Number of times encountered	149
Number of quadrats lacking bryophytes	18
Average bryophyte cover within quadrats	70%
Maximum bryophyte cover within quadrats	100%
Proportion of quadrats on logs of decay class "1" and "2"	98%

The Nowellia curvifolia union is restricted to the rotting wood of decorticated logs. Its boundaries are set by the presence of the Cephalozia union on the log side, and by the development of the Brotherella recurvans in later stages of succession. The only species abundant in this union is Nowellia. Riccardia palmata, occasionally encountered as a plant of high coverage, occurs primarily in pits eroded into the decaying cylinder of the log; Cephalozia has a significant coverage only by

Table 13. *Nowellia curvifolia* Union

Species	Freq.	Mean Cover	Max. Cover
Nowellia curvifolia	8	6	10
Brotherella recurvans	4	0	2
Dicranum fuscescens	4	0	2
Riccardia palmata	3	1	3
Bazzania trilobata	3	0	1
Cephalozia spp.	2	1	5
Hypnum imponens	2	0	3
Sphenolobus exsectus	2	0	1
Sphenolobus michauxii	1	0	4
Lepidozia reptans	1	0	3
Jamesoniella autumnalis	1	0	2
Dicranodontium denudatum	1	0	1
Thuidium delicatulum	1	0	X
Dicranum scoparium	1	0	X

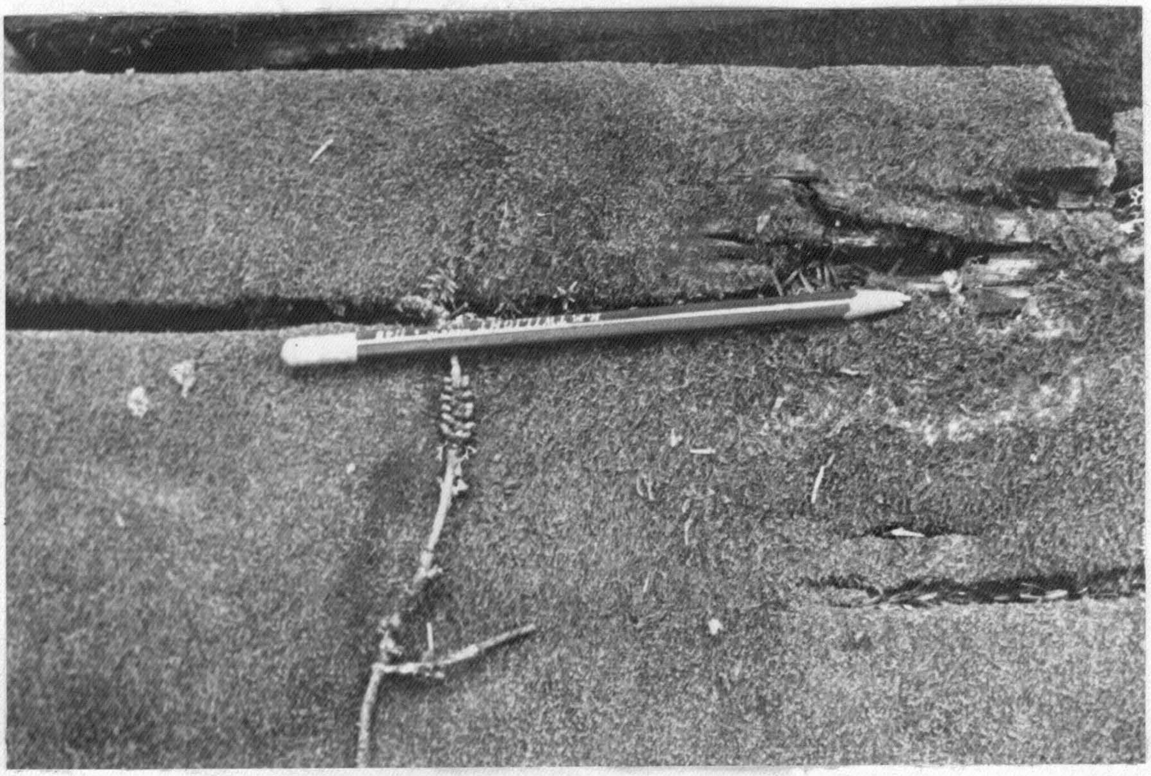

Figure 19. The Nowellia curvifolia union on log of decay class "2" near Rocky Springs Gap, 5800 feet elevation, May, 1964.

transgression from log sides where small diameter of the logs allowed close proximity of the quadrats for sampling sides and tops of logs.

The typical life-form of this community is that of a complanate, dark-colored Leskea type.

This union has a composition identical to the "Cephalozia union" of Cain and Sharp (1938).

The Plagiothecium laetum Union (Pl) (See Table 14, Figure 20)

Number of times encountered	
on living trees	586
on spars and stumps	50
Number of quadrats lacking bryophytes	15
Average bryophyte cover within quadrats	50%
Maximum bryophyte cover in any one quadrat	100%

The Plagiothecium laetum union resembles the Cephalozia union, and it differs primarily in ecological position. Whereas the latter occupies log sides, similarly shaded and high humidity niches formed by root bridges support the former type of union. On dead trees, Tetraphis pellucida and Dicranodontium denudatum appear, while the vegetation of the bridges of living trees primarily includes Plagiothecium laetum and Cephalozia spp.

This vegetation change as decay progresses is accompanied by a significant physiognomic change--from the complanate, light-colored Leskea-type exhibited by Plagiothecium to the Bryum-type life-form of Tetraphis.

The dominance of Plagiothecium laetum on the boles of the trees of stagnant second-growth fir stands is worthy of note. This change in

Table 14. Plagiothecium laetum Union

Species	Spar Bridges			Tree Bridges		
	Freq.	Mean Cover	Max. Cover	Freq.	Mean Cover	Max. Cover
Plagiothecium laetum	6	2	10	9	2	6
Cephalozia spp.	8	1	10	7	1	5
Lepidozia reptans	6	1	4	7	1	6
Dicranodontium denudatum	4	2	10	0	0	7
Blepharostoma trichophyllum	2	0	1	2	0	1
Tetraphis pellucida	3	1	10	0	0	1
Brotherella recurvans	1	0	1	1	0	3
Bazzania trilobata	1	0	1	1	0	X
Hylocomium splendens	1	0	X	1	0	1
Brotherella delicatula	1	0	3	0	0	X
Dicranum fuscescens	1	0	X	0	0	X

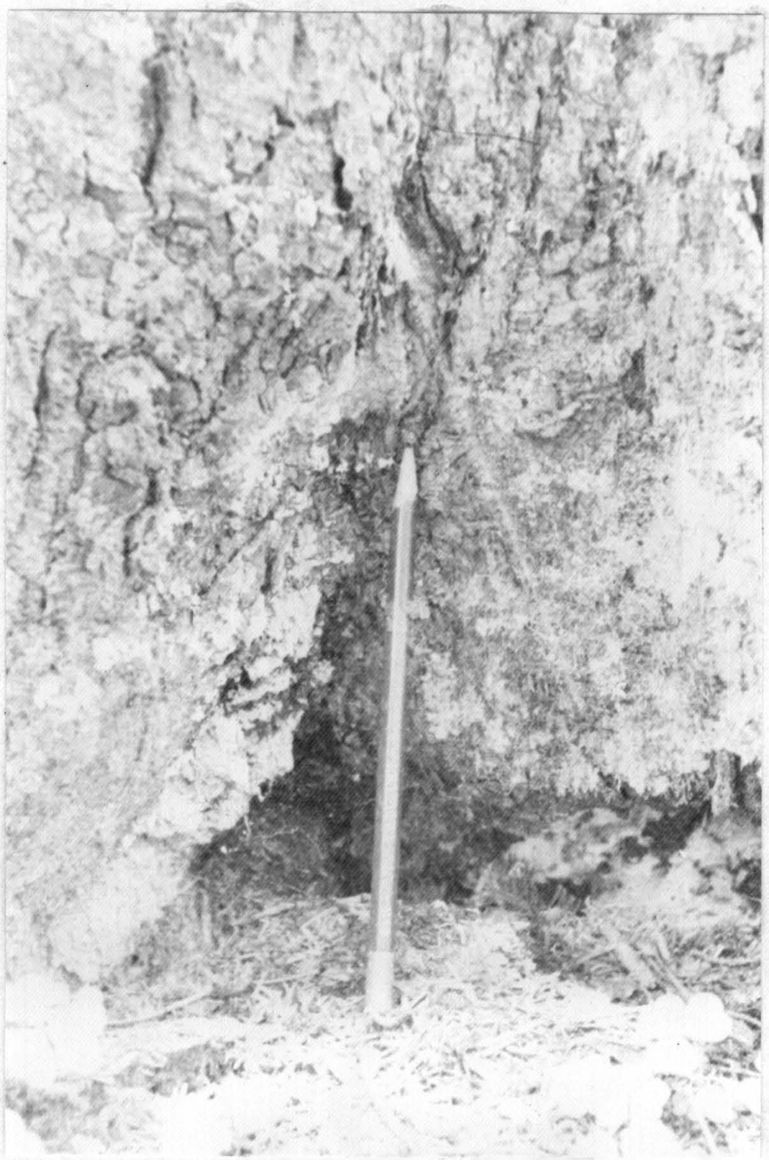

Figure 20. View of bridge of spruce showing normal habitat of the Plagiothecium laetum union. Found on Clingman's Dome, 6600 feet elevation, June, 1964.

habitat is apparently the product of the intense shade and usually high humidity of such sites. P. laetum is the only member of its union to invade tree boles, and on the latter sites its most common associate is Frullania asagrayana. Field observations have indicated that Plagiothecium laetum is abundant on tree bridges subject to occasional drought and this may explain its capacity to grow as a member of the Frullania asagrayana union.

The Polytrichum ohioense Union (Po) (See Table 15, Figure 21)

Number of times encountered	
on logs	80
on soil	37
on rock	106
Average bryophyte cover within quadrats	100%
Minimum bryophyte cover in any one quadrat	100%
Proportion of epilithic quadrats with soil depth greater than "1"	100%
Proportion of epilithic quadrats on ledges and boulder tops	89%
Proportion of epixylic quadrats on logs of decay class "4" or "5"	90%
Proportion of quadrats in light intensities "diffuse" or greater	80%

Wherever well-drained mineral soil of any depth occurs, Polytrichum ohioense forms the prevalent union. Dominance by Polytrichum occurs on logs, rocks, and soil; and it may lie contiguous to nearly any other bryophyte community found in moderate shade. Hylocomium splendens is the most abundant neighboring union and this fact accounts for the significant

Table 15. Polytrichum ohioense Union

Species	Logs and Soil			Rocks		
	Freq.	Mean Cover	Max. Cover	Freq.	Mean Cover	Max. Cover
Polytrichum ohioense	10	9	10	10	10	10
Bazzania trilobata	7	1	4	6	0	2
Hylocomium splendens	3	1	1	6	0	3
Ptillium crista-castrensis	3	1	2	4	0	4
Brotherella recurvans	4	0	2	2	0	1
Lepidozia reptans	2	0	X	3	0	X
Dicranum fuscescens	2	0	1	1	0	1
Hylocomium brevirostre	2	0	3	0	0	1
Calliergonella schreberi	1	0	3	0	0	X
Dicranum scoparium	1	0	1	0	0	1
Hypnum fertile	0	0	0	1	0	2
Pohlia nutans	0	0	X	1	0	X
Dicranella heteromalla	0	0	0	1	0	X

Figure 21. The Polytrichum ohioense union on mineral soil below uprooted tree, near Mt. Kephart, 5800 feet elevation, July 1964.

cover values of Bazzania trilobata, Hylocomium splendens, and Ptilium crista-castrensis.

In most cases, Polytrichum forms an almost unispecific tall turf, and P. ohioense is the most abundant dominant. However, P. commune, P. formosum, and P. gracilis are also recorded from spruce-fir stands, and the difficulties of field identification may account for their not having been regularly recorded in the quadrat data.

The characteristic dominance on mineral soil in the spruce-fir zone by plants of the family Polytrichaceae is worthy of note. The possibility that this dominance is related to mineral translocation along a central strand should be experimentally investigated.

The epilithic expression of this union is identical with the Polytrichum union of Cain and Sharp (1938).

The Rhacomitrium aciculare Union (Ra) (See Table 16, Figure 22)

Number of times encountered	19
Minimum bryophyte cover in any one quadrat	10%
Average bryophyte cover within quadrats	30%
Maximum bryophyte cover in any one quadrat	60%
Minimum light intensity observed	RD
Proportion of quadrats exposed to inundation	100%

Conditions approaching full sun prevail on many of the rocks in water courses in the undisturbed forest. Subaerial habitats on such exposed rocks are subjected to extremes of water availability varying from complete submergence during wet periods of the year to extreme

Table 16. *Rhacomitrium acicularе* Union

Species	Freq.	Mean Cover	Max. Cover
Rhacomitrium aciculare	10	3	6
Scapania nemorosa	2	0	2
Polytrichum commune	1	0	3
Diplophyllum apiculatum	1	0	X
Bazzania trilobata	1	0	X
Dicranum fulvum	1	0	X

Figure 22. The Rhacomitrium aciculare union on boulder in Camp Prong, near Indian Gap, 5000 feet elevation, June 1964.

drought soon after the water retreats. The Rhacomitrium aciculare union is the only important occupant of such sites, and it forms a single species community or it may contain, on its margins, transgressives from nearby unions.

The Rhacomitrium aciculare union typically lies in contact with the Marsupella sphacelata union of frequently submerged rocks and with the Rhacomitrium heterostichum union of shaded tops of rocks which are free from soil.

Rhacomitrium aciculare forms small clumps, and it has thick-walled, darkly pigmented cells.

The Rhabdoweisia denticulata Union (Rd) (See Table 17, Figures 23 and 24)

Number of times encountered	156
Minimum bryophyte cover in any one quadrat	X
Average bryophyte cover within quadrats	40%
Maximum bryophyte cover in any one quadrat	90%
Maximum light intensity observed	VC
Proportion of quadrats occupying recesses, crannies, and caverns	62%

Occupying the darkest portion of the rock outcrops is the Rhabdoweisia denticulata union. It borders upon the Herberta hutchinsiae union in areas of frequent drying conditions; upon the Dicranodontium denudatum union in areas shielded from rain but seldom dry; and upon the Lophozia incisa union in deep incisions which receive small amounts of direct precipitation. The presence of Plagiothecium sylvaticum in the

Table 17. Rhabdoweisia denticulata Union

Species	Freq.	Mean Cover	Max. Cover
Rhabdoweisia denticulata	7	3	6
Plagiothecium sylvaticum	4	1	10
Trichostomum cylindricum	3	1	4
Mnium punctatum	2	0	1
Geocalyx graveolens	1	0	4
Dicranodontium denudatum	1	0	3
Lepidozia reptans	1	0	2
Bazzania tricrenata	1	0	1
Plagiochila austinii	1	0	1
Plagiothecium denticulatum	1	0	1
Blepharostoma trichophyllum	1	0	X
Oncophorus rauei	1	0	X
Pohlia nutans	1	0	X

Figure 23. View of rock cavern showing normal habitat of Rhabdoweisia denticulata union. Found on Mt. Kephart, 5800 feet elevation, July, 1964.

Figure 24. The Plagiothecium sylvaticum facies of the Rhabdoweisia denticulata union on cavern floor near Mt. Kephart, 5800 feet elevation, July, 1964.

R. denticulata union is primarily a function of this proximity to the Lophozia incisa union.

This union exhibits two major facies. The darkest recesses in an outcrop are occupied by Trichostomum cylindricum, and it is in such areas also that the rare bryophyte Gymnomitrion laceratum has been found on Mt. LeConte. In areas of less intense shade, Rhabdoweisia denticulata occurs almost to the exclusion of any other species.

The typical life-form exhibited in this union is that of a low turf, and the plants contained in the union have isodiametric cells with thick walls. The light color of Trichostomum is also worthy of note.

The Rhacomitrium heterostichum Union (Rh) (See Table 18, Figures 25, 26, and 27)

Number of times encountered	181
Minimum bryophyte cover in any one quadrat	10%
Average bryophyte cover within quadrats	50%
Maximum bryophyte cover in any one quadrat	100%
Proportion of quadrats with water availability "2" or "3"	100%

The most widespread and diverse of the epilithic communities is the Rhacomitrium heterostichum union of tops of boulders and outcrops. Light conditions to which this union is subject vary from diffuse shade even to rather direct sun. Five species dominate in sites assigned to the R. heterostichum union. Four of these species form small clumps and these four typically are of rather dark color and have isodiametric cells. Each of these clump-formers are ecologically different in moisture

Table 18. Rhacomitrium heterostichum Union

Species	Freq.	Mean Cover	Max. Cover
Rhacomitrium heterostichum	6	2	5
Thuidium delicatulum	6	1	8
Ulota americana	6	1	2
Dicranum fulvum	5	1	6
Andreaea rothii	5	1	2
Bazzania denudata	3	1	3
Oncophorus rauei	1	0	4
Hypnum fertile	1	0	2
Diplophyllum apiculatum	1	0	2
Herberta hutchinsiae	1	0	2
Hylocomium brevirostre	1	0	X
Lepidozia reptans	1	0	X
Brotherella recurvans	1	0	X
Polytrichum ohioense	1	0	X

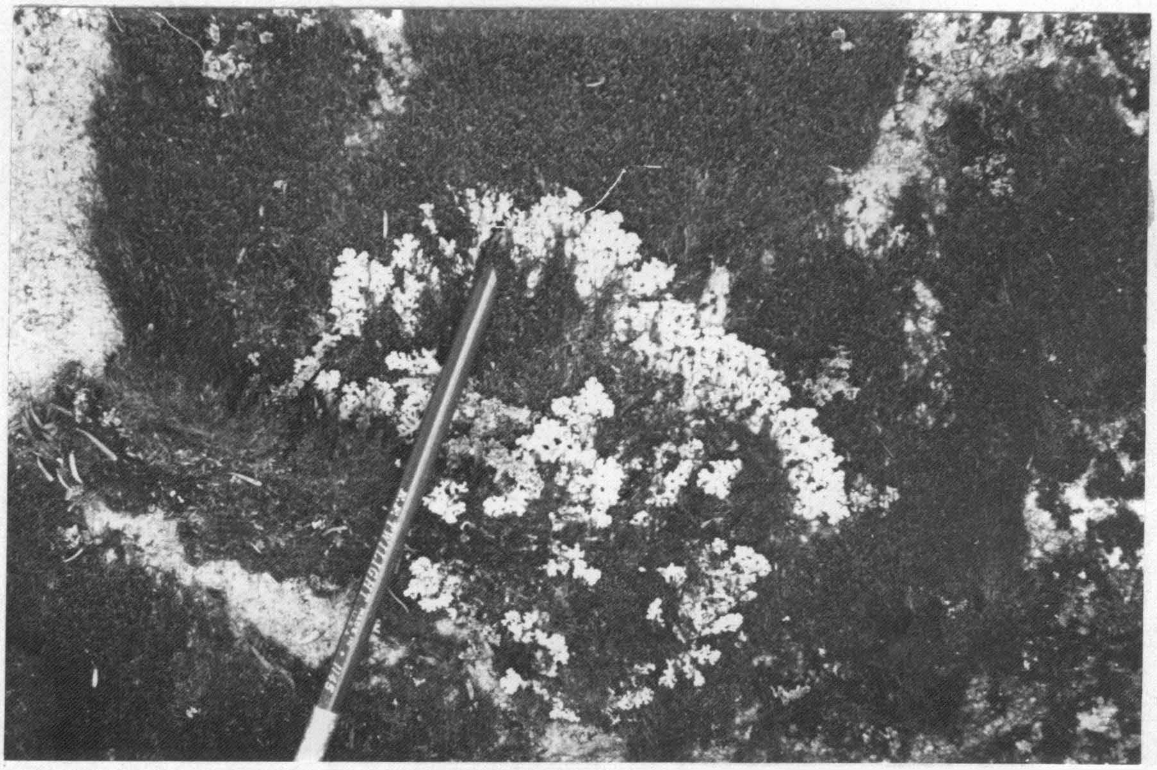

Figure 25. The Rhacomitrium heterostichum union on top of boulder in spruce forest near Newfound Gap, 5200 feet elevation, June, 1964.

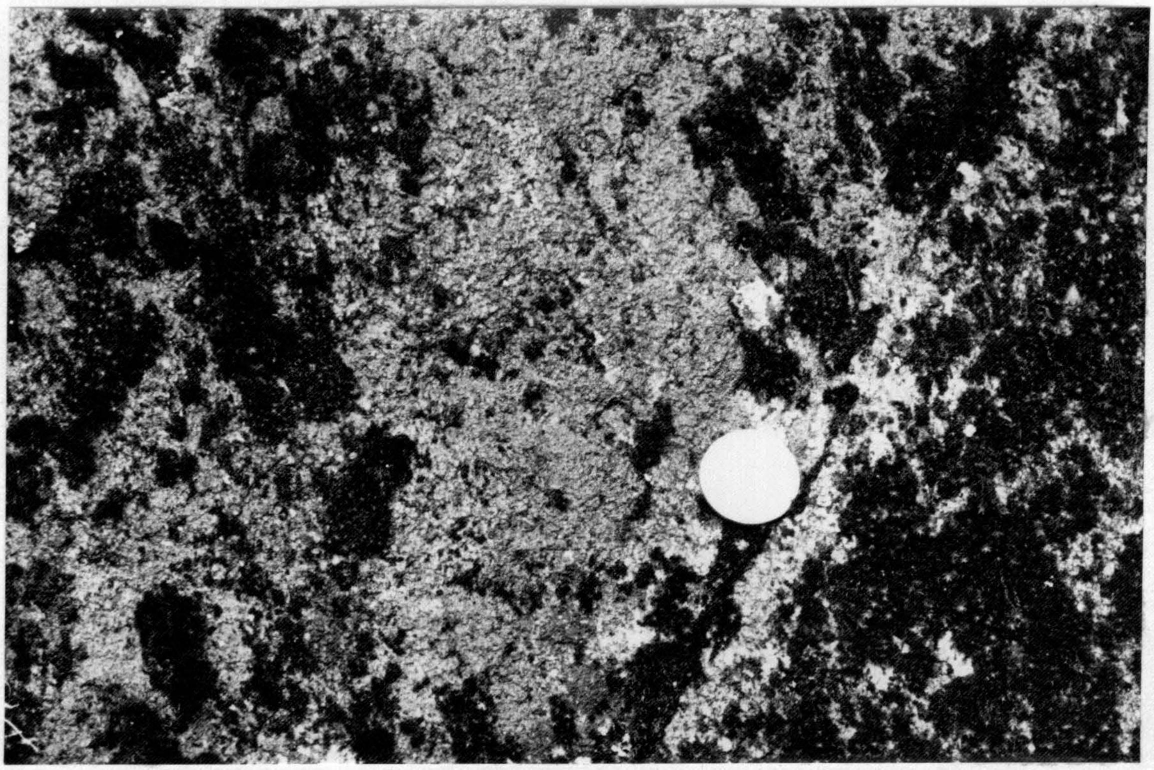

Figure 26. The Ulota americana facies of the Rhacomitrium heterostichum union on top of boulder in spruce forest near Newfound Gap, 5200 feet elevation, June, 1964.

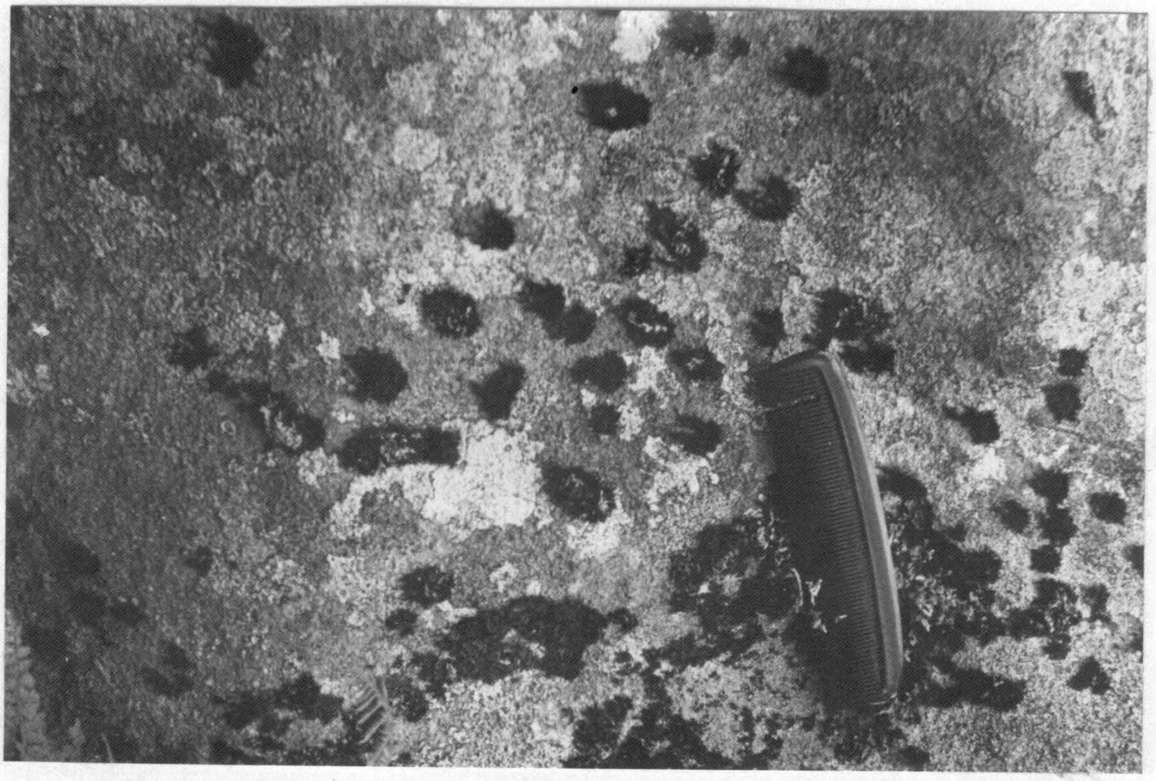

Figure 27. The Andreaea rupestris facies of the Rhacomitrium heterostichum union on 45° face of outcrop near Clingman's Dome, 6600 feet elevation, June, 1964.

requirements: the driest areas are dominated by Rhacomitrium heterostichum, while Dicranum fulvum, Ulota americana, and Andreaea rothii occupy successively wetter sites.

On the margins of the rock, near its contact with soil, or on shallow soil on top of the rock is found Thuidium delicatulum, a plant somewhat similar to Hylocomium splendens in growth-form.

All these plants grow in areas subject to occasional dryness, and moisture differences are primarily those of duration and frequency of drying. Dicranum fulvum, unlike the other four species, may extend off the flat top surface of the rock onto vertical or near-vertical sides, and it here comes in contact with the Herberta hutchinsiae union.

The Riccardia palmata Union (Rp) (See Table 19, Figure 28)

Number of times encountered	62
Minimum bryophyte cover in any one quadrat	20%
Average bryophyte cover within quadrats	50%
Maximum bryophyte cover in any one quadrat	100%
Proportion of quadrats on end of logs	100%
Proportion of quadrats on log decay classes "1" or "2"	81%
Proportion of quadrats above 6000 feet elevation	100%

The Riccardia palmata union occurs on broken or cut faces of logs, and it is there primarily located on the outer ring of wood. The center of the circular area circumscribed by the perimeter of the log is usually bare of bryophytes. The two most important liverworts of the Riccardia

Table 19. Riccardia palmata Union

Species	Freq.	Mean Cover	Max. Cover
Riccardia palmata	10	3	7
Brotherella recurvans	8	0	1
Bazzania trilobata	7	0	1
Lepidozia reptans	3	1	10
Heterophyllium nemorosum	3	1	2
Sphenolobus exsectus	3	1	2
Plagiothecium laetum	3	0	X
Tetraphis pellucida	3	0	X
Cephalozia spp.	2	0	3
Hypnum imponens	2	0	3
Geocalyx graveolens	2	0	1
Hylocomium splendens	2	0	1
Sphenolobus michauxii	1	0	2
Jamesoniella autumnalis	1	0	1
Blepharostoma trichophyllum	1	0	1
Dicranum scoparium	1	0	X
Ptilium crista-castrensis	1	0	X
Calliergonella schreberi	1	0	X
Hylocomium brevirostre	1	0	X
Thuidium delicatulum	1	0	X

Figure 28. The Riccardia palmata union on cut face of spruce log along trail near Rocky Spring Gap, 5800 feet elevation, May, 1964.

palmata union include the title species and Lepidozia reptans. Sphenolobus exsectus is often abundant, but the other species have low coverage. Outside of the just-described location, Riccardia palmata is found primarily in pits and cracks in the upper surfaces of the log, and even in such sites it appears to grow primarily on the sides of those pits and cracks and thus occupies a position analoguous to that of the log end.

The life-form of Riccardia palmata is that of the Metzgeria type, a life-form otherwise occurring in the spruce-fir zone only on broken branch-stubs in the crowns of trees (Metzgeria fruticulosa).

The Sphenolobus michauxii Union (Sm) (See Table 20, Figures 29 and 30)

Number of times encountered	219
Average bryophyte cover within quadrats	100%
Minimum bryophyte cover in any one quadrat	70%
Proportion of quadrats over 6000 feet elevation	91%
Proportion of quadrats on slopes of over 30^{o}	83%
Proportion of quadrats on logs of decay class "1" or "2"	79%

High elevation logs which channel or collect large amounts of seepage water may have large quantities of Sphenolobus michauxii in a position in which Nowellia curvifolia would normally be predominant. This union may cover an entire log, or it may be restricted to the downslope end of a log. It gives way as succession procedes to the Brotherella recurvans union. In addition to the chief species of the union, Dicranodontium denudation may also be an important plant and sometimes approaches

Table 20. Sphenolobus michauxii Union

Species	Freq.	Mean Cover	Max. Cover
Sphenolobus michauxii	8	6	8
Brotherella recurvans	7	1	4
Lepidozia reptans	6	1	2
Dicranodontium denudatum	3	0	6
Sphenolobus exsectus	3	0	3
Bazzania trilobata	3	0	3
Dicranum fuscescens	3	0	2
Jamesoniella autumnalis	3	0	2
Hypnum imponens	3	0	1
Heterophyllium nemorosum	2	1	4
Cephalozia spp.	2	0	1
Riccardia palmata	2	0	1
Dicranum scoparium	2	0	1
Hylocomium splendens	2	0	X
Mnium punctatum	1	0	2
Geocalyx graveolens	1	0	1
Blepharostoma trichophyllum	1	0	X
Lophozia incisa	1	0	X
Ptilium crista-castrensis	1	0	X

Figure 29. The Sphenolobus michauxii union on log of decay class "2" on steep slope near Clingman's Dome, 6600 feet elevation, June, 1964.

Figure 30. The Sphenolobus exsectus facies of the Sphenolobus michauxii union on partially decorticated log of decay class "1" near Rocky Spring Gap, 5800 feet elevation, May, 1964.

dominance. Heterophyllium nemorosum, a plant normally of lower elevations, is common in this union on the highest peaks. Interspersed with the typical Hypnum life-form of the three already-mentioned species, a partial second layer is formed in the union by Lepidozia reptans, which occurs as strands scattered among the larger plants.

This union is identical with the union of the same name described by Cain and Sharp (1938).

The Scapania nemorosa Union (Sn) (See Table 21, Figures 31 and 32)

Number of times encountered	141
Maximum bryophyte cover in any one quadrat	100%
Average bryophyte cover within quadrats	80%
Minimum bryophyte cover in any one quadrat	70%
Proportion of quadrats subject to constant inundation	16%
Proportion of quadrats never subject to inundation	33%

Completely submerged in the water of some of the streams arising in the spruce-fir zone is the Scapania nemorosa union--a community composed of only this one species. It borders, at the waterline, upon the Marsupella sphacelata union.

The Scapania nemorosa union also occurs in areas of constant seepage, where it is subjected to conditions quite different from those of the underwater sites. Several species not present in submerged positions are co-dominants with S. nemorosa in seepage. Areas exposed to occasional complete inundation, have large quantities of Brachythecium rivulare, while

Table 21. Scapania nemorosa Union

Species	Usually Subaerial			Usually Submerged		
	Freq.	Mean Cover	Max. Cover	Freq.	Mean Cover	Max. Cover
Scapania nemorosa	9	2	10	10	8	10
Marsupella sphacelata	1	0	3	7	1	3
Brachythecium rivulare	4	2	8	1	0	1
Sematophyllum marylandicum	3	2	10	0	0	1
Atrichum crispum	1	0	2	2	0	1
Mnium punctatum	2	1	2	0	0	0
M. p. var. elatum	1	1	7	0	0	0
Sciaromium lescurii	1	0	3	0	0	0

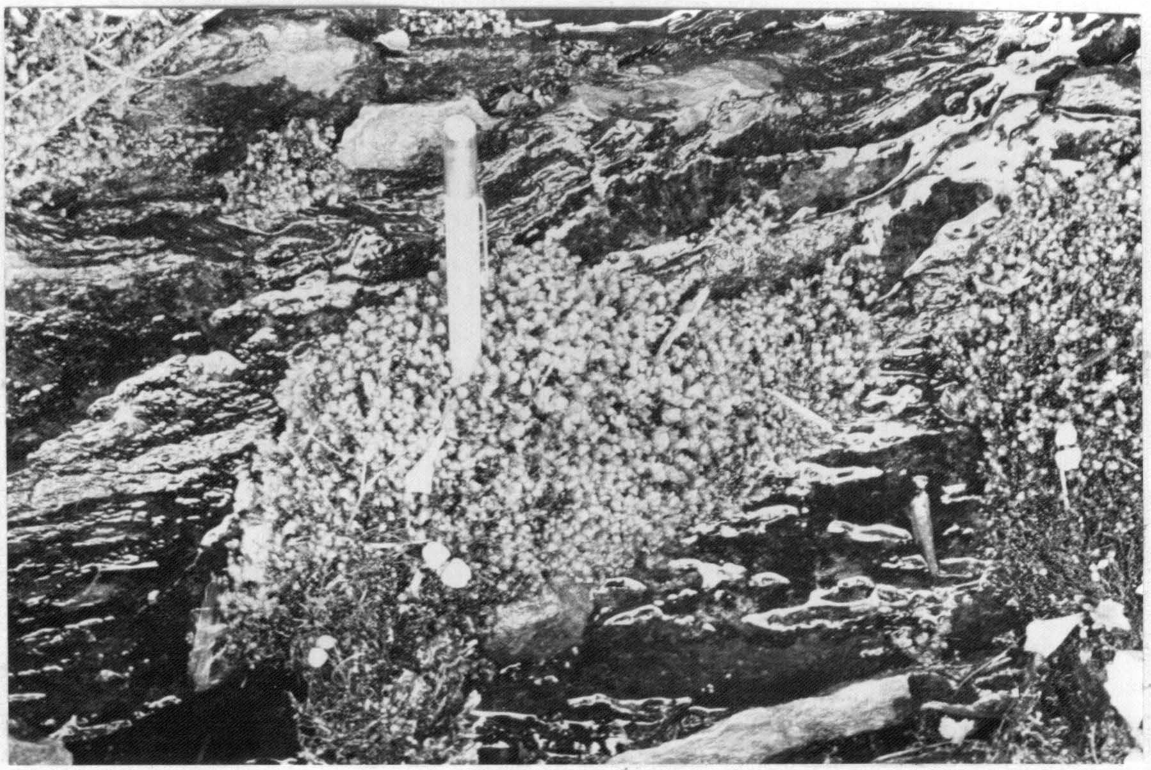

Figure 31. The Scapania nemorosa union in seepage on steep bluff near Clingman's Dome, 6600 feet elevation, June, 1964.

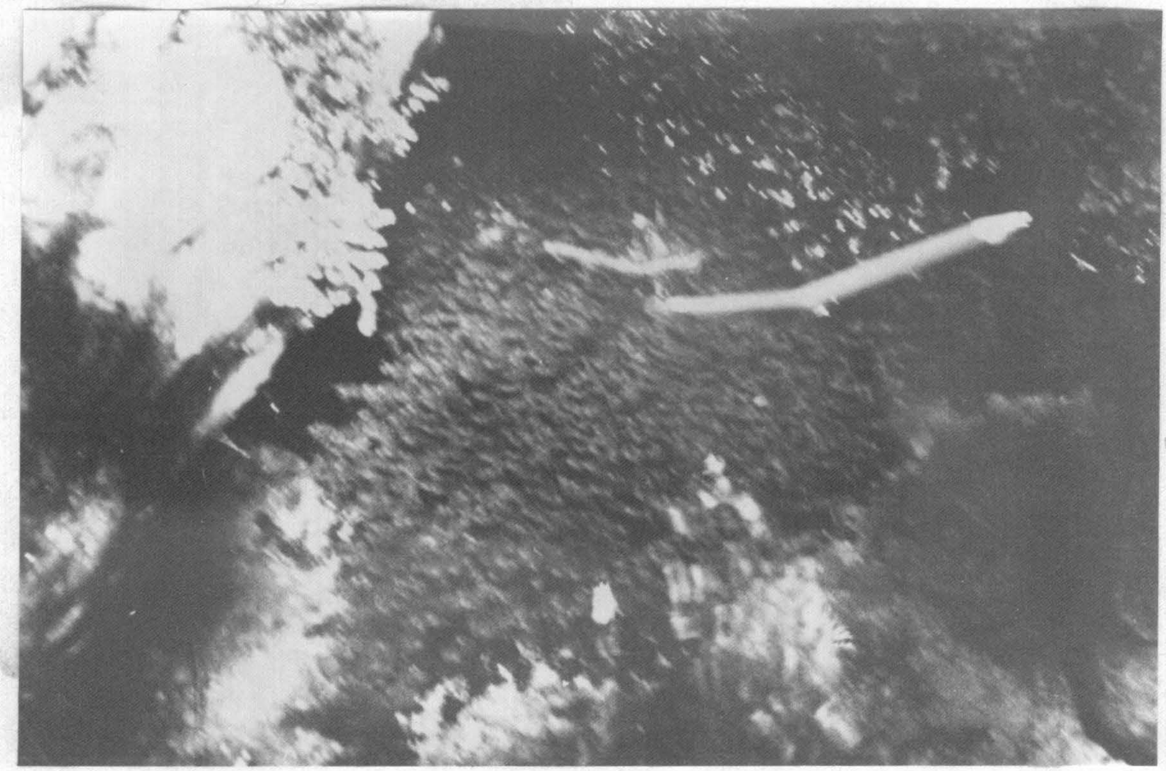

Figure 32. The submerged phase of the Scapania nemorosa union in Camp Prong, near Indian Gap, 5000 feet elevation, June, 1964.

shallower water sites have Sematophyllum marylandicum as an important associate of Scapania.

The present union of seepages typically borders upon the Atrichum crispum union of soils and the Lophozia incisa union of rocks, and these three unions frequently are found so interspersed with one another as to be not easily separable.

The typical growth-form exhibited by Scapania nemorosa is that of a Hypnum mat, and its leaves show a divergent arrangement.

The Sphagnum Union (Sp) (See Table 22, Figure 33)

Number of times encountered	
on logs	84
on soil	41
on rocks	83
Average bryophyte cover within quadrats	100%
Minimum bryophyte cover in any one quadrat	100%
Proportion of quadrats occurring above 6000 feet elevation	59%
Proportion of epixylic quadrats occurring on logs of decay classes "4" and "5"	76%
Proportion of terrestrial quadrats on slopes of less than 10°	100%

On any site on which water accumulates for long periods of time, Sphagnum quinquefarium or S. girgensohnii may be abundant. These two species usually grow separately in mats or clumps of large size, and they are frequently free of any other bryophyte species. Where other bryophytes do occur with the Sphagnum, high coverage may be shown by

Table 22. Sphagnum Union

Species	Freq.	Mean Cover	Max. Cover
Sphagnum quinquefarium	8	6	10
Bazzania trilobata	7	1	4
Polytrichum ohioense	4	1	4
Scapania nemorosa	4	0	3
Lepidozia reptans	4	0	2
Mnium punctatum var. elatum	4	0	1
Brotherella recurvans	4	0	1
Sphagnum girgensohnii	3	2	10
Atrichum crispum	2	0	1
Cephalozia spp.	2	0	X
Dicranum scoparium	1	0	3
Sphenolobus michauxii	1	0	X
Thuidium delicatulum	1	0	X
Ptilium crista-castrensis	1	0	X
Hylocomium splendens	1	0	X
Blepharostoma trichophyllum	1	0	X

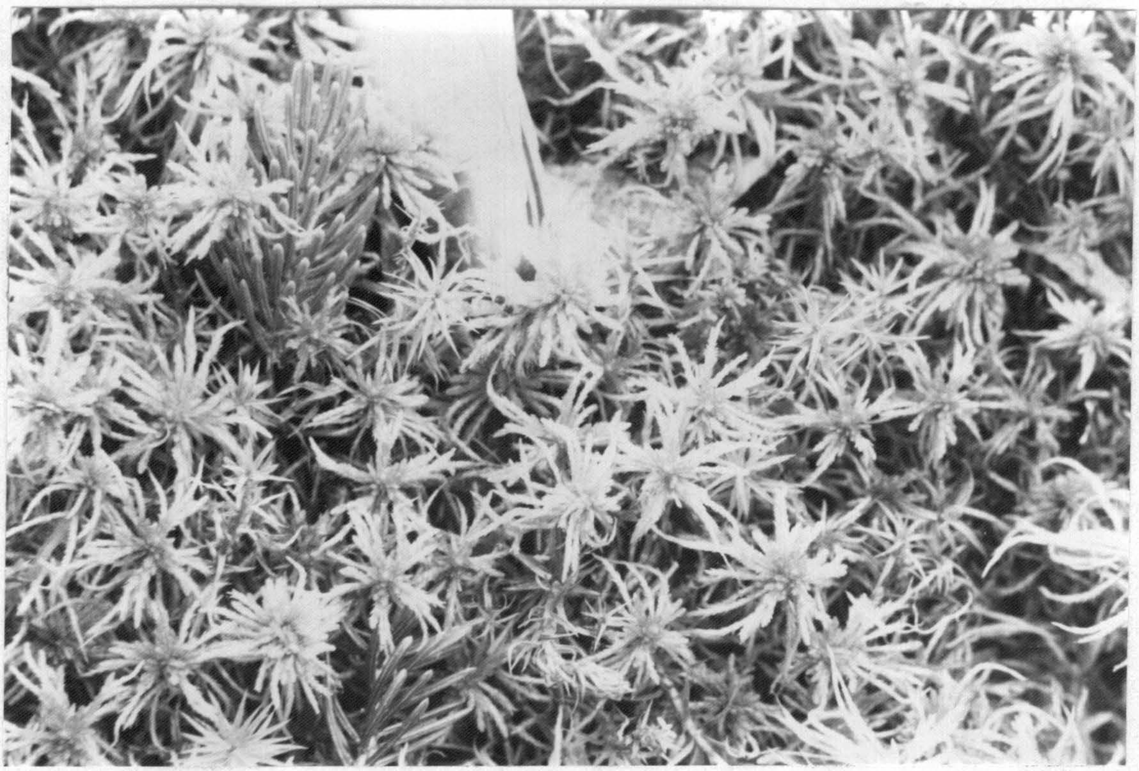

Figure 33. The Sphagnum (quinquefarium) union in wet area on soil at Rocky Spring Gap, 5800 feet elevation, May, 1964.

Bazzania trilobata, Polytrichum ohioense, and sometimes Dicranum scoparium. Strands of Lepidozia reptans are occasionally scattered among the larger Sphagnum plants, while Scaparia nemorosa regularly grows on the outside margins of a Sphagnum clump.

Sphagnum occurs on rocks, soil, and logs, and these substrates appear to have little influence on the nature of the vegetation associated with Sphagnum. Physiognomic change is, however, effected by the substratum. Tall turfs occur on soil, while tall clumps are typical of dripping cliffs.

The Sphagnum union has been described by Cain and Sharp (1938), it being one of the two epilithic types which they recognized from the fir forest in their treatise.

The Ulota crispa Union (Uc) (See Table 23, Figures 34 and 35)

Number of times encountered	274
Minimum bryophyte cover in any one quadrat	20%
Average bryophyte cover within quadrats	60%
Maximum bryophyte cover in any one quadrat	100%
Proportion of quadrats occurring in fir forests	86%
Proportion of quadrats occurring in forests with tree canopy of 80% or less	68%
Proportion of quadrats occurring on north side of tree	72%

Although represented in the data by a clear-cut dominant, Herberta hutchinsiae, the present union has been given the name of a secondary species, Ulota crispa, to avoid confusion with the Herberta community of

Table 23. *Ulota crispa* Union

Species	Freq.	Mean Cover	Max. Cover
Herberta hutchinsiae	10	3	9
Frullania asagrayana	9	1	5
Paraleucobryum longifolium	6	0	4
Ulota crispa	4	2	4
Zygodon viridissimus	4	1	3
Leptodontium excelsum	3	0	2
Bazzania nudicaulis	2	0	3
Plagiochila tridenticulata	2	0	1
Anomylia cuneifolia	2	0	1
Cephaloziopsis pearsonii	1	0	1
Brotherella recurvans	1	0	1
Hypnum reptile	1	0	1

Figure 34. The Leptodontium excelsum facies of the Ulota crispa union on small fir on exposed ridge near Clingman's Dome, 6300 feet elevation, June, 1964.

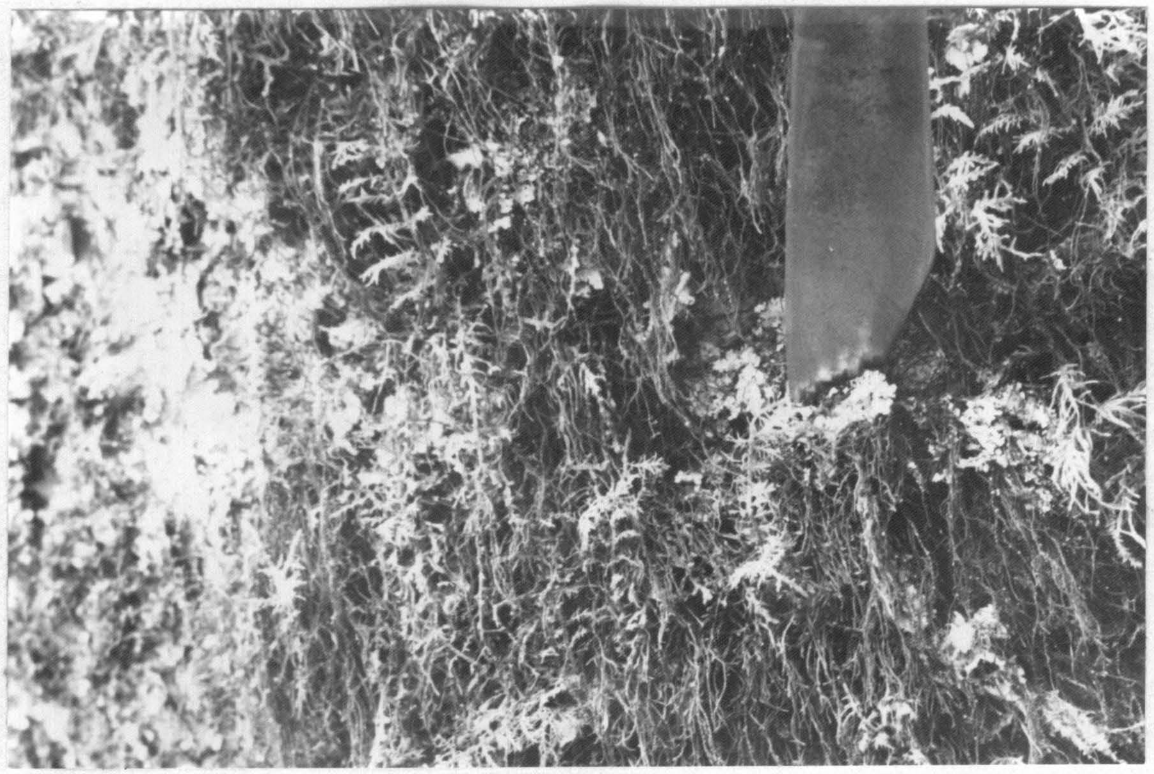

Figure 35. The Herberta hutchinsiae facies of the Ulota crispa union on bark of birch on exposed ridge near Clingman's Dome, 6300 feet elevation, June 1964.

rocks. In the canopies of trees the author has observed high cover of Ulota crispa and Zygodon viridissimus and a correspondingly low cover of Herberta but this information could not be reflected in the data. The information presented in Table 23 is, therefore, taken primarily from marginal communities of the Ulota crispa type.

This union is related to exposure to fog and to rapid drying conditions, and this characteristic of the habitat is reflected in the life-form--pendant or of short clumps. The border along which the Ulota crispa union meets the Frullania asagrayana union is not well defined, due to the continuing abundance of Frullania even into the canopies of the trees.

Although Cain and Sharp (1938) mention the top-limb flora of Abies fraseri, their sampling procedures did not touch upon this union and it was neither given a name nor a quantitative description.

VII. GENERAL OBSERVATIONS ON THE BRYOPHYTE FLORA

Because the sites occupied by some of the more uncommon bryophyte species were neglected by quadrat sampling, supplemental tabulations of the bryophyte flora are presented in Appendix B from the author's field studies and from his examination of the specimens in the University of Tennessee Herbarium. In the herbarium search, elevation was the primary factor in deciding upon inclusion in the list of the spruce-fir bryophytes. Specimens from elevations below 5500 feet were not admitted to the list unless other information was available; but, nevertheless, some specimens from high elevation beech gaps, grassy balds, and heath balds may have been erroneously included.

A few species exhibit such a strong habitat correlation that their occurrence in a particular site is regularly predictable and many of these are inadequately treated in the quadrat analysis. These will now be further described from the often fragmentary notes of the author's field observations.

The most noteworthy bryophyte discovered during the progress of this field work was Brachydontium trichodes known in eastern North America only from Tuckerman's Ravine, Mt. Washington, New Hampshire, before its collection in the southern Appalachians. In the latter region, this bryophyte has been collected only from the spruce-fir zone in the Great Smoky Mountains National Park; it may there be found only in the trails on rough-surfaced rocks such as weathered graywacks. It is common in seepage regions and may be located with ease in the winter by examining the rocks in the footpaths in areas where water-seepage keeps them free of snow. Brachydontium trichodes is apparently a plant which is highly susceptible to competition from larger bryophytes. It grows on sites typical of the Atrichum crispum union, but is almost restricted to those kept free from the expected bryophytes by human trampling.

Metzgeria fruticulosa is found in branch axils, and on broken faces of limbs and on the trunk in the Ulota crispa union of tree canopies. It appears to be most abundant on spruce trees in ridge-top situations, although firs in similar sites may also have significant quantities of this bryophyte species. Its presence in hardwood canopies may be unknown to this writer because very few hardwoods were found broken or uprooted with their camopies available for examination.

A species frequent in the spruce-birch gaps in high elevation ravines in Ulota ludwigii. It is there found on Acer spicatum and Sambucus pubens and is usually intermixed with the related U. crispa. The distinguishing of sterile U. crispa and U. ludwigii is not easy for this writer in the field and so his observation that U. ludwigii is restricted to the spruce-birch gaps and to contiguous forest may not be accurate.

Like the previously treated two species, Cephaloziopsis pearsoni is a plant of the Ulota crispa union. It is found generally throughout the higher peaks of the southern Appalachians (Schuster, 1963), and is restricted to ridges where a high frequency of fog prevails. The present writer has seen this bryophyte species only on trunks of spruce, fir, and mountain ash in approximately that descending order of frequency.

The canopies of such species were cursorily investigated without finding Cephaloziopsis. It is usually restricted to the northwest-facing quadrant of the tree, but was seldom encountered in quadrat analysis because only the most open fir-Senecio and fir-Oxalis-Dryopteris forest site types were suited to its apparent requirements of exposure to light and fog. More commonly it is found on isolated trees crowning ridges in burned or lumbered areas.

Another noteworthy bryophyte found on trees is Ulota americana var. rufescens, a dominant on the trunks and canopies of beech in the beech gaps, but present also on spruces and firs which border these gaps. It has so far been found only in the Frullania asagrayana union in areas where the bryophyte coverage is less than complete. Apparently the considerable availability of propagules from the beech gap Ulota communities allows the occasional development of the species in nearby areas.

Trichostomum cylindricum is one of the most ecologically variable of the bryophytes encountered in this study. This ecological variability parallels an unusual morphological diversity (Anderson, 1958) and contributes to the present writer's suspicion that forms exist which may be worthy of taxonomic recognition. Three separate populations may be distinguished from the data. One of these is especially frequent on beech trees in the beech gaps, but it is also present on many firs in the coniferous forest. It occupies and is frequently dominant in a zone of contact between the Plagiothecium laetum union of bridges and the Brotherella recurvans union of flares.

Another union in which Trichostomum may be found is the Rhabdoweisia denticulata union of rocks. In caverns and deep recesses T. cylindricum is frequently in the darkest zone occupied by bryophytes. Here it may form sparse populations of plants whose leaves are abnormally long for the species.

The only kind of site in which Trichostomum sporophytes have been found by this writer is in moist areas under a diffuse shade cast by overstory plants. It is especially common on narrow ledges of vertically dipping slate where it is a member of the Dicranella heteromalla union.

"Copper mosses" such as Mielichhoferia mielichhoferiana and Merceya ligulata are associated with phyllites and related rock types.

Polytrichum juniperinum is a species of regular occurrence on thin soil in full sun in the Smokies, and it is there found in small crevices on rock stripped bare by landslides. Grasses, herbs, and woody plants have been noted regularly in the larger mats of P. juniperinum and, therefore, its role in succession seems significant.

Calliergonella schreberi is normally a member of the Hylocomium splendens union of soils and logs, and of the Brotherella recurvans union of logs and tree bases. In the Smokies, however, it is frequent only in the Mt. LeConte region, and is elsewhere present but uncommon. A climatic explanation of this unusual geographic restriction of the species seems unlikely because of the central position of LeConte in the Smokies. Edaphic restriction, however, is not ruled out, in spite of the uniformity of the rock of the Smokies. In Tennessee, the range of occurrence of C. schreberi includes low elevation pine forests and heath-balds; it is a dry-site forest floor dominant in the Adirondacks and related mountain systems of New York. A factor in common among these habitats is the extremely low mineral content of the surface soil. The unique position of the heath balds on LeConte's highest region (Myrtle Point) may contribute to a low mineral availability on lower areas of the watershed draining Myrtle Point and result in the observed high abundance of C. schreberi.

Hylocomium splendens exhibits a striking restriction to spruce and fir forests in the southern Appalachians. In lower areas it is replaced by Hylocomium brevirostre. As one approach to an explanation of the lower elevational limits of Hylocomium splendens, a study of the annual increment of growth of the species at various elevations and in various habitats was conducted. This study was possible because the moss produces its annual growth as readily-recognized innovations arising from a central position on the previous year's frond, making it possible to identify and to clip the annual growth of the species. This was done on quadrats located on areas where the species exhibited a one hundred per cent cover and was relatively uncontaminated by fragments of other species.

In Table 24, the growth of H. splendens is plotted against slope, shade, and the presence of hardwood leaves in the litter. No definite correlation can be found with elevation or forest site type. Decreasing elevation, however, produces a restriction of its ecological amplitude although growth rate is maintained at a fairly high level, even on marginal sites. At the higher elevations H. splendens is found on nearly all substrates, but it disappears serially from the mesic and drier soils, from rotten logs, from swampy, shaded soils, and it is last found only on elevated mineral soil of trail banks in flat, wet areas. Competition

Table 24. Hylocomium splendens Productivity

	Hardwood Litter		Light			Aspect and Slope				
	Present	Absent	Very Diffuse	Diffuse	Rather Diffuse	South 20° +	South 5-15°	Level	North 5-15°	North 20° +
Number of Samples	15	33	13	30	4	16	8	11	11	2
lbs./Acre (Min.)	109	89	89	199	264	109	89	201	190	337
lbs./Acre (Mean)	483	329	277	408	425	222	361	416	453	372
lbs./Acre (Max.)	797	606	539	779	797	306	797	580	779	408

from Hylocomium brevirostre appears to this writer the most likely explanation of the growth restriction just described.

Phenological observations of H. splendens were also made. Some of the more noteworthy features of the phenology of the species are its lack of correlation with the elevational belts of climates. The upper elevations in the mountains, if anything, show a slight advance in the seasonal condition as compared with the lower elevations. Most striking is the time of completion of the apparent annual growth, which is over a month advanced (mid-September) on higher elevations, as compared with the lower (late-October) ones. Another phenomenon of note is the probability of growth under a snow cover. The "bud" which produces the next year's growth is usually inconspicuous in mid-December when first covered by snow; but when that snow melts in late March the "bud" is green and prominent. In many cases, it has appeared to this writer that the lower elevational margin of H. splendens coincides with the limits of continuous winter snow cover.

VIII. THE ADIRONDACKS: COMPARATIVE REMARKS

Field work in the Adirondacks was limited to the subalpine fir forest and to the upper reaches of the spruce type (3000 + feet). For brevity, in the chapter which is to follow, comments on the Adirondacks and the southern Appalachians will not specify that they pertain only to the spruce-fir zone, but this should be understood by the reader. To avoid the monotony of repetition, the designation "north" will be used and should be understood to refer to the Adirondacks; "south" will be used as well as "Smokies" to refer to the area of study in the Great Smoky Mountains National Park.

The similarity of the vascular vegetation of the Adirondacks to that of the southern Appalachian spruce-fir zone has already been suggested. This similarity, illustrated in Table 25, is physiognomic, floristic, and vegetational. In the table, the listed southern Appalachian vascular plants are those plants encountered in the writer's quadrat analyses, while the other column is compiled from the most important species listed by Heimburger (1934) from the subalpine zone of the Adirondacks. Bryophytes also illustrate this close floristic relationship--of the one hundred thirty-two species collected by this writer in the Adirondacks and presented in Appendix C, only twenty-seven have not yet been found in the southern Appalachians.

In the Adirondacks, habitats for bryophytes are similar to those of the Smokies. The forest floor is covered with humus and leaf litter and is streaked by belts of exposed mineral soil. The major genera of trees are Picea, Abies, and Betula of species similar to, or identical

Table 25. A Comparison of the Vascular Vegetation of the Adirondacks and the Smokies

Trees and Taller Shrubs	
Smokies	Adirondacks
Abies fraseri (Pursh.) Poin.	Abies balsamea (L) Mill.
Acer pennsylvanicum L.	Acer pennsylvanicum L.
A. rubrum L.	A. rubrum L.
A. spicatum Lam.	A. spicatum Lam.
Amelanchier laevis Wieg.	Amelanchier bartramiana (Tausch.) M. J. Roem
Betula alleghaniensis Britton	Betula papyrifera Marsh.
Cornus alternifolia L. F.	
Hydrangea arborescens L.	
Ilex montanum T. & G.	Nemopanthus mucronata(L) Trel.
Menziesia pilosa (Mx) Juss.	
Picea rubens Sarg.	Picea rubens Sarg.
Prunus pennsylvanica L. f.	Prunus pennsylvanica L. f.
Rhododendron catawbiense Mx.	
R. carolinianum Rehd.	
R. maximum L.	
Ribes rotundifolia Mx.	Ribes glandulosum Graner
Rubus canadensis L.	Rubus idaeus L.
Sambacus pubens Mx.	Sambucus pubens Mx.
Sorbus americana Marsh.	Sorbus americana Marsh.
Tsuga canadensis (L) Carr	
Vaccinium erythrocarpum Mx.	
V. simulatum small	Vaccinium myrtilloides Mx.
Viburnum alnifolium Marsh.	Viburnum alnifolium Marsh.
V. cassinoides L.	V. cassinoides L.

Table 25. (Continued)

Herbs and Low Shrubs: Smokies	Herbs and Low Shrubs: Adirondacks
Arisaema atrorubens (Ait.) Blume	
Aster acuminatus Mx.	Aster acuminatus Mx.
Aster divaricatus L.	
Athyrium filix-femina (L) Roth.	Athyrium filix-femina (L.) Roth.
Carex brunnescens (Pers.) Poir.	
C. intumescens Rudge	
Chelone lyoni Pursh.	
Cimicifuga americana Mx.	
Circaea alpina L.	Circaea alpina L.
Claytonia virginica L.	
Clintonia borealis (Ait.) Raf	Clintonia borealis (Ait.) Raf.
Dennstaedtia punctilobula (Mx.) Moore	
Dryopteris spinulosa (O.F. Muell.) Watt. var. americana (Fisch.) Fern.	Dryopteris spinulosa (O.F. Muell.) Watt. var. americana(Fisch.)Fern.
Eupatorium rugosum Houtt var. roanense (Small) Fern.	
Galax aphylla L.	
Houstonia serpyllifolia Mx.	
Impatiens pallida Nutt.	
Laportea canadensis (L) Wedd.	
Luzula acuminata Raf.	Luzula acuminata Raf.
Lycopodium lucidulum Mx.	Lycopodium lucidulum Mx.
Maianthemum canadense Desf.	Maianthemum canadense Desf.
Medeola virginiana L.	
Mitchella repens L.	
Monotropa uniflora L.	Monotropa uniflora L.
Oxalis montana Raf.	Oxalis montana Raf.
Parnassia asarifolia Vent.	
Polypodium virginianum L.	
Senecio rugelia A. Gray	
Smilacina racemosa (L.) Desf.	Smilacina stellata (L.) Desf.
Solidago glomerata Mx.	Solidago macrophylla Pursh.
Stachys clingmanii Small	
Streptopus roseus Mx.	Streptopus roseus Mx.
Trillium erectum L.	
Trillium undulatum Willd.	Trillium undulatum Willd.
Viola pallens (Banks) Brain.	Viola blanda Willd.
	Aralia nudicaulis L.
	Coptis trifolia (L) T. & G.
	Cornus canadensis L.
	Dryopteris phegopteris(L.) Christens.
	Gaultheria hispidula (L.) Bigel.
	Trientalis borealis Raf.

with those of the south; and the outcropping rocks are, like the south, siliceous and resistant to erosion.

In contrast with the southern Appalachians, however, many streams run through the spruce-fir forest of the north; lakes are also present, and drainage channels are less well-developed due to the more gradual slopes and to the recency of glaciation. A true timberline exists and the climate is colder, subject to occasional summer frosts, less humid, and characterized by smaller amounts of precipitation.

On the forest floor of the Adirondacks, only two unions may be recognized--the Atrichum crispum union being missing or represented only by a Mnium punctatum var. elatum facies. Hylocomium splendens dominated sites are rare and found primarily in the alpine krummholz and in deep, shaded ravines. Elsewhere, a Calliergonella schreberi facies of the H. splendens union is prevalent on all well-drained sites in the fir forest. As a result, however, of the generally poor drainage, Sphagnum is the prevalent union of the forest floor.

On trees in the Adirondacks, only four unions may be recognized. The Ulota crispa union is absent, and Frullania asagrayana is replaced by Ptilidium pulcherrimum. Because of the physiognomic similarity of the latter species to Frullania, this Ptilidium community is here considered a facies of the Frullania union. It is almost restricted to firs in protected sites and the trunks of spruce and birch are usually bare of bryophytes, though, like fir, covered with many lichens.

The three tree-base unions of the Smokies are well developed in the north. On tree flares the Brotherella recurvans union (Table 26)

Table 26. Brotherella recurvans Union of Tree Flares in the Adirondacks

Species	Freq.	Mean Cover	Max. Cover
Calliergonella schreberi	10	6	10
Brotherella recurvans	9	2	10
Dicranum fuscescens	9	1	10
Bazzania trilobata	8	1	6
Mylia taylori	6	0	10
Lepidozia reptans	3	0	2
Hypnum imponens	3	0	X
Ptilium crista-castensis	2	0	1
Plagiothecium denticulatum	2	0	1
Blepharostoma trichophyllum	2	0	1
Barbilophozia barbata	1	0	1
Cephalozia spp.	1	0	X
Cephaloziella spp.	1	0	X

is, in the Adirondacks, only slightly changed, having greater quantities of Calliergonella schreberi and Bazzania trilobata.

Logs in the Adirondacks show four major unions (Table 27), all of which also occur in the Smokies. Logs bare of bark but little decayed are dominated by Nowellia curvifolia and Ptilidium pulcherrimum with lesser amounts of Cephalozia spp. and Gymnocolea inflata. This gives way in later stages of decay to a community dominated by Dicranum fuscescens (a facies of the Brotherella recurvans union). This community has, in comparison with the southern Appalachians, lesser quantities of Brotherella recurvans and more Mylia taylori and Calliergonella schreberi. The last stage of succession is effected by the increasing dominance of Calliergonella schreberi as well as by the establishment of various herbs typical of the forest floor. Until decay is complete, the dark sides of logs are dominated by the Cephalozia union with Cephalozia spp., Tetraphis pellucida, and Plagiothecium muellerianum dominant.

It would appear that the major difference of bryoecological significance between the Adirondacks and the Smokies lies in the greater amount of precipitation and higher humidity of the latter area, and this difference may account for the virtual lack of epiphytic bryophytes in the north and explain the almost complete replacement of Hylocomium splendens on the forest floor.

Table 27. Bryophytes on Logs in the Adirondacks

Species	Log Tops			Log Sides		
	Freq.	Mean Cover	Max. Cover	Freq.	Mean Cover	Max. Cover
Brotherella recurvans	8	0	10	0	0	0
Dicranum fuscescens	8	0	10	0	0	0
Bazzania trilobata	7	1	10	0	0	X
Mylia taylori	6	2	10	0	0	X
Lepidozia reptans	6	0	1	1	0	X
Ptilidium pulcherrimum	3	2	10	0	0	X
Calliergonella schreberi	3	2	10	0	0	0
Nowellia curvifolia	3	1	3	0	0	0
Hylocomium splendens	3	0	10	0	0	0
Hypnum imponens	2	0	4	0	0	0
Barbilophozia barbata	1	0	2	0	0	X
Helodium blandowei	1	0	1	0	0	0
Oncophorus wahlenbergii	1	0	1	0	0	0
Tetraphis pellucida	0	0	X	10	2	8
Plagiothecium muellerianum	0	0	0	6	1	8
Cephalozia spp.	0	0	1	4	0	10
Gymnocolea inflata	2	1	8	1	0	4

IX. DISCUSSION

Succession

Subjective observations of the bryophytes of various successional vascular plant communities within the spruce-fir zone were conducted so that general statements regarding bryophyte succession could be made. These observations took place primarily within three areas of the Smokies--a grove of *Prunus pennsylvanica* with scattered spruce seedlings on southeast slopes near Charlie's Bunion; a fir thicket between Andrew's Bald and Clingman's Dome; and a spruce and fir forest on the slopes above Balsam Mountain Campground. The areas in the order listed exhibit an increasing successional maturity and are as ecologically equivalent a trio as was found by this writer in the Smokies.

Changes in epiphytes and in ground cover were the primary bryophytic differences noted between the three areas. Epiphytic bryophytes on fir are present only as scattered strands of *Frullania asagrayana* in the *Prunus* grove; they include *Plagiothecium laetum* with smaller amounts of *F. asagrayana*, *Brotherella recurvans* and *Paraleucobryum longifolium*; and they present almost a typical *F. asagrayana* union in the Balsam Mountain forest.

Ground cover bryophytes are almost missing except for a thin mat of *Brotherella recurvans* over the leaf litter. The *Hylocomium splendens* union spreads from logs, tree bases, and outcropping boulders, and achieves dominance only in the most mature forest.

Succession on logs and trees differs from that on soil in that, though it may lead toward a self-perpetuating community, any stable group of plants will have a limited duration due to the death of the tree or the decay of the log. Succession on logs has already been discussed in Section VI, but that on trees has been left for the present section. Younger trees are dominated by Frullania asagrayana, with subordinates including (in descending order of abundance) Brotherella recurvans, Brachythecium serrulatum, and Hylocomium brevirostre. Paraleucobryum is present on branches of even the youngest saplings, but it does not appear on the trunk until the tree is free of branches to a height of about ten feet. Other species typical of the Frullania union do not ordinarily appear on the trunk until the tree crown reaches the canopy.

On trunks of mature firs, cyclic changes of the bryophyte vegetation are apparent, especially at high elevations. Mats of Paraleucobryum show indeterminate growth until their own weight causes them to slough from the tree. The recently-exposed bark is colonized primarily by Frullania asagrayana and only later does Paraleucobryum reappear and repeat the cycle.

Information regarding bryophyte succession on rocks is not, in most cases, adequate for study. Rocks, cleared of bryophytes, are not abundant within the Smokies and these are mainly on trails which are kept free, or on roadcuts where those bare rocks are exposed to an environment very different from that in the forest. Information is, however, available from the Scapania nemorosa union of watercourses—a type frequently subject to destruction by flood waters. After destruction of the *Scaparia*, no seral stages are noted, but instead young plants of that species immediately colonize the denuded area.

Bryophyte succession, then within the spruce-fir forest, is of four types: (1) synchronous and parallel with vascular vegetational changes; (2) dependent upon and accompanying substratal change; (3) cyclic, with seral stages; and (4) recurrent, without seral stages. The mosaic of bryophyte vegetation found in the spruce-fir forest appears to be the product of the simultaneous operation of all of these types of succession.

Plant Geography

Studies within the disjunct spruce-fir forest of the southern Appalachians have brought to this writer's attention the problems of the migration of that forest into the area. The question of long-distance dispersal versus uniform range expansion is of particular interest--was there ever a continuous spruce-fir forest extending from New England to the southern Appalachians?

Flora which are distributed primarily by long-distance dispersal should be an aggregate of species of various geographic sources; but those distributed as a result of the extension of a vegetation type into the area would show more uniform geographic origin of the flora.

This uniformity is demonstrated by the *Hylocomium splendens* union which exists with little or no species change, in the spruce-fir forest of the United States, Canada, Europe, and Asia. Its presence in the southern Appalachians would appear to indicate that its migration was by continuous range extension and its restriction to the spruce-fir forest gives support to the argument for original continuity of the forest types of the north and south.

The Hylocomium union also may give evidence of the nature of the southwestern margin of the spruce-fir forest near Siler's Gap in the Smokies. The complete absence of H. splendens south of the margin contrasts with its occasional presence in rock crannies and protected caverns in areas even where the boreal forest has been destroyed. If the forest margin in the south has retreated in the recent past, this retreat should probably have left Hylocomium splendens in protected niches, and its absence, therefore, supports the contention that the forest margin today may not be contracted from its position in the past.

In contrast with the H. splendens union, the Ulota crispa union contains species of Mexican affinities (Leptodontium excelsum), of European derivation (Cephaloziopsis pearsoni) and of lowland hardwoods origin (Ulota crispa). It is not represented as a community type in any other eastern North American forest and appears to be developed as a fog-belt type evolving in place by aggregation from any suitable species which may reach the area.

It would appear that only some habitats are conducive to the establishment of plants distributed over long distances. Such habitats as exposed bark in tree canopies present unusual environmental conditions in which only a few bryophytes can live. Under these conditions, the habitat remains open to bryophyte colonization until an adequate flora is obtained by long-distance dispersal or by change of ecological tolerances of certain species of a nearby area.

The other unions of the spruce-fir forest also may occur in contiguous forests at lower elevations, forests which show at present north-south continuity along the Appalachian mountain range. Explanation of their species composition need rely only on range expansion with occasional species loss and gain because of the environmental change.

X. SUMMARY

A bryoecological study of certain spruce-fir forests in the southern Appalachians is reported, with primary attention being given to the Great Smoky Mountains National Park. Observations for comparison were conducted in the Adirondack Mountains of New York. In the Smokies, the bryophytes on all substrates were sampled and were correlated with subjective habitat descriptions and with vascular plant composition of the area.

Twenty-two unions of bryophytes were recognized. Some of these are restricted to particular substrates, whereas others have a wider ecological range. Major factors in the zonation of bryophytes appear to include source of water, (precipitation contrasted with fog and condensation), frequency and duration of drought, and intensity of light.

The growth forms exhibited by bryophytes in the various unions were found to be correlated with presumed effects of the gross morphology upon water absorption and evaporation, and upon efficiency of photosynthesis.

Many of the bryophyte unions found in the southern Appalachians also occur in the Adirondacks. Noteworthy among these widely distributed unions is that of *Hylocomium splendens*, found in spruce and fir forests in most of the world. Other unions of the southern Appalachians (as *Ulota crispa*) are absent in the Adirondacks and appear to be correlated with local environmental conditions such as fog belts, rather than with a particular forest type.

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APPENDIX A

PARAMETERS USED IN HABITAT DESCRIPTION

EPILITHIC HABITATS

1.	(TPB) top of boulder	- flat top of a rock.
2.	BDP) boulder pit	- a deep interstice among boulders in a boulder field.
3.	(WAL) wall	- a smooth outcropping surface with a slope of 60-120°.
4.	(FAC) face	- a smooth outcropping surface with a slope of less than 60°.
5.	(CVC) cavern ceiling	- a smooth outcropping surface with a slope of more than 120°.
6.	(CVF) cavern face	- back wall or side of an indentation in an outcrop large enough to admit the shoulders of a worker.
7.	(BAS) base	- at line of soil contact with cavern face.
8.	(CRY) cranny	- a miniature cavern admitting only the fist of the worker.
9.	(LDG) ledge	- a nearly horizontal shelf jutting out from the outcrop.
10.	(REC) recess	- the back wall of a ledge set back into face of outcrop.
11.	(SHD) shoulder	- the convex outside margin of a ledge.
12.	(SEP) seepage	- an area wherein ground water appears.
13.	(DRN) drainage	- a channel down which rainwater flows.
14.	(IRD) incised drainage	- a deeply cut drainage.
15.	(INC) incision	- a deeply eroded cut not now draining the area.
16.	(CRK) crack	- a wedge-shaped incision broken into the outcrop.

CRANDALL'S FOREST SITE TYPES

	Site Type	Number of Plots Sampled
1.	(FOH) Fir - Oxalis - Hylocomium	9
2.	(FOD) Fir - Oxalis - Dryopteris	9
3.	(FVVD) Fir - Viburnum - Vaccinium - Dryopteris	9
4.	(FS) Fir - Senecio	9
5.	(FR) Fir - Rhododendron	3
6.	(SFOH) Spruce - Fir - Oxalis - Hylocomium	9
7.	(SFHV) Spruce - Fir - Hylocomium - Vaccinium	9
8.	(SFVVD) Spruce - Fir - Viburnum - Vaccinium - Dryopteris	9
9.	(SFVVS) Spruce - Fir - Viburnum - Vaccinium - Senecio	9
10.	(SFR) Spruce - Fir - Rhododendron	9
11.	(SHV) Spruce - Hylocomium - Vaccinium	9
12.	(SVVD) Spruce - Viburnum - Vaccinium - Dryopteris	9
13.	(SVVL) Spruce - Viburnum - Vaccinium - Lycopodium	9
14.	(SR) Spruce - Rhododendron	9

WATER AVAILABILITY

1. water available only for a short period between the falling of the rain and the completion of the rapid drying to which that site would be exposed.

2. water available from rains or humidity; frequent drying but probably not of long duration.

3. water almost constantly available; never submerged, but almost never dry.

4. in constant seepage; some noticeable moisture always present at least near base of plants.

5. almost completely submerged.

h -a modifier of any of the above indicating occasional high humidity or fog envelopment.

H -a modifier indicating constant high humidity.

LOG DECAY STAGES

1. log intact; entire woody cylinder sound.
2. log mainly untouched by decay, but some erosion of the outer woody cylinder.
3. entire log softened by decay; outer wood cylinder much eroded.
4. entire log very much eroded and often split by decay.
5. entire log completely decayed; location often visible only by the presence of a linear bryophyte community typical of rotten logs.

INTENSITY OF LIGHT

1. (D) direct - sun constantly directed upon the site during unclouded days.
2. (DF) diffuse - in moderate shade, exposed to sunflecks.
3. (C) closed - never receiving direct sunlight or sunflecks; light allowing some visibility.
4. (I) intense - always in very great shade; visibility almost absent.

    (V) very - modifier indicating more shade than the unmodified category.

    (R) rather - modifier indicating less shade than the unmodified category.

SOIL DEPTH

1. virtually no soil.
2. a thin flim of soil preventing direct contact of bryophyte protonemata with the rock.
3. virtually complete soil cover capable even of supporting the growth of many vascular plants.

APPENDIX B

SOUTHERN APPALACHIAN BRYOPHYTE SPECIES LIST

THE BRYOPHYTE UNIONS AND THEIR ABBREVIATIONS

Ac - Atrichum crispum union (soil)

Br - Brotherella recurvans union (tree, log, rock)

Bt - Bazzania trilobata union (tree)

Ce - Cephalozia union (log)

Dd - Dicranodontium denudatum union (rock)

Dh - Dicranella heteromalla union (rock)

Fa - Frullania asagrayana union (tree, log)

Hh - Herberta hutchinsiae union (rock)

Hs - Hylocomium splendens union (soil, rock, log)

Li - Lophozia incisa union (rock)

Ms - Marsupella sphacelata union (rock)

Nc - Nowellia curvifolia union (log)

Pl - Plagiothecium laetum union (tree, log)

Po - Polytrichum ohioense union (soil, log, rock)

Ra - Rhacomitrium aciculare union (rock)

Rd - Rhabdoweisia denticulata union (rock)

Rh - Rhacomitrium heterostichum union (rock)

Rp - Riccardia palmata union (log)

Sm - Sphenolobus michauxii union (log)

Sp - Sphagnum union (soil, log, rock)

Uc - Ulota crispa union (tree)

Coll. - Personal Collection, but not in a quadrat.

Herb. - Present in University of Tennessee herbarium; otherwise unknown to this writer.

L - Collected on log

R - Collected on rock

S - Collected on soil

T - Collected on tree

A CATALOGUE OF THE SOUTHERN APPALACHIAN SPRUCE-FIR BRYOPHYTES

LIVERWORTS

Species	Present in the Following Unions
Acrobolbus ciliatus (Mitt.) Schiffn.	Dd, Rd
Anastrophyllum minutum (Cr.) Schust.	Coll. - S, Herb. - R
A. saxicolus (Schrad.) Schust.	Br, Dh, Rh
Anomylia cuneifolia (Hook.) Schust.	Br, Dh, Hs, Rd, Rh, Uc
Bazzania denudata (Torr.) Trev.	Br, Bt, Dd, Fa, Hh, Hs, Po, Rd, Rh
B. nudicaulis Evans	Br, Dd, Fa, Hh, Pl, Rd, Rh, Sp, Uc
B. tricrenata (Wahlenb.) Trevis	Br, Bt, Ce, Dd, Fa, Dh, Ms, Po, Rd, Rh, Rp, Sm, Sn, Sp, Uc, Herb. - S.
B. trilobata (L.) Gray	Ac, Br, Bt, Ce, Dd, Dh, Fa, Hh, Hs, Li, Ms, Nc, Pl, Po, Ra, Rd, Rh, Rp, Sm, Sn, Sp, Uc
Blepharostoma trichophyllum (L.) Dum.	Br, Bt, Ce, Dh, Fa, Hs, Li, Nc, Pl, Po, Rd, Rh, Rp, Sm, Sp
Calypogeia muelleriana (Schiffn.) K.M.	Herb. - R.
C. suecica (Arn. & Perss.) C.M.	Ac, Br, Hs, Sm, Sp
C. trichomanis (L) Corda	Dh, Ms, Po, Rd
Cephalozia ambigua Massal.	Br, Ce, Coll. - S.
C. bicuspidata (L) Dum.	Br, Ce, Hs, Nc, Pl, Po, Rp, Sm, Sp, Coll. - R.
C. catenulata (Hub.) Spruce	Herb. - L.
C. connivens (Dicks.) Sum.	Dh, Hs, Pl, Sp

C. lammersiana (Hub.) Spruce	Herb. - L.
C. media Lindb.	Br, Ce, Fa, Hs, Nc, Pl, Sp, Coll. - R.
Cephaloziella hampeana (Nees) Schiffn.	Coll. - R.
C. massalongii (Spruce) Muller	Herb. - S.
Cephaloziopsis pearsonii (Spr.) Corrin	Fa, Uc
Diplophyllum apiculatum (Evans) Steph	Br, Dh, Hs, Li, Ms, Ra, Rd, Rh, Sn, Sp
D. obtusifolium (Hook) Dum.	Herb. - S.
Dumortiera hirsuta (Sw.) Nees	Coll. - S.
Frullania asagrayana Mont.	Br, Bt, Ce, Dd, Fa, Hh, Nc, Po, Sm, Uc
F. eboracensis Gottsche	Coll. - T.
F. oakesiana Aust.	Herb. - T.
Geocalyx graveolens (Schrad.) Nees	Br, Bt, Ce, Dd, Dh, Fa, Hs, Nc, Pl, Po, Rd, Rp, Sm, Sp, Herb. - S.
Gymnocolea inflata (Huds.) Dum.	Coll. - R.
Gymnomitrion laceratum (St.) Horik. (= *Dianthelia steerei* Schuster)	Rd
Harpalejeunea ovata (Hook.) Schiffn.	Fa
Harpanthus scutatus (W. & M.) Spruce	Hs, Li, Ms, Herb. - L.
Herberta hutchinsiae (G.) Evans	Br, Bt, Dd, Dh, Fa, Hh, Hs, Nc, Pl, Po, Ra, Rh, Sm, Sp, Uc
Jamesoniella autumnalis (Dc) Steph.	Br, Bt, Ce, Dh, Fa, Hs, Li, Ms, Nc, Pl, Po, Rh, Rp, Sm, Sn, Sp
Jubula pennsylvanica (Steph.) Evans	Hh, Hs, Li, Ms, Po, Ra, Sn

Lejeunea patens Lindb.	Dd, Hh. Hs, Li, Rd, Rh, Herb. - T.
Lepidozia reptans (L.) Dum.	Ac, Br, Bt, Ce, Dd, Dh, Fa, Hs, Li, Ms, Nc, Pl, Po, Ra, Rd, Rh, Rp, Sm, Sn, Sp
Leucolejeunea clypeata (Sch.) Evans	Li, Ms, Rh, Sn
Lophocolea bidentata (L) Dum.	Br, Dh, Ms, Herb. - S.
L. heterophylla (Schrad.) Dum.	Sp
Lophozia attenuata (Mont.) Dum.	Herb. - S.
L. excisa (Dicks.) Dum.	Br, Li, Po, Rh, Rp
L. incisa (Schrad.) Dum.	Ac, Br, Dd, Ce, Fa, Hs, Li, Ms, Pl, Po, Ra, Rh, Rp, Sn
L. silvicola Buch	Herb. - S
M. emarginata (Ehr.) Dum.	Br, Dd, Li, Sn
M. paroica Schust.	Herb. - S.
M. sphacelata (Gies.) Dum.	Dd, Hh, Ms, Ra, Rh, Sn, Coll. - S.
M. sullivantii (DeNot.) Evans	Coll. - R.
Metzgeria fruticulosa (Dicks.) Evans	Dd, Dh, Hh, Sp, Uc
M. furcata (L.) Dum.	Coll. - R., Herb. - T, S.
M. myriopoda Lindb.	Br. Uc
Microlejeunea laetevirens (N. & M.) Evans	Li, Ms, Sn
M. ulicina (Tayl.) Evans	Br, Fa, Nc, Uc
Microlepidozia sylvatica (Evans) Jorg.	Br, Dh, Hh, Hs, Li, Ra, Herb. - L.

Mylia taylori (Hook.) S. F. Gray	Br, Hs, Po, Sp
Nardia crenulata (Sm.) Dum.	Coll. - S., L.
N. scalaris (Schrad.) Cord.	Coll. - S
Nowellia curvifolia (Dicks.) Mitt.	Br, Ce, Fa, Nc, Po, Rp, Sm
Plagiochila asplenioides (L.) Dum.	Dd, Li, Sp
P. austinii Evans	Hh, Rd
P. sharpii Blomq.	Bz, Dd, Hh, Rd, Herb. - T.
P. tridenticulata Tayl.	Br, Bt, Ce, Dh, Fa, Hh, Nc, Po, Rd, Rh, Sm, Sn, Sp, Uc
Plectocolea hyalina (Lyell) Mitt.	Herb. - R. Coll. - S.
Porella platyphylla (L.) Lindb.	Fa
Radula andicola Steph.	Br, Dd, Hh, Li, Ms, Ra, Sn
R. obconica Sull.	Herb. - R.
R. tenax Lindb.	Coll. - R.
Reboulia hemisphaerica (L.) Raddi	Coll. - S.
Riccardia palmata (Hedw.) Carruth.	Br, Fa, Nc, Po, Sm, Rp
Scapania nemorosa (L.) Dum.	Ac, Br, Ce, Dd, Dh, Hh, Hs, Li, Ms, Nc, Pl, Po, Ra, Rd, Rh, Rp, Sm, Sn, Sp
S. undulata (L.) Dum.	Ms, Ra, Sn
Solenostoma obscurum (Evs.) Schust.	Herb. - R.

Sphenolobus exsectiformis (Steph.)	Br, Bt, Ce, Fa, Nc, Po, Rp
S. exsectus (Schmidt) Steph.	Br, Bt, Ce, Fa, Hh, Nc, Po, Rd, Rh, Uc
S. michauxii (Web.) Steph.	Ac, Br, Bt, Ce, Dd, Dh, Fa, Hs, Li, Ms, Nc, Pl, Po, Rh, Rp, Sm, Sn, Sp, Uc
Trichocolea tomentella (Ehrh.) Dum.	Coll. - S.

MOSSES

Species	Present in the Following Unions
Amblystegium varium (Hedw.) Lindb.	Coll. - S.
Amphidium mougeotii (BSG) Schimp.	Coll. - R.
Anacamptodon splachnoides (Froehl.) Brid.	Coll. - T.
Andreaea rupestris Hedw.	Dd, Hh, Rh
A. rothii W. & M.	Br, Dd, Ms, Ra, Rh, Sp
Anomodon attenuatus (Hedw.) Hub.	Coll. - R.
A. minor (P.B.) Lindb.	Coll. - T.
A. rugelii (C.M.) Kies.	Coll. - T.
Atrichum crispum (James) Sull.	Ac, Br, Dh, Hs, Li, Ms, Po, Rh, Sm, Sn, Sp
A. undulatum (Hedw.) Beauv.	Ac, Dh, Hs, Li, Ms, Po, Sn, Sp
Bartramia pomiformis Hedw.	Dh, Hh, Rd
Blindia acuta B.S.G.	Herb. - R.
Brachydontium trichodes (Web.) Fuernr.	Coll. - R.
Brachythecium plumosum (Sw.) Br. & Sch.	Hs, Coll. - R.
B. rivulare B.S.G.	Li, Ms, Sn, Sp, Coll. - L.
B. serrulatum (Hedw.) Robins.	Ac, Br, Fa, Hs, Pl, Sp, Uc
Brothera leana (Sull.) C.M.	Coll. - S.

Brotherella delicatula (James) Fleisch.	Ac, Br, Fa, Hs, Pl, Po, Sm, Sp
B. recurvans (Schwaegr.) Fleisch.	Ac, Br, Bt, Ce, Dd, Dh, Fa, Hh, Hs, Li, Nc, Pl, Po, Rd, Rh, Rp, Sm, Sn, Sp, Uc
B. tenuirostris (Schimp.) Broth.	Ac, Br, Ce, Fa, Hs, Pl, Po, Sm, Sp
Bryhnia novae-angliae (Sull. & Lesq.) Grout	Coll. - S., R.
Bryum argenteum Brid.	Coll. - S.
B. capillare Hedw.	Coll. - R, S.
Calliergonella schreberi (BSG) Grout	Ac, Br, Bt, Ce, Dh, Fa, Hs, Pl, Po, Rh, Sm, Sp
Campylium chrysophyllum (Brid.) Bryhn.	Coll. - R.
C. chrysophyllum brevifolium Grout	Herb. - R.
Ceratodon purpureus (Hedw.) Schimp.	Coll. - S.
Chamberlainia salebrosa (Web. & Mohr) Robins.	Br, Coll. - R.
Dicranella heteromalla (Hedw.) Schimp.	Ac, Br, Dd, Dh, Hs, Li, Ms, Po, Ra, Rd, Sp
D. varia (Hedw.) Schimp.	Coll. - S.
Dicranodontium asperulum (Mitt.) Broth.	Herb. - R.
D. denudatum (Brid.) E.G.B.	Br, Bt, Ce, Dd, Fa, Hh, Hs, Pl, Po, Rd, Rp, Sm
Dicranum bonjeani De Not.	Coll. - S.
D. flagellare Hedw.	Coll. - L.
D. fulvum Hook.	Br, Dd, Dh, Hh, Hs, Li, Ra, Rh, Sn
D. fuscescens Turn.	Ac, Br, Bt, Ce, Dh, Fa, Hs, Nc, Pl, Po, Rd, Sm, Sn, Sp, Uc

D. montanum Hedw.	Herb. - S.
D. scoparium Hedw.	Br, Bt, Ce, Fa, Hs, Pl, Po, Sp
Diphyscium foliosum (Hedw.) Mohr	Coll. - S.
Ditrichum lineare (Sw.) Lindb.	Herb. - S.
D. pallidum (Hedw.) Hampe.	Coll. - S.
D. pusillum (Hedw.) E.G.B.	Coll. - S.
Dolichotheca striatella (Brid.) Loeske	Herb. - R.
Entodon drummondii (B.S.G.) J. & S.	Coll. - L.
Eurhynchium hians (Hedw.) Jaeg. & Sauerb.	Dh, Hs, Rd
Fissidens cristatus Wils.	Dh, Rd, Sp
Forsstroemia trichomitria (Hedw.) Lindb.	Coll. - T.
Funaria hygrometrica Hedw.	Ac, Coll. - R.
Grimmia apocarpa Hedw.	Coll. - R.
Haplohymenium triste (Ces.) Kindb.	Coll. - T.
Hedwigia ciliata (Ehrh.) Hedw.	Coll. - R.
Heterophyllium nemorosum (Schimp.)Kindb.	Br, Fa, Hs, Nc, Pl, Po, Rp, Sm
Homomallium adnatum (Hedw.) Broth.	Herb. - R.
Homalotheciella subcapillata (Hedw.)Broth.	Herb. - T.
Hookeria acutifolia (Hook.) Sull. & Müll.	Rd

Hygrohypnum eugyrium (B.S.G.) Loeske	Li, Ms, Sn
H. micans (Wils.) Broth.	Coll. - R.
H. novae-caesareae (Aust.) Grout	Dd, Dh, Hh, Rd, Sp
H. palustre (Hedw.) Loeske	Ms, Sn
Hylocomium brevirostre (P.B.) B.S.G.	Ac, Br, Bt, Ce, Dh, Fa, Hs, Pl, Po, Rh, Sm, Sp, Uc
H. splendens (Hedw.) B.S.G.	Ac, Br, Bt, Ce, Dd, Fa, Hh, Hs, Ms, Nc, Pl, Po, Ra, Rd, Rh, Rp, Sm, Sp, Uc
H. splendens var. gracilius (Boul.) Husn.	Coll. - R.
H. umbratum (Hedw.) Bry. Eur.	Ac, Br, Dh, Hs, Ms, Po, Rh, Sp
Hypnum fertile Sendt.	Br, Dd, Dh, Hh, Hs, Po
H. imponens Hedw.	Br, Bt, Ce, Dh, Fa, Hs, Po, Ra, Rh, Rp, Sm, Sp
H. pallescens (Hedw.) Bry. Eur.	Fa, Uc
H. reptile Mx.	Br, Bt, Ce, Fa, Nc, Pl, Uc
Isothecium stoloniferum (Hook.) Brid.	Herb. - R.
Leptodontium excelsum (Sull.) E.G.B.	Br. Fa, Hh, Rh, Uc
Leucobryum glaucum (Hedw.) Schimp.	Hs, Rd
Leucodon brachypus Brid.	Coll. - R., T.
L. julaceus (Hedw.) Sull.	Coll. - T.
Merceya ligulata (Spruce) Schimp.	Dh, Rd.
Mielichhoferia mielichhoferiana (Funck.) Limpr.	Dh, Li, Rd

Mnium affine Bland.	Coll. - S.
M. punctatum (Schrad.) Brid.	Ac, Br, Dd, Dh, Li, Ms, Po, Ra, Rd, Rh, Sn, Sp
M. punctatum var. elatum Schimp.	Ac, Dh, Li, Ms, Sn, Sp
M. stellare (Reich.) Hedw.	Herb. - R.
Myurella careyana Sull.	Dd, Dh, Hh, Rd
Neckera complanta (Hedw.) Hueb.	Rd
Oncophorus rauei (Aust.) Grout	Br, Dd, Hh, Rd, Rh
Paraleucobryum longifolium (Hedw.) Loeske	Br, Bt, Ce, Dd, Fa, Hh, Nc, Pl, Po, Uc
Philonotis caespitosa Wils. var. adpressa Dism.	Coll. - S.
P. fontana var. pumila Brid.	Coll. - R.
P. longiseta (Rich.) E.G.B.	Coll. - R.
Plagiothecium denticulatum (Hedw.) B.S.G.	Br, Bt, Dh, Hs, Ms, Pl, Rd, Sn, Sp
P. elegans (Hook.) Sull.	Coll. - R.
P. laetum B.S.G.	Br, Bt, Ce, Dd, Dh, Fa, Hs, Nc, Pl, Po, Rd, Rp, Sm, Sp
P. micans (Sw.) Paris	Coll. - R.
P. sylvaticum (Brid.) B.S.G.	Br, Dh, Hs, Li, Ms, Po, Rd, Sp
Platygyrium repens (Brid.) B.S.G.	Coll. - L.
Pogonatum alpinum (Hedw.) Rohl.	Herb. - S.
P. pennsylvanicum (Hedw.) Paris	Coll. - S.

Pohlia cruda Lindb.	Li, Ms, Sn
P. drummondii (C. Mill.) Andrews	Herb. - R.
P. elongata Hedw.	Ac, Br, Dh, Hh, Hs, Li, Po, Rd, Rh, Sn, Sp
P. nutans (Schreb.) Lindb.	Br, Dh, Hs, Li, Po, Ra, Rd, Rh, Sn, Sp
Polytrichum commune Hedw.	Ac, Dh, Hs, Po, Ra, Rh, Sp
P. formosum Hedw.	Coll. - R.
P. gracile Smith	Herb. - S.
P. juniperinum (Willd.) Hedw.	Dh, Li, Coll. - R.
P. ohioense R. & C.	Ac, Br, Bt, Ce, Dh, Fa, Hs, Ms, Pl, Po, Rd, Rh, Sm, Sn, Sp
P. piliferum Hedw.	Coll. - S.
Porotrichum alleghaniensis (C.M.) Grout	Coll. - R.
Ptilium crista-castrensis (Hedw.) De Not	Ac, Br, Bt, Ce, Dh, Fa, Hs, Nc, Pl, Po, Rh, Sm, Sp
Ptychomitrium incurvum (Wahl.) Sull.	Coll. - R.
Pylaisia intricata (Hedw.) B.S.G.	Coll. - T.
Rhabdoweisia denticulata (Brid.) B.S.G.	Br, Li, Ms, Rd, Rh, Herb. - S.
Rhacomitrium aciculare Brid.	Li, Ms, Ra, Sn
R. heterostichum (Hedw.) Brid. var. *sudeticum* Funck.	Br, Dd, Hh, Ra, Rh
R. microcarpum Brid.	Herb. - R.
Rhodobryum roseum (Bry. Eur.) Limpr.	Br, Herb. - R.

Rhytidiadelphus squarrosus (Hedw.) Warnst.	Hs, Coll. - R.
R. triquetrus (Hedw.) Warnst.	Ac, Br, Bt, Fa, Hs, Pl, Po, Rh, Sm, Sp, Uc
Schwetschkeopsis denticulata (Sull.) Broth.	Br
Sciaromium lescurii (Sull.) Broth.	Li, Ms, Sn
Sematophyllum carolinianum (C. Muell.) Britt.	Br, Dd, Dh, Li, Ms, Ra, Rh
S. marylandicum (C. Muell.) Britt.	Dd, Li, Ms, Ra, Sn
Sphagnum capillaceum (Weiss.) Schrank	Coll. - S.
S. compactum D. C.	Sp
S. girgensohnii Russ.	Br, Bt, Hs, Ms, Po, Sm, Sn, Sp
S. palustre L.	Sp
S. pylaesii Brid.	Herb. - R.
S. quinquefarium (Lind.) Warnst.	Ac, Br, Bt, Ce, Dh, Fa, Hs, Li, Ms, Pl, Po, Sm, Sn, Sp
S. squarrosum Crome	Herb. - S.
Tetraphis pellucida Hedw.	Ac, Br, Bt, Ce, Dd, Dh, Hh, Hs, Nc, Li, Pl, Po, Rd, Rp, Sm, Sp
Thelia hirtella (Hedw.) Sull.	Coll. - T.
Thuidium delicatulum (Hedw.) Mitt.	Br, Bt, Ce, Dd, Dh, Fa, Hh, Hs, Li, Pl, Po, Ra, Rd, Rh, Rp, Sm, Sn, Sp, Uc
Tortella humilis (Hedw.) Jenn.	Coll. - R.
T. tortuosa (Turn.) Limpr.	Coll. - R.
Trichostomum cylindricum (Bruch) C. Muell.	Br, Dd, Dh, Ce, Hh, Hs, Pl, Rd

Ulota americana (P.B.) Limpr. var. rufescens E.G.B.	Fa
U. americana (P.B.) Limpr.	Br, Rh, Ms
U. crispa (Hedw.) Brid.	Fa, Uc
U. ludwigii Brid.	Coll. - T.
Weisia controversa Hedw.	Coll. - S.
Zygodon viridissimus (Dicks.) Brid.	Br, Fa, Rh, Uc

APPENDIX C

BRYOPHYTES OF THE ADIRONDACK SPRUCE-FIR ZONE

LIVERWORTS

Barbilophozia barbata (Schmid.) Dum.

Bazzania trilobata (L.) Gray

Blepharostoma trichophyllum (L.) Dum.

Calypogeia muelleriana Schiffn.

Calypogeia neesiana (Car. & Mass.) K.M.

Cephalozia connivens (Dicks.) Dum.

C. lammersiana (Hüb.) Spruce

C. media Lindb.

Cephaloziella elachista (Jack.) Schiffn.

C. rubella (Nees.) Douin

Chiloscyphus polyanthus (L.) Corda

Gymnocolea inflata Dum.

Lepidozia reptans (L.) Dum.

Lophocolea bidentata (L.) Dum.

Lophozia excisa (Dick.) Dum.

Marsupella emarginata (Ehr.) Dum.

Mylia anomala (Hook.) Gray

M. taylori (Hook.) Gray

Nowellia curvifolia (Dicks.) Mitt.

Pellia epiphylla (L.) Corda

Ptilidium ciliare (L.) Nees

P. pulcherrimum (Web.) Hampe

Scapania apiculata Spruce

S. nemorosa (L) Dum.

Sphenolobus michauxii (Web.) Steph.

MOSSES

Amblystegium serpens (Hedw.) B.S.G.

Andreaea rupestris Hedw.

Anomodon attenuatus (Hedw.) Hüben.

A. minor (Palis) Lindb.

Arctoa blyttii (B.S.G.) Grout

A. fulvella (Dicks.) B.S.G.

Atrichum angustatum (Brid.) B.S.G.

A. undulatum (Hedw.) Palis.

Aulacomnium androgynum (Hedw.) Schwaegr.

A. palustre (Hedw.) Schwaegr.

Bartramia pomiformis Hedw.

Blindia acuta (Hedw.) B.S.G.

Brachythecium serrulatum (Hedw.) Robins.

Brotherella recurvans (Mx.) Fleisch.

Bryhnia novae-angliae (S. & L.) Grout

Bryum argenteum Hedw.

B. capillare Hedw.

B. pseudotriquetrum (Hedw.) Schwaegr.

Ceratodon purpureus (Hedw.) Brid.

Climacium americanum Brid.

Calliergon cordifolium (Hedw.) Kindb.

Calliergonella cuspidata (Brid.) Loeske

C. schreberi (B.S.G.) Grout

Campylium hispidulum (Brid.) Mitt.

Chamberlainia salebrosum (Web. & Mohr) Robins.

Dichodontium pellucidum (Hedw.) Schimp.

Dicranella heteromalla (Hedw.) Schimp.

Dicranum drummondii C. Müll.

D. flagellare Hedw.

D. fulvum Hook

D. fuscescens Turn.

D. montanum Hedw.

D. rugosum Brid.

D. scoparium Hedw.

Diphyscium foliosum (Hedw.) Mohr

Ditrichum pusillum (Hedw. E.G.B.

Drepanocladus uncinatus (Hedw.) Warnst.

Eurhynchium pulchellum (Hedw.) Jenn.

Fissidens cristatus Wils.

Fontinalis antipyretica Hedw. var. gigantea Sull.

Funaria hygrometrica Hedw.

Grimmia apocarpa Hedw.

G. pilifera Palis.

Hedwigia ciliata (Hedw.) Palis.

Helodium blandowii (W. & M.) Warnst.

Heterophyllium haldanianum (Koch) Kindb.

Hygrohypnum eugyrium (B.S.G.) Loeske.

Hylocomium brevirostre (P.B.) B.S.G.

H. pyrenaicum (Spruce) Lindb.

H. splendens (Hedw.) B.S.G.

H. umbratum (Hedw.) B.S.G.

Hypnum fertile Sendt.

H. imponens Hedw.

H. lindbergii Mitt.

H. reptile Mx.

Leucobryum glaucum (Hedw.) Schimp.

Leucodon sciuroides (Hedw.) Schwaegr.

Mnium affine Bland.

M. hornum Hedw.

M. longirostrum Brid.

M. orthorhynchum Brid.

M. punctatum Hedw.

M. p. var. elatum Schimp.

Myurella sibirica (C. Mull.) Reim.

Neckera pennata Hedw.

Oncophorus wahlenbergii Brid.

Orthotrichum pumilum Dicks.

Paraleucobryum longifolium(Hedw.) Loeske

Philnotis fontana (Hedw.) Brid.

Plagiothecium elegans (Hook.) Sull.

P. denticulatum (Hedw.) B.S.G.

P. muellerianum Schimp.

P. turfaceum (Lindb.) Lindb.

Platygyrium repens (Brid.) B.S.G.

Pohlia elongata Hedw.

P. nutans (Hedw.) Lindb.

Polytrichum commune Hedw.

P. juniperinum Hedw.

P. ohioense Ren. & Card.

Ptilium crista-castrensis (Hedw.) De Not.

Rhabdoweisia denticulata (Brid.) B.S.G.

Rhacomitrium aciculare Brid.

R. fasciculare (Hedw.) Brid.

R. heterostichum (Hedw.) Brid.

Rhodobryum roseum (Bry. Eur.) Limpr.

Rhytidiadelphus triquetrus (Hedw.) Warnst.

Schistostega pennata (Hedw.) Hook. & Taylor

Sphagnum capillaceum (Weiss) Schrank

S. compactum D.C.

S. fuscum (Schimp.) H. Klinggr.

S. girgensohnii Russow.

S. palustre L.

S. plumulosum Röll.

S. pylaesii Brid.

S. robustum (Russow) Röll

S. squarrosum Crome

S. warnstorfianum Du Rietz

Tetraphis pellucida Hedw.

Thuidium delicatulum (Hedw.) Mitt.

Tortella tortuosa (Hedw.) Limpr.

Trichostomum cylindricum (Bruch)

Ulota crispa (Hedw.) Brid.

Weissia controversa Hedw.

Zygodon viridissimus (Dicks.) Brid.