To the Graduate Council:

I am submitting herewith a thesis written by Yvonne M. Mescall entitled "The Bryophyte Flora of Savage Gulf, Grundy County, Tennessee." I recommend that it be accepted in fulfillment of the requirements for the degree of Master of Science, with a major in Botany.

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THE BRYOPHYTE FLORA OF SAVAGE GULF, GRUNDY COUNTY, TENNESSEE

A Thesis

Presented for the

Master of Science

Degree

The University of Tennessee, Knoxville

Yvonne M. Mescall

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ABSTRACT

Savage Gulf is a broad, deep gorge located on the western edge of the Cumberland Plateau in Grundy County, Tennessee. Prior to this study, no comprehensive lists of the bryophytes of this area existed, and no attempts had been made to describe the bryophyte flora of the gorge or adjacent plateau. The present study was initiated after discovering several interesting bryophytes on a trip to the gorge in April 1977.

One hundred and eighty-two species of bryophytes from 107 genera in 74 families have been identified for the Savage Gulf area. Of this total, five species are recognized as disjunct Coastal Plain and tropical elements new to Tennessee. One species, Radula voluta, is newly reported for the North American continent. Extensions in known ranges are noted for several species new to the Cumberland Plateau in Tennessee, and lesser extensions on the plateau are reported for several additional species.

The bryophyte floras of various sites within Savage Gulf were compared. The bryophyte flora of the central gorge area is richer and more diverse than that of the adjacent plateau, and contains a number of bryophytes of northern affinity. The richness of the gorge flora is due to the availability of more favorable and diverse habitats.

Unusual collections and range extensions reported for bryophytes in Savage Gulf support the idea that the Cumberland Plateau region is worthy of further intensive bryological investigation.

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CHAPTER I

INTRODUCTION

Savage Gulf is a narrow gorge located on the western edge of the Cumberland Plateau in Grundy County, Tennessee. It is one of three adjacent gorges cut into the plateau that make up the Savage Gulf Natural Area, a National Natural Landmark owned by the State of Tennessee and managed by the Department of Conservation.

To date, no comprehensive list of the bryophyte flora of Savage Gulf exists, and no attempts have been made to investigate and compare the bryophytes of the gorge area with those of the adjacent Cumberland Plateau. The Gulf provides a wide variety of habitats for bryophytes including sandstone bluffs and boulders, calcareous boulders and rock outcrops, streambeds, swales, and swamp areas, as well as two distinct virgin forest communities on the north and south facing slopes.

The gorge itself provides a cool, moist habitat with a mature vascular plant community with distinct canopy, understory and herbaceous layers. The rim floral community is more disturbed and exposed due to past logging activities and includes some young regenerating trees of the Oak-Pine-Hickory forest.

The objectives of this study were threefold:

1. To catalogue the bryophytes of the Savage Gulf area with particular attention to substrate preferences:

2. To compare the bryophyte floras of: (a) the central gorge area with the adjacent portion of the Cumberland Plateau, and (b) the north and south sides of the Savage Creek branch of the Savage Gulf area, with special regard to species richness.

3. To compare the list of bryophytes of Savage Gulf with reports from the literature and herbarium collections to determine the extent and significance of distributional records.

CHAPTER II

THE STUDY AREA

Location and Description

Savage Gulf is a broad, deep gorge of about 1600 hectares cut into the Cumberland Plateau in Grundy County, Tennessee. The gorge is located approximately 56 km (35 mi) northwest of Chattanooga, Tennessee, 35°26-35°28 north latitude by 85°37-85°32 west longitude. Access to the north side of the gorge is via Laager-Cagle road (Highway 4053), northeast of Palmer, access to the south side is along the Old Chattanooga-McMinnville Stage Road.

The gorge is downgraded by Savage Creek which drops approximately 200 m from its headwaters at the eastern end of the gorge to its confluence with the Collins River at the western end, a distance of 8 km (5 miles). The gorge lies in an east-west direction, and except for ravines cut into the slopes by tributaries of Savage Creek, the slopes lie in a nearly perfect north-south orientation.

The rim of Savage Gulf closely follows the 553 m (1800 ft) contour line (U.S. Geological Survey Topographic Map, Collins Quadrangle, 1956), but the elevation drops rapidly to 369 m (1200 ft) at the base of the gorge. The north and south slopes descend at angles of 15-45°, but cliffs of 21-30 m (70-100 ft) are encountered near the rim

where the caprock is often exposed. From the base of these cliffs on the north and south rim, to the creekbed, the slopes are terraced, and often strewn with large (mostly sandstone and conglomerate) boulders. Tributaries of Savage Creek and massive rock slides interrupt the slopes, exposing underlying rock strata (Luther, 1975).

Origin and Geomorphology

The Savage Gulf Natural Area is part of the Appalachian Plateau physiographic province known as the Cumberland Plateau (Fenneman, 1938). The plateau escarpment is characterized by caprocks and cliffs of erosion resistant sandstone and relatively flat upland surfaces into which the gorges are cut.

The recent geologic history has been one of periodic uplift followed by long periods of erosion (Luther, 1975). Fenneman (1938) first proposed this theory for the development of the Cumberland Plateau topography.

The geomorphology of the area is controlled by differences in erosion resistance between the overlying Pennsylvanian and underlying Mississippian rock strata. Gorge formation occurred when the underlying layers of shale and limestone were eroded away by flowing waters, leaving only the more resistant upper layers of sandstone and sandstone conglomerates.

The Savage Gulf area is considered to be in a youthful state of geomorphic development. It is characterized by broad, flat topped interstream divides, deep narrow, V-shaped gorges with actively downcutting streams, and minimal flood plain development (Luther, 1975).

Geology

The recent geologic history of the Cumberland Plateau is one of periodic uplift followed by long periods of erosion. Savage Gulf is stratified with sedimentary rocks of Mississippian and Pennsylvanian age. The deposition of the rock strata has been influenced by fluctuations in ancient sea levels.

The oldest and lowermost layers of exposed rock in the gorge are Mississippian age limestones. This Mississippian series consists of Bangor limestone, the Pennington formation, Hartsells formation, and Monteagle limestone. Although only the Bangor limestone and Pennington formations are present in Savage Creek, the Hartsells formation and Monteagle limestone appear in other branches of the Savage Gulf Natural Area.

Bangor limestone consists of gray to dark gray, fine to medium grain crystalline or fossil-fragmented limestone, which occurs as a layer of about 36 m (120 ft) thick beneath Savage Creek. The upper surface of this layer is exposed at an elevation of 360 m (1200 ft).

The Pennington formation makes up the uppermost Mississippian layer found in Savage Gulf. It is a complex mixture of dolomite, shale, and limestone which forms a layer 94-104 m (310-340 ft) thick situated beneath most of the steep slopes above the 360 m (1200 ft) contour line, yet still well below the caprock.

The more recently deposited Pennsylvanian layer consists of two major strata; the Gizzard group, and the Crab Orchard Mountain group.

The Gizzard group is the older of the two strata. It varies in thickness, 32-49 m (105-160 ft), and represents the main coal bearing layer below the cliff conglomerates. Three formations have been recognized in this group; the Racoon Mountain formation of gray, silty shales intermixed with fine grained sandstones; Warren Point Sandstone, a fine to medium grained, yellowish-gray to yellowish-brown sandstone; and Signal Point Shale, a light to dark gray silty shale. This latter layer is only rarely exposed, often covered by talus from overlying Sewanee conglomerates.

Crab Orchard Mountains group is younger and contains five formations. In Savage Gulf, erosion has obliterated the four youngest and uppermost strata and only the oldest, Sewanee Conglomerate, is present in the Gulf. The other younger formations can be found on ridges to the north and east of the Savage Gulf area. Sewanee conglomerate consists

of medium to course grained quartzose sandstone. It commonly forms rock conglomerates with a high percentage of quartz pebbles of 1.4 cm or larger. The Sewanee layer is very resistant to erosion and forms not only the caprock cliffs of 30-46 m (11-150 ft) in height found throughout the gulf, but also the colluvium that covers the slopes of the gorges following undercutting by streams. This colluvial material can range in size from pebbles less than 1 cm to huge boulders of several meters in diameter. Much of this colluvium rests on slopes underlain by impermeable slippery shales of the Pennington formation, thereby creating conditions conducive to massive rock slides (Luther, 1975).

Soils

Although no published soil survey exists for Grundy County, an unpublished soil survey report for Savage Gulf was prepared by the USDA Soil Conservation Service (1974) for use in planning and management of the Savage Gulf Natural Area by the Tennessee Department of Conservation. The following descriptions are based on this report.

Two soil areas within Savage Gulf and three soil areas on the adjacent plateau have been defined.

Soils located in the bottom of the gorge are described as cobbly soils of the Welchland-Sequatchie Association. Welchland soils are cobbly loam soils making up 90 percent of the soil composition in the gorge basin. They have a

brown cobbly loam A horizon, and a cobbly sandy loam B horizon. Percent stone and cobbles (of diameters of 5-25 cm) ranges from 15-40 percent in the A horizon to 35-80 percent in the B horizon.

Sequatchie sandy loam soils and Allen cobbly loam soils make up the remaining 10 percent of this association. Sequatchie soils have a dark brown A horizon and brown loamy B horizon. These soils occur mostly in areas that have been cleared. The A horizon may contain up to 10 percent 5-15 cm cobbles; the B horizon up to 30 percent. Allen cobbly loam soils are located along the edges of Sequatchie soils. They are characterized by having a brown cobbly loam A horizon and a yellowish-red clay loam B horizon. Up to 25 percent of the A horizon may consist of 5-25 cm cobbles, while the B horizon contains less than 15 percent.

The soils of the upper slopes of the gorge are made up of a series of unstable, bouldery soils including the Bouldin, Allen, and Talbott series.

Bouldin cobbly loam soils make up about 70 percent of this area. They have a dark, grayish-brown cobbly or stoney sandy loam A horizon and a yellowish-red clay loam B horizon. The underlying bedrock from which these soils are derived is limestone. The A horizon may contain up to 40 percent angular sandstone due to rubble from sandstone cliffs above; the size of the sandstone ranging from pebbles to large

boulders. The B horizon in this area may be up to 70 percent rock.

The Allen series, described earlier, makes up about 10 percent of the soils of the upper slopes and occurs in patches on lower slope positions.

The Talbott series makes up the remainder of the upper slope soils. This series is characterized by its brown silt loam A horizon and yellowish-red clay B horizon. Limestone outcrops frequently occur in areas where Talbott soils are found.

Rockland soil is a minor type with a restricted location. It occupies only about 10 percent of the gorge slope, occurring at the base of the sandstone caprocks and cliffs. What little soil that does occur here is a sandy loam surrounding the loose boulders beneath the cliffs.

A third type of soil association is defined for the plateau adjacent to the escarpment. This area consists of Ramsey, Hartsells, and Holston soils.

Ramsey rocky fine sandy loams and fine sandy loam soils make up about 85 percent of this soil association. The Ramsey series is characterized by dark grayish-brown fine sandy or sandy loam A horizons, and a yellowish-brown 1 an B horizon. The Ramsey soils of the plateau range from 25-73 cm in depth and the A horizon may contain 20-35 percent sandstone fragments.

Hartsells loam soils constitute 10 percent of the adjacent plateau area, having a dark grayish-brown loam A horizon and a yellowish-brown sandy clay loam B horizon. Overall, these soils make up 70 percent of the deeper soils of the plateau.

Holston loams make up the remainder of the soils associated with the adjacent plateau. They have a brown loam A horizon and a yellowish-brown B horizon.

Several other soil associations are also described in the soil report for the Savage Gulf Natural Area, however, only the above mentioned soil associations are involved in the present study.

Climate

The climate of Savage Gulf is influenced to a great extent by the varying topography of the region. The Cumberland Plateau acts as a weather barrier and consequently experiences greater precipitation and lower temperature averages than the surrounding areas.

Weather data from the Monteagle Weather Station, according to Dickson (1960), show that the average monthly precipitation ranges from 18.8 cm (7.4 in) in the winter months to 8.6 cm (3.4 in) during the drier summer months. The average annual precipitation at Monteagle is approximately 155 cm (61 in). The average annual temperature is approximately 13.8°C (56.9°F) with winter averages seldom

dropping below 1.6°C (35°F). Dickson noted, however, that the temperatures in this region decrease with the rise in elevation, often up to 1.6°C (3°F) per 1,000 ft elevation.

Although accurate weather data for Savage Gulf itself are not available, it is readily apparent that temperatures in the protected draws and ravines of the gorge are considerably cooler than those of the adjacent plateau.

Sherman (1978) observed that the steep slopes of the gorge act to funnel warm, moist air upward, producing locally heavy rains. Billings and Anderson (1966) recorded similar observations on the Blue Ridge escarpment along the North Carolina-South Carolina-Georgia borders.

Although measurement and interpretation of microclimatic data are beyond the scope of this present study, definite temperature and moisture gradients were observed between habitats. The fact that microclimatic characteristics of bryophyte habitats can be very different from macroclimatic reports was noted by Billings and Anderson (1966). Bryophyte communities studied on the Blue Ridge escarpment appeared to have narrower climatic ranges than the overall area studied.

History of the Area

The earliest inhabitants of the Savage Gulf area were probably Indians who used the gorge as a sacred hunting ground (Prichard, 1977). One of the earliest settlers of the area was Samuel Savage for whom the Gulf is named.

The central gorge area was purchased for logging by Sam Werner of the Werner Lumber Company in 1890; however, only the upland areas of the gorge were logged as a railroad right-of-way dispute in 1905 prevented logging of the central and lower portions of the gulf.

Attention focused on the gulf once again in the mid-sixties when a county tax reassessment program and the possibility of renewed lumbering activities threatened its preservation. Under the direction of Herman Baggenstoss of Tracey City, a major preservation act was begun by the Middle Tennessee Conservation Council, the Tennessee Department of Conservation, and the Tennessee Valley Authority (Zachry, 1977).

In June 1973, funds from the State of Tennessee along with a matching grant of approximately $900,000 from the Federal Bureau of Outdoor Recreation enabled the purchase of the central portion of the gulf and the adjacent rim from Sam Werner III, Carl Werner, and Mrs. Charles Boyd. The area was then established as the Savage Gulf Natural Area (Prichard, 1977).

In 1977, additional funds from the Nature Conservancy in Washington, D.C. purchased an additional 1640 hectares from the Huber Corporation, thereby doubling the preserved area. Additions of adjacent areas of Big Creek and Horsepond Gulf will complete the acquisition of the 10,000 acre proposed natural area.

The Savage Gulf Natural Area is presently designated as a National Natural Landmark by the U.S. Department of the Interior, and was designated as a Class II, Natural-Scientific Area by the State of Tennessee Department of Conservation in 1973.

Floristics

The vascular plant flora of the Cumberland Plateau in Tennessee has been studied by several separate investigators. Caplenor (1955) described the vegetation of the Fall Creek Falls gorge, a relatively undisturbed gorge of the western Cumberland Plateau between Van Buren and Bledsoe counties, 30 miles northeast of Savage Gulf. Sherman (1958) investigated the flora of five gorges on the southern Cumberland Plateau in Alabama and Tennessee, examining the mixed mesophytic forest of the area and pointing out various geographical affinities present in the flora. Clark (1966) described the mixed mesophytic forest of the Fiery Gizzard Gorge on the Cumberland Plateau in south-central Tennessee. Safley (1970) described the forest community types from the Big South Fork of the Cumberland River drainage area.

More recent works on the floristics of the Cumberland Plateau have centered in the Savage Gulf area itself. Quarterman, Turner, and Hemmerly (1972) provided a preliminary analysis of the vegetation of Savage Gulf, classifying the north-facing slope as mixed mesophytic, dominated by

Basswood (Tilia heterophylla), Hemlock (Tsuga canadensis), Sugar Maple (Acer saccharum), and Tulip poplar (Liriodendron tulipifera), and the south-facing slope as an Oak-Hickory-Tuliptree expression of the mixed mesophytic forest, dominated by Chestnut Oak (Quercus prinus), Red Oak (Q. rubra), White Oak (Q. alba), Shagbark Hickory (Carya ovata), and Tulip poplar.

Wade (1977) and Smith (1977) studied the vegetation of the adjacent Cumberland Plateau and described several communities dominated by Chestnut Oak, Scarlet Oak (Quercus coccinea), Short leaf Pine (Pinus echinata), and Red Maple.

Wofford, Patrick, Phillippe, and Webb (in press) completed a floristic survey of the Savage Gulf area, listing 678 species in 358 genera of vascular plants found in the gorge and on the adjacent uplands.

A complete vegetational analysis of the Savage gorge has been recently completed (Sherman, 1978). Eight virgin forest communities and six secondary forest types were described. Distribution of community types was related to slope aspect and position. A more complete discussion of Sherman's work is presented in the descriptions of individual collecting sites.

CHAPTER III

BRYOLOGICAL INVESTIGATIONS IN TENNESSEE

One of the earliest contributors to the knowledge of bryology in Tennessee was William Sterling Sullivant, who traveled throughout East Tennessee in 1843. Bryophyte collections made during this trip were published by Sullivant as an exsiccata series, Musci Alleghanienses. Sullivant made several additional expeditions to Tennessee and other southeastern states, often with his assistant Leo Lesquereux. Between 1844 and 1856 Lesquereux made expeditions to the states of Tennessee, Alabama, and North and South Carolina, to collect mosses for Sullivant. Specimens of mosses resulting from these trips were published by Sullivant and Lesquereux in 1856 as Musci Exsciccati Americani (Andre, 1971).

Between 1856 and 1929, collections of bryophytes from Tennessee were reported by Sullivant and Lesquereux (1865), Howe (1896), Evans (1897, 1905, 1910a, 1910b, 1910c, 1922), Hayes (1916), Andrews (1921) and Grout (1928). The combined list of bryophytes for Tennessee from these early reports totalled only 54 species according to Sharp (1939).

Investigations of bryophytes from Tennessee have been largely of a floristic rather than ecologic nature, and have been limited to a relatively small number of investigators.

These early workers sought to extend the known distributions of bryophyte species, and to provide baseline floristic information. It is also important to note that the vast majority of published bryological information for Tennessee centers around the East Tennessee region.

The most significant contributions to the knowledge and understanding of the bryophyte flora of Tennessee have been made by Dr. Aaron J. Sharp. In 1929, Dr. Sharp accepted employment with the University of Tennessee as an instructor of Botany. Between 1929 and 1938 Sharp published 23 papers adding significantly to the known cryptogamic and vascular floras of the state. His continued efforts in bryology as well as vascular plant studies since that time have provided additional information on the floristics of Tennessee, particularly in the field of cryptogamic botany (Sharp, 1942, 1944, 1948, 1955, 1965, 1967, 1972).

Others, besides Sharp, have also made notable contributions to the knowledge of bryophytes in Tennessee. Cain (1935) presented a list of bryophytes found in the spruce-fir forests of the Smoky Mountains. Wingo (1936) discussed the family Tortulaceae in Tennessee, providing annotated keys to this family. Morrison (1938) presented similar information for the liverwort genus Lejuenea from Tennessee. Other contributions include works by Blomquist (1939, 1940), Clebsch (1947, 1954, 1974), Pursell and Sharp (1959), and Sharp, Clebsch, and Bissell (1968).

Ecological investigations of Tennessee bryophytes have been published by Cain and Sharp (1938), and Billings and Drew (1938), but the most significant work to appear was Sharp's 1939 paper, Taxonomic and Ecological Studies on Eastern Tennessee Bryophytes. In it, Sharp provided habitat information, phytogeographical affinities and correlations, and invasion and successional information for 426 species of bryophytes from the East Tennessee region.

More recent bryoecological investigations have been made by Quarterman (1947, 1950) and Hattaway (1973). Hattaway (1973) described the bryoecology of three limestone sinks in East Tennessee. Hattaway's work is significant in that it describes the bryophyte and woody floras of the sinks using qualitative and quantitative measurements. Microclimatic data were used to describe an environmental gradient between the sinks and the surrounding rim. Ninety-three species of bryophytes from saxicolous and corticolous habitats were studied. The sinks appear to be unique refugia for bryophyte species and inferences from this study imply that they may be useful in making phytogeographical correlations (Hattaway, 1973). That the unglaciated Southern Appalachian mountain region may also act as a refugium for bryophyte species is also well known (Sharp, 1939; Crum, 1972).

Regional bryo-floristic or bryoecological works of the Tennessee region are extremely limited. Clebsch (1947, 1974)

provides the only extensive bryoecological investigations from the Highland Rim in Tennessee. In 1947, he described 184 species of bryophytes from the lower Cumberland River, including 13 taxa new for the state. In his 1974 work, he discussed the relative abundance, substrates, and landscape types for 95 species of mosses and 20 hepatics in the Land Between the Lakes region of Kentucky-Tennessee. Quarterman (1950) provides the only extensive bryoecological work from the Nashville Basin area.

The only work of significance known from West Tennessee is that of Schwarz (1933) which lists common genera and species of bryophytes found in the Reelfoot Lake area of northwestern Tennessee.

CHAPTER IV

COLLECTION AND PREPARATION OF DATA

In as much as field collections provide the core of any floristic work, and that the primary objective of any floral survey is to provide accurate baseline data by means of a complete inventory of all species in a given area, it is important to collect as many different taxa from as many different habitats as possible. To facilitate adequate coverage of the Savage Gulf study area, a U.S. Geological Survey Topographic Map of the Collins quadrangle (1956) was consulted, and unusual sites, as well as generally forested areas of the gulf were noted. This method was used to identify eight primary study areas in the Savage Gulf area based on different slope positions, substrate differences, or unique habitat features such as waterfall areas or swamps.

The study areas include the north swamp (Site 1), the north rim forest (Site 2), the north slope of the central gorge area (Site 3), the south slope of the central gorge area (Site 4), the south rim forest (Site 5), the south plateau swales (Site 6), Savage Creekbed (Site 7), and the Savage Falls area (Site 8) (See Figure 1).

Sampling of lignicolous, saxicolous, and terricolous species was random within all study sites. Where possible, at least five trees of each species present in a study area

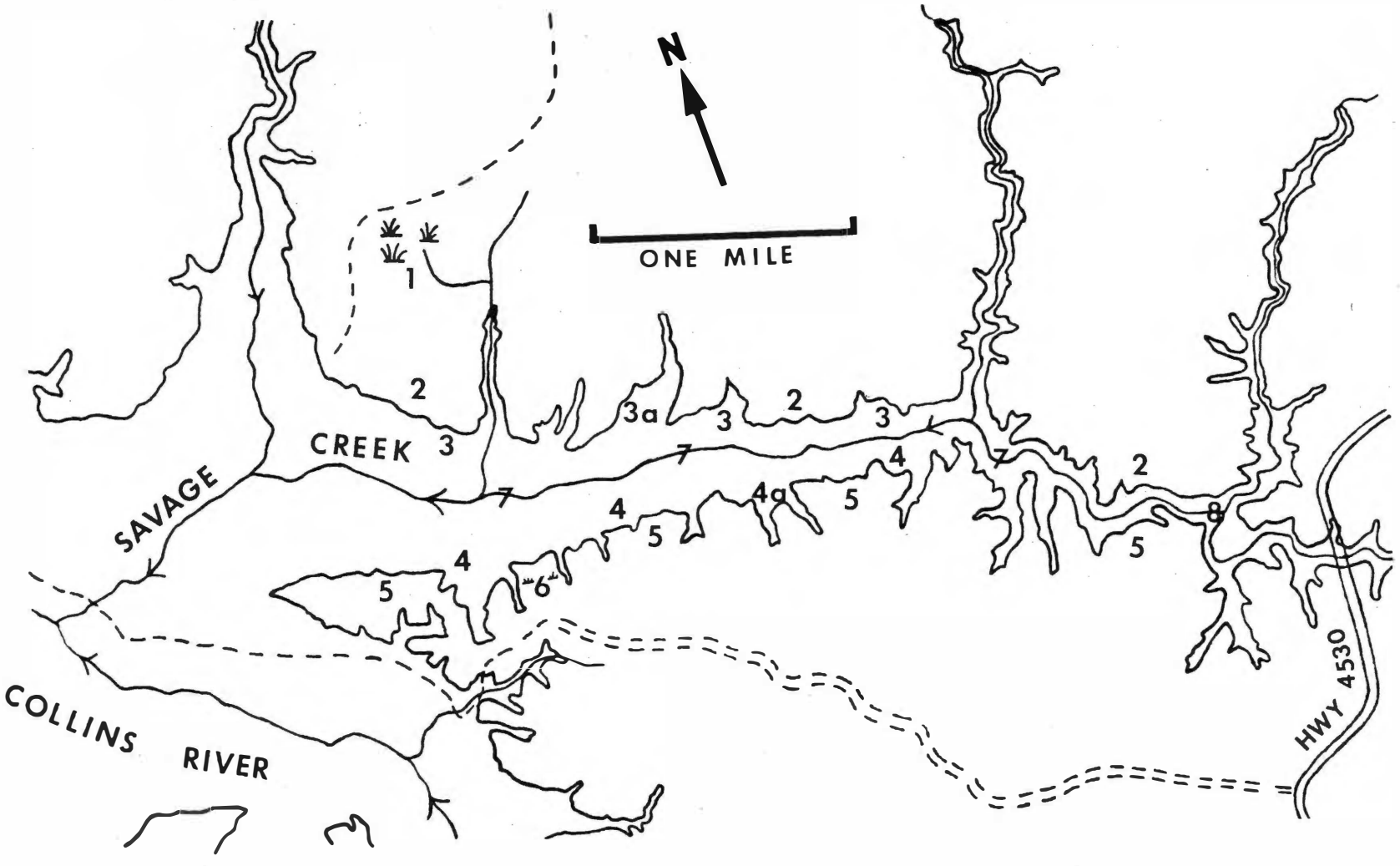

Figure 1. Map of Savage Gulf showing collecting sites. Outline is that of the 1800 ft contour line.

were sampled to insure adequate collection of corticolous species.

Through collections, general habitat descriptions, and notes on bryophyte species known to the author were made in each study area. Specimens unfamiliar to the author as well as species in question were numbered, collected, and taken to the laboratory for further identification. Notes on substrate, moisture, and light intensity were taken for each specimen collected.

Laboratory examination and identification of fresh specimens were made using both binocular and compound microscopes. Specimens of questionable identity and those which the author was unable to identify were submitted to more experienced bryologists for their identification.

Major bryo-floristic works consulted in making determinations were: Grout's Moss Flora of North America (1928-1940), Sharp's Taxonomic and Ecological Studies of Eastern Tennessee Bryophytes (1939), Crum's Mosses of the Great Lakes Forest (1976), Ammon's Liverworts of West Virginia (1940), Frye and Clark's Hepaticae of North America (1937-47), and Schuster's Hepaticae and Anthocerotae of North America (1966). Nomenclature adopted for mosses follows that of Crum, Steere, and Anderson (1973); for liverworts, Stotler and Crandall-Stotler (1977) is followed.

At least one voucher specimen of each taxon reported in this study is in The University of Tennessee Herbarium (TENN).

CHAPTER V

DESCRIPTION OF COLLECTING SITES

The Savage Gulf area contains a number of different, distinctive bryophyte habitats. In order to facilitate collection and interpretation of data, the gorge was divided into eight primary collecting sites based on slope, moisture and unique habitat features. The two major divisions of north and south sides of Savage Creek have been further refined, and are described herein to present more accurate descriptions of the bryophyte habitats within the gulf.

The north side of Savage Gulf is divided into four collecting sites: the north swamp, north plateau forest, the south-facing slope of the central gorge area, and an east-west oriented tributary of Savage Creek designated as the north ravine (Sites 1-3a respectively on Figure 1, page 20).

The south side of Savage Gulf is likewise divided into four general sites including the north-facing slope of the central gorge area, Still Point cove, the south plateau forest, and the south plateau swales (Sites 4-6 respectively on Figure 1, page 20).

Two additional sites are included which are discrete from either side of the gorge. These are the Savage Creekbed and the savage Falls area (Sites 7 and 8 on Figure 1).

The North Swamp (Site 1)

The north swamp collecting site is a wooded, upland swamp located near the western end of the adjacent plateau, approximately one-tenth mile from the northwestern rim of the gorge. Although the area does appear to be drained to some extent, it nevertheless remains relatively wet throughout the summer months.

The area is a partially shaded, wet, almost boggy area with a number of fallen, decorticated, and partially decayed logs throughout. The ground is covered by a thick mat of sphagnum, but a number of herbaceous plants are also common.

A recent floristic survey in this area by Wofford et al. (in press) records dominant woody species of Blackgum (Nyssa sylvatica), Red Maple, Sweetgum (Liquidambar styraciflua), Itea virginica, and Viburnum rufidulum. The herbaceous layer is characterized by a number of fern and sedge species typical of swampy, woodland habitats of the Cumberland Pleateau, however, a number of taxa found in this area, such as Juncus repens, Proserpinaca pectinata, Rhynchospora corniculata, Woodwardia virginica, and Itea virginica have Coastal Plain affinities and may be of phytogeographical importance.

Habitats on the Cumberland Plateau, similar to this one have been described by Smith (1977) and Wade (1977), but reportedly contain a more depauperate flora during summer months.

The underlying soils of the swamp are those of the Ramsey, Hartsells, and Holston series described earlier (USDA, 1974).

The North Plateau Forest (Site 2)

The north plateau forest site consists of the upland woods of the plateau adjacent to the north rim of the gorge. Also included in this site are sandstone bluffs of the north escarpment, and small tributaries that provide drainage of the plateau. The north rim hiking trail of the Savage Gulf Natural Area traverses this site.

The plateau flora has been disturbed to some extent by logging (Sherman, 1978). The regenerating forest is dominated by species of Hickory and Oak. Other frequent woody species in the area include Short Leaf Pine, Sourwood (Oxydendrum arboreum), Sweet Shrub (Calycanthus floridus), and Blackgum; some Hemlock occurs in the streambeds. Shrubs of the area include Viburnum, Vaccinium, and Rhododendron species (Sherman, 1978).

The area is a relatively typical, mesic to dry mixed hardwood forest (Braun, 1950; Smith 1970; Wade 1970).

The South-Facing Slope of the Central Gorge (Site 3)

Site 3 includes the south-facing slope of the central gorge, 3/4 mi. east to 3/4 mi. west of the north ravine site. The area extends from the base of the escarpment bluffs to

the banks of Savage Creek, and includes most of the virgin forest tract on the north side of Savage Creek.

Quarterman et al. (1972) described the forest as an Oak-Hickory-Tuliptree expression of the mixed mesophytic forest. Sherman (1978) describes three different forest communities on this slope; White Oak-Hemlock, Mockernut Hickory-Northern Red Oak, and Chestnut Oak communities.

The White Oak-Hemlock community occurs on the lower slopes. It is dominated by these two species, but Tulip poplar, and Mockernut Hickory are also common. The understory is dominated by Flowering Dogwood (Cornus florida), Red Maple, and Sugar Maple. This forest type also extends into protected draws and ravines (see Site 3). Percent rock content on the soil surface is lowest in this area (Sherman, 1978).

The Mockernut Hickory-Northern Red Oak forest is the largest community in the central gorge area, occurring on middle slope positions as well as on ridges and draws (Sherman, 1978). White Oak and Tulip poplar are also found in this area. The understory is characterized by Dogwood, Red Maple, Sweet Shrub and Smilax species. Occasional sandstone boulders and outcrops are encountered in this area. The soils are deep loams and silt loams formed from the sandstone colluvium and limestone bedrock (Sherman, 1978; USDA 1974).

The Chestnut Oak community occurs on upper slope positions. Although it is dominated by Chestnut Oak, Mockernut Hickory, Northern Red Oak, and Shagbark Hickory also are found here. Smilax, Vitis, and Vaccinium provide a dense understory in some places. The slope is fairly steep and the soils are primarily shallow loams derived from sandstone colluvium (Sherman, 1978). Sherman (1978) also notes that moisture stress is no doubt a factor in determining the flora of this area.

The North Ravine (Site 3a)

A narrow, deep ravine cut into the north slope across from and 1/10 mi. downstream of Still Point constitutes Site 3a.

A major tributary of Savage Creek and drainage channel for the adjacent plateau, the ravine is perpendicular to the gorge, and extends from the 1800 ft. contour line of the plateau to its junction with Savage Creek. The very steep slopes of this narrow ravine as well as the north-south orientation offer a protected habitat for both bryophytes and vascular plants. The ravine is cooler and more moist than the surrounding slope.

The stream cuts through several major rock formations of the gorge, exposing vertical walls of limestone at the lower end and sandstone at the upper end. Sandstone colluvium in the form of massive boulders fills the streambed

from the plateau to the creekbed. Several small waterfall areas are encountered throughout the ravine.

The forest adjacent to the north ravine follows the transition described for the south-facing slope (Site 3).

The North-Facing Slope of the Central Gorge (Site 4)

The north-facing slope of the central gorge area extends 3/4 mi. east and west of Still Point cove, including the virgin forest area of this slope. Sandstone boulders dominate this slope at all positions. The forest communities for this area as described by Sherman (1978) include the Basswood-Tuliptree-Sugar Maple and the Tuliptree-Hemlock communities.

The Basswood-Tuliptree-Sugar Maple community occurs on upper and middle slope positions. Tulip poplar, Basswood, Sugar Maple, Hemlock, Shagbark Hickory, and American Beech (Fagus grandifolia) are listed as important associates. The understory is of low density and is characterized by Sugar Maple, Dogwood, and Witch Hazel (Hamamelis virginiana). The soils of the area are loams and silt loams, derived from sandstone colluvium and underlying shale and limestone bedrock (Sherman, 1978; USDA, 1974).

The Tuliptree-Hemlock community is reported as occurring along the lower slope, adjacent to Savage creek. Tulip poplar is the dominant overstory tree, but Hemlock and

Northern Red Oak are also frequent. Hydrangea and Viburnum species are common shrubs in this area. Soils are loams and sandy loams with a high stone percentage, although the percent rock cover is the lowest in this area.

Still Point Cove (Site 4a)

Still Point cove occurs approximately at the middle of the gorge, extending from the plateau to the creekbed on the north - facing slope. Once a major tributary of Savage Creek, the streambed is only rarely flooded, although it remains moist and cool throughout the year. The streambed is terraced due to erosion resistant strata of sandstone at the upper end, and sandstone colluvium fills the cove from top to bottom. Numerous trees have fallen in the streambed due to massive rock slides. Soils of the area are typically sandy loams derived from the sandstone colluvium.

The forests of the adjacent area follow the transition described for the north - facing slope.

The South Plateau Forest (Site 5)

Site 5 includes the south plateau bluffs and the flat to rolling upland forest adjacent to the rim of the gorge. The area is similar in most respects to the north plateau forest (Site 2) and has a similar history, topography and vascular plant flora.

The bryophyte flora of the Old Chattanooga-McMinnville Stage Road is also included in this collecting site. The

Road area shares characteristics of history and vegetation with the south plateau forest, and although not directly associated with the rim, it is a major access route into the gorge and should be included as part of the gorge flora in the interests of accuracy and completeness.

The South Plateau Swales (Site 6)

A series of swales occur on the south plateau, perpendicular to the rim of the gorge. These wet, sandy depressions support a dense understory of Kalmia latifolia, Hemlock, Ilex opaca, and Euonymous americana (Wofford et al., in press). The swales are otherwise situated within typical plateau vegetation as described earlier.

Soils of the area are sandy loams and sands derived from the underlying Sewanee sandstones, and due to their lowlying position, the depressions remain relatively wet throughout the year. The area is considerably more moist than the surrounding plateau, and although they do occur within the south plateau forest, they are considered to be distinct enough to warrant separate consideration.

Savage Creekbed (Site 7)

Savage Creekbed from just below Savage Falls to the west end of the gorge makes up site 7. The creekbed contains sandstone colluvium that ranges in size from small pebbles to massive boulders. Limestone is also present in the form

of boulders, as well as being the underlying bedrock. The soils of the banks of Savage Creek are sands and sandy loams, occasionally with a thick organic layer. They are shaded and always relatively moist. The forest communities of this area are those described for the lower slopes of the north and south slope respectively.

Savage Falls (Site 8)

Savage Falls is located at the upper end of the gorge. The bed of the creek is shaley sandstone, but even here, sandstone colluvium is evident. On either side of the falls occur limestone and shaley sandstone vertical surfaces and seepage areas, as well as sandy soil banks.

The forest community of the adjacent area is a Hemlock Chestnut Oak association described by Sherman (1978).

A complete listing of all bryophytes identified in this study along with associated collecting sites can be found in Table 1 (Appendix).

CHAPTER VI

FACTORS AFFECTING BRYOPHYTE DISTRIBUTIONS

It is generally known that a number of bryophyte species occur on a wide range of substrates within a variety of habitats, and that other species show particular substrate and habitat preferences.

Environmental factors affecting the distribution of bryophytes involve a number of interacting physical and chemical variables which make up the microhabitat (Barkman, 1958). Light intensity, pH of the substrate, moisture, and temperature are all of primary importance and greatly affect the bryophyte flora of a particular habitat. The physical and chemical nature of bark for example, plays an important role in determining the corticolous bryophyte communities which will inhabit a particular tree species. Sharp (1939) noted that bryophyte communities change as decortication and decay act on fallen trees. These changes correlate well with an increase in acidity of the substrate as the wood breaks down.

Investigations of microclimatic factors that affect bryophyte communities have been made by Sharp (1939), Quarterman (1950), Barkman (1958), Billings and Anderson (1966), and Hattaway (1973). Hattaway investigated several microclimatic factors that influence the bryophyte

composition of limestone sinks. He states "Any environmental aspect is so complex in its interrelationships with other environmental factors that a successful attempt to ascertain the effects produced by one factor alone is almost impossible." It is clear then, that several different environmental factors interact to produce a particular microhabitat. Subtle changes in these variables can lead to major differences in the bryo-floristic composition of an area.

The chemical composition and specific requirements of bryophyte species also play an important part in the distribution of bryophytes in different habitats and on various substrates. A number of species demonstrate substrate specificity and are seldom, if ever collected elsewhere. Exceptions that do occur have been noted by Sharp (1939) and Hattaway (1973). Moisture availability, more than any other factor appears to control the range of substrate preferences.

CHAPTER VII

BRYOPHYTES REPRESENTED IN SAVAGE GULF

The bryophyte flora of Savage Gulf can be divided into four major substrate groups: corticolous species (bryophytes on living trees), lignicolous species (species on decaying wood), saxicolous species (on rock substrates), and terricolous species (soil inhabiting bryophytes). In order to present more accurate habitat information, these groups can be further divided according to specific variations within substrate groupings. A summary of the bryophytes represented in Savage Gulf along with their associated substrates can be found in Table 2 (Appendix).

Corticolous Bryophytes

Corticolous bryophyte species are defined as occurring on the bark at either the trunk or base of aerial trees and shrubs, or on the bark of recently fallen, but still readily identifiable trees.

A total of 50 corticolous species were identified in the Savage Gulf area. A summary of the corticolous bryophytes with their associated phorophyte species can be found in Table 3 (Appendix). In addition to this list, the following bryophytes were collected in small amounts on only one or two trees in the study area: Amblystegium serpens,

Brotherella tenuirostris, Jungermannia gracillima, J. crenuliformis, and Isopterygium tenerum.

Seventeen species appear to be restricted to corticolous substrates. Five of these species demonstrate host specificity for a single phorophyte associate: Calypogeja trichomanis, Frullania brittoniae, Dicranum montanum, Orthotrichum ohioense, and Campylium radicale.

Calypogeja trichomanis and Dicranum montanum are restricted to the bases of Liriodendron tulipifera (tulip poplar). The former species occurs on the south-facing slopes of the gorge and the latter on the north-facing slope and north ravine sites. Although Dicranum montanum is a common corticolous species in the southeastern U.S., Calypogeja trichomanis is not generally considered to be an epiphytic species, growing more typically on saxicolous substrates.

Frullania brittoniae, a leafy liverwort, appears to be restricted to the trunks of Fagus grandifolia (American beech), and occurs only on this species within the Savage Gulf area.

Orthotrichum ohioense, a typically epiphytic species, appears to be restricted to the bark of Juglans nigra (black walnut), a rather uncommon tree in the Savage Gulf area.

Campylium radicale, another atypical epiphyte that normally occurs on wet, sandy soil, is restricted to the bark at the bases of Quercus species within the gorge area.

The remaining species of bryophytes restricted to a corticolous substrate show no difinite preference or specificity, rather, they occur on a number of different phorophyte species in the study area. These species include: Drummondia prorepens, Ulota crispa, Haplohymenium triste, Frullania tamarisci, Thelia hirtella, Haplocladium microphyllum, and H. virginianum.

The remainder of the species occurring on corticolous substrates are not restricted to these substrates, however, they can be segregated into two major groups according to their occurrence on tree species: those which commonly occur on bark at the base of trees, and those which commonly occur higher up on the trunk. Moisture more than any other factor seems to influence this natural segregation pattern.

The dominant corticolous species of bryophytes occurring on the trunks of trees in Savage Gulf include Forsstroemia trichomitria, Leucodon julaceous, Platygyrium repens, and Porella platyphylloidea. In all, 24 species of corticolous bryophytes appear to be limited to the trunks of their associated phorophyte species.

The dominant corticolous bryophyte species occurring on bark at the bases of trees include Anomodon attenuatus, Anomodon rostratus, and Thuidium delicatulum. All three of these species are common and occur on various substrates throughout the deciduous forests of eastern North America. Two species, Campylium radicale and Calypogeja trichomanis,

mentioned earlier, are restricted to the base of their associated phorophyte species.

Several species show no preference to either the trunk or base of their host phorophyte. These species include Anomodon minor and Entodon seductrix. These species appear to have a wide tolerance for a variety of habitats, and occur on other substrates throughout the gulf.

A number of species collected on corticolous substrates in Savage Gulf are not normally considered to be epiphytic. Leucolejuenea clypeata, Fissidens cristatus, Campylium chrysophyllum, and Haplocladium microphyllum are all considered to be saxicolous bryophytes. Cephalozia connivens, Aulacomnium palustre, Fissidens osmundoides, Leptodictyum trichopodium, Mnium ciliare, and Haplocladium virginianum are reported as occurring on moist soil or logs. These species were collected on the bases of trees. Often, the soil accumulations on the bark at the bases of trees may be sufficient to support the growth of terricolous bryophytes. It should also be noted that species such as Cephalozia connivens and Aulacomnium palustre are also very common on lignicolous substrates which are, in fact, later stages of decay of corticolous substrates.

Lignicolous Bryophytes

Lignicolous bryophyte species are defined as those species inhabiting decaying wood substrates. Bryophytes

collected on recently fallen logs or trees of positive identification are included with corticolous species lists, and those bryophytes on logs or trees of questionable identity due to decortication are included as lignicolous bryophyte species.

Lignicolous substrates are available in all study sites within the Savage Gulf area, but are particularly abundant in the swamp site on the north plateau and in ravines where massive rock slides have destroyed a number of large trees. The substrates vary in moisture and light intensity from dark, fully shaded, moist sites on the lower north-facing slope, to open, exposed, drier sites on the north and south plateau. Fallen logs and decaying branches in the swamp and swale sites are considerably more moist than those of the drier forest floors. The bryophyte flora varies accordingly.

Fifty-three lignicolous species were identified in Savage Gulf (Table 4, Appendix). Nine species appear to be restricted to lignicolous substrates within the study area.

Nowellia curvifolia, Odontoschisma prostratum, and Plagiochila asplenioides occur on completely decorticated logs in wet, open sites; Blepharostoma trichophyllum on decaying branches in the swales of the south plateau; and Tetraphis pellucida on decaying tree stumps in mesic to wet sites throughout the gulf. Brachythecium oxcladon, Brotherella recurvans, Hypnum fertile, and Herzogiella

striatella colonize mesic logs that have not yet undergone complete decortication.

A number of species collected on lignicolous substrates are also common terricolous species. Kurzia sylvatica, Leucobryum albidum, L. glaucum, Aulacomnium heterostichum, and Climacium americanum inhabit mesic to moist humic soils as well as decaying logs. Cephalozia bicuspidata, C. macrostachya, and Aulacomnium palustre all occur on wet, sandy soil in the swales of the south plateau. Bryoandersonia illecebra inhabits both lignicolous and sandy soil substrates throughout the Savage Gulf area.

Five lignicolous bryophyte species are also considered to be saxicolous species. These are: Trichocolea tomentella, Calypogeja muelleriana, C. sullivantii, Thamnobryum alleghaniense, and Thuidium pygmaeum. Hattaway (1973) also noted the occurrence of the latter two species on lignicolous substrates in three limestone sinks in Sevier County, Tennessee.

Several additional bryophytes collected on lignicolous substrates are also common corticolous species. Dicranum fuscescens, Entodon macropodus, E. seductrix, Forsstroemia trichomitria, Frullania squarrosa, Lophocolea heterophylla, Platygyrium repens, and Odontoschisma prostratum all occur on upright trees, but were collected on fallen trees as well. Identification of the phorophyte species was impossible due

to partial decortation, and hence, these species are reported as lignicolous bryophytes. It should be noted however, that all of these species are restricted to either corticolous or lignicolous substrates within Savage Gulf, and are common on these two substrates.

Saxicolous Bryophytes

One hundred ten saxicolous bryophytes have been identified from Savage Gulf, 62 of which are restricted to this substrate.

Thirty-four species were found to occur on calcareous rocks with 23 species restricted to this substrate. Seventy-eight species were collected from siliceous rocks with 39 bryophytes unique on this substrate. A complete inventory of saxicolous bryophytes from the Savage Gulf area can be found in Table 5 (Appendix).

A number of species collected on saxicolous substrates show no preference for calcareous or siliceous rocks. All of these species also occur on other substrates throughout the study area: Thuidium delicatulum and T. recognitum on wet rocks along streambeds and beneath waterfall areas; Anomodon attenuatus, A. rostratus, and Thamnobryum alleghaniense on larger, mesic boulders along streams; Pallavicinia lyellii grows in the wet crevices of either calcareous or siliceous rock walls.

Bryophytes restricted to siliceous substrates can be divided into three major groups with respect to the type of rock (small rocks, boulders, or vertical rock surfaces) and moisture. For example, Sematophyllum adnatum, S. demissum, and S. marylandicum are restricted to small, loose rocks and boulders of streambeds; Andreaea rothii, Porella pinnata, and Isopterygiopsis muellerianum to larger, shaded, mesic boulders; and Asterella tenella, Philonotis fontana, and Bartramia pomiformis are restricted to the small crevices and ledges of wet vertical rock surfaces such as those beneath waterfalls or in the spray zone of waterfall areas.

Bryophytes restricted to calcareous habitats can likewise be segregated, with Fissidens bryoides and F. viridulus occurring on small, loose calcareous rocks in Savage creekbed and lower portions of tributaries of Savage Creek; Grimmia apocarpa and Orthotrichum strangulatum on larger, dry, exposed boulders and bluffs; Bryhnia graminicolor and Jubula pennsylvanica on wet, often submerged calcareous boulders in waterfall areas; and Rhabdoweisia crispata and Eucladium verticillatum in the wet, shaded crevices of exposed calcareous rock in the lower portions of the north ravine area.

Several species collected on saxicolous substrates also appear to be common on corticolous or lignicolous substrates. These species include Ctenidium molluscum, and Thamnobryum

alleghaniense on lignicolous substrates on the north-facing slopes of the central gorge area; Taxiphyllum deplanatum on on the bark of Cephalanthus occidentalis in the north swamp site; and Bazzania trilobata, Campylium chrysophyllum, and Mnium cuspidatum, all of which occur on both lignicolous and corticolous substrates in the gulf as well as on sandstone rocks in moist areas of the north-facing slope.

A number of bryophyte species collected in this study occur on both saxicolous and terricolous substrates. Dumortiera hirsuta, Mnium hornum, Rhodobryum roseum, and Eurhynchium hians generally occur in shallow soils on either moist to wet sandstone boulders and vertical rock surfaces or on shaded, moist, sandy soils of the central gorge area.

Three species collected on saxicolous substrates are generally considered atypical for that substrate. Clasmatodon parvulus, Homalotheciella subcapillata, and Schwetschkeopsis fabronia are mosses that are regarded as corticolous epiphytes and are rarely found on any substrate other than bark. However, all three species occur on shaded, mesic calcareous boulders in the central gorge area ws well as on corticolous substrates. Clasmatodon parvulus was also collected once on the north plateau. Hattaway (1973) also reports Clasmatodon and Homalotheciella subcapillata as occurring in limestone or dolomite in Sevier County, Tennessee.

Terricolous Bryophytes

Terricolous species are those bryophytes which inhabit soil or accumulated soil over boulders. This group may be further divided into two major soil types: sandy soils comprised of sandy to sandy loam soils, and humic soils, those containing a large amount of organic material such as those derived from decaying wood.

A total of 58 terricolous species have been identified for the Savage Gulf area. Of this total, 39 species were collected on sandy soils, with 11 species restricted to this substrate. Fourteen species of bryophytes were collected on humic soils with only three restricted species. A summary of the terricolous bryophytes of Savage Gulf with associated soil types is presented in Table 6 (Appendix).

Five bryophytes appear to be restricted to the wet, sandy soils of the plateau region. Sphagnum palustre, S. imbricatum, and S. recurvum are found in the north plateau swamp site as well as in the sandy wet soils of the south plateau swales. Nardia lescurii and Teleranea nematodes are leafy liverworts of wet sandy depressions, the former restricted to the swales of the south plateau while the latter is unique to the north swamp site.

Several terricolous bryophytes appear to be restricted to the wet, sandy soils along the creekbed. These species include Marsupella emarginata and M. sphacelata, two uncommon

leafy liverworts. In addition, a number of terricolous bryophytes also inhabit saxicolous substrates. These species are described with the saxicolous bryophytes.

Terricolous bryophytes also commonly collected on lignicolous or corticolous substrates include: Cephalozia catenulata, C. connivens, Jungermannia crenuliformis, and J. gracillima on corticolous substrates within the gorge area; and Cephalozia bicuspidata and Trichocolea tomentella on decaying branches and twigs. Trichocolea tomentella is of interest as it is usually associated with a lignicolous rather than terricolous substrate, and is reported by Hattaway (1973) as being restricted to this substrate in limestone sinkholes in Sevier County, Tennessee. However, it was collected more frequently on sandy soils at the sides of Savage Creek than on any lignicolous substrate.

Three terricolous species of bryophytes appear to be restricted to humic soils in the Savage Gulf area. These species include Diphyscium foliosum in mesic sites of the plateau forests, and Plagiothecium laetum and Pohlia nutans on moist, humic soil pockets in the central gorge area.

A number of species common to humic soil substrates, but not restricted to this substrate include Climacium americanum and Dicranum scoparium, two very common woodland species often found on lignicolous substrates; and Thuidium delicatulum, Leucobryum glaucum, L. albidum, and Mnium ciliare, four species showing a wide range of hibitats and

frequently collected on lignicolous and saxicolous substrates as well as on humic soils.

CHAPTER VIII

BRYOFLORISTIC COMPARISONS WITHIN SAVAGE GULF

The bryophyte flora of Savage Gulf is rich and diverse, with a number of species restricted to particular habitats within the gorge or on the adjacent plateau. The majority of species recorded are of rather wide distribution in the eastern United States, however, several species show affinities with northern, Coastal Plain, or even tropical floras. These geographical affinities will be discussed in a later section of this paper.

A total of 182 species representing 107 genera of 74 families have been identified for the Savage Gulf area. A number of these species are new reports for Grundy County and represent range extensions onto the Cumberland Plateau. Five species are new reports for Tennessee characteristic of physiographic regions and provinces outside Tennessee. A single species is of extreme interest in that it represents a first report for the North American continent.

In order to present accurate descriptions of the bryophyte vegetation and to determine the similarities and or differences between the floras of the different sites in the Savage Gulf area, several bryo-floristic comparisons have been made. Kulczynski's (1937) community coefficient values have been calculated for each set of sites being

compared. A community coefficient can be used to indicate similarities of species or the degree of resemblance of two communities (Phillips, 1959). Additional literature and a more complete explanation of this method of community comparison can be found in Jaccard (1912) and Oosting (1956). The results of these comparisons are presented below.

Plateau vs. Gorge Bryophytes

A major comparison was made between the bryoflora of the central gorge area and that of the adjacent plateau. Included in the plateau site are the north and south rim forests, the north swamp, and the south plateau swale sites. The gorge flora takes into account all sites located within the gorge itself.

A total of 92 bryophyte species representing 51 percent of the total Savage Gulf bryophyte flora are found on the plateau. One hundred sixty-two bryophytes, representing 89 percent of the total flora are represented in the gorge area. Seventy-six species are common to both sites, resulting in a Kulczynski community coefficient of 59.6 percent.

A number of species are restricted to each site. Among these are two leafy liverworts, Teleranea nematodes and Cephalozia macrostachya which are restricted to the north plateau, and several species of both liverworts and mosses restricted to particular sites within the central gorge area. Despite the rather high degree of resemblance between these

two sites, the number of species that are restricted to each indicates that the gorge and plateau floras are quite distinct.

North Rim Forest vs. South Rim Forest

The north rim forest (Site 2) contains 51 species of bryophytes while the south rim forest (Site 5) contains 52 species. A total of 35 species are held in common by these two sites, resulting in a community coefficient of 68 percent. This value indicates a relatively high degree of similarity between the two sites. Five species collected in the south rim forest appear to be restricted to that site in the Savage Gulf area. These species include: Campylium radicale, Herzogiella striatella, Ulota hutchinsiae, Nardia lescurii, and Lejuenea minutiloba. None of the north rim forest bryophytes appear to be restricted to that site, occurring elsewhere in the Savage Gulf area.

North-Facing Slope vs. South-Facing Slope

The comparison of these two sites excludes both the north cove and Still Point sites found in this area. The north-facing slope contains 90 bryophyte species representing 49 percent of the total Savage Gulf bryoflora. The south-facing slope contains only 54 species, or 29 percent of the total flora contained in the study area. The coefficient of similarity between the two sites is 47 percent, indicating

relatively distinct floristic elements. Two species, Bryhnia novae-angliae and Hypnum curvifolium, are restricted to the north-facing slope. Four species, Dicranella heteromalla, Grimmia pilifera, Metzgeria leptoneura, and Radula voluta are restricted to the south-facing slope.

North Side of Savage Gulf vs. South Side

This comparison of the different floristic elements of the Savage Gulf area includes all north- and south-facing slope sites and north and south plateau sites, but excludes the Savage Falls and Savage Creekbed sites. The latter two sites are excluded since a majority of species found in these areas are common to both sides of the gulf, and their inclusion would not significantly alter the floristic composition of either side.

A total of 135 taxa representing 74 percent of the total bryophyte flora of Savage Gulf are found on the north side of the Gulf. One hundred thirty-one species are found on the south side of the gulf, which accounts for 72 percent of the total flora. Sixty-nine species are common to both sides, resulting in a community coefficient value of 51 percent, thus indicating relatively distinct communities for the two sides of the Gulf.

The drastic differences in species composition between the plateau and gorge sites are readily explained by several

climatic and edaphic factors that are responsible for the availability of habitats suitable for bryophytes.

The gorge provides a shaded, cool, moist, protected habitat, including a mature vascular plant community with a distinct canopy, understory, and herbaceous layer. The plateau floral community is more disturbed, drier and more open than that of the gorge. The regenerating forest of the plateau offers little canopy cover. In addition, the gorge contains extensive amounts of colluvial material in the form of massive siliceous and occasionally calcareous boulders, and a number of exposed bedrock and waterfall areas, thus providing additional habitats not available on the plateau.

The differences in species numbers between the north- and south-facing slopes is due primarily to moisture, light intensity, and temperature differences between these two sites. The north-facing slope is much cooler, more moist, and more heavily forested, and receives only a moderate amount of direct sunlight. These are all conditions conducive to the growth of a lush bryophyte flora. The south-facing slope is much drier, less forested, and is exposed to direct, bright sunlight for a much longer period each day.

The relatively high degree of similarity between the north rim and south rim forest sites is expected, as these two sites share a number of environmental and physical characteristics.

The North Ravine

Special mention should be made concerning the north ravine site located on the south-facing slope of the central gorge area. This large ravine is oriented nearly perpendicular to the gorge itself, and is, in fact, a mini-gorge in its own right. A more thorough description of this area has been made earlier in this text. The north ravine is unique in the Gulf as it contains a total of 92 species of bryophytes, one-half of the total Savage Gulf bryophyte flora, and 3/4 of the total gorge bryoflora. Although this in itself is not striking, the ravine also contains 20 species which are restricted to this site, far more than any other area in Savage Gulf. These restricted species include several rare or uncommon mosses of Tennessee and several species new for the Cumberland Plateau province in Tennessee. The richness of the bryophyte flora of the north ravine site can be explained by its very protected, cool, moist environment. The number of species in this site with northern affinities may also indicate that this site may have served as a refugium for bryophyte species from the north.

CHAPTER IX

RANGE EXTENSIONS AND UNUSUAL COLLECTIONS FROM SAVAGE GULF

A number of interesting and unusual discoveries have been made throughout the course of this investigation. Several bryophyte species collected in the study area represent significant extensions of known bryophyte distributions. Of special interest is a first North American report of Radula voluta and first Tennessee reports of Teleranea nematodes, Cephalozia macrostachya, Plagiochila dubia, Lejuenea minutiloba, and Nardia lescurii. Other important extensions of bryophyte distributions onto the Cumberland Plateau have been noted for a number of species including Homalia trichomanoides var. gracilis and Heterocladium macounii, two very rare species in East Tennessee. Less striking, but still interesting extensions are also noted for several species.

Radula voluta is a saxicolous leafy liverwort, restricted to the north exposure of moist calcareous boulders on the lower south-facing slope of the central gorge area in Savage Gulf. It is reported here for the first time on the North American continent. The plants were matted, and mixed with Brachythecium oxycladon, Bryoandersonia illecebra, and Anomodon attenuatus. Previously its distribution was known

only from the British Isles from Wales to Ayrshire, and West Ireland as reported by DuMortier (1874), Pearson (1902), Cook (1907), and MacVicar (1926). The report of this species in Tennessee significantly extends this range and further investigations of the bryophytes of the Cumberland Plateau region may even further enlarge the distribution of this rare species.

Teleranea nematodes is an austral to tropical leafy liverwort, largely restricted in the U.S. to the extreme outer Coastal Plain. Occasionally its distribution extends into the outer Piedmont (in North Carolina) and upper Coastal Plain in northern Mississippi (Schuster, 1966). It is frequently found along slow moving coastal streams or deeply shaded springs cutting through sand, and often creeping over Spagnum. This species is restricted to the north plateau swamp in Savage Gulf, where it grows intermixed with and creeping over Sphagnum subsecundum. It was associated with several liverwort species including Odontoschisma prostratum, Cephalozia catenulata, and C. macrostachya.

Cephalozia macrostachya is another leafy liverwort species restricted to the north plateau swamp in Savage Gulf. This species is also a Coastal Plain disjunct usually found in the southeastern U.S. in swampy or sphagnous evergreen woods, or on wet, acid soil of ditches. It was collected in the north swamp with Teleranea nematodes, Cephalozia catenulata, and Sphagnum subsecundum.

Plagiochila dubia represents a third species new to Tennessee, found in two sites within the Savage Gulf area. It is a leafy liverwort of neotropical affinity, restricted in the U.S. to the extreme outer Coastal Plain areas from Louisiana to central Florida. It is common on shaded, relatively dry limestone ledges and is reported as often growing in association with members of the leafy hepatic family Lejeneaceae. This species was collected in both the north cove site of the south-facing slope of the central gorge area and on the southwestern slope of the gorge off the Old McMinnville Stage Road. In the cove, the plants were growing on a deeply shaded calcareous boulder; on the south side of the gorge, the plants were collected on a drier, more exposed boulder in association with Lejuenea minutiloba.

Lejuenea minutiloba is an interesting hepatic also new to Tennessee. The plants occur epiphyllously on Plagiochila dubia only on the southwestern slope of the Savage Gulf area. This species is of tropical distribution reported in the West Indies, Bermuda, and Florida.

Nardia lescurii is a final liverwort species new to Tennessee. This species is considered to be an Appalachian endemic and "gorge" species by Schuster (1966). However, he reports two disjunct locations, one in the piedmont of North Carolina and another in the Coastal Plain region of southeast

Virginia. The plants were collected in, and appear to be restricted to the swales of the south plateau. The swale area shows a number of similarities with Coastal Plain habitats and plant associations. This leafy liverwort was found on wet, sandy soil in association with Calypogeja sullivantii, Kurzia sylvatica, Cephalozia bicuspidata, and Odontoschisma prostratum.

In addition to the bryophyte records mentioned above, collections of 34 species from the Savage Gulf area represent first reports for the Cumberland Plateau physiographic province in Tennessee. Twenty-eight of these species are considered by the author to be rare in Tennessee, where that species is known from fewer than five counties in the state. It should be noted, however, that some species present in only one or two counties may be locally abundant within those counties. One example of this is Dicranum fuscescens, a very common species in the mountains of East Tennessee. It is, however, only reported from Blount and Sevier Counties, and is therefore considered to be rare.

Of special interest are two species new to the plateau area. Homalia trichomanoides var. gracilis is an unusually rare species known from only two other collections in Tennessee, one in Anderson County, and one site in a limestone sink in northwest Sevier county. A northern species with a reported distribution of New Jersey, New York, and

Vermont (Grout, 1928), this species is typically found hanging beneath limestone ledges. In Savage Gulf, the plants were found in a moist, limestone crevice in the north ravine site.

A second species of interest is Heterocladium macounii, also restricted to shaded, limestone cliffs in the north ravine site. This species is also extremely rare in Tennessee and is only known from Blount and Monroe Counties. Grout (1928) reported the distribution of this species as Vancouver Island and Washington. Additional collections are known from Southeast Alaska and British Columbia. The report of this species on the Cumberland Plateau significantly extends its range in Tennessee.

Seventeen species of rare or uncommon bryophytes new to the Cumberland Plateau physiographic province represent disjunct populations from the southern Appalachian mountains. Several of these bryophytes are known from only one station in Tennessee prior to this report. These species include: Cephalozia bicuspidata, Campylium polygamum, C. radicale, Pylaisiella selwynii, and Riccardia palmata. These species appear to have affinities with a more boreal flora and they are largely limited to mountainous regions in the Southeast.

Six species of bryophytes new to the Cumberland Plateau have more frequent, but scattered distributions throughout Tennessee. These species include: Plagiochila undata,

Frullania brittoniae, Asterella tenella, Lophocolea heterophylla, Haplocladium microphyllum and Bryhnia novae-angliae.

Seven additional collections represent important extensions of ranges for bryophytes known for the Cumberland Plateau. Two of these collections represent disjuncts from the mountainous region of East Tennessee: Plagiochila sullivantii, and Kurzia sylvatica. One other species is particularly noteworthy. Calypogeja sullivantii is a leafy liverwort known from only three stations in Tennessee. Sharp (1939) reported this species as C. arguta in Morgan, Blount, and Grainger counties. It is frequently found in the Southern Appalachians in shaded, mesic soil banks, or on rocks. It is restricted in Savage Gulf to shaded, steep rock faces of the north-facing slope.

Other Cumberland Plateau extensions of less striking importance include Cephalozia connivens, Ditrichum lineare, Fontinalis dalecarlica, Dichelyma capillaceum, and Hyophila involuta.

An unusually large number of county records and additions to the Cumberland Plateau bryophyte flora have been recorded by this study. However, both Grundy County and the Cumberland Plateau region itself have been little investigated bryologically; most studies of this nature centering instead, on the bryophytes of the Southern Appalachian Mountain region of East Tennessee.

CHAPTER X

GEOGRAPHICAL AFFINITIES OF SAVAGE GULF BRYOPHYTES

A number of bryophyte species found in the southeastern United States show geographical affinities with floristic elements of northern, coastal plain, or even tropical regions. Several investigators have studied these bryogeographical affinities, including Sharp (1939), Schornherst (1943). Schofield and Crum (1972), and Pursell and Reese (1970). In addition, works by Breil (1970), Schuster (1966) and others provide valuable distributional information for a great number of species.

Phytogeographic distribution of bryophytes collected in Savage Gulf range from cosmopolitan species to endemic species with rather narrow distributional ranges.

Cosmopolitan species collected in Savage Gulf include Amblystegium serpens, Hedwigia ciliata, Grimma apocarpa, Leptodictyum riparium, Mnium rostratum, Polytrichum commune, Spagnum subsecundum, and Thuidium delicatulum. All of these species are common throughout Savage Gulf.

Several species represent widespread distributions in Eastern North America, but are not so widely distributed elsewhere in the world. These species include: Kurzia

sylvatica, Anomodon attenuatus, A. rostratus, A. minor, and Calypogeja muellerianum.

A large number of bryophytes of Savage Gulf have affinities with northern (boreal to arctic) floras. These species can be segregated into two groups: those species which are of widespread distribution in Tennessee, and those species with greatest frequency of occurrence in the higher elevations of the southern Appalachian Mountains. Species falling into the former group include: Hypnum fertile, Brachythecium acuminatum, Eucladium verticillatum, Philonotis fontana, Bartramia pomiformis, Isopterygiopsis muellerianum, Thuidium pygmaeum, Cephalozia bicuspidata subsp. ambigua, Marsupella emarginata, and M. sphacelata among others.

Bryophytes of northern affinity which are largely limited to the higher elevations of the Tennessee mountains include: Pellia epiphylla, Blepharostoma trichophyllum, Dicranum fulvum, D. fuscescens, Dicranodontium denudatum, Sciaromium lescurii, Hygrohypnum eugyrium, Plagiothecium laetum, Hylocomium brevirostre, Brotherella recurvans, and Pogonatum pensilvanicum. A majority of these species are restricted in Savage Gulf to the north-facing slope of the central gorge area or to the north ravine site on the south-facing slope.

In addition to northern elements, a number of bryophytes collected in Savage Gulf show affinities with tropical or

subtropical regions. These species are: Pallavicinia lyellii, Radula mollis, Leucolejuenea unciloba, and Thuidium virginianum. Several other species of tropical affinities have a greatest frequency of occurrence in coastal plain are areas of the southeastern United States. Representatives of this element are: Hookeria acutifolia, Mnium hornum, Entodon Syrrhopodon texanus, Sematophyllum adnatum, Odontoschisma prostratum, Teleranea nematodes, Plagiochila dubia, and Lejuenea minutiloba. Other coastal plain elements include: Homalotheciella subcapillata, Cephalozia connivens, Entodon seductrix, Thelia hirtella, and Leucodon julaceous. However, these species also occur frequently elsewhere in the North American continent.

One last species is of particular interest. Nardia lescurii, reported here as new to Tennessee has previously been considered a Southern Appalachian endemic (Schuster, 1966). The occurrence of this species on the Cumberland Plateau significantly extends the known distribution of this rare liverwort.

CHAPTER XI

CONCLUSIONS

Savage Gulf contains a number of northern, coastal plain, and even tropical elements within a relatively small geographical area. The discovery of one continental, and five state records, along with significant additions to the known bryoflora of the Cumberland Plateau emphasizes the need for bryological investigations in this area. Based on the results of this study, it is probable that the Cumberland Plateau region is as worthy of intense bryological investigation as the Southern Appalachian Mountain region, and it is hoped that further bryological investigations will be conducted in this unusual physiographic province.

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APPENDIX

Table 1. Systematic List of Bryophytes of Savage Gulf with Associated Collecting Sites

Systematic Arrangement of Taxa	Collection Site									
	1	2	3	3a	4	4a	5	6	7	8
HEPATICAE:										
PSEUDOLEPICOLEACEAE										
Blepharostoma trichophyllum (L.) Dum.								X		
TRICHOCOLEACEAE										
Trichocolea tomentella (Ehrh.) Dum.									X	
LEPIDOZIACEAE										
Kurzia sylvatica (Evans) Grolle					X			X		X
Teleranea nematodes (Gott. ex Aust.) M. A. Howe	X									
Bazzania trilobata (L.) S. Gray		X	X	X	X	X	X		X	X
CALYPOGEJACEAE										
Calypogeja muelleriana (Schiffn.) K. Muell.					X	X		X		
C. muelleriana (Schiffn.) K. Muell. subsp. *blomquistii* Schust.				X						
C. sullivantii Aust.		X			X		X			
C. trichomanis (L.) Corda					X	X				
CEPHALOZIACEAE										
Cephalozia bicuspidata (L.) Dum.	X							X		
C. bicuspidata (L.) Dum. subsp. *ambigua* (Mass.) Schust.				X						
C. catenulata (Hub.) Lindb.		X								
C. connivens (Dicks.) Lindg.	X							X		X
C. macrostachya Kall.	X									
Nowellia curvifolia (Dicks.) Mitt.	X	X	X	X	X	X	X	X	X	X

Table 1 (continued)

Systematic Arrangement of Taxa	Collection Site									
	1	2	3	3a	4	4a	5	6	7	8
ADELANTHACEAE										
Odontoschisma denudatum (Nees ex Mart.) Dum.	X	X	X		X	X		X	X	X
O. prostratum (Sw.) Trev.	X				X					
LOPHOCOLEACEAE										
Lophocolea heterophylla (Schrad.) Dum.	X									
PLAGIOCHILACEAE										
Plagiochila asplenioides (L.) Dum.				X		X	X			
P. dubia Lindenb, et Gott.				X			X			
subsp. *echinata* (Schust.) Inoue				X						
P. sullivantii Gott. ex Evans				X	X	X				
P. undata Sull.				X						
JUNGERMANNIACEAE										
Nardia lescurii (Aust.) Underw.									X	
Jungermannia crenuliformis Aust.										X
J. gracillima Sm.								X		
GYMNOMITRIACEAE										
Marsupella emarginata (Ehrh.) Dum.									X	X
M. sphacelata (Gieseke) Dum.									X	X
SCAPANIACEAE										
Diplophyllum apiculatum (Evans) Steph.		X	X		X	X	X		X	X
Scapania nemerosa (L.) Dum.		X	X		X	X	X		X	X
S. undulata (L.) Dum.									X	X

Table 1 (continued)

Systematic Arrangement of Taxa	Collection Site 1	2	3	3a	4	4a	5	6	7	8
RADULACEAE										
Radula mollis Lindenb. et Gott.		X	X						X	
R. voluta Tayl.			X							
PORELLACEAE										
Porella pinnata L.	X			X		X			X	X
P. platyphylloidea (Schwein.) Lindb.				X	X	X				
JUBULACEAE										
Frullania brittoniae Evans			X	X	X					
F. eboracensis Gott. ex Steph.	X		X		X					
F. squarrosa (Reinw. et al.) Dum.	X									
F. tamarisci (L.) Dum. subsp. *asagrayana* (Mont.) Hatt.	X	X	X	X	X					X
Jubula pennsylvanica (Steph.) Evans				X						
LEJEUNEACEAE										
Leucolejuenea clypeata (Schwein.) Evans	X		X		X	X	X	X		X
L. unciloba (Lindenb.) Evans			X							X
Lejuenea cladogyna Evans				X						
L. laetivirens Nees et Mont.					X		X			
L. minutiloba Evans							Z			
Cololejuenea ornata Evans			X							
PALLAVICINIACEAE										
Pallavicinia lyellii (Hook.) Carruth.					X	X				X
PELLIACEAE										
Pellia epiphylla (L.) Corda					X		X			X

Table 1 (continued)

Systematic Arrangement of Taxa	Collection Site 1	2	3	3a	4	4a	5	6	7	8
METZGERIACEAE										
Metzgeria furcata (L.) Dum.						X				
M. leptoneura Spruce					X					
ANEURACEAE										
Riccardia palmata (Hedw.) Carruth.				X						
AYTONIACEAE										
Asterella tenella (L.) P.-Beauv.				X						
CONOCEPHALACEAE										
Conocephalum conicum (L.) Lindb.					X	X			X	X
MARCHANTIACEAE										
Dumortiera hirsuta (Sw.) Nees				X	X	X			X	X
MUSCI:										
SHAGNACEAE										
Sphagnum compactum DC. ex Lam. & DC.		X		X	X			X		X
S. imbricatum Hornsch. ex Russ.	X			X						
S. palustre L.	X	X						X		
S. recurvum P.-Beauv.	X				X					
S. subsecundum Nees ex Sturm	X			X	X			X		X
ANDREAEACEAE										
Andreaea rothii Web. & Mohr.					X		X			
FISSIDENTACEAE										
Fissidens bryoides Hedw.				X					X	X
F. cristatus Wils. ex Mitt.	X			X			X		X	

Table 1 (continued)

Systematic Arrangement of Taxa	Collection Site									
	1	2	3	3a	4	4a	5	6	7	8
F. grandifrons Brid.		X					X			
F. osmundoides Hedw.			X		X		X			X
F. subbasilaris Hedw.					X	X			X	
F. taxifolius Hedw.		X	X	X	X	X	X		X	X
F. viridulus (Sw.) Wahlenb.					X				X	X
DITRICHACEAE										
Ditrichum lineare (Sw.) Lindb.				X						
DICRANACEAE										
Dicranella heteromalla (Hedw.) Schimp.					X					
Dicranodontium denudatum (Brid.) Britt. ex Williams					X	X				
Rhabdoweisia crispata (With.) Lindb.				X						
Dicranum flagellare Hedw.	X		X							
D. fulvum Hook.			X	X	X	X			X	X
D. fuscescens Turn.		X		X						
D. montanum Hedw.				X	X					X
D. scoparium Hedw.		X	X	X	X	X	X		X	X
LEUCOBRYACEAE										
Leucobryum albidum (Brid. ex P.-Beauv.) Lindb.		X	X	X	X	X	X	X		X
L. glaucum (Hedw.) Angstr. ex Fr.		X	X	X	X	X	X			X
CALYMPERACEAE										
Syrrhopodon texanus Sull.				X			X			
POTTIACEAE										
Gymnostomum aeruginosum Sm.							X		X	
Eucladium verticillatum (Brid.) B.S.G.				X						

Table 1 (continued)

Systematic Arrangement of Taxa	Collection Site 1	2	3	3a	4	4a	5	6	7	8
Tortella humilis (Hedw.) Jenn.				X					X	
Hyophila involuta (Hook.) Jaeg. & Sauerb.					X					
Didymodon rigidulus Hedw.						X				
GRIMMIACEAE										
Grimmia alpicola Hedw. var. rivularis (Brid.) Wahlenb.		X	X		X		X		X	X
G. apocarpa Hedw.		X	X				X			X
G. pilifera P.-Beauv.					X					
Rhacomitrium aciculare (Hedw.) Brid.				X					X	
BRYACEAE										
Pohlia nutans (Hedw.) Lindb.				X						
Bryum pseudotriquetrum (Hedw.) Gaertn., Meyer, & Scherb. var. bimum (Sherb.) Lilj.				X		X			X	X
Rhodobryum roseum (Hedw.) Limpr.				X	X	X			X	
MNIACEAE										
Mnium ciliare (C. Muell.) Schimp.		X	X	X		X		X		
M. cuspidatum Hedw.		X					X			
M. hornum Hedw.		X	X	X	X	X	X		X	X
M. punctatum Hedw.					X	X				
M. rostratum Schrad.				X					X	
AULACOMNIACEAE										
Aulacomnium heterostichum (Hedw.) B.S.G.			X	X	X	X	X			
A. palustre (Hedw.) Schwaegr.	X			X		X		X		

Table 1 (continued)

Systematic Arrangement of Taxa	Collection Site 1	2	3	3a	4	4a	5	6	7	8
BARTRAMIACEAE										
Bartramia pomiformis Hedw.					X	X				X
Philonotis fontana (Hedw.) Brid.				X		X				
ORTHOTRICHACEAE										
Orthotrichum ohioense Sull. & Lesq. ex Aust.		X		X			X			
O. strangulatum P.-Beauv.							X		X	
Ulota crispa (Hedw.) Brid.		X		X			X			
U. hutchinsiae (Sm.) Hamm.							X			
Drummondia prorepens (Hedw.) Britt	X	X				X		X		
FONTINALACEAE										
Fontinalis dalecarlica Schimp. ex B.S.G.								X		
Dichelyma capillaceum (With.) Myr.		X						X		
CLIMACEACEAE										
Climacium americanum Brid.		X			X	X	X			
HEDWIGIACEAE										
Hedwigia ciliata (Hedw.) P.-Beauv.		X	X	X	X	X	X		X	X
CRYPHAEACEAE										
Forsstroemia trichomitria (Hedw.) Lindb.	X	X	X	X	X	X	X			
LEUCODONTACEAE										
Leucodon julaceous (Hedw.) Sull.	X	X	X	X	X	X	X	X	X	X
NECKERACEAE										
Homalia trichomanoides (Hedw.) B.S.G. (form)				X						
Thamnobryum alleghaniense (C. Muell.) Nieuwl			X	X	X	X			X	

Table 1 (continued)

Systematic Arrangement of Taxa	Collection Site 1	2	3	3a	4	4a	5	6	7	8
HOOKERIACEAE										
Hookeria acutifolia Hook. & Grev.				X	X	X				
THELIACEAE										
Thelia hirtella (Hedw.) Sull.	X		X				X			
FAVRONIACEAE										
Schwetschkeopsis fabronia (Schwaegr.) Broth.			X	X	X					
Clasmatodon parvulus (Hampe) Hook. & Wils. ex. Sull.		X		X	X					
THUIDIACEAE										
Heterocladium macounii Best				X						
Haplohymenium triste (Ces. ex DeNot.) Kindb.	X	X	X	X	X	X	X	X		
Anomodon attenuatus (Hedw.) Hueb.	X	X	X	X	X	X	X	X	X	X
A. minor (Hedw.) Fuernr.			X	X		X				
A. rostratus (Hedw.) Schimp.	X	X	X	X	X	X	X			
Haplocladium microphyllum (Hedw.) Broth.			X				X			
H. virginianum (Brid.) Broth					X	X				
Thuidium delicatulum (Hedw.) B.S.G.	X	X	X	X	X	X	X	X	X	X
T. minutulum (hedw.) B.S.G.			X	X						
T. pygmaeum B.S.G.				X						
T. recognitum (Hedw.) Lindb.					X	X			X	
AMBLYSTEGIACEAE										
Campylium chrysophyllum (Brid.) J. Lange	X	X	X		X					
C. polygamum (B.S.G.) C. Jens.					X	X				
C. radicale (P.-Beauv.) Grout					X					

Table 1 (continued)

Systematic Arrangement of Taxa	Collection Site 1	2	3	3a	4	4a	5	6	7	8
Leptodictyum riparium (Hedw.) Warnst.				X						
Leptodictyum trichopodium (Schultz) Warnst.				X						
Hygroamblystegium tenax (Hedw.) Jenn.			X	X		X			X	
Sciaromium lescurii (Sull.) Broth.				X		X				
Amblystegium serpens (Hedw.) B.S.G.	X		X							
Platydictya jungermannioides (Brid.) Crum				X						
Hygrohypnum eugyrium (B.S.G.) Loeske				X		X				
BRACHYTHECIACEAE										
Homalotheciella subcapillata (Hedw.) Broth.			X			X				
Brachythecium acuminatum (Hedw.) Aust.			X							
B. oxycladon (Brid.) Jaeg. & Sauerb.		X		X	X	X				
B. plumosum (Hedw.) B.S.G.					X					
B. salebrosum (Web. & Mohr.) B.S.G.					X					
Bryhnia graminicolor (Brid.) Grout				X	X					
B. novae-angliae (Sull. ex Lesq. ex Sull.) Grout						X				
Bryoandersonia illecebra (Hedw.) Robins.		X	X	X	X	X	X			
Rhynchostegium serrulatum (Hedw.) Jaeg. & Sauerb.						X	X			
Eurhynchium hians (Hedw.) Sande Lac					X					
E. riparioides (Hedw.) Rich.				X	X	X				
ENTODONTACEAE										
Entodon macropodus (Hedw.) C. Muell.		X	X	X	X	X	X			
E. seductrix (Hedw.) C. Muell.		X			X		X	X	X	
PLAGIOTHECIACEAE										
Plagiothecium cavifolium (Brid.) Iwats.					X	X				
P. denticulatum (Hedw.) B.S.G.		X	X	X	X	X	X	X	X	
P. laetum B.S.G.				X						

Table 1 (continued)

Systematic Arrangement of Taxa	Collection Site 1	2	3	3a	4	4a	5	6	7	8
SEMATOPHYLLACEAE										
Brotherella recurvans (Michx.) Fleisch.				X	X	X	X			
B. tenuirostris (Bruch & Schimp. ex Sull.) Fleisch.				X						
Sematophyllum adnatum (Michx.) Britt.				X	X					
S. demissum (Wils.) Mitt.		X			X				X	X
S. marylandicum (C. Muell.) Britt.		X		X	X	X			X	X
HYPNACEAE										
Platygyrium repens (Brid.) B.S.G.	X	X	X	X	X	X	X			X
Pylaisiella polyantha (Hedw.) Grout			X		X					
P. selwynii (Kindb.) Crum, Steere & Anderson					X					
Homomallium adnatum (Hedw.) Broth.			X				X			
Hypnum curvifolium Hedw.					X					X
H. fertile Sendtn.										X
H. imponens Hedw.		X	X	X	X	X	X		X	X
Isopterygiopsis muelleriana (Schimp.)				X						
Isopterygium distichaceum (Mitt.) Jaeg. & Sauerb.										
I. elegans (Brid.) Lindb.				X	X					
I. tenerum (Sw.) Mitt.	X				X					
Taxiphyllum deplanatum (Bruch. & Schimp. ex Sull.) Fleisch	X			X	X			X	X	X
Herzogiella striatella (Brid.) Iwats.								X		
Ctenidium molluscum (Hedw.) Mitt.				X		X				
HYLOCOMIACEAE										
Hylocomium brevirostre (Brid.) B.S.G.					X	X			X	

Table 1 (continued)

Systematic Arrangement of Taxa	Collection Site									
	1	2	3	3a	4	4a	5	6	7	8
BUXBAUMIACEAE										
Diphyscium foliosum (Hedw.) Mohr.		X		X			X			
TETRAPHIDACEAE										
Tetraphis pellucida Hedw.	X	X	X	X		X	X	X	X	
POLYTRICHACEAE										
Atrichum angustatum (Brid.) B.S.G.		X	X	X	X	X			X	
A. oerstidianum (C. Muell.) Mitt.				X						X
A. undulatum (Hedw.) P.-Beauv.				X	X	X				
Pongonatum pensilvanicum (Hedw.) P.-Beauv.		X	X				X			
Polytrichum commune Hedw.	X	X	X				X	X		
P. ohioense Ren. & Card.		X			X		X			

Table 2. Bryophytes with Associated Substrate Groups

Taxon	Substrate Type			
	Cort	Lign	Sax	Terr
Amblystegium serpens	X			
Andreaea rothii		X		
Anomodon attenuatus	X	X	X	X
A. minor	X			
A. rostratus	X	X	X	X
Atrichum angustatum			X	X
A. oerstidianum			X	X
A. undulatum			X	X
Asterella tenella			X	
Aulacomnium heterostichum	X	X		X
A. palustre	X	X	X	X
Bartramia pomiformis			X	
Bazzania trilobata	X	X	X	
Blepharostoma trichophyllum		X		
Brachythecium acuminatum			X	
B. oxycladon	X	X	X	X
B. plumosum			X	
B. salebrosum				
Brotherella recurvans		X		
B. tenuirostris	X			
Bryhnia graminicolor			X	
B. novae-angliae			X	
Bryoandersonia illecebra				X
Bryum pseudotriquetrum var. bimum			X	
Calypogeja muelleriana		X		X
C. muelleriana subsp. blomquistii			X	
C. sullivantii		X	X	X
C. trichomanis	X			
Campylium chrysophyllum	X	X	X	
C. polygamum			X	
C. radicale	X			
Cephalozia biscuspidata		X		X
C. biscuspidata subsp. ambigua			X	
C. catenulata	X			X
C. connivens	X			X
C. macrostachya		X		
Clasmatodon parvulus	X		X	
Climacium americanum		X		X
Cololejuenea ornata			X	
Conocephalum conicum			X	X
Ctenidium molluscum		X	X	
Dichelyma capillaceum		X		
Dicranella heteromalla			X	

Table 2 (continued)

Taxon	Substrate Type			
	Cort	Lign	Sax	Terr
Dicranodontium denudatum			X	
Dicranum flagellare	X			
D. fulvum			X	
D. fuscescens	X	X		
D. montanum	X			
D. scoparium		X		X
Didymodon rigidulus			X	
Diphyscium foliosum				X
Diplophyllum apiculatum			X	
Ditrichum lineare			X	X
Drummondia prorepens	X			
Dumortiera hirsuta			X	X
Entodon macropodus	X	X		
E. seductrix	X	X		
Eucladium verticillatum			X	
Eurhynchium hians				X
E. riparioides			X	X
Fissidens bryoides			X	
F. cristatus	X	X	X	X
F. grandifrons			X	
F. osmundoides	X		X	
F. subbasilaris			X	X
F. taxifolius			X	X
F. viridulus			X	
Forsstroemia trichomitria	X	X		
Fontinalis dalecarlica			X	
Frullania brittoniae	X			
F. eboracensis	X	X		
F. squarrosa	X	X		
F. tamarsci subsp. asagrayana	X			
Grimmia alpicola var. rivularis			X	
G. apocarpa			X	
G. pilifera			X	
Gymnostomum aeruginosum			X	
Haplocladium microphyllum	X			
H. virginianum	X			
Haplohymenium triste	X			
Hedwigia ciliata			X	
Herzogiella striatella		X		
Homalia trichomanoides var. gravilis			X	
Homalotheciella subcapillata	X		X	
Homomallium adnatum			X	
Hookeria acutifolia			X	
Hygroamblystegium tenax			X	

Table 2 (continued)

Taxon	Substrate Type			
	Cort	Lign	Sax	Terr
Hygrohypnum eugyrium			X	
Hylocomium brevirostre			X	
Hyophila involuta			X	
Hypnum curvifolium		X		
H. fertile		X		
H. imponens	X	X		
Isopterygiopsis muelleriana			X	
Isopterygium distichaceum			X	
I. elegans		X	X	
I. tenerum	X		X	
Jubula pennsylvanica			X	
Jungermannia crenuliformis	X			X
J. gracillima	X			X
Kurzia sylvatica	X			X
Lejuenea cladogyna			X	
L. laetivirens			X	
L. minutiloba			X	
Leptodictyum riparium			X	
L. trichopodium	X			
Leucobryum albidum		X	X	X
L. glaudum		X	X	X
Leucodon julaceous	X	X		
Leucolejuenea clypeata	X		X	
L. unciloba	X		X	
Lophocolea heterophylla	X	X		
Marsupella emarginata				X
M. sphacelata				X
Metzgeria furcata			X	
M. leptoneura			X	
Mnium ciliare	X		X	X
M. cuspidatum	X	X	X	
M. hornum			X	X
M. punctatum				X
M. rostratum			X	X
Nardia lescurii				X
Odontoschisma denudatum		X		X
O. prostratum	X	X		
Orthotrichum ohioense	X			
O. strangulatum			X	
Pallavicinia lyellii		X	X	
Pellia epiphyllum				X
Philonotis fontana			X	
Plagiochila asplenioides		X		
P. dubia			X	
P. eurphyllon subsp. echinata			X	

Table 2 (continued)

Taxon	Substrate Type			
	Cort	Lign	Sax	Terr
P. sullivantii			X	
P. undata			X	
Plagiothecium cavifolium			X	X
P. denticulatum			X	X
P. laetum				X
Platydictya jungermannoides			X	
Platygerium repens	X	X		
Pogonatum pensilvanicum				X
Pohlia nutans				X
Polytrichum commune				X
P. ohioense				X
Pylaisiella polyantha	X			
P. selwynii	X			
Radula mollis			X	
R. voluta			X	
Rhabdoweisia crispata			X	
Rhacomitrium aciculare			X	
Rhodobryum roseum			X	X
Riccardia palmata			X	
Rhynchostegium serrulatum				X
Scanpania nemerosa			X	
S. undulata			X	
Schwetschkeopsis fabronia	X		X	
Sciaromium lescurii				X
Sematophyllum adnatum			X	
S. demissum			X	
S. marylandicum			X	
Sphagnum compactum			X	X
S. imbricatum				X
S. palustre				X
S. recurvum				X
S. subsecundum			X	X
Syrrhopodon texanus				X
Taxiphyllum deplanatum	X		X	
Telleranea nematodes				X
Tetraphis pellucida		X		
Thamnobryum alleghaniense		X	X	
Thelia hirtella	X			
Thuidium delicatulum	X	X	X	X
T. minutulum			X	
T. pygmaeum		X		
T. recognitum		X	X	X
Tortella humilis			X	
Trichocolea tomentella		X		X
Ulota crispa	X			
U. hutchinsiae			X	

Table 3. Corticolous Bryophytes with Associated Phorophyte Species

Corticolous Bryophytes	Associated Phorophyte Species*											
	Ar	Cs	Ct	Fg	Is	Jn	Ls	Lt	Ns	Qs	Tc	Th
Anomodon attenuatus	X		X					X	X			
A. minor								X				
A. rostratus	X		X				X		X			
Aulacomnium heterostichum										X		
A. palustre	X						X		X			
Bazzania trilobata											X	
Brachythecium oxycladon								X		X		
Calypogeja trichomanis								X				
Campylium chrysophyllum								X		X		
C. radicale										X		
Cephalozia catenulata		X										
C. connivens		X			X		X					
Clasmatodon parvulus										X		
Dicranum flagellare	X	X										
D. fuscescens										X		
D. montanum								X				
Drummondia prorepens	X								X			
Entodon macropodus										X		X
E. seductrix							X	X				
Fissidens cristatus	X											
Fissidens osmundoides								X		X		
Forsstroemia trichomitria			X					X		X		X
Frullania brittoniae				X								
F. eborascensis								X		X		
F. squarrosa									X			
F. tamarsci subsp. asagrayana	A						X		X	X		
Haplohymenium triste	X							X	X	X		
Homalotheciella subcapillata						X						
Hypnum imponens											X	
Leucodon julaceous	X						X	X	X	X		

Table 3 (continued)

Corticolous Bryophytes	Associated Phorophyte Species											
	Ar	Cs	Ct	Fg	Is	Jn	Ls	Lt	Ns	Qs	Tc	Th
Leucolejuenea clypeata	X								X	X		
L. unciloba				X								
Lophocolea heterophylla	X											
Mnium ciliare								X		X		
M. cuspidatum	X											
Odontoschisma prostratum	X				X							
Platygyrium repens	X									X		X
Porella platyphylloidea	X			X						X		
Pylaisiella polyantha										X		X
P. selwynii										X		X
Schwetschkeopsis fabronia								X				
Taxiphyllum deplanatum		X										
Thelia hirtella								X		X		
Thuidium delicatulum	X						X		X			
Ulota crispa								X		X		

*Ar=Acer rubrum (Red maple)
Cs=Cephalanthus occidentalis
Ct=Carya tomentosa (Mockernut hickory)
Fg=Fagus grandifolis (American beech)
Is=Ilex sp.
Jn=Juglans nigra (Black walnut)
Ls=Liquidambar styraciflua (Sweetgum)
Lt=Liriodendron tulipifera (Tulip poplar)
Ns=Nyssa sylvatica (Black gum)
Qs=Quercus sp. (Oak)
Tc=Tsuga canadensis (Hemlock)
Th=Tilia heterophylla (Basswood)

Table 4. Lignicolous Bryophytes
Of Savage Gulf

Ablystegium serpens
Aulacomnium heterostichum
A. palustre
Bazzania trilobata
Blepharostoma trichophyllum
Brachythecium oxycladon
Brotherella recurvans
Calypogeja muelleriana
C. sullivantii
Campylium chrysophyllum
Cephalozia bicuspidata
C. catenulata
C. connivens
C. macrostachya
Climacium americanum
Ctenidium molluscum
Dichelyma capillaceum
Dicranum scoparium
Entodon macropodus
E. seductrix
Fissidens cristatus
F. osmundoides
Herzogiella striatella
Hypnum curvifolium
H. fertile
H. imponens
Isopterygium elegans
I. tenerum
Jungermannia gracillima
Kurzia sylavatica
Leucobryum albidum
L. glaucum
Lophocolea heterophylla
Mnium ciliare
M. cuspidatum
Nowellia curvifolia
Odontoschisma denudatum
Plagiochila asplenioides
Plagiothecium cavifolium
P. denticulatum
Taxiphyllum deplanatum
Tetraphis pellucida
Thuidium delicatulum
T. minutulum
T. pygmaeum
T. recognitum

Table 5. Saxicolous Bryophytes with Associated Rock Types

Saxicolous Bryophytes	Type of Rock	
	Calcareous	Siliceous
Andreaea rothii		X
Anomodon attenuatus	X	X
A. rostratus	X	X
Asterella tenella		X
A. angustatum		X
Atrichum oerstidianum		X
A. undulatum		X
Aulacomnium palustre		X
Bartramia pomiformis		X
Bazzania trilobata		X
Brachythecium acuminatum		X
B. oxycladon		X
B. salebrosum		X
Bryhnia graminicolor	X	
B. novae-angliae		X
Bryum pseudotriquetrum var. bimum		X
Calypogeja muelleriana subsp. blomquistii		X
C. sullivantii		X
Campylium chrysophyllum		X
C. polygamum		X
Cephalozia bicuspidata subsp. ambigua		X
Clasmatodon parvulus	X	
Cololejuenea ornata		X
Conocephalum conicum		X
Ctenidium molluscum		X
Dicranella heteromalla		X
Dicranodontium denudatum		X
Dicranum fulvum		X
Didymodon rigidulus	X	
Diplophyllum apiculatum		X
Ditrichum lineare		X
Dumortiera hirsuta		X
Eucladium verticillatum	X	
Eurhynchium riparioides		X
Fissidens bryoides	X	
F. cristatus	X	
F. grandifrons	X	
F. osmundoides	X	
F. subbasilaris	X	
F. taxifolius	X	
F. viridulus	X	
Fontinalis dalecarlica		X
Frullania sp.	X	

Table 5 (continued)

Saxicolous Bryophytes	Type of Rock	
	Calcareous	Siliceous
Grimmia alpicola var. rivularis		X
G. apocarpa	X	
G. pilifera		X
Gymnostomum aeruginosum	X	
Hedwigia ciliata		X
Heterocladium macounii	X	
Homalia trichomanoides (form)	X	
Homalotheciella subcapillata	X	
Homomallium adnatum	X	
Hookeria acutifolia		X
Hygroamblystegium tenax		X
Hygrohypnum eugyrium		X
Hylocomium brevirostre		X
Hyophila involuta	X	
Isopterygiopsis muelleriana		X
Isopterygium distichaceum		X
I. elegans		X
I. tenerum		X
Jubula pennsylvanica	X	
Lejuenea cladogyna	X	
L. laetivirens	X	
L. minutiloba	X	X
Leptodictyum riparium		X
Leucobryum albidum		X
L. glaucum		X
Leucolejuenea clypeata		X
L. unciloba		X
Metzgeria furcata	X	
M. leptoneura	X	
Mnium ciliare		X
M. cuspidatum		X
Mnium hornum		X
M. rostratum		X
Orthotrichum strangulatum	X	
Pallavicinia lyellii		X
Philonotis fontana		X
Plagiochila dubia		X
P. eurphyllon subsp. echinata		X
P. sullivantii		X
P. undata		X
Plagiothecium cavifolium		X
P. denticulatum		X
Platydictya jungermannioides		X
Porella pinnata		X

Table 5 (continued)

Saxicolous Bryophytes	Type of Rock	
	Calcareous	Siliceous
Radula mollis		X
R. voluta	X	
Rhabdoweisia crispata	X	
Rhacomitrium aciculare		X
Rhodobryum roseum		X
Riccardia palmata		X
Scapania nemerosa		X
S. undulata		X
Schwetschkeopsis fabronia	X	
Sciaromium lescurii		X
Sematophyllum adnatum		X
S. demissum		X
S. marylandicum		X
Sphagnum compactum		X
S. palustre		X
S. subsecundum		X
Taxiphyllum deplanatum	X	
Thamnobryum alleghaniense		X
Thuidium delicatulum	X	X
T. minutulum		X
T. pygmaeum		X
T. recognitum		X
Tortella humilis	X	
Ulota hutchinsiae		X

Table 6. Terricolous Bryophytes with Associated Soil Types

Terricolous Bryophytes	Soil Type	
	Sandy	Humic
Anomodon attenuatus		X
A. rostratus		X
Atrichum angustatum	X	
A. oerstidianum	X	
A. undulatum	X	
Aulacomnium heterostichum		X
A. palustre	X	
Bazzania trilobata		X
Blepharostoma trichophyllum	X	
Bracythecium oxycladon		X
Bryoandersonia illecebra	X	
Calypogeja muelleriana	X	
C. sullivantii	X	
Cephalozia bicuspidata	X	
C. catenulata	X	
C. connivens	X	
C. macrostachya	X	
Climacium americanum		X
Conocephalum conicum	X	
Diphyscium foliosum		X
Ditrichum lineare	X	
Dumortiera hirsuta	X	
Eurhynchium hians	X	
E. riparioides	X	
Fissidens cristatus	X	
F. subbasilaris	S	
F. taxifolius	X	
Jungermannia gracillima	X	
J. crenuliformis	X	
Kurzia sylvatica	X	
Leucobryum albidum		X
L. glaucum		X
Mnium ciliare	X	
M. cuspidatum	X	
M. hornum	X	
M. punctatum	X	
M. rostratum	X	
Nardia lescurii	X	
Odontoschisma denudatum	X	
Pallavicinia lyellii	X	
Pellia epiphylla	X	
Plagiothecium cavifolium		X
P. denticulatum		X

Table 6 (continued)

Terricolous Bryophytes	Soil Type	
	Sandy	Humic
P. laetum		X
Pogonatum pensilvanicum	X	
Pohlia nutans		X
Polytrichum commune	X	
P. ohioense	X	
Rhodobryum roseum	X	
Rhynchostegium serrulatum	X	
Scapania nemerosa	X	
Sphagnum compactum	X	
P. imbricatum	X	
P. palustre	X	
P. recurvum	X	
S. subsecundum	X	
Syrrhopodon texanus		X
Teleranea nematodes	X	
Thuidium delicatulum		X
Trichocolea tomentella	X	

VITA

Yvonne Mary Mescall was born to Thomas J. and Lucy M. Mescall in Buffalo, New York, on August 17, 1954. She received both primary and secondary education in Buffalo, graduating from South Park High School in June 1972. In September 1972, she entered the State University of New York College at Buffalo, and received a Bachelor of Arts degree in Biology from that institution in May 1976. During the summer of 1976, she attended the University of Michigan Biological Station in Pellston, Michigan.

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