THE MOSSES OF TERRA NOVA NATIONAL PARK, EASTERN NEWFOUNDLAND; A BRYOFLORISTIC ANALYSIS AND INTERPRETATION

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ABSTRACT

The known moss flora of Terra Nova National Park, eastern Newfoundland, comprises 210 species. Eighty-two percent of the moss species occurring in Terra Nova are widespread or widespread-sporadic in Newfoundland. Other Newfoundland distributional elements present in the Terra Nova moss flora are the northwestern, southern, southeastern, and disjunct elements, but four of the mosses occurring in Terra Nova appear to belong to a previously unrecognized northeastern element of the Newfoundland flora.

The majority (70.9%) of Terra Nova's mosses are of boreal affinity and are widely distributed in the North American coniferous forest belt. An additional 10.5 percent of the Terra Nova mosses are cosmopolitan while 9.5 percent are temperate and 4.8 percent are arctic-montane species. The remaining 4.3 percent of the mosses are of montane affinity, and disjunct between eastern and western North America. In Terra Nova, temperate species at their northern limit are concentrated in balsam fir stands, while arctic-montane species are restricted to exposed cliffs, scree slopes, and coastal exposures. Montane species are largely confined to exposed or freshwater habitats. Inability to tolerate high summer temperatures limits the distributions of both arctic-montane and montane species.

In Terra Nova, species of differing phytogeographic affinities co-occur on cliffs and scree slopes. The microhabitat relationships of five selected species from such habitats were evaluated by Discriminant Functions Analysis and Multiple Regression Analysis. The five mosses have distinct and different microhabitats on cliffs and scree slopes in Terra Nova, and abundance of all but one is associated with variation in at least one microhabitat variable. Micro-distribution of *Grimmia torquata*, an arctic-montane species at its southern limit, appears to be determined by sensitivity to high summer temperatures. Both southern mosses at their northern limit (*Aulacomnium androgynum, Isothecium myosuroides*) appear to be limited by water availability and, possibly, by low winter temperatures. The two species whose distributions extend both north and south of the study area (*Encalypta procera, Eurhynchium pulchellum*) show no clear relationship with microclimate.

Dispersal factors have played a significant role in the development of the Terra Nova moss flora. Compared to the most likely colonizing source (*i.e.* the rest of the island of Newfoundland), species with small diaspores have colonized the study area to a proportionately much greater extent than have species with large diaspores. Hierarchical log-linear analysis indicates that this is so for all affinity groups present in Terra Nova. The apparent dispersal effects emphasize the comparatively recent glaciation of the area, and may also have been enhanced by anthropogenic influences. The restriction of some species to specific habitats, or to narrowly defined microhabitats, appears to strengthen selection for easily dispersed taxa.

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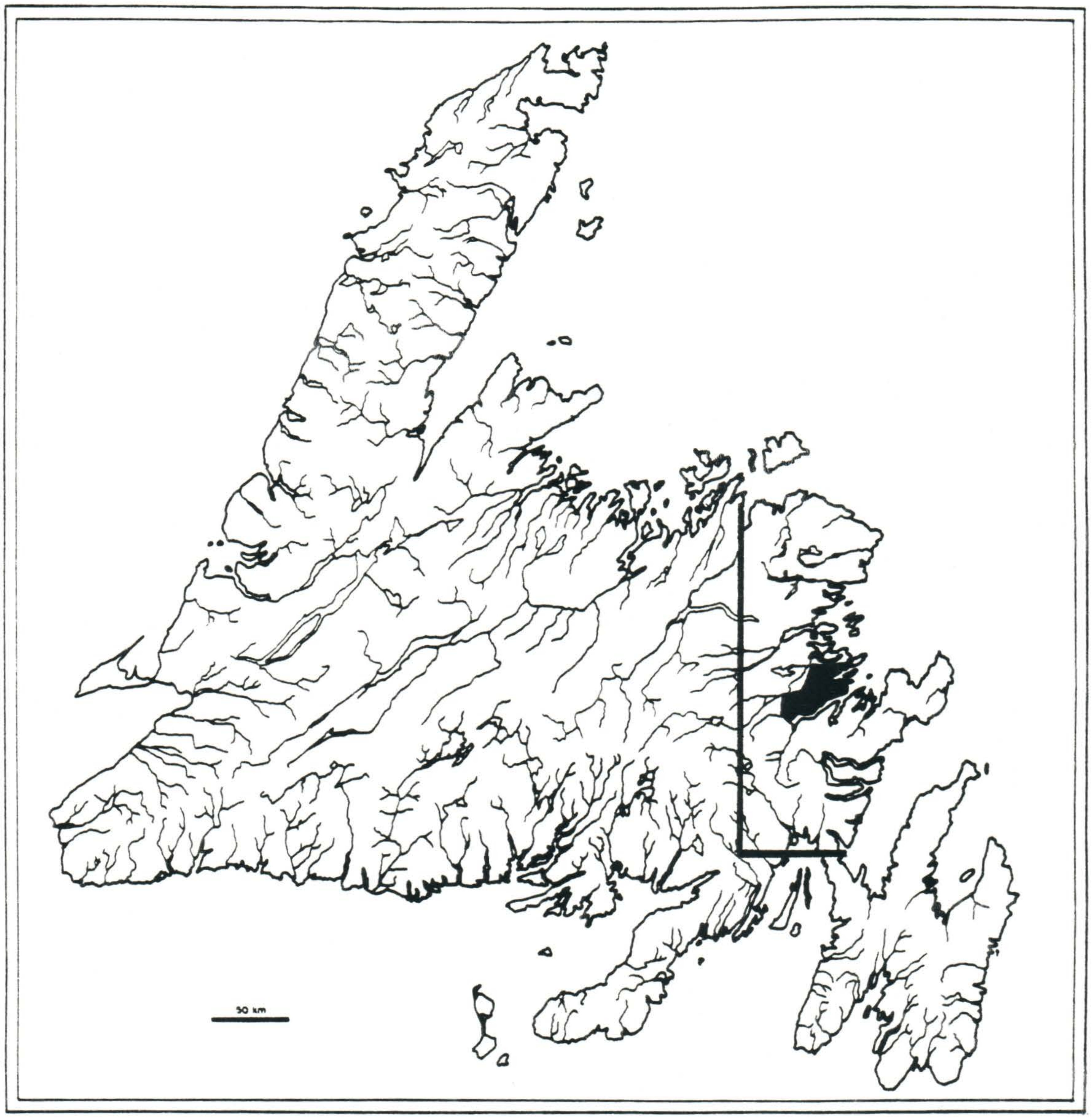
Chapter 1

Introduction

1.1. Research Objectives

The moss flora of the island of Newfoundland and its phytogeographical affinities are reasonably well known (Brassard, 1983a,b; Tuomikoski *et al.,* 1973); however, the east coast of the island (Figure 1-1) has received relatively little attention, and the position and importance of that region relative to the bryogeography of the island has not yet been assessed. Terra Nova National Park (Figure 1-1), located just north of the Bonavista Peninsula, is climatically, geologically and vegetationally representative of the east coast of Newfoundland. The aim of the present study was to evaluate the bryogeographical position of Terra Nova (and by inference, the east coast) within Newfoundland, and furthermore, to understand the composition of the moss flora in terms of local environmental and historical factors. The specific objectives of the present research were:

1. To evaluate the Terra Nova moss flora in terms of the Newfoundland distributions and bryogeographic affinities of its component species.
2. To evaluate the habitat relationships of the various affinity groups present in the area.
3. To evaluate the effects of dispersal ability, and interactions between dispersal ability and species affinity, on the occurrence of moss species in Terra Nova.


50 km

4. To evaluate and compare occurrence and performance of selected species of differing phytogeographical affinity, which co-occur in cliff and scree-slope habitats in Terra Nova, in relation to microhabitat.

1.2. Description of the Study Area

The Biophysical Classification for Terra Nova National Park (Gauthier *et al.*, 1977) includes an extensive biological and physical description of the area. Unless otherwise indicated, the following description is derived from this and is supplemented by personal observations.

1.2.1. Geology, Geomorphology and Physiography

Bedrock Geology

Terra Nova National Park belongs to the Appalachian Mountain System and is underlain almost entirely by Precambrian rocks. Three groups are represented in the park; the Love Cove Group, the Connecting Point Group, and the Musgravetown Group.

The western portions of the park are underlain by rocks of the Love Cove and Musgravetown Groups. The Love Cove Group comprises regionally metamorphosed lavas, clastic sediments, and pyroclastic rocks. These all show pronounced schistosity and include chlorite schists, chlorite sericites, schists, rhyolites and andesites. Rocks of the Musgravetown Group are mostly coarse-grained conglomerates, greywackes, and acidic to very slightly basic lavas.

All the eastern portions of the park are underlain by the Connecting Point Group of rocks. Slates are most abundantly represented in this group, but fine to coarse greywackes are also frequent and a few conglomerates and cherty quartzites also occur.

A few granite batholiths occur at the northernmost extension of the park. These are the only exposed granites in the study area.

Physiography and Geomorphology

Overall relief in Terra Nova National Park is moderate. Along the coast relief is moderately high and the 80 m contour is rarely more than 1 km from shore. A few headlands dominate the coast, with vertical faces rising to 175 m. Inland portions of the park are characterized by low rolling hills with a few summits rising to 200-278 m.

Relief within the park has a general NE-SW trend controlled by monoclinal structure within the bedrock as well as by linear glacial features. This is the trend of Newman and Clode Sounds as well as most of the freshwater bodies in the area. Superimposed on this is a secondary NNE-SSW trend controlled by the major fault lines and contacts between geological formations. This trend is important in determining the stronger relief features of the park, and most of the higher summits are arranged in parallel bands along this orientation.

As a result of coincidence of the NE slope of the terrain and orientation of structural trends within the park, drainage basins generally flow northeastward. Pre-existing drainage patterns were greatly disrupted by the last glaciation, and most of the area is boggy and very poorly drained. With high precipitation, low evaporation and moderate relief, the drainage networks are incapable of rapid removal of excess water. In the few areas of high relief, where drainage is more active, extensive patches of bog between hills hamper effective water removal (Jenness, 1963).

The study area has been extensively glaciated. Glacier ice advanced in a SW-NE direction along local topographic lineaments, further defining these. With postglacial warming, the ice front retreated landward, depositing ground and hummocky moraines. A short interval of cool climate, resulting in the deposition of extensive moraine in the western portions of the park, was followed by a second warming, with rapid ice retreat ca. 8,000-9,000 years B.P. This resulted in the laying down of extensive glacio-fluvial complexes in the present valleys of the major river systems. Glacial, fluvo-glacial, organic and weathering deposits make up the bulk of the park's surficial materials.

On the basis of physiography and geology, the park may be divided into three broad areas. The western portion is dominated by elongated drumlinoid hills, while the eastern portion is characterized by sedimentary rock formations devoid of glacial deposits. A somewhat intermediate central portion has very shallow tills covering the bedrock.

1.2.2. Climate

Terra Nova has a maritime climate characterized by short cool summers and moderate winters. In Banfield's (1981) classification, the study area falls within the East Coast and Hinterlands Climatic Zone characterized as follows:

> "Less wet than South and Southeast coasts and hinterlands (1100-1500 mm per year). Occasional heavy precipitation with north-easterly or northerly airflow, especially in the Gander area. Winters cold with 50-70 % of precipitation falling as snow; snow cover normally continuous at least through February. Cool, late springs with sea ice persisting until mid-May. Summers generally warm and fairly sunny."

Temperature and precipitation data have been recorded at Park

Headquarters since 1962 (Table 1-1). July is the warmest month with a mean daily temperature of 16.4° C. This is one of the warmest mean July temperatures for the entire island. February, the coldest month, has a mean daily temperature of -5.8°C, colder than southern and south-eastern portions of the island but considerably warmer than western and interior regions.

Mean annual precipitation is 1131 mm, with 75% falling as rain. Table 1-1 indicates a fall maximum, with 113 mm falling in November - the wettest month. The driest month is July with a mean total of 71 mm. The study area is drier than areas to the south and southeast (1500-2000 mm total annually) and somewhat wetter than northern and western areas (850-950 mm annually) (Banfield, 1981).

An interesting feature of the park's precipitation climate is the high incidence of freezing precipitation (glitter storms). With an annual average of 178 hours of freezing rain or drizzle, Terra Nova and the immediate vicinity has the highest incidence of this kind of precipitation on the island (Banfield, 1981).

The study area has one of the longest vegetative seasons in Newfoundland (degree days above 5° C (Banfield, 1981)) with an annual average of 1200 degree days above this base. Only a few lowland central and western areas of the island, with ca. 1300 degree days above the 5°C base, have longer vegetative seasons.

Within the park, aspect, elevation, exposure, slope and various other factors affect temperature and precipitation patterns. Precipitation increases with

Table 1-1: Mean monthly Temperature and Precipitation at Park Headquarters (Newman Sound) during the period 1962-1982. (Data from Canadian Climate Normals)

Month	Temperature °C	Precipitation mm
January	-5.3	103.4
February	-5.8	105.4
March	-2.7	92.1
April	1.7	81.8
May	6.7	83.0
June	11.9	75.4
July	16.4	71.5
August	16.0	105.1
September	12.2	88.8
October	6.7	105.4
November	2.7	112.8
December	-3.0	106.1

elevation, and thus the central line of hills receives more snow and rain than any other area. In warmer months thermal inversions may cause frost in the hollows while belts of warm air remain on the hillsides. Southern slopes are generally warmer than those with a northern aspect. Areas next to the coast are most affected by sea temperatures and thus have milder winters and cooler summers than higher and more inland regions. Coastal lowland areas often receive much of their winter precipitation as rain.

1.2.3. Vegetation

Terra Nova lies within the northern portion of the Avalon Section of Rowe's (1972) forest regions. The forests in this section have been decimated by fires and cultural practices and the present vegetation is characterized by patchy, though dense, young coniferous forest interrupted by barrens and peatlands.

Forest Vegetation

Forests cover 72% of the total land area of Terra Nova National Park. *Picea mariana* (Miller) Britton, Sterns *et* Poggenberg is the dominant tree species and occurs on nearly all forest sites. Although best growth is attained in well drained soils, it is an important constituent in many stands, including burn sites, hilltops, upper slopes, and wet sites.

Abies balsamea (L.) Miller is a major component of stands on middle and lower slopes in the study area, and favors moist, deep, well drained soils with minimal seepage. This species is especially common on coastal slopes. *Larix laricina* (DuRoi) K. Koch frequently occurs in mixture with *P. mariana* on lower wet seepage slopes or in linear open stands along brooks. *Pinus strobus* L. is scattered through the park, but never occurs in abundance.

Betula papyrifera Marshall is common throughout the park, usually mixed with the conifers but occasionally forming pure stands. *Populus tremuloides* Michaux is a minor component of the forest vegetation, and occurs scattered on seepage slopes. Only two pure stands occur within the park. The following tree species occur within the park but form only a minor part of the forest vegetation: *Acer rubrum* L., *Alnus rugosa* (DuRoi) Sprengel, *Sorbus decora* (Sargent) Schneider and *Viburnum cassinoides* L. *Acer rubrum* and *Alnus rugosa* may form small thickets in favourable localities.

Forest Succession Trends. Disturbance in the form of logging, fire and insect infestation has had a profound effect on forest vegetation in Terra Nova National Park. Because of its greater resistance to disturbance, black spruce has come to dominate sites normally occupied by balsam fir. The latter has also sufferred from intensive moose browsing, which reduces regeneration. Virtually all the black spruce-moss forests in the study area originated after fires. Balsam fir stands now occur only on the richest sites, and have replaced senescent black spruce stands. These are among the oldest continuously forested stands in the study area.

Repeated disturbance of forests on poor or unstable soils usually leads to the development of *Kalmia* barrens. These are very stable and reforestation is very slow.

Most of the birch forests in the park occur on rich sites that have been burned several times in rapid succession. If left unburned for sufficient time, black spruce stands develop on these, followed by balsam fir. If burning is continued *Kalmia* barrens usually develop.

Wetland Vegetation

Bogs, fens, marshes, and swamps comprise 21% of the park's total area. Two kinds of bogs occur in Terra Nova - ombrogenous raised bogs and mesotrophic bogs which occur on the flanks of the raised bogs or in closed depressions in bedrock crevices. The ground layer of both is dominated by *Sphagnum* species, but *Cladonia* spp., *Scirpus cespitosus* L., *Kalmia polifolia* Wangenheim, *K. angustifolia* L., *Rubus chamaemorus* L., and *Vaccinium* spp. are also common. Species diversity is generally higher in the mesotrophic bogs, and *Carex* spp., *Aster* spp., and *Solidago* spp. are important components of the vegetation.

Seepage fens occur on slopes in the western part of the park and draw fens occur within isolated basins throughout the area. Both fen types have a well developed dwarf shrub layer dominated by *Betula michauxii* Spach. The ground layer of the seepage fens is dominated by various species of *Carex* and *Juncus* but other herbaceous species are also very common. Floristic diversity of the draw fens is higher, and in addition to the species found in the seepage fens, *Aster* spp., *Solidago* spp. and species of the families Orchidaceae and Liliaceae are also common.

Freshwater marshes occur on fluvial outwash, deltas, stream levees, or in conjunction with beaver dams. *Carex* spp. dominate the vegetation in these but *Iris versicolor* L., *Eriophorum angustifolium* Honckeny, *Thalictrum polygamum* Muhlenberg, *Typha latifolia* L., and *Sphagnum* spp. are also common. *Alnus rugosa*, *Betula michauxii*, *Larix laricina*, and *Picea mariana* occur as isolated individuals.

Estuarine marshes are very rare, occurring on sand flats at the mouth of Big Brook, Southwest Brook, and Wings Pond Brook. *Carex salina* Wahlenberg, *Plantago juncoides* Lamark, *Potentilla anserina* L., *Schoenoplectus pungens* (Ehrhart) Durand *et* Jackson, and *Solidago sempervirens* L. are dominant in this vegetation type.

Swamps occur on seepage slopes in local depressions in hilly terrain, and on alluvial soils along stream margins. *Alnus rugosa* dominates the shrub layer in this vegetation unit. Lower layers are dominated by *Spiraea latifolia* (Aiton) Borkhausen, *Myrica gale* L., *Kalmia angustifolia*, *Solidago rugosa* Miller, *Calamagrostis canadensis* (Michaux) Nuttall, *Thalictrum polygamum*, *Carex* spp. and *Juncus* spp. In areas of greater relief *Lycopodium* spp. and ferns dominate the lower layers.

Barrens

Rock barrens, *Kalmia* barrens, and transitional barrens cover 7% of the total land area in the park. Rock barrens occur on the highest summits and in exposed coastal localities where tree growth is limited. Soils are very poorly developed and vegetation is dominated by lichens. *Racomitrium lanuginosum* (Hedw.) Brid. and *Empetrum eamesii* Fernald *et* Wiegand are also important constituents of the vegetation.

Kalmia barrens occur after repeated burning of spruce or fir forests on nutrient poor soils. These are dominated by *Kalmia angustifolia*, *Ledum groenlandicum* Retzius, *Rhododendron canadense* (L.) Torrey and *Vaccinium angustifolium* Aiton.

Transitional barrens represent active successional stages from burn to coniferous forests. *Kalmia angustifolia* plays a much less important role in these than in the preceding, and the vegetation is dominated by *Alnus crispa* (Aiton) Pursh, *Salix* spp., *Vaccinium vitis-idea* L., *V. angustifolium* and various lichen species.

1.2.4. Habitat Classification

The habitat classification proposed by Gauthier *et al.* (1977) includes nine forest types, five wetland types, two barren types, and one each of freshwater, coastal cliff, inland cliff, scree slope, and anthropogenic habitats. These habitats are defined almost entirely on the basis of vascular plant vegetation, and the classification does not include bryophyte vegetation data.

Because of the relatively subordinate position of bryophytes in most ecosystems, moss habitats are determined in very large part by the nature of the vascular vegetation, and Horikawa and Ando (1952) have commented on the "profound interrelationship" between the nature of the higher plant flora of a community and its bryophyte flora. Studies comparing areal distribution of bryophyte associations and vascular plant associations show close agreement between the two (Cain and Sharp, 1938: LaRoi and Stringer, 1976; Nakamura, 1984; Van Reenen and Gradstein, 1983, 1984). Patterns of succession in bryophyte associations also appear to coincide with successional patterns in the higher plant vegetation (Nakamura, 1984). Thus, for the purposes of this study, the habitat classification described above is deemed appropriate.

1.3. The Phytogeographical Position of Newfoundland and Factors Influencing the Island's Floristic Composition

Newfoundland, the easternmost extension of the Boreal biome in North America, has a flora comprised primarily of species characteristic of the coniferous forests of the continent (Brassard, 1983a; Damman, 1965, 1976: Rouleau, 1978; Tuomikoski *et al.*, 1973). Other phytogeographic elements occur within the island's flora, the most important including species of arctic, arctic-montane, montane, or temperate (including coastal plain) affinity. Many of these non-boreal species reach, or nearly reach, their southern or northern limit of eastern North American distribution in Newfoundland; others are known in eastern North America only from Newfoundland. Their distributions within the island are of particular interest - especially the ways in which these relate to historical or environmental factors. A large number of the arctic-montane, arctic, and montane plants, though quite restricted in eastern North America, are widespread in Newfoundland, especially along the coast, while others show varying degrees of restriction (Belland, 1984; Brassard, 1983a, 1984; Damman, 1965, 1976).

Damman (1965, 1976) analyzed the Newfoundland distributions of arctic and temperate vascular plants (as well as some *Sphagnum* species) and related these to ecological factors. Length and warmth of the vegetative season were considered especially important in allowing southern species to persist in Newfoundland, and three groups of species were recognized on the basis of increasing demand for high summer temperatures and consequent restriction of insular range to warmer localities. Another major group, comprised of species most common in southeastern Newfoundland, but occurring in bogs in the Long Range Mountains and the interior, are "apparently sensitive to low winter temperatures, adapted to cool summers, and possibly require high humidity" (Damman, 1965). This group is composed entirely of oceanic species. Arctic species were divided into analogous groups, but here the absence of lethally high summer temperatures and absence of competition on some sites were the major factors implicated in determining insular distribution patterns. Edaphic factors, especially the distribution of calcareous or serpentine soils, were important for both groups.

No similar analysis has been done for temperate and arctic elements in the moss flora of Newfoundland, but within-island patterns of species distribution have been described, and, in a very general way, related to the affinities and broad ecological requirements of species (Brassard, 1983a; Tuomikoski *et al.*, 1973). Species widespread in the island are mostly of boreal affinity or associated with disturbed habitats. A southern element comprises mostly oceanic to sub-oceanic temperate species, while a small group concentrated in rich forest sites of the southwest is predominantly distributed in temperate forests of the continent. The truly northern element in the moss flora (Hedderson, 1984) comprises for the most part high-arctic calciphiles, while the northwestern element includes numerous arctic-montane species, but also a large number of widespread boreal and temperate species limited to calcareous substrata.

History has been implicated as a major factor governing the composition of the flora of Newfoundland since Fernald's (1918a,b, 1925, 1933) controversial proposition that unglaciated surfaces in and near Newfoundland served as glacial refugia for a number of vascular plant species. The theory failed to gain wide acceptance, but, in the last decade or so, has been used to explain the very localized occurrences of numerous bryophytes with centers of North American distribution in the western part of the continent and disjunct to Newfoundland and/or the general Gulf of St. Lawrence area (Belland, 1984; Brassard, 1983a, 1984). Glaciation (or lack thereof) is by no means the only historical event to have affected the flora of Newfoundland. A long history of European settlement has allowed the establishment of many anthropogenic species. These tend to be concentrated around areas of heaviest settlement (Cooper, 1981). Human disturbance has undoubtedly affected the local floras of many regions of the island (Meades, 1983; Rowe, 1977). Fire, for example, has been suggested by Belland (1984) as a possible explanation for the absence of many critical disjuncts from eastern Newfoundland even though unglaciated surfaces are believed to have existed there.

The effects of bryophyte dispersal ability on regional floristic composition within Newfoundland have never been explicitly evaluated. All previous studies of the Newfoundland moss flora have either implicitly assumed that sufficient time has elapsed to mask any dispersal effects, or have not considered such effects at all. Much of the island has been deglaciated and available for plant colonization for only about 8,000 years. For the east coast, which is distant from any likely sources of colonizing species (i.e. the adjacent mainland and proposed refugia), it is conceivable that dispersal effects have significantly influenced the current bryofloristic composition of the region. If dispersal effects exist they may not be equally apparent for all biogeographic groups. If, for example, boreal species arrived in Newfoundland earlier than temperate species, then sufficient time may have elapsed for dispersal effects to have been overruled in the former group but not the latter.

1.4. Microhabitat and Bryophyte Distribution

Bryophytes exist at the interface between substrate and air, where fluctuations in environment may be extreme and may differ markedly from those recorded by standard meteorological stations (Geiger, 1965). The availability of suitable microhabitats may be a major determinant in establishing limits to bryophyte distributions. Microhabitat is likely to be especially important near the limits of bryophyte species' distributions since, under these conditions, even vascular plants are forced to seek out definite, narrowly limited combinations of microhabitat factors (Bocher, 1954). Knowing the microhabitat of individual bryophyte species may allow an evaluation of factors limiting and controlling growth and reproduction, patterns of climatic adaptation, and ultimately the geographic range of these species.

Few studies have considered the role of microhabitat in determining bryophyte distribution patterns. A number of workers have successfully correlated intersite distributions of species with temperature, light intensity, water availability, and evaporation stress (Alpert, 1985; Busby *et al.*, 1978; Clausen, 1952; Foote, 1966; Forman, 1964; Longton, 1980; Seltzer and Wistendahl, 1971; Zehr, 1977). In the only study considering microhabitat in relation to distributions of species occurring near geographic limits, Billings and Anderson (1966) have found that in the southern Appalachian Mountains, endemic or highly disjunct mosses with tropical affinities are restricted to gorges with high and seasonably reliable rainfall and with lower maximum and higher minimum temperatures than is typical for the region.

Preliminary work in Terra Nova National Park in 1984 showed that cliffs and scree slopes in the park have a flora which includes, in addition to the "expected" boreal species, several species of arctic-montane, montane, and temperate oceanic affinity. In Terra Nova, all the non-boreal species are near their latitudinal limits of eastern North American distribution. This offers an opportunity to evaluate their microhabitats and to compare the importance of various microhabitat variables to species of different phytogeographical affinity.

Chapter 2

Methods and Materials

2.1. Collections

Collecting was done to compile a complete list of moss species for the study area, and to determine the floristic composition of each major habitat type within the park. Stands of each habitat type were selected on the basis of accessibility by road, trail, or sea. Within each stand an attempt was made to collect all moss species present, with the exception of a few common and easily identifiable species, for which field identifications were used. For each habitat, the cumulative number of species was plotted against the number of stands visited, and collecting was continued until there was no change in the cumulative number of species for the habitat over three successive stands. In the case of rare habitats (< 5 stands present) all stands in the study area were examined.

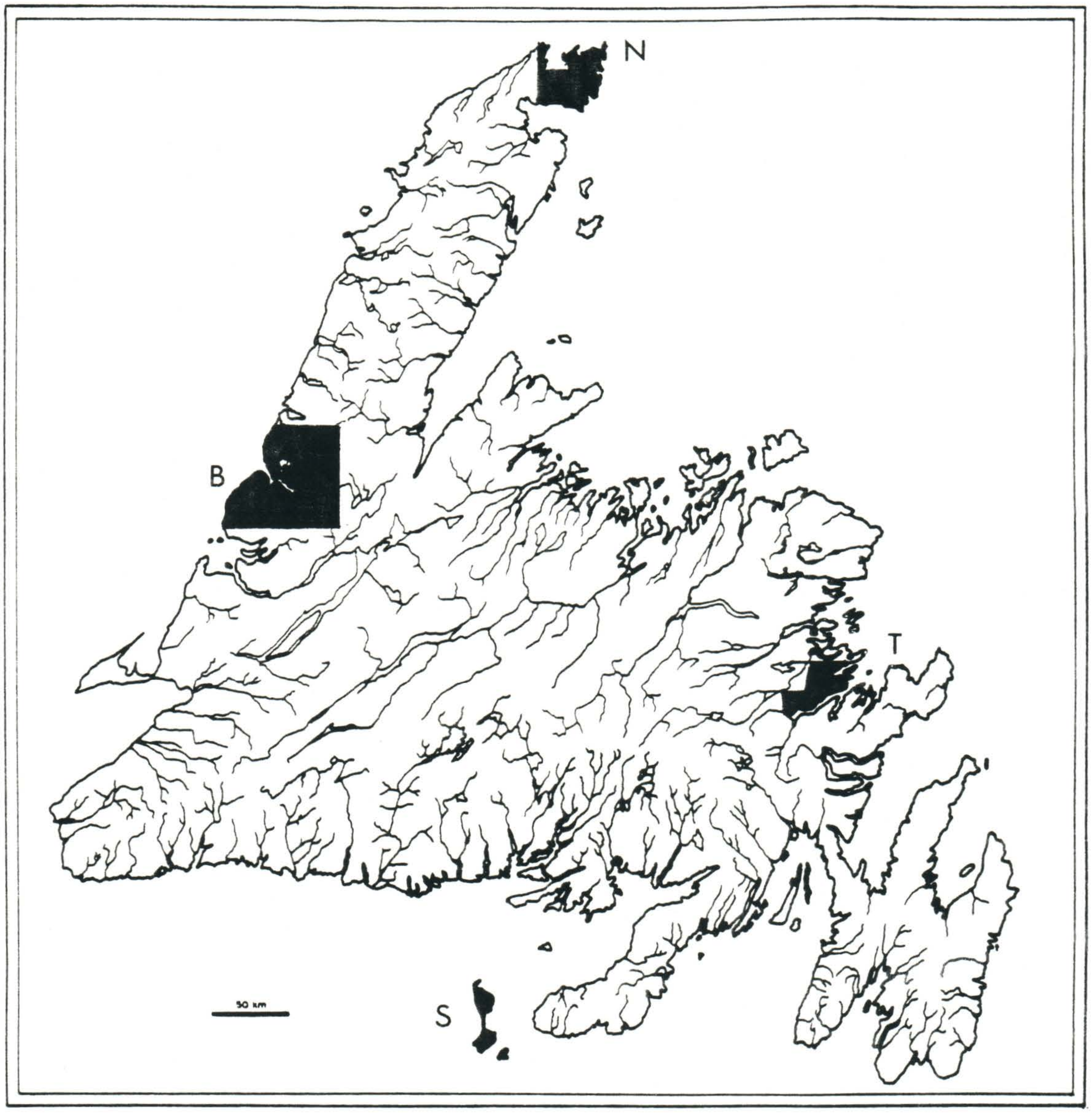
A total of 1102 specimens were collected in the course of the study: 430 were collected between May and October, 1984 and an additional 672 specimens over the same time period in 1985. Specimens were identified at Memorial University. A complete set of voucher specimens is deposited at the Bryophyte Herbarium, Memorial University of Newfoundland (NFLD).

2.2. Bryogeographical Analysis

The moss flora of Terra Nova was described in terms of, i) species distribution within the island, and, ii) the affinities of the flora, with emphasis on North American distribution. The study area was compared to the whole island at both levels of distribution. The list of moss species for Newfoundland is taken from Brassard (1983b). The affinities of Terra Nova's moss flora were compared to those of three other regions of the island (Figure 2-1) for which reliable species lists were available: northernmost Newfoundland (collections by Hedderson, largely unpublished), the Bonne Bay Region (Belland, 1981), and St. Pierre et Miquelon (Etcheberry *et al.*, 1987). Floristic similarity of the study area to these three areas was measured using Jaccard's coefficient of similarity (S_J) (Simberloff and Connor, 1974).

Newfoundland distributional elements generally follow Brassard (1983a) but new data accumulated since then have been incorporated into the present classification. Some of the elements used here are segregates from larger groups proposed by Brassard (1983a) (e.g. Brassard's southern element has been split into a southern and a southeastern element). Species were placed in one of the following categories: widespread, widespread but sporadic, northwestern, northern, southwestern, southern, southeastern, disjunct, unknown.

Affinity classes are based on North American and/or World distribution patterns of species. Important sources of distributional information were Crum (1984), Crum and Anderson (1981), Ireland (1982), Schofield (1972, 1980), Schofield and Crum (1972), and numerous previously published distribution maps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(listed in Sjodin, 1980). Taxonomic revisions were an additional source of information (Bremer, 1980a,b, 1981; Horton, 1982, 1983; Ireland, 1969, 1986; Koponen, 1973, 1974; Lewinsky, 1974; Shaw, 1982; Vitt, 1970). The following affinity classes were recognized: boreal (including boreal/temperate species), temperate, arctic-montane, arctic, montane, cosmopolitan, unknown.

2.3. Dispersal and its Interaction with the Bryogeographical Groups

It is reasonable to assume that most of the flora of Terra Nova is derived from elsewhere on the island. In this study the dispersal potential of species occurring in Terra Nova is compared to that of species which occur in Newfoundland but not in the study area. A two-way contingency table (Sokal and Rohlf, 1981) was used to analyze the independence of diaspore size (as a measure of dispersal ability) and species' presence or absence in Terra Nova National Park. A diaspore is taken to be "any agent capable of moving reproductive germ plasm from one place to another" (Ireland, 1982).

This analysis assumes that diaspore size is an indication of dispersal ability. Experimental evidence (van Zanten and Pocs, 1980) suggests that long distance dispersal, at least, is very improbable at diaspore diameters greater than 25 μm. Species were assigned to one of the following three categories:

1. Diaspores $< 25\mu$m. This category includes species producing spores and/or gemmae.
2. Diaspores $> 25\mu$m but $< 100\mu$m. This includes species producing spores, gemmae, and fragile gametophyte fragments.
3. Diaspores $> 100\mu$m. This category includes species producing fragile

gametophyte fragments, as well as those in which dispersal is by means of whole gametophytes, or large, non-fragile gametophyte fragments. Diaspores of most species in this category are better measured on a scale of millimetres rather than microns.

Data on diaspore sizes was largely derived from Crum and Anderson (1981), Ireland (1982) and Nyholm (1954-1969).

The interactions between dispersal ability and species affinity on the occurrence of species in Terra Nova were evaluated by hierarchical log-linear analysis (Bishop *et al.*, 1975; Fienberg, 1980) of a three way frequency table (BMDP-4F). Only those affinity groups in the Newfoundland flora which were represented in the study area were used in this analysis.

2.4. Microhabitats of Species in Cliff/Scree-slope Habitats

Species were chosen for microhabitat analysis using the following criteria;

1. That at least 8 populations were known to occur on cliffs and/or scree slopes in Terra Nova.
2. That as many of the affinity classes or Newfoundland distributional categories as possible be represented.
3. That the species occurred only in pure populations.

The following five species were chosen for microhabitat analysis:

1. *Aulacomnium androgynum*. A turf forming species of boreal affinity and disjunct within Newfoundland from the east to the west coast. Known from 19 localities in Terra Nova.
2. *Encalypta procera*. A turf forming species, widespread from the arctic to the temperate zone of North America and with a northwestern distribution in Newfoundland. Known from 15 localities in Terra Nova.

3. *Eurhynchium pulchellum.* A weft forming species, widespread from the arctic to the temperate zone in North America and with a northwestern distribution in Newfoundland. Known from 20 localities in Terra Nova.

4. *Grimmia torquata.* A cushion forming species of arctic-montane affinity and with a northeastern distribution in Newfoundland. Known from 18 localities in Terra Nova.

5. *Isothecium myosuroides.* A weft forming species of temperate-oceanic affinity and with a southeastern distribution in Newfoundland. Known from 20 localities in Terra Nova.

All five of the above species are strictly saxicolous on cliffs and scree slopes in Terra Nova.

2.4.1. Field Studies

In the initial 10 days of the 1985 field season, all previously known populations of each of the above five species were located, and an attempt was made to discover as many new populations as possible.

A 75 X 75 cm quadrat was positioned over each population (always less than 75 X 75 cm) and 4 15 X 15 cm quadrats positioned at random within each of these larger quadrats. Within each of the 15 X 15 cm quadrats, species abundance (% cover and total area in cm^2) was measured, along with 7 microhabitat variables; temperature, precipitation, light, pH of substrate, slope, aspect, and elevation.

Temperature. Temperature was measured by the sucrose inversion method (Berthet, 1960; Jones, 1972; Jones and Court, 1980; Pallman *et al.*, 1940).

The inversion solution was made to a concentration of 386.2 g sucrose per litre, and buffered at exactly pH 2.92 with citrate-HCl. A little 2% formaldehyde was added to prevent microbial growth (Berthet, 1960). Stoppered 25 ml glass vials were filled and frozen for transportation to the study sites. Ten vials were used as controls for changes during transport. At the end of the study period the degree of rotation measured in these was not different from the initial rotation of the sucrose solution.

Sucrose vials were placed in the field between May 28 and June 6 1985, with a single vial being placed in each 15 X 15 cm quadrat. Vials were retrieved between October 11 and October 17, 1985, and stored at -20°C until rotational angles could be measured. Rotations were made with a hand-operated Bellingam & Stanley Polarimeter, using a Na-d lamp (λ=589 nm). T_e values were calculated using the equations of Berthet (1960) and Jones and Court (1980).

Precipitation. Total precipitation over the study period was measured in each 15 X 15 cm quadrat using canning tins (110 mm X 60 mm) in which 150 ml of Castor Oil were placed to prevent evaporation. The contents of each tin were emptied and measured at 1.5-3 week intervals, and summed over the study period. The oil was replaced on each visit.

Light. Incident light was measured as often as possible throughout the study period, with an attempt being made to visit each site at many different times of day. Measurements were made on days when there was no cloud cover, to eliminate variability resulting from differing degrees of cloudiness. Readings (in lux) were made with a Gossen Lunasix incident light meter. All lux measurements were converted to micro-moles per square metre per second (μmolm^{-2}s^{-1}) as recommended by Luning (1981). Measurements made over the study period were averaged for each 15 X 15 cm quadrat.

pH of Substrate. A small sample of rock was collected from within each 15 X 15 cm quadrat. Samples were crushed to a coarse powder and mixed at a ratio (by volume) of 1:1 with distilled water. The mixtures were allowed to equilibrate for 2-2.5 hours. pH measurements were made with a single electrode digital pH meter (Fisher Accumet).

Slope, Aspect, and Elevation. Slope was measured to the nearest degree with a clinometer held parallell to the surface of the substrate. Aspect, in degrees deviation from true North, was measured with a magnetic compass. Elevation was measured to the nearest 0.5 metre with an altimeter.

2.4.2. Statistical Analysis

Breakage or loss of sucrose vials (59 of the 344 initially placed in the field) and loss of precipitation gauges occurred for some species' populations. These were discarded. For each species, however, there were complete data sets for at least seven populations and these were used in all the multivariate analyses. Since within-population [*i.e.*, 75 X 75 cm plot] variation in microhabitat variables was small in relation to that between populations, measures obtained for 15 X 15 cm plots were averaged for each population. Each population of a species, therefore, constitutes a sample for that species. Two multivariate statistical methods were employed in analysis of the data, Multiple Discriminant Functions Analysis (DFA) and Multiple Regression Analysis (MRA).

Discriminant Analysis

The DFA is an evaluation of the separation of the five species in a seven-dimensional microhabitat space. Discriminant analysis reduces a set of m measured variables to $k<m$ linear additive functions (Green, 1971; Sokal and Rohlf, 1981). Here, linear relationships are sought among the microhabitat variables, rather than between the species and the microhabitat variables. For ecological factors, relationships are likely to be multiplicative rather than additive, and logarithmic transformations of the data are usually appropriate (Green, 1971, 1974; Green and Vascotto, 1978). Measurements of all the microhabitat variables were log-transformed, with the exception of pH which is measured in logarithmic units. A direct Discriminant Functions Analysis was done using procedure DISCRIMINANT in SPSS-X (Anonymous, 1986). A rotated (VARIMAX) solution was used to interpret the discriminant functions.

Multiple Regression Analysis

Multiple Regression was used to determine the amount of variation in species' performance (abundance) which could be 'explained' by the microsite variables. While significant regressions do not necessarily imply cause-effect relationships, MRA provides an additional basis in this study for comparison of species microhabitats, and, in conjunction with Discriminant Functions Analysis, suggests which microhabitat factors may be controlling patterns of species abundance. Hypotheses suitable for rigorous experimental testing may be generated from the results.

Species abundances, measured as percent cover, were arcsine transformed to help meet the assumptions of linearity (Sokal and Rohlf, 1981, pp. 427). Light measurements (in μmolm^{-2}s^{-1}) were log-transformed and the rest of the data left untransformed for analysis by stepwise multiple regression (SPSS-X, Anonymous, 1986).

Chapter 3

Bryofloristics

3.1. Results and Discussion

The known moss flora of Terra Nova National Park comprises some 210 species in 81 genera, representing ca. 47% of the total known flora of the island of Newfoundland. A complete list of species, along with their occurrences in the major park habitats, Newfoundland distributions, World affinity class, and dispersal ability class is given in Appendix A. An annotated list, fully documenting the Terra Nova occurrences of phytogeographically noteworthy species, is presented in Appendix B.

3.1.1. Affinities of the Terra Nova Moss Flora

The world affinities of the Terra Nova moss flora are summarized in Table 3-1 as are those of the Newfoundland flora. Of the seven affinity groups represented in the Newfoundland moss flora, five occur in Terra Nova; no species present in the study area have arctic or unknown affinities. The other affinity groups are discussed below and a brief discussion of habitat relationships (summarized in Table 3-2) is also included under each group.

The moss flora of Terra Nova National Park is dominated by species of

Table 3-1: The frequency and relative importance of the 7 world affinity classes in the moss flora of Terra Nova and the total Newfoundland flora.

Element	Terra Nova #	Terra Nova %	Newfoundland #	Newfoundland %
Cosmopolitan	22	10.5	29	6.5
Boreal	149	70.9	245	55.3
Temperate	20	9.5	56	12.5
Arctic-Montane	10	4.8	57	12.7
Arctic	0	0.0	10	2.2
Montane	9	4.3	41	9.2
Unknown	0	0.0	5	1.1
Total	210	100.0	447	100.0

Table 3-2: The number of species from each of the affinity groups in each of the habitats of Terra Nova. Habitat abbreviations are given in parentheses. AA, Arctic-montane. Bo, Boreal. Co, Cosmopolitan. Mo, Montane, Te, Temperate.

Habitat		Affinity Group Co	Bo	Te	AA	Mo
Kalmia-Black spruce	(KB)	00	06	01	00	00
Carex-Black spruce	(Ca)	00	06	00	00	00
Black spruce-moss	(Bs)	05	29	02	00	00
Cladonia-Black spruce	(Cl)	05	05	01	00	00
Balsam fir-moss	(Bf)	11	52	09	02	01
Dryopteris-Hylocomium -Balsam fir	(DH)	01	29	02	00	00
Rubus-Balsam fir	(Ru)	01	12	01	00	00
White birch	(Wb)	05	24	01	00	00
Trembling Aspen	(TA)	01	21	02	00	00
Rock barrens	(RB)	06	17	01	02	00
Kalmia barrens	(KA)	06	14	00	00	00
Bogs	(Bg)	06	38	02	01	00
Fens	(Fn)	07	35	03	01	00
Freshwater marshes	(FM)	04	13	01	00	00
Estuarine marshes	(EM)	01	07	00	00	00

Table 3-2 continued

Swamps	(Sw)	04	39	02	00	00
Freshwater	(Fw)	07	46	06	01	05
Coastal exposures	(Co)	10	25	01	05	02
Inland Cliffs	(IC)	06	38	03	04	02
Scree slopes	(SS)	05	36	03	04	01
Anthropogenic	(An)	09	31	02	01	00
Total in affinity group		22	149	19	10	09

boreal affinity, with 149 species (70.9%) falling in this class. An additional 10.5% of the flora is made up of cosmopolitan species. These are not further discussed.

The Temperate Element

Twenty (9.5%) of the moss species occurring in Terra Nova are of temperate affinity. Included in this group are four *Sphagnum* species (*S. angermannicum*, *S. molle*, *S. pylaisii* and *S. strictum*), whose North American distributions largely coincide with the eastern coastal plain. Of these four coastal plain species, all except *S. strictum* reach their northern limit north of the study area, in northernmost Newfoundland or in southern Labrador (Crum, 1984; Lavoie and Gauthier, 1983). *S. strictum* is near its northeastern limit of North American distribution in the study area.

The remainder of the temperate species have the greater portion of their range within the limits of the temperate forest biome. Eight of these have northern limits either in northern Newfoundland or in southern Labrador:

Atrichum altecristatum
Brotherella recurvans
Bryhnia novae-angliae
Callicladium haldanianum
Dicranella heteromalla
Pohlia annotina
Rhizomnium appalachianum
Rhizomnium punctatum

The remaining species reach, or nearly reach, their northeastern limit of North American distribution in the study area:

Atrichum crispum
Hypnum fertile
Isothecium myosuroides
Kindbergia praelonga
Plagiothecium latebricola
Pogonatum pensilvanicum
Polytrichastrum formosum
Ulota drummondii

Considered together, the temperate species show a pattern of distribution among the park habitats similar to that of the boreal element. Examination of individual species distributions (Table 3-3), however, reveals differences between the temperate species that attain a northern limit in, or just north of, the study area, and those that extend their distributions to northern Newfoundland or southern Labrador. The majority of species in the former category occur in a quite restricted range of habitats, and balsam fir forests appear to be particularly important to these. Six of the eight species at northern limits in Terra Nova are either restricted to balsam fir stands or occur in only one other habitat type. *Isothecium myosuroides* has the broadest habitat range of the species at northern limits, occurring in balsam fir-moss forests and on wet cliffs, shaded scree slopes and on rocks in the spray zone of major stream gorges. Temperate species with distributional limits far north of the study area tend to occur in a broader range of habitats and show no consistent among-species patterns.

The virtual restriction of temperate species at northern limits to balsam fir stands is not easily explained. It is perhaps related to the fact that virtually all other forest types in the study area are post-fire successional habitats. As noted above, the balsam fir stands are the oldest and least disturbed forest sites in the study area. LaRoi and Stringer's (1976) analysis of the bryophyte flora of the North American taiga showed that bryophyte species richness of white spruce-fir stands is higher than that of black spruce. This difference was attributed to the greater age of white spruce-fir stands as well as to their higher productivity; a combination of these two gives a greater diversity and quantity of woody

Table 3-3. The distribution of temperate elements in major habitats of Terra Nova. Presence in a habitat is indicated by a 1. Habitat abbreviations are given in Table 3-2.

Species	Habitat																				
	KB	Ca	Bs	Cl	Bf	DH	Ru	Wb	TA	RB	KA	Bg	Fn	FM	EM	Sw	Fw	Co	IC	SS	An
Atrichum altecristatum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Atrichum crispum	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Brotherella recurvans	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Bryhnia novae-angliae	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0
Callicladium haldanianum	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Dicranella heteromalla	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	1	1	1	1	0
Hypnum fertile	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Isothecium myosuroides	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0
Kindbergia praelonga	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Plagiothecium la tebricola	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pogonatum pensilvanicum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Pohlia annotina	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Polytrichastrum formosum	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Rhizomnium appalachianum	1	0	0	0	1	1	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0
Rhizomnium punctatum	0	0	1	0	1	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0
Sphagnum angermannicum	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Sphagnum molle	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0
Sphagnum pylaisii	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0	0
Sphagnum strictum	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1	0	0
Ulota drummondii	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Number of species/habitat:	01	00	02	01	09	02	01	01	02	01	00	03	03	00	01	02	06	02	04	03	02

Total Moss species: 20

substrates for microsuccesional species. It is possible that some substrate type on which the more strongly temperate species are dependent is lacking from all but balsam fir stands in Terra Nova.

The Arctic-Montane Element

The Arctic-montane element, including 10 species, represents 4.8% of Terra Nova's moss flora. Five of the species (*Bartramia ithyphylla, Bryum knowltonii, Orthotrichum pylaisii, Racomitrium lanuginosum* and *Ulota curvifolia*) are more or less continuously distributed in arctic regions of North America, extending southwards in mountains on both sides of the continent. The remainder (*Grimmia donniana, G. torquata, Kiaeria blyttii, Oligotrichum hercynicum*, and *Tayloria serrata*) are disjunct between eastern and western North America, tending to be more common northwards on both sides of the continent. Newfoundland is at or very near the southern limit of all ten of these species' eastern North American distributions.

Arctic-montane species are clearly concentrated in various exposure types (*i.e.,* coastal exposures, and scree slopes and cliffs with a northern aspect) throughout the study area (Table 3-4). Of the ten arctic montane species present in Terra Nova, eight are present in, and five are restricted to, this group of habitats. With the exception of the occurrence of *Tayloria serrata* in a balsam fir-moss stand, the arctic-montane element is absent from forests.

Damman (1965) has suggested three factors which might specifically limit

Table 3-4. The Distribution of Arctic-Montane Elements In Major Habitats of Terra Nova. Presence in a habitat is indicated by a 1. Habitat abbreviations are given in Table 3-2.

	Habitat																				
Species	KB	Ca	Bs	Cl	Bf	DH	Ru	Wb	TA	RB	KA	Bg	Fn	FM	EM	Sw	Fw	Co	IC	SS	An
Bartramia ithyphylla	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Bryum knowltonii	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0
Grimmia donniana	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0
Grimmia torquata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0
Kiaeria blyttii	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Oligotrichum hercynicum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Orthotrichum pylaisii	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Racomitrium lanuginosum	0	0	0	0	0	0	0	0	0	1	0	1	1	0	0	0	0	0	0	1	0
Tayloria serrata	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ulota curvifolia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0
Number of species/habitat:	00	00	00	00	01	00	00	00	00	02	00	01	01	00	00	00	01	05	04	04	01

Total Moss species: 10

distributions of arctic vascular plants in Newfoundland: 1) the absence of competition in certain habitats, 2) requirement of high light intensity for most arctic species and hence their exclusion from closed plant canopies, and 3) inability of arctic plants to tolerate high summer temperatures. The among-habitat distribution of arctic-montane mosses in Terra Nova is not likely to result from either of the first two factors. Five of the ten species occur in closed vegetation on coastal barrens, indicating that competitive ability of these mosses is not limiting. Of the species that occur on cliffs and scree slopes, the majority occur at least part of the time in very shaded sites, and this would appear to exclude light requirements as a major determinant of habitat distribution of these mosses. A common feature of the major habitats occupied by arctic-montane mosses in the study area is relatively low summer temperature. Thus it seems probable that their inability to tolerate high summer temperatures restricts the arctic-montane species to habitats where the cooling influence of the sea, or cold air flow through shaded gorges creates suitably "northern" conditions.

The occurrence of *Oligotrichum hercynicum* in a disturbed habitat is of particular interest. This species is mostly known in Newfoundland from high altitude snowbeds in the Long Range Mountains (Belland, 1981; Tuomikoski *et al.*, 1973) but has recently been found at several disturbed roadside localities in the southeastern part of the island. The species commonly occurs as a weed in Europe (Nyholm, 1969; Smith, 1978), and it is possible that the eastern Newfoundland populations, including those in Terra Nova, are a result of anthropogenic introduction to the island while the populations from the western part of the island are native.

The Montane Element

The montane element includes 9 species, representing 4.3% of the flora. *Bryum alpinum, Grimmia incurva* and *G. trichophylla* are widespread in mountains of western North America, but in the east are either restricted to Newfoundland or else occur in one or two other montane localities (especially the Gaspe Peninsula, New England, or the Torngat Mountains). The remaining species (*Bryum muehlenbeckii, Dryptodon patens, Grimmia anomala, G. tenerrima, Orthotrichum rupestre* and *Schistidium agassizii*) are either broadly distributed in the east or have intermediate stations around the Great Lakes.

As a group, the montane species show the greatest degree of habitat restriction of any of the elements present in Terra Nova, being almost completely confined to freshwater habitats or various exposure types throughout the study area (Table 3-5). The element is particularly well represented in freshwater habitats where five of the nine species occur, usually in the rocky gorges of the major rivers in the study area. The montane element is represented in forest habitats only by the single occurrence of *Orthotrichum rupestre* on a dry rock outcrop in a balsam fir-moss stand. It is not clear why the montane species should show such remarkable restriction of habitat. They may, like the arctic-montane taxa, be relatively intolerant of high summer temperatures, but this still fails to explain why many of the species appear to prefer rock cliffs near fresh

Table 3-5. The distribution of Montane elements in the major habitats of Terra Nova. Presence in a habitat indicated by a 1. Habitat abbreviations are given in Table 3-2.

	Habitat																				
Species	KB	Ca	Bs	Cl	Bf	DH	Ru	Wb	TA	RB	KA	Bg	Fn	FM	EM	Sw	Fw	Co	IC	SS	An
Bryum alpinum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Bryum muehlenbeckii	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Dryptodon patens	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Grimmia incurva	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Grimmia anomala	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Grimmia tenerrima	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Grimmia trichophylla	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0
Orthotrichum rupestre	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Schistidium agassizii	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Number of species/habitat:	00	00	00	00	01	00	00	00	00	00	00	00	00	00	00	00	05	02	02	01	00

Total Moss species: 9

water. It is possible that a requirement for high moisture levels is also involved in the distribution of these species.

3.1.2. Newfoundland Distributions

The relative importance of the 9 Newfoundland distributional elements to the moss flora of Terra Nova and the total insular flora is given in Table 3-6. Seven of the nine Newfoundland elements are present in the flora of Terra Nova National Park; the northern and southwestern elements are not represented.

The Widespread Elements

Most (82.3%) of the species occuring in Terra Nova are widespread or widespread-sporadic in Newfoundland, but these elements together represent only 47.6% of the total moss flora of the island. The dominance of these elements in the Terra Nova flora merely reflects the weak representation of most other Newfoundland distributional groups. I have included in the widespread group the nine species considered by Brassard (1983) to have distinctly coastal distributions. Five of these coastal species (*Bartramia ityphylla*, *Bryum salinum*, *Schistidium maritimum*, *Tortella fragilis*, and *Ulota phyllantha*) occur in Terra Nova. The remaining four elements are discussed separately below.

The Northwestern Element

Seventy nine (17.7%) of the mosses in Newfoundland are primarily distributed on the Northern Peninsula and along the west coast of the island. Five of these species occur in Terra Nova. *Brachythecium erythrorrhizon*, *Encalypta procera*, *Eurhynchium pulchellum*, *Heterocladium dimorphum* (Figure 3-1) and

Table 3-6: The distribution of the Terra Nova and Newfoundland moss floras among the nine Newfoundland distributional elements.

Element	Terra Nova		Newfoundland	
	#	%	#	%
Widespread	128	60.9	138	30.9
Widespread/ Sporadic	45	21.4	75	16.8
Northwestern	5	2.4	79	17.7
Northern	0	0.0	36	8.1
Southwestern	0	0.0	17	3.8
Southern	6	2.9	09	2.0
Southeastern	4	1.9	20	4.5
Disjunct	17	8.1	50	11.4
Unknown	5	2.4	23	5.1
Total	210	100.0	447	100.0


50 km

Tomenthypnum nitens are, in the study area, at or near their southeastern limits of distribution within Newfoundland. All five of these are widespread boreal or boreal-arctic species that are at least weakly calciphilic (Amann, 1928) and their Newfoundland distributions may reflect this edaphic preference. Brassard (1983a) has suggested that the absence or rarity of calcareous substrata in eastern and central Newfoundland is one of the major factors contributing to the insular distribution of many of the boreal calciphilic species that have predominantly northwestern distributions in Newfoundland. This is almost certainly why the northwestern element is so poorly represented in the study area, even though many of the species in that element are widespread in boreal and subarctic regions of North America.

The Southern Element

The Southern element in Newfoundland's flora includes the 9 species (2% of the flora) that are most frequent along the South Coast, and absent from the Northern Peninsula. This element is well represented in Terra Nova, where six of these species occur. *Atrichum crispum* (Figure 3-2), *A. undulatum*, *Plagiothecium latebricolă*, *Pogonatum pensilvanicum*, and *Ulota drummondii* show a marked increase in frequency toward the South Coast, and are at or near the northern limit of their island distribution in the study area. *Polytrichastrum formosum* is somewhat more widespread, but has not been recorded from the Northern Peninsula. Nearly all of the southern species occurring in Terra Nova are species of temperate affinity which are nearing their northeastern limit of North American distribution in the study area.


50 km

The Southeastern Element

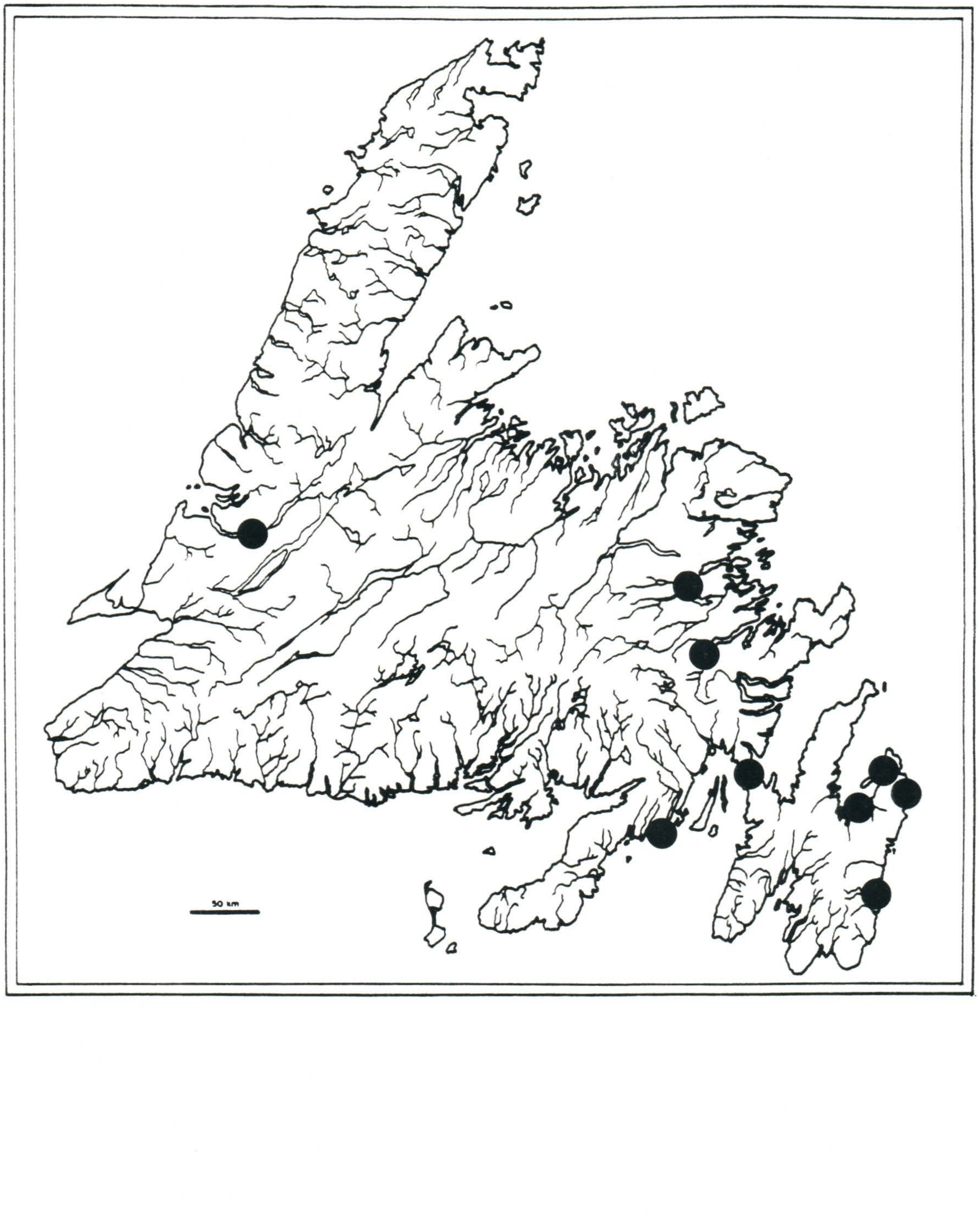
Twenty species (4%) in the Newfoundland flora have southeastern distributions within the island, and are largely confined to the Avalon and Burin Peninsulas. Only four of the southeastern species (*Isothecium myosuroides* (Figure 3-3), *Sphagnum centrale*, *S. fimbriatum*, and *S. strictum*) occur in Terra Nova, and all four are very near their northwestern limit of known Newfoundland distribution. Both *S. centrale* and *S. fimbriatum* are widespread boreal species (Crum, 1984, 1986) that are almost certainly more widespread in Newfoundland than the few collections indicate. The remaining two species (*Isothecium myosuroides, Sphagnum strictum*) have strongly oceanic distributions in both North America (Crum and Anderson, 1981) and Europe (Nyholm, 1965; Smith, 1978), and their distribution in Newfoundland very likely reflects a similar oceanic tendency.

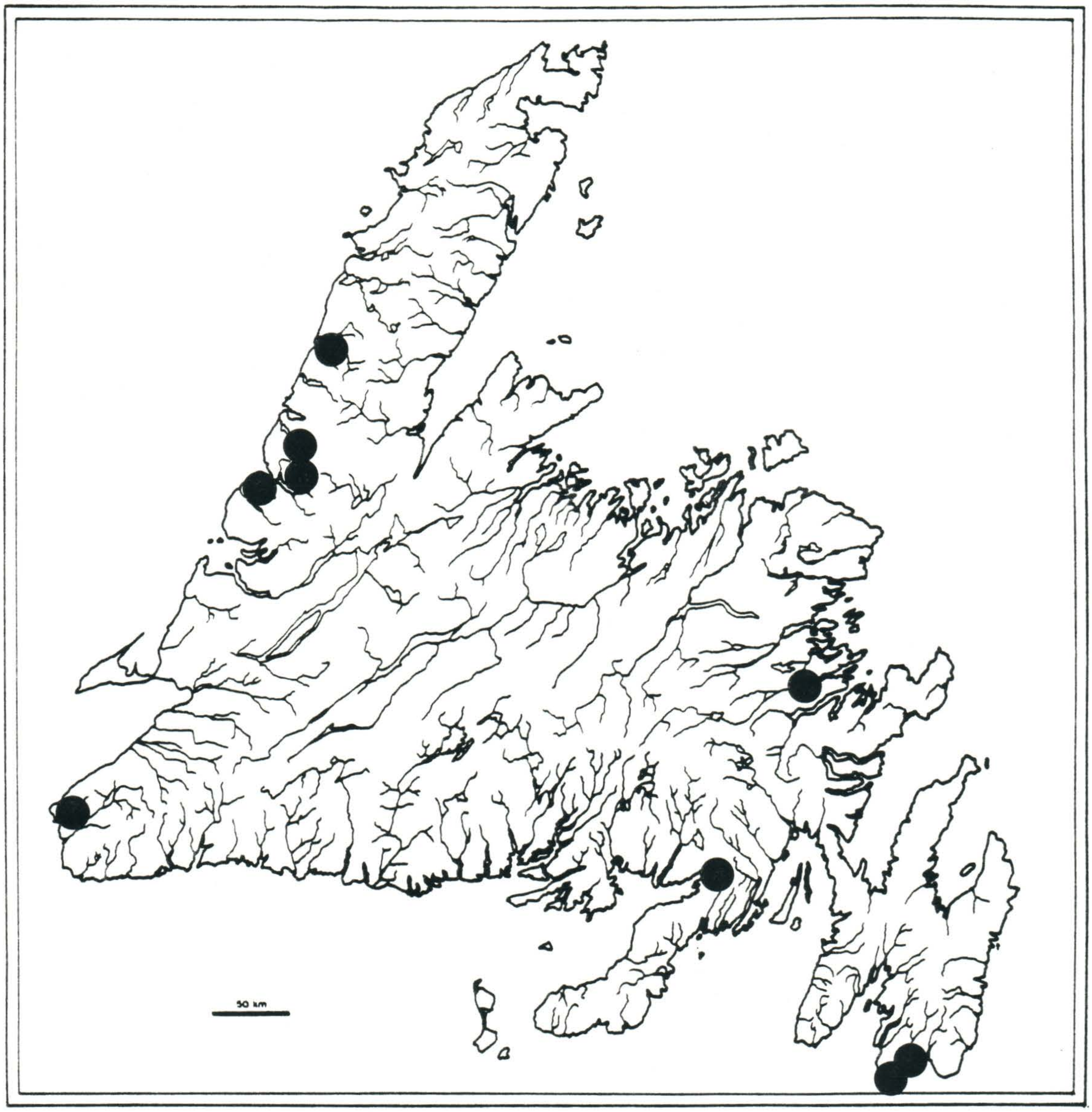
Given the proximity of Terra Nova National Park to southeastern Newfoundland, more species with predominantly southeastern distributions might be expected to occur in the Terra Nova moss flora. However, many of the species which have southeastern distributions in Newfoundland are suspected human introductions that are restricted, even within southeastern Newfoundland, to major centers of human population, particularly the St. John's area (Belland, 1984; Brassard, 1983a).


50 km

The Disjunct Element

Fifty Newfoundland moss species (11.4% of the total flora) have major gaps in their distributions within the island, while 17 (8.1%) of the species occurring in Terra Nova show such disjunctions in their Newfoundland distributions: Six of these are more frequent in western Newfoundland and have one or two populations in the eastern part of the island: *Dicranella subulata*, *Dryptodon patens*, *Grimmia tenerrima*, *Isopterygiopsis muelleriana*, *Racomitrium canescens* and *Scorpidium scorpioides*. Six of the disjuncts are more common in the eastern parts of the island but have one or two populations in western Newfoundland. Of these, *Aulacomnium androgynum*, and *Tetraplodon angustatus* have a more north-easterly bias, while *Bryum muehlenbeckii* (Figure 3-4), *Buxbaumia aphylla*, *Hypnum fertile*, and *Kindbergia praelonga*, tend to be more common in the southeast. The remainder of the disjuncts occur with roughly equal frequency in both eastern and western Newfoundland. *Bryum caespiticium*, *Grimmia anomala*, and *Oligotrichum hercynicum* (Figure 3-5) are known from several localities on both parts of the island while *Bryum alpinum* and *Tayloria serrata* are each known from Terra Nova and single west coast localities.


50 km


50 km

The Unknown Element

Twenty-three species (5.1%) in the Newfoundland flora were assigned to an "unknown" element. This group includes species whose distributions are not well enough known to categorize, or that did not fit into one of the elements, or their segregates, as defined by Brassard (1983a) and modified for this study. Five of these species occur in Terra Nova. One of these, *Sphagnum subnitens*, is not very well known in Newfoundland - perhaps because of confusion with *S. subfulvum* (Crum, 1984). *S. subnitens* is a boreal species, wide ranging in eastern North America, that is probably widespread on the island, but underrepresented in herbaria. The remaining Terra Nova species in the unknown category (*Bryum knowltonii*, *Grimmia torquata*, *Orthotrichum pylaisii*, and *O. rupestre*) may belong to a previously unrecognized distributional element in the Newfoundland moss flora. All four have a markedly northeasterly bias in their Newfoundland distributions (e.g. *Orthotrichum pylaisii* (Figure 3-6)), and are mostly known from White Bay to Bonavista Bay, but may also occur along the east coast of the Northern Peninsula. Several other species in the Newfoundland flora which are not known from Terra Nova also appear to belong to this northeastern element: *Mnium stellare, Philonotis yezoana, Saelania glaucescens.* Continued bryofloristic exploration of eastern and northeastern Newfoundland may result in the addition of species to this distributional category.


50 km

3.1.3. Comparison to Other Areas of Newfoundland

Table 3-7 presents a bryofloristic comparison of the Terra Nova moss flora to that of Bonne Bay, northernmost Newfoundland, and St. Pierre and Miquelon.

The study area shows the greatest overall bryofloristic similarity to St. Pierre and Miquelon (S_J= 0.70). The moss flora of the latter area, however, completely lacks montane species, and includes relatively few that are of arctic-montane affinity. The two areas also differ in that the moss flora of St. Pierre and Miquelon includes temperate-oceanic species and a few boreal calciphiles (mostly comprising rich fen species) that are absent from the flora of Terra Nova.

Similarity between the Bonne Bay moss flora and that of Terra Nova is only slightly less, with S_J= 0.68. Differences between the two floras are largely due to the presence in Bonne Bay of a large number of species that are absent from Terra Nova. The Bonne Bay flora includes sizeable arctic-montane and montane elements, both of which are only weakly represented in Terra Nova. Also present in Bonne Bay are a considerable number of boreal and temperate calciphiles which are absent in Terra Nova.

Terra Nova's moss flora is least similar to that of the northernmost part of Newfoundland (S_J= 0.64). As noted, the arctic-montane and montane elements are only weakly represented in Terra Nova, but these constitute a major component of the northern Newfoundland flora. The temperate element, which ranks third in order of importance to the Terra Nova moss flora, is virtually absent from northern Newfoundland. The flora of northern Newfoundland also

Table 3-7: A bryofloristic comparison of the Terra Nova moss flora to that of Bonne Bay, northern Newfoundland, and St. Pierre and Miquelon.

Element	Terra Nova # (%)	Bonne Bay # (%)	Northern Newfoundland # (%)	St. Pierre & Miquelon # (%)
Cosmopolitan	22 (10.5)	24 (7.6)	23 (8.6)	19 (10.9)
Boreal	149 (70.9)	195 (61.5)	164 (61.4)	131 (74.9)
Temperate	20 (9.5)	29 (9.1)	6 (2.2)	20 (11.4)
Arctic-Montane	10 (4.8)	37 (11.7)	43 (16.1)	5 (2.8)
Arctic	0 (0.0)	3 (0.9)	9 (3.4)	0 (0.0)
Montane	9 (4.3)	26 (8.2)	17 (6.4)	0 (0.0)
Unknown	0 (0.0)	2 (0.6)	4 (1.5)	0 (0.0)
Total	210	316	266	175
S_J	1	0.68	0.64	0.70

has a small group of truly arctic mosses that is absent from the rest of the island. Further floristic differences between the two areas result from the presence of a substantial group of boreal calciphiles in northern Newfoundland, and, as noted above, the absence of most of these from Terra Nova.

3.2. Summary

The Terra Nova flora is not particularly distinct within Newfoundland. No mosses are restricted in Newfoundland to the Terra Nova region, and most are quite widespread within the island, being largely species of wide distribution in boreal North America. Other regions of the island for which bryofloristic data are available also show a dominance of boreal species with widespread distributions in Newfoundland, but differ in the degree to which such elements preponderate.

The temperate element is also well represented in Terra Nova and several species appear to reach or nearly reach their northeastern limit of continental distribution in the area. The arctic-montane and montane distributional elements present in the Newfoundland flora are but poorly represented in the study area. These generally show marked restriction to specific habitat types. Scarcity of such suitable habitats in Terra Nova is possibly a major factor contributing to floristic differences between the study area and both Bonne Bay and northern Newfoundland.

The predominantly acidic nature of the bedrock underlying Terra Nova has profoundly influenced the character of the moss flora, and those species with a strong affinity for calcareous substrata are virtually absent. This is responsible for some of the differences between the moss flora of Terra Nova and those of other parts of the island where calcareous or basic bedrock is present.

Chapter 4

Evaluation of Dispersal Effects

4.1. Results

4.1.1. Overall Dispersal Effects

Table 4-1 shows that the null hypothesis of independence of diaspore size and occurrence in Terra Nova must be rejected (G-test; $p = 1 \times 10^{-11}$). The present data indicate that of the total pool of available species (*i.e.* the total Newfoundland moss flora), those species with smaller diaspores have colonized Terra Nova to a proportionately greater extent than those with larger diaspores.

4.1.2. The Log-Linear Model

Attempts to model relationships between diaspore size, species affinity and occurrence in Terra Nova were unsuccessful when all five of the affinity groups occurring in the study area were included in the analysis (G-tests, $p < 0.001$). Failure to find a model of good fit was due to the very high frequency of boreal and cosmopolitan species with small diaspores in the Terra Nova flora, and the relatively low frequency in the study area of species in other categories. Reanalysis of the data, excluding cells containing boreal and cosmopolitan species occurring in Terra Nova and having small diaspores (Quasi log-linear analysis), produced several models of good fit (G-tests, $p > 0.05$), but these, like all quasi

Table 4-1: Summary of data used to test the independence of diaspore size and occurrence in Terra Nova for the Newfoundland moss flora. Numbers in parentheses are expected frequencies based on a model of independence.

Distribution Type	Number of species in Diaspore size class <25μm	 25-100μm	 >100μm
In Terra Nova	171 (139.91)	28 (36.03)	11 (35.56)
Not In Terra Nova	127 (159.09)	48 (40.97)	64 (40.44)

$G = 50.652$; $p = 1 \times 10^{-11}$

log-linear models (Fienberg, 1980) are difficult to interpret. Their only practical value in the present study is that they indicate the gross over-representation in the Terra Nova moss flora of boreal and cosmopolitan mosses with small diaspores.

Since the above models allow little to be said of the relationship between affinity, diaspore size and occurrence in Terra Nova of the arctic-montane, montane and temperate species, a second series of log-linear models was tested using only these elements of the Newfoundland moss flora. Results of the hierarchical log-linear analysis are presented in Table 4-2. The model DO,WO was found to provide the best fit to the data (Table 4-3; G-test, $p>0.29$), and the only apparent departure from frequencies predicted by this model is the higher than expected number of montane species with diaspores $> 100\mu m$ in Terra Nova. Estimates of the parameters of this model, presented in full below, are given in Table 4-4.

$$\ln(f_{ijk})=\mu+\alpha_i+\beta_j+\gamma_k+\alpha\beta_{ij}+\alpha\gamma_{ij}$$

where;

- f_{ijk} is the expected frequency in cell ijk.
- μ is the mean of the ln of the expected frequencies.
- α is the main effect of occurrence (O).
- β is the main effect of affinity (W).
- γ is the main effect of diaspore size (D).

Table 4-2: Summary of Hierarchical Log-linear Analysis on Data of Table 4-3. D,Diaspore class. O, Occurrence in Terra Nova. W, Affinity class.

Model	Degrees of Freedom	G	p
D.	15	65.37	0.0000
W.	15	91.42	0.0000
O.	16	53.28	0.0000
D,W.	13	62.12	0.0000
W,O.	14	50.03	0.0000
O,D.	14	23.97	0.0462
D,W,O.	12	20.72	0.0546
DW.	9	60.60	0.0000
DO.	12	17.13	0.1448
WO.	12	45.78	0.0000
D,WO.	10	16.47	0.0000
W,DO.	10	13.88	0.1787
O,DW.	8	19.21	0.0138
DW,DO.	6	12.36	0.0544
DO,WO.	8	9.63	0.2923
WO,DW.	6	14.96	0.0206
DW,DO,WO.	4	8.80	0.0663

Table 4-3: Frequency data on occurrence in Terra Nova and diaspore size class for the arctic-montane, montane, and temperate elements in the Newfoundland moss flora. Numbers in parentheses are expected frequencies based on the log-linear model DO,WO.

Occurrence	Affinity	Diaspore Size Class <25μm	 25-100μm	 >100μm
	Temperate	14 (13.5)	3 (2.5)	2 (3.0)
In Terra Nova	Arctic-Montane	9 (7.1)	1 (1.3)	0 (1.6)
	Montane	4 (6.4)	1 (1.2)	4 (1.4)
	Temperate	19 (17.5)	7 (7.3)	11 (12.1)
Not In Terra Nova	Arctic-Montane	20 (22.3)	9 (9.3)	18 (15.4)
	Montane	16 (15.2)	7 (6.3)	9 (10.5)

Table 4-4: Parameter estimates for the log-linear model DO,WO for the data of Table 4-3.

μ = 1.7792

α_1 = -0.703, α_2 = 0.703
β_1 = 0.216, β_2 = 0.015, β_3 = -0.230
γ_1 = 0.739, γ_2 = -0.540, γ_3 = -0.198

Estimates of $\alpha\beta$

	j		
i	1	2	3
1	0.247	-0.193	-0.054
2	-0.247	0.193	0.054

Estimates of $\alpha\gamma$

	k		
i	1	2	3
1	0.325	-0.082	-0.242
2	-0.325	0.082	0.242

- $\alpha\beta_{ij}$ is the effect of dependence of category i of occurrence on category j of affinity (WO interaction).
- $\alpha\gamma_{ik}$ is the effect of dependence of category i of occurrence on category k of diaspore size (DO interaction).

This model implies that both diaspore size and species affinity are associated with occurrence in Terra Nova, but diaspore size and species affinity are conditionally independent (i.e. diaspore size and species affinity are independent for each level of occurrence in Terra Nova). Since the present study is directly concerned with effects of the other two variables on occurrence in Terra Nova, it is convenient to rewrite the above model in explicit terms of the log-odds (Sokal and Rohlf, 1981) of occurrence versus non-occurrence in the study area:

$$\ln f_{1jk}/f_{2jk} = [\alpha_1 - \alpha_2] + [\alpha\beta_{1j} - \alpha\beta_{2j}] + [\alpha\gamma_{1k} - \alpha\gamma_{2k}]$$

The first term in this equation (α_1-α_2 = -1.406) indicates the overall odds ratio of occurring versus not occurring in Terra Nova. The second term indicates the effect of species affinity on the odds ratio and assumes the following values: 0.492 for temperate, -0.386 for arctic-montane, and -0.108 for montane. Thus, of the three affinity groups considered, the relative odds of occurring in the study area are increased for temperate species, and decreased for both arctic-montane and montane species. The final term in the model gives the contribution of diaspore size to the log-odds ratio: 0.740 for species with diaspores $<25\mu$m, -0.164 for species with diaspores 25-100μm, and -0.484 for species with diaspores $>100\mu$m. For the three affinity groups considered, the odds of occurring in Terra Nova obviously decrease with increasing diaspore size.

The null hypothesis of independence of occurrence in Terra Nova and diaspore size was tested for the boreal and cosmopolitan species in the Newfoundland bryoflora. This hypothesis was rejected for the former (G-test, $p < 0.0001$), but accepted for the cosmopolitan taxa (G-test; $p > 0.25$). In the case of the boreal taxa, the Terra Nova flora was found to have a great overrepresentation of species with small diaspores.

4.2. Discussion

The results are consistent with the hypothesis that dispersal factors have played a major role in the development of the moss flora of Terra Nova (and probably of all of eastern Newfoundland). Given its distance from potential colonizing sources, and relatively recent deglaciation, it is scarcely surprising that the region's floristic composition should be biased toward species producing small, easily dispersed diaspores. The massive depredations of man throughout the last century, and continuing until the area was made a National Park *ca.* 30 years ago, may also have favoured species with high dispersal ability. Extensive destruction and alteration of habitat has probably resulted in the complete extinction of some rarer species in Terra Nova, and this is likely to be particularly true for forest species. More vagile taxa should have been able to reestablish themselves in the area more quickly than species with lower dispersal ability. In any case it is highly likely that the present flora of Terra Nova is not at equilibrium, and additional slowly migrating or dispersing species may become established there in the future.

The relatively high incidence in the Terra Nova moss flora of montane species with large diaspores is noteworthy. Departure from the pattern exhibited by other elements is possibly due to the predominant occurrence of montane species in stream gorges. This may have permitted hydrochoric dispersal of plant fragments into the area, and subsequent establishment of new populations.

Especially interesting are the implications of the log-linear analysis for an understanding of the occurrence of the arctic-montane and temperate elements in the eastern Newfoundland bryophyte flora. It is sometimes supposed that postglacial development of the Newfoundland flora (and, indeed, the Canadian flora as a whole) was by orderly northward migration of vegetation zones as climates ameliorated. Arctic-montane taxa existing in essentially boreal settings are thus considered relicts of a periglacial band of arctic vegetation which advanced northward prior to the establishment of forests. It is unlikely that the arctic-montane element in eastern Newfoundland arose directly from such a process, for it is difficult to imagine how this should selectively leave species with high dispersal ability. Rather, the present data suggest immigration events that need not have been co-ordinated with the northward migration of any supposed arctic vegetation zone. The effects of anthropogenic disturbance (as outlined above) would probably be minimal for the arctic-montane elements since these occur in habitats that have generally remained unaffected by man.

The high incidence of easily dispersed taxa in the temperate element of the Terra Nova moss flora likewise appears to argue against the development of the eastern Newfoundland bryophyte flora by slow, orderly migration from south to north. There is an increased likelihood however, that the effects of disturbance would be more pronounced for this element since most of the temperate moss species are found in forest habitats. This group of habitats has been more affected than any other by past activities in the study area.

Analysis of Holocene pollen sequences by Lamb (1980) and Macpherson (1981) have led these workers to the conclusion that postglacial vegetational development in (respectively) southern Labrador and Newfoundland was not by simple migration of belts of vegetation, but through stages related to immigration and dispersal of specific taxa, and their complex interaction with processes of climate and soil development. The present analysis certainly supports these earlier hypotheses, and the restriction of some taxa to specific habitats (Chapter 3) or, as discussed below, to restricted areas of suitable microhabitat conditions, are factors that could only enhance the selection of easily dispersed taxa.

Chapter 5

Microhabitats of Selected Cliff/Scree-slope Mosses

5.1. Results

The untransformed means and standard deviations of each of the seven microhabitat variables are given for each species in Table 5-1.

5.1.1. Discriminant Functions Analysis

Three significant discriminant functions, accounting for 91.3% of the between species variation, were extracted from the data set (Table 5-2). Figure 5-1 shows the separation of the five mosses on these three discriminant axes, accounting respectively for 38.4, 36.0 and 15.9 % of the total among species variation.

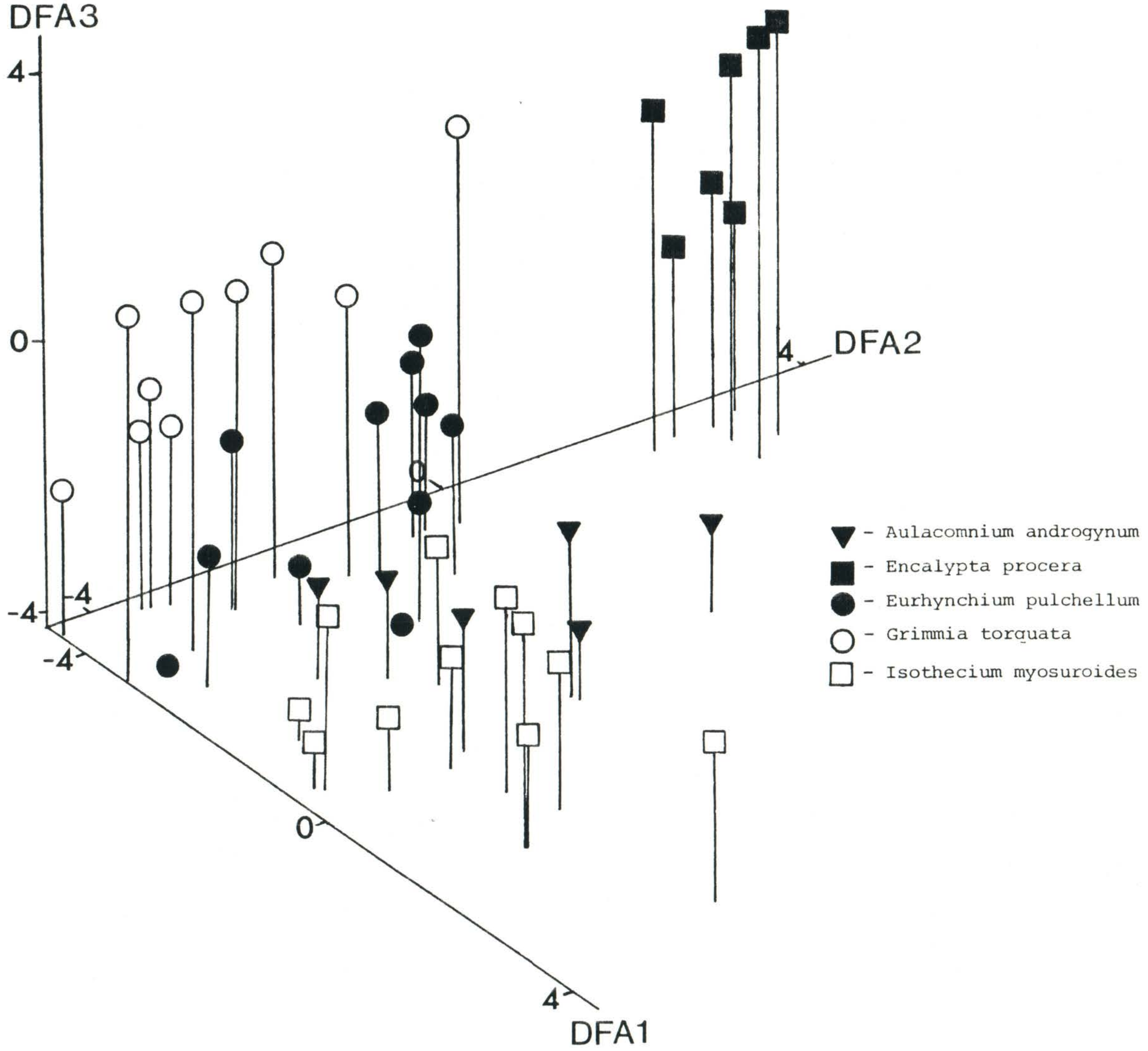
Discriminant Function 1 loads heavily on precipitation and light but with opposite sign. The empirical interpretation is the amount of precipitation received relative to incident solar radiation, and I have interpreted this function as a water deficit gradient. The basis of separation on this function is the occurrence of *Encalypta procera* and *Grimmia torquata* in microhabitats which receive very little precipitation (Table 5-1). Populations which receive moderate

Table 5-1 Means and standard deviations (parentheses) of the seven microhabitat variables measured for each of five selected cliff/scree-slope mosses.

	Microhabitat Variable						
Species	Precip (ml)	Temp T_e	Slope (deg)	Elev (m)	Light $(\log\mu\mathrm{mol}^2\mathrm{s}^1)$	Aspect (deg)	pH
Aulacomnium androgynum	298	15.4	70.5	15.5	4.5	74.7	6.06
	(74)	(2.7)	(21)	(4.0)	(0.2)	(19)	(0.4)
Encalypta procera	32	13.6	24.9	62.0	2.6	64.4	7.28
	(5)	(0.5)	(14)	(32)	(0.4)	(49)	(0.1)
Eurhynchium pulchellum	68	15.6	53.7	19.5	3.9	80.6	5.93
	(49)	(3.1)	(18)	(4)	(0.9)	(51)	(0.4)
Grimmia torquata	19	11.8	62.7	58.3	3.2	32.4	5.64
	(4)	(1.4)	(22)	(34)	(0.4)	(27)	(0.4)
Isothecium myosuroides	326	17.6	30.3	22.3	5.1	64.5	5.32
	(126)	(1.6)	(31)	(5)	(1.0)	(31)	(0.3)

Table 5-2: Summary of Discriminant Functions Analysis on microhabitat data for five moss species. DF coefficients greater than 0.5 indicated by asterisks

	Function No.		
	1	2	3
Percent of among-species variation accounted for	38.4	36.0	15.9
Cumulative percent of variance accounted for	38.4	75.4	91.3
Microhabitat variables and DF coefficients			
Precipitation	1.224*	-0.151	-0.175
Light	-0.532*	-0.291	0.378
Aspect	0.235	0.034	0.118
pH	-0.014	0.979*	0.159
Temperature	-0.049	0.158	-0.772*
Elevation	-0.070	-0.072	0.596*
Slope	-0.034	-0.064	-0.132


DFA3
4
0
-4
-4
-4
0
4
DFA1
0
4
DFA2
▼ - Aulacomnium androgynum
■ - Encalypta procera
● - Eurhynchium pulchellum
○ - Grimmia torquata
☐ - Isothecium myosuroides

amounts of precipitation also receive more solar radiation and therefore have higher evaporation rates. *Aulacomnium androgynum* and *Isothecium myosuroides* occur in microhabitats with the highest light intensities but these also receive the most precipitation (Table 5-1). The mean total precipitation for populations of *I. myosuroides* for example, is more than twice that for *Grimmia torquata*. Water deficits for *A. androgynum* and *I. myosuroides* are undoubtedly less than for the two species previously discussed.

Discriminant Function 2 is an obvious pH gradient. This function separates *Encalypta procera* and *Isothecium myosuroides* from the other three species, with *E. procera* occurring only on substrates with high pH (minimum 7.07) and *I. myosuroides* on quite acidic substrates (pH < 5.56).

Discriminant Function 3 is largely a function of temperature and elevation with opposite loading sign. *E. procera* and *G. torquata* occur at higher elevations where temperatures are generally low, but *G.torquata* also occurs near sea level at exposed coastal localities where the proximity of the ocean reduces temperatures. *Aulacomnium androgynum* and *I. myosuroides* occur at warmer sites at low elevation and away from the exposed coast.

Classification Results

The Discriminant Functions were highly successful in their ability to correctly assign populations to species on the basis of their microhabitat characteristics; 89% of the 45 populations used in the analysis were correctly assigned on these grounds (Table 5-3). 100% classification was achieved for *Aulacomnium androgynum*, *Encalypta procera*, and *Grimmia torquata*. For *Isothecium myosuroides* only a single population was incorrectly assigned (to *Aulacomnium androgynum*). The worst classification was obtained for *Eurhynchium pulchellum*, with only 64% of the populations of that species being correctly assigned. Of the four misclassified populations, two were assigned to each of *Aulacomnium androgynum* and *Isothecium myosuroides*, indicating that *E. pulchellum* occurs in the microhabitats of these two species.

5.1.2. Multiple Regression Analysis

Results of the stepwise multiple regressions are summarized in Table 5-4. The analysis was very successful, and highly significant regression equations accounting for 78% to 91% of the variation in abundance were developed for all of the species except *Eurhynchium pulchellum*. Analysis of residuals (Daniel and Wood, 1971) in each case produced no evidence to suggest that the assumptions of normality were violated.

5.1.3. Microhabitat Relationships of the Individual Species

In this section I have attempted to integrate the results of the Discriminant and Regression analyses in an evaluation of the microhabitat characteristics of each species studied.

Aulacomnium androgynum

A. androgynum occurs at warm sites, generally very near sea level, with

Table 5-3: Discriminant Functions classification of the five cliff/scree-slope mosses. Numbers in parentheses are percentages.

	Predicted species membership				
Species	1	2	3	4	5
1) Aulacomnium androgynum	6	0	0	0	0
	(100)	-	-	-	-
2) Encalypta procera	0	7	0	0	0
	-	(100)	_	_	_
3) Eurhynchium pulchellum	2	0	7	2	0
	(18)	-	(64)	(18)	-
4) Grimmia torquata	0	0	0	10	0
	_	_	_	(100)	-
5) Isothecium myosuroides	1	0	0	0	10
	(9)	-	-	-	(91)

Overall classification success = 89%.

Table 5-4 Summary of Multiple Regression Analysis of Abundance on seven microhabitat variables for five cliff/scree-slope mosses.

Species	N	Step	R^2	Equation*	p
Aulacomnium androgynum	8	1	0.64	$y = 0.26 + 0.007A$	< 0.05
		2	0.91	$y = -1.22 + 0.007A + 0.32L$	< 0.01
Encalypta procera	7	1	0.89	$y = -4.9 + 0.727H$	< 0.001
Eurhynchium pulchellum	11	1	_	none	______
Grimmia torquata	10	1	0.80	$y = 2.11 - 0.13T$	< 0.001
		2	0.89	$y = 2.48 - 0.13T - 0.02P$	< 0.001
Isothecium myosuroides	11	1	0.67	$y = 0.44 + 0.002P$	< 0.001
		2	0.78	$y = 0.21 + 0.002P + 0.003A$	< 0.001

* P = Precipitation (ml); T = Temperature (T_e); L = Light (log μmolm^{-2}s^{-1});
A = Aspect; H = pH; y = Arcsine [(proportion cover)$^{0.5}$].

abundant precipitation and high light intensity. Substrates of this species are only moderately acidic. Abundance is most closely associated with aspect, and tends to be greater on south facing exposures. There is also a strong positive association of abundance with increased light intensity, and this variable accounts for an additional 27% of the variation in abundance.

Encalypta procera

The dependence of *E. procera* on basic substrates is indicated by both discriminant analysis and multiple regression. The apparent restriction of this species to cold microhabitats with little precipitation, as indicated by the discriminant analysis, is probably a reflection of the distribution of basic subtrata in Terra Nova. As noted (Chapter 1), the area is predominantly underlain by acidic bedrock, but in a few very deep crevices small deposits of precipitated carbonate occur, and *E. procera* is restricted to these. Such crevices receive a minimal amount of precipitation and light.

Eurhynchium pulchellum

On the basis of the present work, there is little that can be said regarding microhabitat relationships of *Eurhynchium pulchellum*. Performance of this species is not significantly correlated with any of the measured variables. The discriminant analysis indicates that the species occurs in microsites with intermediate water availability (as determined by precipitation/radiation ratios) and with intermediate temperature and substrate pH.

Grimmia torquata

The tendency for *G. torquata* to occur in cold, dry sites is evident from the discriminant analysis, and regression analysis indicates a strong negative association between abundance of the species and both temperature and precipitation.

Isothecium myosuroides

It is clear from both multivariate analyses that water availability is a major factor in the microsite distribution of *Isothecium myosuroides*. Discriminant functions analysis also indicates that the species has a strong affinity for acidic sites, with high mean temperatures through the vegetative season. Abundance of the species is, in addition to being strongly associated with water availability, positively correlated with increasing aspect (ie, abundance tends to be higher on southerly slopes).

5.2. Discussion

The five species studied have distinct and different microhabitats on the scree-slopes and cliffs of Terra Nova National Park, and the performance (abundance) of most species is clearly associated with variation in some microhabitat variable or variables. It is generally assumed that the role of interspecific interaction in determining bryophyte species distribution is relatively unimportant in habitats like the one studied here since vegetation is generally very sparse and species are rarely associated (Alpert, 1985; Yarranton, 1970). Consequently, explanations for microhabitat distributions of bryophyte taxa in these habitats are sought in relationships between microhabitat (especially microclimate) and physiological adaptation of the species in question. In the present study, especial emphasis is placed on interpreting differences in microhabitat relationships among species in light of their natural geographic range.

Very strong association with microclimate is exhibited by the three species nearing latitudinal limits of distribution (*i.e. Aulacomnium androgynum, Grimmia torquata, Isothecium myosuroides*). The clear association between the distribution and performance of *Grimmia torquata* and the distribution of cold dry microsites on cliffs and scree slopes strongly suggests that sensitivity to high summer temperatures is a major determinant of micro-distribution in this arctic-montane moss. Lethal effects of high summer temperatures have been documented for many vascular plants of arctic affinity (Dahl, 1951), and ample experimental data indicate that physiological processes in polar bryophytes and vascular plants have lower optimum temperatures than do the same processes in temperate plant species (Atanasiu, 1971; Dilks and Proctor, 1975; Kallio and Karenlampi, 1975; Mooney *et al.*, 1964; Savile, 1972). Photosynthesis, for example, has an optimum temperature of 25 - 35°C in most temperate mosses studied, but in polar mosses this optimum is only 5 - 10°C. The negative relationship between precipitation and performance of *Grimmia torquata*, and its restriction to relatively dry habitats, is likely a reflection of more pronounced temperature stress in wet habitats. (Dilks and Proctor, 1975; Norr, 1974).

The two mosses of southern affinity (*Aulacomnium androgynum* and *Isothecium myosuroides*) occur in relatively warm, wet microsites. The marked restriction of *I. myosuroides* to habitats with low water deficits (indicated by position on DFA1), and the strong dependence of abundance of this species on precipitation, implicate water availability as a major factor governing the micro-distribution of this temperate-oceanic taxon. The strong dependence of this species on water availability may be related in part to its loose, pleurocarpous growth form which is less capable of water retention than other, more compact forms (Birse, 1958a,b; Gimingham and Birse, 1957; Hamilton, 1953).

The performance of *A. androgynum* is most closely related to aspect, and this microhabitat variable is also partly associated with performance of *Isothecium myosuroides*; abundance in both cases is higher on southern aspects. Aspect, while not likely to directly affect the performance of species, may be strongly associated with other microclimatic factors (Alpert, 1985; Bates, 1982; Grime and Lloyd, 1973). In the present instance it appears that winter climate is implicated, and it is particularly tempting to suggest a relationship with mild winter temperatures since the distribution in Newfoundland of many vascular plants of southern affinity tends to be strongly dependent on the distribution of such temperatures (Damman, 1965).

The two mosses with extensive distribution both north and south of the study area (*i.e. Encalypta procera, Eurhynchium pulchellum*) do not show clear patterns of association with microclimate. As noted above, the apparent restriction of *E. procera* to cold, dry microhabitats appears to be a reflection of the distribution of calcareous substrates rather than an indication of a microclimatically imposed constraint.

Plant species nearing latitudinal limits may depend more strongly on well defined, narrow ranges of microhabitat than do species which are well within their range limits (Bocher, 1954). The present analysis supports this, and provides evidence that such dependence is related to patterns of physiological adaptation, which are presumably constrained by the evolutionary histories of the different species; distributional histories must be superimposed on these.

Statistical association of species distribution and/or performance with a given microhabitat variable does not constitute proof of cause and effect. However, the explanations offered for the observed patterns (where these were discernable) constitute testable hypotheses. Validation or refutation of these hypotheses can perhaps be best accomplished by a comparative experimental approach (*e.g.*, phytotron growth studies); such studies constitute the next logical step in the work initiated here.

Chapter 6

General Discussion

The present phytogeographic structure of the Terra Nova moss flora betrays an intricate interplay between history, species dispersability, and plant-environment relationships. Interpretation of this regional flora must involve synthesis and integration of information pertaining to all three of these broad areas, and it is primarily this interpretive task that the present chapter seeks to accomplish.

The entire bryoflora of the northern portion of North America has been greatly affected by Pleistocene glaciations (Crum, 1966, 1972; Schofield, 1972, 1981), and that of Terra Nova is no exception. The apparent effects of species dispersability on the structure of the Terra Nova moss flora are inextricably linked to the history of the region, and particularly to its glacial and immediate postglacial history. Most of eastern Newfoundland was ice covered until *ca.* 8,500 years B.P., and even after ice retreated much of the territory was unavailable for plant colonization because of somewhat higher sea levels and the existence of several large lakes in what are now the major river valleys of the region (Gauthier *et al.*, 1977). Colonization may have been further delayed since the study area is isolated from potential colonizing sources in southern and western portions of the island. The flora of Terra Nova must, therefore, have been recently derived.

The effects of regional climate are evident in the essentially boreal character of the Terra Nova moss flora; it is dominated by species with broad distributions in the vast boreal forest belt of North America. Oceanic tendencies in the climate of the study area, the most important expression of which is moderated winter temperatures (Banfield, 1981), are reflected in the occurrence of a small, distinctly oceanic element in the Terra Nova moss flora.

Edaphic factors exert a clear influence on bryofloristic composition of the study area. The uniformly acidic nature of the underlying bedrock is reflected in the preponderance of acidophilic and edaphically undemanding species in the flora, and the virtual absence of calciphilic species.

Human activity in Terra Nova has resulted in alteration of much of the forest in the area. Past logging practices and extensive fires have favoured black spruce at the expense of balsam fir. Bryophyte species diversity (especially of temperate species) in black spruce forests is low compared to that in the now infrequent and small balsam fir stands. Thus the distinct possibility exists that anthropogenic influence in Terra Nova may have eradicated certain elements in the original (postglacial) bryoflora.

Environmental restrictions coupled with constraints imposed by species dispersal ability are likely responsible for the low representation of extraneous elements (*sensu* Cain, 1944) in the Terra Nova moss flora (*i.e.* arctic-montane elements, temperate species at northern limits, and montane elements). Given that a species possesses the ability for rapid dispersal, its occurrence in the study area is dependent not only on its reaching there, but also on its ability to establish itself, and persist under prevailing and variable local conditions. Species belonging to the extraneous elements are able to persist only in a narrow range of habitat types, and consequently are of restricted distribution in the study area (and often in much of Newfoundland). Furthermore, there is strong evidence (Chapter 5) that the extraneous species are highly dependent on narrowly defined microclimatic ranges. Even if such species are able to reach the study area, they can only become established if diaspores reach suitable habitats and microclimatically favourable sites. Thus, species establishment is dependent on the probability of a diaspore "finding" a favourable site. This should provide even stronger selection for species with high dispersal ability.

Evidence for such selection is provided by the log-linear model, which indicates that the likelihood of an arctic-montane species occurring in Terra Nova is very low relative to that of temperate or montane species. This former element shows strong habitat restriction, (and if *Grimmia torquata* is representative, strong microhabitat restriction) and the total available habitat in the study area is less for this group than for the other two. It seems more than coincidental that, of the three extraneous elements, the proportion of taxa in the study area with small diaspores is highest in the arctic-montane group.

Chapter 7

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Appendix A

List of Moss Species known from Terra Nova National Park

The following table lists all moss species currently known from Terra Nova National Park. Authorities for taxa listed are given in Brassard (1983b). For each species, occurrence in the park habitats, Newfoundland distribution, Affinity class, and diaspore size class is indicated. Habitat abbreviations are as in Table 3-2, and occurrence in a given habitat is indicated by a 1. Newfoundland distributions (ND) are: 1-Widespread, 2-Widespread but sporadic, 3-northwestern, 6-southern, 7-southeastern, 8-disjunct, 9-unknown. Affinity classes (WA) are: 1-Boreal, 2-Temperate, 3-Arctic-montane, 5-Montane, 6-Cosmopolitan. Diaspore size classes (DA) are: 1-$<$ 25μm, 2-$>$25 but $<$100μm, 3-$>$ 100μm.

Habitat

SPECIES	KB	Ca	Bs	Cl	Bf	DH	Ru	Wb	TA	RB	KA	Bg	Fn	FM	EM	Sw	Fw	Co	IC	SS	An	ND	WA	DA
Amphidium lapponicum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	1	1	1
Amphidium mougeotii	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	1
Andreaea rothii	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	0	1	1	2
Andreaea rupestris	0	0	1	0	1	0	0	1	0	1	1	0	0	0	0	0	1	0	1	0	0	1	6	2
Atrichum altecristatum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	2	2	1
Atrichum crispum	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	2	3
Atrichum oerstedianum	0	0	0	0	1	1	1	1	0	0	0	0	0	0	0	1	1	0	0	0	0	1	1	1
Atrichum undulatum	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	0	0	0	0	6	1	1
Aulacomnium androgynum	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	1	8	1	1
Aulacomnium palustre	0	0	0	0	1	0	0	1	0	0	0	1	1	1	0	0	1	1	0	0	1	1	1	1
Barbula unguiculata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2	1	1
Bartramia ithyphylla	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	2	3	1
Bartramia pomiformis	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	1	1	1
Blindia acuta	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	1	1	1
Brachythecium albicans	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2	1	1
Brachythecium campestre	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	1
Brachythecium erythrorrhizon	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	3	1	1
Brachythecium plumosum	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	1	1	1
Brachythecium populeum	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1
Brachythecium reflexum	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	1	1
Brachythecium rivulare	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1	1

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Brachythecium rutabulum	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	2	1	1
Brachythecium salebrosum	0	0	0	0	1	1	1	1	1	0	0	0	0	0	0	1	0	0	0	1	0	1	1	1
Brachythecium starkei	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1
Brotherella recurvans	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	2	1
Bryhnia novae-angliae	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	1	2	1
Bryoerythrophyllum recurvirostrum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	6	1
Bryum alpinum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	8	5	3
Bryum argenteum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	6	1
Bryum caespiticium	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	8	1	1
Bryum capillare	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	2	1	2
Bryum knowltonii	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	9	3	1
Bryum lisae var cuspidatum	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	1	2	6	1
Bryum muehlenbeckii	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	8	5	3
Bryum pallescens	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	2	1	1
Bryum pseudotriquetrum	0	0	1	0	1	0	0	1	1	0	0	1	1	0	1	1	1	1	0	0	0	1	6	1
Bryum salinum	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	2	1	1
Bryum stenotrichum	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	1	6	1
Buxbaumia aphylla	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	8	1	1
Callicladium haldanianum	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	2	1
Calliergon cordifolium	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	2	1	1
Calliergon stramineum	0	0	0	0	0	0	0	0	0	1	0	1	0	1	1	0	0	0	0	0	0	1	1	1

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Campylium chrysophyllum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1	1
Campylium polygamum	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1	0	0	0	0	0	1	1	1
Campylium stellatum	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	1	1	1
Ceratodon purpureus	0	0	0	1	1	0	0	0	0	1	1	0	0	0	0	0	0	1	0	1	1	1	6	1
Climacium dendroides	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1	1	1
Cynodontium alpestre	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	1	1	1
Cynodontium strumiferum	0	0	0	0	1	0	0	0	0	1	1	0	0	0	0	0	1	1	1	1	0	1	1	1
Dicranella cerviculata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2	1	1
Dicranella subulata	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8	1	1
Dicranella heteromalla	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	1	1	1	1	0	1	2	1
Dicranum bonjeanii	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	1	1	0	1	1	1
Dicranum fuscescens	0	1	1	0	1	1	1	1	1	1	0	0	0	0	0	1	1	1	1	1	0	1	1	1
Dicranum leioneuron	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	1
Dicranum majus	0	0	1	0	1	1	0	1	0	0	0	0	0	0	0	1	0	0	1	0	0	1	1	1
Dicranum ontariense	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1
Dicranum polysetum	0	0	1	0	1	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	1	1	1	1
Dicranum scoparium	0	1	1	0	1	6	1	1	1	1	0	0	0	1	0	1	1	0	0	1	1	1	1	1
Dicranum spurium	0	0	0	1	0	0	0	0	0	1	1	0	0	0	1	0	0	0	0	0	1	1	1	1
Dicranum undulatum	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	1	0	0	0	0	0	1	1	1
Diphyscium foliosum	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	1	1	1
Distichium capillaceum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	2	6	1
Ditrichum lineare	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1

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Ditrichum pusillum	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2	1	1
Drepanocladus ex annulatus	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	1	0	0	0	0	0	1	1	1
Drepanocladus fluitans	0	0	1	0	0	0	0	0	0	0	0	1	1	0	1	0	0	1	0	0	0	1	1	1
Drepanocladus revolvens	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	1	1	1
Drepanocladus uncinatus	0	0	1	0	1	1	1	1	1	0	1	1	0	0	0	1	0	0	0	1	1	1	1	1
Dryptodon patens	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	8	5	3
Encalypta procera	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	3	1	2
Eurhynchium pulchellum	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	3	1	1
Fissidens adiantoides	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1	1	1
Fissidens osmundoides	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	1	1	1
Fontinalis dalecarlica	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	2	1	1
Fontinalis novae-angliae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1	1
Funaria hygrometrica	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	6	1
Grimmia anomala	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	8	5	2
Grimmia donniana	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	2	3	1
Grimmia incurva	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	2	5	3
Grimmia tenerrima	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	8	5	1
Grimmia torquata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	9	3	2
Grimmia trichophylla	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	2	5	1
Gymnostomum aeruginosum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1	1

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Mnium hornum	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	1	1	0	1	1	1	1	2
Neckera complanata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0	2	1	3
Neckera pennata	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	1
Oligotrichum hercynicum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	8	3	1
Oncophorus wahlenbergii	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1
Orthodicranum flagellare	0	0	0	0	1	0	0	0	0	1	1	1	0	0	0	0	0	1	1	1	0	1	1	1
Orthodicranum montanum	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	1	1	1
Orthotrichum gymnostomum	0	0	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	2	1	1
Orthotrichum obtusifolium	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	2	1	1
Orthotrichum pylaisii	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	9	3	1
Orthotrichum rupestre	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	9	5	1
Orthotrichum speciosum	0	0	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	2	1	1
Paraleucobryum longifolium	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0	1	1	2
Philonotis fontana	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	1	0	1	0	1	1	1
Plagiothecium cavifolium	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	1	1	1
Plagiothecium denticulatum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1	1	1
Plagiothecium laetum	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	1	0	1	1	0	1	1	1
Plagiothecium la tebricola	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	2	1
Pleurozium schreberi	1	1	1	1	1	1	0	1	1	0	0	1	1	1	0	1	1	0	0	1	1	1	1	1
Pogonatum dentatum	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1
Pogonatum pensilvanicum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	6	2	1

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Pogonatum urnigerum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1
Pohlia annotina	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	2	2
Pohlia cruda	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	1	6	1
Pohlia nutans	0	0	1	1	1	0	0	0	0	1	0	0	0	0	0	1	0	1	1	0	1	1	6	1
Polytrichastrum alpinum	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	1	1	1	1	0	1	1	1
Polytrichastrum formosum	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	6	2	1
Polytrichastrum longisetum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1
Polytrichastrum pallidisetum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	1
Polytrichum commune	0	0	1	1	1	0	0	1	0	0	0	1	1	1	0	1	0	0	0	0	1	1	6	1
Polytrichum juniperinum	0	0	1	1	1	0	0	1	0	1	1	1	1	0	0	1	0	0	0	1	1	1	6	1
Polytrichum piliferum	0	0	0	1	1	0	0	1	0	0	1	1	1	0	0	0	0	0	1	0	1	1	6	1
Polytrichum strictum	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	1	1	1
Pterygynandrum filiforme	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	1	1	2
Ptilium crista-castrensis	0	0	1	1	1	1	0	1	1	0	0	1	1	0	0	1	1	0	0	1	0	1	1	1
Racomitrium aciculare	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	1	0	1	0	0	1	1	1
Racomitrium canescens	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	8	1	3
Racomitrium fasciculare	0	0	0	0	1	0	0	1	0	0	1	0	0	0	0	0	1	0	1	0	1	1	1	1
Racomitrium heterostichum	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	1	1	0	0	0	1	1	1
Racomitrium lanuginosum	0	0	0	0	0	0	0	0	0	1	0	1	1	0	0	0	0	0	0	1	0	1	3	1
Racomitrium microcarpon	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	1	0	1	1	1

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Rhabdoweis ia crispata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	1	1	1
Rhizomnium appalachianum	1	0	0	0	1	1	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	2	2	1
Rhizomnium magnifolium	1	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1	2
Rhizomnium punctatum	0	0	1	0	1	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	1	2	2
Rhytidiadelphus loreus	0	0	1	0	1	1	0	1	1	0	0	0	0	0	1	1	0	1	0	1	0	1	1	1
Rhytidiadelphus squarrosus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1
Rhytidiadelphus subpinnatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	2	1	1
Rhytidiadelphus triquetrus	0	0	1	0	1	1	0	1	1	0	0	1	0	0	1	1	0	0	1	1	0	1	1	1
Schistidium agassizzii	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	2	5	1
Schistidium apocarpum	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1	0	0	0	1	6	1
Schistidium gracile	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1	1	1
Schistidium maritimum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1	1
Schistidium rivulare	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	2	1	1
Scorpidium scorpioides	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	8	1	1
Sphagnum angermannicum	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	2	1
Sphagnum capillifolium	0	0	1	0	1	0	1	0	0	0	1	1	1	0	0	0	0	0	1	0	1	1	1	1
Sphagnum centrale	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	7	1	2
Sphagnum compactum	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	1	1	2
Sphagnum cuspidatum	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	1	1	2

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Sphagnum fallax	0	1	0	0	0	0	0	0	0	0	0	1	1	1	0	1	0	0	0	0	1	1	1	1
Sphagnum fimbriatum	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	7	1	1
Sphagnum flavicomans	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	1	1	2
Sphagnum fuscum	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	1	1	1
Sphagnum girgensohnii	0	1	1	0	1	1	1	0	0	0	0	1	1	0	0	1	1	0	0	0	1	1	1	1
Sphagnum imbricatum	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	1	1	3
Sphagnum lindbergii	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0	0	2	1	1
Sphagnum magellanicum	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	1	6	1
Sphagnum majus	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	1	1	2
Sphagnum molle	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	2	2	2
Sphagnum palustre	0	0	0	0	1	1	1	0	0	0	0	1	1	1	0	0	1	0	0	0	0	1	6	2
Sphagnum papillosum	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	1	1	2
Sphagnum pulchrum	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	1	1	2
Sphagnum pylaisii	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0	0	1	2	3
Sphagnum quinquefarium	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1	1
Sphagnum rubellum	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	1	0	0	1	1	1
Sphagnum recurvum	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	1	1	1
Sphagnum russowii	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	1	1	1	1
Sphagnum squarrosum	0	0	0	0	1	1	0	0	0	0	0	1	1	1	0	1	0	0	0	0	0	1	1	1
Sphagnum strictum	0	0	0	0	0	0	0	0	0	1	0	1	1	0	0	0	0	0	1	0	0	2	1	2

Appendix A continued-

Sphagnum subfulvum	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	1	1	1
Sphagnum subnitens	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	9	1	2
Sphagnum subsecundum	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	1	0	0	0	0	0	2	1	1
Sphagnum tenellum	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0	0	1	1	2
Sphagnum teres	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2	1	1
Sphagnum torreyanum	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	1	1	0	0	0	0	2	1	2
Sphagnum warnstorfii	0	0	0	0	0	1	0	0	0	0	0	1	1	0	0	1	0	0	0	0	0	2	1	1
Splachnum ampullaceum	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	2	1	1
Tayloria serrata	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8	3	1
Tetraphis pellucida	0	0	1	0	1	0	1	0	1	0	0	0	0	0	0	1	0	0	0	0	0	1	1	1
Tetraplodon angustatus	0	0	1	0	1	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	1	8	1	1
Tetraplodon mnioides	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	1	1
Thuidium delicatulum	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1	1	1	1
Tomenthypnum nitens	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	3	1	1
Tortella fragilis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1	2
Tortella tortuosa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0	1	1	1

Appendix A continued_

Tortula ruralis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2	1	1
Trematodon ambiguus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	1
Trichostomum tenuirostre	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	1
Ulota coarctata	0	0	1	0	1	1	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1	1
Ulota crispa	0	0	1	0	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1
Ulota curvifolia	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	1	3	1
Ulota drummondii	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	6	2	1
Ulota hutchinsiae	1	0	0	0	1	1	0	0	1	0	1	0	0	0	0	0	1	1	0	1	0	1	1	1
Ulota phyllantha	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1	2
Zygodon viridissimus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	2	1	2

Appendix B

Annotated List of Phytogeographically Noteworthy Species

All collection numbers cited in the following list are mine unless otherwise indicated.

Atrichum crispum (James) Sull. *3146.* A species of temperate affinity which is its north-eastern limit of North American distribution in the study area.

Atrichum undulatum (Hedw.) P.Beauv. *3310, 3327, 3468.* A species of boreal affinity, disjunct between eastern and western North America. Not well known in the east (Ireland, 1982); the populations in the study area represent the northern limit of the species' known distribution in easte North America.

Aulacomnium androgynum (Hedw.) Schwaegr. *2307, 2321, 2330, 2459, 2699, 2714, 3090, 3093, 3170, 3216, 3256, 3295.* A species of boreal affinity, disjunct between eastern and western North America. According to Crum and Anderson (1981), rare and scattered in the eastern part of the continent. In Newfoundland, known mostly from the northeast, but also from two west coast stations.

Bartramia ithyphylla Brid. *Hedderson, s.n.* An arctic-montane species which in Newfoundland is mostly restricted to the coast but also occurs in the mountains of the Northern Peninsula and west coast.

Brachythecium erythrorrhizon B.S.G. *2316.* In Newfoundland, this species occurs predominantly in the calcareous regions of the northwest, and the Terra Nova population is the southeastern limit of the species' known insular distribution.

Bryum alpinum With. *2468.* This predominantly montane species is rare in eastern North America where it is known from only one station outside Newfoundland. On the island, it is known from the study area and a single west coast locality (Tuomikoski et al, 1973).

Bryum knowltonii Barnes *3385.* An arctic-montane species known in eastern North America (outside the arctic) only from Newfoundland. On the island, known from several collections on the tip and east side of the Northern Peninsula, and along the northeast coast.

Bryum muehlenbeckii B.S.G. *3068.* Rare in eastern North America, and disjunct from a broad western range, this montane species is mostly known in Newfoundland from the Avalon Peninsula and adjacent areas, as well as from a single west coast locality.

Dryptodon patens (Hedw.) Brid. *Brassard, 9256.* A montane species, known in eastern North America only from Newfoundland, but with intermediate populations in the Great Lakes area (Crum and Anderson, 1981). In Newfoundland the species is known from several west coast localities, but in the east only from the study area.

Encalypta procera Bruch *2532b, 3008.* A calciphilic moss, widespread in North America from the high arctic to temperate forests. In Newfoundland, known previously from the calcareous regions of the northwest. The present specimens were collected from limey deposits in crevices of granite bedrock .

Eurhynchium pulchellum (Hedw.) Jenn. *2676, 3021, 3024.* A widespread species in North America, occurring from arctic to temperate regions. In Newfoundland, the species has a markedly northwestern bias in its distribution and is most frequent on calcareous substrates. Study area populations are the southeastern-most extension of the species range within Newfoundland.

Grimmia anomala Hampe *ex* Schimp. *3677.* A boreo-montane species (Vitikainen, 1969) disjunct in North America between the Rocky Mountains and Newfoundland with intermediate populations in the Great Lakes area. In Newfoundland, the species occurs at several west coast stations and at several localities in the southeast.

Grimmia donniana Sm. *3670, 3674.* These are the first eastern Newfoundland records of an arctic-montane species, rare in eastern North America. Otherwise widespread in Newfoundland and especially common on the south and west coasts.

Grimmia incurva Schwaegr. *3676.* A predominantly montane species widespread in Newfoundland but known elsewhere in eastern North America only from a few collections in the Maritime Provinces (Belland, 1984), and the Torngat Mountains of northern Labrador (Hedderson and Brassard, 1986).

Grimmia tenerrima Ren. & Card. *3664.* A montane species, disjunct between eastern and western North America, with intermediate populations in the Great Lakes region. In Newfoundland the species has a disjunct distribution, being known previously from the Bonne Bay area and from northernmost Newfoundland. The population in the study area is on schist, and is the only known Newfoundland population that is not on heavily serpentinized rock.

Grimmia torquata Hornsch. *ex* Grev. *2342, 2353, 2368, 2535, 2707, 2752, 3095, 3175.* An arctic-montane species that is widespread but sporadic in eastern North America. In Newfoundland it is known only from the north-east coast and one Burin Peninsula locality (Brassard, 1983a).

Heterocladium dimorphum (Brid.) B.S.G. *3166.* A widespread boreal-temperate species mostly known in Newfoundland from the calcareous northwest. The specimen cited here, however, was collected from siliceous boulders where it was associated with such acidophiles as *Hedwigia ciliata* and *Racomitrium microcarpon*.

Homalothecium sericeum (Hedw.) B.S.G. *3439, 3473.* In North America this species is known only from the island of Newfoundland where it is quite broadly distributed. The species may have been introduced from Europe, but many specimens, like those cited here, are from natural, undisturbed habitats, suggesting that at least some of the populations are native.

Hypnum fertile Sendtn. *2647, 3158, 3245.* A species of temperate affinity, known in Newfoundland from several stations in the southeast, and a single west coast station, at Bonne Bay.

Isopterygiopsis muelleriana (Schimp.) Iwats. *2264.* A species of boreal affinity, disjunct between eastern and western North America (Crum and Anderson, 1981; Ireland, 1969). In Newfoundland, this species is known from several west coast localities but the specimen cited here appears to constitute the first record from the eastern part of the island.

Isothecium myosuroides Brid. *2393, 2462, 3009, 3010, 3011, 3091, 3242, 3264, 3265, 3270, 3422.* A temperate-oceanic species, disjunct between eastern and western North America, with an intermediate station in the Great Lakes (Allen, 1983). It reaches its northern limit of eastern North American distribution in the study area, and in Newfoundland has a distinctly southeastern distribution (Brassard, 1983a).

Kiaeria blyttii (Schimp.) Broth. *3339.* An arctic-montane species widespread in Newfoundland, but otherwise uncommon in eastern North America south of the arctic.

Kindbergia praelonga (Hedw.) Ochyra. *3481.* A species of temperate affinity, common in western North America and disjunct to the eastern part of the continent where it is largely restricted to the Gulf of St. Lawrence region (Crum and Anderson, 1981). In Newfoundland this species is most frequent in the southeast but is also known from a single station in the southwestern part of the island.

Oligotrichum hercynicum (Dicks.) Schwaegr. *3193.* An arctic-montane species disjunct between eastern and western North America (Long, 1985). Outside Newfoundland, this species is known in the east only from one collection in Nova Scotia (Allen, 1984) and from the Torngat Mountains (Hedderson and Brassard, 1986). Within Newfoundland, *O. hercynicum* has mostly been collected from snowbeds in the Long Range Mountains, but recently has also been found in disturbed roadside habitats at several stations on the Avalon Peninsula.

Orthotrichum gymnostomum Brid. x *O. obtusifolium* Brid. *2279, 2336.* These specimens with gametophytes of *O. gymnostomum* bear sporophytes which are intermediate between that species and the closely related *O. obtusifolium*. The intermediate sporophytes, interpreted as naturally occurring hybrids, are discussed in detail in Hedderson (1986).

Orthotrichum rupestre Schleich. *ex* Schwaegr. *3373.* A montane species, widespread in western North America but known elsewhere on the continent only from a few Great Lakes localities, the White Mountains of New

Hampshire, and Newfoundland (Crum and Anderson, 1981; Vitt, 1974). The present record is only the second from Newfoundland; the species was previously collected at Exploits.

Plagiothecium latebricola B.S.G. *3415.* In North America, a rare species that is largely confined to the eastern temperate forest region (Ireland, 1986). Populations in the study area represent the northeastern limit of this species' North American distribution.

Pogonatum pensilvanicum (Hedw.) P.Beauv. *Norris, 3934, 3935.* A species of temperate affinity, widespread in eastern North America and reaching its northeastern limit of continental distribution in Newfoundland (Crum and Anderson, 1981). In Newfoundland *P. pensilvanicum* is known from a few scattered southern localities and is at its northern limit of known distribution just north of the study area, near Gander.

Racomitrium canescens (Hedw.) Brid. *3211.* This species is suprisingly rare in Newfoundland where it is otherwise known only from a few stations in the southwest. It is almost certainly undercollected.

Scorpidium scorpioides (Hedw.) Limpr. *3735.* A predominantly calciphilic species widespread in arctic and boreal regions of North America. In Newfoundland, very common in the calcareous northwest but otherwise known only from a few southern and southeastern stations.

Sphagnum angermannicum Melin *3206.* In North America, predominantly associated with the American coastal plain, from which the Newfoundland, and other Gulf of St. Lawrence populations, are disjunct (Lavoie and Gauthier, 1983; Maass, 1967).

Sphagnum molle Sull. *2994*. In North America, this species is almost exclusively associated with the eastern coastal plain where it is distributed in several disjunct areas. Crum (1984) gives its continental range as eastern Texas to Florida and north to North Carolina; New Jersey, New York, eastern Quebec, and Newfoundland; also inland in the mountains of North Carolina and the Cumberland Plateau of Kentucky and Tennessee. In Newfoundland the species is known from less than a dozen sporadically distributed localities.

Sphagnum strictum Sull. *3358, 3364, 3405*. Like the two foregoing species, largely associated with the eastern coastal plain in North America, but perhaps less patchily distributed than either (Crum, 1984). In Newfoundland, *S.strictum* has a distinctly southeastern distribution.

Tayloria serrata (Hedw.) B.S.G. *3412*. An arctic-montane species, disjunct between eastern and western North America. In Newfoundland, *T. serrata* was previously known only on the basis of a single collection from the Bay of Islands area on the west coast of the island (Brassard, 1975).

Tomenthypnum nitens (Hedw.) Loeske. *2435*. A widespread boreal-arctic species known previously in Newfoundland from calcareous fens on the west coast and the Northern Peninsula, from an east coast station in a coastal fen near Gambo (Tuomikoski *et al.*, 1973) and from a fen on the island of Miquelon (Etcheberry *et al.*, 1987). The Terra Nova specimen is from a population in a roadside salt dump where the presence of salt may compensate for the lack of calcareous conditions.

Tortella fragilis (Drumm.) Limpr. *3438.* A widespread calciphile which in Newfoundland is common in the northwest, but otherwise associated primarily with coastal habitats (Brassard, 1983a).

Ulota curvifolia (Wahlenb.) Lilj. *2387, 2513, 3086, 3296.* A low-arctic and montane species which nears its southern limit of eastern North American distribution in Newfoundland (Vitt, 1973). Widespread in Newfoundla nowhere common.

Ulota drummondii (Hook. & Grev. *ex* Grev.) Brid. *3057, 3154.* An essentially boreal species, broadly disjunct in North America from Newfoundland and Bonaventure Island to southeast Alaska and the Queen Charlotte Islands (Crum and Anderson, 1981; Vitt, 1970). In Newfoundland, *U. drummondii* has a markedly southern distribution.