

THE BRYOPHYTE FLORA OF BRIDAL VEIL FALLS, BRITISH COLUMBIA:
AN ANALYSIS OF ITS COMPOSITION AND DIVERSITY

by

NATHALIE DJAN-CHEKAR

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Department of Botany

The University of British Columbia
Vancouver, Canada

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Abstract

Bridal Veil Falls is a small provincial park located at the eastern extremity of the Fraser Lowland in southwestern British Columbia. This study presents an inventory of the bryophyte flora of Bridal Veil Falls Provincial Park and an adjacent boulder slope. This inventory provided the basis for a discussion of the ecology and geographical affinities of the bryoflora emphasizing the environmental and historical factors that are determinant of its composition. A key to the mosses is provided.

Field work conducted between 1991 and 1992 and examination of herbarium specimens revealed a diverse bryoflora in comparison to areas of similar size in British Columbia's Lower Mainland. This bryoflora is composed of 210 species (150 mosses and 60 liverworts). In addition, *Barbula convoluta* var. *gallinula* was found new to British Columbia.

An analysis of bryophyte occurrence in habitats showed that high species diversity can be attributed to the wide variety of both habitats available at the site and microenvironments associated with these different habitats. Variations of light, moisture, and edaphic conditions were found to be generally important sources of diversity.

The bryoflora of Bridal Veil Falls has a strong circumboreal component. Its affinity with the rich bryoflora of coastal British Columbia is reflected by a large proportion of Pacific North American endemics and species of humid coastal regions. The availability of suitable microenvironments allows the occurrence of species of arctic-montane, mediterranean and strictly oceanic distribution. The bulk of the flora is probably derived from bryophyte populations that colonized the Lower Mainland of British Columbia from southern refugia after the retreat of the Wisconsin ice.

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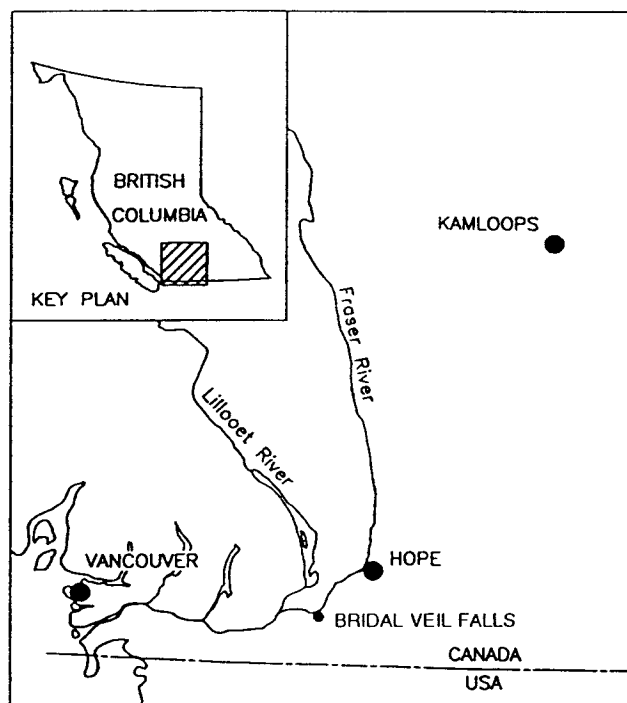
Chapter 1. Introduction

1.1. Objectives

Floristic studies provide the foundation for an understanding of biodiversity in plants. They also present the background for studies of the environment. In British Columbia's Provincial Parks, such detailed studies are rare, and there are none of bryophyte diversity. Bridal Veil Falls Provincial Park was chosen for its ready accessibility, and because earlier bryophyte collections made there suggested an exceptional diversity for its size and presented a number of intriguing phytogeographical problems. The aim of this study was thus to prepare a detailed documentation of the bryophyte flora of Bridal Veil Falls area with consideration of the environmental and historical factors that determine its composition.

Bridal Veil Falls Provincial Park is located in the coastal region of British Columbia about 100 km east of Vancouver in the Lower Fraser River Valley (Fig. 1.1). The climate of coastal British Columbia is especially favourable for bryophytes (Schofield 1992). It is characterized by year-round moderate temperatures, high rainfall and mild winters (Hare and Thomas 1974). Although the area was almost completely covered by ice during the Wisconsin glaciation, favourable coastal refugia south of the glacial boundary and along the southern coast of Alaska helped preserve this rich bryoflora (Schofield 1984, 1992). The mild and humid coastal climate and historical circumstances combine with the variety of microhabitats available at Bridal Veil Falls to create a high potential for an abundant and rich bryophyte flora.

Figure 1.1. Location of Bridal Veil Falls Provincial Park, British Columbia.



Specific objectives of this study were:

1. To present an inventory of the bryophytes of Bridal Veil Falls area.
2. To design a key to the mosses of the area.
3. To describe and discuss bryophyte occurrence in the various habitats and substrata found at the site.
4. To analyse geographical affinities of the species composing the flora.
5. To examine the relationship between habitat and geographic affinity.
6. To examine bryophyte diversity at Bridal Veil Falls in light of late-Pleistocene and Holocene history of coastal British Columbia and the Fraser Lowland.

1.2. Description of the study area

Bridal Veil Falls Provincial Park was established in 1965 and comprises an area of 32 hectares (British Columbia Parks Branch 1990). The study area includes the park, and a boulder slope immediately adjacent to the west of the park. The boulder slope was included in the study area because it represents a habitat very different from those found in the park. It also appears of particular bryological and phytogeographical interest based on earlier collections. The whole of the study area therefore covers approximately 60 hectares. Figure 1.2 presents a schematic diagram showing the different environments found in the study area.

1.2.1. Physiography, geology and geomorphology.

Bridal Veil Falls is located near the eastern extremity of the Fraser Lowland in British Columbia's Lower Mainland (Fig 1.3). The Fraser Lowland belongs to the Georgia

Figure 1.2. Schematic diagram of the study area (not to scale).

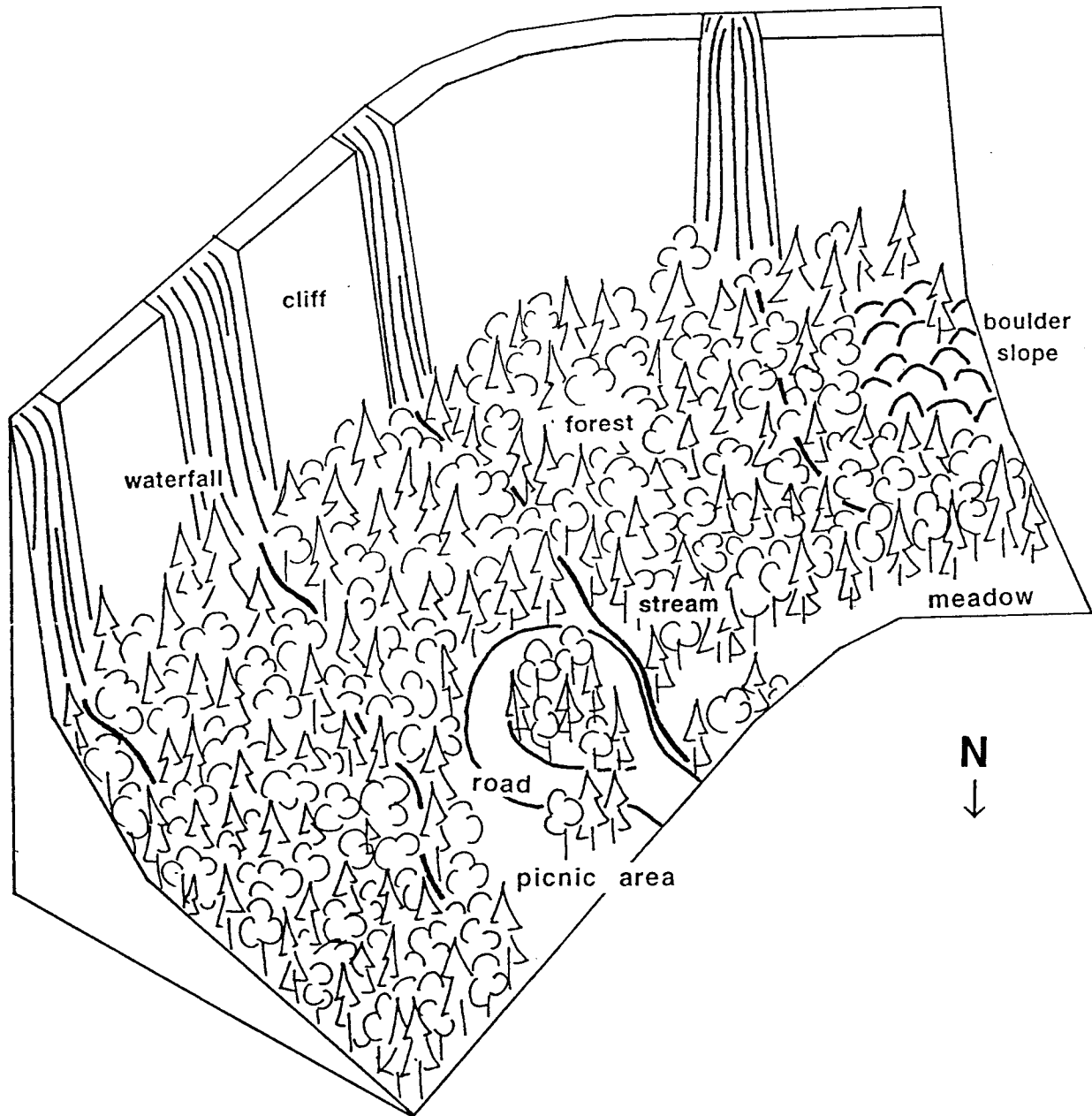
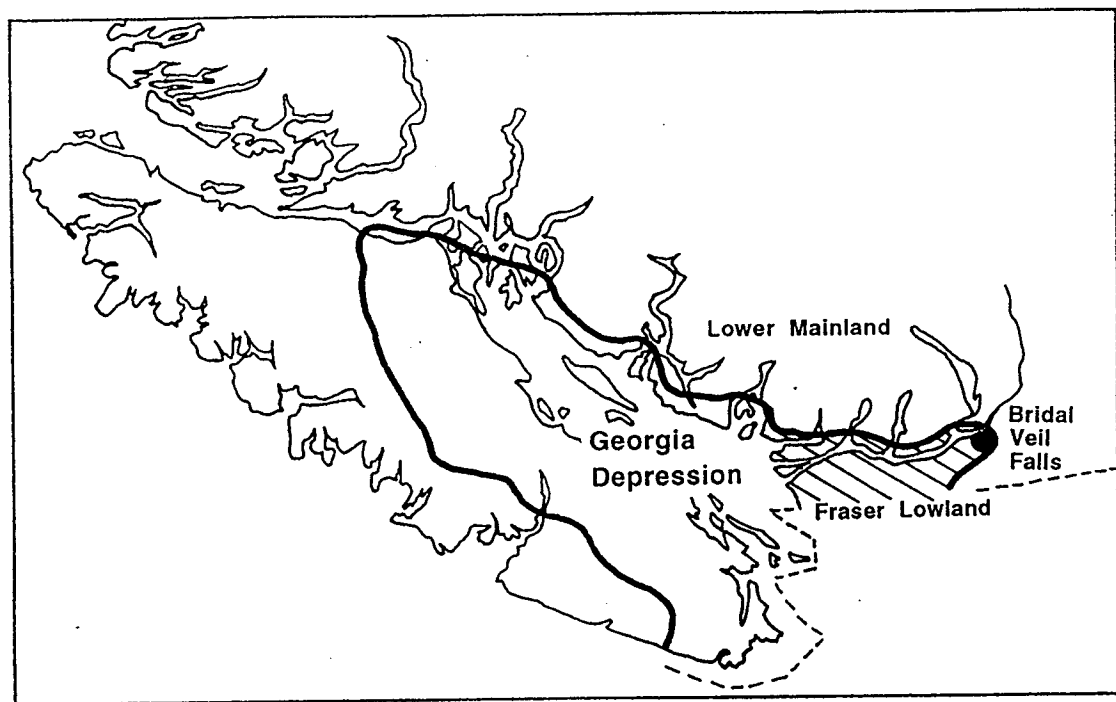


Figure 1.3. Physiographical setting of Bridal Veil Falls. (from Campbell *et al.* 1990)



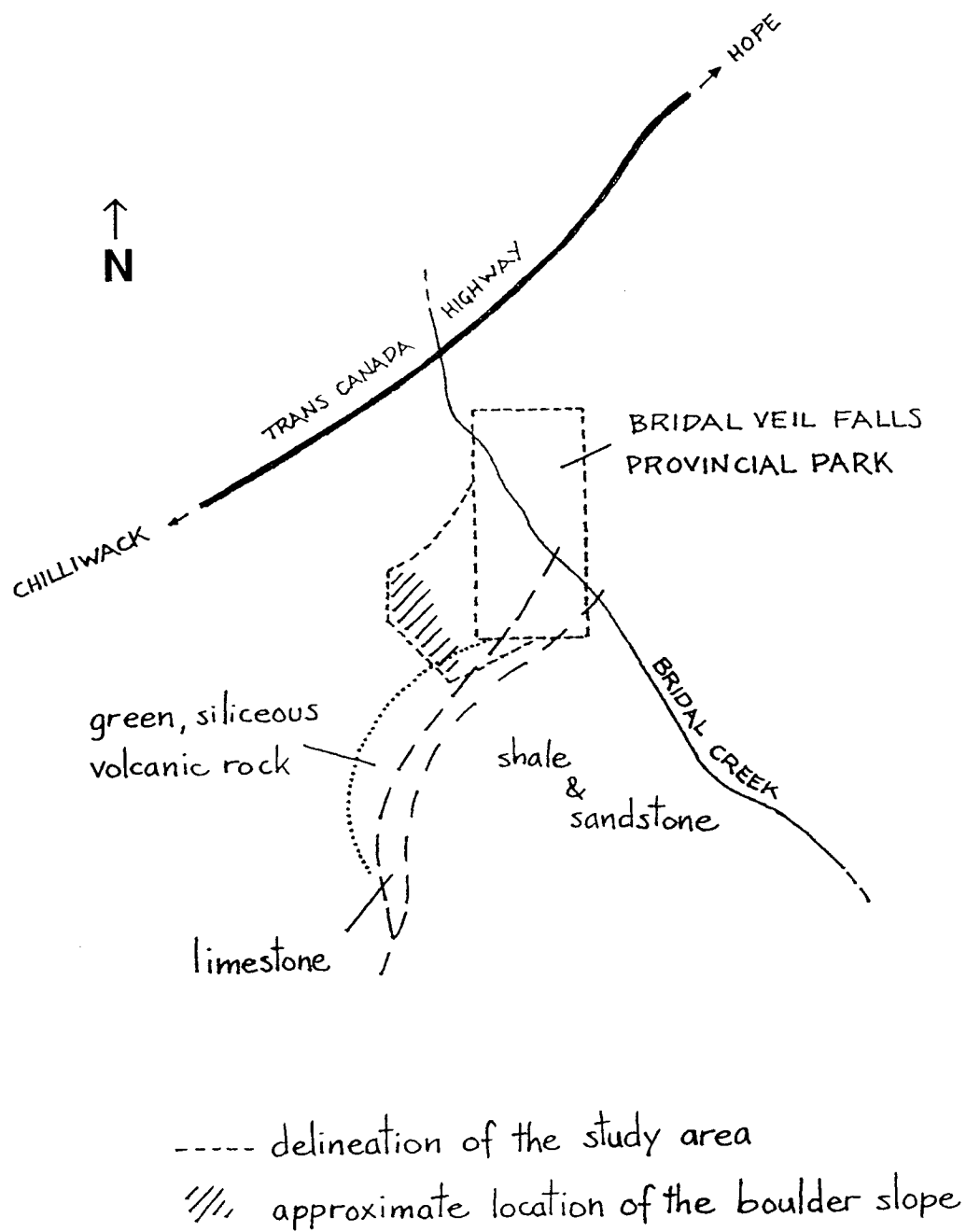
Depression, a large basin between the highlands of Vancouver Island and the coastal mountain ranges of the mainland (Campbell *et al.* 1990). The Fraser Lowland is a low lying area of depositional origin between the Coast mountain range to the north and the Cascade mountain range to the south (Holland 1976). Bridal Veil Falls is at the base of the lowland's southern escarpment. The study area is thus bordered to the south by northwest facing cliffs (Fig. 1.2). It lies between 100 and 400 meters above sea level.

The bedrock geology of the area of Bridal Veil Falls is very complex. An outline of the nature of the bedrock in the study area and immediate surroundings is presented in Figure 1.4. The cliffs found in the study area are predominantly of sedimentary calcareous rock. They are outcrops of the zone of limestone seen in Figure 1.4. Non-calcareous cliffs are found above the boulder slope. Rocks in the boulder slope are also non-calcareous.

The boulder slope probably represents one of the rockfalls that Armstrong (1984) described as common along the Trans-Canada highway east of Rosedale. These rockfalls consist of free fall or precipitous movement of fragments of bedrock of various sizes detached from cliffs or very steep slopes. Rockfalls are usually caused by freeze-thaw action. It is possible that the process resulting in the boulder slope at Bridal Veil Falls was not sudden. Rock fragments detached from the cliff above could have accumulated over a period of time, and this could still be happening (K.W. Savigny, pers. communication). It is clear, however, that the bulk of the rockfall near Bridal Veil Falls had already occurred by 1963; the boulder slope is visible on air photos taken that year.

Four waterfalls are found along the cliffs in the study area (Fig. 1.2). In several places, as well, water dribbles over the rock faces. Four streams are associated with the waterfalls, at

Figure 1.4. Bedrock geology of the study area, 1:25 000. (modified from Monger 1966)



least one of which is intermittent. The water is likely to have a very high content of calcium carbonate. There is evidence for this in the abundant marl deposits found along the Fraser River below Bridal Veil Falls (Smith 1971; J.W.H. Monger, Geological Survey of Canada, pers. communication). In the form of calcite, calcium carbonate is a main constituent of limestone (Cole 1983). Calcium could be dissolved into the water as it flows over the limestone outcrops (Fig. 1.4). Furthermore, above Bridal Veil Falls on the slope of Cheam Peak are other areas of limestone and large areas of shales and sandstones of the Cultus Formation (not shown in Figure 1.4). These shales and sandstones contain calcium feldspar (J.W.H. Monger, pers. communication). In addition, the large amount of rainfall in the area and the cool temperatures of the northwest-facing mountain slope are conducive to the dissolution of relatively important quantities of calcium into the water (K.W. Savigny, pers. communication). Solubility of calcium carbonate increases as temperature falls from 35°C to 0°C (Cole 1983).

1.2.2. Climate

Bridal Veil Falls is located in the Coastal Western Hemlock zone as defined by the biogeoclimatic system of ecosystem classification of British Columbia. This zone lies at low to middle elevations all along the coast of British Columbia, and penetrates the coastal mountain barrier in the Fraser River Valley (Pojar *et al.* 1991). It is characterized as the rainiest zone in the province. Typically, it has cool summers and mild winters, with mean annual temperatures of about 8°C (Pojar *et al.* 1991). The growing season in the Lower Fraser River Valley is among the longest in British Columbia (Campbell *et al.* 1990).

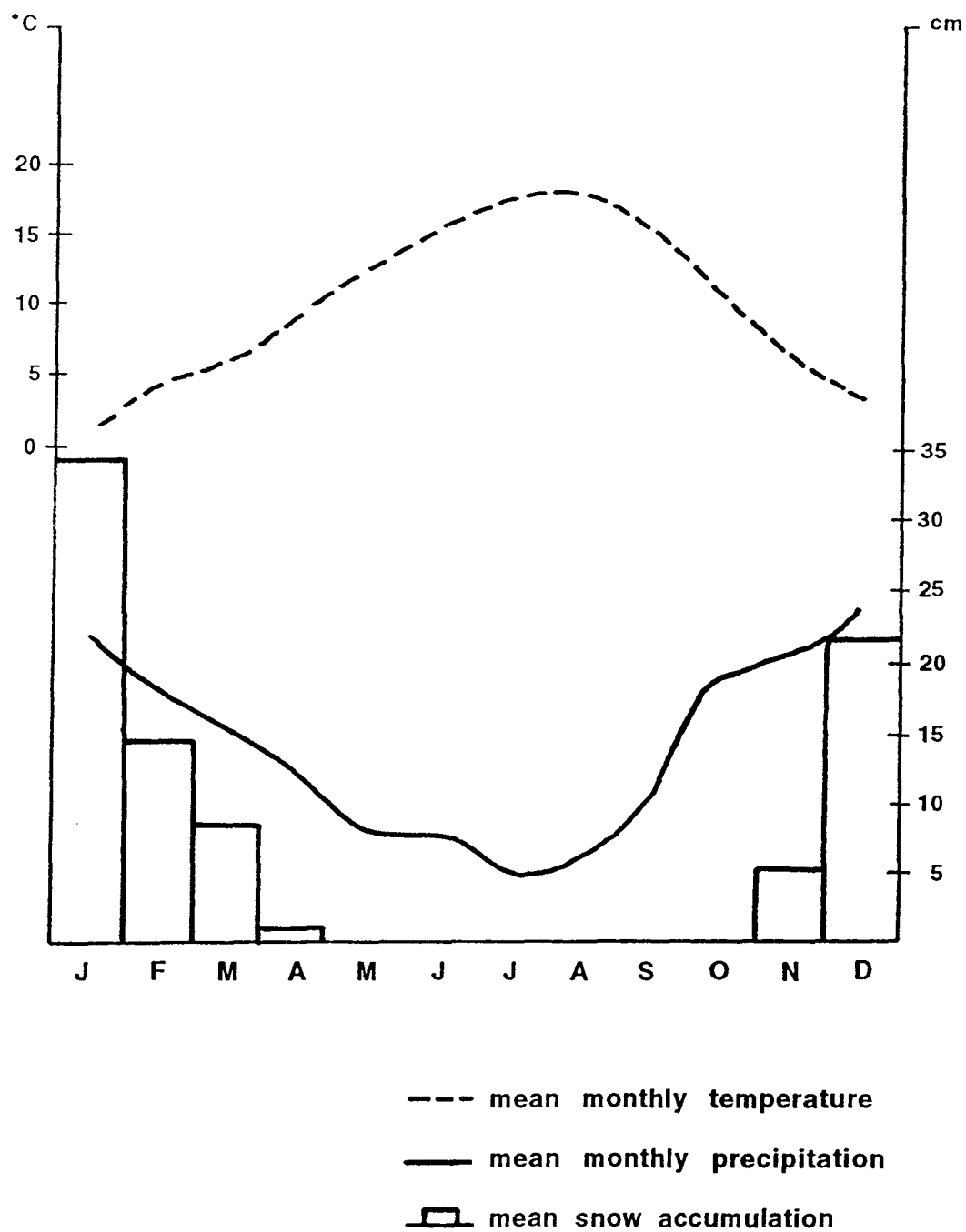
Figure 1.5 presents data from a climatic station in Agassiz, on the opposite side of the Fraser River from Bridal Veil Falls. The mean monthly temperatures peak at 18°C during July and do not fall below 0°C. Snowfall is light, with snow accumulation reaching a mean monthly maximum of around 35 cm in January. Precipitation is highest during the fall and winter, and lowest during the summer. Nevertheless, more than 80% of the plants' water requirements are met by precipitation during the growing season (Farley 1979). Within the study area itself, the northwest-facing escarpment undoubtedly exaggerates the cool summer temperatures, especially near the cliff bases, by reducing periods of direct sunlight. The cliffs thus remain cool and mesic throughout the year.

1.2.3. Vegetation

The forest of the study area has been logged during the past century. Most of the trees are estimated to be between 35 and 50 years old (S. Doubinin, British Columbia Ministry of Forest, pers. communication). The area would thus have been logged in the 1940's and 1950's, not long before the creation of the park in 1965. The British Columbia Ministry of Forest has no record of major fires in the area (S. Doubinin, pers. communication). Burnt stumps scattered in the forest are likely to be the remains of individual trees struck by lightning.

Two tree species dominate the forest: bigleaf maple (*Acer macrophyllum* Pursh) and western redcedar (*Thuja plicata* Donn ex D.Don). They serve to support an abundant epiphytic flora of bryophytes, lichens and licorice fern (*Polypodium glycyrrhiza* D.C. Eat.).

Figure 1.5. Temperature and precipitation at Agassiz, British Columbia. (data from Farley 1979)



Other tree species found in the area include western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), paper birch (*Betula papyrifera* Marsh.), red alder (*Alnus rubra* Bong.), and black cottonwood (*Populus trichocarpa* Torr. & Gray). The understory is rather sparse. Vine maple (*Acer circinatum* Pursh) is common, as are ferns, notably the western sword fern (*Polystichum munitum* (Kaulf.) Presl.), and near the cliffs and streams, the maidenhair fern (*Adiantum pedatum* L.). Under clearings in the canopy, shrubs such as devil's club (*Oplopanax horridum* (J.E.Sm.) Miq.), salmonberry (*Rubus spectabilis* Pursh) and thimbleberry (*Rubus parviflorus* Nutt.) are abundant.

The dominant vegetation in the boulder slope is of bryophytes. In the open portions of the slope, *Selaginella wallacei* Hieron. is common. Other vascular cryptogams to be found there are mainly: *Huperzia myoshiana* (Makino) Ching, *Asplenium trichomanes* L., *Cryptogramma acrotichoides* R.Br. in Richards, *Woodsia* R.Br. spp., and *Polypodium glycyrrhiza* which flourishes during the rainy season. Among flowering plants, *Geranium robertianum* L., and three species of miner's lettuce (*Montia parvifolia* (Moc. ex DC.) Greene, *Claytonia perfoliata* Donn ex Willd., and *C. sibirica* L.) are common. Ocean spray (*Holodiscus discolor* (Pursh) Maxim.), false azalea (*Menziesii ferruginea* Smith), Douglas maple (*Acer glabrum* Torr.), stinging nettle (*Urtica dioica* L.), and *Ribes* L. spp. dominate the shrubby areas.

1.3. Late-Pleistocene and recent history

1.3.1. Geology

During the last glaciation, the Cordilleran ice sheet occupied most of British Columbia. In southwestern British Columbia, the ice flowed eastward from the Vancouver Island ranges and westward from the Coast mountains (Holland 1976). The Fraser Lowland was entirely covered by ice by around 17 000 B.P., as the ice sheet reached the Vancouver area (Fulton 1984). At glacial maximum, the ice extended to the Puget Lowland, about 250 km south of British Columbia's Lower Mainland (Mullineaux *et al.* 1965, as reported in Fulton 1984). Thirteen thousand years B.P., the retreating ice allowed the sea to invade the Strait of Georgia (Clague 1981; Fulton 1984). While the sea was invading the western part of the Fraser Lowland, in the eastern part, there was a short, local re-advance of a piedmont glacier referred to as the Sumas advance (Clague 1981). Piedmont glaciers are the spreading, terminal part of valley glaciers that occupy broad lowlands at the base of steep mountain slopes (Flint 1971). The Sumas glacier eroded the mountain slopes in which it was embedded. The steep cliffs found along the base of the escarpments bordering the Fraser Lowland, such as those found at Bridal Veil Falls, are the products of erosion by this glacier (K.W. Savigny, pers. communication). The Sumas glacier receded rapidly from the Fraser Lowland. The lowland was then probably free of glacial ice by 11 000 years B.P. (Clague 1981). Following the retreat of the ice, the eastern portion of the lowland was not invaded by the sea; the drift deposited by the Sumas glacier was not overlain by marine sediments (Clague 1981).

More recently, the mountain slope at the base of which Bridal Veil Falls is located was the site of a major rock avalanche. This avalanche, referred to as the Cheam Slide,

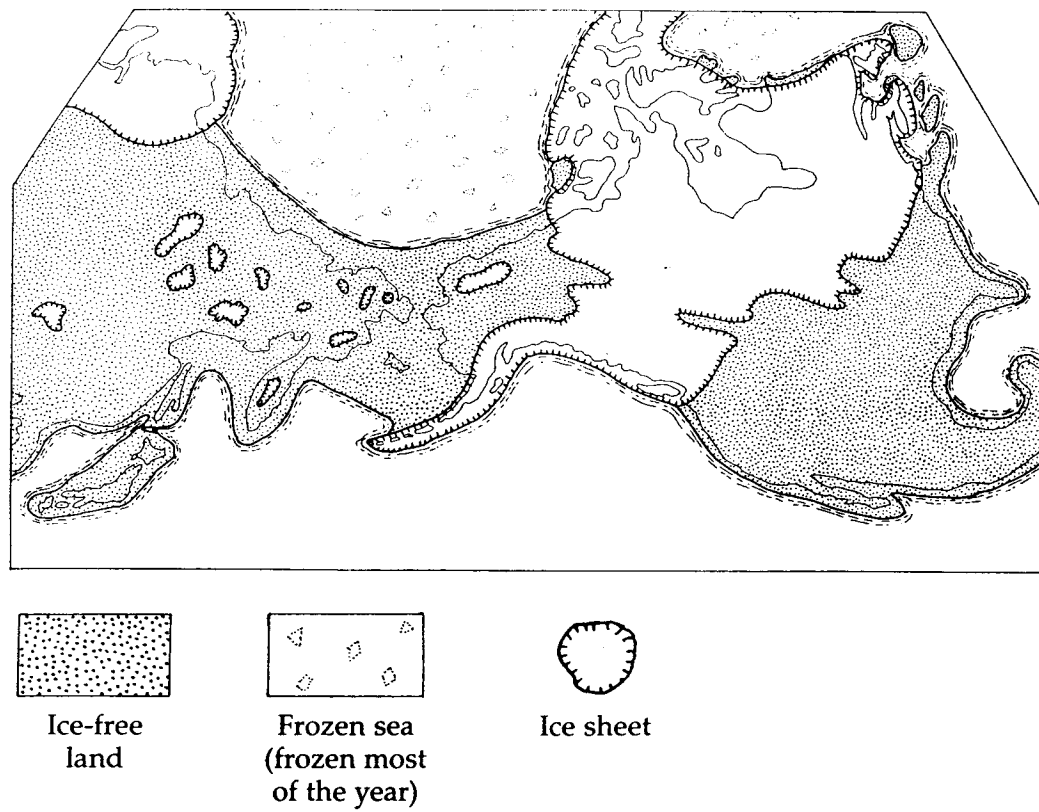
occurred at some time between 4 300 and 5 100 years B.P. (Naumann and Savigny 1991). Its debris overlies the Fraser River floodplain (Smith 1971). The source was located just above Bridal Veil Falls at an elevation of 1 200 m on Cheam Peak (Smith 1971, as reported in Armstrong 1984).

1.3.2. Vegetation and climate

During full-glacial times, two major ice-free areas could have served as refugia for the plants that colonized the glaciated lands after the retreat of the ice (Fig. 1.6). To the south of the ice, most of the United States were ice-free. To the north, ice-free conditions existed over major portions of Alaska and Yukon, which were united to the Siberian peninsula by the Bering Land Bridge (Ritchie 1987). On a smaller scale, numerous lowland refugia are believed to have been scattered along the shores and the offshore islands of Alaska and British Columbia (Pielou 1991). For example, geological and biological evidences have shown that small areas in the Queen Charlotte Islands probably served as refugia during the last glaciation (Heusser 1960; Calder and Taylor 1968; Schofield 1969a, 1989; Mathewes *et al.* 1982, as reported in Hebda 1983; Pielou 1991). Some bryophytes could also have survived the glaciation in high mountain refugia, or nunataks (Pielou 1991).

After the retreat of the ice, it is probable that lowland coastal vegetation promptly invaded southwestern British Columbia. Considering the region's proximity to the southernmost extent of the ice, the most likely source of propagules was southern refugia. Plants of the modern west coast flora could have survived glaciation quite close to the ice

Figure 1.6. Schematic diagram of the pattern of land, sea, and ice during the Wisconsin glacial maximum. The fine lines show modern coastline. (from Pielou 1991)



margin, possibly in valleys protected from the generally harsh climatic conditions (Barnosky 1985, as reported in Pielou 1991). In mountainous regions, very different climates can prevail in adjacent areas. As well, the proximity of the ocean was likely to attenuate climatic extremes.

Around 10 500 years B.P., temperature rose rapidly and precipitation declined, such that between approximately 10 000 B.P. and 7 500 B.P., conditions in the Lower Mainland would have been generally warmer and drier than at present (Mathewes 1973; Mathewes and Heusser 1981). The effect of this so-called, xerothermic period (the Hypsithermal) on vegetation is not clear, however. According to Mathewes (1973), the effect of macroclimatic changes on vegetation during the Hypsithermal could have been attenuated by the wide tolerance ranges of most tree species and the ameliorating oceanic influence along the coast. For example, in Hypsithermal deposits from the Lower Mainland, Mathewes (1973) found macrofossil of species of mosses characteristic of humid regions of the coast and interior. His findings support the arguments for the prevalence of humid coastal conditions in the Fraser Lowland since the retreat of the ice. It is also possible that humid conditions existed throughout the Hypsithermal as a microclimate in protected sites.

From 7 500 to 6 000 B.P., a trend toward cooler and wetter microclimatic conditions marked the end of the xerothermic period. Since then, climatic conditions in the region appear to have been more or less constant (Mathewes and Heusser 1981).

1.4. Earlier bryological work at Bridal Veil Falls

Throughout the years, Bridal Veil Falls has been extensively collected for bryophytes. Most of the specimens are housed at the herbarium of the University of British Columbia (UBC). As early as the 1940's, V.J. Krajina collected in the area and it is possible he visited the site later to become Bridal Veil Falls Provincial Park. Early specimens from the Bridal Veil Falls proper date from the 1960's. The collections are mainly those of W.B. Schofield, who first collected at the site in 1964. Among his students, J.L.D. Godfrey collected at Bridal Veil Falls for the preparation of a flora of the hepatics and hornworts of southwestern British Columbia (Godfrey 1977). Another student of W.B. Schofield, J.P. van Velzen, also sampled at the site for his work on epilithic bryophyte communities in southwestern British Columbia (Van Velzen 1981). D.H. Vitt also did some bryological work at Bridal Veil Falls, collecting specimens for a study of foliicolous bryophytes and lichens of *Thuja plicata* in western British Columbia (Vitt *et al.* 1973). Four foliicolous species of *Orthotrichum* were found growing in abundance at Bridal Veil Falls, the first report of foliicolous mosses in North America north of the tropics. Two species of bryophytes rare to British Columbia, *Hymenostylium insigne* and *Barbula amplexifolia* were first collected at Bridal Veil Falls (Zander and Eckel 1982). The collection of *Hymenostylium insigne* by W.B. Schofield was the first collection of this species in the New World. *Seligeria tristichoides* was also first collected in British Columbia on the cliffs at Bridal Veil Falls by F.J. Hermann (Crum 1975), the first report of this species in western North America.

Chapter 2. Inventory and keys

2.1. Materials and methods

2.1.1. Collection

A list of the bryophytes found at Bridal Veil Falls was compiled primarily from collections made at the site during the course of this study. Field work was conducted during 1991 and 1992. Of 661 specimens collected, a total of 996 bryophytes were identified. For completeness, I also examined specimens collected at Bridal Veil Falls by earlier bryologists and deposited at the herbarium of the University of British Columbia (UBC). These were included in the flora.

Field collections were made from as many types of microhabitats as could be recognized, taking into account accessibility and time constraints. Each specimen was given a collection number and ecological information and date of collection were recorded. Ecological data recorded included type of habitat and substratum, moisture and light conditions, and exposure (compass direction faced), when applicable.

2.1.2. Identification and preparation of the keys

For the identification of the mosses collected during this study, I referred primarily to the *Moss flora of the Pacific Northwest* by E. Lawton (1971). Keys to the mosses of Bridal Veil Falls were prepared based mainly on personal observations made in the process of identification. In the case of species that were not collected during the course of this study, I examined herbarium specimens collected by other bryologists at Bridal Veil Falls. The work

of the following authors guided my observations and provided useful characters to be used in the construction of the keys:

Crum and Anderson (1981);	Nyholm (1975);
Dixon and Jameson (1924);	Schofield (1969b);
Frisvoll (1983, 1985, 1988);	Schofield and Talbot (1991);
Gangulee (1972);	Shaw (1982);
Hill (1984);	Smith (1978);
Hoisington (1979);	Vitt (1973);
Ireland (1969a, 1969b, 1970, 1976, 1982);	Vitt and Buck (1992);
Jamieson (1976);	Vitt <i>et al.</i> (1988);
Koponen (1974);	Zander (1978, 1979);
Lawton (1965, 1967, 1971);	Zander and Eckel (1982).

For the identification of the liverworts, I used the flora of the hepatics and hornworts of southwestern British Columbia prepared by Godfrey (1977). Much information on the liverwort flora of Bridal Veil Falls can be derived from Godfrey's work, as all the species of liverworts found are treated in her keys and descriptions. I also used the following floras and taxonomic treatments which provided helpful additional descriptions and illustrations:

Frye and Clark (1937-1947);
Hicks (1992);
Macvicar (1960);
Schuster (1966, 1969, 1974, 1980, 1992a, 1992b);
Smith (1990).

A set of voucher specimens is deposited in the herbarium of the University of British Columbia (UBC). UBC accession numbers for these specimens are given in Appendices A and B. In most cases, voucher specimens were collected during the course of this study. The exception is for species not found during this study, but collected by others. In such cases, carefully examined herbarium specimens serve as vouchers.

2.1.3. Nomenclature

The nomenclature used in this study follows current checklists of the mosses and liverworts of North America (Stotler and Crandall-Stotler 1977; Anderson 1990; Anderson *et al.* 1990). My interpretation of certain species however, occasionally differed from that of the authors of these checklists. In these particular cases, the following nomenclature was used:

a) Mosses:

-*Barbula coreensis* (Card.) Saito is treated as a synonym of *Barbula amplexifolia* (Mitt.) Jaeg. based on Zander (1979);

- *Brachythecium frigidum* (C.Muell.) Besch. and *Brachythecium asperrimum* (Mitt.) Sull. are considered distinct species based on the work of Hoisington (1979);

-*Ditrichum flexicaule* (Schwaegr.) Hampe and *Ditrichum crispatisimum* (C.Muell.) Par. are considered distinct species based on Frisvoll (1985);

- *Schistidium apocarpum* var. *strictum* (Turn.) Moore is treated as distinct from *S. apocarpum* var. *apocarpum* (Hedw.) Bruch & Schimp. in B.S.G. as described in Lawton (1971).

b) Liverworts:

-*Chiloscyphus pallescens* (Ehrh. ex Hoffm.) Dum. is considered as a synonym of *Chiloscyphus polyanthos* (L.) Corda based on Godfrey (1977) and Smith (1990);

-*Plagiochila asplenioides* (L.) Dum., *P. porelloides* (Torrey ex Nees) Lindenb. and *P. satoi* Hatt. are treated together as *P. asplenioides sensu lato* based on Godfrey (1977) (see Section 2.2.3 for discussion).

2.2. Results and discussion

2.2.1. Diversity of the flora

The known bryophyte flora of Bridal Veil Falls Provincial Park and adjacent boulder slope area was found to be composed of 210 species. This includes 150 species of mosses and two additional varieties in 86 genera, and 60 species of liverworts in 36 genera. It represents 22% of the moss flora of the province and 27% of its liverwort flora (data from Schofield 1968a and Ireland *et al.* 1987). The bryophytes known from Bridal Veil Falls are listed in Appendices A and B.

Prior to this study, only 184 species were known for the study area. Species added to the flora by virtue of this study are indicated in the annotated list of species (Appendices A and B). A variety of *Barbula convoluta*, *B. convoluta* var. *gallinula* Zander, was found to be new to British Columbia (see Section 2.2.4). Two other species, *Hymenostylium insigne* and *Anastrophyllum assimile* are known from only very few other localities in British Columbia. Finally, *Barbula amplexifolia* is known in British Columbia only from Bridal Veil Falls.

The number of bryophyte species at Bridal Veil Falls is relatively high compared to places of similar area in the Lower Mainland of British Columbia. Lynn Canyon Park (25 ha) in North Vancouver, for instance, has a bryophyte flora composed of 100 species of mosses (Krause and Schofield 1977) and approximately 54 species of liverworts (W.B. Schofield, pers. communication). Similarly, the bryoflora of Pacific Spirit Park (763 ha) in Vancouver consists of 122 species of mosses and 38 species of hepatics (Schofield 1992, unpublished data). Of the 166 species composing the hepatic flora of Southwestern British Columbia (Godfrey 1977), 36% are present at Bridal Veil Falls; 56% of the 64 genera described by Godfrey (1977) are represented.

2.2.2. Keys to the mosses of Bridal Veil Falls Provincial Park and adjacent boulder slope.

The following dichotomous keys treat the moss flora of Bridal Veil Falls Provincial Park and adjacent boulder slope area. They should be used in conjunction with Lawton's *Moss Flora of the Pacific Northwest* (1971) which provides illustrations and descriptions of most of the species treated here. Her flora also provides a glossary of specialized terminology used throughout the following keys. A list of synonyms for the species named differently than in Lawton or references for species not treated in Lawton is provided in Appendix D.

The first key leads to genera. Genera can then be keyed to species in a following set of keys. The exceptions are unispecific genera or isolated species within certain genera in which case species is given in the first key. In some cases, several different routes will lead to the same species. This was done to accommodate possible differences in interpretation by different observers.

The keys are based primarily on gametophytic characters. Sporophytic characters are used only when providing determinant additional information or in the case of species which are otherwise difficult or impossible to distinguish. Most characters are microscopic requiring the use of dissecting and compound microscopes.

Keys to the mosses of Bridal Veil Falls and adjacent boulder slope

1-General key

1. Leafy plants not apparent, sporophyte solitary; seta stout, capsule inclined with the upper face flattened; plant small. *Buxbaumia piperi*
1. Leafy plant apparent, with or without sporophyte. 2
2. Leaf cells arranged in a reticulate pattern with narrow, elongate, chlorophyllous cells surrounding large, swollen, porose, fibrillose, dead, hyaline cells; branches in fascicles. *Sphagnum* (p. 48)
2. Leaf cells mostly chlorophyllous (with the exception of marginal, alar, or basal cells); branching uncommon, irregular, pinnate, or dendroid. 3
3. Gemmae lens-shaped, contained in terminal gemmae cups; peristome of four, rigid teeth. *Tetraphis* (p. 48)
3. Gemmae, if present, never in gemmae cups, or gemmae absent; peristome absent, or of more than four teeth, or sporophyte absent. 4
4. Leaves with lamellae on the upper surface. 5
4. Leaves without lamellae on the upper surface. 9
5. Leaves bordered by elongate cells, undulate; lamellae few, restricted to the upper surface of the costa. *Atrichum* (p. 38)
5. Leaves not bordered, not undulate; lamellae usually numerous, not restricted to the upper surface of the costa. 6
6. Lamellae found on the lower surface of the leaf, and on the upper surface of the costa. *Oligotrichum aligerum*
6. Lamellae restricted to the upper surface of the leaf. 7
7. Apical cells of the lamellae smooth. *Polytrichum* (p. 45)
7. Apical cells of the lamellae papillose. 8

8. Apical cells of the lamellae longer than broad in cross-section, somewhat ovate, with the outer wall strongly thickened; leaves somewhat flexuose when dry.
..... *Polytrichastrum alpinum*
8. Apical cells of the lamellae not longer than broad in cross-section, rounded at the top, with the walls more or less evenly thickened; leaves stiff and erect when dry.
..... *Pogonatum urnigerum*
9. Leaves bordered by a band of narrowly elongate cells sharply contrasting with the cells within; leaf cells smooth. 10
9. Leaves not bordered, marginal cells not strongly differentiated from the rest of the lamina, or cells gradually longer, and narrower toward the margin; leaf cells smooth or papillose. 15
10. Leaf bases split in two flaps at the base, clasping the stem and the leaf above; leaves complanate, distichous; plant small. *Fissidens bryoides*
10. Leaf bases not of two flaps, not clasping the stem. 11
11. Leaf margins recurved, and unistratose. *Bryum* (p. 39)
11. Leaf margins plane, unistratose or multistratose. 12
12. Leaf margins entire, and multistratose. *Rhizomnium glabrescens*
12. Leaf margins toothed, or if entire, then unistratose. 13
13. Costa extending to about 3/4 the length of the leaf; leaf cells elongate, 2:1 or longer; leaf margins unistratose; plant small and delicate. *Epipterygium tozeri*
13. Costa extending to near apex, percurrent or excurrent; leaf cells (with exception of marginal cells) short, usually less than 2:1. 14
14. Leaf margins multistratose, marginal teeth double. *Mnium* (p. 43)
14. Leaf margins unistratose, marginal teeth single, or absent. *Plagiomnium* (p. 44)
15. Leaves complanate (flattened) on stem 16
15. Leaves not complanate on stem, regularly distributed around the stem. 27
16. Leaves arranged in two rows. 17
16. Leaves arranged in more than two rows. 19

17. Leaves with a long, narrow, papillose awn; leaf bases sheathing the stem; plant green above, brown below. *Distichium capillaceum*
17. Leaves not awned. 18
18. Costa extending to about mid-leaf; leaves spatulate, widest above middle, apex broadly rounded; leaf bases not of two flaps. *Homalia trichomanoides*
18. Costa extending well beyond mid-leaf to apex or just below; leaves not spatulate, widest at or below the middle, apex acute or obtuse; leaf bases split in two flaps at the base, clasping the stem and the leaf above. *Fissidens* (p. 42)
19. Costa single, to mid-leaf or beyond. 20
19. Costa absent, or short, or short and double. 22
20. Stem with abundant paraphyllia; leaves undulate, lingulate, apex rounded, abruptly ending in a short point; capsule immersed; flagelliform branches often present. *Metaneckera menziesii*
20. Stem without, or with occasional paraphyllia; leaves not undulate; capsule exserted. 21
21. Median leaf cells short to broadly elongate, usually less than 5:1. 22
21. Median leaf cells narrowly elongate, more than 5:1. 27
22. Leaves spatulate, widest above the middle, apex broadly rounded; plant strongly complanate, and glossy. *Homalia trichomanoides*
22. Leaves narrower above than at mid-leaf, apex acute or obtuse; plant more or less complanate, dull or glossy. *Porotrichum* (p. 46)
23. Plant with tiny, filiform, branch-like propagula clustered in leaf axils. *Pseudotaxiphyllum elegans*
23. Plant without asexual reproductive bodies, or if present, not branch-like. 24
24. Leaves decurrent. *Plagiothecium* (p. 45)
24. Leaves not decurrent. 25
25. Alar cells differentiated, forming a distinct group of swollen cells. . *Hypnum lindbergii*
25. Alar cells not differentiated, or if differentiated then not swollen. 26

26.	Leaves ovate-lanceolate, apex gradually narrowing into a point.	<i>Pseudotaxiphyllum elegans</i>	
26.	Leaf lingulate to ovate-lanceolate, more or less rounded below the pointed apex, often undulate.	<i>Neckera</i> (p. 43)	
27.	Leaf cells conspicuously sinuose; leaves costate, usually imbricate when dry (with the exception of hair-points, if present, which are often squarrose or reflexed, and more or less twisted).		28
27.	Leaf cells not sinuose, or leaves without a costa, or crisped and contorted when dry.		31
28.	Leaf cells multipapillose, or leaves muticous and rounded at apex, or hair-points papillose.	<i>Racomitrium</i> (p. 46)	
28.	Leaf cells smooth, or with papillae on the back of the costa and scattered sparsely on the lamina in the upper leaf; leaves acute at apex, hyaline hair-points, if present, denticulate but not papillose.		29
29.	Cells at mid-leaf elongate, more than 2:1, commonly 3-4:1. . .	<i>Racomitrium</i> (p. 46)	
29.	Cells at mid-leaf short, 1-2:1.		30
30.	Plant dark green to nearly black; leaf cells smooth.	<i>Schistidium apocarpum</i> var. <i>apocarpum</i>	
30.	Plant often reddish brown; leaf cells at the back of the costa and upper lamina papillose.	<i>Schistidium apocarpum</i> var. <i>strictum</i>	
31.	Plants minute, up to 4 mm including the sporophyte (gametophyte 1 or 2 mm high); leaves costate, lanceolate, with smooth cells.	<i>Seligeria</i> (p. 47)	
31.	Plants larger, or if not, leaves ecostate, or leaf cells multipapillose.		32
32.	Leaf cells papillose.		33
32.	Leaf cells smooth.		65
33.	Stems papillose.		34
33.	Stems smooth.		35

34. Leaves ovate-lanceolate, somewhat cordate; costa obscure, usually forked, ending at or before mid-leaf; plant with many lateral branches at right angles with the main branch. *Heterocladium macounii*
34. Leaves linear to lanceolate; costa strong, single, ending just before apex; plant unbranched, or with few irregular, erect branches. . . . *Hymenostylium recurvirostre*
35. Leaves without a costa, or with a short single costa ending before mid-leaf, or with a double costa. 36
35. Leaves with a well-defined single costa ending above mid-leaf. 41
36. Leaves with a long double costa extending to mid-leaf or beyond; leaves plicate. *Rhytidiadelphus triquetrus*
36. Leaves without a costa, or costa single, or if double, not extending beyond mid-leaf. 37
37. Stems and branches with abundant paraphyllia; plant much branched, bi- to tripinnate, frond-like; new growth arising from the middle of previous year's stem. *Hylocomium splendens*
37. Stems and branches without paraphyllia, or if paraphyllia present, plant irregularly branched. 38
38. Leaves ending in a whitish hair-point. 39
38. Leaves lacking a whitish hair-point. 40
39. Leaf cells with forked papillae; capsule immersed. *Hedwigia ciliata*
39. Leaf cells with simple papillae; capsule exserted. *Pseudobraunia californica*
40. Costa single, often forked, obscure; leaves with 2 or more papillae per cell; stem papillose. *Heterocladium macounii*
40. Costa double, or absent; leaves with one papilla per cell, papillae formed by projecting upper ends of cells; stem smooth. *Pterigynandrum filiforme*
41. Plants with numerous branches, forming a mat over the substratum or dendroid. . 42
41. Plants erect, scarcely branched, usually in tufts. 45

42. Stems with numerous paraphyllia; leaf cells with 1 papilla per cell located at the upper end of the cells; upper leaves without hair-points. 43
42. Stems without paraphyllia, or paraphyllia scarce; leaf cells multipapillose, or unipapillose with the papillae not associated with the upper end of the cell; upper leaves usually with hair-points. 44
43. Plants dendroid; branch leaves obtuse and serrate at apex; costa rough with projections on the dorsal surface; branches circinate when dry. *Dendroalsia abietina*
43. Plants forming a mat over the substratum; branch leaves entire, or slightly serrulate above; costa smooth. *Pseudoleskea stenophylla*
44. Leaves imbricate when dry, margins recurved; papillae scarce, restricted to costa and cells in upper leaf; costa percurrent; plants dark green to reddish brown. *Schistidium apocarpum* var. *strictum*
44. Leaves crisped and contorted when dry, margins plane; papillae abundant, found on cells throughout most of the leaf; costa ending before apex, pellucid; plants green to yellow-green. *Claopodium* (p. 40)
45. Leaf margins coarsely serrate near apex. 46
45. Leaf margins entire or serrulate, or if toothed, the teeth very distant, or few and restricted to the very tip of the leaf. 50
46. Leaf cells with numerous cuticular thickenings resembling papillae; leaf apices rough, with teeth on the margins, on the back of the costa, and often on the lamina. *Plagiopus oederiana*
46. Leaf cells mammillose (bulging), or with one papilla per cell. 47
47. Plant with clusters of orange-brown rhizoids matting the base of the stem, dull, yellowish-green; leaf margins bistratose above, teeth often double; capsule green, globulose when young, ribbed when dry. *Bartramia pomiformis*
47. Plant without clusters of rhizoids matting the base of the stem, or if so, plants not dull, but somewhat shiny; leaf margins unistratose, teeth single 48
48. Leaves linear-lanceolate from an orange-brown, sheathing leaf base, apex acute. *Timmia austriaca*
48. Leaves long lingulate, ovate-lanceolate, or lanceolate, base not sheathing, apex acute to rounded. 49

49. Leaf cells mammillose (bulging) on one or both surfaces; leaves crisped and contorted when dry. *Dichodontium pellucidum*
49. Leaf cells with one large papilla on each surface; leaves imbricate-flexuose when dry; gemmae frequent, borne in a globular head at the tip of a leafless stalk at the tip of the shoot. *Aulacomnium androgynum*
50. Plants with ovoid, multicellular, often massive gemmae borne in leaf axils; leaves ovate to ovate-lanceolate; leaf cells multipapillose, short above, short rectangular below; plants small.
. *Barbula* (p. 38)
50. Plants without gemmae, or gemmae otherwise; leaves linear, lanceolate, ovate-lanceolate, oblong, lingulate or spatulate. 51
51. Leaves broad throughout, oblong, lingulate, or spatulate, apex usually rounded to broadly pointed; costa often excurrent in a stiff point or awn; upper leaf cells short and multipapillose, lower leaf cells elongate and smooth. 52
51. Leaves narrowed toward apex, apex acute or narrowly obtuse, or leaf cells with only 1 papilla per cell on each surface of the leaf. 55
52. Plants with abundant gemmae clustered in leaf axils, gemmae consisting of branched, uniseriate filaments. *Encalypta procera*
52. Plants without gemmae. 53
53. Leaf margins differentiated, cells longer and narrower than within, smooth or with low papillae; costa excurrent as a coloured point or awn. *Tortula subulata*
53. Leaf margins not differentiated; costa variable. 54
54. Calyptra long campanulate; peristome single or double, teeth not twisted; basal leaf cells (best observed near the base of the costa) with thickened, coloured crosswalls; costa ending before apex, percurrent, or excurrent as a short point not readily visible under low magnification (10x), or if so, the long hair-point hyaline, smooth, and flexuose. *Encalypta* (p. 41)
54. Calyptra cucullate; peristome single, teeth long, fused below, and twisted together; basal leaf cells with evenly thickened crosswalls; costa excurrent as a long, toothed awn readily visible at low magnification (10x). *Tortula* (p. 48)
55. Leaves (at least the upper ones) with hyaline, denticulate hair-points; plants dark green to reddish brown. *Schistidium apocarpum* var. *strictum*
55. Leaves without hyaline hair-points, sometimes apiculate, apiculus never denticulate.
. 56

56. Gemmae usually abundant, borne in leaf axils near the tip of the stem, consisting of 3- to 4-celled elliptic bodies; leaf cells multipapillose, papillae more than 2 per cell.
..... *Zygodon viridissimus*
56. Gemmae absent, or if present leaf cells with 1-2 or no papillae. 57
57. Leaves ovate-lanceolate, broadened at the base. 58
57. Leaves linear to lanceolate, not broadened at the base. 59
58. Plants usually on trees; basal leaf cells usually very thick-walled (often as thick as the cells are wide) and coloured, often pitted; calyptra hairy and campanulate.
..... *Ulota* (p. 48)
58. Plants usually on rock or soil, occasionally on logs; basal leaf cells usually hyaline and not pitted; calyptra smooth and cucullate. *Didymodon* (p. 41)
59. Basal leaf cells hyaline, forming a "V" at the base of the leaf (i.e. hyaline cells extending higher along the margins of the leaf than along the costa).
..... *Tortella tortuosa*
59. Basal leaf cells not hyaline, or if hyaline, not arranged in a conspicuous "V". ... 60
60. Alar cells differentiated, forming a large group of swollen cells; leaves usually falcate-secund, costa long excurrent. *Dicranum fuscescens*
60. Alar cells not differentiated, or not inflated; leaves straight, costa ending before apex to shortly excurrent. 61
61. Leaf cells with 1 or 2 papillae on each surface; plants usually on trees.
..... *Orthotrichum* (p. 44)
61. Leaf cells multipapillose, with more than 2 papillae on each surface; plants usually on rock. 62
62. Costa often shortly excurrent as a smooth terminal point, and extreme tip of the leaves often with a few smooth teeth; capsule wrinkled when dry, peristome single, of 16 teeth; plants green above, reddish brown below, leaf bases sheathing the stem.
..... *Bryoerythrophyllum recurvirostre*
62. Costa usually ending below apex, or if excurrent in a smooth terminal point, then leaf apex not denticulate; capsule ribbed or smooth when dry, peristome absent. 63

63. Leaves usually tightly twisted and contorted when dry; upper basal leaf cells with numerous oval papillae resembling cuticular ridges; papillae often found on the crosswalls of leaf cells; capsule ribbed when dry. *Amphidium* (p. 38)
63. Leaves usually loosely twisted and contorted when dry, or somewhat imbricate; upper basal leaf cells smooth, or with a few, rounded papillae similar to the papillae on the upper leaf cells; papillae not on the crosswalls of the leaf cells; capsule smooth when dry. 64
64. Leaf margins usually plane and entire, or often crenulate along the upper basal region where the leaves curve back; capsule pale brown, reddish at the mouth; operculum not attached to the columella. *Gymnostomum aeruginosum*
64. Leaf margins usually recurved at middle on one or both sides, entire; capsule dark brown; operculum often attached to the columella. *Hymenostylium* (p. 42)
65. Costa absent, or double, or short, ending before mid-leaf. 66
65. Costa single (occasionally forked), extending to mid-leaf or beyond. 78
66. Stems with abundant paraphyllia; stem leaves with a long, attenuate, twisted apex; branching regularly bi- to tripinnate; new growth arising from the middle of the previous year's stem. *Hylocomium splendens*
66. Stems without paraphyllia, or paraphyllia scarce; stem leaves not twisted at apex; branching irregular, or mostly once pinnate. 67
67. Leaves plicate. *Rhytidiadelphus* (p. 46)
67. Leaves smooth, not plicate. 68
68. Alar cells with a distinctly differentiated single row of 3-4 elongated and inflated cells. *Brotherella roellii*
68. Alar cells not differentiated, or if differentiated, never with a single row of 3-4 elongated and inflated cells. 69
69. Cortical cells of stem enlarged and thin-walled; alar cells inflated. 70
69. Cortical cells of stem small and thick-walled; alar cells not inflated, or if so, leaves squarrose. 71
70. Leaves obtuse to rounded at apex, straight. *Calliergonella cuspidata*
70. Leaves acute at apex, usually falcate-secund. *Hypnum lindbergii*

71. Stem red; alar cells differentiated, smaller, thick-walled and coloured (orange-brown).
..... *Pleurozium schreberi*
71. Stem green or brown. 72
72. Leaves narrowly acuminate from a cordate base, squarrose or wide-spreading (upper, lanceolate portion of the leaf pointing away from the stem). 73
72. Leaves ovate-lanceolate to lanceolate, imbricate to spreading, or leaves falcate. . . 74
73. Alar cells clearly differentiated, short rectangular to rounded, or enlarged and inflated; leaves often shortly decurrent. *Campylium stellatum*
73. Alar cells not clearly differentiated, hyaline, shorter and wider than surrounding cells; leaves not decurrent. *Rhytidiadelphus squarrosus*
74. Leaves concave, entire, or serrate to serrulate at apex. 75
74. Leaves not concave, entire, or serrulate at leaf base and occasionally at apex. . . . 76
75. Leaves decurrent, decurrent portion narrow, of elongate, hyaline cells tapering to the stem (often remaining on the stem); leaf apices often recurved.
..... *Plagiothecium cavifolium*
75. Leaves not decurrent; leaf apices not usually recurved. *Hygrohypnum luridum*
76. Leaves falcate to circinate, slenderly acuminate to a filiform point; plants irregularly or more or less regularly pinnate, branches numerous. *Hypnum* (p. 43)
76. Leaves straight to somewhat falcate-secund, never circinate; plants irregularly branched, branches few. 77
77. Leaves less than 0.5 mm long; plants minute, filiform. *Platydictya jungermannioides*
77. Leaves more than 0.5 mm long; plants short, thin. *Isopterygiopsis pulchella*
78. Leaves lanceolate from an orange-brown sheathing leaf base; leaf cells in cross-section bulging on the upper surface of the leaf. *Timmia austriaca*
78. Leaves not lanceolate, or leaf bases not sheathing, or if sheathing, not coloured. . . 79
79. Plants dendroid, branches clustered at the top of a usually erect stem. 80
79. Plants not branching, or branching irregular or pinnate. 81

80. Branch leaves decurrent; alar cells not differentiated. . . . *Leucolepis acanthoneuron*
80. Branch leaves not decurrent, rounded at insertion, forming auricles just above the alar region; alar cells coloured and swollen. *Climacium dendroides*
81. Leaves ovate, strongly concave, imbricate, barely changed when dry; costa strong, ending just before apex, percurrent or excurrent. 82
81. Leaves lanceolate, or not concave or imbricate, or if so, costa shorter, ending well before leaf apex. 84
82. Leaves apiculate; plants whitish green above, pinkish below. *Plagiobryum zierii*
82. Leaves rounded to broadly acute, without an apiculus. 83
83. Plant yellow-green. *Anomobryum filiforme*
83. Plant with a reddish wine tinge. *Bryum miniatum*
84. Alar cells differentiated, forming a distinct group of inflated cells. 85
84. Alar cells not differentiated, or if differentiated, not forming a distinct group of inflated cells. 91
85. Leaves plicate, falcate-secund. 86
85. Leaves not plicate, or leaves straight. 87
86. Stem with abundant paraphyllia; alar cells often coloured. . . *Palustriella commutata*
86. Stem without paraphyllia (pseudoparaphyllia sometimes present); alar cells hyaline. *Sanionia uncinata*
87. Alar cells coloured; costa strong, often excurrent; leaves narrowly ovate to lanceolate. 88
87. Alar cells hyaline, or if coloured, costa never excurrent; leaves ovate to ovate-lanceolate. 89
88. Costa excurrent from an ovate leaf base. *Blindia acuta*
88. Costa excurrent or ending before apex, leaves long, lanceolate. . . *Dicranum* (p. 40)

89. Median leaf cells mostly shorter than 5:1; costa extending well into leaf apex.
..... *Cratoneuron filicinum*
89. Median leaf cells mostly longer than 5:1; costa not extending to leaf apex. 90
90. Leaves straight to often falcate, acute or obtuse, not decurrent, smooth, margin entire.
..... *Hygrohypnum luridum*
90. Leaves straight, acute, usually decurrent at the base, plicate or smooth, margin usually serrulate nearly to the base, or entire. *Brachythecium* (p. 39)
91. Stem with abundant paraphyllia; plants usually on trees. 92
91. Stem without abundant paraphyllia or paraphyllia scarce. 93
92. Leaves rounded at apex. *Metaneckera menziesii*
92. Leaves gradually acuminate. *Pseudoleskea stenophylla*
93. Plant blackish or brownish, erect, scarcely branched; leaves often with hair-points; leaf cells thick-walled. 94
93. Plant yellow-green, green or dark green (sometimes reddish), erect or prostrate, branching scarce, or pinnate, or irregular; leaves without hair points. 97
94. Cells in upper part of the leaf elongate. *Pohlia nutans*
94. Cells in upper part of the leaf short, somewhat quadrate or rounded. 95
95. Leaves tightly crisped and contorted when dry; plants in dense tufts. *Grimmia torquata*
95. Leaves imbricate or loosely contorted when dry. 96
96. Hair-points present on upper leaves. *Schistidium apocarpum* var. *apocarpum*
96. Hair-points absent. *Didymodon rigidulus* var. *gracilis*
97. Plants usually prostrate (sometimes erect), forming mats over the substratum; branching irregular or pinnate. 98
97. Plants usually erect, forming tufts; branching absent or scarce. 116
98. Leaf margins recurved from base to near apex. 99
98. Leaf margins plane or recurved at the base only. 100

99.	Leaves plicate, not concave; costa single.	<i>Homalothecium</i> (p. 42)
99.	Leaves not plicate, concave; costa often with supplementary costae flaring at its base.	<i>Antitrichia</i> (p. 38)
100.	Branch leaves squarrose, entire or minutely serrulate at the base. .	<i>Campylium</i> (p. 40)
100.	Branch leaves erect or spreading, not squarrose, or if so, leaves serrate.	101
101.	Leaves plicate.	102
101.	Leaves not plicate.	104
102.	Leaf margins often recurved, serrate or toothed at the apex and often at the base.	<i>Homalothecium</i> (p. 42)
102.	Leaves margins plane or recurved at the very base only, entire to serrulate or serrate.	103
103.	Alar cells more or less inflated; operculum conic.	<i>Brachythecium</i> (p. 39)
103.	Alar cells not inflated; operculum long rostrate.	<i>Eurhynchium</i> (p. 41)
104.	Median leaf cells short, 1-2(3):1; leaves ovate to lingulate, with a broad apex. .	105
104.	Median leaf cells long and narrow, more than 3:1, or if shorter, leaves ovate-lanceolate with an acuminate apex.	106
105.	Costa strong, ending before apex, toothed at the back near apex; leaves coarsely irregularly toothed at apex; plant coarse.	<i>Thamnobryum neckeroides</i>
105.	Costa short, extending to the middle or 3/4 of the leaf, not toothed at the back; leaves serrate to serrulate at apex; plant small, in thin mats. . .	<i>Porotrichum vancouveriense</i>
106.	Leaf margins serrate or serrulate from apex to nearly base.	107
106.	Leaf margins entire or serrulate above (occasionally to below mid-leaf, but never to base).	111
107.	Leaf margins irregularly toothed; alar cells differentiated, forming a distinct, small group of dense and thick-walled, quadrate, rounded or irregular cells.	<i>Isothecium myosuroides</i>
107.	Leaf margins regularly toothed.	108

108. Leaf apices broadly acute to rounded; cells at the extreme apex of the leaves usually short, 2:1 or less. 109
108. Leaf apices acute to acuminate, never obtuse or rounded; cells at the extreme apex of the leaves elongate, mostly longer than 2:1. 110
109. Alar cells not clearly differentiated, elongate, wider than other cells, occasionally slightly inflated. *Platyhypnidium riparioides*
109. Alar cells differentiated, short, quadrate, rounded or irregular. *Eurhynchium pulchellum* (see generic key for variety, p. 41)
110. Stem and branch leaves different in form (branch leaves ovate, stem leaves larger, cordate, decurrent, and often squarrose); operculum long rostrate. *Eurhynchium* (p. 41)
110. Stem and branch leaves not different in form; operculum conic. *Brachythecium* (p. 41)
111. Leaves narrowly ovate-lanceolate, tapering to a long, channelled (margins rolled inward) apex. *Campylium polygamum*
111. Leaves ovate to ovate-lanceolate, apex not long and channelled. 112
112. Leaves concave. 113
112. Leaves not concave. 115
113. Costa single, often ending in a tooth at the back (look at several leaves). *Scleropodium* (p. 47)
113. Costa single or often double or forked, not ending in a tooth. 114
114. Leaves often falcate, entire at apex. *Hygrohypnum luridum*
114. Leaves straight, usually finely serrulate at apex. *Brachythecium* (p. 39)
115. Leaves small, mostly less than 1 mm long, not plicate or decurrent; alar cells not inflated. *Amblystegium serpens*
115. Leaves larger, mostly more than 1 mm long, often plicate and more or less decurrent; alar cells usually more or less inflated. *Brachythecium* (p. 39)
116. Leaf margins involute, at least above. 117
116. Leaf margins plane or recurved. 119

117. Leaves erect, narrowly lanceolate, gradually tapering from base to apex.
..... *Ditrichum crispatisimum*
117. Leaves spreading or squarrose, lanceolate from a broadened, sheathing leaf base. . 118
118. Capsules long and narrow, cylindric; stems rarely taller than 5 mm.
..... *Trichodon cylindricus*
118. Capsules short, zygomorphic; stems up to 30 mm. *Dicranella schreberiana*
119. Leaf margins toothed above. 120
119. Leaf margins entire or serrulate above. 124
120. Leaf cells elongate, more or less uniform throughout the length of the leaf.
..... *Pohlia* (p. 45)
120. Leaf cells short above and elongate below, or vice-versa. 121
121. Leaf cells elongate above, quadrate at the base. *Anacolia menziesii*
121. Leaf cells quadrate above, elongate at the base. 122
122. Leaf margins bistratose above, teeth often double. *Bartramia pomiformis*
122. Leaf margins unistratose throughout, teeth single. 123
123. Leaf apices rough with teeth on the margins, on the back of the costa, and often on the lamina; stem with clusters of reddish-brown rhizoids. *Plagiopus oederiana*
123. Leaf apices with teeth on the margin only, and papillae on the back of the costa; stem without clusters of rhizoids. *Dichodontium pellucidum*
124. Leaf cells thick-walled, short, uniform throughout the length of the leaf.
..... *Tetraphis* (p. 48)
124. Leaf cells thick- or thin-walled, elongate throughout or short above to gradually elongate below. 125
125. Leaves abruptly lanceolate from a broad apex. 126
125. Leaves linear, lingulate, ovate, or lanceolate, gradually tapering towards apex. . 128
126. Leaves crisped and contorted when dry; plants on trees. *Ulota*
126. Leaves spreading and loosely contorted when dry; plants on soil. 127

127. Capsules long and narrow, more than 4X longer than wide, cylindric; stem rarely higher than 5 mm. *Trichodon cylindricus*
127. Capsules short, less than 3X longer than wide, zygomorphic; stem up to 30 mm. *Dicranella schreberiana*
128. Leaves cells elongate throughout, thin-walled, gradually longer and narrower towards the margin. 129
128. Leaves cells short, or if elongate, cells somewhat thick-walled, or not gradually differentiated towards the margin. 130
129. Costa extending to 3/4 the length of the leaf or above; stem usually more than 1 cm long. *Pohlia* (p. 45)
129. Costa not extending above 3/4 the length of the leaf; stem usually less than 1 cm long. *Epipterygium tozeri*
130. Leaves crisped and contorted when dry. 131
130. Leaves erect or spreading when dry, sometimes slightly contorted. 132
131. Leaf margins recurved from near base to near apex; leaf margins bistratose above. *Dicranoweisia cirrata*
131. Leaf margins plane or more or less recurved below; leaf margins unistratose. *Dichodontium pellucidum*
132. Costa excurrent as a short awn. *Pottia truncata*
132. Costa ending before apex, percurrent or shortly excurrent, but never as an awn. 133
133. Leaf cells short and quadrate above, gradually longer below. . . *Ceratodon purpureus*
133. Leaf cells more or less elongate throughout. 134
134. Leaf margins bistratose above. *Dicranella varia*
134. Leaf margins unistratose. 135
135. Median leaf cells narrow, less than 20 μm wide; capsule symmetric. . *Pohlia nutans*
135. Median leaf cells broad, more than 20 μm wide; capsule zygomorphic. *Funaria hygrometrica*

2-Keys to multispecific genera.

Amphidium

1. Leaf margins plane (or only slightly recurved below) and more or less entire; papillae on leaf cells round and wide. *A. lapponicum*
1. Leaf margins usually recurved and often with distant, blunt teeth above; papillae on leaf cells elliptical, small, resembling cuticular ridges. *A. californicum*

Antitrichia

1. Supplementary costae strong; leaf cells pitted; leaves loosely imbricate when dry, tips often spreading. *A. curtispindula*
1. Supplementary costae weak or absent; leaf cells not pitted, or very weakly so; leaves tightly imbricate when dry. *A. californica*

Atrichum

1. Monoicous. *A. undulatum*
1. Dioicous. 2
2. Leaf cells more or less rounded with pronounced corner thickenings; dioicous or monoicous. *A. undulatum*
2. Leaf cells more or less angular, most corner thickenings not well defined, walls more or less evenly thickened; always dioicous. *A. selwynii*

Barbula

1. Leaves rounded at apex, not sheathing at the base; costa ending a few cells before apex; gemmae usually larger than 100 μm *B. convoluta* var. *gallinula*
1. Leaves acute at apex, somewhat sheathing at the base; costa excurrent in a short point; gemmae usually 100 μm or shorter. *B. amplexifolia*

Brachythecium

1. Leaves concave, tapering more or less abruptly to a short point. 2
1. Leaves not concave, usually narrowly acuminate. 4
2. Alar cells short-rectangular or quadrate, not inflated and often dense and more or less opaque. *B. plumosum*
2. Alar cells rectangular or hexagonal, more or less inflated and hyaline. 3
3. Alar cells forming distinct decurrent auricles of inflated cells, sharply set-off, easily distinguished at low magnification (20X on the dissecting microscope). . . . *B. rivulare*
3. Alar cells not forming distinct decurrent auricles, more or less inflated, not sharply set-off. *B. rutabulum*
4. Leaves straight to falcate, sometimes asymmetric, usually not plicate, narrowly ovate below, gradually tapering to a long, narrowly acuminate apex; alar cells few, quadrate, irregular or short rectangular, not swollen. *B. velutinum*
4. Leaves straight, symmetric, usually plicate, broad below, narrowly attenuate at apex. 5
5. Stem leaves deeply plicate, most with at least two laminal (not marginal) plications on either side of the costa. *B. frigidum*
5. Stem leaves plane, wrinkled or with only one plication on either side of the costa. 6
6. Inflated alar cells in a well defined, often decurrent, group of ten or more oval or round cells; inflated cells plainly visible under low magnification (40X). . . *B. frigidum*
6. Enlarged alar cells less numerous, (usually 6-9), these being more oblong or rectangular in outline rather than round, not plainly visible under low magnification (40X). *B. asperrimum*

Bryum

1. Marginal leaf cells not differentiated; leaves rounded at apex, margins plane; plant with a wine red tinge, leaves imbricate when dry. *B. miniatum*
1. Marginal leaf cells differentiated, longer and narrower than within; leaves pointed at apex, margins recurved. 2

2. Leaves widest above the middle, not decurrent; costa in upper leaves excurrent in an awn. *B. capillare*
2. Leaves widest below the middle, decurrent; costa ending before apex to shortly excurrent. *B. pseudotriquetrum*

Campylium

1. Costa absent, or short, usually ending below mid-leaf; leaves squarrose or wide-spreading, tapering from a cordate base into a long, fine point. *C. stellatum*
1. Costa extending to mid-leaf or beyond. 2
2. Leaves lanceolate from a broadly ovate base, lanceolate apex recurved. *C. chrysophyllum*
2. Leaves ovate-lanceolate, gradually tapering, straight and spreading. . . . *C. polygamum*

Claopodium

1. Leaf cells multipapillose with two or more papillae per cell. *C. bolanderi*
1. Leaf cells unipapillose. *C. crispifolium*

Dicranella

1. Leaves lanceolate from a broad sheathing leaf base; leaf margins plane. *D. schreberiana*
1. Leaves lanceolate, gradually narrowed from base to apex, leaf base not sheathing; leaf margins recurved in lower leaf. *D. varia*

Dicranum

1. Leaf cells papillose on the dorsal surface with one papilla per cell. . . . *D. fuscescens*
1. Leaf cells smooth. 2
2. Leaf cells strongly pitted; leaves falcate-secund to straight and erect; leaf tips not usually broken; costa ending before apex to shortly excurrent. *D. scoparium*
2. Leaf cells not pitted; leaves straight and erect; leaf tips often broken; costa long excurrent. *D. tauricum*

Didymodon

1. Leaf cells smooth. *D. rigidulus* var. *gracilis*
1. Leaf cells papillose. 2
2. Ventral cells of the costa elongate at mid-leaf; leaves squarrose when moist.
. *D. fallax* var. *reflexus*
2. Ventral cells of the costa quadrate at mid-leaf; leaves spreading when moist.
. *D. vinealis* var. *flaccidus*

Encalypta

1. Plants with abundant gemmae clustered in leaf axils, gemmae consisting of branched uniseriate filaments. *E. procera*
1. Plants without gemmae. 2
2. Leaf margins recurved at mid-leaf; dorsal surface of the costa smooth, or papillose above; capsule smooth, calyptra fringed, seta green for most of its length, red just below the capsule, peristome single, consisting of short red teeth. *E. ciliata*
2. Leaf margins plane at mid-leaf; dorsal surface of the costa papillose by projecting of cell ends; capsule ribbed, calyptra fringed or not. 3
3. Capsule ribbed longitudinally; calyptra not fringed; seta red. *E. rhaptocarpa*
3. Capsule (not observed) ribbed spirally; calyptra fringed. *E. procera*

Eurhynchium

1. Stem and branch leaves different in size but similar in shape; leaf apices more or less acute to commonly obtuse or rounded (best seen in branch leaves). 2
1. Stem and branch leaves different in shape¹; leaf apices acute, never obtuse or rounded. 3

¹ In *Eurhynchium praelongum* and *E. oreganum*, stem and branch leaves are differentiated; branch leaves are ovate, not markedly decurrent and not squarrose, while stem leaves are cordate with a very broad, more or less auriculate base and a lanceolate, more or less squarrose apex, and are strongly decurrent. This difference in leaf shape can be used to distinguish between branches and lateral stems.

2. Branch leaves usually < 1 mm. *E. pulchellum* var. *pulchellum*
2. Branch leaves usually > 1 mm. *E. pulchellum* var. *barnesii*
3. Plant usually slender; branching variable, regular or irregular; lateral stems usually common on main stem; stems usually more or less sparsely and irregularly pinnate, or more or less regularly and/or closely branched in which case commonly bipinnate; leaves not (or rarely slightly) plicate. *E. praelongum*
3. Plant usually coarse; branching more or less regular; lateral stems usually few on main stem; stem evenly and closely pinnate (mostly once pinnate, rarely sparsely bipinnate), somewhat frond-like; leaves, mostly those of stem and larger branches, often plicate. *E. oreganum*

Fissidens

1. Plant very small, less than 1 cm long; leaf margins bordered by elongate cells; plants of dry habitats. *F. bryoides*
1. Plant usually more than 1 cm long; leaf margins not differentiated from the rest of the lamina; plants of wet habitats. *F. grandifrons*

Homalothecium

1. Leaf margins serrulate at apex, and occasionally also slightly serrulate at base. *H. fulgenscens*
1. Leaf margins toothed at apex and base, the teeth curved toward leaf base (hook-like). *H. nuttallii*

Hymenostylium

1. Leaves gradually lanceolate, curved toward the stem when dry, usually broadly recurved with the recurved portion several (2 or more) cells wide; costa usually 80 or more μm wide at base; stem smooth. *H. insigne*
1. Leaves linear, tapering into a point near apex, appressed to contorted when dry, narrowly recurved on one or both sides with the recurved portion 1 or 2 (occasionally 3) cells wide; costa usually 40 to 60 μm wide at base; stem smooth or papillose. *H. recurvirostre*

Hypnum

1. Cortical cells of stem thick-walled, similar to the cells within; leaves rounded at insertion. *H. circinale*
1. Cortical cells of stem thin-walled, hyaline, larger than the cells within; leaves straight at insertion. 2
2. Alar cells differentiated, forming a distinct group of swollen cells. . . . *H. lindbergii*
2. Alar cells not clearly differentiated, few, quadrate, or occasionally with a few, enlarged, hyaline cells at the alar margin. *H. subimponens*

Mnium

1. Leaf margins with inner core of stereids visible in cross-section; leaf cells angular, walls not thickened at the corners; leaves not contorted when dry. . . *M. spinulosum*
1. Leaf margins without an inner core of stereids; leaf cells rounded or somewhat angular, walls thickened or not at the corners; leaves contorted when dry. 2
2. Median leaf cells mostly more than 20 μm (often up to 40), rounded, thickened at the corners with the walls otherwise not markedly thickened; dioicous or synoicous. . . 3
2. Median leaf cells mostly less than 20 μm (up to 25), rounded to somewhat angular, thickened or not at the corners with the walls generally thick and firm; dioicous. *M. thomsonii*
3. Synoicous; costa not toothed at the back near apex (look at several leaves). *M. marginatum*
3. Dioicous; costa usually toothed at back near apex. *M. ambiguum*

Neckera

1. Leaves abruptly rounded below the pointed apex; leaf apices serrulate; plant shiny; capsules immersed. *N. pennata*
1. Leaves only slightly rounded below the pointed apex; leaf apices toothed, the teeth long, sharp, and often recurved toward leaf base; plant dull; capsules exerted. *N. douglasii*

Orthotrichum

1. Dioicous. *O. lyellii*
1. Autoicous, or sexuality unknown. 2
2. Leaves flexuose to crisped and contorted when dry; capsule exserted, with immersed stomata; endostome of 16 fine, linear (or hair-like) teeth; calyptra glabrous or hairy. 3
2. Leaves erect, and appressed when dry; capsule immersed to shortly exserted; with superficial stomata; endostome of 8 or 16 lanceolate teeth; calyptra hairy. 4
3. Leaves flexuose when dry; stomata abundant, found on the middle and lower portion of the capsule; exostome of 8 whitish teeth (often split to 16 when dry). *O. consimile*
3. Leaves crisped and contorted when dry; stomata found on the middle and upper portion of the capsule; exostome of 16 reddish teeth. *O. pulchellum*
4. Exostome and endostome of 8 teeth each; capsule emergent to shortly exserted, slightly ribbed below the mouth when dry. *O. speciosum*
4. Exostome and endostome of 16 teeth each; capsule immersed to emergent, ribbed or smooth when dry. 5
5. Capsule ribbed when dry; dioicous. *O. lyellii*
5. Capsule smooth when dry; autoicous; endostome teeth irregularly notched, ragged. *O. striatum*

Plagiomnium

1. Leaf margins toothed or entire, the teeth short and blunt; leaf apices rounded, usually apiculate; prostrate stems creeping on the substratum with rhizoids scattered throughout the length of the stem; leaves not or only slightly decurrent; operculum rostrate. *P. rostratum*
1. Leaf margins toothed, the teeth sharp; leaf apices more or less pointed, apiculate; prostrate stems if present, usually arching with rhizoids at both ends; operculum conic. 2
2. Plants with prostrate stems; leaves strongly decurrent; costa with stereids. . *P. insigne*
2. Plants without prostrate stems; leaves not or only slightly decurrent; costa without stereids. *P. venustum*

Plagiothecium

1. Leaves mostly symmetric. 2
1. Leaves asymmetric. 3
2. Leaves undulate, complanate; plants robust, whitish green. *P. undulatum*
2. Leaves smooth, usually concave and not complanate (occasionally complanate).
. *P. cavifolium*
3. Decurrent portion of leaves tapering, with the cells usually elongate, never swollen;
median leaf cells narrow, less than 12 μm wide. *P. laetum*
3. Decurrent portion of leaves often bulging, with the cells rounded, often swollen;
median leaf cells wide, more than 12 μm wide. *P. denticulatum*

Pohlia

1. Leaves with a metallic shine; leaf cells narrowly elongate, commonly over 10:1.
. *P. cruda*
1. Leaves not shiny; leaf cells broadly elongate, less than 10:1 (except for marginal
cells). 2
2. Leaf cells thick-walled; plant green to brownish; leaves erect, margins plane or
recurved, costa strong. *P. nutans*
2. Leaf cells thin-walled, or not conspicuously thickened; plant whitish green; leaf
margins plane. *P. wahlenbergii*

Polytrichum

1. Leaf margins sharply toothed, and plane when moist; apical cells of the lamellae
rounded in cross-section, with the walls more or less evenly thickened. . *P. formosum*
1. Leaf margins entire, and incurved when moist; apical cells of the lamellae pear-shaped
in cross-section, with the upper wall distinctly thickened. 2
2. Costa long excurrent as a hyaline, toothed awn. *P. piliferum*
2. Costa shortly excurrent as a reddish awn. *P. juniperinum*

Porotrichum

1. Alar cells not differentiated from surrounding cells, elongate; leaf apices acute; leaf margins toothed in upper leaf with coarse sharp, irregular teeth. *P. bigelovii*
1. Alar cells differentiated, quadrate; leaf apices acute to obtuse; leaf margins serrate to serrulate in upper leaf. *P. vancouveriense*

Racomitrium

1. Leaves with hyaline hair-points. 2
1. Leaves without hair-points. 7
2. Hair-points papillose. 3
2. Hair-points usually denticulate, but not papillose. 4
3. Leaf cells smooth (with the exception of the hair-point). *R. lanuginosum*
3. Leaf cells papillose. 4
4. Costa ending around mid-leaf; marginal leaf cells above the alar cells usually elongate and thin-walled. *R. canescens*
4. Costa ending near apex; marginal leaf cells above the alar cells short (usually quadrate) and thick-walled. *R. elongatum*
5. Leaves bordered at the basal margin by elongate, esinuose, thin-walled, more or less hyaline cells, and alar cells differentiated, smooth, esinuose and thin-walled; leaf cells papillose, with several low papillae per cell. *R. varium*
5. Leaves not bordered at the basal margins and alar cells not differentiated, or if so, leaf cells smooth. 6
6. Hair-points strongly decurrent, not strongly denticulate; alar and supra-alar marginal cells not differentiated; leaves linear-lanceolate; costa usually bistratose, strongly canaliculate; leaf cross-sections at mid-leaf V-shaped and showing round, thick-walled laminal cells; upper marginal leaf cells elongate. *R. lawtonae*
6. Hair-points shortly decurrent or abruptly ending , denticulate to spinulose; alar and supra-alar marginal cells differentiated or not; leaves linear-lanceolate to ovate-lanceolate; costa usually 2 to 4-stratose, strongly canaliculate or not; leaf cross-sections at mid-leaf variable, and showing round or elliptic laminal cells; upper marginal leaf cells short to shortly elongate. *R. heterostichum s.l.*

7. Apical leaf cells elongate (more than 3:1), apex narrowly long lanceolate; in section, papillae seen as large rounded thickenings on the cross-walls. *R. fasciculare*
7. Apical leaf cells short (less than 3:1) or mixed. 8
8. Leaves lingulate, broadly obtuse to rounded at apex; leaf margins usually with blunt teeth toward apex. *R. aciculare*
8. Leaves ovate-lanceolate, narrowly obtuse to acute at apex; leaf margins not toothed, smooth or finely crenulate at apex. 9
9. Leaf cells with several low papillae per cell. *R. varium*
9. Leaf cells smooth. *R. pacificum*

Rhytidiadelphus

1. Leaf cells in the upper portion of the leaves papillose on the back by projecting cell ends; costa long and double, usually extending beyond mid-leaf. *R. triquetrus*
1. Leaf cells smooth throughout; costa absent, or short and double, ending below mid-leaf. 2
2. Leaves plicate; alar cells not differentiated. *R. loreus*
2. Leaves not plicate; alar cells differentiated, shorter, wider, and hyaline. *R. squarrosus*

Scleropodium

1. Basal leaf cells (last few rows) elongate; median leaf cells very long, often to 15-20:1. *S. touretii* var. *colpophyllum*
1. Basal leaf cells (last few rows) short, rounded, quadrate or short rectangular; median leaf cells shorter, usually around 10:1. *S. cespitosum*

Seligeria

1. Peristome absent. *S. donniana*
1. Peristome present. 2

2. Capsule hemispherical; seta straight when moist; columella long, often retaining the operculum once detached or sticking out after the latter has fallen off; spores large (18-32 μm). *S. tristichoides*
2. Capsule ovoid; seta usually curved when moist; columella short; spores small (8-18 μm). *S. campylopoda*

Sphagnum

1. Plants green, never with red coloration; stem leaves lingulate, broadly truncate, apex fringed. *S. girgensohnii*
1. Plants often red coloured; stem leaves triangular, apex narrow, often involute. *S. capillifolium*

Tetraphis

1. Seta straight and smooth. *T. pellucida*
1. Seta bent in the middle, and papillose above the bend. *T. geniculata*

Tortula

1. Costa excurrent as a coloured point or short awn, not readily visible at low magnification (10x); leaf margins differentiated at mid-leaf, cells longer and narrower than within, smooth or with low papillae. *T. subulata*
1. Costa usually long excurrent as a white (often reddish at the base), denticulate awn readily visible at low magnification (10x); leaf margins not differentiated. 2
2. Leaves erect-spreading when moist, more or less straight, not curved. . . *T. princeps*
2. Leaves recurved when moist, curved backward, apices pointed down toward the base of the plant. *T. ruralis*

Ulota

1. Spores large, more than 30 μm in diameter. *U. megalospora*
1. Spores small, less than 30 μm in diameter. *U. obtusioscula*

2.2.3. Notes on problematic taxa

Atrichum

Atrichum selwynii and *A. undulatum* are both common species in southwestern British Columbia (Lawton 1971, Vitt *et al.* 1988). They are thus both likely to be found at Bridal Veil Falls. The main difference between the two species involves their sexuality. *A. selwynii* is always dioicous, while *A. undulatum* can be either monoicous or dioicous (Ireland 1969a). Treatments of the genus by Ireland (1969a, 1971) suggested a series of other characters to differentiate the two species. Such characters involve the nature of the calyptra, the curvature of the capsule, the number of sporophytes borne on each plant, and the characteristics of the leaf cells. However, based on observation of my material and of herbarium specimens, these characters appear variable and greatly overlapping. Hispid-tipped calyptrae, which Ireland attributed to *A. undulatum*, were found to occur in dioicous material of *A. selwynii*. Curvature of the capsule was variable even within a single population. Similarly, numbers of sporophytes per plant varied between populations of the same species. Finally, Ireland attributed smaller, thick-walled, collenchymatous, rounded leaf cells to *A. undulatum*, and larger, thin-walled, non-collenchymatous, angular leaf cells to *A. selwynii*. This characterization, though observable, was not consistent in our material. The nature of the leaf cells often varied between leaves of the same plant and even within a single leaf.

Monoicous sexuality remained the only character that positively distinguished *A. undulatum* from *A. selwynii*. In the case of dioicous specimens or of those that could not be sexed, careful observation of the nature of the leaf cells appeared to be the preferable solution.

Only one specimen collected during the course of this study was monoicous, confirming the presence of *A. undulatum* at Bridal Veil Falls. Other specimens were either seemingly dioicous, or did not bear sporophytes and/or sex organs at the appropriate stage for assessing sexuality. They were identified based on the characteristics of leaf cells, as mentioned above.

Dicranella schreberiana* versus *Trichodon cylindricus

Sterile material of *Dicranella schreberiana* is not easily distinguishable from *Trichodon cylindricus*. Furthermore, the two species occur in the same types of habitat. Dixon and Jameson (1924), Smith (1978), and Crum and Anderson (1981) suggested the roughness of the subula as a discriminant character. The subula is said to be toothed-papillose all around in *Trichodon cylindricus*, while in *Dicranella schreberiana*, the teeth should be found only on the margin of the subula. Lawton (1971) also indicated a difference in size between the two species. According to her descriptions, stems of *Dicranella schreberiana* reach up to 30 mm in height, while *Trichodon cylindricus* is smaller, rarely reaching more than 5mm in height.

The presence of both species at Bridal Veil Falls was confirmed by sporophytic material of *Trichodon cylindricus*, and by material with the long shoots attributable to *Dicranella schreberiana*. As a guide for the identification of small gametophytic material also collected, we examined and compared the roughness of the subula between the latter specimens. We were unable, however, to observe the difference in roughness described above.

All sterile material collected during the course of this study was therefore classified as *Dicranella schreberiana*.

Plagiochila

Godfrey (1977) derived a key to separate *Plagiochila asplenioides* from *P. satoi* from papers by Inoue and Schuster. The characters use in that key proved to be greatly variable. Although this key worked well for some specimens, Godfrey encountered many transitional specimens. She concluded that there were no satisfactory means of separating the two species in southwestern British Columbia. Specimens belonging to this problematic group were treated as the *P. asplenioides* complex.

Godfrey (1977) pointed out that a detailed study of the group was needed to solve the problem. Hong (1992), who worked on the genus *Plagiochila* in Western North America, proposed key characters which are essentially the same as those unsuccessfully used by Godfrey. The problem thus remains unsolved.

To avoid problems with transitional specimens, Godfrey's treatment was adopted here: species of the *P. asplenioides/P.satoi* group were identified as *P. asplenioides sensu lato*.

Plagiomnium

Taxonomic treatments of *Plagiomnium* (Lawton 1971; Koponen 1974) are based primarily on fertile material. They refer to characteristics of leaves of mature material, sexuality, and sporophytic characters. Neither keys nor descriptions account for different growth forms, life stages or environmental variants. In the course of this study, we

encountered difficulties identifying sterile and plagiotropous material.

The ecological aspects of the study, required the collection of material to record its presence in a certain habitat, rather than the collection of ideal material for the purpose of taxonomic work. In general, taxonomic treatments that treat variability would undoubtedly be useful in ecological work.

Racomitrium

The classification of *Racomitrium* sect. *Laevifolia* (or *heterostichum* group) is problematic, reflecting the inherent variability of this taxon. A complete and thorough taxonomic treatment of this complex had been lacking. Recently, the taxonomy of the group was revised by Frisvoll (1988). His treatment has been used here as a reference for the identification of the specimens of the *heterostichum* group found at Bridal Veil Falls.

Frisvoll (1988) based his treatment on taxonomic characteristics which he recognized as stable and therefore useful for species recognition. They include the structure of the costa, the alar cells and supra-alar marginal cells, the leaf margin, and the perichaetial leaves. Based upon Frisvoll's treatment we were able to recognize two species of the *heterostichum* group in the Bridal Veil Falls collection: *Racomitrium pacificum*, and *R. lawtonae*. The former is characterized by the absence of hair-points and unistratose leaf margins. The latter is characterized by its long lanceolate leaves with weakly denticulate, long decurrent hair-points, unistratose margins, undifferentiated alar cells, elongate upper marginal cells, median leaf cells rounded in cross-section, and bistratose, canaliculate costae (Ireland 1970, 1976; Frisvoll 1988).

My material also included several specimens which did not conform satisfactorily to the description of either of the above species. We encountered the same difficulties of high variability mentioned by other taxonomists (Frisvoll 1988). Unfortunately, I had at my disposal only very few specimens identified by Frisvoll. Such specimens would have helped clarify the concepts developed by Frisvoll (1988) and familiarize ourselves with the variability permitted within the different species concepts.

The specimens that would not fit into the segregate species were classified as *Racomitrium heterostichum sensu lato*. They usually possessed strongly denticulate hair-points that were not or only shortly decurrent, short to slightly elongated upper marginal leaf cells, median leaf cells elliptic in cross-section, and predominantly unistratose leaf margins. The specimens probably include some material of *Racomitrium heterostichum* (e.g. Djan-Chékar & Dagenais 91-106) with a costa broad and bistratose at mid-leaf, and of *R. affine* (e.g. Djan-Chékar & Schofield 91-544; Djan-Chékar & Reid 91-69) with a costa narrower and tri-stratose at mid-leaf. Our concept of these taxa, however, is not sufficiently clear to positively identify them as such. Some specimens might also be variations of *Racomitrium lawtonae* (e.g. UBC b20413, b20439, and b20418). These specimens typically possessed bistratose, canaliculate costae, unistratose margins and undifferentiated alar cells, but hair-points were relatively short decurrent, upper marginal leaf cells were short, or some differentiated cells occurred at the basal margin. Among all specimens encountered unistratose leaf margins predominated. This eliminates as possible species, *Racomitrium brevipes*, *R. occidentale*, and *R. obesum*.

2.2.4. *Barbula convoluta* var. *gallinula*, new to British Columbia.

Barbula convoluta var. *gallinula* Zander is reported here as new to British Columbia.

Three specimens were collected during the course of this study and a duplicate of one of them was sent to R.H. Zander for confirmation.

While *Barbula convoluta* var. *convoluta* is common and widely distributed (Smith 1978, Zander 1979), var. *gallinula* has been reported only from the Northwest Territories, Yukon and Alaska (Zander 1979, and pers. communication (1992)). Southwestern British Columbia becomes the southernmost known locality for this variety. The wide gap in its distribution is most likely to be the result of a lack of collection of this small and inconspicuous plant.

Chapter 3. Ecology

3.1. Introduction - Species diversity

The species diversity of a community is normally expressed in terms of number of species present (species richness) and in terms of the relative abundance of these species (evenness). The results of the present study include estimates of species richness; relative abundance was not measured with any precision. Therefore, any reference to diversity alludes to species richness only. Species richness by itself can be considered as a simple, unweighed measure of diversity (Pielou 1975).

Several hypotheses have been proposed to indicate which community factors determine diversity. Such factors include: time, productivity, succession, stability, environmental extremes, predictability, competition, and habitat complexity and heterogeneity (Slack 1977; Putman and Wratten 1984). As noted by Pielou (1975), some factors play a role at a local scale, that is in a particular community at a particular time. These small scale, short term factors are the proximate causes of diversity. They are the concern of ecology. Other factors related to diversity play a role over areas of wider geographic extent and over considerable periods of time. These large scale, long term factors are the ultimate causes of diversity. They are the concern of biogeography and are considered in Chapter 4.

More specifically, this chapter emphasizes the role of habitat complexity and heterogeneity as a promoter of diversity. Substratum-patchiness, for instance, has been associated with increased diversity of small organisms, such as bryophytes (Pielou 1975). Because of their small size, bryophytes are affected by very local variations in environmental conditions.

3.2. Materials and methods

The data used for this general analysis of bryophyte ecology at Bridal Veil Falls were derived from ecological information recorded when specimens were collected (see Section 2.1.1). Therefore, only specimens collected during the course of this study were included in the analysis. As specimens were determined, other bryophytes found in mixture with the principal species were also identified and recorded. A total of 807 records of mosses and 189 records of liverworts were compiled for this ecological analysis. Eighty-three percent of the bryophytes composing the flora are represented. They are listed in Appendix C.

3.2.1. Definition of habitat categories

For the purpose of this analysis, habitats where bryophytes were collected were classified into six different categories. These different categories were defined as follows (see Figure 1.2):

1) Anthropogenic habitats: Anthropogenic habitats are the direct result of human activity. They comprise the park installations, parking lot, trails, lawn and picnic area, and a clear-cut strip, or meadow, over a buried pipeline.

2) Forest habitats: Most forested sites found throughout the study area are treated as forest habitats. Also included within the forest habitats are edges of the forest and the forested scree slopes found at the base of the cliffs. The exceptions are the forested cliffs, streams, spray-zones and edges of the boulder slope which are treated as other habitat categories.

3) Boulder slope habitats: Habitats within this category are all part of the boulder slope west of the park. This includes not only the open portion of the slope, but also the forested edges and a shrubby area at the top.

4) Cliff habitats: Cliff habitats include the series of cliffs that define the southern border of the study area and a few vertical outcrops found in the forest below. They comprise open cliffs and also those shaded by the adjacent forest, as well as the sites of waterfalls.

5) Stream habitats: Stream habitats encompass the banks and beds of the four forest streams found in the study area. This includes an intermittent stream which dries up during the summer months.

6) Spray-zone habitats: This category includes areas at the base of waterfalls which receive spray from the falls throughout most of the year (during the summer months, water levels being low, spray can be much reduced). Excluded from this category are cliffs within the spray zones; these are classified as cliff habitats.

3.2.2. Definition of substratum categories

Within each type of habitat, bryophytes occur on a variety of substrata. The different substrata were further classified independent of habitat. Substratum categories were:

1) Rock: Rock as a substratum comprises cliffs, boulders, smaller rocks, projecting outcrops and gravel. It can include vertical surfaces such as cliffs and boulder faces, horizontal surfaces such as rocks and projecting outcrops on the forest floor or the crests of boulders, or finally loose surfaces such as gravel. Rocks found in the study area were divided into two types: calcareous and non-calcareous.

2) Vegetation: Trees and shrubs in the study area support epiphytic communities of bryophytes. Some bryophytes were also found to grow on other species of bryophytes. Epiphytes were classified on the basis of the species on which they were collected, as well as

on the basis of where they grew on the tree or shrub. The roots and the base of the tree (>25 cm from the ground) were considered as one category, and the trunk another. Branches in the understory, as well as branches and stems of shrubs, formed a third category. Branches of the canopy, accessible from recently-fallen trees and branches, formed the last category.

3) Soil: Soil as a substratum consists of either the upper surface of mineral soil, soil accumulated over rock, soil accumulated between rocks, or earth banks. In any of these cases, the soil involved can be of different types. Those encountered in this study were classified as litter, organic (which includes humus), sand, clay, and silt.

4) Wood: Wood in various stages of decay is also an important substratum for bryophytes. It is represented by logs, stumps or snags, and branches. Three different states of decay were recognized in this study: recently-fallen (still with bark), decaying (has lost its bark, but is still solid), and finally rotten (falls apart easily).

3.2.3. Similarity indices

Similarity indices were used to determine the degree of similarity between pairs of habitats in terms of the species composition of their respective floras. The Jaccard Index of Similarity, which is based on binary (or presence/absence) data, was chosen for this purpose. This index is the proportion of species which co-occur in two sites to the total number of species found in at least one of the two sites, or:

$$JI = \frac{a}{a+b+c}$$

where a is the number of species occurring at both sites, b is the number of species occurring only in the first site, and c is the number of species occurring only at the second site (Digby

and Kempton 1987; Ludwig and Reynolds 1988). The minimum value for this index is 0, that is, when the two sites have no species in common. The maximum value is 1, that is, when the two sites have identical floras. Conjoint absences of species are ignored in this index.

The relationship between habitats based on similarity in species composition was represented graphically using multidimensional scaling (Wilkinson 1990).

3.3. Results and discussion

3.3.1. Floristic diversity in terms of habitats and substrata

The habitats recognized at Bridal Veil Falls can be separated into two groups based on the number of bryophyte species they contain (Table 3.1): boulder slope, cliff and forest habitats are more diverse, whereas, anthropogenic, stream and spray zone habitats are less diverse. Such results reflect, at least in part, the relative area occupied by each of these habitats at Bridal Veil Falls. Although precise measurements are not available, the forest certainly occupies the largest area. Cliffs and boulder slope are also relatively extensive. Anthropogenic habitats are probably comparable in size to the latter. On the other hand, streams and spray zones both occupy much smaller areas than any of the other habitats. Furthermore, sampling was focused on the largest habitats, those where bryophytes were most abundant, and those that seemed, at first glance, the most diverse - in other words, forest, cliffs and boulder slope. However, area and sampling effort are not the only factors affecting diversity. The following discussion will outline how other factors also affect the number of species observed in the different habitats.

Table 3.1. The distribution of bryophytes between habitats, between substrata, and between substrata within each habitat. (Total numbers of bryophytes are given in bold, numbers of mosses are in parentheses (), numbers of liverworts are in brackets [].)

		Substrata				
		Vegetation	Rock	Soil	Wood	
Habitat types	Anthropogenic	0 (0) [0]	7 (7) [0]	15 (15) [0]	0 (0) [0]	20 (20) [0]
	Boulder slope	1 (1) [0]	54 (46) [8]	30 (21) [9]	13 (8) [5]	78 (61) [17]
	Cliff	1 (1) [0]	61 (48) [13]	43 (30) [13]	0 (0) [0]	78 (60) [18]
	Forest	60 (46) [14]	14 (14) [0]	24 (23) [1]	45 (32) [13]	88 (67) [21]
	Stream	5 (5) [0]	18 (16) [2]	12 (8) [4]	18 (16) [2]	35 (29) [6]
	Spray zone	3 (3) [0]	9 (8) [1]	8 (7) [1]	21 (13) [8]	33 (25) [8]
		64 (50) [14]	107 (88) [19]	94 (73) [21]	73 (52) [21]	Total number of species ¹

¹Species totals are independent of the body of the table. They report total species number on each habitat or substratum. As species can occur on more than one habitat/substratum combination, column or row totals will always be less than or equal to species totals.

In terms of substrata, the highest species diversity was found on rocks and on soil, while diversity on vegetation and on wood is lower (Table 3.1). Such results are not surprising considering that rock and soil are the most important substrata both in the boulder slope and on cliffs, two of the three most diverse habitats (Table 3.1). Combined, the flora of the boulder slope and cliffs comprise 71% of all species found at Bridal Veil Falls.

It should be noted that 82% of the species growing on soil throughout the study area occur on soil over rock. Soil in cliff and boulder slope habitats, particularly, is usually soil over rock. Rock thus serves as a secondary substratum. This further emphasizes the importance of rock as a substratum at Bridal Veil Falls.

The differences observed between substrata in terms of species diversity are also partly a reflection of the general ecology of bryophytes. For instance, Smith (1982) observed that the number of epiliths (species growing on rock) in a flora is usually greater than the number of epiphytes - this applies to both obligate or facultative epiliths or epiphytes. Corroborating this observation, Schofield (1976) reported that the majority of moss genera in British Columbia are able to grow on rock.

3.3.2. Widely distributed versus restricted species

Among the bryophytes found at Bridal Veil Falls, some species occurred in a wide variety of habitats and substrata, while others were restricted to a certain type of habitat or substratum. Examples of widely distributed taxa are: among mosses, *Claopodium crispifolium*, *Eurhynchium praelongum*, *Homalothecium fulgescens*, *Isothecium myosuroides*, *Mnium marginatum*, *M. thomsonii*, *Plagiomnium rostratum*, *Rhytidiadelphus triquetrus*, and *Tortella*

tortuosa, and among liverworts, *Conocephalum conicum*, *Plagiochila asplenoides s.l.*, and *Scapania americana*. Examples of species restricted (or unique) to a certain substratum in a certain habitat are: for the mosses, *Seligeria* spp., *Hypnum lindbergii*, *Racomitrium elongatum*, *R. canescens*, *Bryum miniatum*, *Buxbaumia piperi*, *Dicranella varia*, *Platyhypnidium riparioides*, and *Ulota* spp., and for the liverworts, *Preissia quadrata*, *Porella cordaeana*, *Anastrophyllum minutum*, *Gymnomitrium obtusum*, *Moerckia hibernica*, and *Lepidozia reptans*.

Species occurring in a wide variety of habitats and substrata can be regarded as species with a wide range of ecological tolerance, that is, in terms of the different microenvironments found at Bridal Veil Falls. On the other hand, species unique to a certain habitat or substratum can be regarded as species with a relatively limited range of ecological tolerance (again in terms of the different microenvironments found at Bridal Veil Falls only). Evidently, there exists a gradient of ecological tolerance among species. The majority of species have varying degrees of ecological tolerance intermediate to that of the species mentioned above.

The restriction of a species to a certain type of habitat or substratum is considered as a key element of this study. The exclusive presence of a species in a certain habitat confers a well defined role to this particular habitat as a determinant of diversity in the study area. It also provides an indication of how this habitat might differ from the others. Among the species found at Bridal Veil Falls, a high proportion were restricted to a certain habitat or to a certain substratum - respectively 45% and 43% (Table 3.2 and 3.3). This illustrates how variety in terms of habitat is important to the diversity of an area.

Table 3.2. Number of bryophytes unique to each habitat.

Habitat types	Number of bryophytes unique to each habitat			% of the entire flora of each habitat
	Mosses	Liverworts	Total	
Anthropogenic	6	0	6	30
Boulder slope	15	8	23	29
Cliff	10	4	14	18
Forest	21	6	27	31
Stream	4	1	5	14
Spray zone	2	2	4	12
Total	58	21	79	45

Table 3.3. Number of bryophytes unique to each substratum.

Substrata	Number of bryophytes unique to each substratum			% of the entire flora of each substrata
	Mosses	Liverworts	Total	
Vegetation	5	3	8	12.5
Rock	26	7	33	31
Soil	17	4	21	22
Wood	7	7	14	19
Total	55	21	76	43

The number of species restricted to each habitat (Table 3.2) reflects species diversity within each habitat (Table 3.1). The most diverse habitats (forest, boulder slope and cliff) had the largest number of unique species, while few species were restricted to habitats with low species diversity (anthropogenic, stream and spray zone). However, closer examination of the results shows that high species diversity and large number of unique species are not necessarily correlated. This is best illustrated by the percentage of species in the flora of each habitat, confined to that habitat (Table 3.2). Both forest and boulder slope, which had high species diversity, had a relatively high proportion of unique species, and both stream and spray zone, which had low species diversity, had a relatively low proportion of unique species. On the other hand, cliff habitats, despite high species diversity, had a relatively low proportion of unique species, and anthropogenic habitats, the least diverse, had a relatively high proportion of unique species.

The number of species unique to each substratum (Table 3.3) also reflects species diversity (Table 3.1). In this case however, the pattern is consistent. Substrata with high species diversity (rock and soil) had a large number of unique species, while few species were restricted to the less diverse substrata (vegetation and wood). The substratum with the highest percentage of unique species was rock. Vegetation had the lowest percentage. Again, these results corroborate observations by Smith (1982) who noted that the number of obligate epiliths in a flora is usually larger than the number of obligate epiphytes. Schofield (1976) made similar observations, noting that few mosses in British Columbia's flora are confined to an epiphytic habitat.

3.3.3. Floristic similarity between habitats

Table 3.4 describes the similarity in species composition between the moss flora of each pair of habitats using the Jaccard Index of Similarity. None of the indices of similarity obtained are particularly high, ranging only between 0.09 and 0.31. This indicates that the habitat categories defined for this project generally discriminate relatively well between actual habitats occupied by bryophytes. This is not to say that overlap does not occur, or that it has been reduced to a minimum. To do so a much larger number of categories, as well as tools such as statistical classification of communities, would be required. Classification would also need to be done at a much smaller scale. The categories used here are artificial, defined mainly for the purpose of a broad discussion of ecology.

Among the indices of similarity obtained, there are nevertheless some relatively important differences. This is best illustrated in Figure 3.1 which provides a graphic representation of the similarity matrix given in Table 3.4.

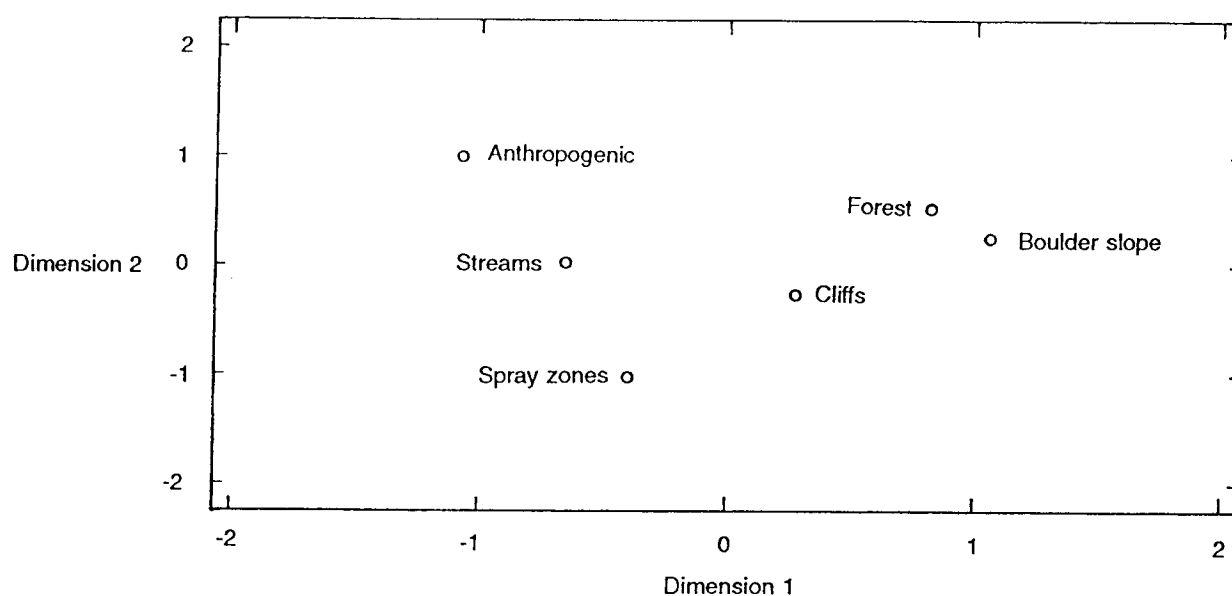
Anthropogenic habitats had among the lowest indices of similarity for all habitats (Table 3.4). In other words, anthropogenic habitats shared only a small portion of their flora with each of the others. Such results reflect the fact that anthropogenic habitats have the lowest diversity of mosses (Table 3.1), absence of liverworts, as well as one of the highest percentage of unique species (Table 3.2).

Cliffs, forest and boulder slope show a relatively high degree of similarity. This is not surprising considering that these three habitats have the highest species diversity (Table 3.1). Cliff, forest and boulder slope habitats all have a large number of unique species (Table 3.2). Nevertheless, the results indicate that a large number of widely occurring species would also

Table 3.4. Similarity between habitats based on composition of the moss flora using the Jaccard Index of Similarity.

Habitat types	Boulder slope	Cliff	Forest	Stream	Spray zone
Anthropogenic	0.09	0.14	0.13	0.17	0.10
Boulder slope		0.27	0.31	0.14	0.10
Cliff			0.22	0.24	0.25
Forest				0.17	0.12
Stream					0.23

Figure 3.1. Relationship between habitats based on similarity in species composition using multidimensional scaling (stress value of 0.00028¹).



¹Stress is very low indicating that this graphic representation fits the data generally well. The Shepard diagram (not shown), however, resembles a stepwise function indicating that a degenerate solution was achieved. Therefore, although the general picture is appropriate, the graphical distances between points are not an entirely accurate depiction of the Jaccard similarities between habitats. The use of a three-dimensional plot did not sensibly correct this problem.

be shared between them. Examples would be *Claopodium crispifolium*, *Homalothecium fulgens*, *Hylocomnium splendens*, *Hypnum subimponens*, *Isothecium myosuroides*, *Neckera douglasii*, *Plagiomnium rostratum*, *Rhytidiadelphus triquetrus*, *Scleropodium cespitans*, *Conocephalum conicum*, and *Scapania americana*, all of which occurred in all three habitats. Several others occurred in two of the three. Between boulder slope and cliff habitats, epilithic communities shared the largest proportion of species, with a coefficient of similarity of 0.25. Such a result is expected since rock is the predominant substratum in both of these habitats. Examples of species found on rock in both cliff and boulder slope habitats were *Anacolia menziesii*, *Bartramia pomiformis*, *Brachythecium plumosum*, *Grimmia torquata*, *Gymnostomum aeruginosum*, *Heterocladium macounii*, *Plagiopus oederiana*, *Polytrichastrum alpinum*, *Racomitrium heterostichum s.l.*, *Herbertus aduncus*, and *Marsupella emarginata*. Between the boulder slope and the forest, the substrata sharing the largest number of species were rock in the boulder slope and forest vegetation, with a coefficient of similarity of 0.23. Here again both of these substrata are predominant in their respective habitat. Furthermore, there are many bryophyte genera in which species are able to grow either as epiphytes or epiliths (Schofield 1976). Examples of such species found both in the forest and on the boulder slope are: *Antitrichia* spp., *Dicranum tauricum*, *Plagiomnium venustum*, *Pseudotaxiphyllum elegans*, and *Rhytidiadelphus loreus*. Between cliff and forest habitats, no pairs of substrata showed a particularly high degree of similarity in species composition of their respective flora. The highest degree of similarity was a coefficient of 0.17 between rock in cliffs and forest vegetation. Again, this result points out how a portion of epiphytic species are often found growing on rock surfaces. Examples of species found in both cliff and forest

habitats are: *Brachythecium asperrium*, *Dicranella schreberiana*, *Eurhynchium pulchellum* var. *pulchellum*, *Metaneckera menziesii*, *Platydictya jungermannioides*, *Thamnobryum neckeroides*, *Apometzgeria pubescens*, *Plagiochila asplenoides* s.l., and *Porella roellii*.

Stream, cliff and spray zone habitats also show a relatively high degree of similarity. This could be attributed to these habitats harbouring, at least in part, high-moisture microenvironments. Wide-ranging mesic and hydric species, such as *Hygrohypnum luridum*, *Hymenostylium insigne*, *Fissidens grandifrons*, *Campylium stellatum*, and *Lophozia gillmanii*, are more likely to be shared between streams, cliffs and spray zones than with any other types of habitat. This is illustrated by the low degree of similarity that streams and spray zones have with forest and boulder slope. As described above, cliffs, nevertheless, have a higher degree of similarity with forest and boulder slope, for they include a large portion of drier microenvironments as well as high-moisture ones. Combined with the high species diversity observed on cliffs (Table 3.1), the above results outline the richness of cliffs in terms of microhabitats. Furthermore, the relatively large proportion of species shared by cliff habitats with each of the others, except anthropogenic ones, explains the relatively low proportion of species to be found only on cliffs (Table 3.2).

3.3.4. The occurrence of species in habitats and on substrata

The following examines the flora of the different habitats and substrata in more detail and provides further discussion of the results given above.

Anthropogenic habitats

The results have shown that the species composition of anthropogenic habitats is unique to those habitats. This is related to the uniqueness of anthropogenic habitats among all habitats in the area in having soil - in this case bare ground - as a dominant substratum. As shown in Table 3.1, soil was the important substratum in anthropogenic habitats in terms of species diversity. Seventy-five percent of all the species found in this habitat grew on soil. Furthermore, nearly all the species unique to this habitat were growing on soil. They are *Atrichum selwynii*, *Calliergonella cuspidata*, *Funaria hygrometrica*, *Hypnum lindbergii*, and *Rhytidiadelphus squarrosus*.

The importance of soil as a substratum in anthropogenic habitats reflects an early stage in plant succession. Schofield (1985) pointed out that the persistence of bryophytes on soil is sometimes brief. Successional changes usually permit colonization by seed plants which outcompete the bryophytes present in earlier stages. This is what is happening in the meadow (the area cleared for a pipeline). As weeds and grasses have grown more abundant at the site, the abundance and variety of bryophytes has declined (W.B. Schofield, pers. communication). On the other hand, other anthropogenic sites are kept at early successional stages by continued use and maintenance by humans.

Sauer (1988) commented on the colonization of abandoned fields. His comments apply to the meadow and seem to apply also to other artificially modified anthropogenic habitats, such as the lawn and picnic area. He suggested that abandoned fields are invaded from outside rather than reclaimed by species *in situ*. His observations are for seed plants, but seem to apply to bryophytes as well. Considering dispersal distances, the most likely invaders of

anthropogenic habitats are species from the adjacent forest. However, it is likely that appropriate microhabitats for forest species are scarce in anthropogenic habitats. Unlike the forest, the soil here does not include a thick layer of organic matter. The habitat being more open, light and moisture conditions also often differ, especially away from the edges between the two habitats. Nevertheless, some of the more widely distributed species occurring in the forest are present also in anthropogenic habitats. They are *Bryum capillare*, *Claopodium crispifolium*, *Eurhynchium praelongum*, *Homalothecium fulgens*, *Plagiomnium insigne*, *P. rostratum*, and *Rhytidiadelphus triquetrus*. On the other hand, we also observed a high proportion of weedy species in anthropogenic habitats, such as *Atrichum selwynii*, *Calliergonella cuspidata*, *Funaria hygrometrica*, and *Rhytidiadelphus squarrosus*. Among them are the species restricted to anthropogenic habitats. Presumably, they invaded from lawns and fields or other disturbed habitats in the vicinity. It is possible that they were accidentally introduced from other lawns via moss fragments on lawnmowers.

Boulder slope

The boulder slope was found to be among the habitats with high species diversity, as well as a high proportion of unique species. To some extent, such results can be related to the very different environmental conditions found in the boulder slope in contrast to other habitats. Unlike any of the others, the boulder slope is open and exposed. Consequently, it experiences much stronger extremes in terms of climatic conditions. Of the species occurring at Bridal Veil Falls exclusively in the boulder slope, several are species tolerant of long periods of drought. Examples would be species like: *Amphidium californicum*, *Pogonatum*

urnigerum, *Polytrichum piliferum*, *Racomitrium* spp., and *Gymnomitrium obtusum*.

The boulder slope also differs edaphically from the other habitats. The rock is non-calcareous while in the rest of the study area, calcareous rock dominates. The only exception is a portion of cliff just above the slope where the rock surface is also non-calcareous. Therefore, several species restricted to the boulder slope and the cliff above are usually associated with acidic substrata. Examples are: *Encalypta ciliata*, *Pleurozium schreberi*, *Racomitrium* spp., *Sphagnum* spp., *Anastrophyllum* spp., *Frullania californica*, *Gymnomitrium obtusum*, and *Herbertus aduncus*. Nevertheless, some species usually associated with calcareous substrata also were found to occur in the boulder slope and the cliff above. Examples are species such as: *Barbula convoluta* var. *gallinula*, *Encalypta raptocarpa*, *Gymnostomum aeruginosum*, *Palustriella commutata*, *Plagiopus oederiana*, *Timmia austriaca*, *Tortella tortuosa*, *Tortula ruralis*, *Conocephalum conicum*, and *Preissia quadrata*.

It has been found that other elements may partially replace calcium (Brown 1982). Species usually associated with calcium could tolerate low calcium environments by substituting calcium with other elements. This might be the case for some of the species mentioned above. Among species where such a substitution has been observed, Brown reported *Palustriella commutata*. Another possible explanation is that run-off of calcium-rich water occurs over the rock where these bryophytes grew. It was mentioned previously that the water in the area has a very high concentration of calcium. It is probable, especially on cliffs, that water running over the non-calcareous rock could provide the appropriate amounts of calcium for the growth of calcicoles. This argument is supported by the presence of species predominantly associated with calcareous rock on tree trunks or wood at the base of the cliffs

or in spray zones. Examples are *Encalypta procera*, *Palustriella commutata*, *Timmia austriaca*, and *Tortella tortuosa*.

Another important factor, with regard to high species diversity in the boulder slope, is microtopography. The large size of the boulders and their arrangement makes for very complex relief. It creates a wide variety of conditions in terms of exposure and consequently, a wide range of temperature and moisture conditions. Such differentiation in environmental conditions also occurs between the open part of the slope and the edges. It is interesting to note here that regardless of the substratum, most of the 36 species found in both the forest and the boulder slope were restricted in the boulder slope to partially or fully shaded sites, such as edges of the slope, north faces of boulders, overhangs, or depressions among boulders. Examples are *Rhytidiadelphus triquetrus*, *Pseudotaxiphyllum elegans*, *Hypnum subimponens*, *Tortella tortuosa*, *Bryum capillare*, *Jamesoniella autumnalis*, *Conocephalum conicum*, and *Scapania umbrosa*. Exceptions, or species that were found in open microhabitats in the boulder slope, are: the widely occurring *Hylocomium splendens*; *Dicranoweisia cirrata* which occurred in the forest in the canopy of cedar where humidity is low and light intensity high in comparison to lower on the trees (Smith 1982); *Polytrichum juniperinum* found on soil at the forest edge, again a presumably drier and more illuminated habitat; and *Aulacomnium androgynum*, *Scapania americana*, and *Lophozia ventricosa*, all three occurring on wood in the forest.

The assemblage of species found on wood in the boulder slope differed from that on wood in the other habitats: coefficients of similarity were 0.08 with wood in forest, 0 with wood in streams, and 0.05 with wood in spray zones. This could reflect the difference in

moisture and light conditions between the boulder and the three other habitats. During the summer, temperatures remain cooler in the partial or full shade of the forest. Therefore, wood in forest or stream habitats retains some degree of moisture throughout most of the year. The situation is somewhat similar in spray zones which can be more open, but nevertheless are kept cool and moist by the spray. On the other hand, the open boulder slope becomes dry during the summer months, as moisture quickly evaporates on warm and sunny days. However, only the liverwort *Odontochisma denudatum* was found to grow exclusively on wood in the boulder slope. The presence of this species in the boulder slope and at Bridal Veil Falls will be discussed in the following chapter. Most of the other species that were growing on wood in the boulder slope were also found either as forest epiphytes (e.g. *Dicranoweisia cirrata*, *Dicranum tauricum*, and *Scapania bolanderi*), or on other substrata in the boulder slope, especially on soil (e.g. *Dicranum scoparium* and *Pohlia nutans*), or on both wood and soil (e.g. *Rhytidiadelphus triquetrus* and *Jamesoniella autumnalis*). In terms of moisture conditions, wood and soil in the boulder slope and trees in the forest could be seen as middle grounds between the extreme of forest and boulder slope. Trunks and branches of trees where these species are usually found in the forest are likely to be among the driest of forest microhabitats. On the other hand, soil and wood are likely to be among the microhabitats of the boulder slope which retain moisture the longest.

Cliffs

The results have shown that cliff habitats are markedly diversified in terms of microenvironmental conditions. This was reflected by a relatively high species diversity

(Table 3.1) and a large number of species shared with nearly all of the other habitats (Table 3.4, Fig. 3.1). As mentioned earlier, a key factor to species diversity is likely to be the variety of moisture conditions found along the cliffs. In very wet sites are found species like *Cratoneuron filicinum*, *Fissidens grandifrons*, *Hymenostylium insigne*, and *Palustriella commutata*. Moist sites harboured species such as *Campylium stellatum*, *Didymodon rigidulus* var. *gracilis*, *Hymenostylium recurvirostre*, *Blepharostoma trichophyllum*, *Moerckia hibernica*, and *Pellia neesiana*. In more mesic situations, we encountered species such as *Anomobryum filiforme*, *Ditrichum crispatisimum*, *Encalypta* spp., *Mnium thomsonii*, *Plagiopus oederiana*, *Seligeria donniana*, *S. tristichoides*, *Tortella tortuosa*, *Jungermannia atrovirens*, *Preissia quadrata*, and *Reboulia hemisphaerica*. Finally, in dry sites, grew species such as *Heterocladium macounii*, *Racomitrium aciculare*, *Schistidium apocarpum* var. *apocarpum*, *Frullania californica*, and *Scapania americana*. It is in the two latter sites that occurred a large proportion of the species shared with the forest and the boulder slope (examples of these species were given earlier in the text). Light conditions along the cliffs are also variable. Although all cliffs have more or less the same northwestern exposure, some are open while others are shaded to varying degrees by the adjacent forest. Finally, although most rock surfaces along the cliffs are calcareous, non-calcareous rock is also present. The difference between rock types is not only chemical. Different types of rock also have different water-holding capacity (Smith 1982). For instance, limestone holds more water than siliceous rock.

Several species found on cliffs were closely associated with very particular combinations of conditions. In many cases, although conditions between two sites seemed superficially similar, bryophyte communities differed. For instance, species such as

Anomobryum filiforme, *Seligeria donniana* and *S. tristichoides*, and *Pellia neesiana* were found only at very specific sites along the cliffs, while their microhabitat seems repeated in several places.

Forest

Like the boulder slope, the forest contained a large number of species, as well as a high proportion of species unique to it. Again, such results can be attributed to environmental conditions unique to the forest. As seen in Figure 3.1, of all the species occurring on vegetation throughout the study area, the majority (94%) were forest species. It is a similar situation for a large proportion of the species occurring on wood (62%). In other words, epiphytes and species growing on wood are best represented in the forest. From such results we can conclude that abundance of vegetation, and consequently abundance of wood, as substrata is particular to the forest. Several of the species found only in the forest are associated with trees or wood, for example: *Buxbaumia piperi*, *Dicranum fuscescens*, *Hypnum circinale*, *Neckera pennata*, *Orthotrichum* spp., *Plagiothecium undulatum*, *Ulota* spp., *Calypogeia fissa*, *Lepidozia reptans*, *Metzgeria temperata*, and *Porella cordaeana*. It is of interest to note that most of these species can grow on rock surfaces elsewhere.

Considerable variation exists in the composition of bryophyte communities on trees and on wood. In the case of trees, the variation observed has been related to a series of interacting factors which influence light conditions, relative humidity, nutrient availability and the chemical and physical nature of the substratum. These factors include the age of the host tree, height on the tree, direction of exposure, inclination, and chemical and physical

characteristics of the bark, such as porosity, roughness, exfoliation, chemistry, pH. (Slack 1976, 1977; Smith 1982; Kenkel and Bradfield 1981, 1986; and Schofield 1985). Such a large number of interacting factors makes it difficult to discern clear patterns in the distribution of epiphytic species in the results of this study. This would require precise measurements of microhabitat characteristics and systematic sampling of epiphytic communities. Nevertheless, some trends are apparent. For example, desiccation-tolerant species, such as *Dicranoweisia cirrata*, *Orthotrichum* spp., and *Tortula ruralis*, were found in the canopy of the trees where there is higher illumination and lower relative humidity. On the other hand, at the base of trees we found species associated with rich, moist habitats, such as *Plagiothecium undulatum*, *Pseudotaxiphyllum elegans*, and *Rhizomnium glabrescens*.

As pointed out by Slack (1976), the nature of epiphytic communities is dynamic. As a tree grows, surrounding environmental conditions are modified, and the nature of the bark changes. This results in changes in the structure and composition of epiphytic communities throughout the life of the tree. After the tree falls, moisture and illumination of the tree changes and the epiphytic communities which occupied the living tree are replaced by others (Schofield 1985). These new communities are in turn replaced as the wood decays and as the surrounding vegetation responds to the local disturbance. For instance, we found species of *Orthotrichum* only on recently-fallen wood. Other species, like *Leucolepis acanthoneuron*, *Metzgeria temperata* and *Scapania americana*, occurred on wood in an early stage of decay. Finally, some species were associated with rotten wood. Examples are *Buxbaumia piperi*, *Plagiothecium laetum*, *Pseudotaxiphyllum elegans*, *Tetraphis pellucida*, *Calypogeia fissa*, and *Lepidozia reptans*.

Although the forest harboured a large number of epiphytes, only a small number of species were restricted to trees. This corroborates results presented by Smith (1982) and Slack (1977). Results presented by Smith (1982) concerning British mosses showed that the majority of epiphytes are not restricted to epiphytic conditions. In the British flora, there are 33 obligate epiphytic mosses versus 44 facultative ones. Similarly, Slack (1977), working in forest stands on Ampersand Mountains in the Adirondack, found that only nine of 36 epiphytic bryophyte species grew exclusively on trees. Similarly, few of the numerous species growing on wood are restricted to that substratum. In fact, several forest species occur both on wood and on living trees. The index of similarity between forest vegetation and forest wood is relatively high (0.5). Examples of species growing both as epiphytes and on wood (apart from species found on recently-fallen wood) are: *Dicranum fuscescens*, *Hypnum circinale*, *Isothecium myosuroides*, *Plagiothecium undulatum*, *Rhizomnium glabrecens*, *Lophocolea cuspidata*, *Metzgeria conjugata*, *M. temperata*, and *Scapania bolanderi*. Furthermore an important proportion of forest epiphytes are also forest floor species. The index of similarity between the two latter habitats was 0.23. When on trees, the species involved were often found growing at tree bases. Examples are *Antitrichia californica*, *Eurhynchium oreganum*, *E. praelongum*, *Leucolepis acanthoneuron*, *Plagiomnium insigne*, *P. rostratum*, *Rhytidiadelphus loreus* and *Thamnobryum neckeroides*. Several of the latter species can grow also on wood. Therefore, our results also show a relatively high degree of similarity between the forest floor flora and the flora of forest wood (0.25).

Streams and spray zones

As described above, stream and spray zone habitats both had low species diversity. It has been related to their small area. This low species diversity could also be related to the higher degree of specificity associated with habitats such as streams and spray zones. The environmental conditions found in these habitats can be viewed as somewhat restrictive. Slack and Glime (1985), for instance, describe stream habitats as unstable. They note that only a very small proportion of species can establish themselves and survive under stream conditions. They pointed out the problems associated with withstanding currents and abrasion, and survival of repeated desiccation and flooding according to varying water levels. To these restrictive conditions, we could add the accumulation of sediments, and more particularly to the study area, the water's high concentration of calcium. With the exception of currents and abrasion, all these conditions are found also in spray zones.

Nevertheless, despite the certain degree of specificity which can be attributed to these two habitats, streams and spray zones had only a relatively low proportion of unique species. Species unique to stream habitats are *Brotherella roellii*, *Campylium chrysophyllum*, *Platyhypnidium riparioides*, *Porotrichum bigelovii*, and *Chiloscyphus polyanthos*. Species found only in spray zone habitats are *Dicranella varia*, *Eurhynchium pulchellum* var. *barnesii*, *Jungermannia leiantha*, and *Riccardia chamedryfolia*. As described above, this low proportion of unique species partly reflects the fact that several species were shared with high-moisture habitats found along the cliffs. However, it could be related also to an edge effect. The habitat categories that were defined for this study overlap to a certain degree. This is true especially as edges between habitats provide environmental conditions intermediate between

those characteristic of each habitat. The effect of edges on habitat categorization is particularly important in smaller habitats, such as streams and spray zones, where the proportion of edges to the bulk of the habitat is much greater. It is even more pronounced in a long and narrow type of habitat such as streams. The precise limits of stream banks, for instance, are not clear. A similar situation prevails in the extent of spray zones. The transition between stream, or spray zone habitats, and forest habitats is not sudden. It involves gradual changes in environmental conditions, particularly relative humidity. There is also a temporal element involved, dictated by fluctuations in water levels. Spray zones, for instance, are wider during periods of higher precipitation.

3.4. Conclusion

The results of this study provide the basis for a general discussion of the ecology of bryophytes at Bridal Veil Falls. Although discussion of these results involves considerable speculation, it has raised a series of hypotheses and highlighted trends that could serve as a basis for more detailed ecological work.

General differences between habitats in terms of environmental conditions were found to play a role as a promotor of overall species diversity at the site. Such differences involved exposure, light and moisture conditions, edaphic conditions, and type of substratum dominant in the habitat. At a smaller scale, habitat complexity was found to be a source of diversity. A wide variety of microhabitats available to bryophytes characterized the most diverse habitats. Involved here were again light, moisture and edaphic conditions, as well as factors such as microtopography and cyclic successional changes.

Chapter 4. Phytogeography

4.1. Materials and methods

4.1.1. Definition of phytogeographic elements

The bryophyte species of Bridal Veil Falls were grouped by affinities between their distributions. The approach used, based upon the recognition of phytogeographic elements, has been described by Stott (1981). Phytogeographic elements were defined in terms of the distribution of the bryophytes in the Northern Hemisphere, north of the tropics (Table 4.1). A second set of phytogeographic elements was used to describe their regional distributions within Pacific North America (Table 4.2). The Pacific North American region includes the Pacific coast of Alaska, and the regions west of the Rockies in Yukon, British Columbia and the United States.

Northern hemisphere distributions of the various species were determined primarily on the basis of distributional information provided by Nyholm (1975), Ireland (1982), and Smith (1978) for the mosses; and by Godfrey (1977) for the liverworts. Regional distributions of the mosses were assessed based primarily upon distributional information provided by Vitt *et. al.* (1988), Lawton (1971), and Schofield (unpublished data). Taxonomic treatments by Hoisington (1979), Vitt (1973), Frisvoll (1983, 1988), and Ireland (1970) provided additional sources of distributional information. Regional distributions of liverworts were derived from Vitt *et. al.* (1988), Schofield (unpublished data), Godfrey (1977), and Schuster (1966, 1969, 1974, 1980, 1992a, and 1992b). In addition, taxonomic treatments by Hong (1980, 1992) and Hong *et.al.* (1990) were also useful.

Table 4.1. Phytogeographic elements based on distributions within the Northern Hemisphere.
(modified from Godfrey 1977)

I. Continuous distributions

A. Circumboreal distributions

1. Circumboreal (CB)
2. Circumboreal, missing in Eastern Asia (CB(-EA))
3. Arctic-alpine (AA)

B. Endemic distributions

1. Endemic to Western North America (WNA)
2. Endemic to North America (NA)

II. Discontinuous, or disjunct, distributions

A. Disjuncts of european affinities

1. North America/Western Eurasia (NA/WE)
2. Western North America/Western Eurasia (WNA/WE)
3. Western North America/Newfoundland and/or Greenland/Western Europe (WNA/ENA/WE)

B. Disjuncts of eastern asian affinities

1. North America/Japan (NA/J)
2. Western North America/Eastern Asia (WNA/EA)

C. Disjuncts of mixed affinities

1. Western North America/Western Eurasia/Eastern Asia (WNA/WE/EA)
 2. Western North America/Eastern North America/Western Eurasia/Eastern Asia (WNA/ENA/WE/EA)
-

Table 4.2. Phytogeographic elements based on regional (Pacific North American) distributions.

I. Northern Distributions - with southern British Columbia, or northern Washington populations marking the southern limit of the range

1. Widespread (nw)
2. Coastal - restricted to the coast (nc)
3. Discontinuous - restricted to the coast and humid interior (nd)

II. Southern Distributions - with southern British Columbia populations marking the northern limit of the range

1. Widespread (sw)
2. Coastal - restricted to the mediterranean (winter wet/summer dry) climate of the coast (sc)
3. Discontinuous - restricted to the mediterranean climate (winter wet/summer dry) of the coast and dry sites of the interior (sd)

III. Widespread Distributions - with southern British Columbia populations more or less in the middle of the range

1. Widespread (w)
2. Coastal - restricted to the coast (c)
3. Discontinuous - restricted to the coast and humid interior (d)

IV. Arctic-montane Distributions - of arctic/alpine or subarctic/subalpine affinity

1. Arctic-montane (am)
-

4.2. Results and discussion

4.2.1. Affinities of the flora - broad geographic perspective.

Twelve phytogeographical elements were used to describe the Northern Hemispheric range of the bryophytes of Bridal Veil Falls (Table 4.1). The element to which each species was assigned is given in Appendices A and B. Table 4.3 summarizes the elements represented at Bridal Veil Falls. The following presents a general discussion of these various distributional elements. Predominant patterns are discussed. The detailed discussion of particular cases is beyond the scope of this study.

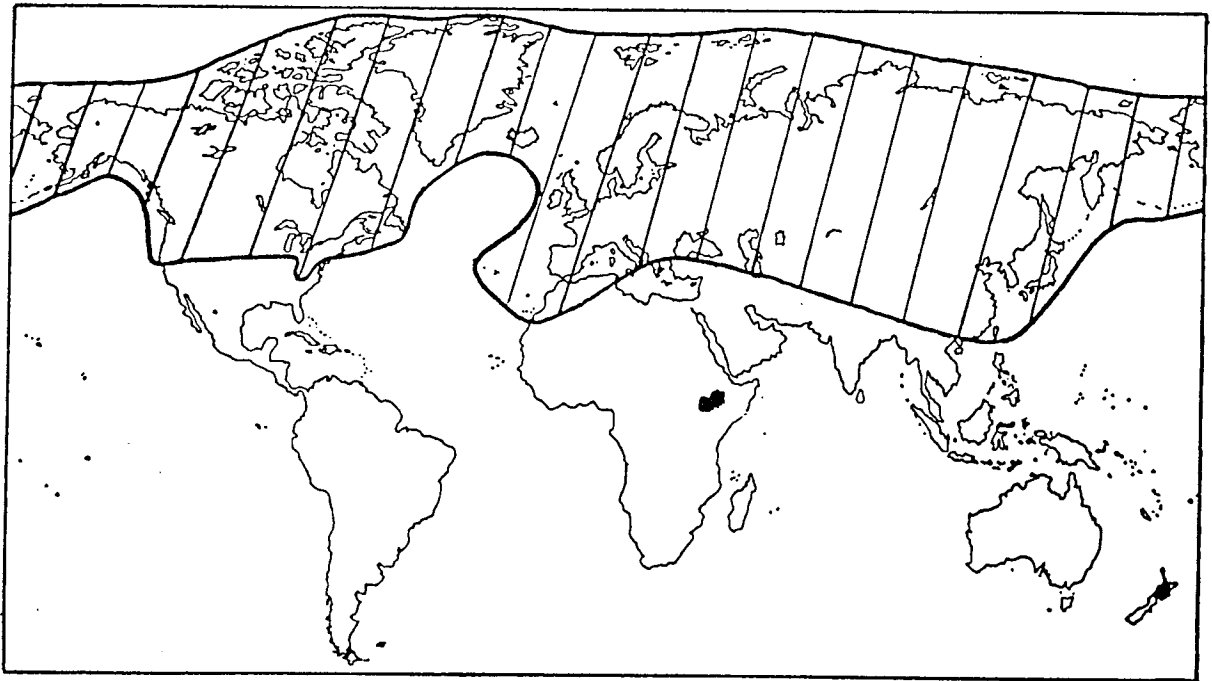
Most of Bridal Veil Falls' flora (60%) is circumboreal (Table 4.3, elements 1 to 3). The circumboreal elements include species that have a more or less continuous distribution throughout the Northern Hemisphere (e.g. *Ceratodon purpureus*, *Climacium dendroides*, *Cratoneuron filicinum*, *Dicranum scoparium*, *Funaria hygrometrica*, *Hylocomium splendens* (Figure 4.1), *Neckera pennata*, *Plagiothecium denticulatum*, *Sanionia uncinata*, *Tetraphis pellucida*, *Conocephalum conicum*, and *Lepidozia reptans*). Circumboreal species dominate the bryophyte flora of the holarctic. The large number of species showing such a distribution is attributable to a number of factors (Godfrey 1977; Schofield 1980, 1992). The ice sheets that spread over large portions of the northern continents during the Pleistocene shaped a similar landscapes. After their retreat, they left vast tracts of land available for colonization. The large number of circumboreal taxa reflects also climatic uniformity throughout much of the Northern Hemisphere. Finally, the land masses involved are relatively continuous at present and have been since long in the past. As noted in Godfrey (1977), extended periods of geographical contact or proximity provided the opportunities for dispersal.

Table 4.3. The number of bryophytes belonging to each circumboreal phylogeographic elements.

Abbreviations of phylogeographic elements is as follows: **AA**=arctic-alpine, **CB**=circumboreal, **EA**=eastern Asia, **ENA**=eastern North America, **J**=Japan, **NA**=North America, **WE**=western eurasia, **WNA**=western North America. (see Table 4.1)

Phylogeographic elements	Number of mosses	Number of liverworts	Total	Percent of the flora (%)
1. CB	88	31	119	56
2. CB(-EA)	0	4	4	2
3. AA	0	4	4	2
4. WNA	29	5	34	16
5. NA	3	1	4	2
6. NA/WE	9	3	12	6
7. WNA/WE	13	1	14	7
8. WNA/ENA/WE	1	2	3	1
9. NA/J	1	2	3	1
10. WNA/EA	4	3	7	3
11. WNA/WE/EA	2	0	2	1
12. WNA/ENA/WE/EA	2	4	6	3

Figure 4.1. World distribution of *Hylocomium splendens*. (from Schofield 1974).



In the case of arctic-alpine species, although their distribution is continuous, they predominate at high northern latitudes, extending southward in higher elevations of mountains or in other microenvironments that closely match the macroenvironment of arctic regions (Schofield 1969a). For instance, the extension of arctic bryoflora to western Newfoundland coincides with the southerly flow of cold Labrador ocean current that produces cold summers (Schofield 1992). Examples of arctic-alpine species at Bridal Veil Falls are *Lophozia alpestris* and *Tritomaria quinquedentata*.

Twenty-two percent of the flora is of species that have discontinuous distributions throughout the Northern Hemisphere (Table 4.3, elements 6 to 12). These species show wide gaps, or disjunctions, in their range. Large continental disjunctions are generally thought of as remnants of more continuous distributions of the past. Most disjunct species are restricted to very specific climatic regions that have probably been interconnected in the very distant past and are markedly disjunctive at present. Such disjunctions thus originate over extensive geological time periods - the results of various historical factors such as changes in the continental positions or variation in climate through time (Belland 1987; Schofield 1985, 1988; Schofield and Crum 1972). In most cases, it is unlikely that long distance dispersal was involved, despite the fact that most bryophytes have diaspores highly suitable for long distance wind-dispersal. The disjunctive distribution patterns observed in bryophytes coincide mostly to the same patterns observed in vascular plants. It is thus likely that disjunctions of vascular plants and bryophytes followed the same historical development (Schofield 1980). Furthermore, a high proportion of disjunctive species are dioicous, and do not produce any specialized vegetative propagules for dissemination (Schofield 1980, 1984; Schofield and

Crum 1972). Disjunctive species are also often associated with highly humid oceanic climates, often in mountainous regions where the effects of strong winds and the opportunities for propagules to become air-borne are considerably reduced (Schofield 1980; Schofield and Crum 1972; Schuster 1983). This is especially true of species that have long-established association with forest vegetation (Schofield 1984). Furthermore, disjunctive species are found mostly in or near regions that escaped the harshest extremes of the glaciation (Schofield 1988).

At Bridal Veil Falls, species of the discontinuous elements are usually disjunct to one or more of the following regions: western North America, eastern North America, eastern Asia, and western Eurasia. A large proportion are disjuncts between western North America and western Eurasia. These western North American-western Eurasian disjuncts represent two main types of disjunction as described in Schofield (1985, 1988). The first type involves disjunctive species which occur in the oceanic (or highly humid) climates of western North America and western Europe (e.g. *Dicranoweisia cirrata*, *Dicranum tauricum*, *Hymenostylium insigne* (Figure 4.2), *Plagiothecium undulatum*, and *Porella cordaeana*). In western North America, oceanic climates are found eastward of the mountain chains, predominantly the coastal ones, which act in generating moist climates under the influence of dominant westerly winds. The greatest diversity of oceanic species is in northern coastal regions of Pacific North America. The second type of western Eurasian-western North American disjunction involves species found in the mediterranean (or winter wet, summer dry) climates of the southern portion of the coast of western North America and the coastal regions of the Mediterranean in Europe and northern Africa (e.g. *Antitrichia californica* (Figure 4.3), *Metaneckera menziesii*,

Figure 4.2. World distribution of *Hymenostylium insigne*. (modified from Schofield 1989).

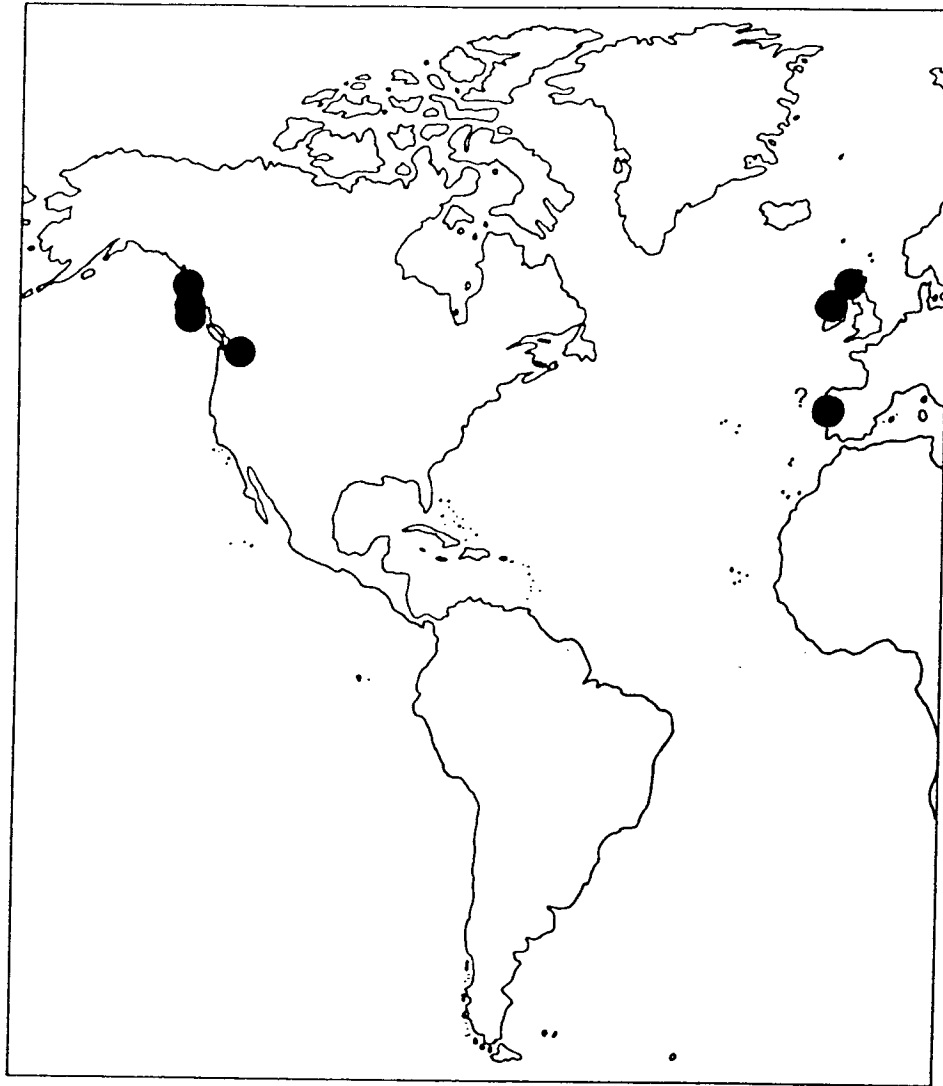


Figure 4.3. World distribution of *Antitrichia californica*. (from Schofield 1988).



Orthotrichum lyellii, *Scleropodium cespitans*, and *Tortula princeps*). In western North America, the range of mediterranean species can extend from southern California to southern British Columbia, and in some cases northward as far as southwestern Alaska in suitable, drier microclimates. Some of the species can occur also inland in edaphically favourable areas (Schofield 1980).

Oceanic climates, as those described above, tend to be particularly rich in disjunctive taxa (Schofield and Crum 1972). Such climates occur not only in Pacific North America and western Eurasia but also in eastern Asia. Disjuncts are common also between oceanic regions of western North America and eastern Asia (Hong 1987; Schofield 1965; and Schofield and Crum 1972). Among the western North American-eastern Asian disjuncts found at Bridal Veil Falls are *Claopodium crispifolium* (Figure 4.4a), *Hypnum subimponens* (Figure 4.5a), *Oligotrichum aligerum*, and *Pogonatum contortum*. In a few cases, oceanic disjuncts occur also in eastern North America. Examples are *Antitrichia curtipendula*, *Bryum miniatum*, *Pseudotaxiphyllum elegans* (Figure 4.6a), *Rhytidiadelphus loreus*, and *Tetraphis geniculata*.

As seen above, most disjunctive species are environmentally restricted (Schofield 1969a). However, in a few cases, disjunct species do not seem associated with a well-defined set of environmental conditions. Examples are *Epipterygium tozeri*, *Grimmia torquata*, and *Tortula subulata*. *Epipterygium tozeri*, for instance, occurs not only in mediterranean climates in western North America and western Eurasia, but extends to different climates in southeast Asia and Britain. The disjunct distribution of such species could represent fragments of a circumboreal Tertiary flora (Schofield 1965, 1980).

Figure 4.4. *Claopodium crispifolium*, a) world distribution (modified from Schofield 1965), b) Pacific North American distribution (from Schofield, unpublished data).

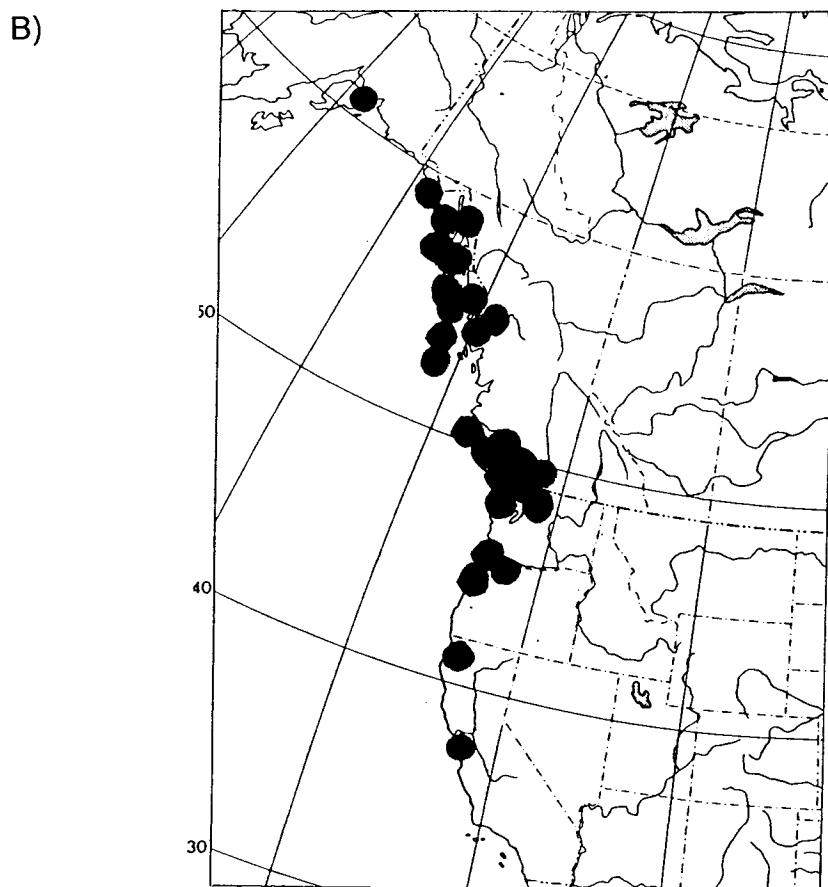
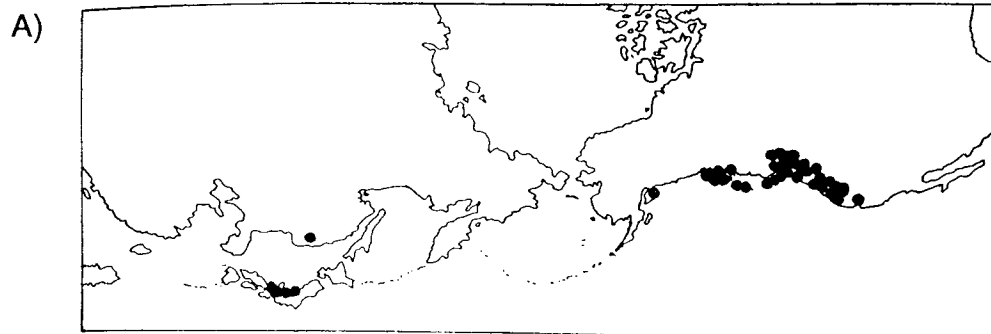


Figure 4.5. *Hypnum subimponens*, a) world distribution (from Schofield 1965), b) Pacific North American distribution (from Schofield, unpublished data).

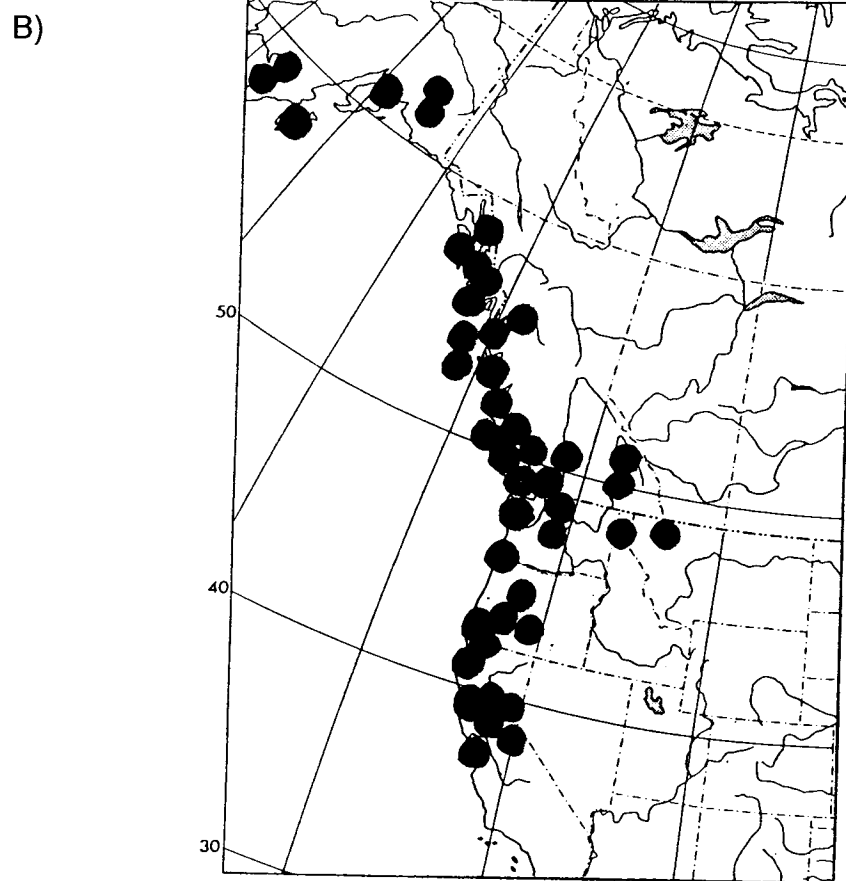
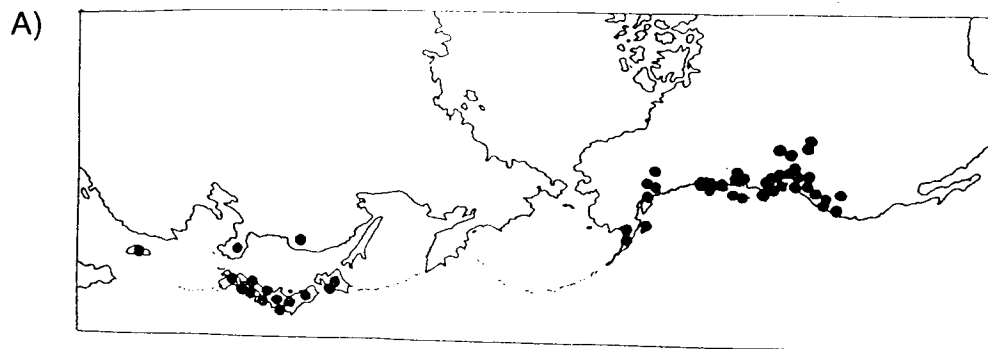
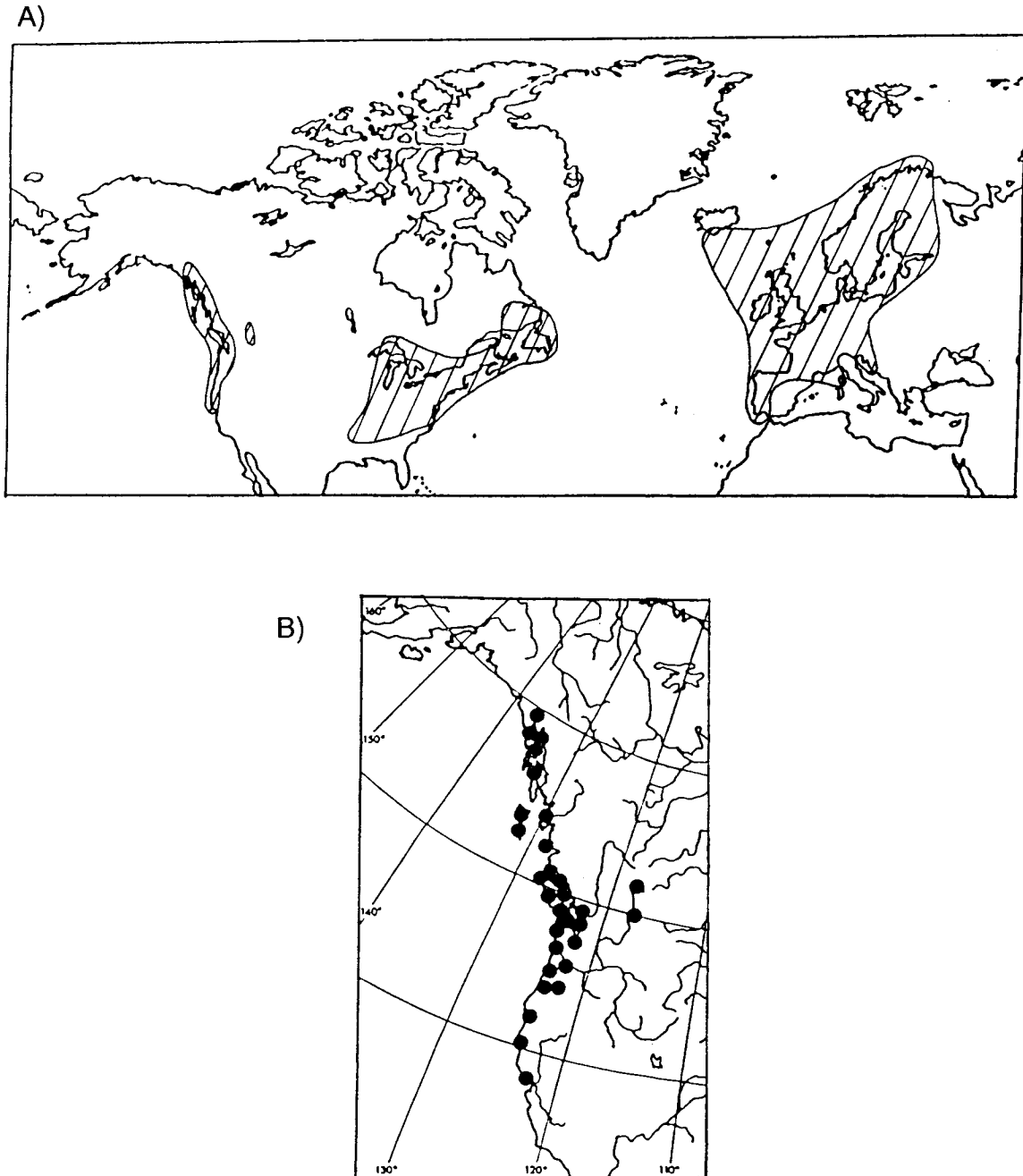


Figure 4.6. *Pseudotaxiphyllum elegans*, a) world distribution (data from Belland 1987, and Störmer 1969), b) Pacific North American distribution (from Schofield, unpublished data).



Finally, eighteen percent of the bryophytes at Bridal Veil Falls are restricted to North America (Table 4.3, elements 4 and 5). The majority are western North American endemics. These are confined mainly to areas in, or west of, the Rocky Mountains (Schofield 1969a). Like the western North American-western Eurasian disjuncts, western North American endemics found at Bridal Veil Falls can be of two types: 1) oceanic, associated with highly humid climates found primarily west of the mountain ranges of the Cordillera (e.g. *Buxbaumia piperi*, *Eurhynchium oreganum*, *Leucolepis acanthoneuron*, *Plagiomnium venustum*, *Racomitrium lawtonae* (Figure 4.7), *Thamnobryum neckeroides*, *Porella navicularis*, and *Scapania americana*), or 2), mediterranean, associated with the more southern, winter wet, summer dry climates (e.g. *Amphidium californicum*, *Anacolia menziesii*, *Dendroalsia abietina*, *Pseudobraunia californica* (Figure 4.8), *Racomitrium pacificum*, and *Frullania californica*). In both cases some species are restricted to the coast, while others occur also inland in suitable microclimates. According to Schofield (1980, 1984), the bulk of this western North American endemic flora, like the disjunctive flora of the region, would have survived the glaciations south of the glacial boundary in the western United States.

A small proportion of the species that are confined to North America are found also outside of Pacific North America. In most cases, these species are disjuncts between western and eastern North America. As discussed in Belland (1987) and Belland and Schofield (1988), the absence of many North American species in the central portion of the continent coincides with the presence of the prairie biome. There are several examples of species that show disjunctions between western and eastern North America, and are not found in the Great Plains. Examples of such species at Bridal Veil Falls are: *Grimmia torquata*, *Heterocladium*

Figure 4.7. Pacific North American distribution of the endemic *Racomitrium lawtonae* (from Frisvoll 1988, and Schofield, unpublished data). (Also known from the Aleutians)

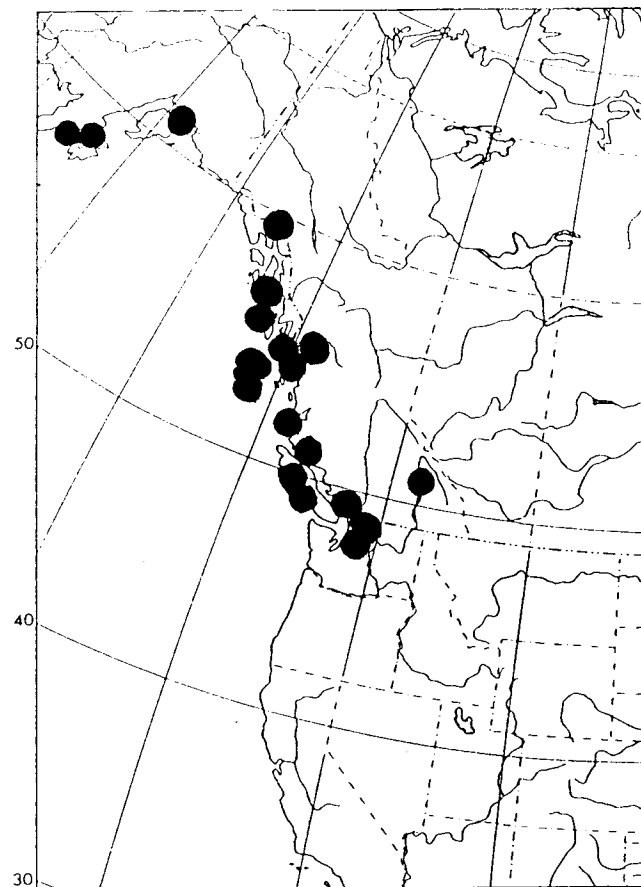
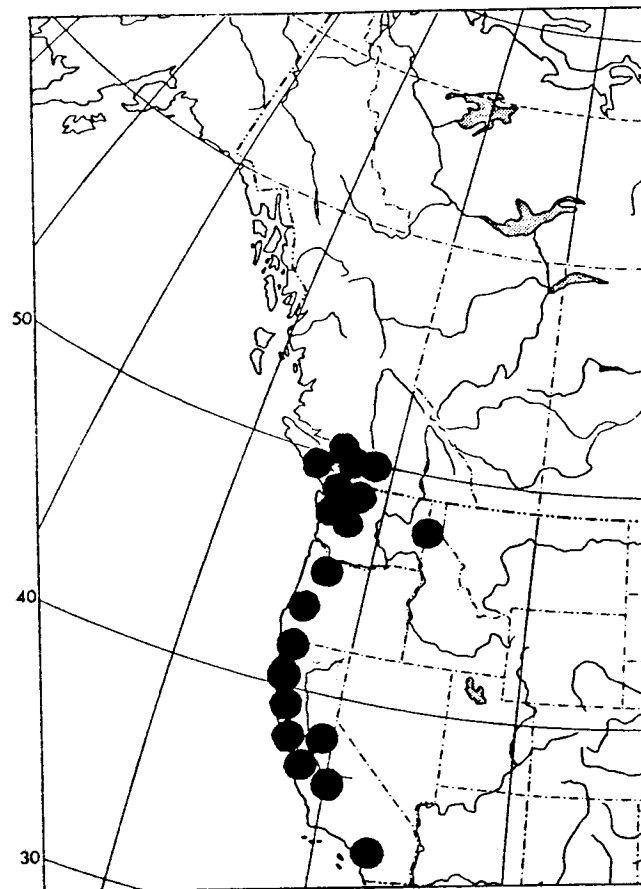


Figure 4.8. Pacific North American distribution of the endemic *Pseudobraunia californica* (from Schofield, unpublished data).



macounii, *Pseudoleskea stenophylla*, *Pseudotaxiphyllum elegans* (Figure 4.6a), *Rhytidiadelphus loreus*, *Tetraxis geniculata*, and *Frullania tamarisci* subsp. *nisquallensis*.

In summary, at Bridal Veil Falls, the distribution of species between broad phytogeographic elements is typical of the bryophyte flora of northwestern North America as described by Schofield (1968b, 1968c, 1969a, 1984 and 1988). The bulk of the flora is circumboreal. It also is rich in endemics. Finally, it is characterized by the presence of wide disjuncts, usually to western Eurasia and to eastern Asia, and predominantly associated with oceanic environments.

4.2.2. Affinities of the flora - regional geographic perspective.

Ten phytogeographical elements were defined (Table 4.2) to describe the Pacific North American distributions of the species collected at Bridal Veil Falls. The phytogeographical element to which each species was assigned is indicated in Appendices A and B. Table 4.4 provides a summary. Two percent of the species remained unclassified either because their distribution was poorly understood or because it did not accommodate any of the distributional elements defined and it seemed superfluous to create categories to accommodate them individually.

The majority of the species found at Bridal Veil Falls (55%) are widespread throughout Pacific North America. Most of these species have circumboreal distribution.

Also representing an important percentage of the flora are widespread discontinuous and widespread coastal species with 20% and 10% of the flora respectively. These are mostly endemic or disjunctive species associated with the humid oceanic climates of western North

Table 4.4. The number of bryophytes belonging to each regional phylogeographic elements.

Phytogeographic elements	Number of mosses	Number of liverworts	Total	Percent of the flora (%)
Widespread	89	27	116	55
Widespread coastal	8	14	22	10
Widespread discontinuous	32	10	42	20
Arctic-montane	2	5	7	3
Southern widespread	0	1	1	0.5
Southern coastal	4	2	6	3
Southern discontinuous	7	0	7	3
Northern widespread	4	0	4	2
Northern coastal	1	0	2	0.5
Northern discontinuous	2	0	1	1
Unclassified	3	1	4	2

America. Coastal species are restricted to the humid coastal regions (e.g. *Claopodium crispifolium* (Figure 4.4b)), while discontinuous species occur as well into the interior, mainly in the Columbia Mountain ranges (e.g. *Hypnum subimponens* (Figure 4.5b) and *Pseudotaxiphyllum elegans* (Figure 4.6b)). The Columbia region shows many similarities to the coast in terms of climate and vegetation (Schofield 1976, 1988). Easterly moving air masses produces cool wet winters and warm dry summers, and as in the coastal forest, the tree species that dominate in mature stands are *Tsuga heterophylla* and *Thuja plicata* (Ketcheson *et al.* 1991).

The remaining 13% of the flora consists of species of northern, southern, or arctic-montane distributions. The Bridal Veil Falls populations of these species are at the limit of their range, or in the case of arctic-montane species, represent unusual extension of the range. Northern coastal or northern discontinuous species are, as above, endemic or disjunct species associated with the humid climates of the coast and the interior. In this case, however, they have a generally more northern distribution. Examples are *Hymenostylium insigne* (Figure 4.2), *Racomitrium lawtonae* (Figure 4.7), and *Tetraphis geniculata*. Unlike the more widespread coastal or discontinuous species which are probably immigrants from populations that survived south of the glacial boundary, these more northern species are thought to be descendants of relictual populations in unglaciated areas along the coast (Schofield 1976).

Southern coastal or southern discontinuous species are also mostly endemics or disjuncts. These, however, are associated with mediterranean climates. Examples are *Amphidium californicum*, *Anacolia menziesii*, *Pseudobraunia californica* (Figure 4.8), and *Frullania californica*.

Northern and southern widespread species are species that are more widely distributed in the holarctic. In the case of northern ones, their range is restricted to northern temperate and/or boreal regions (e.g. *Polytrichum formosum*, *Seligeria campylopoda*, and *S. donniana*). On the other hand, southern widespread species are restricted to southern temperate regions (e.g. *Reboulia hemisphaerica*).

4.2.3. Relationship between habitat and geographic affinity.

This section examines the relationship between the Pacific North American distribution of species and their occurrence in the various types of habitat available at Bridal Veil Falls. Table 4.5 gives details as to how the different regional phytogeographic elements are represented in each habitat. The distribution of widespread species between habitats corresponds to the way the whole of the Bridal Veil Falls' flora is generally distributed between habitats (see Table 3.1). Diversity of widespread species is higher in the habitats with higher species diversity and lower in the ones with lower species diversity. On the other hand, although coastal and discontinuous species are generally more numerous in the more diverse habitats, they are the most numerous in the forest. Such results could be related to the more even character of forest habitats. Climatic conditions in forest are not subject to as much fluctuation as in more open habitats such as the boulder slope. The high humidity of coastal regions which is favourable to growth of bryophytes is maintained more uniformly under forest conditions. The different types of microhabitats available to bryophytes in forest environments are also less variable than in other habitats like cliffs or boulder slope. The latter can show considerable variation in terms of edaphic conditions, exposure, humidity,

Table 4.5. Number of bryophytes species of each regional phytogeographic element occurring in each habitat type.

Abbreviation of phytogeographic elements is as follows: **am**=arctic-montane, **c**=coastal, **d**=discontinuous, **n**=northern, **s**=southern, and **w**=widespread. (see Table 4.2)

Habitat types	Number of species of each affinity										
	W	C	D	NW	NC	ND	SW	SC	SD	AM	U
Anthropogenic	15	1	4	0	0	0	0	0	0	0	0
Boulder slope	44	5	20	0	0	1	1	0	3	3	0
Cliff	49	6	15	2	1	0	1	1	1	2	0
Forest	41	10	31	1	0	0	0	2	2	0	1
Stream	23	2	7	0	0	0	0	0	2	0	1
Spray zones	23	5	4	0	1	0	0	0	0	0	0

Note: This table includes only data on the species collected at Bridal Veil Falls during the course of this study.

etc. Humid forest habitats hence form a more uniform unit through space and time allowing the wider dispersal of the bryophytes associated with them.

Godfrey (1977) examined regional distribution patterns of hepatics in southwestern British Columbia. She observed that regional distribution patterns appear to reflect patterns of availability of particular microclimatic conditions. Therefore, the wide variety of microenvironments available at a particular site would not only promote species diversity (see Chapter 3), but it could also promote the diversity of phytogeographic elements represented at the site. As stated in Godfrey (1977), suitable microclimate can affect regional distribution in extending the local opportunities for occurrence of species of different affinities at a site.

Bryophytes near the limit of their range are particularly susceptible to the availability of particular microclimatic conditions. Reporting Böcher (1954), Hedderson (1987) remarked on the importance of microhabitats for bryophytes, especially near the limits of species distributions, where plants depend more strongly on definite and limited combinations of microhabitat factors. Different authors (Belland and Brassard 1988; Hedderson 1987; Vaarama and Laine 1974) have observed how species at the limit of their range in their respective study areas were restricted in terms of habitat to a narrow range of favourable microhabitat conditions. At Bridal Veil Falls, bryophytes near the limit of their range include species of northern, southern and arctic-montane distribution. As expected, these species are often narrowly restricted in terms of the habitats and substrata on which they were found; several of them are among the species that were found confined to one habitat or substratum.

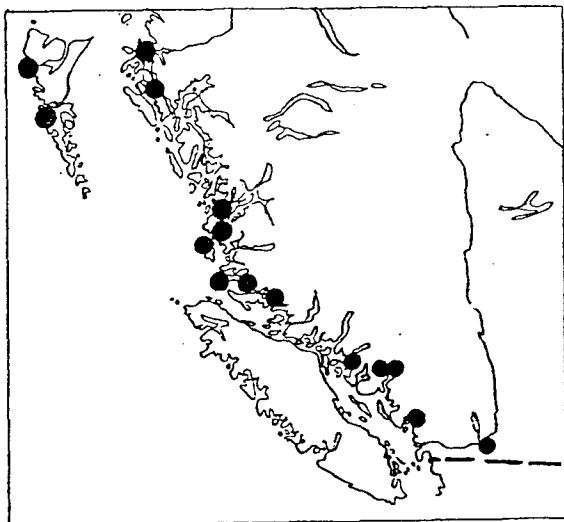
In the previous chapter, boulder slope, cliff and forest habitats were identified as the most diverse in terms of microenvironments available to bryophytes. It is interesting to note

that it is in these three habitats that species of northern, southern and arctic-montane distribution are mainly found (Table 4.5). This could be simply an artefact of the large number of species found in these habitats. Nevertheless, the wide variety of microenvironments in these habitats is likely to be also an important factor considering the importance of particular microhabitats for the establishment and survival of bryophytes at the limit of their range. If a wide variety of microhabitats are available at a site, it is more likely that this site will offer suitable conditions.

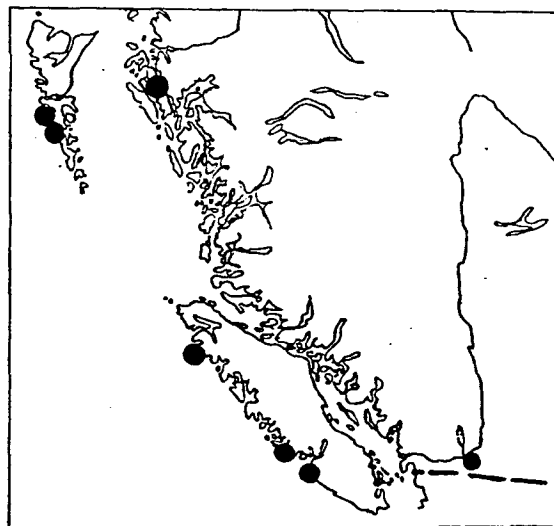
Godfrey (1977) classified the liverworts she collected in southwestern British Columbia according to patterns of local distribution for the region. Among the species of liverworts found at Bridal Veil Falls are species that she classified as strictly oceanic: *Chandonanthus filiformis*, *Moerckia hibernica*, and *Odontochisma denudatum*. She described these species as restricted to coasts along the Pacific Ocean, occurring along the west coast of Vancouver Island and northward along mainland inlets. These species were said to be rare or absent in the Lower Mainland. Their local distribution is shown in figure 4.9. Although Godfrey (1977) was not aware of the presence of these species at Bridal Veil Falls, this would probably not have changed their strictly oceanic status. Bridal Veil Falls' populations are isolated populations of these species and their presence inland remains exceptional. A few species of mosses could also be classified as strictly oceanic. Among the mosses found at Bridal Veil Falls, the only truly strictly oceanic species is *Hymenostylium insigne* which is known elsewhere in western North America only from the Queen Charlotte Islands (Figure 4.2). The presence of these strictly oceanic species inland at Bridal Veil Falls is unusual. It suggests the availability of microhabitats where humidity is exceptionally high for the region.

Figure 4.9. Regional distribution of a) *Chandonanthus filiformis*, b) *Moerckia hibernica*, and c) *Odontochisma denudatum*.

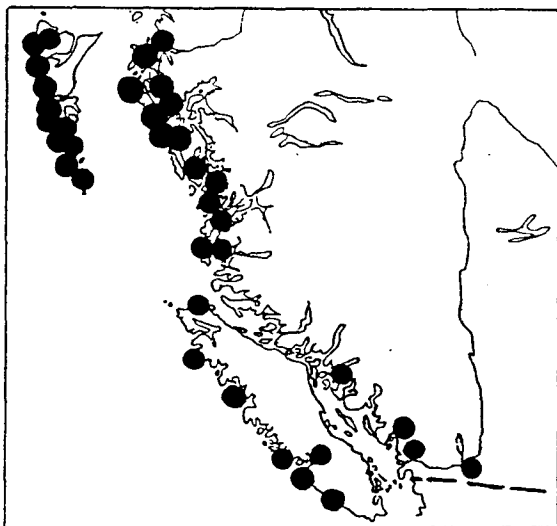
A) *Chandonanthus filiformis*



B) *Moerckia hibernica*



C) *Odontochisma denudatum*



Odontochisma denudatum, for example, was found on a rotten log high in the boulder slope. The site was shaded by high cliffs, thus moisture persisted there most of the year. Similarly, *Hymenostylium insigne* and *Moerckia hibernica* were both associated with damp cliff faces, usually in proximity of waterfalls. *Chandonathus filiformis*, although on a dry rock surface, was found in a shaded and sheltered site. In general, the relatively cooler and more mesic climate characterizing Bridal Veil Falls (see Chapter 1) is likely to be an important factor accounting for the presence of the above species. Availability of calcareous substrata is also a factor for calcicoles such as *Moerckia hibernica* and *Hymenostylium insigne*.

The presence of arctic-montane species at Bridal Veil Falls is also unusual (e.g. *Barbula convoluta* var. *gallinula*, *Plagiobryum zierii*, *Anastrophyllum assimile*, *Lophozia alpestris*, and *Tritomaria quinquedentata*). Such species were described by Godfrey (1977) as subalpine-descending. In other words, these species are chiefly high elevation, but occasionally descend to low elevations in microclimatically suitable sites. Godfrey mentioned waterfalls and cold, humid boulder slopes or rock outcrop-slopes as examples of such sites. As expected, arctic-montane species at Bridal Veil Falls were associated with north-facing cliffs and the boulder slope (Table 4.5). The availability of cold, humid microsites along the cliffs has already been mentioned. It is in such a site that the arctic-montane species *Barbula convoluta* var. *gallinula* and *Plagiobryum zierii* were found. Both species were found in adjacent sites on a moist, shaded cliff. In the case of the boulder slope, the emphasis throughout the text has been that it was an open, dry and warm site. It could, however, also be described as a cold, humid habitat. In fact, there is a seasonal pattern in the microclimatic conditions characterizing the boulder slope. During the fall and winter, precipitation is greater

(Figure 1.5), and duration of direct sunlight is considerably reduced, even more so considering the high elevation of the adjacent cliffs; the boulder slope thus becomes a cold, humid habitat. For example, the presence of *Polypodium glycyrrhiza* in the boulder slope is not noticeable in the summer. By late fall and throughout winter, this fern flourishes in masses over the boulders. Such cold, humid conditions as described above are likely to lag behind, as summer approaches, in microsites on the north sides of boulder and closer to the cliff bases. Furthermore, if snow accumulates during the winter, it is likely to stay longer in these microsites keeping them cooler. Arctic-montane bryophytes are usually associated with these colder, moister microsites in the boulder slope (e.g. *Anastrophyllum assimile*).

Also found at Bridal Veil Falls is a group of species that Godfrey (1977) classified as species of dry southern habitats. This group includes most species described earlier as southern (e.g. *Frullania bolanderi*, *F. californica*, and *Reboulia hemisphaerica*). Godfrey (1977) observed that these species generally occupy dry, relatively sunny areas. Although specific requirements vary between species, these dry, southern species usually do, in fact, occupy drier and warmer habitats at Bridal Veil Falls. Those that occur as epiphytes were found on trunks, branches, and in the canopy of trees rather than at tree bases where conditions are presumably moister (e.g. *Antitrichia californica*, *Dendroalsia abietina*, *Tortula subulata*, and *Frullania bolanderi*). Species occurring on cliffs were associated with dry rock surfaces (e.g. *Frullania californica*). Finally, dry southern species occurring in the boulder slope (e.g. *Amphidium californicum*, *Anacolia menziesii*, *Pseudobraunia californica*, and *Reboulia hemisphaerica*) were found mostly on open, exposed sites or on dry boulder faces.

4.2.4. An interpretation of the development of the flora.

As seen above, the flora of Bridal Veil Falls contains a number of species that are phytogeographically significant. These would include species that are closely associated with very specific microenvironmental conditions found at the site, rare species, and species that show important gaps in their regional distribution. High species diversity at the site and presence of numerous phytogeographically significant species raises questions as to the origin and development of the bryoflora.

Considering the late-Pleistocene and Holocene history of the area, the flora of Bridal Veil Falls is relatively recent. The vegetation that colonized and flourished at the site following the retreat of the Sumas glacier at the end of the last glaciation was probably completely destroyed as a result of the Cheam Slide. Subsequent plant communities that established themselves at the site were in turn disturbed by more recent events, such as logging and rockfall, as well as smaller scale events, such as the installation of a pipeline and of park facilities. As seen in chapter three, these recent events have been mostly promoters of bryophyte diversity as they enhanced the variety of habitats available for bryophytes.

The bulk of the bryoflora of Bridal Veil Falls has its source in adjacent areas of the Fraser Lowland. Bryophytes from these adjacent areas were undoubtedly the main source of propagules for colonization after disturbances. As seen earlier, the flora of the region is predominantly of circumboreal affinity, with a strong humid coastal component. It probably derives primarily from bryophyte populations that survived the Wisconsin glaciation south of the glacial boundary. In a few cases, floristic elements could possibly derive from bryophyte populations that survived in coastal refugia along the coast of southern British Columbia, or

in mountain refugia in adjacent regions (Godfrey 1977). Some species could have invaded the area preceding the establishment of the modern vascular plant vegetation, while others probably moved in with the latter and depend on its presence for survival. *Acer macrophyllum*, for example, a tree that harbours abundant and diverse bryophyte communities, is likely to be a late-comer in the Fraser Lowland and at Bridal Veil Falls. It is a species of more southern distribution and it characterizes mostly second growth stands.

The expansion of the range of mediterranean elements to the Fraser Lowland has been associated with the Hypsithermal period (Schofield 1988). It is possible that the southern species took advantage of this warmer and drier period to extend the limit of their range northward, and, at the outset of that period, survived in these northern areas where favourable microenvironments were available. Nevertheless, as argued by Godfrey (1977), a xerothermic period is not necessary to explain the occurrence of species of dry southern climates in southwestern British Columbia. Their presence might simply be the result of their movement northward, as any other species displaced southward during the glaciation, into any site which offers favourable microenvironmental conditions.

While the bulk of the modern bryoflora at Bridal Veil Falls is shared with adjacent areas, some species, however, are rare or unknown from elsewhere in the Lower Mainland. In interpreting the phytogeography of such species, the extent of our knowledge of bryophyte distribution becomes an important limitation. The question arises as to whether a species is really absent from an area, or whether the area simply has not been thoroughly explored yet. Apparent disjunction can be the result of scarcity of records. This is likely to be the case of *Barbula convoluta* var. *gallinula*, for example. There is a gap in the distribution of this

species between northern areas (Alaska, Yukon, and the Northwest Territories) and southern British Columbia. It is unlikely that this wide regional disjunction is the result of long distance dispersal. Firstly, this moss reproduces essentially by means of large, bulky gemmae. Secondly, there are important geographical barriers between the two disjunct parts of its range.

The case of oceanic species is also puzzling. These species are also often rare or unknown from the Lower Mainland. Some of these species could have dispersed inland to Bridal Veil Falls from nearby western coastal regions, such as Vancouver Island (e.g. *Odontochisma denudatum* and *Moerckia hibernica*). Nevertheless, several of them are not known to produce sporophytes or gemmae locally (*Anastrophyllum assimile* and *Chandonanthus filiformis*). Other species, not only do not readily produce propagules, but are unknown from nearby coastal regions. *Hymenostylium insigne* is an example; its only known localities, apart from Bridal Veil Falls, are on the Queen Charlotte Islands. Its presence at Bridal Veil Falls suggests strongly that coastal populations of this species could exist elsewhere in the south of the province.

Because of the scarcity of records, any attempt to interpret the phytogeography of the above species should be approached with caution. It is possible that each of these species has its own history of survival through the ice age and subsequent post-glacial dispersal.

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Appendix A

Annotated list of mosses at Bridal Veil Falls.

Species and authority is given first, followed by UBC accession number of the voucher specimen, distribution in the Northern Hemisphere, and distribution in the Pacific North America. Finally, species added to the flora by virtue of this study are marked new.

Distribution in the Northern Hemisphere: **AA**=arctic-alpine, **CB**=circumboreal, **EA**=eastern Asia, **ENA**=eastern North America, **J**=Japan, **NA**=North America, **WE**=western eurasia, and **WNA**=western North America. (see Table 4.1)

Distribution in the Pacific North America: **am**=arctic-montane, **c**=coastal, **d**=discontinuous, **n**=northern, **s**=southern, and **w**=widespread. (see Table 4.2)

-
- Amblystegium serpens* (Hedw.) Schimp. in B.S.G.; b136197; CB; w
Amphidium californicum (Hampe ex C.Muell.) Broth.; b136198; WNA; sc
Amphidium lapponicum (Hedw.) Schimp.; b136199; CB; w
Anacolia menziesii (Turn.) Par.; b136200; WNA; sd
Anomobryum filiforme (Dicks.) Solms in Rabenh.; b136201; CB; w
Antitrichia californica Sull. in Lesq.; b136202; WNA/WE; sd
Antitrichia curtipendula (Hedw.) Brid.; b136203; WNA/ENA/WE/EA; d
Atrichum selwynii Aust.; b136329; NA; w
Atrichum undulatum (Hedw.) P.Beauv.; b136204; CB; w
Aulocomnium androgynum (Hedw.) Schwaegr.; b136205; CB; w
Barbula amplexifolia (Mitt.) Jaeg.; b136375; WNA/EA; unclassified, widely disjunct between northern Canada and Alaska, southern British Columbia, and Arizona (Zander 1979)
Barbula convoluta var. *gallinula* Zand.; b136206; WNA; am; new to British Columbia
Bartramia pomiformis Hedw.; b136207; CB; w
Blindia acuta (Hedw.) Bruch & Schimp. in B.S.G.; b136208; CB; w
Brachythecium asperrimum (Mitt.) Sull.; b136209; WNA; d
Brachythecium frigidum (C.Muell.) Besch.; b136210; WNA; w
Brachythecium plumosum (Hedw.) Schimp. in B.S.G.; b136211; CB; d
Brachythecium rivulare Schimp. in B.S.G.; b136212; CB; w
Brachythecium rutabulum (Hedw.) Schimp. in B.S.G.; b136213; CB; w; new to Bridal Veil Falls
Brachythecium velutinum (Hedw.) Schimp. in B.S.G.; b23910 ; CB; w
Brotherella roellii (Ren.& Card. in Roell) Fleisch.; b136214; WNA; unclassified, local in humid, lowland, coastal forests of southwestern British Columbia (Schofield 1976)
Bryoerythrophyllum recurvirostre (Hedw.) Chen; b136215; CB; w
Bryum capillare Hedw.; b136216; CB; w
Bryum miniatum Lesq.; b136217; WNA/ENA/WE; d
Bryum pseudotriquetrum (Hedw.) Gaertn. et al.; b136218; CB; w
Buxbaumia piperi Best; b136219; WNA; d; new to Bridal Veil Falls

Calliergonella cuspidata (Hedw.) Loeske; b136220; CB; w
Campylium chrysophyllum (Brid.) J.Lange; b136221; CB; w
Campylium polygamum (Schimp. in B.S.G.) C.Jens.; b18181; CB; w
Campylium stellatum (Hedw.) C.Jens.; b136222; CB; w
Ceratodon purpureus (Hedw.) Brid.; b136223; CB; w
Claopodium bolanderi Best; b94616; WNA; d
Claopodium crispifolium (Hook.) Ren. & Card.; b136224; WNA/EA; c
Climacium dendroides (Hedw.) Web. & Mohr; b136225; CB; w
Cratoneuron filicinum (Hedw.) Spruce; b136226; CB; w
Dendroalsia abietina (Hook.) Brid.; b136227; WNA; sd
Dichodontium pellucidum (Hedw.) Schimp.; b136228; CB; w
Dicranella schreberiana (Hedw.) Hilf. ex Crum & Anderson; b136229; CB; w
Dicranella varia (Hedw.) Schimp.; b136230; CB; w
Dicranoweisia cirrata (Hedw.) Lindb. ex Milde; b136231; WNA/WE; d
Dicranum fuscescens Turn.; b136232; CB; w
Dicranum scoparium Hedw.; b136233; CB; w
Dicranum tauricum Sapeh.; b136234; WNA/WE; w
Didymodon fallax var. *reflexus* (Brid.) Zand.; b136235; CB; w
Didymodon rigidulus var. *gracilis* (Schleich. ex Hook. & Grev.) Zand.; b136236; NA/WE; w
Didymodon vinealis var. *flaccidus* (Bruch & Schimp. in Schimp.) Zand.; b136237; WNA/WE;
d
Distichium capillaceum (Hedw.) Bruch & Schimp. in B.S.G.; b41198; CB; w
Ditrichum crispatisimum (C.Muell.) Par.; b136238; CB; w
Encalypta ciliata Hedw.; b136239; CB; w
Encalypta procera Bruch; b136240; CB; w
Encalypta rhaptocarpa Schwaegr.; b136241; CB; w; new to Bridal Veil Falls
Epipterygium tozeri (Grev.) Lindb.; b136242; WNA/WE/EA; sc; new to Bridal Veil Falls
Eurhynchium oreganum (Sull.) Jaeg.; b136243; WNA; d
Eurhynchium praelongum (Hedw.) Schimp. in B.S.G.; b136244; CB; d
Eurhynchium pulchellum var. *barnesii* (Ren. & Card.) Grout; b136245; WNA; c
Eurhynchium pulchellum var. *pulchellum* (Hedw.) Jenn.; b136246; CB; w
Fissidens bryoides Hedw.; b136247; CB; w
Fissidens grandifrons Brid.; b136248; CB; w
Funaria hygrometrica Hedw.; b136249; CB; w; new to Bridal Veil Falls
Grimmia torquata Hornsch. in Grev.; b136250; NA/WE; w
Gymnostomum aeruginosum Sm.; b136251; CB; w
Hedwigia ciliata (Hedw.) P.Beauv.; b20213; CB; w
Heterocladium macounii Best; b136252; NA; d
Homalia trichomanoides (Hedw.) Schimp. in B.S.G.; b136253; CB; w
Homalothecium fulgescens (Mitt. ex C.Muell.) Lawt.; b136254; WNA; d
Homalothecium nuttallii (Wils.) Jaeg.; b136255; WNA; c
Hygrohypnum luridum (Hedw.) Jenn.; b136256; CB; w
Hylocomium splendens (Hedw.) Schimp. in B.S.G.; b136257; CB; w
Hymenostylium insigne (Dix.) Podp.; b136258; WNA/WE; nc

Hymenostylium recurvirostre (Hedw.) Dix.; b136259; CB; w
Hypnum circinale Hook.; b136260; WNA; d
Hypnum lindbergii Mitt.; b136261; CB; w; new to Bridal Veil Falls
Hypnum subimponens Lesq.; b136262; WNA/EA; d
Isopterygiopsis pulchella (Hedw.) Iwats.; b114080; CB; w
Isothecium myosuroides Brid.; b136263; NA/WE; d
Leucolepis acanthoneuron (Schwaegr.) Lindb.; b136264; WNA; d
Metaneckera menziesii (Hook. in Drumm.) Steere; b136265; WNA/WE; w
Mnium ambiguum H.Muell.; b64819; CB; w
Mnium marginatum (With.) Brid. ex P.Beauv.; b136266; CB; w
Mnium spinulosum Bruch & Schimp. in B.S.G.; b136267; CB; w
Mnium thomsonii Schimp.; b136268; CB; w
Neckera douglasii Hook.; b136269; WNA; d
Neckera pennata Hedw.; b136270; CB; w
Oligotrichum aligerum Mitt.; b136271; WNA/EA; d; new to Bridal Veil Falls
Orthotrichum consimile Mitt.; b136272; WNA/WE; d
Orthotrichum lyellii Hook. & Tayl.; b136273; WNA/WE; d
Orthotrichum pulchellum Brunt. in Winch. & Gateh.; b136274; WNA/WE; d
Orthotrichum speciosum Nees in Sturm; b136275; NA/WE; w
Orthotrichum striatum Hedw.; b136276; WNA/WE; d
Palustriella commutata (Brid.) Ochyra; b136277; CB; w
Plagiobryum zierii (Hedw.) Lindb.; b136278; CB; am
Plagiomnium insigne (Mitt.) T.Kop.; b136279; WNA; d
Plagiomnium rostratum (Schrader) T.Kop.; b136280; CB; w
Plagiomnium venustum (Mitt.) T.Kop.; b136281; WNA; d
Plagiopus oederiana (Sw.) Crum & Anderson; b136282; CB; w
Plagiothecium cavifolium (Brid.) Iwats.; b136283; CB; w
Plagiothecium denticulatum (Hedw.) Schimp. in B.S.G.; b136284; CB; w
Plagiothecium laetum Schimp. in B.S.G.; b136285; CB; w
Plagiothecium undulatum (Hedw.) Schimp. in B.S.G.; b136286; WNA/WE; d
Platydictya jungermannioides (Brid.) Crum; b136287; CB; w
Platyhypnidium riparioides (Hedw.) Dix.; b136288; CB; sd
Pleurozium schreberi (Brid.) Mitt.; b136289; CB; w
Pogonatum urnigerum (Hedw.) P.Beauv.; b136290; CB; w; new to Bridal Veil Falls
Pohlia cruda (Hedw.) Lindb.; b136291; CB; w
Pohlia nutans (Hedw.) Lindb.; b136292; CB; w
Pohlia wahlenbergii (Web. & Mohr) Andrews; b136293; CB; w; new to Bridal Veil Falls
Polytrichastrum alpinum (Hedw.) G.L.Sm.; b136294; CB; w
Polytrichum formosum Hedw.; b106819; CB; nw
Polytrichum juniperinum Hedw.; b136295; CB; w
Polytrichum piliferum Hedw.; b136296; CB; w
Porotrichum bigelovii (Sull.) Kindb.; b136297; WNA; d
Porotrichum vancouveriense (Kindb. in Mac.) Crum; b136298; WNA; c

Pottia truncata (Hedw.) Fuernr. ex B.S.G.; b84386 ; CB; unclassified, confined to essentially coastal agricultural areas of the Fraser River Delta (Schofield 1968b, 1976)
Pseudobraunia californica (Lesq.) Broth.; b136330; WNA; sd
Pseudoleskea stenophylla Ren. & Card. in Roell; b94158; NA; d
Pseudotaxiphyllum elegans (Brid.) Iwats.; b136299; NA/WE; d
Pterigynandrum filiforme Hedw.; b136300; CB; w
Racomitrium aciculare (Hedw.) Brid.; b136301; CB; w
Racomitrium canescens (Hedw.) Brid.; b136302; CB; w
Racomitrium elongatum Ehrh. ex Frisv.; b136303; NA/WE; w
Racomitrium fasciculare (Hedw.) Brid.; b64806; CB; w
Racomitrium heterostichum (Hedw.) Brid. *sensu lato*; b136304; CB; w
Racomitrium lanuginosum (Hedw.) Brid.; b136305; CB; w
Racomitrium lawtonae Irel.; b136306; WNA; nd; new to Bridal Veil Falls
Racomitrium pacificum Irel. & Spence; b136333; WNA; sc
Racomitrium varium (Mitt.) Jaeg.; b136307; WNA; c
Rhizomnium glabrescens (Kindb.) T.Kop.; b136308; WNA; d
Rhytidiadelphus loreus (Hedw.) Warnst.; b136309; NA/WE; d
Rhytidiadelphus squarrosus (Hedw.) Warnst.; b136310; CB; w
Rhytidiadelphus triquetrus (Hedw.) Warnst.; b136311; CB; w
Sanionia uncinata (Hedw.) Loeske; b136312; CB; w
Schistidium apocarpum var. *apocarpum* (Hedw.) Bruch & Schimp. in B.S.G.; b136313; CB; w
Schistidium apocarpum var. *strictum* (Turn.) Moore; b136314; CB; w
Scleropodium cespitans (C.Muell.) L.Koch; b136315; WNA/WE; d
Scleropodium touretii var. *colpophyllum* (Sull.) Lawt. ex Crum; b136316; WNA; sc; new to Bridal Veil Falls
Seligeria campylopoda Kindb. in Mac. & Kindb.; b136317; NA/WE; nw
Seligeria donniana (Sm.) C.Muell.; b136318; CB; nw
Seligeria tristichoides Kindb.; b136319; NA/WE; nw
Sphagnum capillifolium (Ehrh.) Hedw.; b23923; CB; w
Sphagnum girgensohnii Russ.; b136320; CB; w
Tetraphis geniculata Girg. ex Milde; b136332; NA/J; nd
Tetraphis pellucida Hedw.; b136321; CB; w
Thamnobryum neckeroides (Hook.) Lawt.; b136322; WNA; d
Timmia austriaca Hedw.; b136323; CB; w
Tortella tortuosa (Hedw.) Limpr.; b136324; CB; w
Tortula princeps De Not.; b112430; WNA/WE; sd
Tortula ruralis (Hedw.) Gaertn. *et al.*; b136325; CB; w
Tortula subulata Hedw.; b136331; WNA/WE/EA; sd
Trichodon cylindricus (Hedw.) Schimp.; b44319; WNA/ENA/WE/EA; w
Ulotia megalospora Vent. in Roell; b136326; WNA; c
Ulotia obtusiuscula C.Muell. & Kindb. in Mac. & Kindb.; b136327; WNA; c
Zygodon viridissimus (Dicks.) Brid.; b136328; CB; c

Appendix B

Annotated list of liverworts at Bridal Veil Falls.

Species and authority is given first, followed by UBC accession number of the voucher specimen, distribution in the Northern Hemisphere, and distribution in the Pacific North America. Finally, species added to the flora by virtue of this study are marked new.

Distribution in the Northern Hemisphere: **AA**=arctic-alpine, **CB**=circumboreal, **EA**=eastern Asia, **ENA**=eastern North America, **J**=Japan, **NA**=North America, **WE**=western eurasia, and **WNA**=western North America. (see Table 4.1)

Distribution in the Pacific North America: **am**=arctic-montane, **c**=coastal, **d**=discontinuous, **n**=northern, **s**=southern, and **w**=widespread. (see Table 4.2)

-
- Anastrophyllum assimile* (Mitt.) Steph.; b136334; WNA/ENA/WE/EA; am
Anastrophyllum minutum (Schreb.) Schust.; b136335; CB; w
Apometzgeria pubescens (Schrank) Kuwah.; b136336; CB; w
Barbilophozia barbata (Schmid. ex Schreb.) Loeske; b78630; CB; w
Bazzania denudata (Torrey ex Gott. et al.) Trev.; b136337; NA/J; d
Bazzania tricrenata (Wahlenb.) Lindb.; b68270; CB; c
Blepharostoma trichophyllum (L.) Dum.; b136338; CB; w
Calypogeia fissa (L.) Raddi; b136339; NA/WE; unclassified
Calypogeia trichomanis (L.) Corda; b76692; CB; d
Cephalozia bicuspidata (L.) Dum.; b136340; CB; d; new to Bridal Veil Falls
Cephalozia lunulifolia (Dum.) Dum.; b136341; CB; w
Cephaloziella divaricata (Sm.) Schiffn.; b136342; CB; w
Chandonanthus filiformis Steph.; b20411; WNA/EA; c
Chandonanthus setiformis (Ehrh.) Lindb.; b20441; CB-EA; am
Chiloscyphus polyanthos (L.) Corda; b136343; CB; w
Conocepalum conicum (L.) Lindb.; b136344; CB; w
Diplophyllum albicans (L.) Dum.; b20424; CB; c
Diplophyllum taxifolium (Wahlenb.) Dum.; b91021; CB; w
Douinia ovata (Dicks.) Buch; b20434; WNA/ENA/WE; c
Frullania bolanderi Aust.; b121766; WNA/ENA/WE/EA; sc
Frullania californica (Aust.) Evans; b136345; WNA; sc
Frullania tamarisci subsp. *nisquallensis* (Sull.) Hatt.; b16229; NA; c
Geocalyx graveolens (Schrader) Nees; b95635; CB; w
Gymnomitrium obtusum (Lindb.) Pears.; b136346; WNA/ENA/WE; w
Herbertus aduncus (Dicks.) S.Gray; b136347; WNA/ENA/WE/EA; d
Jamesoniella autumnalis (DC.) Steph.; b136348; CB; w
Jungermannia atrovirens Dum.; b136349; AA; w
Jungermannia leiantha Grolle; b136350; NA/WE; w
Lepidozia reptans (L.) Dum.; b136351; CB; w

Lophocolea cuspidata (Nees) Limpr.; b136352; CB; d
Lophocolea heterophylla (Schrader) Dum.; b136353; CB; w
Lophozia alpestris (Schleich. ex Web.) Evans; b136354; AA; am; new to Bridal Veil Falls
Lophozia excisa (Dicks.) Dum.; b20214; CB; w
Lophozia gillmanii (Aust.) Schust.; b136355; CB-EA; w; new to Bridal Veil Falls
Lophozia guttulata (Lindb. et H. Arnell) Evans; b80952; CB; w
Lophozia heterocolpos (Thed.) M.A. Howe; b79770; CB; w
Lophozia incisa (Schrader) Dum.; b136356; CB; w
Lophozia ventricosa (Dicks.) Dum.; b136357; CB-EA; w
Marsupella emarginata (Ehrh.) Dum.; b136358; CB; d
Metzgeria conjugata Lindb.; b136359; CB; c
Metzgeria temperata Kuwah.; b136360; NA/J; c
Moerckia hibernica (Hook.) Gott.; b136361; CB-EA; c
Odontoschisma denudatum (Nees ex Mart.) Dum.; b136362; WNA/ENA/WE/EA; c
Pellia neesiana (Gott.) Limpr.; b136363; CB; w; new to Bridal Veil Falls
Plagiochila asplenoides (L.) Dum. *sensu lato*; b136364; CB; w
Porella cordaeana (Hueb.) Moore; b136365; WNA/WE; d
Porella navicularis (Lehm. et Lindenb.) Lindb.; b136366; WNA; c
Porella roellii Steph.; b136367; WNA; c
Preissia quadrata (Scop.) Nees; b136368; CB; w
Ptilidium californicum (Aust.) Underw.; b65568; WNA/EA; d
Ptilidium pulcherrimum (G. Web.) Hampe; b67657; CB; w
Radula bolanderi Gott.; b18147; WNA; c
Radula complanata (L.) Dum.; b102608; CB; w
Reboulia hemisphaerica (L.) Raddi; b136369; CB; sw
Riccardia chamedryfolia (With.) Grolle; b136370; CB; c
Scapania americana K. Muell.; b136371; WNA; c
Scapania bolanderi Aust.; b136372; WNA/EA; d
Scapania umbrosa (Schrader) Dum.; b136373; NA/WE; d
Tritomaria quinqueidentata (Huds.) Buch; b136374; AA; am
Tritomaria scitula (Tayl.) Joerg.; b86715; AA; am

Appendix C

Occurrence in habitats and on substrata of species collected at Bridal Veil Falls during the course of this study.

Habitats are: **ha**-anthropogenic, **hb**-boulder slope, **hc**-cliffs, **hf**-forest, **hs**-streams, **hp**-spray zones. Substratum are: **se**-vegetation, **sr**-rock, **ss**-soil, **sw**-wood.

Species	ha	hb	hc	hf	hs	hp	se	sr	ss	sw
Mosses										
Amblystegium serpens	1	0	0	0	0	0	0	1	0	0
Amphidium californicum	0	1	0	0	0	0	0	1	0	0
Amphidium lapponicum	0	1	0	0	1	0	0	1	0	0
Anacolia menziesii	0	1	1	0	0	0	0	1	0	0
Anomobryum filiforme	0	0	1	0	0	0	0	0	1	0
Antitrichia californica	0	1	0	1	1	0	1	1	1	1
Antitrichia curtipendula	0	1	0	1	0	0	1	1	0	1
Atrichum selwynii	1	0	0	0	0	0	0	0	1	0
Atrichum undulatum	0	1	0	1	0	0	0	1	1	0
Aulocomnium androgynum	0	1	0	1	0	0	0	0	0	1
Barbula convoluta	0	0	1	0	0	0	0	1	1	0
Bartramia pomiformis	0	1	1	0	0	0	0	1	1	0
Blindia acuta	0	0	1	0	0	0	0	1	0	0
Brachythecium asperrimum	0	0	1	1	0	0	1	1	1	1
Brachythecium frigidum	0	1	1	0	0	0	0	1	1	0
Brachythecium plumosum	0	1	1	0	0	0	0	1	1	0
Brachythecium rivulare	1	0	1	0	1	0	0	1	1	1
Brachythecium rutabulum	0	0	0	1	0	0	0	0	1	0
Brotherella roellii	0	0	0	0	1	0	0	0	0	1
Bryoerythrophyllum recurvirostre	0	0	0	0	1	1	0	1	0	1
Bryum capillare	1	1	1	1	0	0	0	1	1	0
Bryum miniatum	0	0	1	0	0	0	0	0	1	0
Bryum pseudotriquetrum	0	0	1	0	0	1	0	1	1	1
Buxbaumia piperi	0	0	0	1	0	0	0	0	0	1
Calliergonella cuspidata	1	0	0	0	0	0	0	0	1	0
Campylium chrysophyllum	0	0	0	0	1	0	0	1	1	0
Campylium stellatum	0	0	1	0	0	1	0	0	1	0
Ceratodon purpureus	0	0	0	1	0	0	0	1	1	0
Claopodium bolanderi	0	1	0	0	0	0	0	1	0	0
Claopodium crispifolium	1	1	1	1	1	1	1	1	1	1
Climacium dendroides	1	0	0	1	0	0	1	0	1	0
Cratoneuron filicinum	0	0	1	0	0	0	0	1	1	0
Dendroalsia abietina	0	1	0	1	0	0	1	1	0	0
Dichodontium pellucidum	0	0	1	0	1	0	0	1	1	1
Dicranella schreberiana	1	0	1	1	0	0	0	0	1	0
Dicranella varia	0	0	0	0	0	1	0	0	1	0
Dicranoweisia cirrata	0	1	0	1	0	0	1	0	0	1
Dicranum fuscescens	0	0	0	1	0	0	1	0	0	1
Dicranum scoparium	0	1	1	0	0	0	0	1	1	1
Dicranum tauricum	0	1	0	1	0	0	1	1	0	1

Species	ha	hb	hc	hf	hs	hp	se	sr	ss	sw
Mosses (cont'd)										
Didymodon fallax	0	1	0	0	1	0	0	1	1	1
Didymodon rigidulus	0	0	1	0	0	0	0	1	1	0
Didymodon vinealis	1	0	1	0	0	1	0	1	1	1
Ditrichum crispatisissimum	0	1	1	0	1	1	0	1	1	0
Encalypta ciliata	0	1	1	0	0	0	0	1	1	0
Encalypta procera	0	0	1	0	0	1	0	1	1	1
Encalypta rhaptocarpa	0	0	1	0	0	0	0	1	0	0
Epipterygium tozeri	0	0	0	1	0	0	0	0	1	0
Eurhynchium oreganum	0	1	0	1	0	0	1	0	1	1
Eurhynchium praelongum	1	1	0	1	1	0	1	1	1	1
Eurhynchium barnesii	0	0	0	0	0	1	0	0	0	1
Eurhynchium pulchellum	0	0	1	1	0	0	1	1	0	0
Fissidens bryoides	1	0	0	1	0	1	1	1	1	0
Fissidens grandifrons	0	0	1	0	1	0	1	1	1	0
Funaria hygrometrica	1	0	0	0	0	0	0	0	1	0
Grimmia torquata	0	1	1	1	0	0	0	1	0	0
Gymnostomum aeruginosum	0	1	1	0	0	0	0	1	1	0
Heterocladium macounii	0	1	1	0	0	0	0	1	0	0
Homalia trichomanoides	0	0	0	1	1	0	1	0	0	0
Homalothecium fulgescens	1	1	1	1	1	0	1	1	1	1
Homalothecium nuttallii	0	1	0	1	0	0	1	0	0	1
Hygrohypnum luridum	0	0	1	0	1	1	0	1	0	0
Hylocomium splendens	0	1	1	1	0	0	1	1	1	0
Hymenostylium insigne	0	0	1	0	0	1	0	1	1	0
Hymenostylium recurvirostre	0	0	1	1	0	0	0	1	1	0
Hypnum circinale	0	0	0	1	0	0	1	0	0	1
Hypnum lindbergii	1	0	0	0	0	0	0	0	1	0
Hypnum subimponens	0	1	1	1	1	0	1	1	0	0
Isothecium myosuroides	0	1	1	1	1	0	1	1	1	1
Leucolepis acanthoneuron	0	0	1	1	1	0	1	0	1	1
Metaneckera menziesii	0	1	1	1	0	1	1	1	0	1
Mnium ambiguum	0	0	0	1	0	1	0	1	1	0
Mnium marginatum	0	0	1	1	1	1	1	1	1	1
Mnium spinulosum	0	0	0	1	0	0	0	0	0	1
Mnium thomsonii	0	0	1	1	1	1	1	1	1	1
Neckera douglasii	0	1	1	1	0	0	1	1	1	1
Neckera pennata	0	0	0	1	0	0	1	0	0	1
Oligotrichum aligerum	0	0	0	1	0	0	0	0	1	0
Orthotrichum consimile	0	0	0	1	0	0	1	0	0	1
Orthotrichum lyellii	0	0	0	1	0	0	1	0	0	1
Orthotrichum pulchellum	0	0	0	1	0	0	1	0	0	0
Orthotrichum speciosum	0	0	0	1	0	0	1	0	0	0
Orthotrichum striatum	0	0	0	1	0	0	1	0	0	1
Palustriella commutata	0	0	1	0	1	1	0	1	1	1
Plagiobryum zierii	0	0	1	0	0	0	0	0	1	0
Plagiomnium insigne	1	1	0	1	0	0	1	0	1	1
Plagiomnium rostratum	1	1	1	1	1	1	1	1	1	1
Plagiomnium venustum	0	1	0	1	0	0	1	1	1	0

Species	ha	hb	hc	hf	hs	hp	se	sr	ss	sw
Mosses (cont'd)										
Plagiopus oederiana	0	1	1	0	0	0	0	1	1	0
Plagiothecium cavifolium	0	1	0	0	0	0	0	0	1	0
Plagiothecium denticulatum	0	1	0	1	0	0	1	0	1	1
Plagiothecium laetum	0	0	0	1	1	0	0	0	0	1
Plagiothecium undulatum	0	0	0	1	0	0	1	0	0	1
Platydictya jungermannioides	0	0	1	1	0	0	0	1	1	0
Platyhypnidium riparioides	0	0	0	0	1	0	0	1	0	0
Pleurozium schreberi	0	1	0	0	0	0	0	1	1	0
Pogonatum urnigerum	0	1	0	0	0	0	0	0	1	0
Pohlia cruda	0	1	0	0	0	0	0	1	1	0
Pohlia nutans	0	1	0	0	0	0	0	0	1	1
Pohlia wahlenbergii	0	0	1	0	0	1	0	1	0	0
Polytrichastrum alpinum	0	1	1	0	0	0	0	1	1	0
Polytrichum juniperinum	0	1	0	1	0	0	0	1	1	0
Polytrichum piliferum	0	1	0	0	0	0	0	1	0	0
Porotrichum bigelovii	0	0	0	0	1	0	0	1	0	0
Porotrichum vancouveriense	0	0	0	1	0	0	0	1	0	1
Pseudotaxiphyllum elegans	0	1	0	1	0	0	1	1	0	1
Pterigynandrum filiforme	0	0	0	1	0	0	1	0	0	1
Racomitrium aciculare	1	0	1	0	1	0	0	1	0	0
Racomitrium canescens	0	1	0	0	0	0	0	1	0	0
Racomitrium elongatum	0	1	0	0	0	0	0	1	0	0
Racomitrium heterostichum s.l.	0	1	1	0	0	0	0	1	0	0
Racomitrium lanuginosum	0	1	0	0	0	0	0	1	0	0
Racomitrium lawtonae	0	1	0	0	0	0	0	1	0	0
Racomitrium varium	0	1	0	0	0	1	0	1	1	0
Rhizomnium glabrescens	0	0	0	1	1	1	1	0	0	1
Rhytidiadelphus loreus	0	1	0	1	0	0	1	1	1	1
Rhytidiadelphus squarrosus	1	0	0	0	0	0	0	0	1	0
Rhytidiadelphus triquetrus	1	1	1	1	0	0	1	1	1	1
Sanionia uncinata	0	1	0	0	0	0	0	1	0	0
Schistidium apocarpum	1	0	1	0	1	0	0	1	0	0
Schistidium strictum	0	1	0	0	0	0	0	1	0	0
Scleropodium cespitans	0	1	1	1	0	0	1	1	0	0
Scleropodium touretii	0	0	0	1	0	0	0	0	0	1
Seligeria campylopoda	0	0	0	1	0	0	0	1	0	0
Seligeria donniana	0	0	1	0	0	0	0	1	0	0
Seligeria tristichoides	0	0	1	0	0	0	0	1	0	0
Sphagnum girgensohnii	0	1	0	0	0	0	0	0	1	0
Tetraphis pellucida	0	1	0	1	0	1	1	0	0	1
Thamnobryum neckeroides	0	0	1	1	0	0	1	1	1	0
Timmia austriaca	0	1	1	0	0	1	0	1	1	1
Tortella tortuosa	0	1	1	1	1	1	1	1	1	1
Tortula ruralis	0	0	1	1	0	0	1	1	0	0
Ulota megalospora	0	0	0	1	0	0	1	0	0	0
Ulota obtusiuscula	0	0	0	1	0	0	1	0	0	0
Zygodon viridissimus	0	0	1	0	0	1	1	1	0	0

Species	ha	hb	hc	hf	hs	hp	se	sr	ss	sw
Liverworts										
Anastrophyllum assimile	0	1	0	0	0	0	0	1	1	0
Anastrophyllum minutum	0	1	0	0	0	0	0	1	0	0
Apometzgeria pubescens	0	0	1	1	0	0	1	1	1	0
Bazzania denudata	0	0	0	1	0	0	1	0	0	0
Blepharostoma trichophyllum	0	0	1	0	0	1	0	1	1	1
Calypogeia fissa	0	0	0	1	0	0	0	0	0	1
Cephalozia bicuspidata	0	0	0	1	0	1	0	0	0	1
Cephalozia lunulifolia	0	0	0	1	0	1	1	0	0	1
Cephaloziella divaricata	0	1	0	0	0	0	0	1	1	0
Chiloscyphus polyanthos	0	0	0	0	1	0	0	0	1	0
Conocephalum conicum	0	1	1	1	1	1	0	1	1	1
Frullania californica	0	0	1	0	0	0	0	1	0	0
Gymnomitrium obtusum	0	1	0	0	0	0	0	1	0	0
Herbertus aduncus	0	1	1	0	0	0	0	1	0	0
Jamesoniella autumnalis	0	1	0	1	0	0	1	0	1	1
Jungermannia atrovirens	0	0	1	0	1	0	0	1	1	1
Jungermannia leiantha	0	0	0	0	0	1	0	0	0	1
Lepidozia reptans	0	0	0	1	0	0	0	0	0	1
Lophocolea cuspidata	0	0	1	1	0	0	1	0	1	1
Lophocolea heterophylla	0	0	0	1	0	0	1	0	0	0
Lophozia alpestris	0	1	0	0	0	0	0	1	0	0
Lophozia gillmanii	0	0	1	0	1	1	0	0	1	1
Lophozia incisa	0	1	0	0	0	0	0	0	1	0
Lophozia ventricosa	0	1	0	1	0	0	0	1	1	1
Marsupella emarginata	0	1	1	0	0	0	0	1	0	0
Metzgeria conjugata	0	0	1	1	0	0	1	0	1	1
Metzgeria temperata	0	0	0	1	0	0	1	0	0	1
Moerckia hibernica	0	0	1	0	0	0	0	1	0	0
Odontoschisma denudatum	0	1	0	0	0	0	0	0	0	1
Pellia neesiana	0	0	1	0	0	0	0	1	1	0
Plagiochila asplenoides s.l.	0	0	1	1	0	0	1	1	1	1
Porella cordaeana	0	0	0	1	0	0	1	0	0	0
Porella navicularis	0	0	0	1	1	0	1	0	1	1
Porella roellii	0	0	1	1	0	0	1	1	0	0
Preissia quadrata	0	0	1	0	0	0	0	0	1	0
Radula complanata	0	0	1	1	1	0	1	0	1	0
Reboulia hemisphaerica	0	1	1	0	0	0	0	1	1	0
Riccardia chamedryfolia	0	0	0	0	0	1	0	0	0	1
Scapania americana	0	1	1	1	0	0	0	1	1	1
Scapania bolanderi	0	1	0	1	0	0	1	0	0	1
Scapania umbrosa	0	1	0	1	0	1	0	0	0	1
Tritomaria quinquedentata	0	1	0	0	0	0	0	0	1	0

Appendix D

Synonyms and alternative references.

Some of the nomenclature used in this report differ from that used in Lawton (1971) or Godfrey (1977). This table provides synonyms to the names used in Lawton or Godfrey. Names used in this report are to the lefthand side, synonyms used by Lawton or Godfrey are to the righthand side. In the case of species not treated by these two authors, alternate references are provided.

Anomobryum filiforme = *Pohlia filiformis*

Barbula amplexifolia - not treated in Lawton (1971), see Zanders (1979)

Barbula convoluta var. *gallinula* - not treated in Lawton (1971), see Zanders (1979)

Bryoerythrophyllum recurvirostre = *Didymodon recurvirostris*

Campylium polygamum = *Amblystegium polygamum*

Didymodon fallax var. *reflexus* = *Barbula reflexa*

Didymodon rigidulus var. *gracilis* = *Barbula acuta*

Didymodon vinealis var. *flaccidus* = *Barbula vinealis* var. *flaccida*

Ditrichum crispatisimum - referable to *D. flexicaule*, see Frisvoll (1985) for details

Encalypta rhabdocarpa = *E. vulgaris* var. *rhabdocarpa*

Herberta adunca = *Herbertus aduncus*

Hymenostylium insigne - not treated in Lawton (1971), see Zanders and Eckel (1982)

Hymenostylium recurvirostre = *Gymnostomum recurvirostre*

Isopterygiopsis pulchella = *Isopterygium pulchellum*

Isothecium myosuroides = *I. stoloniferum*

Leucolepis acanthoneuron = *L. menziesii*

Metaneckera menziesii = *Neckera menziesii*

Mnium ambiguum = *M. lycopodioides*

Mnium thomsonii = *M. orthorrhynchum*

Palustriella commutata = *Cratoneuron commutatum*

Plagiopus oederiana = *P. oederi*

Plagiothecium cavifolium = *P. roeseanum*
Platyhypnidium riparioides = *Eurhynchium riparioides*
Polytrichastrum alpinum = *Polytrichum alpinum*
Porotrichum bigelovii = *Porothamnium bigelovii*
Porotrichum vancouveriense = *Bestia vancouveriensis*
Pseudoleskea stenophylla = *Lescuraea stenophylla*
Pseudotaxiphyllum elegans = *Isopterygium elegans*
Racomitrium spp. = *Rhacomitrium* spp.
Racomitrium canescens s.str. - not treated in Lawton (1971), see Frisvoll (1983), or Hill (1984)
Racomitrium elongatum - not treated in Lawton (1971), see Frisvoll (1983), or Hill (1984)
Racomitrium lawtonae - see discussion under *R. heterostichum* var. *heterostichum* in Lawton (1971), for more information see Frisvoll (1988)
Racomitrium pacificum - not treated in Lawton (1971), see Frisvoll (1988)
Sanionia uncinata = *Drepanocladus uncinatus*
Sphagnum spp. - not treated in Lawton (1971), see Ireland (1982)
Schistidium apocarpum = *Grimmia apocarpa*
Trichodon cylindricus = *Ditrichum cylindricum*
Ulotia obtusiuscula = *U. crispa* var. *alaskana*
Zygodon viridissimus = *Z. vulgaris*

Appendix E

Similarity between habitat/substratum combinations based on composition of their respective moss flora using the Jaccard Index of Similarity.

Habitat substratum combinations are named with two letters. The first letter refers to the habitat, where **a**=anthropogenic, **b**=boulder slope, **c**=cliff, **f**=forest, **s**=stream, and **p**=spray zone. the second letter refers to the substratum, where **e**=epiphyte, **r**=rock, **s**=soil, and **w**=wood.

Habitat/ substratum combinations ⁸	Jaccard index of similarity (X 10 ²)																			
	as	be	br	bs	bw	ce	cr	cs	fe	fr	fs	fw	se	sr	ss	sw	pe	pr	ps	pw
ar (7)	10	17	6	0	0	0	10	3	4	11	8	5	20	21	7	10	0	0	0	5
as (15)		0	7	9	5	0	7	10	11	16	23	9	11	7	15	15	6	10	0	4
be (1)			2	0	0	0	2	0	2	0	4	3	20	6	0	6	0	0	0	0
br (54)				18	6	2	24	12	23	7	15	15	6	11	6	11	2	4	2	5
bs (30)					12	0	10	6	14	6	19	13	0	6	7	3	0	4	4	0
bw (13)						0	2	0	10	0	3	8	0	0	0	0	0	0	0	5
ce (1)							2	3	0	7	0	0	0	6	0	0	0	0	0	8
cr (61)								42	17	13	9	7	6	19	8	14	4	10	0	0
cs (43)									6	7	8	3	6	12	12	12	0	12	12	23
fe (60)										9	23	50	9	7	8	19	2	6	2	9
fr (14)											19	7	6	11	10	11	6	5	5	8
fs (24)												25	12	8	15	22	4	11	0	3
fw (45)													6	7	8	20	3	3	0	5
se (5)														17	18	17	0	8	0	6
sr (18)															26	19	0	9	5	4
ss (12)																26	0	14	7	11
sw (18)																	0	20	5	21
pe (3)																		0	0	0
pr (9)																			0	24
ps (8)																				11
pw (21)																				

⁸ Numbers in brackets represent total number of moss species found in each habitat substratum combination.

Note: Habitats ae, aw, and cw had no species and were dropped from the analysis.

Appendix F

A note of caution.

The following species are documented by specimens at the herbarium of the University of British Columbia and are labelled from Bridal Veil Falls. Based on the habitats in the area, the thoroughness of the field studies of the past two seasons, and the ecology of these species, it seems very possible that the specimens were not collected from Bridal Veil Falls. It is probable that they are from some site closer to the coast, probably around Howe Sound, where the collector (J.P. van Velzen) also made collections. All of the species noted are known from the latter area and are unknown (except for van Velzen's specimens) from Bridal Veil Falls. It is not impossible that the specimens are correctly labelled, but on the basis of field experience at Bridal Veil Falls, their presence there should be considered as uncertain until new collections are made.

These species are: *Andreaea rupestris* Hedw.;

Chandonanthus filiformis;

Chandonanthus setiformis;

Diplophyllum albicans;

Douinia ovata.

Unlike the four other species, *Andreaea rupestris* had not been included in the flora because the herbarium material was not available for examination. However, B.M. Murray (University of Alaska Museum) recently confirmed that van Velzen's records of *A. rupestris* from Bridal Veil Falls (UBC B20440, B20431, B20421) were correctly identified.

A. rupestris is easily distinguishable from the other species of mosses found at Bridal Veil Falls. It is a small plant, brown or reddish-brown in colour, with ecostate leaves, and a sporophyte which opens along four longitudinal slits.