A TAXONOMIC REVISION OF THE GENERA *ANTENNARIA* AND *SYMPHYOTRICHTHUM* (ASTERACEAE) IN BRITISH COLUMBIA, CANADA

With Additional Perspectives on the Role of Taxonomy Within the Biological Sciences

by

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_A taxonomic revision of the genera Antennaria and Symphyotrichum (Asteraceae) in British Columbia, Canada - with additional perspectives on the role of taxonomy within the biological sciences

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ABSTRACT

*Antennaria* and *Symphyotrichum* represent two of the most taxonomically complex genera of the family Asteraceae in North America. Extensive hybridization and polyploidy contribute to many of the taxonomic difficulties encountered within both genera, and in *Antennaria* these are compounded by the presence of widespread apomixis. This suite of factors has contributed to considerable taxonomic uncertainty in these genera, particularly in the Pacific Northwest where they are both diverse and understudied. This study uses a traditional, specimen-based alpha-taxonomic methodology to investigate the taxonomy of these two genera within the western Canadian province of British Columbia. It uses both a detailed review of existing herbarium collections from within the region of interest, as well as a comprehensive review of existing taxonomic and floristic literature pertaining to these genera, to provide a taxonomic framework that is better representative of these genera in British Columbia. This study provides clarification on a number of unresolved taxonomic and floristic uncertainties, including the incorrect application of nomenclature, poorly defined species limits, incomplete or erroneous morphological circumscriptions, incorrect geographic distributions, and inadequate identification criteria. Several taxa that had not previously been recognized formally in the region, both native and exotic, are documented here and provided a full accounting of their occurrence. It also provides the first comprehensive summary of putative hybrids within these genera in the Pacific Northwest. Dichotomous keys for the identification of taxa within these genera in British Columbia were developed that capture new developments that have resulted from this study. Finally, the importance of taxonomy to the biological sciences is elucidated in the context of this study, and perspectives on the Taxonomic Impediment and the relationship between academia and taxonomy are detailed and discussed.
LAY SUMMARY

This study assesses the classification of species within two genera of the sunflower family (Asteraceae) in British Columbia, Canada. The two genera in question – *Antennaria* (the pussytoes) and *Symphyotrichum* (the American asters) – are notorious for the difficulties encountered in defining the boundaries between the component species, and both have been poorly studied in western Canada. These difficulties are largely the result of widespread hybridization, polyploidy (chromosome doubling), and asexual reproduction that often blur the distinctions among the species. This study employed a traditional herbarium-based taxonomic methodology to refine the species boundaries within these two genera in British Columbia to provide a stronger taxonomic basis for other biodiversity studies. It also re-circumscribes the attributes of the species in these genera, refines their geographic distributions in the region, and provides novel identification criteria to aid in their diagnosis.
PREFACE

This dissertation is the original, unpublished, independent product of the author, James D.A. Fenneman.
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DEDICATION

To Erin and Abby. You guys have been SO understanding during all of this.
CHAPTER ONE:
INTRODUCTORY CHAPTER

The family Asteraceae, with c. 24,000 – 30,000 known species (Funk et al. 2009), is among the largest families of plants in the world. Members of this family occur naturally on all continents except Antarctica (Stevens 2001), and many have been introduced as exotic weeds in areas far from their native range. Asteraceae is also among the most taxonomically complex families of vascular plants due in part to factors such as hybridization, polyploidy, reticulate evolution, and apomixis within many of its genera. This complexity is reflected in the unresolved taxonomy within many of the component genera, whereby the species limits often remain uncertain and their associated species definitions ambiguous. In this thesis, I investigate the taxonomy and diversity of two such genera within the western Canadian province of British Columbia – Antennaria (Chapter 2) and Symphyotrichum (Chapter 3) – to provide enhanced taxonomic clarity to those genera within the context of the flora of the Pacific Northwest. These genera are well-known as among the most taxonomically unresolved in the region, despite their inclusion in several earlier regional floristic and taxonomic studies.

The first floristic treatment to address these genera in British Columbia was Henry (1915), where they were treated alongside the rest of the flora of southern British Columbia, without any specific taxonomic attention being paid to them. Subsequent important taxonomic papers such as Cronquist (1943) (for Symphyotrichum) and Porsild (1950) (for Antennaria) contributed substantially to refining the species limits of the component taxa and better defining their attributes in northwestern North America, but it was not until Hitchcock et al. (1955) and its later companion volume, Hitchcock & Cronquist (1973), that an attempt was made to describe the taxonomy of these genera in a floristic fashion that was widely available to botanists throughout the region. The taxonomic concepts of these and other genera presented in Hitchcock et al. (1955) and Hitchcock
& Cronquist (1973) were widely adopted throughout the Pacific Northwest, as they represented the only region-specific taxonomic study of these groups at the time. These taxonomic concepts were also adopted by later regional floristic efforts such as Douglas et al. (1989) and Douglas et al. (1998), where they were restated with only minimal additional taxonomic insight provided. Douglas (1995), which included a floristic and taxonomic review of Antennaria and Symphyotrichum (as Aster) specifically within the province of British Columbia, contributed little to the taxonomic circumscriptions of these groups beyond what had been presented half a century earlier. As a result, the concepts of Hitchcock et al. (1955) persisted as the default taxonomy of these groups in the Pacific Northwest throughout the latter half of the 20th century. The publication of the Flora of North America treatments of these genera (Bayer 2006 [Antennaria], Brouillet et al. 2006 [Symphyotrichum]) brought an additional taxonomic perspective to them for the Pacific Northwest, as it was the first major revision of the family to incorporate insights from the many molecular and evolutionary findings of the previous two decades. As the focus of these treatments was continental in scope, however, there was little emphasis on regionally-specific aspects of taxonomy. Thus, even after this monumental effort, the resulting taxonomy of these genera in the Pacific Northwest remained largely reflective of that of Hitchcock et al. (1955) and Hitchcock & Cronquist (1973), and taxonomic errors in these works often remained unaddressed. It is this dearth of region-specific taxonomic attention, and the resultant persistence of taxonomic errors and ambiguities, that prompted my study of these genera in British Columbia.

British Columbia is a floristically diverse region of North America, yet has remained relatively understudied in comparison to many other areas of the continent. The floristic diversity of the province largely reflects the influences of pronounced physiographic and climatological variation combined with the post-glacial convergence of several floristic elements (McLaughlin 1994) representing different glacial refugia. Specifically, the floristic diversity of the province
combines floristic elements from eastern North America, Beringia, and the western United States, with no other region of the continent supporting a similar post-glacial convergence of such widely divergent floristic elements. Adding to this floristic complexity is the influence of multiple coastal and nunatak refugia within the current boundaries of British Columbia during the Wisconsinan glaciation (75,000-11,000 yr B.P.), which supported plant communities throughout the most recent glacial event (Marr et al. 2008). The unique convergence of these various floristic elements within British Columbia has resulted in a diverse selection of region-specific floristic interactions, as well as an associated diversity of taxonomic questions that can be addressed only through a familiarity with the floristic characteristics of the region. However, the limited representation of British Columbia within most taxonomic studies has left many of these questions unaddressed, or even unrecognized, and has contributed to the perpetuation of unsatisfactory taxonomic treatments for many genera within the province. This study represents the first detailed, region-specific review and revision of the morphological, phytogeographic, ecological, cytological, phylogenetic, and nomenclatural attributes of species of *Antennaria* and *Symphyotrichum* in the province. The resulting monographic treatment is intended to address previous taxonomic uncertainties and ambiguities by utilizing specimens from within the province of British Columbia, many of which have never been reviewed for other taxonomic studies. The methodology involved both the testing of existing taxonomic approaches, as well as the development of novel taxonomic hypotheses to address any shortcomings in existing approaches. The revised taxonomy presented in this study will not only better define these taxa within the Pacific Northwest, but will also lay the foundations for further research to address the many taxonomic questions that remain.

1.1 General methodology

The traditional alpha-taxonomy methodology that was employed during this herbarium-based taxonomic study involved five primary steps: (i) the selection of an appropriate species
concept to apply during the study; (ii) a review of specimens pertaining to the genera of interest, and the application of the chosen species concept to these specimens; (iii) the refinement of the morphological, ecological, and phytogeographic circumscriptions of the accepted taxa; (iv) the assignment of nomenclatural synonyms to the accepted taxa; and (v) the construction of a dichotomous identification key to the accepted taxa. This methodology is largely consistent with that described in Henderson (2005), although it differs most significantly in its emphasis on taxonomic deduction over statistical or computational diagnosis of specimens. It further differs from the approach of Henderson (2005) in its reliance on the downstream application of the concepts by others for validation of the concepts, rather than the significance associated with statistical analyses of the morphological variation among the specimens.

(i) Selection of a species concept

This initial stage of the study provided the theoretical or conceptual background for all subsequent stages, as per Henderson (2005). Although the species concept applied in this study does not directly correspond to any of the twelve most widely accepted species concepts of De Quieroz et al. (2007), the theoretical underpinnings overlap broadly with the Cohesion Species Concept (CSC) of Templeton (1989). The concept of a species under the CSC, as described by Templeton (1989), reflects “the most inclusive population of individuals having the potential for phenotypic cohesion through intrinsic cohesion mechanisms.” These cohesion mechanisms reflect both the potential for reproductive exchangeability within a species (and simultaneous limits on reproductive exchangeability with other species) as well as the role of evolutionary processes such as natural selection and genetic drift in sculpting the characteristics of the species. Thus, the factors contributing to the definition of a species under the CSC include not just mechanisms promoting isolation from other groups, but more importantly the mechanisms involved in promoting intragroup cohesion and integrity. This species concept also considers the evolutionary processes
responsible for speciation in addition to the attributes and characteristics of the biodiversity that results from those processes. Table 1 further describes the cohesion mechanisms considered when defining species under the CSC.

**TABLE 1. Classification of cohesion mechanisms under the CSC.** From Templeton (1989)

<table>
<thead>
<tr>
<th>I. Genetic Exchangeability: the factors that define the limits of spread of new genetic variants through <em>gene flow</em>.</th>
</tr>
</thead>
<tbody>
<tr>
<td>A. Mechanisms promoting genetic identity through gene flow</td>
</tr>
<tr>
<td>1. <em>Fertilization system</em>: the organisms are capable of exchanging gametes leading to successful fertilization.</td>
</tr>
<tr>
<td>2. <em>Developmental system</em>: the products of fertilization are capable of giving rise to viable and fertile adults.</td>
</tr>
<tr>
<td>B. Isolating mechanisms: genetic identity is preserved by lack of gene flow with other groups</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>II. Demographic Exchangeability: the factors that define the fundamental niche and the limits of spread of new genetic variants through <em>genetic drift</em> and <em>natural selection</em>.</th>
</tr>
</thead>
<tbody>
<tr>
<td>A. Replaceability: genetic drift (descent from a common ancestor) promotes genetic identity</td>
</tr>
<tr>
<td>B. Displaceability</td>
</tr>
<tr>
<td>1. <em>Selective Fixation</em>: natural selection promotes genetic identity by favouring the fixation of a genetic variant</td>
</tr>
<tr>
<td>2. <em>Adaptive Transitions</em>: natural selection favours adaptations that directly alter demographic exchangeability. The transition is constrained by:</td>
</tr>
<tr>
<td>a. Mutational constraints on the origin of heritable phenotypic variation</td>
</tr>
<tr>
<td>b. Constraints on the fate of heritable variation:</td>
</tr>
<tr>
<td>i. Ecological constraints</td>
</tr>
<tr>
<td>ii. Developmental constraints</td>
</tr>
<tr>
<td>iii. Historical constraints</td>
</tr>
<tr>
<td>iv. Population genetic constraints</td>
</tr>
</tbody>
</table>

The species concept used for this study differed slightly from the classical CSC of Templeton (1989) in its incorporation of a wider selection of evidentiary lines during application. While the CSC is primarily centred around the evolutionary and reproductive mechanisms responsible for the biological cohesion of individuals within a species and their associated isolation from other species, the species concept applied here also considers extant patterns within the phytogeography, cytology, ecology, and morphology of the proposed species as evidence of these evolutionary forces. The species concept used for this study thus approaches the concept of
‘Integrative’ (Will et al. 2005) or ‘Iterative’ (Yeates et al. 2005) taxonomy that has sprung from the tradition of Hennig’s (1966) promotion of a ‘holomorphological’ taxonomy. The assumption underlying my application of this species concept is that definable species under the CSC will be diagnosable by signals in their distributions, habitat characteristics, chromosome counts, or morphological characteristics, and that these can then be used as a means by which to discern the limits between the taxonomic units (= ‘species’) that comprise the system. Ultimately, this species concept sought the congruence of multiple lines of taxonomically relevant evidence about the taxa being investigated to determine their applicability under the CSC. Thus, species recognized for this study were required to demonstrate the congruence of at least three lines of evidence (phylogenetic, cytological, ecological, phytogeographic, or morphological), with these evidentiary lines being mutually supportive of the same taxonomic solution.

(ii) Specimen review

The specimens reviewed for this study included the entirety of specimens of the two focal genera (*Antennaria*, *Symphyotrichum*) housed at the herbarium of the Beaty Biodiversity Museum of the University of British Columbia (UBC). Although specimen review was centred on collections of these genera from within British Columbia, all available extralimital collections of the taxa present within the province were also reviewed so as to provide context for understanding the characteristics of the provincial specimens. The total number of specimens reviewed for this study included c. 1700 specimens of *Antennaria* (including c. 1200 from British Columbia) and c. 1000 specimens of *Symphyotrichum* (including c. 700 from British Columbia).

The specimens were first reviewed primarily to determine the strength of their agreement with existing taxonomic systems. For this, all available floras, monographs, and technical taxonomic papers pertaining to these genera within the Pacific Northwest and beyond were reviewed. As most of these publications present slightly, or sometimes pronounced, differences in
the taxonomic interpretation of these groups, each different approach was applied systematically to each individual specimen to determine how well the approach corresponded to the morphological and other characteristics of the specimen. Misidentified specimens that were detected during this stage of the study were corrected via traditional herbarium protocol (research annotations) before these specimens were further assessed to determine their correlation with proposed taxonomy. This stage was also an opportunity to assess the strengths and weaknesses of different technical identification keys and identify shortcomings within the tools used for diagnosing the taxa. This stage was particularly critical in identifying individual taxa or groups of taxa wherein ambiguity existed in their taxonomic definition, prompting a more detailed critical evaluation of those particular taxa. The structure of that critical evaluation differed among the different sorts of taxonomic ambiguities that were detected, but in all cases involved repeated testing within the herbarium to determine the taxonomic system that best met the above-mentioned requirements for multiple mutually-supportive lines of evidence. The ultimate result of this stage of the study was the production of the list of accepted taxa in the monographic treatments that comprise the later chapters of this study.

(iii) **Refining circumscriptions of the taxa**

Once the taxa to be included within the taxonomic treatments had been determined through the application of a species concept to the specimens, the morphological, ecological, and phytogeographic attributes of the taxa were further assessed and characterized. Morphological attributes of the specimens comprising each accepted taxon were reviewed against existing published descriptions of the taxa to verify their applicability to British Columbia specimens. Although in many cases the morphology of B.C. specimens was consistent with published descriptions, in other cases underemphasized or even novel characteristics were identified to better diagnose or define the taxa. In taxa for which comprehensive morphological circumscriptions had
not previously been provided, a full morphological description was prepared based on the specimens reviewed for this study. Occasional errors in published species circumscriptions were identified and corrected through the systematic assessment of all morphological characters of each specimen and their comparison against these published descriptions. The refined circumscriptions of the taxa were subsequently re-applied to the specimens to ensure their compatibility with existing herbarium material, and thus this stage typically occurred in concert with the previously-mentioned stage of specimen review.

(iv) **Assignment of synonyms**

Digital images of type specimens (holotypes, isotypes, syntypes, isosyntypes, and occasionally paratypes) were reviewed for all published names pertaining to taxa recognized in this study. These images were available via JSTOR Global Plants (https://plants.jstor.org), which houses the world’s largest database of digitized plant specimens. The type specimens were assessed morphologically, ecologically, and phytogeographically and assigned to a particular recognized taxon based on this assessment. In some cases, the assignment of these type specimens to the concept of a particular species was reflected through changes in the morphological diagnosis of the taxon.

(v) **Construction of a dichotomous identification key**

As a final stage, a novel dichotomous key for the identification of species within the focal genera was constructed based on a determination of the clearest criteria for permitting the diagnosis of specimens of these in British Columbia. In some cases, well-known and widely used criteria that appear throughout many floristic and taxonomic publications were incorporated, as these remain the most important and most easily assessed characteristics for specimen determination. In many other instances, however, novel criteria were introduced into the
dichotomous key to better enable the diagnosis of specimens based on the most clearly defined and easily interpretable characteristics. These identification keys will provide a mechanism by which future botanists can assess the strengths and weaknesses of this proposed taxonomy.

1.2 Landscapes of British Columbia

The province of British Columbia is physiographically, climatically, and ecologically diverse relative to other Canadian provinces, and is home to c. 3,400 taxa (species, subspecies, and varieties) of vascular plants (British Columbia Conservation Data Centre 2018). To best describe the distributions of species of *Antennaria* and *Symphyotrichum* in the presence of these complexities, I have divided the province into eight discrete regions of relatively consistent physiography, climate, and vegetation (Figure 1) for the purposes of this study. The physiographic setting, biogeoclimatic setting, and vegetation characteristics of each of these regions is described here, including a detailed discussion of the diversity of *Antennaria* and *Symphyotrichum*. Although a provincial map of the biogeoclimatic zones is provided in Appendix 1, Meidinger & Pojar (1991) and Mackenzie & Meidinger (2006) should be consulted for more detailed descriptions of the climatological and ecological characteristics of each zone.
FIGURE 1. Geographic regions of British Columbia used to describe the distribution of *Antennaria* and *Symphyotrichum* species in this study. SW = southwest region; SC = south-central region; SE = southeast region; WC = west-central region; C = central region; EC = east-central region; NW = northwest region; NE = northeast region. The heavy red line denotes the coastal (to the west) and interior (to the east) metaregions.

Southwest Region

Physiographic Setting

This region consists of Vancouver Island and the southern mainland coast, east to the crest of the southern Coast-Cascade Mountains. The Georgia Depression, which includes southeastern Vancouver Island, the Gulf Islands, the lower Fraser River Valley, and the Sunshine Coast, is a central feature of this region. This is the most densely populated region of British Columbia, with important population centres including Vancouver, Surrey, Abbotsford, Chilliwack, Hope, Victoria, Nanaimo, Comox, Campbell River, Sechelt, and Powell River.

Biogeoclimatic Setting

The southwest region is largely characterized by two biogeoclimatic zones: the Coastal Douglas-Fir (CDF) zone in the warm, summer-dry lowlands of southeastern Vancouver Island, the Gulf Islands, and local areas of the southern mainland coast; and the much wetter Coastal Western
Hemlock (CWH) zone at low elevations throughout the rest of the region. These zones give way to the Mountain Hemlock (MH) zone at middle and upper elevations (c. 900-1800 m), and, at the highest elevations (above c. 1600 m), the Coastal Mountain-heather Alpine (CMA) zone. These upper elevations typically experience very heavy snowpacks and relatively long winters, with the summers being short and cool (Meidinger & Pojar 1991).

**Vegetation**

Low elevation forests within this region are dominated by Coastal Douglas-fir (*Pseudotsuga menziesii* var. *menziesii*), Western Redcedar (*Thuja plicata*), Western Hemlock (*Tsuga heterophylla*), Sitka Spruce (*Picea sitchensis*), Grand Fir (*Abies grandis*), Bigleaf Maple (*Acer macrophyllum*), Red Alder (*Alnus rubra*), and Black Cottonwood (*Populus trichocarpa*). Arbutus (*Arbutus menziesii*) and Garry Oak (*Quercus garryana*) are locally frequent in the drier climates of the Georgia Depression, especially on well-drained or rocky substrates. Middle and upper elevation forests of the MH zone are comprised of few tree species, with Amabilis Fir (*Abies amabilis*), Mountain Hemlock (*Tsuga mertensiana*), and Yellow-cedar (*Xanthocyparis nootkatensis*) dominating these elevations throughout the region. Subalpine and alpine areas of the CMA zone are uniformly dominated by members of the family Ericaceae, particularly mountain-heathers (*Phyllodoce, Cassiope*), White-flowered Rhododendron (*Rhododendron albiflorum*), and blueberries/huckleberries (*Vaccinium spp.*).

This region supports relatively few *Antennaria* species, although both subspecies of *A. howellii* (most commonly subsp. *howellii*) occur widely at low elevations of the Georgia Depression, and both *A. media* and *A. racemosa* are fairly common at middle and upper elevations throughout the region. *Antennaria rosea* is frequent in the Coast-Cascade Ranges, but is rare within the Georgia Depression (where it is known from collections of both native and adventive populations). *Antennaria pallida* occurs rarely at the highest elevations of both Vancouver Island
and the adjacent mainland coast, while *A. lanata* is restricted to the Cascade Ranges, where it is fairly common. A single disjunct historical collection of *A. dimorpha* has been made from southernmost Vancouver Island, but the species is likely now extirpated from the region.

Nine species of *Symphyotrichum* occur regularly within the southwestern region, including both native and introduced species; it is the only region of the province where exotic species of *Symphyotrichum* are widely established. Low elevations within the Georgia Depression are dominated by *S. douglasii* and various cultivars of the introduced *S. novi-belgii*, while *S. frondesum* var. *caurinum* is the only representative of the genus to regularly inhabit middle and upper elevations within this region (except along the crest of the Cascade Ranges, where it overlaps slightly in distribution with, and hybridizes with, *S. frondesum* var. *frondeum*). *Symphyotrichum chilense* is common along maritime and estuarine shorelines along the outer coast of Vancouver Island, but is infrequent in the Georgia Depression; this species is replaced by *S. subspicatum* from northern Vancouver Island north. Four taxa that are typically associated with the southern interior of the province (*S. bracteolatum*, *S. ciliolatum*, *S. falcatum* var. *falcatum*, and *S. lanceolatum* subsp. *hesperium*) are rare on the southern mainland coast, where they are primarily restricted to the shorelines of the lower Fraser River or adjacent uplands. Four additional taxa (*S. ciliatum*, *S. frondosum*, *S. laeve* subsp. *laeve*, and *S. pilosum* var. *pilosum*) occur as rare waifs or tenuously-established species in and around Vancouver.

**South-central Region**

**Physiographic Setting**

This region encompasses the eastern slopes of the Coast and Cascade Mountains, the Thompson-Nicola Plateau, the Okanagan Highlands, and the arid basins along the Okanagan, Similkameen, South Thompson, Nicola, and lower Fraser Rivers. The northern extent of this
region extends to the southern Chilcotin Plateau, the lower reaches of the North Thompson River, and the Shuswap Lake area. The densest areas of human habitation within this region are along the Okanagan Valley, and important population centres include Osoyoos, Penticton, Kelowna, Vernon, Salmon Arm, Kamloops, Cache Creek, Lillooet, Keremeos, and Princeton.

Biogeoclimatic Setting

Low elevation basins (below c. 900 m) of this region are hot and dry, and are dominated by the Bunchgrass (BG) and Ponderosa Pine (PP) biogeoclimatic zones, which transition sequentially through the Interior Douglas-fir (IDF) and Montane Spruce (MS) zones with increasing elevation and/or latitude. The highest montane areas (above c. 1500 m) support examples of the Engelmann Spruce-Subalpine Fir (ESSF) zone, although this biogeoclimatic zone is not particularly widespread in the region. Relatively little true alpine habitat occurs in this region, where it is largely restricted to the highest elevations (above c. 2000 m) of the Coast and Cascade Mountains. Alpine vegetation in this region is characteristic of the Interior Mountain-heather Alpine (IMA) zone.

Vegetation

The vegetation of the lowest elevations, which are extremely dry due to the rainshadow effects of the Coast and Cascade Mountains, is dominated by species such as Bluebunch Wheatgrass (*Pseudoroegneria spicata*), Big Sagebrush (*Artemisia tridentata*), Ponderosa Pine (*Pinus ponderosa*), Interior Douglas-fir (*Pseudotsuga menziesii* var. *glauca*), and a diverse assemblage of dryland shrubs, forbs, and grasses. Interior Douglas-fir and Interior Spruce (*Picea engelmannii* x *glauca*), alongside occasional Western Redcedar and Western Larch (*Larix occidentalis*), generally dominate mid-elevation forests; Pinegrass (*Calamagrostis rubescens*) is very common and widespread at these elevations, and is often ubiquitous within the understory.
Upper montane forests primarily support low-diversity forests of Engelmann Spruce (*Picea engelmannii*) and Subalpine Fir (*Abies lasiocarpa*). At the highest elevations, alpine habitats are dominated by mountain-heathers (*Phyllodoce, Cassiope*) and other members of the family Ericaceae, and typically experience lower snowpacks, shorter winters, and drier summers than comparable alpine habitats to the east or west.

The south-central region supports a high diversity of *Antennaria* species relative to most other regions of the province. *Antennaria anaphaloides, A. dimorpha, A. microphylla, A. parvifolia, A. rosea,* and *A. umbrinella* are all widespread and frequent at low to moderate elevations throughout the region, while *A. howellii* (both subspecies) and *A. racemosa* occur widely in forested habitats of middle and upper elevations. The higher mountains of this region support additional *Antennaria* species, with *A. lanata, A. media,* and locally *A. pulvinata* all frequent to common at these elevations. The only Canadian locations for the rare *Antennaria flagellaris* occur in this region of British Columbia, on the eastern slopes of the Cascade Mountains near Princeton. Two additional taxa, *A. pulcherrima* subsp. *pulcherrima* and *A. luzuloides* subsp. *luzuloides,* occur marginally in this region, where they are restricted to the northwestern and southeastern peripheries, respectively.

The genus *Symphyotrichum* is similarly diverse within this region, where it is represented by thirteen native species. The lowest elevations support an abundance of *S. bracteolatum, S. ciliatum, S. falcatum var. falcatum,* and *S. lanceolatum* subsp. *hesperium* in wet, shoreline habitats, while *S. campestre* and *S. ericoides var. pansum* are widespread and characteristic of drier upland habitats. *Symphyotrichum ciliolatum, S. frondeum var. frondeum,* and the hybridogenous *S. x maccallae* become common at middle and upper elevations, where they are more characteristic of forested environments than the open, arid landscapes that dominate the lowest basins. Rarer *Symphyotrichum* taxa of the south-central region include two species of shoreline habitats in the
southern Okanagan Valley (S. x columbiaun, S. frondosum) and S. spathulatum var. intermediate of the Shuswap Lake area, while the northerly S. boreale occurs locally along the northern periphery of the region. Symphyotrichum laeve subsp. laeve and the garden escapee S. x versicolor occur as non-established waifs in this region, and apparent collections of S. falcatum var. commutatum from the Okanagan Valley may similarly be representative of adventive populations.

**Southeast Region**

**Physiographic Setting**

The mountainous southeast region includes the southern and central Columbia Mountains (including the Selkirk, Monashee, Purcell, and southern Cariboo Ranges), most of the Shuswap and Okanagan Highlands, the Kettle River Valley and associated lowlands (the ‘Boundary’ region), and the southern Rocky Mountain Trench and adjacent Rocky Mountains (north to central Kinbasket Lake). This region of British Columbia supports a relatively small human population, with important population centres including Grand Forks, Castlegar, Trail, Nelson, Creston, Cranbrook, Kimberley, Nakusp, Revelstoke, Golden, and Clearwater.

**Biogeoclimatic Setting**

The lower elevations (below c. 1500 m) of much of the southeast region are dominated by the relatively wet Interior Cedar-Hemlock (ICH) zone, although the drier climates of the Kettle River area and the southern Rocky Mountain Trench support localized pockets of the Ponderosa Pine (PP) and Interior Douglas-fir (IDF) zones. Although middle and upper elevations throughout this region (above c. 1500 m) are typically dominated by the Engelmann Spruce-Subalpine Fir (ESSF) zone, the Montane Spruce (MS) zone occasionally occurs along the western and eastern boundaries of this region where the climate is somewhat drier. At the highest elevations (above c.
2300 m), alpine areas throughout this region (which are widespread) support examples of the Interior Mountain-heather Alpine (IMA) zone.

**Vegetation**

The wet climates that dominate throughout much of this region support forested habitats that are very similar to those found along the coast of British Columbia, with Western Redcedar, Western Hemlock, Black Cottonwood, and a variety of otherwise coastal shrubs, forbs, and grasses often dominating. The presence of typical interior species such as Western Larch, Ponderosa Pine, Interior Spruce, Interior Douglas-fir, and Paper Birch (*Betula papyrifera*) in this region is also notable, and the combination of ‘coastal’ and ‘interior’ floras results in a relatively high plant diversity. Along the Kettle River and throughout the southern Rocky Mountain Trench, the vegetation is more reminiscent of the arid basins of the south-central interior than of the wetter climates of the Columbia Mountains, with species such as Ponderosa Pine, Big Sagebrush, Bluebunch Wheatgrass, and a high diversity of dryland shrubs, forbs, and grasses being characteristic. Engelmann Spruce and Subalpine Fir dominate the upper elevations throughout this region, while mountain-heathers, blueberries/huckleberries, and sedges (*Carex* spp.) are characteristic of the alpine zone.

The southeast supports an *Antennaria* flora that is similar to that of the south-central region, at least within the drier areas of the region. *Antennaria anaphaloides, A. dimorpha, A. microphylla, A. parvifolia, A. rosea,* and *A. umbrinella* all occur in the dry lowlands of the southern Rocky Mountain Trench and Kettle River valley, with some of these (*A. rosea, A. umbrinella*) occurring upslope through middle and upper elevations as well. Forested habitats support *A. howellii* (both subspecies), *A. racemosa,* and locally *A. luzuloides* subsp. *luzuloides,* with the Kettle River area and southernmost Columbia Mountains representing the provincial centre of abundance for the latter species. *Antennaria lanata* and, in areas of calcareous substrates, *A. pulvinata* are widespread
and common within this region at middle and upper elevations but do not occur within the lowlands. *Antennaria pulcherrima* subsp. *pulcherrima* occurs locally in calcareous meadows and shorelines of the Rocky Mountains and southern Rocky Mountain Trench, where it appears to potentially hybridize with the closely related *A. anaphaloides*.

The most common and widespread species of *Symphyotrichum* at low elevations throughout the southeastern region are *S. bracteolatum*, *S. lanceolatum* subsp. *hesperium*, *S. ciliolatum*, *S. x maccallae*. The drier climates of the southeastern corner of this region, which include the southern Rocky Mountain Trench and adjacent Rocky Mountains, support additional species that are otherwise associated with the dry climates of south-central British Columbia to the west or the prairies of southern Alberta to the east (*S. ericoides* var. *pansum*, *S. campestre*, *S. ciliatum*, *S. laeve* subsp. *laeve*). Two species that are more common and widespread across central British Columbia, *S. boreale* and *S. falcatus* var. *falcatus*, occur sporadically at lower elevations across the northern portions of this region. Middle and upper elevations also support robust populations of *S. frondeum* var. *frondeum* along with peripheral populations (in the southern Cariboo Range) of *S. frondeum* var. *frondeum*. The provincially rare *S. ascendens* and *S. falcatus* var. *commutatum*, which occur much more commonly to the east in adjacent southern Alberta, are largely restricted in British Columbia to the southern Rocky Mountain Trench. The similarly rare *S. cusickii* and *S. hendersonii* are restricted in Canada to the southernmost Columbia Mountains near the United States border. *Symphyotrichum spathulatum* var. *intermedium*, which has been erroneously noted as occurring more widely throughout British Columbia in the past, is a rare inhabitant of the Arrow Lakes area of the southern Columbia Mountains (although it may be slightly more widespread than the few collections suggest).
West-central Region

Physiographic Setting

The west-central region of British Columbia includes the central and northern mainland coast, all associated islands, and the islands of Haida Gwaii, extending eastwards as far as the crest of the central Coast Mountains. The outlets of the Skeena and Nass Rivers are major physiographic features of this region, and the coastline is largely characterized by a complex landscape of glacially-carved fiords and islands. This region of the province is sparsely populated, with Prince Rupert, Stewart, Terrace, Kitimat, Bella Coola, and Masset representing the primary areas of human habitation.

Biogeoclimatic Setting

Low elevations throughout the west-central region (below c. 400 m) are characterized by the wettest subzones of the Coastal Western Hemlock (CWH) zone, which give way to similarly wet examples of the Mountain Hemlock (MH) zone with increasing elevation. Above c. 1000 m, the highest mountain peaks support alpine vegetation that is characteristic of the Coastal Mountain-heather Alpine (CMA) zone.

Vegetation

The ecological variation within the west-central region is not as pronounced as in most other areas of the province, resulting in a depauperate flora when compared to adjacent regions. It is the wettest region of British Columbia, and one of the wettest regions on the North American continent, with the vegetation largely dominated by extensive coniferous forests and littoral, shoreline habitats along the seacoasts. Low elevations are characterized by ubiquitous forests of Western Redcedar, Western Hemlock, Sitka Spruce, and, in some of the coldest or wettest areas, Amabilis Fir, Mountain Hemlock, and Yellow-cedar. Boggy areas are widespread throughout the
region, and support extensive communities of peat moss (*Sphagnum* spp.), Shore Pine (*Pinus contorta* var. *contorta*), sedges (*Carex, Eriophorum*), grasses, and a variety of shrubs in the family Ericaceae such as Western Bog-laurel (*Kalmia microphylla*), Bog-rosemary (*Andromeda polifolia*), and Crowberry (*Empetrum nigrum*). The generally low-diversity montane forests of the MH zone primarily comprise Mountain Hemlock, Amabilis Fir, and Yellow-cedar, while alpine areas are dominated by mountain-heathers (*Phyllodoce, Cassiope, Harrimanella*), grasses, and sedges. The islands of Haida Gwaii were the largest refugial area in British Columbia during the Wisconsinan Glaciation (Pruett *et al.* 2013), and as such these areas support almost all of British Columbia’s endemic vascular plants (Douglas *et al.* 2002a).

Both *Antennaria* and *Symphyotrichum* are very poorly represented in the west-central region. *Antennaria rosea*, *A. pallida*, and *A. media* are all widespread along the Coast Mountains, but are absent from lower elevations along the mainland coast and from all coastal islands (including Haida Gwaii). Additionally, *A. monocephala* subsp. *angustata* and *A. pulvinata* occur locally along the Coast Mountains, the latter primarily in areas of calcareous influence, but neither species is particularly frequent within the region. *Antennaria howellii* subsp. *howellii* is rare in this region, where it is restricted to low elevation forests of the Skeena River and adjacent lowlands. The only species of *Symphyotrichum* to occur widely in the west-central region are *S. frondeum* var. *caurinum*, which is widespread at middle and upper elevations of the Coast Mountains but absent from low elevations and all islands, and *S. subspicatum*, which is widespread along maritime and estuarine shorelines throughout the region (including Haida Gwaii and other coastal islands). *Symphyotrichum chilense* occurs rarely along maritime shorelines of Haida Gwaii, where it appears to hybridize locally with the much more common *S. subspicatum*. 
Central Region

Physiographic Setting

The central region of British Columbia is dominated by an intermontane plateau system comprised of the Nechako Plateau, Nechako Lowlands, northern Chilcotin Plateau, and Cariboo Plateau. It extends westwards to encompass the eastern slopes of the central Coast Mountains and eastwards to the foot of the northern Columbia Mountains (Cariboo Range) and central Rocky Mountains. This region also extends northwestwards to encompass the Bulkley Valley and adjacent mountains, with the northernmost extent reaching the southern Williston Reservoir. The major population centres of this region include Prince George, Quesnel, Williams Lake, Vanderhoof, Smithers, and Mackenzie.

Biogeoclimatic Setting

The Sub-boreal Spruce (SBS) zone is dominant throughout most of this region. The SBS zone is largely replaced by the Sub-boreal Pine-Spruce (SBPS) zone and, at higher elevations (above c. 1200 m), the Montane Spruce (MS) zone in the drier climates of the Chilcotin and Cariboo Plateaus, and by the Interior Cedar-Hemlock (ICH) in the wet climates of the northwestern portion of the region. Middle and upper elevations throughout most of this region (above c. 1500 m) are dominated by the Engelmann Spruce-Subalpine Fir (ESSF) zone. Alpine areas within this region are infrequent and largely confined to the western, northern, and eastern peripheries. Alpine environments along the Coast Mountains (above c. 1700-2100 m) represent the southernmost extent of the otherwise northerly Boreal Altai Fescue Alpine (BAFA) zone, while elsewhere these same elevations support examples of the Interior Mountain-heather Alpine (IMA) zone.
Vegetation

The mixed and coniferous forests that occur throughout this region are characterized by Interior Spruce, Subalpine Fir, Lodgepole Pine (*Pinus contorta* var. *latifolia*), Trembling Aspen (*Populus tremuloides*), Black Cottonwood, and Paper Birch, while Interior Douglas-fir dominates in the warmer, drier southern portions of the region. The wetter climates in northwestern parts of the region support forests of Western Redcedar, Western Hemlock, and Lutz Spruce (*Picea x lutzii*). Like elsewhere across the southern interior of the province, montane forests of this region support relatively low-diversity coniferous forests of Engelmann Spruce and Subalpine Fir, giving way to communities of mountain-heathers (*Phyllodoce, Cassiope*), grasses, and sedges in the alpine zones. The drier, colder alpine areas that occur along the Coast Mountains, and which are representative of the BAFA biogeoclimatic zone, support vegetation that is more characteristic of subarctic ecosystems than of alpine vegetation elsewhere at comparable latitudes of the province.

The largely forested inter-montane plateaus of this region, which are situated between the Coast Mountains to the west and the Columbia and Rocky Mountains to the east, support a relatively small diversity of *Antennaria* species relative to adjacent regions to the north and south. *Antennaria rosea, A. racemosa,* and *A. howellii* (both subspecies) are the most common and widespread members of the genus in these areas, with *A. parvifolia, A. umbrinella,* and *A. microphylla* occurring locally in the drier climates of the southern portions of the region. The higher elevations associated with mountainous areas along the western, northern, and eastern peripheries of this region support *A. media, A. pallida, A. monocephala* subsp. *angustata,* and *A. pulvinata,* with the subalpine and alpine habitats of the Coast Mountains supporting the highest diversity of these montane species.

*Symphyotrichum ciliolatum* is the most widespread and abundant member of the genus throughout the central region, where it is essentially ubiquitous in the forested environments that
dominate the lower elevations. The central region also represents the provincial centre of abundance of the wetland-associated *S. boreale*, which is otherwise absent or much less common to the north and south, as well as sporadic populations of *S. lanceolatum* subsp. *hesperium* (especially along major river systems). *Symphyotrichum frondeum* var. *caurinum* is the primary species of *Symphyotrichum* at middle and upper elevations along the western, northern, and eastern peripheries of the region, especially where the forests are characteristic of wetter climates. The drier southern portions of this region support the northern extent of several *Symphyotrichum* species of south-central or southeastern regions of the province, including *S. bracteolatum*, *S. ciliatum*, *S. ericoides* var. *pansum*, and *S. falcatum* var. *falcatum*.

**East-central Region**

**Physiographic Setting**

This is the smallest region of the province, and encompasses the northernmost Columbia Mountains (Cariboo Range) as well as the central Rocky Mountains and adjacent Rocky Mountain Trench (from Kinbasket Lake north to the Pine Pass). Mount Robson Provincial Park, within which sits the tallest mountain in the Canadian Rocky Mountains (Mount Robson), is a central feature of this region. The human population of this region is very small, with McBride and Valemount being the only significant areas of human habitation.

**Biogeoclimatic Setting**

The lower elevations of this mountainous region (below c. 1100 m), which are distributed primarily along the Rocky Mountain Trench, support examples of the Interior Cedar-Hemlock (ICH) zone and Sub-boreal Spruce (SBS) zone. Montane areas, which are widespread throughout this zone, are dominated by the Engelmann Spruce-Subalpine Fir (ESSF) zone above c. 1100 m,
while the highest mountains (above c. 1700 m) support the Interior Mountain-heather Alpine (IMA) zone.

**Vegetation**

The vegetation of the east-central region represents an interface between southern floras of the southeastern region of the province and northern/subarctic floras that characterize the northern Rocky Mountains and areas across the northwestern region of the province. As such, many plant species reach either their northernmost or southernmost limits within this region. The low elevation forests of the region, which are dominated by Western Redcedar, Western Hemlock, Lodgepole Pine, Interior Spruce, Subalpine Fir, Trembling Aspen, Black Cottonwood, and Paper Birch, represent a mixture of species from the wetter climates of southeastern British Columbia and the sub-boreal forests of central British Columbia. As with most of the southern half of the B.C. interior, montane forests are dominated by Engelmann Spruce and Subalpine Fir, while ericaceous shrubs such as mountain-heather (*Phyllodoce, Cassiope*) and blueberries/huckleberries, along with a variety of grasses, sedges, and forbs, dominate the subalpine and alpine zones.

The most widespread and frequent species of *Antennaria* within the east-central region include *A. howellii* (both subsp.), *A. rosea*, and, at higher elevations, *A. media*. Several species of *Antennaria*, including *A. pallida* and *A. monocephala* subsp. *angustata*, reach or approach their southern geographic limits in eastern B.C. in this region of the province, while others (*A. lanata, A. microphylla*) reach or approach their northern geographic limits. *Antennaria pulcherrima* subsp. *pulcherrima* and *A. pulvinata* occur in this region primarily along the Rocky Mountains, especially in areas of strong calcareous influence. The normally grassland- or dry forest-associated *Antennaria parvifolia* is rare and is restricted in this region to the Valemount area.

Few species of *Symphyotrichum* occur in this region of the province, with the forest-associated *S. ciliolatum* and the wetland-associated *S. boreale* being the only species that are
widespread. Additionally, the more southerly *S. bracteolatum* reaches its northernmost extent in British Columbia in this region, where it is restricted to wetlands and shorelines at the lowest elevations, while *S. frondium* var. *caurinum* occurs occasionally in forest and wetland habitats at middle and upper elevations.

**Northwest Region**

**Physiographic Setting**

This mountainous region, which is the largest in British Columbia, extends from the northern Rocky Mountains westwards to the U.S. border along the Alaska Panhandle. It includes the Cassiar, Omineca, Liard, Skeena, St. Elias (Alsek), and northern Coast Mountains, as well as the northern Rocky Mountain Trench, Liard Basin, and the plateaus of the Stikine, upper Skeena, and upper Yukon River watersheds. This area supports the lowest density of human habitation in the province, with Telegraph Creek, Dease Lake, and Atlin representing the only notable communities.

**Biogeoclimatic Setting**

The lower elevations of this region are largely dominated by the Boreal White and Black Spruce (BWBS) zone, although localized areas of Interior Cedar-Hemlock (ICH) and Sub-boreal Spruce (SBS) zones occur in the southwestern portions of the region. Isolated examples of the Coastal Western Hemlock (CWH) zone penetrate the western boundary of this region along the lowermost reaches of the Stikine, Iskut, Taku, Umuk, and Whiting Rivers, and are continuous with similar habitats across the border in southeastern Alaska. Middle and upper elevations (above c. 700 m) are dominated by the Engelmann Spruce-Subalpine Fir zone across southern portions of this region, but give way to extensive areas of the Spruce-Willow-Birch (SWB) zone across the northern two-thirds of the region. Alpine areas of the northwestern region, which often extend
downslope to as low as 1000 m, are uniformly characterized by the Boreal Altai Fescue Alpine (BAFA) zone.

**Vegetation**

*White Spruce (Picea glauca), Black Spruce (Picea mariana), Lodgepole Pine, Subalpine Fir, and Trembling Aspen* are the most common species throughout the low elevations of this region, although Western Cedar, Western Hemlock, and, at higher elevations, Engelmann Spruce occur locally in southwestern areas. Much of the region is characterized by extensive areas of willow-birch scrub with scattered pockets of White or Engelmann Spruce, with a correspondingly high diversity of willow species present. Alpine areas, which are widespread and extensive in this region, are generally dominated by Altai Fescue (*Festuca altaica*) grasslands, although wetter regions in the southwestern portion of the region support mountain-heather (*Phylloodoce, Cassiope, Harrimanella*) communities that are similar to those found to the south and west. Many plant species of otherwise more northerly distribution, especially those of Beringian origin, reach their southern geographic limits within this region.

*Antennaria* diversity is higher in this region of British Columbia than in adjacent areas to the south or east, due specifically to the occurrence of several taxa of northern affinities. *Antennaria rosea* and *A. media* are widespread throughout the region. Northern species such as *Antennaria pallida* and *A. monocephala* (both subspecies) have their provincial centres of distribution in this region, while more southern species such as *A. pulvinata, A. racemosa* and *A. howellii* subsp. *howellii* reach their northern limits in the southern portion of this region. Isolated populations of *Antennaria umbrinella*, which otherwise occurs primarily in south-central British Columbia, occur in pockets of drier, rainshadow climates to the east of the Coast and St. Elias Mountains, including in the areas of Telegraph Creek and the Haines Triangle. *Antennaria*
*pulcherrima* subsp. *pulcherrima* occurs locally in calcareous wetlands and seepages in northern portions of this region.

Although the genus *Antennaria* is well represented in the northwest region, very few species of *Symphyotrichum* occur. *Symphyotrichum ciliolatum* and *S. boreale* occur locally along the eastern and southern peripheries of the region, and *S. frondeum* var. *caurinum* occurs in the Coast Mountains (Boundary Ranges) along its western margins, but much of the region is unpopulated by members of this genus.

**Northeast Region**

**Physiographic Setting**

The northeast region includes the eastern slopes of the northern Rocky Mountains and all areas east to the Alberta border, and includes prominent physiographic features such as the Peace River valley, the Fort Nelson lowlands, and the eastern foothills of the Rocky Mountains. Human population in this region is concentrated along the Peace River valley, and much of the region remains unpopulated. Important population centres in the northeast region include Dawson Creek, Fort St. John, Chetwynd, Tumbler Ridge, Hudson Hope, and Fort Nelson.

**Biogeoclimatic Setting**

Most of the region is at a lower elevation and uniformly supports the forests of the Boreal White and Black Spruce (BWBS) zone, which gives way to either the Engelmann Spruce-Subalpine Fir (ESSF) zone (southern portions) or the Spruce-Willow-Birch (SWB) zone (northern portions) at middle and upper elevations. Alpine areas throughout the northeast region, which are restricted to its western margins, support the Boreal Altai Fescue Alpine (BAFA) zone.
Vegetation

Boreal forests of White Spruce, Black Spruce, Tamarack (*Larix laricina*), Trembling Aspen, and Balsam Poplar (*Populus balsamifera*) dominate throughout this region, although Engelmann Spruce and Subalpine Fir become important at higher elevations along portions of the Rocky Mountains. Bogs and fens occur widely in this region, especially in the northern portions. The Peace River valley supports extensive forests of Trembling Aspen interspersed with grassland habitats dominated by species such as Thickspike Wildrye (*Elymus lanceolatus*), Kentucky Bluegrass (*Poa pratensis*), Junegrass (*Koeleria macrantha*), and Short-awned Porcupinegrass (*Hesperostipa curtiseta*). Subalpine communities along the northern portion of the Rocky Mountains in this region supports extensive areas of willow-birch scrub, giving way to grass-dominated alpine habitats at the highest elevations. Much of the vegetation of this region, particularly that of the lower elevations away from the Rocky Mountains, is more characteristic of boreal and prairie ecosystems of Alberta than of the ecosystems that characterize most of the rest of British Columbia, and many otherwise easterly plant species reach their westernmost outposts in this region of British Columbia.

Although the Peace River lowlands and Rocky Mountains support a moderate diversity of *Antennaria* species, much of the rest of the region is extremely depauperate in members of this genus. Within the Peace River lowlands, where prairie and parkland ecosystems are widespread and the genus is well-represented, species such as *A. rosea*, *A. parvifolia*, *A. howellii* subsp. *howellii* (rare), *A. racemosa* (rare), and the prairie-associated *A. neglecta* occur; the Peace River region is the sole area of occurrence of the latter species in British Columbia. Higher elevations along the Rocky Mountains support populations of *A. pallida*, *A. media* (local), and *A. monocephala* (both subspecies). The northerly *A. pulcherrima* subsp. *pulcherrima* occurs
sporadically in calcareous meadows and wetlands within this region, particularly along the Rocky Mountains and associated foothills.

The genus *Symphyotrichum* is relatively well represented in this region of the province, with a diversity of species that mirrors that of adjacent Alberta. The northeast is the only region of the province where the otherwise easterly *S. puniceum* var. *puniceum* occurs, where it is primarily restricted to the Peace River and Fort Nelson lowlands. The region is also one of the primary provincial centres of distribution for *S. laeve* subsp. *laeve*, which is ubiquitous throughout open and disturbed habitats of the Peace River valley. *Symphyotrichum ciliolatum* is widespread in forested habitats throughout the region, while *S. lanceolatum* subsp. *hesperium* is often abundant along the shorelines of the Peace River and its tributaries; *S. boreale* occurs sporadically in fens and other calcareous wetlands. Several species with prairie affinities, *S. ericoides* var. *pansum*, *S. falcatum* var. *falcatum*, and *S. ciliatum*, range westward from Alberta into the Peace River valley, with *S. ericoides* var. *pansum* being the most common member of this assemblage. The otherwise more westerly *S. frondeum* var. *caurinum* occurs locally along the eastern slopes of the Rocky Mountains in southern portions of this region, but is neither widespread nor common.

### 1.3 Summary of Research

The traditional alpha-taxonomic study presented here addresses the unresolved taxonomy of two important, diverse, and taxonomically complex genera in the family Asteraceae in British Columbia – *Antennaria* (Chapter 2) and *Symphyotrichum* (Chapter 3). The restricted geographic focus of the study was specifically chosen to enable a more detailed, region-specific assessment of the taxonomy of these genera and to address information gaps or uncertainties that have been identified in previous studies. Given the unique phytogeographic complexity of the province of British Columbia, the disregard of provincial specimens in many of these earlier studies left a variety of taxonomic questions unaddressed and many species concepts unclear. The taxonomic
revisions presented herein are thus intended to clarify the species limits, morphological circumscriptions, distributions, and ecological associations of these species in the province and better represent their diversity in this region of North America. It is hoped that the incorporation of these taxonomic approaches more widely beyond British Columbia will improve the taxonomy of these groups elsewhere in North America.

In this treatment, I accept 17 species of *Antennaria* and 23 species of *Symphyotrichum* as occurring within the boundaries of British Columbia. In comparison to the most recent and widely adopted taxonomic and floristic studies of these genera in the Pacific Northwest (e.g., Hitchcock & Cronquist 1973, Douglas 1995, Douglas *et al.* 1998, Bayer 2006, Brouillet *et al.* 2006), I have accepted two previously unrecognized taxa of *Antennaria* (*A. pallida, A. pulvinata*) and seven previously unrecognized taxa of *Symphyotrichum* (*S. x columbianum, S. cusickii, S. douglasii, S. falcatum var. commutatum, S. hendersonii, S. x maccallae, S. novi-belgii var. novi-belgii*); several of these (*S. cusickii, S. falcatum var. commutatum, S. hendersonii*) have been adopted as part of the British Columbia flora by the B.C. Conservation Data Centre (2018) prior to this monographic summary of their occurrence. These additions are the result of both new collections following the most recent floristic publications as well as new taxonomic circumscriptions resulting from this study. In addition, several previously recognized taxa in these genera have been excluded as part of the provincial flora due to misidentification or recircumscription. The widely recognized, but difficult to define, concept of *S. subspicatum* is also recircumscribed here so as to align the concept with the holotype, with other components of this ‘trash bin’ concept distributed amongst several other taxa and their hybrids. Finally, the name *Symphyotrichum frondeum* is proposed herein to accommodate the species that has previously been recognized as *S. foliaceum* in regional floras due to the conspecificity of the holotype with that of *S. subspicatum*. 
I present this example of specimen-based, alpha-taxonomic research so as to demonstrate the depth and value of such studies in the academic system, where they are rarely afforded the attention or respect that they deserve. The long decline of baseline taxonomic research, such as that which is represented by this study, has become an important challenge within the biological sciences. As taxonomy has continued to suffer from inadequate funding and other forms of support from the academic community, the implications of this inattention (which have come to be known as the ‘Taxonomic Impediment’ [Coleman 2015]) have rippled out to affect both other academic biologists (particularly in the fields of ecology, conservation biology, and phylogenetics) as well as non-academic end-users of taxonomy and natural history that are dependent on the application of accurate taxonomic concepts. The history of the Taxonomic Impediment, the current challenges that it poses to the biological sciences, and a selection of proposed future opportunities for overcoming these challenges are presented at the end of this study (Chapter 4). The perspective presented in this chapter is motivated by my concern over the current state of taxonomic research, as well as my experiences within and outside of the university system, particularly my relationship with the British Columbia Conservation Data Centre and experiences within the fields of environmental consulting, restoration ecology, and conservation biology. The development of this perspective was largely facilitated by the University of British Columbia’s Public Scholar’s Initiative (PSI), which aims to promote partnership between academic non-academic and non-academic institutions. This component of the study is presented as a means to both draw attention to this critical issue as well as to provide a launching pad for the further involvement of academic and non-academic biologists alike in confronting the Taxonomic Impediment and supporting the role of taxonomy in the global study of biodiversity.
CHAPTER TWO:

A TAXONOMIC REVISION OF *ANTENNARIA* (ASTERACEAE: GNAPHALIEAE) IN BRITISH COLUMBIA, CANADA

2.1 Introduction

*Antennaria* is well known as one of the most taxonomically complex genera in the Asteraceae due to the presence of extensive hybridization, polyploidy, and apomixis (Bayer 1993), particularly within the Catipes clade of species (Bayer *et al.* 1996). It is most diverse in North America (especially western and northern North America), but is also found across northern Eurasia and disjunctly in South America. As is typical of agamic complexes, the considerable morphological variation within the genus is difficult to capture taxonomically, and arises through hybridization among the sexually reproducing, usually diploid (sometimes tetraploid) species followed by extensive polyploidy and gametophytic apomixis (in this case, diplospory [Stebbins 1932b, Bayer 1984]) among the hybrid offspring. The resulting apomictic lineages, which propagate asexually, can be considered ‘microspecies’ (Jauhar & Joshi 1973) and grouped into aggregates or agamospecies (Turesson 1926, Babcock & Stebbins 1938) with similar morphology and, presumably, sexual progenitor species. Due to the morphological variation among the microspecies, however, the resulting aggregates are often difficult to define morphologically, especially when considered at larger geographic scales. A typical result of this is that some microspecies may fall within the morphological definition of more than one aggregate, or conversely may fall between two or more aggregates or between an aggregate and its progenitor species. All of these conditions are prevalent within *Antennaria* and have confounded taxonomists working on the genus for more than a century.

Early workers in the genus in North America, such as E.L. Greene (1897, 1898, 1899, 1901, 1904a, 1904b, 1906a, 1906b, 1908, 1911a, 1911b, 1911c), P.A. Rydberg (1897, 1899, 1900,
M.L. Fernald (1898, 1899a, 1914a, 1914b, 1916, 1921, 1924), E.E. Nelson (1899a, 1899b, 1900, 1901), and A.E. Porsild (1939, 1949, 1950) attempted to reflect the variation in the genus through the publication of a large number of species-level taxa, most of which were apomictic microspecies and differed only marginally from other described taxa. This approach is similar to that employed for many other apomictic complexes, such as European Taraxacum (Richards & Sell 1976) and Hieracium (Sell & West 1976). The result, however, was a huge number of published names in the genus, as exemplified by the recognition of 135 synonyms here for the seventeen accepted species in British Columbia. Later taxonomists such as Bayer (1984, 1985, 1987a, 1987b, 1988a, 1988b, 1989a, 1989b, 1989c, 1989d, 1990a, 1990c, 1991, 1993, 2006), Bayer & Stebbins (1981, 1982, 1987, 1993), Bayer et al. (1996), Chmielewski & Chinnappa (1986, 1988a, 1988b, 1988c, 1990, 1991), Chmielewski et al. (1990a, 1990b), and Chmielewski (1993, 1994, 1995, 1997, 1998, 2006) shifted away from the recognition of such a large number of apomictic microspecies and towards an approach that amalgamated these into a smaller number of aggregates, which were generally recognized at the species (or, occasionally, subspecies) level. This latter approach, which is similar to that commonly applied to North American Taraxacum (Brouillet 2006) and Crepis (Sears 2011), has been the dominant method of representing the taxonomy of the genus in recent decades.

Two major, and largely concurrent, taxonomic research programs investigated the genus Antennaria in the 1980s and 1990s: that of Bayer (with contributions from Stebbins and others) and that of Chmielewski (with contributions from Chinnappa and others). These two research programs used a variety of methods to investigate the taxonomy of the genus and relationships among the component taxa in North America, including morphometric approaches (Bayer 1985, 1987a, 1987b, 1988a, 1989a, 1989c, 1990a, 1990c; Chmielewski & Chinnappa 1988a, 1991; Chmielewski et al. 1990a, 1990b; Chmielewski 1993, 1997, 1998), chromosome counts (Bayer &
Stebbins 1981, 1987; Chinnappa 1984, 1986; Bayer 1984; Chmielewski & Chinnappa 1988a, 1990; Chmielewski 1995, 2006), crossing studies (Bayer & Stebbins 1982; Bayer 1985), and isozyme/allozyme analysis (Bayer 1988b, 1989b, 1991; Bayer & Crawford 1986), sometimes with the incorporation of ecological or phytogeographic evidence (Bayer & Stebbins 1987; Chmielewski & Chinnappa 1988b, 1988c; Chmielewski 1988, 1996; Bayer 1989c, 1990b; Bayer et al. 1996). Although complimentary in many ways, the taxonomic conclusions reached by the Bayer and Chmielewski lines of research often differ rather strikingly. With the publication of a continent-wide taxonomy of the genus by Bayer & Stebbins (1993), and its subsequent adoption in the Flora of North America project (Bayer 2006), the taxonomic approaches of the Bayer et al. research stream have become the most widely adopted across the United States and Canada, and alternative approaches are now rarely seen in floras or other biodiversity publications. There exists no published comparison of these approaches at either the continental or regional scales, however, and therefore no means by which to evaluate the potential for alternative taxonomic hypotheses to aid in clarifying aspects of the taxonomy or identification criteria that remain problematic. Given the challenges still faced by those working with the taxonomy of Antennaria in North America, such alternative approaches may be valuable in providing additional perspectives through which to view the genus. In light of this, this study attempts to compare these two approaches directly by applying them to a large collection of herbarium specimens from a single geographic region – in this case the western Canadian province of British Columbia.

The objectives of this study are: (i) to determine which elements of these two proposed taxonomies (Bayer, Chmielewski) best represent the genus in British Columbia; (ii) to refine the descriptions of the characteristics (morphological, ecological, phytogeographic) that define the component taxa; (iii) to refine the identifications of the reviewed specimens in a way that is reflective of the most suitable taxonomic system; and (iv) to present the results as a revised
monographic taxonomic treatment of the genus in British Columbia. Accepted taxa in this treatment, at least within the apomictic aggregates, are intended to maximize the intrataxon homogeneity (morphological and otherwise) while simultaneously minimizing the intertaxon overlap in any of these characteristics. However, given the structure of the system, as described above, ambiguity between taxa will be an inevitable element of the genus, and some *Antennaria* specimens and populations are expected to fall between or otherwise outside of the taxa presented here. This should be considered an unavoidable part of working with this fascinating group of plants, as well as a source of inspiration for continued study of the genus.

2.2 Materials & Methods

A review of existing taxonomic literature pertaining to *Antennaria*, along with extensive field and herbarium experience of the author and others, revealed that the accepted taxonomy of the genus did not reflect the taxonomic variation observed in British Columbia. Most notably, many taxa were poorly defined and many identifications seemed incompatible with the circumscriptions of the taxa that they purported to represent. In response, I reviewed more than 1700 specimens of *Antennaria* housed at the University of British Columbia herbarium (UBC), including more than 1200 collections from British Columbia, in order to revise the taxonomy so as to better capture the variation within that province. This collection is among the largest, most comprehensive (geographically, temporally, and taxonomically), and most active collections of vascular plant specimens in British Columbia, and was thus considered an ideal collection from which to base this type of taxonomic study. In addition to the specimens at UBC, specimens were reviewed from BABY as well as digitally from ALA (University of Alaska 2016), the Consortium of Pacific Northwest Herbaria (CPNH 2016), and the Intermountain Region Herbarium Network (IRHN 2016). Review of these latter collections primarily represented specimens from
jurisdictions adjacent to British Columbia and provided important context for the collections at UBC. Note that only specimens housed at UBC are specifically referenced and mapped within the provided taxonomic treatment as these were the specimens that informed the taxonomic conclusions. In addition, all accessible type specimens pertaining to the taxa accepted here for British Columbia were reviewed digitally via JSTOR Global Plants (JSTOR 2016), and assigned to a particular taxon based on morphological, phytogeographic, and in some cases ecological (where noted) similarity.

During this specimen review, two main taxonomic approaches were applied to the specimens: that of Bayer and collaborators (which resulted in the taxonomy presented in Bayer 2006) and that of Chmielewski and collaborators. Other taxonomic approaches, such as that of A.E. Porsild (1950), were also considered so as to better represent the breadth of taxonomic opinions on the genus. In order to determine which taxonomic approach was most applicable, individual specimens were systematically identified using the published identification criteria of the various approaches, and the successes or shortcomings of each taxonomy noted. Furthermore, published morphological descriptions were refined in areas where these descriptions failed to adequately represent the morphology encountered in the reviewed specimens.

Taxonomic concepts that are presented here represent four primary types of taxa: (i) sexual, diploid taxa that are recognized at the species level (e.g., \textit{A. dimorpha}, \textit{A. racemosa}); (ii) suspected autoploid, apomictic aggregates that differ little, if at all, morphologically from their progenitor diploids and are synonymized with the parental diploid (e.g., \textit{A. parvifolia}, \textit{A. pulvinata}); (iii) suspected autoploid, apomictic aggregates that differ consistently morphologically from their progenitor diploids and are recognized at the subspecies level (e.g., \textit{A. monocephala} subsp. \textit{angustata}); and (iv) alloploid, apomictic aggregates that are hypothesized to have originated through the hybridization of 2+ parental diploids and are
recognized at the species level (e.g., *A. rosea*, *A. howellii* s.l., *A. borealis*). For apomictic aggregates (both allopolyploid and autoployploid), the concept of the aggregate presented here is intended to maximize the intrataxon morphological homogeneity while simultaneously minimizing the morphological overlap with other aggregates. The inclusion of phytogeographic, cytological, and ecological evidence related to these aggregates is further included to ensure that the resulting taxa are consistent in these factors relative to what would be expected in a sexually-reproducing taxon.

Based on the results of this study, a revision of the taxonomy of the genus in British Columbia is presented below which also incorporates new insights into the morphology, distribution, and ecology of the component taxa. The morphological descriptions of the taxa have been revised as well, and are presented herein. Reviewed specimens were mapped within the British Columbia portion of their range, and an approximation of the regional distribution of each species was constructed based on specimens that were reviewed for this study in combination with distributional information that has been published in other regional floras and monographs. A fully revised dichotomous key is provided to aid in the identification of specimens.

### 2.3 Discussion

The taxonomy of *Antennaria* presented in this treatment is the result of a thorough comparison of existing taxonomic concepts have been systematically tested against a large collection of specimens from within a defined geographic region (in this case, the Canadian province of British Columbia). This comparison has enabled the identification of concepts that best reflect the taxonomy of the genus within this jurisdiction, as well as those that fail to adequately capture the variation of the group or are otherwise inappropriate for use in its taxonomy. Most published taxonomic treatments of the genus in the past two decades have
reflected the taxonomic opinions presented in Bayer & Stebbins (1993) and Bayer (2006), but significant difficulty in applying these concepts in the field and herbarium has led to a limited understanding of the genus amongst active botanists in the region. The incorporation here of many concepts that had been published by Chmielewski and collaborators, and which were found to be more readily applicable to the patterns of variation seen within the genus, should render the taxa better defined and more easily identified while also improving the relationship of the taxonomy to the evolutionary history of the taxa.

When the treatment presented here is compared with Bayer & Stebbins (1993) and Bayer (2006), or with other regional floristic accounts that present a taxonomy that is similar to or derived from these approaches such as Hitchcock & Cronquist (1973) and Douglas et al. (1998), a number of differences will be apparent. Several taxa that have been previously recognized as occurring in the region have been excluded from consideration due to misapplication of concepts (i.e., *A. alpina*) or misidentification of specimens (i.e., *A. corymbosa, A. densifolia*). Additionally, several other concepts that have been well described by Chmielewski (i.e., *A. borealis* [= *A. pallida* of Chmielewski], *A. pulvinata*) are considered fully deserving of recognition as species-level taxa due to pronounced morphological, ecological, and phytogeographic consistency within the concepts and their notable divergence in these factors from other recognized taxa. Indeed, the recognition of these latter two taxa simplifies the recognition of several taxa within the genus, with some of the prior confusion attributed to the scattering of the synonyms associated with these taxa amongst other aggregates (as in Bayer 2006). One novel morphological character that has otherwise not been reported is presented here for the identification of *A. pulvinata* (cypsela length), providing an additional line of evidence for synonymizing apomictic *A. pulvinata* and sexual populations that have previously been recognized as *A. ‘aromatica.’
Although many of the taxonomic concepts of Chmielewski and collaborators were found to represent the genus in British Columbia better than those presented in Bayer & Stebbins (1993) or Bayer (2006), and have therefore been adopted here as a result, there remain some concepts originating from this research stream that failed to align with the specimens reviewed for this study. In particular, the infraspecific taxonomy presented for *A. media* (Chmielewski 1997) was found to be unrepresentative of the specimens observed, with the supposedly diagnostic characters of the taxa not co-varying in the way suggested by the paper. A similar approach taken for *A. alpina* (Chmielewski 1998) was similarly difficult to resolve, and the application of this infraspecific taxonomy was further complicated by the apparent misapplication of the name *A. alpina* in the region. Other concepts that have been promoted by Chmielewski as representative of species-level taxa, such as *A. ‘alborosea’* and *A. ‘stolonifera’* (Chmielewski & Chinnappa 1988), were not found to be diagnosable within the morphological variation of the *A. rosea* and *A. media* concepts, respectively, and were synonymized with these concepts. Thus, the taxonomic treatment presented here includes only the aspects of the two major taxonomic approaches that best represent the characteristics of the genus, at least as they relate to the British Columbia flora.

A number of other elements of this taxonomic revision do not specifically originate from the review of these differing taxonomic approaches, but rather from the review of the specimens and species concepts that they represent. This includes: (i) the revision of the morphological circumscriptions of a number of taxa (e.g., *A. media, A. rosea*); (ii) the revision of the geographic distributions of a many taxa through the re-identification and mapping of specimens within the UBC herbarium (e.g., *A. dimorpha, A. howellii* subspecies, *A. monocephala* subspecies, *A. microphylla, A. neglecta, A. umbrinella*); (iii) the revision of the infraspecific taxonomies of several taxa (e.g., *A. howellii, A. monocephala*); (iv) the highlighting of important but generally under-recognized or under-utilized identification criteria (e.g., *A. neglecta, A. umbrinella*); (v) the
reattributio n of many synonyms based on review of the corresponding type specimens, (vi) the recognition of several putative hybrid combinations occurring within the province; and (vii) a completely revised and updated dichotomous identification key that reflects the taxonomy presented. The inclusion of these elements beyond those specifically incorporated from other existing taxonomic approaches has improved the taxonomic circumscription of the genus in British Columbia and suggests a framework for evaluating these concepts and this approach elsewhere in North America. Such an approach also yields numerous taxonomic predictions that can be tested using further phylogenetic studies.

2.4 Conclusions

The taxonomic approach presented in this treatment has now been applied by myself and several other botanists on Antennaria populations across much of British Columbia and has been reported to noticeably improve the identification rates of specimens while providing stronger and better-defined taxonomic concepts. It should be considered a further step in the conversation regarding the taxonomy of Antennaria, however, rather than a final word, and there remains considerable uncertainty about the genus, particularly within the apomictic aggregates of the Catipes clade. The morphological variation within most of these apomictic taxa remains moderate to pronounced, and the boundaries between some of the taxa overlap more than is desirable. The result of this is the inevitable difficulty in attributing a certain percentage of specimens to any of the concepts presented here. This difficulty is most apparent in regions of the province with a more complex glacial history, such as the northwestern mountains, the Rocky Mountains of the southeast, and the Coast-Cascade Ranges along the western parts of the province. Within these areas, specimens and populations occur that may appear as morphological ‘bridges’ between recognized taxa, or represent a morphology that is otherwise out-of-place among these taxa. It is in areas such as these that future targeted taxonomic research has the opportunity to shed
considerable further light on the genus, perhaps including the recognition of additional taxa or, at least, a better understanding of the variation among individual apomictic microspecies. Regarding the taxonomy presented in this treatment, I am in full agreement with Bayer & Stebbins (1993) that a major proof of the utility of a taxonomy is in its workability by other users, and hopefully further insights will arise from both the successes and failures associated with the application of this taxonomy.

2.5 Taxonomic treatment

**ANTENNARIA** Gaertn. PUSSYTOES

Herbaceous perennials (sometimes subshrubby in *A. umbrinella*), dioecious or gynoecious, rhizomatous, sometimes from a branched woody stem base, often stoloniferous, often mat-forming; stolons (when present) horizontal to suberect or erect (rarely arcuate), usually leafy (rarely naked, or leaves reduced and scale-like), sometimes subligneous\(^1\) (*A. umbrinella*).

**Flowering stems** ascending to erect, simple below the capitulescence, sparsely to densely lanate to floccose, eglandular or sparsely to densely stalked-glandular. **Leaves** basal and cauline; basal leaves linear or narrowly lanceolate to narrowly or broadly oblanceolate or spatulate, apices acute or obtuse to rounded or mucronate, entire, usually grey-pubescent on both surfaces or adaxial surface green and glabrescent, eglandular or sparsely to densely stalked-glandular; cauline leaves alternate, sessile, linear to lanceolate, apices usually acute to acuminate, sometimes with inconspicuous to prominent flags\(^2\) (especially distally), entire, usually grey-pubescent to floccose or lanate, eglandular or sparsely to densely stalked-glandular (especially distally).

**Capitulescences** of a single terminal head or multiple heads in a capitate to corymbose (or

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\(^1\) **Subligneous**: slightly woody; snapping when bent

\(^2\) **Flags**: naked, scarious leaf apices that are coloured differently (tan, brown, or blackish) from the remainder of the leaf
racemose to paniculiform in *A. racemosa*) arrangement. **Pistillate capitulae** discoid; involucres campanulate, phyllaries sometimes reflexed at anthesis; phyllaries in 3-6+ rows, lanceolate to narrowly or broadly ob lanceolate, inner phyllaries usually longer and narrower than outer phyllaries, apices acute or obtuse to rounded, margins often erose, whitish or creamy-white to pink, tan, brownish, olive, or blackish, often with a dark brownish or blackish central spot, glabrous (*A. luzuloides*) or sparsely to densely lanate basally, often ciliate basally; pistillate corollas narrowly tubular to filiform, white or yellowish to reddish; pappus of 12-20+ capillary to barbellate bristles. **Staminate capitulae** usually wider and shorter than pistillate heads; phyllaries usually broader, paler, and more consistently reflexed at anthesis than those of pistillate heads; corollas funnelform or tubular, 5-lobed, whitish to creamy-white; pappus of 10-20+ clavate or barbellate bristles. **Cypsela** yellowish to reddish or brownish, ovoid to ellipsoid, smooth to minutely papillate, rarely stalked-glandular.

Species ca. 45 (17 spp. in B.C.). Eurasia, North America, Mexico, South America. \(x = 14\).

The genus *Antennaria* is widespread throughout the northern hemisphere, with three species occurring disjunctly in the southern hemisphere (southern South America). It reaches its greatest diversity in western North America, where representatives occur widely from the arctic and subarctic regions of Alaska and Canada to the arid deserts and mountains of the southwestern United States and Mexico, and east through the woodlands of the southeastern United States. Within British Columbia, species of *Antennaria* are most abundant in relatively dry, open or lightly forested environments at all elevations, although some species occur in either wetter (e.g., *A. pulcherrima*) or more densely forested (e.g., *A. howellii, A. racemosa*) habitats. The genus is relatively poorly represented in coastal regions of the province, especially away from the Georgia Depression, with the greatest diversity of species in British Columbia occurring in the southern interior, the Rocky Mountains, and the subarctic mountains of the northwest.
Although the base chromosome number of *Antennaria* is widely recognized as $n = 14$, and plants with $2n = 28$ considered diploids, comparison with closely related genera (e.g., *Gnaphalium*) has suggested that such plants are likely paleotetraploids rather than true diploids (Bayer & Stebbins 1981, Bayer 1990a); however, as $2n = 14$ is not found in *Antennaria*, these plants are recognized here as diploid. Taxonomically, *Antennaria* comprises five (Bayer 1990a) or six (Bayer 2006) unranked clades, four of which (Catipes, Pulcherrimae, Dimorphae, and Argenteae) are represented in British Columbia (Table 2). The majority of the species are placed in the Catipes clade, and these are the species from which the bulk of the taxonomic complexity arises. In British Columbia, the Catipes clade contains six sexual, diploid or tetraploid taxa and seven apomictic, polyploid aggregates (Table 2), the latter being treated as species in this treatment so as to provide a more standard and consistent taxonomy.

**TABLE 2. Placement of B.C. species of *Antennaria* among the four clades present in the province.** * = sexual species, in which both staminate and pistillate plants occur; a = apomictic species (or aggregates) in which only pistillate plants occur. Note that both symbols are presented for *A. monocephala*, as its two subspecies differ in their respective breeding biology.

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<tr>
<th>PULCHERRIMAE</th>
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<tr>
<td><em>A. anaphaloides</em></td>
<td><em>A. howelli</em></td>
<td><em>A. parvifolia</em></td>
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<tr>
<td><em>A. lanata</em></td>
<td><em>A. media</em></td>
<td><em>A. pulvinata</em></td>
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<td><em>A. pulcherrima</em></td>
<td><em>A. microphylla</em></td>
<td><em>A. racemosa</em></td>
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<td>CATIPES</td>
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<td><em>A. dimorpha</em></td>
<td><em>A. monocephala</em></td>
<td><em>A. rosea</em></td>
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<td><em>A. flagellaris</em></td>
<td><em>A. neglecta</em></td>
<td><em>A. umbrinella</em></td>
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<td>DIMORPHAE</td>
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<td><em>A. luzuloides</em></td>
<td><em>A. borealis</em></td>
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An identification key to the accepted species of *Antennaria* in British Columbia is presented below. All species of *Antennaria* are dioecious but, as only some species are sexually
reproducing, staminate plants are not represented in all taxa. When present, staminate plants contribute greatly to species identification by narrowing the number of potential candidate species, and therefore should be sought in the field whenever collections are made. Staminate plants are identifiable by their 5-lobed, funnelform corollas and protruding anthers (corollas generally filiform in pistillate plants, with the stigmas included or, if slightly exserted, then the stigma lobes remaining closed) (Figure 2). They also typically have shorter, wider involucres than pistillate plants, with broader, usually whitish or pale phyllaries that are often reflexed at anthesis, as well as shorter, often somewhat clavate (vs. capillary) pappus bristles. Bayer & Stebbins (1993) and Bayer (2006) provide additional considerations to improve the success rate for identification of Antennaria specimens.

**FIGURE 2.** Comparison of staminate and pistillate capitulae (A, B) and florets (C, D) in Antennaria. A, C = staminate plant; B, D = pistillate plant. All images are of the sexual diploid Antennaria racemosa (specimen: R.L. Taylor, Beil, Marchant, & Oliver 5686 [UBC]).
Dichotomous Key to *Antennaria* Species in British Columbia

1a. Flowering heads solitary ............................................................... 2
1b. Flowering heads borne in capitulescences of 2 or more .................. 4

2a. Cauline leaves with prominent scarious flags at apices; plants of moist to mesic, subalpine and alpine habitats across the northern half of the province…. 10. *A. monocephala* [in part]
2b. Cauline leaves without scarious apical flags; plants of dry habitats in the steppe and lower montane zones of south-central B.C. ................................................................. 3

3a. Plants lacking stolons, usually strongly mat-forming; widespread throughout south-central B.C ................................................................. 3. *A. dimorpha*
3b. Plants with long, arching, naked stolons that terminate in a leafy propagative bud, not mat-forming; rare in south-central B.C., where known only from the Princeton area……

4a. Plants lacking stolons, not mat-forming ........................................ 5

5a. Phyllaries glabrous; involucres 3.5-5 (6) mm; basal leaves linear to narrowly oblanceolate ................................................................. 7. *A. luzuloides*
5b. Phyllaries moderately to densely lanate basally; involucres (4) 4.5-8 mm; basal leaves narrowly oblanceolate to lance-elliptic or narrowly spatulate ....................... 6

6a. Cauline leaves with prominent flags; basal leaves 3-veined; flowering stems (1) 3-20 (30) cm tall, of middle and upper elevations .......................................... 6. *A. lanata*
6b. Cauline leaves lacking flags or, if present, then linear and inconspicuous; basal leaves 3- to 5-veined; flowering stems 15-65 cm tall, primarily of low to middle elevations (occasionally to subalpine) ......................................................... 7

7a. Phyllaries wholly whitish to creamy-white, or with a small (< 1 mm) blackish spot at the base; involucres (4) 5-6.5; plants of dry to mesic, open to lightly forested, upland habitats across the southern interior of B.C ........................................ 1. *A. anaphaloides*
7b. Phyllaries with a large (1-3 mm), prominent blackish spot on the proximal half; involucres 5-8 mm; plants of moist, shrubby, often streamside habitats in northern
and eastern B.C., as well as disjunctly to the western Chilcotin......13. *A. pulcherrima*

4b. Plants stoloniferous, usually mat-forming…………………………………………………………..8

  8a. Plant staminate…………………………………………………………………………………...9

  9a. Basal leaves 3-veined, adaxial surface green and glabrous, 25-100 mm; capitulescence open, racemose or paniculiform at maturity……………………………………16. *A. racemosa* [in part]

  9b. Basal leaves 1-veined, adaxial surface grey-pubescent, 5-30 (45) mm; capitulescence dense, capitate or subcorymbose at maturity………………………………………………10

  10a. Stolons 2.5-18 cm, stolon leaves greatly reduced (often nearly scale-like) relative to leaves of terminal stolon rosette; capitulescences densely capitate; plants restricted to Peace River region of northeastern B.C…………………..11. *A. neglecta* [in part]

  10b. Stolons 1-7 (10) cm, stolon leaves similar in size or only slightly reduced relative to leaves of terminal stolon rosette (never greatly reduced or scale-like); capitulescences subcorymbose to capitate; plants widespread…………………………………………11

  11a. Plants eglandular; stolons erect or suberect, subligneous; phyllaries creamy-white to tan or brownish-olive (sometimes tinged with pinkish)……………………………………18. *A. umbrinella* [in part]

  11b. Plants sparsely to densely stalked-glandular, especially distally; stolons spreading horizontally, herbaceous (not subligneous); phyllaries whitish to creamy-white….
……………………………………………………………………………9. *A. microphylla* [in part]

8b. Plant pistillate…………………………………………………………………………………………12

  12a. Capitulescence open, racemose or paniculiform at maturity; basal leaves 25-100 mm, 3-veined…………………………………………………………………………16. *A. racemosa* [in part]

  12b. Capitulescences open to dense, capitate to subcorymbose or corymbose (never racemose or paniculiform); basal leaves (4) 4.5-40 (45) mm, 1- to 3-veined…….13

  13a. Capitulescences composed of one larger, dominant terminal head and 1-2 small, much reduced lateral heads subtending the terminal head…………………………….10. *A. monocephala* [in part]

  13b. Capitulescences composed of 3 or more flowering heads of similar size and shape….
14a. Adaxial leaf surface glabrous or glabrescent, bright to dark green; leaves 1- to 3-veined

5. *A. howellii* [in part]

14b. Adaxial leaf surface usually grey-pubescent or lanate, rarely becoming greenish and glabrescent with age; leaves typically 1-veined

15. *A. howellii* [in part]

15a. Stolon leaves greatly reduced (often nearly scale-like) relative to leaves of terminal stolon rosette; plants restricted to the Peace River region of northeastern B.C.

11. *A. neglecta* [in part]

15b. Stolon leaves similar in size or only slightly reduced relative to leaves of terminal stolon rosette (never greatly reduced or scale-like); plants widespread throughout B.C.

16. *A. howellii* [in part]

16a. Phyllaries conspicuously medium to bright pink

17. *A. parvifolia* [in part]

17a. Cauline leaves 4-7 per flowering stem; flowering stems 2-15 (18) cm tall; involucres 8-11 (15) mm; basal leaves broadly oblanceolate to spatulate, apices rounded to mucronate

12. *A. parvifolia* [in part]

17b. Cauline leaves (5) 7-16 per flowering stem; flowering stems 3-30 (40) cm tall; involucres 4-10 mm; basal leaves narrowly oblanceolate to narrowly spatulate, apices mucronate

17. *A. rosea* [in part]

16b. Phyllaries whitish, creamy-white, tan, olive-brown, or blackish, often with a dark central spot, rarely with a faint pinkish tinge

18. *A. umbrinella* [in part]

18a. Stolons suberect to erect, subligneous

18. *A. umbrinella* [in part]

18b. Stolons horizontal or, if erect or suberect, then herbaceous

19. *A. umbrinella* [in part]

19a. Basal leaves (15) 20-40 mm

20. *A. umbrinella* [in part]

20a. Phyllaries with a prominent brownish or blackish central spot

20. *A. umbrinella* [in part]

20b. Phyllaries not prominently dark-spotted

21. *A. umbrinella* [in part]

21a. Outer phyllaries lanceolate, apices acute to acuminate
5. *A. howellii* [in part]

21b. Outer phyllaries narrowly obleng or narrowly to broadly oblanceolate, apices obtuse to rounded.................................22

22a. Cauline leaves 4-7 per flowering stem; flowering stems 2-15 (18) cm tall; involucres 8-11 (15) mm; basal leaves broadly oblanceolate to spatulate, apices rounded to mucronate........12. *A. parvifolia* [in part]

22b. Cauline leaves (5) 7-16 per flowering stem; flowering stems 3-30 (40) cm tall; involucre 8-10 mm; basal leaves narrowly oblanceolate to narrowly spatulate, apices mucronate..........18. *A. rosea* [in part]

19b. Basal leaves (4) 4.5-15 (20) mm.........................................................23

23a. Phyllaries whitish to tan or pale olive with a prominent brownish or blackish central spot.................................................................24

24a. Basal leaves broadly cuneate-spatulate (rarely spatulate), < 2x as long as wide, 4.5-10 (12) mm; cypselae (1.2) 1.5-2 mm; phyllaries usually erect at anthesis; flowering stems (0.5) 1.5-5.5 (8) cm tall; plants occurring across the southern two-thirds of B.C.........................15. *A. pulvinata*

24b. Basal leaves oblanceolate, > 2x as long as wide, (6) 9-15 (20) mm; cypselae 0.7-1.5 mm; phyllaries usually reflexed at anthesis; flowering stems (2.5) 4-16 (20) cm tall; plants occurring across the northern half of B.C.................................................................2. *A. borealis*

23b. Phyllaries not dark-spotted or, if dark spot present, then overall phyllary colour blackish-green to dark olive-brown..........................25

25a. Phyllaries blackish-green to dark olive-brown..............8. *A. media*

25b. Phyllaries whitish or creamy-white to tan..................................26

26a. Plants sparsely to densely stalked-glandular, especially distally......27

27a. Basal leaves spatulate to broadly oblanceolate, 6-16 mm...........

.................................................................9. *A. microphylla* [in part]

27b. Basal leaves narrowly oblanceolate to narrowly spatulate, (6) 8-40
mm……………………………………………..17. *A. rosea* [in part]

26b. Plants eglandular…………………………………………………………..28

28a. Cauline leaves 4-7 per flowering stem; flowering stems 2-15 (18) cm tall; involucres 8-11 (15) mm; basal leaves broadly oblanceolate to spatulate, apices rounded to mucronate.....12. *A. parvifolia* [in part]

28b. Cauline leaves (5) 7-16 per flowering stem; flowering stems 3-30 (40) cm tall; involucres 4-10 mm; basal leaves narrowly oblanceolate to narrowly spatulate, apices mucronate……………….

…………………………………………………………………………18. *A. rosea* [in part]

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**Monograph of *Antennaria* species in British Columbia**

1. *Antennaria anaphaloides* Rydb.

**TALL PUSSYTOES; Pearly Pussytoes; Tall Everlasting**


**Plants** dioecious, sexual, short-rhizomatous or sometimes from a branched woody stem base, lacking stolons, not mat-forming. **Flowering stems** erect, densely tomentose to floccose, not stalked-glandular, 15-35 (60) cm tall. **Basal leaves** erect to ascending, narrowly oblanceolate to lance-elliptic, apices mostly acute to acuminate, grey-tomentose to lanate on both surfaces, not stalked-glandular, 3- to 5-veined, (25) 50-150 (200) mm. **Cauline leaves** 7-12, linear or linear-ob lanceolate to lance-elliptic, reduced upwards, apices acuminate, lacking scarious tips, not stalked-glandular, 10-80 mm. **Capitulescences** capitate or glomerulate to corymbose, dense to open, peduncles of lower heads/clusters to 40 mm, 20-90 mm in diameter. **Pistillate capitulae** 8-
30 (50+), subsessile to long-stalked; involucres broadly campanulate, phyllaries usually reflexed at anthesis, sparsely to moderately lanate basally, 4.5-7 mm; outer phyllaries obovate to obleng, apices rounded to truncate and often erose, whitish to creamy-white (sometimes pink-tinged), often with a small brown spot near the base, 4-6 mm; inner phyllaries narrowly oblong to obovate, apices rounded to truncate and often erose, whitish to creamy-white, often with a small brown spot near the base, 3.5-5.5 mm; pistillate corollas 3-4.5 mm; pappus 3.5-4.5 (5.5) mm. **Staminate capitulae**

8-30 (50+); similar to pistillate heads but involucres slightly broader, (4) 5-6.5 mm; staminate corollas 3-4.5 (5) mm; pappus 3.5-4.5 (5.5) mm. **Cypselae** smooth, 1-1.8 mm.

Flowering May-Jul. Mesic to dry grasslands, open forests, aspen copses, and thickets in the steppe and montane (rarely subalpine) zones; 450-1500 (2300) m. Frequent in south-central BC, from the Coast-Cascade Mts. east to the Boundary region [Grand Forks, Christina Lake] and north to the southern Chilcotin region and Shuswap Lake; locally frequent in southeast BC [southern Rocky Mountains and adjacent Rocky Mountain Trench], north to Kootenay National Park. BC east to SK, south to NV, UT, CO. 2n = 28 (2x) (Appendix E).

This is a grassland- and parkland-associated species of the Great Basin, southern Rocky Mountains, and northern/western Great Plains that extends its range northward into suitable habitats of southern Canada (Figure 3) is closely related to the similar *A. pulcherrima* of more northerly regions, and the two species have in the past been considered conspecific due to their morphological similarities (e.g., Douglas 1995, Douglas *et al.* 1998). Although similar in many respects, *A. anaphaloides* is most easily separable from *A. pulcherrima* by its smaller, more numerous capitula and conspicuous whitish phyllaries that have a smaller and browner basal spot than those of *A. pulcherrima* (the spot is typically larger, blacker, and more centrally situated on the phyllary in *A. pulcherrima*, giving the involucres an overall dark or blackish aspect).
Furthermore, these species inhabit different habitats in their respective ranges, with *A. anaphaloides* being a species of dry, upland grasslands and open forests, whereas *A. pulcherrima* occurs in shrubby alluvial habitats, along shorelines, and in wet meadows, especially in areas of extensive *Salix* thickets. The distributions of these two species overlap locally in the Rocky Mountains of British Columbia and Alberta, and the presence of intermediate specimens from this region suggests a potential zone of hybridization between them; see *A. pulcherrima* for further discussion of these possible hybrids. In addition to potential hybridization between *A. anaphaloides* and *A. pulcherrima*, putative hybrids between *A. anaphaloides* and *A. lanata* have also been collected rarely in subalpine habitats of south-central and southeast B.C. (e.g., Mount Kobau, Limestone Ridge [East Kootenays]), where the elevational ranges of these two species marginally overlap. Individuals proposed as representative of this hybrid combination are intermediate between the two parental taxa in a variety of features, and tend to present a mixture of the characters of these taxa. This applies to characters such as basal leaf shape, basal leaf venation, phyllary colouration, cauline leaf flags, and overall stature. Such hybrids may be expected to occur more widely across the southern interior of British Columbia, as the geographic distributions of *A. anaphaloides* and *A. lanata* overlap extensively across this region.
FIGURE 3] Distribution of British Columbia specimens of Antennaria anaphaloides that were reviewed for this study (left), and approximate distribution of the species in northwestern North America (right).

2. Antennaria borealis Greene

PALLID PUSSYTOES; Pale Pussytoes

Antennaria borealis Greene (1899: 85), auct. non. Gandoger (1887). Type:—UNITED STATES. Alaska: Disenchantment Bay, 10 August 1892, Funston 101 (holotype NDG!).

Antennaria pallida E.E. Nelson (1901: 700). Type:—UNITED STATES. Alaska: Disenchantment Bay, 10 August 1892, Funston 101 (holotype NDG!).


Antennaria isolepis Greene (1911b: 41). Type:—CANADA. Nunavut: Cape Eskimo, 26 August 1910, J.M. Macoun 79270 (lectotype [designated by Bayer (1989a: 59)] NDG!, isolecotypes NY!, GH!).

Antennaria rousseauii A.E. Porsild (1949: 80) [as rousseaiui]. Type:—CANADA. Quebec: Payne River, 07 August 1947, Rousseau 991 (holotype CAN, isotypes GH!, S!).
Antennaria pedunculata A.E. Porsild (1950: 15). Type:—CANADA. Yukon: upper Moose River valley, Canol Road, 12 July 1944, A.E. Porsild & Breitung 10447 (holotype CAN, isotype GH!).

Plants gynoecious, apomictic, rhizomatous, stoloniferous, often mat-forming; stolons leafy, 0.5-2 (3) cm. **Flowering stems** erect, lanate, sometimes sparsely to moderately stalked-glandular (at least distally), (2.5) 4-16 (20) cm tall. **Basal leaves** oblongate, apices rounded to broadly acute or mucronate, moderately to densely grey-pubescent on both surfaces, 1-veined, (6) 9-15 (20) mm. **Cauline leaves** 6-14, narrowly to broadly lanceolate or oblanceolate, apices acute to acuminate, middle and upper leaves with strap-shaped to acuminate scarious tips, 8-20 mm. **Capitulescences** usually subcorymbose to corymbose (sometimes capitate, especially when young), slightly to moderately open, 10-30 mm in diameter. **Pistillate heads** 3-11; involucres campanulate, phyllaries usually reflexed at anthesis, moderately to densely lanate basally, 5-7.5 mm; outer phyllaries ovate to broadly oblanceolate, apices rounded to obtuse, whitish to tan or pale olive (rarely tinged with pink) with a dark brown central spot, 3-5.5 mm; inner phyllaries oblanceolate, apices obtuse, whitish to pale brown or olive (rarely tinged with pink) with a dark brown central spot, 4.5-7 mm; pistillate corollas 2.5-4.5 mm; pappus 4-5.5 mm. **Cypselae** dark brownish, smooth to finely papillate or stalked-glandular, 0.7-1.5 mm.

Flowering Jun-Jul (Aug). Dry to mesic meadows, high-elevation grasslands, talus slopes, scree, streambanks, shorelines, forest openings, rocky ridges, fellfields, gravelly areas, and tundra, especially on sandy or other well-drained soils, in the upper montane, subalpine, and alpine zones; (800) 1200-2000 (2300) m. Locally frequent in northwest BC, becoming infrequent south along the Coast Mts of western BC; locally frequent in east-central BC [central Rocky Mts., Cariboo Mts.]; rare in southwest [Vancouver Is., southern Coast Mts., Cascade Mts.] and southeast [Rocky
This tetraploid agamic complex is widespread and fairly common in northern parts of the province. It ranges south locally along the Coast Mountains to the Cascade Mountains of southwestern B.C., as well as along the Rocky Mountains to extreme west-central Alberta (Willmore Wilderness Park; possibly also Jasper National Park) and the Cariboo Mountains of eastern British Columbia. *Antennaria borealis* occurs in a wide variety of open habitats, particularly where the soils are sandy, gravelly, or otherwise well-drained, and is generally restricted to middle and upper elevations wherever it occurs. It is unclear whether the absence of records from the northern Rocky Mountains of British Columbia (Figure 5) is reflective of a true absence of the species or collecting deficiencies, although the abundance of collections of other taxa (including a number of other *Antennaria* species) from this region suggests the former explanation.

The name *Antennaria borealis*, as applied here, corresponds with the concept of *A. pallida* of Chmielewski (1995) and encompasses the formerly-recognized synonyms *isolepis*, *pedunculata*, and *pallida*. Although Chmielewski (1995) applied the name *A. pallida* to this complex due to the synonymization of *pallida* and *borealis* in Nelson (1901), the circumstances that resulted in the synonymization of these two names are rectified by the invalidation of most taxonomic binomials associated with the microspecies of Gandoger (1887), including *A. borealis* Gand., as per Stafleau & Cowan (1976). As a result, the name *A. borealis* Greene is here resurrected as the correct nomenclature for the agamic complex that Chmielewski (1995) recognized as *A. pallida*, and information pertaining to *A. pallida* in Chmielewski (1995) is here adopted as pertaining to *A. borealis*. 
The proposed progenitors of *A. borealis*, based on morphological similarities, are *A. media*, *A. rosea*, and *A. pulvinata* (Chmielewski 1995), although only the latter species is known to have sexual populations in areas approaching the distribution of *A. borealis*. Despite being among the more distinctive and morphologically coherent apomictic *Antennaria* complexes in North America, this taxon has long been neglected among regional and continental floras, and its component synonyms distributed among several other species complexes (*alpina, rosea*) (e.g., Bayer & Stebbins 1993, Bayer 2006). Importantly, representative specimens of *A. borealis* have commonly been included within a very broad, and morphologically inconsistent, concept of *A. alpina*, contributing much to the confusion surrounding the application of that name in North America.

*Antennaria borealis* can generally be identified by its broad, pale (usually whitish, sometimes pale dingy-brown or olive-brown), dark-spotted phyllaries that are typically sharply reflexed at anthesis (Figure 4: B, D); in most other similar *Antennaria* species, the phyllaries do not become reflexed until at or near seed dispersal. Furthermore, mature individuals of *A. borealis* commonly have long-stalked lower flowering heads, producing an open, subcorymbose to corymbose capitulescence (Figure 4: A, D). This feature can aid in distinguishing such plants from species such as *A. media*, in which the dense capitulescences are characteristically rounded or capitate. Note, however, that young *A. borealis* often have capitate capitulescences, and in some populations these may persist into maturity, relegating this feature to a supporting, rather than definitive, morphological characteristic. Interestingly, the unusually broad and usually reflexed phyllaries, which closely resemble those of staminate individuals of sexual *Antennaria* species, have led some authors (e.g., Greene 1911, Hultén 1968) to posit that the species *A. isolepis* (which is included within *A. borealis* here) was entirely staminate, despite the biological and
developmental constraints that would make such a situation essentially impossible in an agamic complex.

Although morphologically well-defined relative to most other agamic complexes in Antennaria, there is nonetheless variation across A. borealis that may inhibit identification of some individuals or populations. The morphology of the species merges with that of A. media and A. rosea in some portions of its range, perhaps suggesting the shared influences of particular diploid parental contributors in these regions. Specifically, many populations of A. borealis in south-coastal and south-central Alaska tend to have phyllaries that are tinged darker (blackish-green to olive-brown) towards the apices than typical pale-phyllaried forms. These populations in many ways bridge the morphological gap between A. borealis and A. media, particularly as many of the plants do not have the characteristically reflexed phyllaries of typical A. borealis. Such individuals are distinguished from A. media in this treatment, however, by the similarly broad, pale-tipped (although dark-tinged) phyllaries that differ from the darker, narrower phyllaries of A. media. Similarly, some populations of A. rosea – specifically those that correspond with the “elegans” form of that aggregate – share the broad, pale, dark-spotted, reflexed phyllaries and subcorymbose capitulescences of A. borealis, but are distinguished by their taller, more slender habit and, particularly, their consistently narrower (linear-oblanceolate to narrowly oblanceolate) basal leaves. Interestingly, Chmielewski (1995) notes that local populations of A. borealis tend to flower and mature 2-3 weeks earlier than sympatric populations of the A. rosea aggregate.
FIGURE 4. General morphology of Antennaria borealis. A = plant habit, showing the typically elongated lower peduncles and resulting subcorymbose capitulescence; B = detail of capitula and phyllaries, showing the broad, pale phyllaries with prominent blackish central spots/bases; C = detail of cauline leaves, showing the prominent pale, strap-like apical flags; D = whole plants in the field, showing the overall habit and the reflexed or spreading nature of the pale phyllaries at anthesis. [A: Straley & Nicholls 6895 (UBC); B-C: R.L. Taylor, Beil, Marchant, & Oliver 554 (UBC); D: V. Skilton (ph.); 15 June 2013; White Pass, BC (used with permission)].

FIGURE 5. Distribution of British Columbia specimens of Antennaria borealis that were reviewed for this study (left), and approximate distribution of the species in northwestern North America (right).
3. *Antennaria dimorpha* (Nutt.) Torr. & A. Gray

**LOW PUSSYTOES; Two-form Pussytoes; Cushion Pussytoes; Low Everlasting; Cushion Everlasting**


**Plants** dioecious, sexual, from a branched woody stem base, lacking stolons, usually mat-forming.

**Flowering stems** ascending to erect, densely tomentose to floccose, not stalked-glandular, 0.5-4 (6) cm tall. **Basal leaves** linear to narrowly spatulate, apices acute, densely grey-tomentose on both surfaces, not stalked-glandular, 1-veined, 8-25 mm. **Cauline leaves** 0-2 (4), linear to narrowly oblanceolate, not reduced upwards, apices acute, lacking scarious tips, not stalked-glandular, 7-15 mm. **Capitulescences** of solitary terminal flowering heads. **Pistillate capitulae** 1; involucres narrowly campanulate to turbinate, phyllaries not reflexed, sparsely to moderately lanate basally, 10-15 (18) mm; outer phyllaries broadly lanceolate to ovate, apices acuminate, brownish-green with a dark brown central spot, broadly hyaline-marginated, 6-7 mm; inner phyllaries linear-
lanceolate, apices long-acuminate, brownish-green (sometimes pink-tinged), broadly hyaline- margined, 10-15 mm; pistillate corollas 8-10 mm; pappus 10-12 mm. **Staminate capitulae** 1; involucres campanulate, phyllaries not reflexed, sparsely to moderately lanate basally, 6-8 mm; outer phyllaries oblong to ovate, apices obtuse to acute to short-acuminate, olive-brown with a darker brown central spot, broadly hyaline-margined, 3-5 mm; inner phyllaries similar to outer phyllaries; staminate corollas 3-5 mm; pappus 4.5-6 mm. **Cypselae** finely short-pubescent, 2-3.5 mm.

Flowering Apr-Jun. Dry grasslands, shrub steppe, open forests, and rock outcrops in the steppe and lower montane zones; 175-900 (1050) m. Common in south-central BC, from the Coast-Cascade Mts. east to the Okanagan Valley and north to the southern Chilcotin region; rare in southwest [southern Vancouver Island] and southeast [southern Rocky Mtn. Trench] BC. BC east to SK, south to CA, AZ. 2n = 28, 56 [2x, 4x] (Appendix E).

**Antennaria dimorpha** is a distinctive spring-blooming species that is a common and characteristic component of grassland and sagebrush habitats of the arid basins of the southern interior. A single collection from Mount Douglas, near Victoria, in 1950 (*Krajina & Spilsbury s.n. [UBC!]*) is the only reported occurrence of this species on the immediate coast; it has not been observed at this site since its original collection and may now be extirpated. Although the validity of the location data associated with this specimen has in the past been questioned as a potential example of a mislabelling, the specimens that the collectors secured at the same location on the same day (as accessioned into the UBC herbarium) are clearly coastal species that are known to occur at Mount Douglas; therefore, the location data associated with this specimen is presumed to be correct, and it is mapped as such in this treatment. Another collection (*T.M.C.Taylor, Krajina, & Tusko 6 [UBC!]*) from west of the Coast-Cascade Mountains, at Harrison Hot Springs east of
Vancouver, has similarly been considered mislabelled given the lack of suitable habitat anywhere near the site. This speculation is supported by the field notes of the collectors, which describe collecting in the Lytton and Lillooet areas of the southern interior (where *A. dimorpha* is common) on the same day as their collecting at Harrison Hot Springs. Because of the questions surrounding the accuracy of the data associated with this specimen, it is omitted from the distribution map (Figure 6) and other consideration herein, pending additional evidence.

The pistillate and staminate involucres of this sexual, dioecious *Antennaria* differ more from each other than in any other sexual species of *Antennaria* in B.C., thus giving rise to the specific epithet ‘*dimorpha*.’ The flowering stems of *A. dimorpha* are extremely short (sometimes almost non-existent), and the solitary, terminal flowering heads rarely exceed the dense basal leaves; taller plants (to 10 cm) from southeastern Washington and northeastern Oregon, in which the flowering stems distinctly exceed the basal leaves, have been called *A. latisquama* or *A. dimorpha* var. *latisquama*, but these are now considered to fall within the normal range of variation of *A. dimorpha* and are no longer given formal taxonomic recognition. Other infraspecific names that have been described within *A. dimorpha*, such as var. *integra* (slender caudex, greater abundance of simple hairs), var. *macrocephala* (overall larger size of all parts), and var. *nuttallii* (leaves relatively small, styles slightly exserted), are all considered to similarly represent variation within typical *A. dimorpha*, and are generally not recognized floristically.

Among British Columbia species of *Antennaria*, only the closely-related *A. flagellaris* has both similarly short flowering stems and solitary flowering heads, but that species is immediately distinguishable from *A. dimorpha* by its naked, arching stolons, each of which ends in a propagative bud.
4. *Antennaria flagellaris* (A. Gray) A. Gray

**STOLONIFEROUS PUSSYTOES;** Flagellate Pussytoes; Whip Pussytoes; Dwarf Spreading Everlasting; Stoloniferous Everlasting


**Plants** dioecious, sexual, fibrous-rooted or from a slender caudex, stoloniferous, not mat-forming; stolons leafless, wiry, glabrous to loosely floccose, terminating in a leafy propagative bud, erect or ascending when young, becoming spreading and arching in age, 3-10 (15) cm. **Flowering stems** ascending to erect, sparsely to moderately floccose, not stalked-glandular, 0.5-1.5 cm tall. **Basal leaves** linear-oblanceolate, apices acute, densely tomentose to lanate on both surfaces, not stalked-glandular, 1-veined, 10-20 (35) mm. **Cauline leaves** (4) 6-10, linear-oblanceolate, usually slightly reduced upwards, apices acute, lacking scarious tips, not stalked-glandular, 10-20 mm. **Capitulescences** of solitary terminal flowering heads. **Pistillate capitulae** 1; involucres narrowly
campanulate, phyllaries not reflexed, sparsely to moderately lanate basally, 7-9 (13) mm; outer phyllaries ovate to lanceolate, apices acute to acuminate, yellowish-brown to brownish, usually with a darker brown central spot, 3-6 mm; inner phyllaries lanceolate, apices long-acuminate, yellowish-brown to brownish, 5-7 mm; pistillate corollas 5-7 mm; pappus 6-8 mm. **Staminate capitulae** 1; involucres campanulate, phyllaries not reflexed, sparsely to moderately lanate basally, 4-7 mm; outer phyllaries ovate to lanceolate, apices acute, olive-brown, sometimes with a darker brown central spot, 3-5 mm; inner phyllaries similar to outer phyllaries; staminate corollas 3-4.5 mm; pappus 3.5-4.5 mm. **Cypselae** papillate, 2-3 mm.

Flowering May-Jun. Seasonally moist to dry grassy slopes, meadows, sagebrush steppe, and unstable banks, especially on clayey or gravelly calcareous substrates, in the lower montane zone; 860-920 (1350) m. Rare in south-central BC [Princeton area]. BC south to CA, east to WY, SD. \(2n = 28\) [2x] (Appendix E).

*Antennaria flagellaris* is a very rare species in British Columbia, being first reported from the province as recently as 1996. It is currently known in the province from fewer than ten populations within an area of ca. 13 km\(^2\) along the eastern slopes of the Cascade Mountains near Princeton, with these populations being disjunct by ca. 200 km from the nearest populations to the south in Washington (Figure 7). The habitat occupied by this species in British Columbia is highly specialized, being composed of open, south-facing sites with calcareous, gravelly-clay or gravelly-sand substrates that experience seepage during the spring but dry out during the summer months, especially where the ground is unstable and prone to slumping or erosion (Douglas *et al.* 2004).

The short flowering stems, solitary capitulae, and, especially, the long, arching, naked stolons render this species perhaps the most easily identifiable *Antennaria* in British Columbia;
only *A. dimorpha* approaches this distinctive morphology, but that species is nonetheless easily distinguished from *A. flagellaris* by a number of features (see *A. dimorpha*).

![Figure 7](image)

**FIGURE 7.** Distribution of British Columbia specimens of *Antennaria flagellaris* that were reviewed for this study (left), and approximate distribution of the species in northwestern North America (right).

5. **Antennaria howellii** Greene

**HOWELL’S PUSSYTOES; Field Pussytoes; Small Pussytoes (= subsp. *neodioica*); Northern Pussytoes (= subsp. *neodioica*); Common Pussytoes (= subsp. *neodioica*); Tomentose Pussytoes (= subsp. *neodioica*); Howell’s Everlasting**


*Antennaria pedicellata* Greene (1897: 175). Type:—UNITED STATES. Oregon: Blue Mountains, no collection date reported, *Cusick 1522* (lectotype [designated by Bayer (1989d: 397)] NDG!, isolectotype OSC!). [= *subsp. neodioica*]


Antennaria canadensis Greene var. randii Fernald (1898: 247). Type:—UNITED STATES. Maine: nr Indian Pond, Mount Desert Island, Hancock County, 03 July 1897, Rand s.n. (lectotype [designated by Bayer & Stebbins (1982: 309)] GH!); A. neglecta Greene var. randii (Fern.) Cronquist (1945: 184); A. neodioica Greene var. randii (Fern.) B. Boivin (1972: 60). [= subsp. howellii]

Antennaria petasites Greene (1898: 277). Type:—CANADA. British Columbia: Drew’s Harbour, 14 May 1876, G.M. Dawson 11292 (lectotype [designated on specimen by Bayer (1987)] NDG!, isolecotype NY!). [= subsp. howellii]

Antennaria neodioica Greene var. grandis Fernald (1899a: 73). Type:—UNITED STATES. Maine: Town Hill Road, Somesville, Mount Desert Island, Hancock County, 01 July 1897, Rand s.n. (lectotype [designated by Bayer & Stebbins (1982: 309)] GH!); A. grandis (Fern.) House (1916: 60). [= subsp. neodioica]
Antennaria rupicola Fernald (1899a: 74). Type:—UNITED STATES. Maine: Matawamkeag River, Island Falls, Aroostook County, 09 June 1899, Fernald 2361 (syntypes GH!, US!, VT!, NY!, NEBC!); A. neodioica Greene var. rupicola (Fern.) Fernald (1914a: 132). [= subsp. neodioica]


Antennaria stenolepis Greene (1904a: 201). Type:—CANADA. British Columbia: Chilliwack Valley, 30 June 1901, J.M. Macoun 26187 (holotype NDG!, isotypes GH!, DAO!). [= subsp. neodioica]

Antennaria callilepis Greene (1904a: 201). Type:—CANADA. British Columbia: Chilliwack Valley, 08 August 1901, J.M. Macoun 26186 (holotype NDG!, isotypes NY!, GH!). [= subsp. neodioica]

Antennaria lanulosa Greene (1904b: 38). Type:—CANADA. British Columbia: Chilliwack Valley, 29 August 1901, J.M. Macoun 26194 (lectotype [designated by Bayer (1989a: 56)] NDG!, isolectotypes NY!, GH!). [= subsp. neodioica]

Antennaria eximia Greene (1906b: 71). Type:—CANADA. British Columbia: Skagit Valley, 12 July 1905, J.M. Macoun 69338 (holotype NDG!, isotypes NY!, US!). [= subsp. howellii]

Antennaria concolor Piper (1906: 604). Type:—UNITED STATES. Oregon: Mount Scott, Clackamas County, 06 June 1904, Piper 6189 (holotype US!, isotypes US!, F!, WTU!). [= subsp. neodioica]


Antennaria neodioica Greene var. chlorophylla Fernald (1921: 296). Type:—UNITED STATES. Maine: Orono, Penobscot County, 04 June 1898, Fernald 2364 (holotype GH!, isotype: NEBC!). [= subsp. neodioica]
*Antennaria appendiculata* Fernald (1921: 295). Type:—CANADA. Quebec: banks of the Grand River, Gaspé County, 01 July 1904, *Fernald s.n.* (syntypes GH!, MICH!). [= subsp. *howellii*]  


**Plants** gynoecious, apomictic, rhizomatous, stoloniferous, often mat-forming; stolons leafy, leaves usually slightly to moderately reduced relative to terminal rosette, 1-9 (12) cm. **Flowering stems** erect, lanate to moderately or densely floccose, not stalked-glandular, (6) 15-35 cm tall. **Basal leaves** oblanceolate to spatulate or obovate, apices broadly obtuse or rounded to mucronate, adaxial surface green and glabrous (sometimes with some sparse, loose floccose vestiture, especially when young) to moderately to densely short-pubescent with greyish hairs, abaxial surface densely grey-tomentose, 1- to 3-veined, 15-40 mm. **Cauline leaves** (6) 7-11, linear to narrowly lanceolate, apices acuminate, middle and upper leaves occasionally with small linear scarious tips, (8) 12-40 mm. **Capitulescences** capitate to subcorymbose, dense to moderately open, (15) 20-55 mm in diameter. **Pistillate capitulae** (3) 5-13; involucres campanulate, phyllaries not reflexed at anthesis, moderately to densely lanate basally, 6-9 (11) mm; outer phyllaries lanceolate, apices acute to obtuse, whitish to tan or pale greenish-brown, often with a reddish or pinkish central spot, (3) 4-6 mm; inner phyllaries similar to outer phyllaries but narrower, 4-7 mm; pistillate corollas (3.5) 4-6.5 (8) mm; pappus 5.5-8 (9) mm. **Cypselae** papillate, 0.8-1.7 (2) mm.

Flowering May-Jul. Mesic to dry forests, clearings, meadows, pastures, and disturbed areas in the lowland, steppe, montane, parkland, and (rarely) subalpine zones; 0-1500 (2000) m. Frequent in southwest BC [Georgia Depression east to Coast-Cascade Mts.]; frequent in south-central, southeast, and central BC [Coast-Cascade Mts. east to Alberta, north to the Skeena River and Williston Reservoir]; infrequent in northeast BC [Peace River lowlands and adjacent Rocky
Antennaria howellii is a widespread and variable apomictic polyploid complex of temperate North America, ranging widely from the Pacific coast east to the Canadian Maritimes and the northeastern United States. It is more closely associated with forested environments than most other Antennaria species in the Pacific Northwest, with the exception of the similarly forest-associated A. racemosa. Antennaria howellii is most likely to be confused in British Columbia with pistillate plants of two of its apparent progenitor diploids, the aforementioned A. racemosa and the very similar A. neglecta. The distribution of A. howellii overlaps extensively with A. racemosa in B.C. and, although typical individuals of the latter species are generally easily identifiable by their distinctly open and racemose capitulescences, younger plants in which the capitulescence is more compact may be misidentified as A. howellii. Even when young, however, A. racemosa is easily distinguished from A. howellii by the densely stalked-glandular stems and peduncles (these being eglandular in A. howellii). Separation from pistillate A. neglecta is more challenging, but, given the localized distribution of A. neglecta in the province (Peace River lowlands), it is not a widespread identification issue. Pistillate A. neglecta can usually be distinguished from A. howellii subsp. neodioica (with which it shares short pubescence on the adaxial leaf surfaces) by the reduced, often scale-like leaves of its stolons that contrast greatly in size with the enlarged terminal rosette. In comparison, the stolon leaves of A. howellii subsp. neodioica are only slightly reduced in size relative to the terminal rosette, and are never so greatly reduced as to appear scale-like. The basal leaves of A. neglecta can sometimes become essentially glabrous and green towards the end of the growing season, thus prompting confusion with the sympatric A. howellii subsp. howellii, but the stolon differences mentioned above remain relevant.
The parental diploid taxa of the *A. howellii* complex have been investigated extensively (Bayer 1985), with the eastern species *A. neglecta, A. plantaginifolia,* and *A. virginica,* as well as the western *A. racemosa,* identified as likely sexual contributors based on the morphology of offspring from experimental crosses among these taxa. The relative genetic contribution of these parental diploids, and the resulting morphological expression, varies across the range of the species, and has resulted in numerous named taxa and infrataxa in this complex throughout North America. This morphological variation can be translated into two subspecies based primarily on leaf pubescence, as in this treatment. These two subspecies are generally distinct and easily identified in British Columbia, but some individuals may be difficult to place due to intermediate characteristics (particularly adaxial leaf vestiture.) The morphological discrepancies are much less distinct in northeastern regions of North America, where a great deal of the morphological variation in the species resides, and renders the treatment of these entities as species-level taxa difficult. As a result, they are treated as subspecies here, with the recognition that they are relatively distinct within this particular portion of their distribution. The two subspecies may be distinguished as follows:

a. Adaxial leaf surfaces usually green and glabrous, or with a sparse, loose, floccose vestiture when young, rarely uniformly floccose when very young; stolons 1-4 (6) cm long; leaves 1-to 3-veined............................................................i. *A. howellii subsp. howellii*

aa. Adaxial leaf surfaces moderately to densely grey-pubescent, occasionally becoming glabrescent in age; stolons 3-9 (12) cm long; leaves mostly 1-veined.........................................................ii. *A. howellii subsp. neodioica*

i. *Antennaria howellii subsp. howellii* is the more widespread and common subspecies in British Columbia, and occurs throughout the range of the species in the province (Figure 8). Although usually easily identifiable by its distinctly green, glabrous or nearly so adaxial leaf surfaces, the presence of leaf pubescence in some populations may render distinction from subsp.
neodioica locally challenging. In particular, the leaves of many A. howellii subsp. howellii individuals are uniformly tomentose or floccose when very young and emerging, and, although this leaf vestiture is usually quickly lost, confusion with subsp. neodioica is particularly likely at this stage. Indeed, this leaf vestiture persists on the leaves of many mature individuals of subsp. howellii; however, unlike the uniform short pubescence of subsp. neodioica, this vestiture becomes sparse, loose, and cobwebby, and the green, glabrous adaxial leaf surface is easily visible beneath it (the leaves remain uniformly pubescent in subsp. neodioica, usually with an overall greyish aspect). A further point of confusion between these subspecies is the tendency for the adaxial leaf surfaces on the largest leaves of some subsp. neodioica to become essentially glabrous in age, and thus mature plants of this species may sometimes show glabrous adaxial leaf surfaces on some of the oldest, largest leaves. Such plants may be especially difficult to place into one or the other of the subspecies treated here, and identification may ultimately rely on the relative abundance of glabrous leaves (dominating the plant in subsp. howellii; few and only on the oldest leaves in subsp. neodioica).

Bayer (1985) identified A. racemosa and A. neglecta as the most dominant diploid parental contributors to subsp. howellii, at least in western portions of its range that correspond with subsp. howellii s.s.; the southwestern A. marginata Greene is also cited (Bayer 2006) as a potential contributor to some southern populations. Populations in northeastern North America that have recently been treated as A. howellii subsp. canadensis (e.g., Bayer 1985; Bayer 2006) are morphologically indistinguishable from many populations of subsp. howellii in western North America. These northeastern populations share the green, glabrous adaxial leaf surface that otherwise characterizes subsp. howellii, and the morphological distinctions that have been proposed to exist between them (number of leaf veins, leaf size, presence of leaf flags, and phyllary colour) are extremely variable in both regions, overlap considerably, and do not show the
biogeographic structuring that has been proposed based on the specimens examined. As a result, these two populations are treated as synonymous in this treatment. Interestingly, the glabrous adaxial leaf surface in this polyploid complex has been directly attributed to the parentage of *A. racemosa* (Bayer 1985; Bayer 2006), a species of western North America that does not have any know populations within the range of these northeastern populations (= “*canadensis*”). This may hint at a historically more extensive, transcontinental distribution of *A. racemosa* that has left traces in the apomictic polyploid agamospecies that originated during its occupation of the region, or a post-glacial migration eastward of subsp. *howellii* away from its region of origin.

ii. *Antennaria howellii* subsp. *neodioica* (Greene) Bayer is widespread throughout the southern half of British Columbia (Figure 8), but is considerably less frequent than subsp. *howellii* at most locations; see the account of subsp. *howellii* and the above key to subspecies for more information on distinguishing these two taxa. The two subspecies often occur in the same areas, even growing together at some sites, but, given apomictic reproduction (and the absence of males), maintain their morphological distinctions in sympatry. The concept of subsp. *neodioica* adopted in this treatment also includes plants that have commonly been treated as *A. howellii* subsp. *petaloidea* or *A. neodioica* subsp. *petaloidea*, and which have been cited as occurring in British Columbia (e.g., Bayer 2006). Plants attributable to *petaloidea* are described as differing from subsp. *neodioica* in their less distinctly spatulate and less distinctly petiolate leaves, as well as their slightly longer stolons (Bayer 2006). There is extensive overlap in these characters based on published identification keys, however, as well as extensive geographic overlap between the taxa. As the majority of individuals are left unassignable based on current published literature, the two taxa are merged here in recognition of their poorly defined morphological and taxonomic boundaries.
6. *Antennaria lanata* (Hook.) Greene

**WOOLLY PUSSYTOES;** Woolly Everlasting; Greyish Everlasting

*A. carpatica* (Wahlenb.) Bluff & Fingerhuth β *lanata* Hooker (1834a: 329).

Type:—UNITED STATES. “Summits of the most elevated among the Rocky Mountains, lat 52°”, no collection date reported, *Drummond s.n.* (holotype K!); *A. lanata* (Hook.) Greene (1898: 288).

**Plants** dioecious, sexual, short-rhizomatous or from a branched woody stem base, lacking stolons, not mat-forming. **Flowering stems** erect, densely grey-tomentose to floccose, not stalked-glandular, (1) 3-20 (30) cm tall. **Basal leaves** erect to ascending, narrowly oblanceolate to oblanceolate, apices acute, densely grey-tomentose on both surfaces, not stalked-glandular, 3-veined, 10-60 (100) mm. **Cauline leaves** 6-8, narrowly lanceolate, slightly reduced upwards, apices acute to acuminate, middle and upper leaves with strap-shaped scarious tips, not stalked-glandular, 5-40 mm. **Capitulescences** capitate to subcorymbose or corymbose, dense to slightly open, peduncles of lower heads/clusters to 15 mm, 15-35 mm in diameter. **Pistillate capitulae** 6-
12; involucre campanulate, phyllaries sometimes reflexed at anthesis, moderately to densely lanate basally, 5-8 mm; outer phyllaries broadly lanceolate to ovate, apices obtuse to acute, dark brownish or olive-brown to blackish-brown (sometimes paler towards the apices), often with a blackish central spot, 3-4.5 mm; inner phyllaries lanceolate, apices obtuse to acute, brownish to olive-brown, usually paler or whitish distally, 4-6 mm; pistillate corollas 2.5-4 mm; pappus 3.5-5 mm. **Staminate capitulae** 6-12; involucre broadly campanulate, phyllaries usually reflexed at anthesis, moderately to densely lanate basally, 4.5-6 mm; phyllaries oblanceolate to oblong or narrowly obovate, apices rounded, brownish to dark olive-brown proximally, pale brownish to whitish distally, 4-5.5 mm; staminate corollas 3-4.5 mm; pappus 4-5 mm. **Cypselae** smooth, 1-1.6 mm.

Flowering Jun-Aug. Moist to mesic meadows, heath, snowbed sites, forest openings, ridges, and tundra in the upper montane, subalpine, and alpine zones; 1500-2500 m. Common in south-central [Cascade Mts. and associated eastern ranges] and southeast BC [Columbia Mts. and Rocky Mts., north to Wells Gray and Mount Robson Provincial Parks]; locally common in southwest BC [western slopes of Cascade Mts.]. BC east to AB, south to CA, UT, WY. $2n = 28$ [2x] (Appendix 3).

**Antennaria lanata** is a common and characteristic species of moderate to high elevations across southern British Columbia from the Cascade Mts. east to the Rocky Mts. (Figure 9), being a frequent, and often abundant, member of many subalpine and alpine meadow communities in this region. Among North American species, it is most closely related to *A. anaphaloides* and *A. pulcherrima*, and together these three species comprise the Pulcherrimae clade of Bayer 1990a and Bayer 2006. Occasional taxonomic treatments (e.g., Urbanska 1983) have treated these three taxa (along with the Eurasian *A. carpatica*) as representatives of a single circumboreal species (*A. carpatica s.l.*), but these entities are now widely recognized as representing distinct species-level
taxa. *Antennaria lanata* is distinctive relative to most other members of the genus in B.C., both in morphology and ecology, although some plants may approach small individuals of *A. anaphaloides* in appearance. See *A. anaphaloides* for notes on potential hybridization with that species in British Columbia.

![Distribution map of Antennaria lanata](image)

**FIGURE 9.** Distribution of British Columbia specimens of *Antennaria lanata* that were reviewed for this study (left), and approximate distribution of the species in northwestern North America (right).

7. *Antennaria luzuloides* Torr. & A. Gray subsp. *luzuloides*

**WOOD-RUSH PUSSYTOES;** Rush Pussytoes; Silvery-brown Pussytoes; Silvery Everlasting; Wood-rush Everlasting

*Antennaria luzuloides* Torrey & A. Gray (1843: 430). Type:—UNITED STATES. “N.W. coast” (= Oregon or Rocky Mts.), no collection date reported, *Drummond or Douglas (uncertain)* s.n. (holotype GH!).

**Plants** dioecious, sexual, from a branched woody stem base, lacking stolons, not mat-forming. **Flowering stems** ascending to erect, sparsely to moderately tomentose to floccose, not stalked-glandular, 7-35 (70) cm tall. **Basal leaves** erect to ascending, linear to oblanceolate or narrowly spatulate, apices acuminate, grey-tomentose on both surfaces, 1- to 3-veined, (18) 30-55 mm. **Cauline leaves** 7-15, linear to narrowly oblanceolate, reduced upwards, apices long-acuminate, lacking scarious tips, not stalked-glandular, 5-60 mm. **Capitulescences** capitate to corymbose, dense to moderately open or open, peduncles of lower heads/clusters to 60 mm, 20-45 mm in diameter. **Pistillate capitulae** 10-110; involucres narrowly campanulate, phyllaries not reflexed at anthesis, glabrous, 3.5-5 (6.5) mm; outer phyllaries oblong to broadly oblanceolate, apices obtuse to rounded, usually shrivelling into concentric wrinkles, pale brownish-green, often paler or whitish distally, 1-2 mm; inner phyllaries lance-oblong to oblanceolate, apices mostly obtuse, pale greenish-brown, paler or whitish to translucent distally, 2-3 mm; pistillate corollas 2.5-4 mm; pappus 3-4 mm. **Staminate capitulae** similar to pistillate heads but broader, inner phyllaries broader and whiter distally; staminate corollas 3-4 mm; pappus 3-4.5 mm. **Cypselae** sparsely papillate or strigose, 1-2 mm.

Flowering May-Jul. Dry grasslands, shrub steppe, meadows, gravelly slopes, and open forests in the steppe and montane zones; 500-1500 (1900) m. Infrequent in south-central and southeast BC [Boundary region and southern Columbia Mts., disjunct north to Kamloops area (Tod Mtn.).] BC east to AB, south to CA, NV, UT, CO, disjunct to SD. **2n = 28** (2x) (Appendix 3).

*Antennaria luzuloides* subsp. *luzuloides* is a diploid, sexual, grassland- and dry forest-associated species that is highly distinctive among members of the genus in British Columbia. It is generally easily identifiable in the region by its narrow leaves, small and numerous flowering heads, pale greenish-brown involucres, glabrous phyllaries with concentric wrinkles, and its
typically broad, open, corymbose capitulescences. It is primarily restricted in B.C. to the dry climates of the south-central interior, being most abundant along the United States border in the Boundary region east of the Okanagan Valley (e.g., Grand Forks, Midway, Christina Lake) (Figure 10). It has also been collected from the Kamloops area (Tod Mountain); as there are no known collections from the intervening areas (despite considerable collecting effort), the Tod Mountain population is considered to be disjunct from the remainder of the species’ range.

The name *A. oblanceolata* Rydb. (= *A. luzuloides* var. *oblanceolata*) has been applied to collections with unusually broad, narrowly oblong or narrowly elliptic leaves; however, these collections appear to represent part of the normal range of morphological variation in the species and are therefore not afforded taxonomic recognition in this treatment. Most collections from British Columbia are consistent with the typical, narrower-leaved morphology of the species, and the “oblanceolata” morphology appears to be considerably less frequent.

**FIGURE 10.** Distribution of British Columbia specimens of *Antennaria luzuloides* subsp. *luzuloides* that were reviewed for this study (left), and approximate distribution of the species in northwestern North America (right).
8. Antennaria media Greene

ROCKY MOUNTAIN PUSSYTOES; Dark Pussytoes; Alpine Pussytoes; Sierra Pussytoes


Antennaria media Greene subsp. ciliata E.E. Nelson (1901: 700). Type:—UNITED STATES. California: White Mountains, Mono County, 22 July 1886, Shockley 444 (holotype US!).


Antennaria austromontana E.E. Nelson (1901: 703). Type:—UNITED STATES. Utah: Marysvale, Piute County, 28 August 1894, M.E. Jones 5922 (holotype US!, isotypes NY!, RSA!).


Antennaria acuta Rydberg (1910b: 323). Type:—CANADA. Alberta: marsh near Lake O’Hara, 08 August 1904, J.M. Macoun 65423 (holotype NY!; isotype US!).


Antennaria candida Greene (1911: 151). Type:—UNITED STATES. Washington: Mt. Rainier, Pierce Co., 14 August 1895, O.D. Allen 141 (holotype US!, isotypes RM!, GH!, CAS!).


Antennaria atriceps Fernald ex Raup (1934: 207). Type:—CANADA. British Columbia: Mount Selwyn, 26 July 1932, Raup & Abbe 4134 (holotype GH!, isotypes S!, MIN!, NY!, F!, G!).

Antennaria stolonifera A.E. Porsild (1950: 16). Type:—CANADA. Yukon: MacMillan River, Canol Road, 28 August 1944, A.E. Porsild & Breitung 11377 (holotype CAN, isotypes NY!, S!, WTU!).

Plants gynoecious, apomictic (sexual outside of B.C.), rhizomatous, stoloniferous, often mat-forming; stolons leafy, 0.5-6 cm. Flowering stems erect, densely lanate, not stalked-glandular, 2-10 (12) cm tall. Basal leaves oblong-lanceolate to spatulate, apices broadly acute to obtuse or rounded, usually densely grey-pubescent on both surfaces (sometimes becoming glabrescent and greenish with age), 1-veined, (4) 5-15 (20) mm. Cauline leaves 3-8, linear-lanceolate to lanceolate or narrowly oblanceolate, apices obtuse to acute or acuminate, middle and upper leaves often with
linear or acuminate to strap-shaped scarious tips, not stalked-glandular, (6) 8-22 mm. **Capitulecences** capitate to slightly subcorymbose, usually dense, lower peduncles rarely to 10 mm, 7-25 mm in diameter. **Pistillate capitulae** 3-8; involucres campanulate, phyllaries usually not reflexed at anthesis, moderately to densely lanate basally, (3.5) 4-6 (7) mm; outer phyllaries broadly lanceolate or oblanceolate to ovate, apices rounded or obtuse to acute or acuminate, blackish-green to dark olive-brown, usually with a slightly darker blackish or dark brown central spot, (2) 2.5-5 mm; inner phyllaries lanceolate to oblanceolate, apices obtuse to acute or acuminate, greenish-black to blackish-olive or olive-brown (rarely paler and dingy-white), usually with a blackish or dark brown central spot, 3-6.5 mm; pistillate corollas (1.5) 2-5 mm; pappus (2.5) 4-5 mm. **Cypselae** smooth to basally papillate, 0.7-1.3 mm.

Flowering (Jun) Jul-Aug. Mesic to dry meadows, talus slopes, scree, rocky ridges, fellfields, streambanks, gravelly areas, and tundra in the upper montane, subalpine, and alpine zones; (850) 1300-2500 (2700) m. Frequent throughout BC, from the Coast-Cascade Mts. east to the Rocky Mts., except infrequent in south-central and central BC and rare in the northern Rocky Mts. of northeast BC; locally frequent on Vancouver Island [southwest BC]. AK east to NWT, south to CA, NV, UT, CO. \(2n = 28, 56, 70, 76, 84, 98, 112 [2x-8x]\) (Appendix E).

**Antennaria media** is a widespread and common member of the genus throughout most of British Columbia, although it is scarce in the northern Rocky Mountains and is absent from Haida Gwaii and the lowlands east of the Rocky Mountains in northern B.C. (Figure 12). It is primarily a species of alpine, subalpine, and upper montane elevations throughout its range, and as such is local throughout much of the south-central and central interior of the province where suitable high elevation habitats are scarce. Among **Antennaria** species in northwestern North America, **A. media** is relatively distinctive due to its usually dark-coloured (blackish-green to dark olive-brown)
phyllaries, although it may be confused with multicephalous individuals of the similarly dark-phyllaried *A. monocephala* subsp. *angustata* in northern regions of the province. These two taxa can nonetheless normally be distinguished, however, by the fewer capitula of *A. monocephala* subsp. *angustata* (1-3, vs. 3-8 in *A. media*) and the typically reduced size of the lateral capitula in that taxon when they are present.

*Antennaria media* in British Columbia is an agamic complex that appears to be an autopolyploid derivative of sexually-reproducing, diploid populations from the mountains of California and Oregon (Bayer 2006). These sexual populations have been recognized taxonomically as *A. pulchella* or *A. media* subsp. *pulchella* by some authors in the past (e.g., Bayer 1990c; Chmielewski 1997; Bayer 2006); however, the morphological distinctions between the proposed sexual progenitor (*pulchella*) and its presumed autopolyploid derivative (*media*) are minimal and consistent with enlarged floral organs (involucre, pistillate corollas, pappus) resulting from the polyploid ‘gigas effect’ (Stebbins 1971), which is not traditionally reflected taxonomically. As a result, the sexual populations that have been referred to as *pulchella* are here treated as conspecific with the widespread apomictic populations that have been treated as *A. media*. Such an approach has commonly been taken with other *Antennaria* species in which localized sexual populations are not known to differ morphologically in a consistent or taxonomically significant way from their more widespread apomictic, autopolyploid derivatives. Examples of such an approach include current treatments of *A. parlinii* and *A. parvifolia* in Bayer (2006), as well as the taxonomic approach to *A. pulvinata* of Chmielewski (1993), which is followed in this treatment.

*Antennaria media*, as treated here, includes much of what has formerly been considered *A. alpina* in B.C., with the remaining *alpina* being dispersed among what are here treated as *A. borealis* and *A. pulvinata*. There is a long history of confusion around the names *alpina* and *media*
in North America, and populations in northwestern North America have been treated as either entirely *A. alpina* (Hitchcock et al. 1955, Moss 1959, Welsh 1974, Packer 1983), entirely *A. alpina* var. *media* (Davis 1952, Hitchcock & Cronquist 1973, Taylor & MacBryde 1977, Douglas et al. 1989, Douglas 1995), entirely *A. media* (Abrams & Ferris 1960, Hultén 1968, Scoggan 1979, Qian & Klinka 1998), or as a mixture of *A. alpina* and *A. media* (Cody 1996, Douglas et al. 1998, Bayer 2006). Furthermore, many older floristic references (e.g., Henry 1915) or those from arctic regions of the continent (e.g., Porsild 1950, Anderson 1959, Porsild & Cody 1980), treat members of this complex under one or more of the many currently-recognized synonyms, further complicating the taxonomy of the group. For resources that treat *alpina* and *media* as separate taxa in northwestern North America, only the presence (*alpina*) or absence (*media*) of naked, scarious flags at the tips of the middle and upper cauline leaves is cited as a definitive characteristic in distinguishing them (Douglas et al. 1998, Bayer 2006); all other potential characters are considered too variable to be taxonomically informative. However, the presence or absence of scarious flags on the leaves appears to be no less variable in this complex than other characters such as phyllary shape and colour, leaf shape, stolon length, and overall habit, and as a result is considered equally inappropriate for use in the taxonomy of the complex. For example, there is a continuum in the size, shape (strap-shaped, acuminate, linear, absent), and distribution (upper leaves only, both middle and upper leaves) of these flags among collections from the province, with the variation showing neither biogeographic/ecological structuring nor correlation with any other morphological characters. Interestingly, even many type specimens of *A. media* have prominently flagged cauline leaves, including the lectotype (*Sonne s.n. [US]*) and isolectotypes (NY, RM) as well as at least one of the paratypes (*J.M. Macoun 11242 [NY]*) and in other paratypes (*Howell s.n. [NDG], J.M. Macoun 11243 [NDG]*) these flags are absent or nearly so (Figure 11). The occurrence of leaf flags on many of the type specimens of *A. media* directly contradicts all current
concepts of the species that are in widespread use. The erroneous assumption that *A. media* consistently lacks leaf flags appears to have been largely responsible for the considerable confusion regarding the presence of *A. alpina* in northwestern North America.

**FIGURE 11.** Examples of scarious leaf flags on isolecotype (A) and paratype (B) of *A. media*. A = Sonne s.n. (NY); B = J.M. Macoun 11242 (NY).

Variation within this polyploid agamic complex is extensive and difficult to characterize, although some attempts have been made to represent the variation through the recognition of infraspecific taxa. Chmielewski (1997), using a detailed phenetic analysis, proposed that this variation could be represented through the recognition of five subspecies across the range of the species. One of these subspecies, subsp. *compacta*, occurs in the western North American arctic and is considerably more morphologically distinct than other forms; it is perhaps better recognized as either a distinct agamospecies or as part of the northern *A. friesiana* polyploid complex (based on morphological and biogeographic considerations). It is excluded from the species concept of *A. media* presented in this treatment, although all known populations occur outside of British Columbia. Of the remaining four subspecies proposed by Chmielewski (1997), one (*ciliata*) was treated as being restricted to the western United States, while the remaining three (*media, pulchella, fusca*) were mapped as occurring northward into British Columbia. The morphological
characters used to distinguish among these subspecies included the length of the corollas, length of the pappus, shape of the leaves, length of the stolons, overall plant height, length of the cauline leaves, vestiture type, and tendency for mat-forming habit. Furthermore, Chmielewski (1998) treated the (as-then-recognized) *A. alpina* complex in a similar fashion, resulting in the recognition of three North American subspecies (*alpina, porsildii, canescens*), two of which (*alpina, canescens*) were mapped as occurring in British Columbia and would be encompassed within the concept of *A. media* in this treatment. During the review of British Columbia specimens of these complexes for this treatment, few were found to correspond convincingly with any of the proposed subspecies of either *alpina* or *media*, and the proposed diagnostic characters did not co-vary in the fashion suggested by these infraspecific taxonomies. The application of the infraspecific characters of Chmielewski (1997) was found to be particularly challenging with the inclusion of the subspecies of *A. alpina* of Chmielewski (1998) into the concept of *A. media* here (see Excluded Species, below, for a justification of this transfer), although, even without the inclusion of these, the existing morphological variation within the *A. media* aggregate precluded infraspecific designation for most specimens. For example, leaf shape and vestiture were found to vary widely between the extremes that were cited by Chmielewski (1997) as being definitive for the subspecies *media* (leaves spatulate-obovate and remaining densely woolly-hairy in age) and *fusca* (leaves cuneate and becoming glabrous above with age). Many specimens presented alternative correlations between these characters (i.e., cuneate leaves combined with densely woolly adaxial leaf surfaces, or vice versa) or were otherwise intermediate with regards to the supposedly diagnostic characters, suggesting that these characters were poorly correlated and expressed as continua rather than as discrete character states. This multi-dimensional, continuous character variation and poor correlation between supposedly diagnostic characters renders infraspecific
determination futile in most cases. The species *Antennaria media* is thus treated here as monotypic and variable, in a fashion that is similar to the treatment of other agamic complexes in the genus.

Although known only as an apomict within the British Columbia portion of its distribution, there is some evidence that hybridization may occur between this taxon (as the pistillate parent) and other sexual members of the genus in the region. For example, the type specimen of *Antennaria x macounii* Greene (*J.M. Macoun 11241 [phototype S!]*) is seemingly intermediate morphologically between *A. media* and *A. umbrinella*, which are generally recognized as the potential parental taxa of this specimen (Bayer & Stebbins 1993). The morphology of this specimen, which itself is of rather poor condition, does indeed suggest intermediacy between these two species, although it was collected from an area that is outside of the known distribution of one of the proposed parents (*A. umbrinella*). Nonetheless, the specimen is here considered to represent the hybrid *A. media x umbrinella* given the convincingly intermediate morphology, as well as to maintain consistency with current taxonomic approaches. The regional absence of *A. umbrinella* is perhaps explained as either an artifact of inadequate collecting effort or an indication of the historical presence of *umbrinella* in an area where it no longer occurs.

**SMALL-LEAVED PUSSYTOES;** Littleleaf Pussytoes; White Pussytoes; Rocky Mountain Pussytoes; Small-leaved Everlasting.


*Antennaria foliacea* Greene (1898: 279). Type:—UNITED STATES. Montana: Little Belt Mountains, 18 August 1896, *Flodman 867* (holotype US!, isotypes NY!, MIN!).


Plants dioecious, sexual, rhizomatous, stoloniferous, mat-forming; stolons leafy, 1-5 (6) cm. Flowering stems erect, sparsely to densely tomentose to floccose, sparsely to moderately stalked-glandular (especially distally), 8-30 cm tall. Basal leaves spatulate to broadly oblanceolate, apices mucronate, densely grey-pubescent on both surfaces, 1-veined, 6-16 mm. Cauline leaves 10-19, linear to linear-lanceolate, apices acute, lacking scarious tips, usually sparsely to moderately stalked-glandular (especially middle and upper leaves), 5-25 mm. Capitulescences usually subcorymbose, dense to slightly open (rarely open), lower peduncles to 10 (20) mm, 15-30 (35) mm in diameter. Pistillate heads 6-13; involucres campanulate, phyllaries usually not reflexed at anthesis, moderately to densely lanate basally, 5.5-7 mm; outer phyllaries oblong to broadly oblanceolate, apices rounded to obtuse, whitish to creamy-white (rarely faintly tinged with pink), 2-3.5 (4) mm; inner phyllaries narrowly oblanceolate, apices obtuse, whitish to creamy-white, 3-4 mm; pistillate corollas 3-4.5 mm; pappus 3-5 mm. Staminate heads 6-13; involucre broadly campanulate, phyllaries usually reflexed at anthesis, 5-6.5 mm; phyllaries broadly oblanceolate to spatulate, apices rounded to nearly truncate, whitish to creamy-white, 3.5-5 mm; staminate corollas 2.5-3 mm; pappus 3-4 mm. Cypselae smooth to sparsely papillate, 0.6-1.2 mm.

Flowering May-Aug. Mesic to dry meadows, grasslands, grassy slopes, alluvial areas, alkaline depressions, open forests, and gravelly disturbed areas in the steppe and montane zones; 450-1200 (1350) m. Locally frequent in southeast BC [southern Rocky Mtn. Trench, Rocky Mountains] and infrequent in south-central BC [north to the Chilcotin region]; rare and disjunct
north to central BC [Bulkley Valley]. AK east to QC, south to CA, AZ, NM. $2n = 28, 42, 56$ [2x, 3x, 4x] (Appendix E).

_Antennaria microphylla_ is a species of open, low to moderate elevations across the southern interior of British Columbia (Figure 13), especially in grassland or parkland ecosystems. It commonly occurs in association with alkaline soils, and northern populations, for which the name _A. nitida_ has been applied, are also known for being associated with areas of calcareous influence (Porsild 1950). It is a primarily diploid, sexual member of the taxonomically complex ‘Catipes’ group, and is listed as a major sexual progenitor of the _Antennaria rosea_ polyploid complex (Bayer 1989c, Bayer 2006). Although staminate plants are frequent throughout much of the range of the species, the scarcity, or even lack, of staminate plants from northernmost parts of its range (Porsild 1950) suggests that these populations are likely apomictic. Staminate plants are frequent in provincial collections, however, and thus most B.C. specimens appear to be representative of sexually-reproducing populations.

The status of _A. microphylla_ in British Columbia has been poorly defined in many past treatments due to the synonymization with apomictic allopolyploids that are here treated as _A. rosea_ (e.g., Hitchcock _et al._ 1955, Hitchcock & Cronquist 1973, Douglas 1995). Although the relationship between these taxa is now much better established, many collections (and the floristic efforts to which they contributed) remain affected by these past confusions. _Antennaria microphylla_ is indeed similar to pale-phyllaried forms of _A. rosea_, but can usually be distinguished by the presence _microphylla_ or absence _rosea_ of stalked glands throughout the middle and upper stem, cauline leaves, and capitulescence bracts. This distinction is not absolute, however, and is neither as definitive nor as obvious as is often stated in the floristic literature. Specifically, some northern forms of _A. rosea_ (especially those consistent with the _alborosea_ form) are similarly glandular throughout the upper portions of the plant, although the pink phyllaries of this form
should minimize or eliminate confusion with the white-phyllaried *A. microphylla*. Furthermore, the glands of *A. microphylla* are often difficult to detect, even with the assistance of high magnification, as they may be very sparse or otherwise obscured by the vestiture of the stem and leaves. The glands are thus best detected by observing areas of the leaves and bracts where the vestiture is sparse enough to permit observation of the underlying green leaf tissue, especially within the capitulescence where the glands tend to be most dense.

*Antennaria microphylla* has been proposed to hybridize with *A. racemosa* to form the hybrid *A. x foliacea* (Bayer 1987a), based on specimens from western Montana. Review of these specimens, however, suggests that they may conversely represent an aberrant *A. microphylla* with unusually ample cauline leaves, or perhaps even a member of the *A. howellii* subsp. *neodioica* aggregate. As a result, the interpretation of these specimens as *microphylla x racemosa* hybrids is not maintained in this treatment, and they are instead treated as aberrant *A. microphylla*.

![FIGURE 13. Distribution of British Columbia specimens of *Antennaria microphylla* that were reviewed for this study (left), and approximate distribution of the species in northwestern North America (right).](image)
10. *Antennaria monocephala* DC.

**ONE-HEADED PUSSYTOES; Pygmy Pussytoes**


*Antennaria pygmaea* Fernald (1914a: 129). Type:—CANADA. Newfoundland (Labrador): Labrador (without specific locality), 1870, *Unitas Fratrum s.n.* (holotype GH!). [= *subsp. angustata*]


*Antennaria tweedsmuirii* Polunin (1940: 356). Type:—CANADA. Quebec: Cape Smith, 03 August 1936, *Polunin 1374* (holotype CAN, isotype GH!). [= *subsp. angustata*]

*Antennaria tansleyi* Polunin (1940: 357). Type:—CANADA. Quebec: (Cape) Wolstenholme, Hudson Strait, 01 August 1936, *Polunin 1272* (holotype BM). [= *subsp. angustata*]

*Antennaria fernaldiana* Polunin (1947: 100). Type:—CANADA. Nunavut: inland of Coral Harbour, Southampton Island, 20 August 1946; *Polunin 17728* (holotype not located). [= *subsp. angustata*]


**Plants** dioecious or gynoecious, sexual or apomictic, rhizomatous, usually not mat-forming; stolons leafy, 2-4.5 cm. **Flowering stems** erect, glabrous-strigose or sparsely to moderately tomentose or floccose, usually stalked-glandular, often purplish, (2) 5-13 (19) cm tall. **Basal leaves** oblanceolate to narrowly spatulate, apices mucronate, glabrous or glabrescent to grey-pubescent adaxially, tomentose abaxially, 1-veined, (5) 9-18 (20) mm. **Cauline leaves** 3-11, linear, apices with prominent strap-shaped scarious tips, 4-11 mm. **Capitulescences** of solitary terminal flowering heads (rarely with 1-2 much reduced lateral heads subtending primary head). **Pistillate capitulae** 1 (-3); involucres turbinate, phyllaries not reflexed at anthesis, sparsely to moderately lanate basally, 5-8 mm; outer phyllaries narrowly to broadly lanceolate or oblanceolate, apices acute, brownish to olive-brown, often with a blackish or dark brown central spot, 4-6 mm; inner
phyllaries similar to outer phyllaries but narrower, 5-6 mm; pistillate corollas 3.5-4 mm; pappus 4-5 mm. **Staminate capitulae** 1; involucres campanulate to short-turbinate, phyllaries sometimes reflexed at anthesis, 4-5 mm; phyllaries narrowly to broadly oblanceolate, apices obtuse to rounded, whitish or creamy white to brownish or blackish-olive, 3.5-4.5 mm; staminate corollas 2.5-3.5 mm; pappus 3-4 mm. **Cypselae** usually smooth, 1-1.3 mm.

Flowering (May) Jun-Aug. Moist to mesic meadows, snowbed sites, rocky ridges, scree, open slopes, heath, streambanks, and alpine tundra in the subalpine and alpine zones; (600) 1100-2100 (2350) m. Common in northern BC, except absent from low elevations east of the Rocky Mountains; locally frequent south along the Coast Mts. and Rocky Mts. to west-central [Itcha-Ilgachuz Ranges] and east-central [Cariboo Mts.] BC; rare in southeast BC [southern Rocky Mts.]. AK east to NL, south to WY, disjunct to WA; Greenland; ne Asia. **2n** = 28, 56, 72 [2x, 4x, 5x] (Appendix E).

*Antennaria monocephala* is among the more distinctive species of *Antennaria* in B.C. by virtue of its (usually) solitary flowering heads, distinctly northerly distribution, and restriction to alpine and subalpine habitats. It is one of the most common *Antennaria* species in northern parts of the province, extending its distribution southward along the Coast Mountains to central B.C. and along the Rocky Mountains to southeastern B.C. (Figure 14). Contrary to its name, occasional specimens occur in which there are one or two small lateral heads subtending the primary flowering head, and these can cause confusion with other dark-phyllaried northern species such as *A. media* and, especially, the extralimital *A. friesiana* (Trautv.) Ekman of arctic and subarctic regions. Such individuals should nonetheless be identifiable as *A. monocephala*, however, as the terminal flowering head is generally clearly larger and better developed than the subtending heads.
This species is generally treated in recent floristic and taxonomic literature (e.g., Bayer 2006) as comprising two subspecies: the sexual diploid subsp. *monocephala* and the apomictic autopolyploid subsp. *angustata*. Some authors (e.g., Porsild 1950, Hulten 1968, Porsild & Cody 1980) have recognized a number of taxa at either the specific or subspecific level that are now treated as synonymous with *A. monocephala s.l.*, of which *philonipha*, *megacephala*, and *pygmaea* have been reported for British Columbia and adjacent regions. Chmielewski & Chinnappa (1991) demonstrated that most of the variation used to discriminate these taxa was neither discrete nor definitive, and recommended the recognition of only a single diploid, sexual subspecies (subsp. *monocephala*) and its apparently autopolyploid derivative (subsp. *angustata*). Although a general taxonomic approach of treating sexual diploids and their autopolyploid derivatives as synonymous has been followed elsewhere in this treatment (see *A. media*, *A. microphylla*, *A. parvifolia*, *A. pulvinata*), the two subspecies of *A. monocephala* are recognized as distinct here in recognition of the consistent, and usually readily identifiable, morphological distinctions between them that correspond directly with ploidy and breeding biology.

A number of past authors, including Douglas *et al.* (1998), Bayer & Stebbins (1993), and Bayer (2006), have suggested that the sexual diploids (= subsp. *monocephala*) and apomictic polyploids (= subsp. *angustata*) are indistinguishable except by the presence (subsp. *monocephala*) or absence (subsp. *angustata*) of staminate plants in the populations. Chmielewski & Chinnappa (1991), however, demonstrated that the two ploidy levels are clearly separable morphologically based primarily on aspects of the vestiture of the leaves and stems, and that these were taxonomically stable characteristics that were not subject to environmentally-induced variation. Examination of specimens of *A. monocephala* collected from British Columbia strongly supports this conclusion, and the two subspecies can be recognized as follows:

**a.** Adaxial leaf surfaces moderately to densely grey-pubescent; stems usually greenish,
moderately to densely floccose-tomentose; staminate plants absent

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\textit{i. A. monocephala subsp. angustata}

\textbf{aa.} Adaxial leaf surfaces glabrous or glabrate, green; stems greenish to purplish, glabrous-strigose or sparsely to moderately tomentose, not floccose; pistillate and staminate plants more or less in equal frequencies in populations........\textit{ii. A. monocephala subsp. monocephala}

\textbf{i. } \textit{Antennaria monocephala subsp. monocephala} \((2n = 28 \ [2x])\) is a sexual taxon with a distribution that is largely centred on the Beringian region of northwestern North America (Chmielewski and Chinnappa 1991), ranging into adjacent areas, including northern British Columbia. It is the more common subspecies in British Columbia and occurs throughout most of the range of the species in the province, although it appears to be absent from the southernmost extent (Figure 14). It is immediately identifiable when the presence of staminate plants in the population can be confirmed, but identification of pistillate plants in the absence of staminate plants is nonetheless relatively straightforward based on the stem and leaf characters noted in the above key. Additionally, this subspecies tends to be somewhat shorter and stockier than subsp. \textit{angustata}, and is more frequent in wetter habitats (streambanks, moist tundra), but there is considerable overlap between the subspecies in both habit and habitat.

Several sexual, monocephalous \textit{Antennaria} taxa have been formally recognized in the past, but appear better placed within a more broadly circumscribed subsp. \textit{monocephala} given the morphological continuities among the forms. Two such taxa have been reported for British Columbia, \textit{A. philonipha} and \textit{A. megacephala}, with the latter having been described based on material collected from the northern Rocky Mountains of the province. The name \textit{philonipha} has been attributed to unusually tall, slender plants with long stolons, thinner pubescence, and large flowering heads, and which are generally associated with moist grassy habitats; this form is represented in the UBC herbarium by a single collection from the extreme northwestern parts of the British Columbia (Haines Triangle). The name \textit{megacephala} has been attributed to populations
of large-headed plants with unusually well-developed scarious tips on the cauline leaves, relatively broad and dark phyllaries, and a greater propensity for polycephaly. Both of these forms appear to fall within the range of variation of typical subsp. *monocephala* and are thus not treated formally here, although further work with *philonipha* in particular may lead to its eventual taxonomic recognition given its rather pronounced morphological and ecological distinctions.

**ii. Antennaria monocephala** subsp. *angustata* (*2n = 56, 70 [4x-5x]*) is hypothesized to be the apomictic, autopolyploid derivative of subsp. *monocephala* (Bayer 2006), and is widespread across arctic and subarctic regions of North America. It is considerably more widespread than subsp. *monocephala* in North America, ranging east across the central and eastern Canadian arctic and south into the U.S. Rocky Mountains where subsp. *monocephala* is absent. It is less frequent in British Columbia than subsp. *monocephala*, however, being distributed primarily along the Boundary and Coast Ranges of northwestern and west-central B.C., as well as along the northern and central Rocky Mountains and associated ranges (Figure 14). The treatment of subsp. *monocephala* (above) discusses the characters that distinguish the two infraspecific taxa. It should also be noted that populations of subsp. *angustata* tend to occur on drier, rockier substrates than those that harbour populations of subsp. *monocephala*. The name *pygmaea* has been applied to populations of subsp. *angustata* with somewhat broader, paler inner phyllaries, but there appears to be little justification in formally recognizing such plants given the lack of morphological discontinuities within the subspecies.
11. *Antennaria neglecta* Greene

**FIELD PUSSYTOES; Prairie Pussytoes**

*A. neglecta* Greene (1897: 173). Type:—UNITED STATES. District of Columbia: Catholic University grounds, 03 May 1897, *Greene s.n.* (lectotype [designated by Bayer & Stebbins (1982: 308)] NDG!).


**Antennaria wilsonii** Greene (1911c: 78). Type:—UNITED STATES. Indiana: near Cold Creek, Hamilton County, 18 Apr 1892, *G.W. Wilson s.n.* (lectotype [designated by Bayer & Stebbins (1982: 308)] US, isolectotype NDG!).

**Antennaria erosa** Greene (1911c: 78). Type:—UNITED STATES. Illinois: Odin, Marion County, 08 May 1909, *Greene s.n.* (lectotype [designated by Bayer & Stebbins (1982: 308)] NDG!, isolectotypes NDG!).

**Antennaria longifolia** Greene (1911c: 79). Type:—UNITED STATES. Missouri: Grain Valley, Jackson County, 07 May 1899, *B.F. Bush 6* (lectotype [designated by Bayer & Stebbins (1982: 308)] US!, isolectotype NDG!).

**Antennaria parvula** Greene (1911c: 81). Type:—UNITED STATES. South Dakota: near Fort Meade, Black Hills, Meade County, 1887, *Forwood s.n.* (lectotype [designated by Bayer & Stebbins (1982: 309)] US!).


**Plants** dioecious, sexual, rhizomatous, stoloniferous, sometimes mat-forming; stolons not leafy, leaves usually greatly reduced (often scale-like) relative to terminal rosette, 2.5-18 cm. **Flowering stems** erect, lanate to moderately to densely floccose, not stalked-glandular, (6) 10-25 cm tall (pistillate) or (2.5) 4-15 cm tall. **Basal leaves** ob lanceolate to spatulate, apices broadly obtuse or rounded to mucronate, adaxial surface moderately to densely short-pubescent with greyish hairs (sometimes becoming green and glabrate with age), abaxial surface grey-tomentose, 1-veined, 15-30 mm. **Cauline leaves** 3-7, linear, apices acuminate, middle and upper leaves with linear to narrowly strap-shaped scarious tips, 1.5-25 mm. **Capitulescences** globose or capitate (staminate) to subcorymbose or racemose (pistillate), dense to slightly open (rarely open), lower peduncles to
20 (30) mm, 15-35 mm in diameter. **Pistillate capitulae** 2-8; involucres campanulate, phyllaries not reflexed at anthesis, moderately to densely lanate basally, 6-10 mm; outer phyllaries lanceolate to narrowly oblanceolate, apices acute to obtuse, whitish to creamy-white, often with a brownish or reddish central region; inner phyllaries similar to outer phyllaries but narrower, 7-8 mm; pistillate corollas 4.5-7 mm; pappus 6-9.5 mm. **Staminate capitulae** (1) 2-4; involucres campanulate, phyllaries reflexed at anthesis, moderately to densely lanate basally, 4-7 mm; phyllaries broadly oblanceolate to spatulate, apices rounded, whitish, often with a small reddish central spot, 4-5.5 mm; staminate corollas 2.5-5 mm; pappus 3.5-6.5 mm. **Cypselae** minutely papillate, 0.9-1.4 mm.

Flowering May-Jul. Mesic to dry grasslands, pastures, aspen parkland, and forest edges in the parkland zone; 400-850 m. Locally frequent in northeast BC [Peace River lowlands]. BC east to NS, north to NWT, south to OK, AR, KY, VA. \(2n = 28\) [2x] (Appendix E).

**Antennaria neglecta** is a common and widespread species of the Great Plains and eastern North America. It is localized in British Columbia, however, where it is restricted to prairie and parkland habitats in the Peace River lowlands of the northeast (Figure 16). It is a sexual, diploid species that has had a major role as a progenitor of several apomictic polyploid complexes, including the *A. howellii* complex (Bayer 1985); these taxa were considered conspecific by many past authors (e.g., Cronquist 1955, Moss 1959, Hitchcock & Cronquist 1973, Packer 1983, Douglas 1995). Although the presence of staminate plants in the population immediately distinguishes *A. neglecta* from its allopolyploid derivatives, identification of pistillate plants in the absence of staminate plants can be problematic. **Antennaria neglecta** is particularly similar to *A. howellii* subsp. *neodioica*, with which it shares short-pubescent adaxial leaf surfaces (adaxial leaf surfaces green and nearly or completely glabrous in *A. howellii* subsp. *howellii*). In the absence of
Staminate individuals, *A. neglecta* can be best distinguished from *A. howellii* subsp. *neodioica* by its fewer cauline leaves (3-7 in *A. neglecta* vs. 6-11 in *A. howellii* subsp. *neodioica*) and, especially, its very small (often scale-like) stolon leaves that contrast greatly in size with the much larger and well-developed leaves that are borne in the rosette that terminates the stolon (Figure 15).

![A. neglecta, A. howellii subsp. howellii, A. howellii subsp. neodioica](image)

**FIGURE 15.** Comparison of stolons and stolon leaves of *A. neglecta* with those of *A. howellii* subsp. *howellii* and subsp. *neodioica*. *Antennaria neglecta*: Lomer 4098 (UBC); *Antennaria howellii* subsp. *howellii*: Bell s.n. (UBC); *Antennaria howellii* subsp. *neodioica*: Krajina 650624118 (UBC).

![Distribution maps](image)

**FIGURE 16.** Distribution of British Columbia specimens of *Antennaria neglecta* that were reviewed for this study (left), and approximate distribution of the species in northwestern North America (right).
12. *Antennaria parvifolia* Nutt.

**NUTTALL’S PUSSYTOES; Small-leaf Pussytoes; Littleleaf Pussytoes; Low Everlasting**

*Antennaria parvifolia* Nuttall (1841: 406). Type:—UNITED STATES. North Dakota: on the Black Hills and plains of the upper part of the Platte, no collection date reported, *Anon. s.n.* (holotype BM!, isotype PH!); *Antennaria dioica* (L.) Gaertn. var. *parvifolia* (Nutt.) Torrey & A. Gray (1843: 431).


*Antennaria holmii* Greene (1899: 81). Type:—UNITED STATES. Colorado: Long’s Peak, Larimer County, 08 August 1899, *Holm s.n.* (holotype NDG!, isotype WIS!).


*Antennaria obtusata* Greene (1908: 241). Type:—UNITED STATES. Utah: Dyer Mine, Uintah Mountains, 30 June 1902, *Goodding 1209* (holotype US!).

*Antennaria aprica* Greene var. *rosea* Lunell (1908: 8). Type:—UNITED STATES. North Dakota: Towner, McHenry County, 29 May 1908; *Lunell 1131* (holotype MIN!); *A. aureola* Lunell var. *rosea* (Lunell) Lunell (1917: 61) [as ‘roseata’].


Plants gynoecious, apomictic (sexual outside of B.C.), rhizomatous, stoloniferous, mat-forming; stolons leafy, 1-6 cm. Flowering stems erect, moderately to densely lanate to floccose, not stalked-glandular, 2-15 (18) cm tall. Basal leaves spatulate to oblanceolate, apices rounded to mucronate, densely grey-tomentose on both surfaces (adaxial surface sometimes becoming greenish with age), 1-veined, (8) 10-35 mm. Cauline leaves 4-7, linear or lanceolate to narrowly oblanceolate, apices acute, lacking scarious tips, not stalked-glandular, 8-20 mm. Capitulescences mostly subcorymbose to corymbose, dense to slightly open, lower peduncles to 10 (12) mm, 20-35 mm in diameter. Pistillate heads 2-7; involucres campanulate to slightly turbinate, phyllaries usually reflexed at anthesis, densely lanate basally, 8-11 (15) mm; outer phyllaries narrowly oblong to oblanceolate, apices rounded to obtuse, whitish to pink-tinged (rarely darker pink), 4-5 mm; inner phyllaries narrowly oblanceolate to lanceolate, apices obtuse to acute or acuminate, whitish to pink-tinged, 5-6 mm; pistillate corollas 5-8 mm; pappus 6.5-9 mm. Cyselae glabrous to minutely papillate, 1-1.8 mm.

Flowering May-Jun. Dry grasslands, sagebrush steppe, pastures, open forests, and disturbed areas in the steppe, parkland, and lower montane zones; 350-950 (1100) m. Frequent in south-central BC [north to the Chilcotin region]; locally frequent in southeast [southern Rocky Mountain Trench and adjacent Rocky Mountains; disjunct north to Valemount] and northeast [Peace River lowlands] BC. BC east to ON, south to AZ, NM, TX; Mexico. 2n = 56, 70, 84, ca. 99, ca. 100, 112, 126, ca. 130, 140 [4x-10x] (Appendix E).
This early-flowering *Antennaria* is characteristic of dry, open habitats in the arid basins of the southern interior, as well as the grasslands of the Peace River region of northeastern British Columbia (Figure 17). It is a relatively distinctive member of the genus in the province, being characterized by its large flowering heads, short stature, strongly mat-forming habit, and distinctly spatulate leaves. It is less variable than some other similar polyploid aggregates, such as *A. rosea* and *A. media*, with the exception of occasional variation in phyllary colour and shape. The broad phyllaries, which are typically reflexed at anthesis, are usually whitish or pinkish-white; however, occasional specimens with moderately to strongly pink phyllaries occur that may cause confusion with forms of *A. rosea*. Such plants should be identifiable as *A. parvifolia*, however, by their larger flowering heads, broader and more distinctly spatulate basal leaves, and fewer cauline leaves. Pink-phyllaried forms have been recognized in the past as *A. aprica* fo. *roseoides* Boivin or *A. aprica* var. *rosea* Lunell, but have not appeared in any recent taxonomic or floristic works and are no longer considered taxonomically significant given the relationship between phyllary colour and environmental conditions (Chmielewski et al. 1990a, Chmielewski et al. 1990b; see discussion under *A. rosea*, below). Similarly, specimens with brown-tinged phyllaries have sometimes been recognized as *A. aprica* fo. *brunnea* Boivin, but such variation is no longer considered taxonomically informative as the brownish colour, in some cases, may be the result of age-related morphological changes in addition to environmentally-induced variation. Plants with the specific or varietal epithet *aureola*, a name that is occasionally seen in some publications (e.g., Chmielewski et al. 1990), differ only in being somewhat larger in floral and foliar measurements and having narrower phyllaries. As noted by Chmielewski et al. (1990a), however, there is no single character that distinguishes *aureola* from nominate *parvifolia* and, as a result, the two are synonymized here and in other recent treatments.
Antennaria parvifolia is a polyploid complex that is hypothesized to have been derived from a variety of sexual progenitors, including *A. marginata*, *A. dioica*, *A. media* (sexual populations), and *A. neglecta* (Bayer 2006). The species concept includes both sexual and apomictic forms, although only apomictic forms are known from northern regions of the species’ range, including British Columbia; sexual populations are restricted to the southwestern United States (New Mexico, Colorado) (Bayer 2006). The name *A. microphylla* has occasionally been incorrectly applied to this species, such as in Packer (1983), but this appears to be the result of confusion derived from the comparable translations of *parvifolia* and *microphylla* (= small leaves). Similarly, the application of the name *A. parviflora* to this species is an orthographic error resulting from a misspelling of *A. parvifolia*, but is occasionally present in floristic treatments of the genus (e.g., Moss 1959).

![FIGURE 17. Distribution of British Columbia specimens of Antennaria parvifolia that were reviewed for this study (left), and approximate distribution of the species in northwestern North America (right).](image-url)
13. *Antennaria pulcherrima* (Hook.) Greene subsp. *pulcherrima*

**SHOWY PUSSYTOES; Showy Everlasting**

*Antennaria carpatica* (Wahlenb.) Bluff & Fingerhuth var. *pulcherrima* Hooker (1834a: 329). Type:—UNITED STATES. “swamps of the plains among the Rocky Mountains”, no collection date reported; *Drummond s.n.* (holotype K!); *A. pulcherrima* (Hook.) Greene (1897: 176).


**Plants** dioecious, sexual, short-rhizomatous or sometimes from a branched woody stem base, lacking stolons, not mat-forming. **Flowering stems** erect, densely tomentose to floccose, not stalked-glandular, (15) 30-65 cm tall. **Basal leaves** erect to ascending, oblanceolate to narrowly spatulate, apices mostly acute, grey-tomentose to lanate on both surfaces, not stalked-glandular, 3- to 5-veined, 50-200 mm. **Cauline leaves** 5-15, linear, reduced upwards, apices acuminate, upper leaves often with linear scarious tips, not stalked-glandular, 8-140 mm. **Capitulescences** capitate to subcorymbose, dense to slightly open, peduncles of lower heads/clusters to 20 mm, 20-45 mm in diameter. **Pistillate heads** 3-30; involucres campanulate to somewhat turbinate, phyllaries usually not reflexed at anthesis, moderately to densely lanate basally, 7-12 mm; outer phyllaries ovate or oblong to oblanceolate, apices obtuse to rounded and often erose, brownish to blackish-brown basally, pale brownish or darker olive-brown distally, usually with a darker brown or blackish central spot, usually shrivelling into concentric wrinkles, 2.5-6 mm; pistillate corollas 4-6 mm; pappus (7) 8-10 mm; inner phyllaries oblanceolate, apices obtuse, pale brownish to darker olive-brown, sometimes paler distally, 6-8 mm. **Staminate heads** 3-30; involucres broadly
campanulate, phyllaries usually reflexed at anthesis, moderately to densely lanate basally, 5-8 mm;
outer phyllaries oblong to obovate, apices rounded, brownish basally, whitish to brownish-white
distally, often with a darker brown central spot, 3-4 mm; inner phyllaries similar to outer
phyllaries, but broader and more conspicuously white distally, 4-5 mm; staminate corollas 3.5-5
mm; pappus 4-6 mm. *Cypselae* smooth, 1-1.5 mm.

Flowering Jun-Jul (Aug). Moist to wet meadows, streambanks, alluvial flats, shrubby
thickets, forest openings, and wetland margins in the montane and subalpine zones; (500) 750-
1300 (2100) m. Locally frequent in extreme northern and eastern [Rocky Mts.] BC, disjunct to
south-central BC [Chilcotin region]. AK east to QC, south to BC, UT, CO. 2n = 28, 56 [2x, 4x]
(Appendix E).

*Antennaria pulcherrima* is the boreal counterpart of the similar *A. anaphaloides*, and the
two have occasionally been considered conspecific by past authors (e.g., Douglas 1995, Douglas
*et al.* 1998). It is a species of wet streamsides, willow thickets, and riverine flats in montane and
boreal regions of the province, but is absent from the dry forests and grasslands of the southern
interior that support *A. anaphaloides* (Figure 18). Where the two species occur sympatrically in
British Columbia, such as in the Chilcotin region and the southern Rocky Mountains, these
ecological differences are maintained. Additionally, the two species differ cytologically, with *A.
pulcherrima* being a tetraploid species in British Columbia and *A. anaphaloides* being diploid
throughout its range (Urbanska 1983). Diploid populations of *A. pulcherrima* do occur south of
Canada in the U.S. Rocky Mountains (Urbanska 1983), however, rendering ploidy of only regional
utility in distinguishing the taxa. The fewer, larger flowering heads and conspicuously darker
phyllaries (each with a prominent dark brownish or blackish base, and often a darker central spot)
are the primary means by which to distinguish the two species morphologically. It should be noted,
however, that staminate plants of *A. pulcherrima* have broader, whiter phyllaries than pistillate plants and more closely resemble *A. anaphaloides*, rendering gender determination an important consideration during the identification of these species. Further identification problems may arise with populations of *A. pulcherrima* in and adjacent to the southern Rocky Mountains of the province (e.g., Kinbasket Lake, Golden, Yoho National Park, Kootenay National Park), which often have more extensively whitish phyllaries and more closely resemble *A. anaphaloides* than populations elsewhere. The occurrence of these populations near areas of sympathy between *A. pulcherrima* and *A. anaphaloides* suggests the potential for a hybrid origin, but as the size and number of the flowering heads, as well as the ecological preferences, are more consistent with *A. pulcherrima* than *A. anaphaloides*, such populations are included within the former species in this treatment.

FIGURE 18. Distribution of British Columbia specimens of *Antennaria pulcherrima* subsp. *pulcherrima* that were reviewed for this study (left), and approximate distribution of the species in northwestern North America (right).
14. *Antennaria pulvinata* Greene

**PULVINATE PUSSYTOES**; Aromatic Pussytoes (= ‘aromatica’); Scented Pussytoes (= ‘aromatica’)


*Antennaria sedoides* Greene (1904b: 37). Type:—CANADA. Alberta: Banff, 28 May 1901, *Sanson 26861* (lectotype [designated by Bayer 1989a: 58]) CAN, isolectotype NDG!).


*Antennaria vexillifera* Fernald (1924: 99). Type:—CANADA. Quebec: between Mt. Mattaouisse and Mt. Collins, Matane County, 08 July 1923, *Fernald, Griscom, Mackenzie, Pease, & L.B. Smith 26056* (holotype GH!, isotypes NY!, K!).


**Antennaria brunnescens** Fernald (1933: 336). Type:—CANADA. Newfoundland: Killdevil, Bonne Bay, 23 August 1929, *Fernald, Long, & Fogg* 2105 (holotype GH!, isotypes US!, NY!, PH!, MIN!, K!, WIS!, C!, F!, S!).


**Plants** gynoecious, apomictic (sexual outside of B.C.), rhizomatous, usually stoloniferous, pulvinate to mat-forming; stolons absent to very short, leafy, 0-0.5 (1) cm. **Flowering stems** erect, lanate, often sparsely to moderately stalked-glandular (at least distally), (0.5) 1.5-5.5 (8) cm tall.

**Basal leaves** widely cuneate-spatulate (rarely spatulate), apices rounded to broadly obtuse or somewhat truncate, moderately to densely grey-pubescent on both surfaces, 1-veined, 4.5-10 (12) mm. **Cauline leaves** 3-9, lanceolate or oblanceolate to lance-elliptic, apices acute to acuminate, middle and upper leaves usually with strap-shaped to acuminate scarious tips (sometimes absent), 6-14 mm. **Capitulescences** capitate to subcorymbose, dense to slightly open, (13) 16-28 mm in diameter. **Pistillate heads** 3-7, nearly sessile to short-stalked; involucre campanulate, phyllaries sometimes reflexed at anthesis, moderately to densely lanate basally, 5.5-6.5 mm; outer phyllaries broadly oblanceolate (rarely broadly lanceolate or ovate), apices usually obtuse, whitish to tan or pale olive with a dark brown or blackish central spot, 3-4.5 mm; inner phyllaries oblanceolate (rarely lanceolate), apices obtuse (rarely acute to acuminate), whitish to pale brown or olive with a dark brown central spot, 5-6 mm; pistillate corollas 3.5-5 mm; pappus 5-5.5 mm. **Cypselae** smooth to finely papillate or stalked-glandular, (1.2) 1.5-2 mm.
Flowering (Jun) Jul-Aug. Dry to mesic, often calcareous talus slopes, scree, fellfields, cliffs, rocky ridges, and tundra in the upper montane, subalpine, and alpine zones; (900) 1500-2400 m. Infrequent to locally frequent in south-central, southeast, and central BC [Coast-Cascade Mts. east to the Rocky Mts. and north to Williston Lake and the Skeena River]; rare in northwest BC [north to the Stikine River]. BC east to AB, south to WA, ID, WY, disjunct east to NL, QC. \(2n = 28, 56, 60, 84\) [2x-6x] (Appendix E).

*Antennaria pulvinata* is a low, strongly mat-forming species of moderate to high elevations that is widespread, though often uncommon and local, across the southern two-thirds of the British Columbia interior. Although it occurs on a variety of substrates, populations tend to be most frequent in areas of calcareous influence. It is most easily distinguished from other similar *Antennaria* species in the province by its short, broad leaves (typically < 2x longer than wide), short flowering stems, near complete lack of stolons, and unusually large cypselae (typically > 1.5 mm) that minimally overlap in size with other species (Fenneman & Chan, unpubl.); the lattermost character has not been reported previously by taxonomic works treating this species. The phyllaries are often pale, broad, and with a dark central spot, thus most closely resembling *A. borealis*, but the presence of some populations with narrower, darker phyllaries may cause confusion with *A. media*; as such, phyllary characters are not considered definitive for identification of this species.

*Antennaria pulvinata* includes both sexual and apomictic populations, and has a highly convoluted taxonomic and nomenclatural history; Chmielewski (1993) provides a concept of this taxon that is consistent with British Columbian material. Although most recent authors (e.g., Bayer 1989a, Bayer & Stebbins 1993, Bayer 2006) have included *pulvinata* within a very broad circumscription of *A. rosea*, such a treatment fails to account for the morphological consistency of the taxon and its marked morphological divergence from any other elements of the *rosea* complex, as was noted by Chmielewski (1993). Furthermore, the apomictic, polyploid populations of this
taxon (which are the only forms known to occur in B.C.) were shown to be morphologically indistinguishable from sexual, diploid populations in the Rocky Mountains that have been treated as the range-restricted *Antennaria aromatica* in recent floristic and taxonomic works (e.g., Chmielewski 1988, Bayer & Stebbins 1993, Bayer 2006). These two taxa are thus considered synonymous in this treatment, with “*aromatica*” representing the presumed diploid sexual progenitor and “*pulvinata*” representing the autopolyploid derivative. To incorporate this change, the morphological description of the taxon is broadened and certain characters (e.g., glandularity) are de-emphasized, following Chmielewski (1993). Although a case could be made for treating sexual diploids as taxonomically distinct from their autopolyploid derivatives, such an approach is considered inappropriate here in the absence of any consistent morphological distinctions between them. All *Antennaria* taxa in British Columbia with both apomictic and sexual populations, and which lack morphological discontinuities between the two (e.g., *A. pulvinata*, *A. parvifolia*, *A. media*, *A. microphylla*), are treated similarly here so as to ensure consistency among the taxonomic concepts.

The closely-related *Antennaria densifolia* of limestone substrates in the unglaciated portions of Alaska, the Yukon, and the Northwest Territories is similar to *A. pulvinata* in its short, broad basal leaves. Considerable confusion has resulted regarding the distributions of the two taxa in the Pacific Northwest due to this similar morphology, and there have been a number of reports of *A. densifolia* occurring in southern British Columbia (e.g., Chmielewski 1996); see Excluded Species for further discussion. The distributions of these two taxa suggest a close relationship, with *A. densifolia* and sexual populations of *A. pulvinata* (= *A. aromatica*) each with distributions that closely align with areas that were unglaciated during the Wisconsin glaciation (as mapped in Bayer 1989c). Their distributions strongly suggest that this glacial period (or perhaps an earlier
glaciation with a similar extent) was the vicariance event that promoted their speciation, as was suggested by Bayer (1989c).

Although outside of the geographic scope of this treatment, the concept of *A. pulvinata* presented here includes populations from the Atlantic coast of Canada, particularly the island of Newfoundland, that are similar morphologically and ecologically (i.e., limestone-associated). Such an approach is consistent with that proposed by Chmielewski (1994), who showed these populations to be morphologically nearly indistinguishable from *A. pulvinata* of western North America, and posited a post-glacial eastward migration across the continent and subsequent vicariance as an explanation for the wide disjunction. Review of type specimens pertaining to the taxa that Chmielewski (1994) included in his morphometric study (*bayardi*, *brunnescens*, and *foggii*) supports the notion that these are morphologically similar (though not identical) to typical *A. pulvinata*, and they are treated as such herein. Furthermore, the concept is expanded here to include as synonyms other named taxa from the region that fit this same morphology (*cana*, *vexillifera*, *columnaris*, *confusa*). However, as digital specimen review precludes detailed assessment of cypsela characters (which are the most diagnostic character of *A. pulvinata*), the synonymization of these disjunct eastern populations with *A. pulvinata* is considered tentative and worthy of additional verification. If recognized as distinct from *A. pulvinata*, and thus representative of morphological convergence rather than a geographic disjunction, the name *Antennaria cana* (Fern. & Wieg.) Fern. appears to have priority in the naming of these east coast populations.
FIGURE 19. General morphology of *Antennaria pulvinata*. A = plant habit, showing the short stature, few capitula, and distinctly short, broad, compact basal leaves (R.L. Taylor, Beil, Marchant, & Oliver 5856 [UBC]); B = whole plants in the field, showing the overall structure and the strongly mat-forming habit (R. Batten (ph.), Rocky Mts., AB [used with permission]).

FIGURE 20. Distribution of British Columbia specimens of *Antennaria pulvinata* that were reviewed for this study (left), and approximate distribution of the species in northwestern North America (right).

**RACEMOSE PUSSYTOES**; Hooker’s Pussytoes; Racemose Everlasting; Slender Everlasting

*Antennaria racemosa* Hooker (1834a: 330). Type:—UNITED STATES. “Rocky Mountains”, no collection date reported, *Drummond s.n.* (holotype K!).


**Plants** dioecious, sexual, rhizomatous, stoloniferous, not mat-forming; stolons leafy, 3-8 cm. **Flowering stems** ascending to erect, very sparsely lanate, moderately to densely stalked-glandular (especially distally), 10-60 cm tall. **Basal leaves** elliptic to oblong or obovate, apices obtuse to mucronate, adaxial surface green and glabrous, abaxial surface grey-tomentose, 3-veined, 25-100 mm. **Cauline leaves** 4-7, linear to broadly lanceolate, apices acute to acuminate, lacking scarious tips, 10-30 mm. **Capitulescences** subcorymbose (when young) to racemose or paniculate, open, peduncles to 40 mm, to 200+ mm in height. **Pistillate capitulae** 3-20; involucres campanulate, phyllaries not reflexed at anthesis, subglabrous to sparsely lanate basally, 6-8 (9) mm; outer phyllaries lanceolate to narrowly ob lanceolate, apices acute to acuminate, greenish-white, 4-5 mm; inner phyllaries similar to outer phyllaries, 5-7 mm; pistillate corollas 3-4 mm; papus 3.5-5.5 mm. **Staminate capitulae** 3-17; involucres broadly campanulate, phyllaries often reflexed at anthesis, subglabrous to sparsely lanate basally, 4-5 (8) mm; phyllaries oblong to ovate, apices rounded or obtuse to acute, greenish-white to greenish-brown, sometimes tinged with reddish, 2.5-5 mm; staminate corollas 3-4 mm; pappus 3-4.5 mm. **Cypselae** smooth to slightly papillate, 1-1.5 mm.

Flowering May-Jul. Mesic forests, woodlands, meadows, thickets, and grasslands in the lowland, steppe, montane, and subalpine zones; 500-2000 (2300) m. Locally frequent in southwest BC [Vancouver Island]; common in south-central and southeast BC [west to the Coast Mts.,

This common, distinctive, forest-associated Antennaria is easily distinguished when mature by its open, racemose or paniculate capitulescences, densely stalked-glandular stems and peduncles (with only a sparse scattering of longer, eglandular hairs), and large, broad basal leaves that are adaxially green and glabrous (adaxial surface contrasting conspicuously with the grey- to white-tomentose abaxial surface). Young capitulescences are more compact than those of mature plants, sometimes appearing dense and subcorymbose, and may be confused with those of \(A. howellii\); the extensive glandularity on the stems and peduncles of such plants, however, is immediately diagnostic of \(A. racemosa\).

Based on morphological similarities, and supported by the largely overlapping distributions of the two taxa, this sexual, diploid member of the genus appears to be one of the primary progenitors of the apomorphic, polyploid \(A. howellii\). The relatively large, broad basal leaves of \(A. howellii\) var. \(howellii\), with their characteristically green and glabrous (or nearly so) adaxial surfaces, are particularly indicative of \(A. racemosa\) parentage (Bayer 1985). Bayer (2006) also suggests the contribution of \(A. racemosa\) to the \(A. rosea\) apomorphic complex, although this appears to be speculative and unsupported, and is perhaps unlikely given the minimal morphological similarity between the two taxa. Potential hybridization with \(A. umbrinella\) (= \(A. x oblanicifolia\) E.E. Nelson [\(E.E. Nelson & A. Nelson 5640\) (lectotype RM!, isolectotypes NY!, US!, MO!, P!)], \(A. microphylla\) (= \(A. x foliacea\) Greene [\(Flodman 867\) (lectotype US!, isolectotypes NY!, MIN!)]), and \(A. corymbosa\) (= \(A. x erigeroides\) Greene [\(J.M. Macoun 69346\) (lectotype CAN, isolectotypes NY!, GH!, NDG!)]) has also been reported by Bayer (1988a). Although the hypothesized hybridization with \(A. umbrinella\) (= \(A. x oblanicifolia\)) seems reasonable based on the morphology of the specimens in question, the morphologies of \(A. x foliacea\) and \(A. x erigeroides\) are not
particularly supportive of a hybrid origin, at least not involving the purported parental taxa. See the account of *A. microphylla* (above) for further discussion of *A. x foliacea*, where it is included as a synonym. The attribution of hybridization with *A. corymbosa* resulting in *A. x erigeroides* is unexpected given that the type location of this purported hybrid (Cascade Mountains of British Columbia) is ca. 600 km northwest of the nearest confirmed populations of *A. corymbosa* in central Idaho. The type specimen of *A. x erigeroides* (as well as a second, more recent, collection from the type locality [*Lomer 99-117* (UBC!)]) does indeed suggest hybridization between *A. racemosa* and another species, but the non-*racemosa* parent is more likely to be *A. rosea* rather than *A. corymbosa*, based on both morphological and phytogeographic considerations.

**FIGURE 21.** Distribution of British Columbia specimens of *Antennaria reacemosa* that were reviewed for this study (left), and approximate distribution of the species in northwestern North America (right).

16. **Antennaria rosea** Greene

**ROSY PUSSYTOES; Pink Pussytoes; Red Pussytoes; Desert Pussytoes (= ‘arida’); Arid Pussytoes (= ‘arida’); Pink Everlasting; Rosy Everlasting**


Type:—UNITED STATES. “In Nevada and Utah, from the Havallah Mountains to the Uintas, 6,000-10,000 feet elevation”, July 1869, *S. Watson 652* (isotype YU!).

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Antennaria rosea Greene (1898: 281). Type:—UNITED STATES. Idaho: Kootenai County, July 1891, Leiberg 646 (lectotype [designated by Bayer (1989a: 56)] NDG!).


Antennaria scariosa E.E. Nelson (1899a: 210). Type:—UNITED STATES. Wyoming: Leroy, Uinta County, 07 June 1898, A. Nelson 4587 (holotype RM!, isotypes NY!, RM!).


Antennaria polyphylla Greene ex C.F. Baker (1903: 19), nom. nud. Type:—UNITED STATES. Nevada: Fall Creek, Ormsby County, July 1902, C.F. Baker 1328 (holotype CAN, isotypes NDG!, VT!, MO!, MSC!, MICH!, P!, E!).


Antennaria straminea Fernald (1914a: 130). Type:—CANADA. Newfoundland: Twillingate, 20 July 1911, Fernald, Wiegand, & Bartram 6340 (holotype GH!, isotypes RM!, NY!, YU!, PH!, S!, P!).

Antennaria subviscosa Fernald (1914a: 131). Type:—CANADA. Quebec: Point aux Corbeaux to Cap Caribou, 08 July 1907, Fernald & Collins 1195 (holotype GH!, isotypes GH!, NY!, PH!).

Antennaria peasei Fernald (1924: 101). Type:—CANADA. Quebec: Mount Logan, 13 July 1923, Pease & Smith 26057 (holotype GH!, isotypes GH!, NY!, K!).
Antennaria laingii A.E. Porsild (1939: 293). Type:—UNITED STATES. Alaska: Chitina River, 13 June 1925, Laing 210 (holotype CAN!).

Antennaria leuchippii M.P. Porsild (1946: 85) [as leuchippi]. Type:—CANADA. Yukon: Whitehorse, 11 July 1944, A.E. Porsild & R.T. Porsild s.n. (holotype CAN, isotypes CAN, C!).

Antennaria alborosea M.P. Porsild (1946: 85). Type:—CANADA. Yukon: Rose River valley, Canol Road, 06 July 1944, A.E. Porsild & Breitung 10190 (holotype CAN, isotypes GH!, US!, S!, LE!).

Antennaria breitungii A.E. Porsild (1950: 18). Type:—CANADA. Yukon: east of Lewes River, Whitehorse, 01-05 June 1944, A.E. Porsild & Breitung 9229 (holotype CAN, isotypes GH!, S!).

Antennaria elegans A.E. Porsild (1950: 18). Type:—CANADA. Yukon: upper Rose River, Canol Road, 14 July 1944, A.E. Porsild & Breitung 10411 (holotype CAN, isotypes US!, GH!, S!, C!).

Antennaria incarnata A.E. Porsild (1950: 19). Type:—CANADA. Yukon: upper Rose River valley, Canol Road, 11 July 1944, A.E. Porsild & Breitung 10412 (holotype CAN, isotypes NY!, GH!, US!, WTU!, S!).

Antennaria leontopodioides Cody (1956: 127). Type:—CANADA. Northwest Territories: Indin Lake, Mackenzie District, 12 August 1949, Cody & McCane 3473 (holotype DAO!).

Plants gynoecious, apomictic (possibly rarely sexual), rhizomatous, stoloniferous, mat-forming; stolons leafy, 1-7 cm. Flowering stems ascending to erect, usually floccose, sometimes sparsely to moderately stalked-glandular (at least distally), 3-30 (40) cm tall. Basal leaves narrowly oblanceolate to narrowly spatulate, apices mucronate, moderately to densely grey-pubescent on both surfaces or sometimes green and glabrescent adaxially, 1-veined, (6) 8-40 mm. Cauline leaves (5) 7-16, linear to lanceolate, apices acute to acuminate, middle and upper leaves sometimes with lanceolate to strap-shaped scarious tips, 5-36 mm. Capitulescences capitate to subcorymbose, dense to slightly open, 18-30 mm in diameter. Pistillate capitulae 3-20, nearly
sessile to short-stalked; involucres campanulate, phyllaries sometimes reflexed at anthesis, moderately to densely lanate basally, 4-10 mm; outer phyllaries narrowly to broadly oblanceolate, apices mostly rounded, whitish, dingy-white, or tan to pale or dark pink, sometimes with a darker brownish central spot or band, 3-5 mm; inner phyllaries narrowly lanceolate to oblanceolate, apices acute or obtuse to rounded, whitish, dingy-white, or tan to pale or dark pink, 4-5 mm; pistillate corollas 2.5-6 mm; pappus 3.5-6.5 mm. Cypselae smooth to finely papillate, 0.6-1.8 mm.

Flowering May-Jul. Mesic to dry grasslands, shrub steppe, open forests, meadows, tundra, and disturbed areas in the lowland, steppe, montane, parkland, boreal, subalpine, and alpine zones; (300) 500-1900 (2400) m. Common throughout BC in and east of the Coast-Cascade Mountains, except absent from extreme northeast BC [Fort Nelson lowlands]; rare in southwest BC [Georgia Depression]. AK east to NL, south to CA, AZ, NM, MI, ME. 2n = 28, 42, 56, 60, ca. 62, ca. 68, 70, ca. 72 [2x-5x] (Appendix E).

Antennaria rosea is both the most common and the most widespread member of the genus in British Columbia (Figure 33), as well as the most morphologically and ecologically variable. It occupies open or lightly forested environments at all elevations and latitudes, from arid grassland basins of the southern interior to high alpine and subarctic habitats of northern areas. It is conspicuously absent from most areas of the coast, although it has been collected from the Georgia Depression (Powell River, Vancouver [adventive]) and has been reported from Vancouver Island by Chmielewski et al. (1990b). It is primarily or entirely gynodioecious and apomictic throughout its distribution, although Chmielewski & Chinnappa (1988a), Chmielewski & Chinnappa (1988b), and Chmielewski et al. (1990b) report staminate plants from the western United States and southwestern Canada (including British Columbia). The presence of staminate, sexual A. rosea has been questioned by Bayer (1989), who has suggested that reports likely pertain to
misidentifications of closely related sexual taxa (i.e., *A. corymbosa*, *A. microphylla*, *A. parvifolia*, *A. umbrinella*) or are representative of rare, sterile ‘aberrant males’ that do not contribute to the reproductive effort of the population. Further to this, the staminate specimens cited by Chmielewski *et al.* (1990b) were all either white-phyllaried or with, at most, a slight tinge of pink and, as such, are perhaps more likely to be misidentified than those with the near-diagnostic pink phyllaries. It should be noted, however, that a single staminate individual is present on the holotype of *A. arida* subsp. *viscidula* [*A. Nelson 7570 (RM!)*], which is synonymized with *A. rosea* s.l. here and in Bayer (1989a), thus confirming the rare occurrence of staminate plants within elements that are included within the *A. rosea* aggregate. The absence of staminate *A. rosea* in the collections of the UBC herbarium would appear to support the conclusions of Bayer (1989), at least insofar as they pertain to British Columbia.

Although commonly characterized as a species with pink or reddish phyllaries (contributing to both the scientific and common names), approximately one-third of the collections at the UBC herbarium are from whitish- or creamy-phyllaried populations. Chmielewski & Chinnappa (1988b) have shown that the presence and intensity of pinkish colouration on the phyllaries is at least partially influenced by environmental factors. For example, transplant experiments showed that white-phyllaried plants commonly became pinkish, and pinkish-phyllaried populations reddish, following transplantation to new environments, but the reverse (i.e., a loss or lightening of the pink colouration) was never observed. As a result, this character appears to be of only marginal utility taxonomically, and attempts at infraspecific taxonomies that incorporate it are not accepted as appropriate, at least given current understanding. Other characteristics that were found to be under partial environmental control in this species included stem height (which also varies phenologically), cauline leaf size and shape, number of capitulae,
leaf pubescence, and peduncle length (Chmielewski & Chinnappa 1988b, Chmielewski et al. 1990b).

When lacking pinkish or reddish phyllaries, representatives of *A. rosea* can generally be distinguished from other similar pale-bracted species by the absence of ascending woody stolons (as would be found in *A. umbrinella*), the relatively small flowering heads (smaller than *A. parvifolia*), and the relatively long, slender, narrowly oblanceolate leaves (longer and narrower than either *A. microphylla* or *A. parvifolia*). Although the presence of stalked glands is generally treated as the primary means of distinguishing white-phyllaried *A. rosea* from the sexual *A. microphylla*, with which it has been treated as conspecific in the past (e.g., Hitchcock & Cronquist 1973, Douglas 1995), some populations of *A. rosea* - particularly those that correspond with the ‘*alborosea*’ morphotype, discussed below - are equally glandular. The glandular hairs on *A. rosea* are most often purplish when present, but some populations bear yellowish or greenish glands that are similar to those found in *A. microphylla*. As such, the presence of glands on the stems and leaves should not be considered fully indicative of *A. microphylla* (or their absence indicative of *A. rosea*), and basal leaf shape and size should be consulted for difficult specimens.

Based on morphological considerations, Bayer (1987b, 2006) has suggested that the progenitor diploids of the *Antennaria rosea* aggregate (excluding *A. rosea* subsp. *pulvinata*, which is here treated as the species *A. pulvinata*) may include *A. corymbosa*, *A. marginata*, *A. media* (as *A. pulchella*), *A. microphylla*, *A. racemosa*, *A. rosulata*, *A. suffrutescens*, and *A. umbrinella*. Conversely, Chmielewski et al. (1990b) restrict the potential progenitor taxa to *A. corymbosa*, *A. microphylla*, and *A. umbrinella*. Curiously, the potential contribution of the Eurasian *A. dioica*, which is the only sexual diploid in the northern hemisphere with similarly pink phyllaries, has not been considered by either of these authors. Although *A. dioica* does not occur in North America other than in the Aleutian Islands of Alaska (Hultén 1968, Bayer 2006), it may have historically
been present and capable of contributing to allopolyploidization. Being an aggregate species of considerable morphological complexity, and combining the characters of as many as 3-8 sexual progenitor species, individual clones of *A. rosea* can vary immensely with respect to virtually any character, including plant size, overall structure, propensity for stolon development and mat-forming habit, leaf size, leaf shape, leaf vestiture, stem vestiture, glandularity, capitulescence structure, number of capitulae, phyllary shape, and phyllary colour. Populations also often comprise several different clones, averaging three clones per population (Bayer 1990b), resulting in considerable intrapopulation variation.

The pronounced variation within *A. rosea*, and the apomictic or clonal nature of the species, has led to an extensive list of published names that each represent a component of the variation. These names often appear in older floras or taxonomic publications, where they are occasionally treated as full species (e.g., Porsild 1950, Porsild & Cody 1980). Although they represent only a portion of the total variation within the species, their recognition (or at least discussion) considerably improves the interpretation of that variation. Eleven such names, which can be considered to represent particular ‘morphotypes’ or ‘forms’ within the broader *A. rosea* aggregate, have been recognized from British Columbia in various floristic and taxonomic publications, and these are discussed in greater detail below. As phyllary colour is generally the first character used to distinguish among forms of *A. rosea*, Table 3 lists the distribution of phyllary colours among the eleven recognized morphotypes to aid in the interpretation of the morphological variation in the species and link it to published names, even if these names are not recognized taxonomically in this treatment. It should be noted that this list and the subsequent discussion only includes names that apply to morphotypes that have been recognized as occurring in the province in published literature, and will undoubtedly only capture a portion of the variation in the species. Many, or perhaps even most, specimens would be expected to fall between two or more of these forms, so
observers should expect relatively few specimens to be easily pigeonholed into only a single form. This is reflected in some of the ambiguity around definitions of these forms, both in this treatment and others, which further complicates the assignment of these names.

**TABLE 3.** Reported phyllary colour of *Antennaria rosea* morphotypes occurring in British Columbia. X = colour occurs in all/most populations; (X) = colour is rare.

<table>
<thead>
<tr>
<th>Morphotype</th>
<th>Phyllary Colouration</th>
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<tbody>
<tr>
<td></td>
<td>Pink</td>
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<tr>
<td>alborosea</td>
<td>X</td>
</tr>
<tr>
<td>arida</td>
<td>(X)</td>
</tr>
<tr>
<td>breitungii</td>
<td>X</td>
</tr>
<tr>
<td>confinis</td>
<td></td>
</tr>
<tr>
<td>elegans</td>
<td>(X)</td>
</tr>
<tr>
<td>incarnata</td>
<td>X</td>
</tr>
<tr>
<td>laingii</td>
<td></td>
</tr>
<tr>
<td>leuchippii</td>
<td>(X)</td>
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<tr>
<td>rosea</td>
<td>X</td>
</tr>
<tr>
<td>subviscosa</td>
<td></td>
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</table>

“*alborosea*”: this morphotype (as the species *A. alborosea*) has been reported for British Columbia by Porsild (1950), Hultén (1968), Porsild & Cody (1980), and Chmielewski & Chinnappa (1988c). Although recognized at the species level in these publications, other treatments (Bayer 1989a, Bayer 1993, Bayer & Stebbins 1993, Bayer 2006) have synonymized the form with *A. rosea* subsp. *rosea*. It is a pink-phyllaried morphotype (Table 3; Figure 21) that is characterized by the conspicuous glandularity of the stems, leaves, and peduncles, as well as the usually green-glabrate surfaces of the basal and cauline leaves (Chmielewski & Chinnappa 1988c, 1990a). Analysis of specimens at the UBC herbarium, however, has demonstrated that glandularity, although infrequent, is widespread in *A. rosea*, and the presence of glandular hairs does not appear to co-vary with the leaf characters mentioned by Chmielewski & Chinnappa (1988c, 1990a). Although
some specimens were found to correspond closely with the original description of *A. alborosea*, glandular hairs were also occasionally encountered on specimens representing a wide range of other morphologies, including those lacking adaxially green and glabrous leaves, such as the *arida*, *elegans*, and *incarnata* morphotypes, as well as specimens falling between or otherwise outside of the morphotypes that are discussed in this treatment. Indeed, variation in the structure and colour (purplish to yellowish or greenish) of glandular hairs suggests that glandularity may possibly be of multiple origins in the aggregate. Leaf vestiture is also highly variable across the taxon, although most specimens with green-glabrate leaves that were assessed for this study did tend to have glandular hairs, as per descriptions of *A. alborosea*. Although *alborosea* has been described as being among the most discrete and distinctive entities within the *A. rosea* aggregate (J.G. Chmielewski, pers. comm. [2015]), the review of specimens at the UBC herbarium has not supported this claim.

**FIGURE 22.** Isotype of *Antennaria alborosea*. A.E. Porsild & Breitung 10190 (GH). A = whole plant habit; B = whole plant detail; C = capitulescence detail; D = basal leaf detail.
“arida”: this morphotype is of southern origin and is associated primarily with drier environments across the western United States and southwestern Canada. It has been recognized as the infraspecific taxon *A. rosea* subsp. *arida* in Bayer and Stebbins (1993) and Bayer (2006), being distinguished from other treated subspecies primarily by quantitative characters of the leaves, involucres, and phyllaries. The type series of ‘arida’ represents a form with whitish or creamy phyllaries (Figure 23), as does the original description of the taxon (Nelson 1899), but Bayer & Stebbins (1993) and Bayer (2006) expand the concept to include plants with a variety of phyllary colours, including white, pink, green, red, and brown. Such an approach renders the taxon nearly undiagnosable, however, given that both the quantitative and colour characters mentioned as diagnostic overlap almost entirely with the other recognized infraspecies under this taxonomy. Furthermore, the association of phyllary colour with environmental influences (Chmielewski & Chinnappa 1988b) limits the taxonomic application of even this character, despite its importance in the original description. The *arida* morphotype has been treated as an F1 hybrid between *A. microphylla* and the extralimital *A. corymbosa* by Chmielewski *et al.* (1990b), although, if it is indeed the result of one or more hybridization events between these species, the hybrid has become stabilized through apomixis and spread far beyond the range of *A. corymbosa*. Whitish-phyllared specimens with an overall morphology consistent with the type specimens of *arida* are widespread across southern British Columbia, but were found to grade seamlessly into other morphologies in a variety of characters (including phyllary colour). The *arida* morphotype is here included within *A. rosea* s.l. in recognition of the confusion surrounding its morphology and taxonomy, its generally poor taxonomic circumscription, the limitations of applying phyllary colour taxonomically, and the multi-dimensional intergradation of its morphology with other components of the *A. rosea* aggregate.
“breitungii”: this morphotype (as the species *A. breitungii*) has been reported for areas immediately adjacent to British Columbia in the southern Yukon and western Alberta by Porsild (1950) and Chmielewski & Chinnappa (1988), suggesting a presence in northern or eastern parts of British Columbia. It is synonymized with *A. rosea* subsp. *confinis* in Bayer & Stebbins (1993) and Bayer (2006), along with a large number of names that are here either included within a broad *A. rosea* s.l. or synonymized with other members of the genus. The *breitungii* morphotype is characterized as being a relatively low, strongly mat-forming, pink- to white-phyllaried form with short, crowded basal leaves that often become glabrous adaxially in age (Chmielewski & Chinnappa 1988) (Figure 24). It is perhaps most similar to *A. microphylla* in many respects (particularly the size and shape of the leaves), but can be distinguished by its often pink phyllaries and lack of glandular hairs. Specimens consistent with the overall habit and leaf shape of *breitungii*
were found to occur sporadically across northern British Columbia, but most specimens reviewed shared neither the pink phyllaries nor the often glabrescent adaxial leaf surfaces that are associated with the type series and published literature on the form. As a result, this form is here subsumed within *A. rosea s.l*.

**FIGURE 24. Isotype of *Antennaria breitungii*. A.E. Porsild & Breitung 9229 (GH). A = whole plant habit; B = whole plant detail (flowering stems immature); C = capitulescence detail; D = basal leaf detail.**

“*confinis*”: this name has been applied to British Columbia material primarily as the taxon *A. rosea* subsp. *confinis*, based on the circumscription of Bayer (1989a, 2006) and Bayer & Stebbins (1993), and encompasses a number of other morphotypes that are discussed here separately. It has traditionally been recognized primarily by its dingy-whitish to pale brownish phyllaries (Figure 25), but the expanded definitions of Bayer & Stebbins (1993) and Bayer (1989a, 2006) result in the inclusion of a slightly wider variety of phyllary colours (greyish, yellowish) within their taxonomic concept. Based on the synonymies provided, their concept of *confinis* would include
other forms that are discussed here as part of the *A. rosea* aggregate, including *breitungii*, *elegans*, *incarnata*, *laingii*, *leuchippii*, and *subviscosa*. Some of these synonyms (*breitungii*, *incarnata*) represent names that are specifically associated with pink-phyllariated morphologies, however, thus directly contradicting the morphological description of *confinis* that is presented in these sources. Moreover, several of the other names included within the concept of Bayer & Stebbins (1993) and Bayer (1989a, 2006) do not appear to be part of the *A. rosea* aggregate at all, including *sedoides* (here included in *A. pulvinata*), *kernensis* (here included in *A. umbrinella*), and *tomentella* (here included in *A. howellii* subsp. *howellii*). Finally, the role of hybridization in the origin of the holotype – specifically hybridization between *A. microphylla* and *A. umbrinella* – has been hypothesized by Chmielewski et al. (1990b), and this seems reasonable, perhaps even likely, based on the morphology of the (admittedly scanty) specimen. Thus, given the inconsistent application of the name across morphologies that do not correspond with either the holotype or original description, the inclusion of names in synonymy that appear not to represent components of the *A. rosea* aggregate, and the potential hybrid origin of the holotype, this name (and the morphology that it represents) is probably best disregarded as part of morphological variation of *A. rosea* in British Columbia. It is included in this discussion, however, so as to provide a point of comparison with Bayer (2006) and other taxonomic approaches that recognize *A. rosea* subsp. *confinis*. 
“elegans”: this name is applied to northern plants with relatively broad, whitish or creamy-white to dingy-brown (sometimes faintly pink-tinged, especially when immature), usually dark-spotted phyllaries that are typically reflexed at anthesis (Figure 26). It has been reported, as *A. elegans*, for northwestern British Columbia by Chmielewski & Chinnappa (1988b) and from northeastern B.C. by Porsild & Cody (1980), and is represented by a number of specimens from these areas in the UBC herbarium. It is one of the more distinctive forms of *A. rosea* in British Columbia, and, in many ways, is morphologically intermediate between other pale-phyllaried morphotypes of *A. rosea* and the similarly apomictic *A. borealis*. Although it resembles some forms of *A. borealis*, the *elegans* morphotype of *A. rosea* is generally distinguishable by its tall, slender stature and longer, narrower basal leaves. It also closely resembles *A. corymbosa*, which occurs in the western United States and is generally recognized as one of the progenitor diploids of the *A. rosea*
aggregate, but differs from that more southerly species in its smaller basal leaves and, often, its larger and more open capitulescences. The morphological similarity of *elegans* to *A. corymbosa* appears to be responsible for the only reported collection of *A. corymbosa* in British Columbia (Björk 2008), and the representative specimen from east-central B.C. [Björk 9415 (UBC!)] is here referred to *A. rosea* as a representative of the *elegans* morphotype; see Excluded Species (below) for further discussion of this specimen.

**FIGURE 26. Isotype of Antennaria elegans. A.E. Porsild & Breitung 10411 (S).** A = whole plant habit; B = whole plant detail; C = capitulescence detail; D = basal leaf detail.

“*incarnata*”: this morphotype has been reported from southwestern British Columbia, as well as areas of western Alberta and the southern Yukon Territory that are adjacent to the B.C. border, by Chmielewski & Chinnappa (1988b). Among specimens at the UBC herbarium, provincial collections corresponding with this morphotype have been made primarily along the Coast Mountains and adjacent North Cascades of western British Columbia. The *incarnata* morphotype is characterized by its relatively small stature, dark brownish band across the midpoint of the
otherwise pinkish phyllaries (giving the capitulae an overall brownish-pink aspect), and its consistently exerted styles (Chmielewski & Chinnappa 1988b) (Figure 27). Although rather distinctive in its purest form, it grades into other morphotypes such as *elegans* (which also shows a dark band/spot on the phyllaries) and *rosea* s.s. and, in many ways, is intermediate between these two morphologies. Thus, none of the morphological characters upon which the description of the form was based are unique, and all can be found widely (if infrequently) throughout the *A. rosea* aggregate. As a result, this form is here included within the greater *A. rosea* aggregate, and identified as a morphological “bridge” between *rosea* s.s. and the *elegans* morphotype.

**FIGURE 27. Isotype of Antennaria incarnata. A.E. Porsild & Breitung 10412 (GH). A = whole plant habit; B = whole plant detail; C = capitulescence detail; D = basal leaf detail.**

“*laingii*”: plants referable to this name have been reported from northwestern and southeastern British Columbia (Chmielewski & Chinnappa 1988b), as well as adjacent areas of Alberta and the Yukon Territory (Porsild 1950, Chmielewski & Chinnappa 1988b). This form is described as being
a low-growing (usually < 20 cm tall) plant with narrow, scarious, obtuse, whitish to brownish-white phyllaries and densely white-tomentose basal leaves (Porsild 1950, Chmielewski & Chinnappa 1988b) (Figure 28). It is most similar to *A. microphylla* (particularly northern, apomictic populations that have been called *A. “nitida”*), but can be distinguished by its eglandular stem, cauline leaves, and peduncles as well as its longer, narrower basal leaves. Within the *A. rosea* aggregate, the *laingii* morphotype is most similar to the *arida* type (which occurs to the south of *laingii*), and many specimens may be equally at home under either of these names. This is a relatively poorly defined form that overlaps morphologically with other pale-phyllarie forms of *A. rosea s.l.* and, as such, it is maintained as part of that apomictic aggregate in this treatment.

“*leuchippii*”: this morphotype has been reported for southeastern British Columbia by Chmielewski & Chinnappa (1988b), as well as adjacent areas of Alberta and the Yukon Territory (Porsild 1950, Chmielewski & Chinnappa 1988b). It is a tall, slender member of the *A. rosea*
aggregate, with scarious, whitish or pink-speckled to faintly pink-tinged phyllaries, (Figure 29) and is most similar to the alborosea and oxyphylla morphotypes of A. rosea. In its truest form, the leuchippii morphotype differs from the alborosea morphotype in its paler and less consistently pinkish phyllaries (phyllaries usually whitish, unlike alborosea), smaller cauline leaves, smaller flowering heads, and its densely tomentose adaxial leaf surfaces (Porsild 1950, Chmielewski & Chinnappa 1988b). It differs from the oxyphylla morphotype primarily in its narrower basal leaves and lack of short, ascending stolons (Chmielewski & Chinnappa 1988b). Numerous intermediates between leuchippii, alborosea, and oxyphylla occur widely, as well as between leuchippii and other forms (e.g., elegans, laingii), with many specimens difficult to place into any of these forms. As a result, this poorly defined morphotype is included within the broader A. rosea aggregate in this treatment.

**FIGURE 29.** Isotype of Antennaria leuchippii. A.E. Porsild & R.T. Porsild s.n. (C). A = whole plant habit; B = whole plant detail; C = capitulescence detail; D = basal leaf detail.
“oxyphylla”: this morphotype has been reported from northwestern (Porsild 1950) and southeastern (Chmielewski & Chinnappa 1988b) British Columbia, as well as adjacent areas of Alberta and the Yukon Territory. This morphotype has been distinguished from other similar elements of the A. rosea aggregate (e.g., leuchippii) by the basal leaf shape (spatulate-ovate) as well as the presence of short, erect or suberect stolons (Porsild 1950, Porsild & Cody 1980, Chmielewski & Chinnappa 1988b) (Figure 30). Chmielewski & Chinnappa (1988b) note regional differences in phyllary colour of the oxyphylla form, with northern (e.g., Yukon) populations having pink phyllaries and Rocky Mountain populations tending to have whitish phyllaries. Within this form, there is considerable variation in other morphological characters in addition to phyllary colour, such as achene morphology (Chmielewski & Chinnappa 1988b), rendering the above-mentioned leaf and stolon characters as the primary means of diagnosing the form. Both of these characters (especially leaf shape) are expressed widely throughout other forms in the A. rosea, aggregate, however, and thus their application in the circumscription of this particular morphological form is problematic. As a result, the oxyphylla morphotype is here included within the broader A. rosea aggregate.

“rosea”: this form represents the most widespread and best-known element of the A. rosea aggregate in British Columbia. Populations referable to the rosea morphotype are found throughout the species’ range in the province, although they represent a smaller proportion of the overall A. rosea diversity in northern (especially northwestern) parts of the province. The rosea morphotype is characterized by its tall, slender flowering stems, lack of glandularity, relatively compact capitulescences, pale to bright pink (sometimes darker pinkish-red) phyllaries, and long, narrow leaves that typically exceed 20 mm in length (Figure 31). Although quite distinctive in its purest form, the relationship between the pink colour of the phyllaries and both environmental
influences (Chmielewski & Chinnappa 1988b; see above) and phenological state (i.e., pink colour fades during anthesis and seed dispersal) renders that character difficult to apply taxonomically. The intensity of pink colouration on the phyllaries ranges from a slight pinkish wash on otherwise whitish phyllaries to a deep, intense reddish-pink, and does not covary consistently with other characters such as overall size and habit, leaf shape, or capitulescence structure. Moreover, several other forms of *A. rosea* exhibit similar pink colouration on the phyllaries (see Table 3), or grade into the typical *rosea* morphology in a variety of different characters, and thus this seemingly distinctive form is difficult to diagnose in many instances.
“subviscosa”: although described from disjunct populations in eastern North America, the *subviscosa* morphotype has been recognized as occurring more widely in northern North America by several authors (Porsild 1950, Porsild & Cody 1980, Chmielewski & Chinnappa 1988b). It has been reported for northernmost British Columbia by Porsild and Cody (1980), as well as areas of the southern Yukon Territory that are immediately adjacent to the B.C. border (Porsild 1950, Chmielewski & Chinnappa 1988b). It is one of several low-growing, long-stoloniferous, whitish-phyllaried morphotypes of *A. rosea*, and is characterized primarily by its tendency to have open capitulescences with long-peduncled lower capitula, as well as the presence of ob lanceolate-spatulate basal leaves (Figure 32). It is particularly similar to the *elegans* morphotype of *A. rosea*, but can be distinguished by its longer, usually ascending stolons, less conspicuous dark bands.
across the phyllaries, and glabrous to thinly pubescent flowering stems (vs. floccose in *elegans*). It is also similar to the *oxyphylla* morphotype, particularly in its basal leaf shape, but is distinguished by its shorter stature, lack of erect or ascending stolons, and more open capitulescences. In many ways, the *subviscosa* form is morphologically intermediate between several of these other co-occurring forms and, without any unique or diagnostic characters upon which to recognize it, it is best retained within a broad concept of the *A. rosea* aggregate.

**FIGURE 32.** Isotype of *Antennaria subviscosa*. Fernald & Collins 1195 (GH). A = whole plant habit; B = whole plant detail; C = capitulescence detail; D = basal leaf detail.
FIGURE 33. Distribution of British Columbia specimens of Antennaria rosea that were reviewed for this study (left), and approximate distribution of the species in northwestern North America (right).

17. **Antennaria umbrinella** Rydb.

**UMBER PUSSYTOES;** Brown-bracted Pussytoes; Brown Everlasting; Brown-bracted Mountain Everlasting


*Antennaria aizoides* Greene (1898: 283). Type:—CANADA. Saskatchewan: Cypress Hills, 09 June 1884, *J.M. Macoun 11245* (lectotype [designated by Bayer (1988a: 297)] CAN, phototype S!).

*Antennaria reflexa* E.E. Nelson (1899a: 208). Type:—UNITED STATES. Wyoming: Centennial Valley, 09 June 1895, *A. Nelson 1265* (holotype RM!, isotypes RM!, CS!).


Antennaria dioica (L.) Gaertn. var. kernensis Jepson (1925: 1071). Type:—Volcano Meadows, upper Kern River, Tulare County, 25 July 1904, Hall & Babcock 5473 (syntypes UC!, US!, RM!, CAS!).

Plants dioecious, sexual, rhizomatous, stoloniferous, mat-forming; stolons leafy, usually suberect to erect, subligneous, 1-7 cm. Flowering stems erect, moderately to densely floccose, not stalked-glandular, 6-16 (22) cm tall. Basal leaves oblaneolate to narrowly spatulate, apices acute to mucronate, densely grey-pubescent on both surfaces, 1-veined, (5) 10-17 (20) mm. Cauline leaves 7-12, linear to linear-lanceolate, apices acute, lacking scarious tips, 8-18 mm. Capitulescences capitate to subcorymbose (rarely corymbose), dense to slightly open, lower peduncles to 7 (10) mm, 10-20 (30) mm in diameter. Pistillate capitulae 3-10; involucres campanulate, phyllaries not reflexed at anthesis, sparsely to densely lanate basally, 4-6.5 mm; outer phyllaries lanceolate to ob lanceolate, apices mostly obtuse, creamy-white to tan or brownish-olive (sometimes tinged with pinkish), 3.5-4.5 mm; inner phyllaries narrowly lanceolate to ob lanceolate, apices obtuse to acute, creamy-white to tan or brownish-olive, 4-5 mm; pistillate corolla 2.5-3.5 mm; pappus 3-5 mm. Staminate capitulae 3-10; involucres broadly campanulate, phyllaries often reflexed at anthesis, sparsely to densely lanate basally, 3-6 mm; phyllaries broadly ob lanceolate to spatulate, apices obtuse to rounded, 2.5-3.5 mm; staminate corolla 2.5-3.5 mm; pappus 3-4.5 mm. Cypselae smooth, 0.5-1.2 mm.

Flowering (Apr) May-Jun (Jul). Mesic to dry grasslands, meadows, shrub steppe, rock outcrops, open forests, and rocky ridges in the steppe, montane, subalpine, and alpine zones; (200) 400-2200 (2500) m. Common in south-central BC [north to the Chilcotin region]; locally frequent in southwest [southern Coast Mts., Cascade Mts.] and southeast [southern Rocky Mts., southern Rocky Mtn. Trench] BC; rare in west-central [Bulkley Valley] and northwest [Stikine River,
Antennaria umbrinella is an early-flowering, sexual species that is most common in the dry basins and forested plateaus of the southern interior; it also occurs locally in dry, rocky, higher-elevation habitats elsewhere across the southern half of the province (e.g., southern Coast Mountains, North Cascades, southern Rocky Mountains) (Figure 35). The species occupies rather distinct low and high elevation ranges that are separated by areas where the species is scarce or absent, with low elevation populations occurring primarily between 400-1300 m and high elevation populations occurring primarily between 1700-2200 m. Although the species is generally recognized as sexual throughout its range, the absence of staminate collections from most high-elevation populations suggests that these may in fact be largely apomictic; in contrast, staminate plants are widespread and common among low-elevation populations in British Columbia. Although largely a species of the southern interior of the province, Antennaria umbrinella occurs sporadically northward into northwestern B.C., where it inhabits isolated areas of relatively warm, dry grassland or parkland habitats in the rainshadow of the Coast Mountains (e.g., Bulkley Valley, Telegraph Creek). The northernmost occurrence is in extreme north-western B.C. (Haines Triangle), and is staminate; these populations appear be continuous with populations inhabiting the rainshadow climates of the southwestern Yukon.

Being superficially similar to a number of other Antennaria species with brownish or tan phyllaries, A. umbrinella is best characterized by its erect to suberect, somewhat woody (subligneous) stolons that commonly give the plant a ‘bushy,’ rather than matted, appearance in the field (Figure 34). This character has been underemphasized in many floristic and taxonomic publications, despite its importance in the identification of A. umbrinella. The subligneous stolons are often shorter and less conspicuous in high elevation populations, which also tend to have darker
(olive-brown vs. tan) phyllaries, and may appear intermediate between typical *A. umbrinella* and *A. media*. Long-standing confusion between this species and other pale- or brownish-phyllaried species (e.g., *A. pulvinata*, *A. borealis*, *A. media*, some forms of *A. rosea*) has led to a relatively high proportion of misidentifications of this species in provincial herbaria, clouding an understanding of its distribution in British Columbia and rendering many published distribution maps (e.g., Douglas 1995, Douglas *et al.* 2002b) inaccurate.

The holotype of *Antennaria macounii* Greene, which was collected near Revelstoke, appears to represent a hybrid between *A. umbrinella* and *A. media*, and it is here recognized as such (as *Antennaria x macounii*). There are no collections of *A. umbrinella* from the areas surrounding the collection site, however, which suggests that *A. umbrinella* is either present in the area and has been missed by collectors, or that the species had a strictly historical presence in the area but has left some traces of its presence in apomictic lines derived from historical hybridization.

![FIGURE 34. Erect, subligneous stolons around the bases of the flowering stems in *Antennaria umbrinella*.](image)

A = Goward 81-1238D, Merritt, BC, UBC; B = McIntosh, Sadler, Dyer, Safford, & Robinson 2011_36, Princeton, BC, UBC.
Antennaria Species Excluded from the British Columbia Flora

i. Antennaria alpina (L.) Gaertn.  ALPINE PUSSYTOES

   This name has long been applied in floristic and taxonomic literature to Antennaria collections from subalpine, alpine, subarctic, and arctic areas of North America, including British Columbia and elsewhere in the Pacific Northwest (Douglas 1995, Douglas et al. 1998). In some cases (e.g., Hitchcock et al 1955, Hitchcock & Cronquist 1973, Packer 1983, Douglas et al. 1989, Douglas 1995), the name has been used to represent the taxon that is here treated as A. media (usually treating it as A. alpina var. media), but in other cases (e.g., Bayer & Stebbins 1993, Cody 1996, Chmielewski 1998, Douglas et al. 1998, Bayer 2006) the name has been used to represent a morphology/taxon that is distinct from the concept of A. media presented herein. Where these two names have been treated as separate taxa, only the presence (alpina) or absence (media) of scarious flags on the cauline leaves has been presented as a consistently distinguishing character. Scarious
leaf flags are widespread and variable throughout typical *A. media*, however, even being present on a number of the type specimens (see Figure 8), and thus this is an inappropriate character for taxonomic use in this case. What has been presented as *A. alpina* in northwestern North America is here distributed among three other taxa: *A. media*, *A. borealis*, and *A. pulvinata*. The concept of *A. alpina* is here restricted to European/amphi-Atlantic populations that are morphologically similar to *A. media* but which are considerably disjunct geographically and likely of independent origin. The lectotype of *Gnaphalium alpinum* L. (Anon. s.n. [LINN!]), which is the basionym of *Antennaria alpina* [L.] Gaertn., differs from *A. borealis* (which accounts for most of what has been called *A. alpina* in North America) in its narrow, wholly brownish phyllaries and green, glabrous leaf surfaces.

ii. *Antennaria corymbosa* E.E. Nelson  FLAT-TOPPED PUSSYTOES

This species of the western United States was reported for British Columbia by Björk (2008) and Björk & Goward (2011) based on a single collection from Wells Gray Provincial Park [*Björk 9415 (UBC!)*]; the species otherwise ranges no farther north than central Idaho and northeastern Washington, ca. 400 km and ca. 600 km to the south, respectively. *Antennaria corymbosa* is a sexual, diploid species that has been hypothesized by both Bayer (1987b, 1989a, 2006) and Chmielewski *et al.* (1990b) to be among the progenitor species of the *A. rosea* agamic complex. It has been considered morphologically distinct due to the presence of several characters, including the broad, whitish phyllaries with a dark basal or central spot, the ascending capitula that form a subcorymbose or corymbose capitulescence, and the relatively long, slender basal leaves. The species is more morphologically consistent throughout its range than most other *Antennaria* species, exhibiting minimal morphological variation among populations (Chmielewski *et al.* 1990a). It is also distinctive ecologically, being a species that commonly inhabits moist to wet meadows and fens (Cronquist *et al.* 1994, Bayer 2006) – an otherwise unusual habitat for
Antennaria. The British Columbia specimen was indeed collected from a fen and possesses phyllary and capitula characters that are suggestive of *A. corymbosa* (e.g., phyllaries with a dark basal spot and broad, pale apices); however, the specimen diverges from *A. corymbosa* in the morphology of the basal leaves, which are much shorter (5-7 mm) than has been reported for *A. corymbosa* (18-45 mm) (Bayer 2006). Further to this, the *elegans* form of *A. rosea*, which has not been recognized or discussed in recent floristic literature, similarly possesses the phyllary and capitulescence characters that are otherwise associated with *A. corymbosa*. As the identification of the British Columbia specimen was largely determined based on characters that are not unique to *A. corymbosa*, and given that it departs from the morphology of *A. corymbosa* in the only character that is considered reliable for identification (basal leaf size/shape), the species is excluded from the treatment presented here. The large disjunction from the remainder of the species’s range (which is otherwise confined to areas south of the Pleistocene glacial limits) further calls into question its identification, or, at least, suggests the need for incontrovertible specimen evidence. The specimen instead appears to represent an example of the *elegans* morphotype of *A. rosea*, to which it is attributed here.

iii. *Antennaria densifolia* A.E. Porsild  DENSE-LEAVED PUSSYTOES

This northern, sexual, diploid species of the unglaciated portions of Alaska, the Yukon Territory, and the Northwest Territories has been reported for British Columbia by Chmielewski (1996), Bayer (2006), and Björk & Goward (2011). Review of specimens pertaining to these reported *A. densifolia* populations in B.C., and comparison to material of *A. densifolia* from the Yukon Territory, indicates that they fall well within the circumscription of *A. pulvinata* presented here. Specifically, the involucres of true *A. densifolia* are conspicuously smaller (4.5-5.5 mm) than those of the B.C. specimens that have been attributed to the species (5.5-6.5 mm), and the basal leaves are smaller, denser, and typically (though not always) much more strongly imbricate. The
morphology of the British Columbia specimens is thus entirely consistent with collections of *A. pulvinata* in the province, to which they are attributed in this treatment. Such a conclusion is not unexpected given that the large disjunction of *A. densifolia*, whose distribution is so closely aligned with unglaciated regions of Beringia, into previously glaciated regions of southern Canada would be very unexpected, and nearly unprecedented. A reported population of *A. densifolia* from western Montana was analyzed by Chmielewski (1996) and similarly determined to be *A. pulvinata*. Conversely, a report of *A. densifolia* from Montana in Bayer (1989c) was determined to truly represent this more northerly taxon by the author; however, the applicable specimens were not reviewed as part of this study and the veracity of this claim is unknown.
CHAPTER THREE:  
A TAXONOMIC REVISION OF SYMPHYOTRICHUM (ASTERACEAE: ASTEREAE) IN BRITISH COLUMBIA, CANADA

3.1 Introduction

The taxonomic complexity of *Symphyotrichum* Nees [= *Aster* subg. *Symphyotrichum* (Nees) A.G. Jones] has long confounded attempts to develop a consistent taxonomic system for the genus in North America. The frustration encountered by taxonomists attempting to either develop infrageneric taxonomies or define species limits within the genus is well captured by the following quote by Asa Gray in 1882 (Semple & Brouillet 1980), describing his feelings following a taxonomic review of North American *Aster* (which included *Symphyotrichum* at the time) and *Solidago*:

“I am not very confident of the success of my prolonged endeavours to put these genera into proper order and to fix the nomenclature of the older species; and in certain groups absolute or practical definition of the species by written characters or descriptions is beyond my powers.”

Nearly 140 years after it was written, much of the sentiment expressed in the quote remains as true as it was in the late 19th century, despite the extraordinary advancements made in understanding the evolutionary processes and associated biosystematics of the genus during the intervening years.

Until recently, species that are here attributed to the genus *Symphyotrichum* were recognized as comprising a diverse New World radiation of the widespread genus *Aster*, which is also very diverse and widespread across Eurasia. Such was the case in 1943, when A. Cronquist identified a group of western North American *Aster* species (the *Aster foliaceus* group [= *Symphyotrichum* subg. *Symphyotrichum* sect. *Occidentales* of this treatment]) as taxonomically
unresolved and in need of monographic attention. The widespread adoption of the taxonomy presented in his monograph of the group greatly influenced the taxonomic understanding of the subgenus for the following 50 years. During the latter part of the 20th century, important workers in the genus such as A.G. Jones, J.C. Semple, L. Brouillet, and G.A. Allen attempted to further elucidate the taxonomy of Aster subg. Symphyotrichum, with some (e.g., Semple & Brouillet 1980) advocating for the recognition of segregate genera to represent natural and identifiable groupings of species within the complex. The comprehensive review of the taxonomy of North American Aster presented in Nesom (1994) argued for the dissolution of traditional concepts of Aster in North America and the elevation of many subgenera to genus status. The resultant taxonomic system was adopted by virtually all subsequent taxonomic and floristic authors, and its adoption by Brouillet et al. (2006) in the Flora of North America Project formally entrenched it as the default taxonomic system for the group among North American taxonomists and florists. Thus, since the 1990s, the genus Symphyotrichum has been treated as distinct from the genus Aster as well as from the numerous other Aster segregates that were elevated to genus in Nesom (1994). However, despite clarity on the relationships among these newly-erected genera, many of the taxonomic complexities inherent within the Symphyotrichum clade itself remain unresolved.

The complexity that is inherent in the genus, both in British Columbia and elsewhere in North America, stems primarily from the following factors: (i) extensive hybridization among the species, including inter-subgeneric hybridization between subgenera of different base chromosome numbers; (ii) widespread auto- and allopolyploidy, ranging from tetraploid to duodecaploid, with relatively few diploid species in many regions (i.e., in the Pacific Northwest); (iii) close morphological similarity of many of the taxa, with few or no singular diagnostic features for many of the component species; (iv) extensive morphological variation of most taxa in association with both geography and environmental influences, often affecting characters that are
considered important for identification; and (v) a long-standing presence in the horticultural trade and the resultant production of many ornamental hybrids and cultivars, some of which have escaped and become established within the natural range of the genus. Further to this, the limitations provided by herbarium specimens (i.e., inability to assess intrapopulation variation, absence of important characters from specimens) have presented additional difficulties for herbarium taxonomists attempting to define and describe the component taxa or better understand their relationships to each other. These factors together render the morphological discrepancies between many species difficult, or in some cases nearly impossible, to detect. As a result, *Symphyotrichum* has remained among the most taxonomically complex genera in North America for nearly 200 years.

This study endeavours to provide a regional context to the taxonomy of this group by specifically focusing on its diversity in the western Canadian province of British Columbia – a region that has otherwise rarely featured prominently in taxonomic studies of the genus. The most comprehensive taxonomic and floristic studies of the genus in British Columbia are Douglas 1995 and Douglas *et al.* 1998, both of which were based largely on concepts adopted from Hitchcock *et al.* (1955) and Hitchcock & Cronquist (1973) and provided few novel taxonomic advances to understanding the genus in the province. The limitations of applying the taxonomic concepts of Hitchcock *et al.* (1955) and Hitchcock & Cronquist (1973) to British Columbia, and the uncertainty surrounding the definitions of the component taxa, ultimately resulted in the extensive incorporation of poorly identified herbarium material into the studies of Douglas (1995) and Douglas *et al.* (1998). The study presented herein thus has the following objectives to address this issue: (i) to review the entirety of the collection of British Columbia *Symphyotrichum* specimens housed at the UBC herbarium to determine the extent to which existing identifications accurately correspond with established taxonomic systems; (ii) to identify and address uncertainties
surrounding accepted species concepts and the limitations of applying these concepts to British Columbia material; (iii) to develop a revised taxonomic system that better represents the diversity of *Symphyotrichum* taxa in British Columbia; (iv) to refine the descriptions of the characteristics (morphological, ecological phytogeographic) that define the component taxa as they are represented in this taxonomic system; and (v) to present the results as a revised monographic treatment of the genus in British Columbia.

### 3.2 Materials & Methods

A review of existing taxonomic literature pertaining to *Symphyotrichum*, along with extensive field and herbarium experience of the author and others, revealed that the accepted taxonomy of the genus did not reflect the taxonomic variation observed in British Columbia. Most notably, many taxa were poorly defined and many identifications seemed incompatible with the circumscriptions of the taxa that they purported to represent. In response, I reviewed more than 1000 specimens of *Symphyotrichum* housed at the University of British Columbia herbarium (UBC), including over 700 collections from British Columbia, in order to revise the taxonomy in a way that better captures the variation within that province. This collection is among the largest, most comprehensive (geographically, temporally, and taxonomically), and most active collections of vascular plant specimens in British Columbia, and was thus considered an ideal collection from which to base this type of taxonomic study. The review of herbarium specimens was augmented by additional field collection in a variety of areas of the province, including the Rocky Mountains, Kootenays, Peace River lowlands, Georgia Depression, and Cascade Mountains. In addition to the specimens at UBC, digital specimens were also reviewed from ALA (University of Alaska 2016), the Consortium of Pacific Northwest Herbaria (CPNH 2016), and the Intermountain Region Herbarium Network (IRHN 2016). Review of these latter collections primarily represented
specimens from jurisdictions adjacent to British Columbia and provided important context for the collections at UBC. Note that only specimens housed at UBC are specifically referenced and mapped within the provided taxonomic treatment as these were the specimens that informed the taxonomic conclusions. In addition, all accessible type specimens pertaining to the taxa accepted here for British Columbia were reviewed digitally via JSTOR Global Plants (JSTOR 2016), and assigned to a particular taxon based on morphological, phytogeographic, and in some cases ecological (where noted) similarity. Reviewed specimens were mapped within the British Columbia portion of their range, and an approximation of the regional distribution of each species was constructed based on specimens that were reviewed for this study in combination with distributional information that has been published in other regional floras and monographs.

Based on the results of this study, a revision of the taxonomy of *Symphyotrichum* in British Columbia is presented below which also incorporates new insights into the morphology, distribution, and ecology of the component taxa. The morphological descriptions of the taxa have been revised and are presented herein, and nomenclatural issues are addressed. A fully revised dichotomous key that incorporates these changes is provided to aid in the identification of specimens.

### 3.3 Discussion

The taxonomic challenges presented by *Symphyotrichum* in British Columbia were thoroughly reviewed, assessed, and addressed as part of this study, which has resulted in a number of alterations to the taxonomy, nomenclature, distribution, and identification criteria of the component taxa in the province. The intraspecific morphological variation encountered during this study was supportive of the roles of hybridization and environmentally-induced plasticity as contributing significantly to these taxonomic challenges, and much of the taxonomic uncertainty
that remains in this treatment reflects the influence of these two factors. However, although uncertainties remain, the thorough specimen review associated with this study has enabled significant clarification of the taxonomy of the genus in British Columbia, particularly as it relates to alternative taxonomic approaches that have been presented in Hitchcock et al. (1955), Douglas et al. (1998), Brouillet et al. (2006), and other influential regional floras.

In comparison to Douglas et al. (1998), which represents the most recent floristic treatment of the genus that is specific to the Pacific Northwest, the number of accepted species-level taxa in British Columbia is increased from 17 to 23. The increase in taxa is the result of several factors, including the discovery of native taxa that were previously unknown to occur in the province (S. cusickii, S. falcatum var. commutatum, S. hendersonii), the recognition of established exotic species that had previously been overlooked (S. novi-belgii var. novi-belgii), and the recognition of hybridogenous taxa that have been attributed to other taxa in previous treatments (S. x columbianum, S. x maccallae). For example, the dissolution of the species S. subspicatum that is presented here has resulted in the recognition of three taxa (the native, hybridogenous S. x maccallae, the native S. douglasii, and the exotic S. novi-belgii var. novi-belgii) that had long been overlooked within the regional Symphyotrichum flora due to their morphological similarity to other taxa as well as uncertainties around the morphological definitions of most of the taxa that comprise Symphyotrichum subg. Symphyotrichum sect. Occidentales. Similarly, the recognition of S. x columbianum in this treatment raises the status of a population of asters that have in the past been attributed to the provincially rare S. ascendens but which are clearly misplaced within that species based on the glandularity of the plants. Given the extremely limited distribution of this taxon in the province and its association with threatened habitats within its range, its taxonomic recognition is crucial to ensuring the its conservation within the province.
In addition to recognizing the presence of additional *Symphyotrichum* species in British Columbia, this study also addressed numerous issues related to the nomenclature, morphological descriptions, distributional information, and identification criteria of the component taxa. In particular, the taxon that has widely been treated as *Symphyotrichum foliaceum* in almost all previous floristic and taxonomic accounts was found not to correspond with the holotype of the name. The long history of attribution of the name ‘foliaceum’ (or ‘foliaceus’) to this taxon thus reflects historical misapplication of the name, and the name should accurately be considered a junior synonym of the name ‘subspicatum. This has necessitated several nomenclatural changes in the species, including the renaming of the species as *S. frondeum* and the description and typification of a new variety that would correspond with the taxon formerly treated as *S. foliaceum var. foliaceum* (here designated as *S. frondeum var. caurinum*.)

The poorly defined species concepts that have arisen as a result of this nomenclatural and taxonomic confusion surrounding the species of *Symphyotrichum* have resulted in a considerable rate of misidentification of herbarium specimens in herbaria, and this was noted as a widespread issue within the UBC herbarium during this study. The reidentification of many specimens clarified the geographic distributions of many of the species in the province, particularly narrow-leaved species such as *S. boreale, S. bracteolatum, S. lanceolatum subsp. hesperium*, and *S. spathulatum* for which there was an unusually high rate of misidentifications detected. The revised distribution maps presented in this treatment reflect an improved understanding of the morphological definitions of the component taxa and their identification criteria that was gained over the course of this study, and the presentation of a fully revised dichotomous identification key for the species that incorporates these insights is intended to improve the rate of correct identification of these taxa in the future. Thus, this taxonomic revision aids in further understanding of the genus *Symphyotrichum* in British Columbia and elsewhere in the Pacific
Northwest by clarifying species concepts, providing a comprehensive discussion of the taxonomy, ecology, nomenclature, and distribution of the taxa, and providing a dichotomous key to their identification.

3.4 Conclusions

The *Symphyotrichum* flora of British Columbia has been investigated taxonomically by several past authors, but has never been the focus of the type of detailed, comprehensive specimen review that is presented in this study. As a result, many misconceptions, uncertainties, and erroneous conclusions have persisted in the literature that have resulted in an incomplete understanding of the genus in the province. The taxonomically and geographically focused study presented here resulted in the detection of species that had been overlooked in the region due to misidentification or taxonomic confusion, corrected long-standing nomenclatural issues, refined the boundaries between the component taxa in a way that better defined them, and corrected incorrect distributional information that resulted from the issues surrounding misidentification. The recognition of a previously undetected, potentially threatened species (*S. x columbianum*) and a potentially invasive exotic species (*S. novi-belgii var. novi-belgii*) demonstrate the critical importance of the taxonomic review presented here, as these insights provide opportunities for either conservation of endangered populations or eradication of invasive populations. Although many uncertainties remain in the taxonomic understanding of this genus, the breadth of the information presented here provides a wealth of potential hypotheses to help guide future experimental research into the systematics, ecology, and evolution of this group of plants. Thus, such herbarium-based taxonomic research as is presented here can be seen as a critical component in all aspects of biodiversity research and conservation biology, as well as an indispensable element in helping to direct future research.
3.5 Taxonomic Treatment

**SYMPHYOTRICHUM** Nees  ASTER

Annual to perennial herbs, usually short- to long-rhizomatous (taprooted in annual spp.), often colonial. **Stems** solitary to several, sometimes clumped from a branched caudex or woody cormoid stem base, prostrate (rare) to ascending or erect, simple to few-branched or much-branched distally, glabrous to pubescent (often becoming glabrescent proximally), pubescence often arranged in lines proximal to leaf bases, (3) 10-120 (200) cm tall. **Leaves** basal and cauline, glabrous to short-pubescent, margins usually stiff-ciliate with antrorse hairs; basal and lower cauline leaves often withering prior to anthesis, often petiolate or subpetiolate (rarely sessile to subsessile), lanceolate or elliptic to ovate or occasionally cordate, apices obtuse to acute or acuminate, margins entire to serrate; cauline leaves often reduced distally, sessile or subsessile, linear or lanceolate to oblanceolate or ovate, apices obtuse to acute or acuminate, bases sometimes clasping or auriculate. **Capitulescences** of solitary terminal capitulum or a few- to much-branched raceme or panicle, sometimes subcorymbose, branches spreading or recurved (i.e., *S. ericoides*) to ascending; peduncle bracts 0-6 (25+), linear to elliptic or ovate, often recurved, sessile, apices sometimes minutely spinulose, bases sometimes clasping, distinct from or grading into phyllaries, distalmost sometimes enlarged and foliaceous. **Flowering heads** solitary to many; involucres campanulate to somewhat turbinate; phyllaries strongly graduated to subequal, in 3-6 series, often spreading-ciliate, faces glabrescent to pubescent, sometimes glandular, greenish to purplish, often whitish-hyaline over basal 1/4-2/3, apices sometimes minutely spinulose or rarely greenish-subulate; outer phyllaries linear or lanceolate to elliptic; inner phyllaries linear to linear-lanceolate or narrowly oblanceolate; ray florets 0 (*S. ciliatum*) or (10) 15-60 or 90-110 (*S. frondosum*), whitish or pinkish to bluish or purplish, laminae (1.5) 3-20 (21) mm; disc florets (5) 10-150+, yellowish, often becoming reddish or purplish in age, 5-lobed, lobes deltate to lanceolate.
Cypselae cylindric to obovoid or oblong (rarely oblanceoloid or obconic), compressed or not, yellowish to brownish to dark purplish-brown, (1-) 2- to 9-nerved, glabrous to sparsely or densely short-hairy; pappus of numerous barbellate bristles, bristles equal to subequal, whitish to tawny, sometimes reddish-tinged.

Species ca. 90-100 (23 spp. in B.C.). North America, Mexico, Caribbean, Central America, South America, c/e Asia; introduced in Europe. $x = 5, 7, 8, 13$.

The genus *Symphyotrichum* is widespread and highly diverse throughout North America, with a smaller number of species occurring south through the New World to South America and in eastern and central Asia (Brouillet *et al.* 2006). Within North America, centres of diversity for the genus include the eastern/midwestern United States and eastern Canada, the southern Great Plains, and the western United States/Pacific Northwest (BONAP 2018). The genus is relatively poorly represented in arctic and subarctic areas of the continent, although several locally-distributed taxa (*S. yukonense*, *S. pygmaeum*, *S. nahanniense*) are endemic to that region (Brouillet *et al.* 2006). Members of this genus are found in a wide variety of habitats, ranging from natural grasslands, prairies, shrub-steppe, dry forests, and other dry, upland habitats to ditches, wetlands, shorelines, estuaries, seacoasts, and other wet habitats. Many species are well-adapted to disturbed environments, and several have become established exotic species beyond their natural range. Indeed, several North American species have become problematic invasive species in Europe (Tutin *et al.* 1976, Botanical Society of Britain & Ireland 2018), where both natural species and garden-derived hybrids have spread along waterways, shorelines, and roadsides throughout the continent and displaced native species. The genus is well-known for its late flowering period, with most species flowering from July through October, or occasionally even into December. It is also well-known for its taxonomic complexity, which stems from extensive hybridization among the
species, widespread polyploidy (commonly 6x-12x), poorly-defined species limits, and pronounced morphological variation within taxa (due to both genetic and environmental factors).

Taxa that are here recognized as comprising the genus Symphyotrichum have long been incorporated into a broad definition of the genus Aster L., and are recognized as such in many floristic and taxonomic references. Following Nesom (1994), the genus Symphyotrichum Nees was widely resurrected to represent a diverse radiation of New World asters, while other British Columbia members of the genus were dispersed among the genera Canadanthus, Eucephalus, Eurybia, Ionactis, and Sericocarpus; only a single British Columbia species (Aster alpinus L.) now remains in the genus Aster. Within the genus Symphyotrichum itself, several systems of infrageneric classification have been proposed, and the following system is adopted here (Table 4), which is based on that presented in Brouillet et al. (2006):

### TABLE 4. Infrageneric classification of British Columbia Symphyotrichum species adopted in this treatment.
The placement of S. x columbianum in subg. Ascendentes is considered speculative and is based on its presumed progenitor taxa.

<table>
<thead>
<tr>
<th>Subg. Virgulus (n = 5)</th>
<th>Subg. Symphyotrichum (n = 7, 8)</th>
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<tbody>
<tr>
<td><strong>Sect. Grandiflori</strong></td>
<td><strong>Sect. Conyzopsis (n = 7)</strong></td>
</tr>
<tr>
<td>S. campestrum</td>
<td>S. ciliatum</td>
</tr>
<tr>
<td><strong>Sect. Eriocoei</strong></td>
<td>S. frondosum</td>
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<tr>
<td>S. ericoides</td>
<td>S. x maccallae</td>
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<tr>
<td>S. falcatum</td>
<td>S. boreale</td>
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<tr>
<td><strong>Subg. Ascendentes (n = 13)</strong></td>
<td><strong>Sect. Symphyotrichum (n = 8)</strong></td>
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<tr>
<td>S. ascendens</td>
<td>S. ciliolatum</td>
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<td>S. x columbianum</td>
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i. **Symphyotrichum** subg. **Virgulus** (Raf.) G.L.Nesom

Symphyotrichum subgenus Virgulus [= Aster subg. Virgulus (Raf.) A.G. Jones] has a base chromosome number of $n = 5$. It has sometimes been recognized at the generic level as the genus Lasallea Semple & Brouillet (Semple & Brouillet 1980), but this name is illegitimate and has subsequently been replaced by Virgulus (Reveal & Keener 1981). The three British Columbia
representatives of subg. *Virgulus* are recognized here as comprising two sections: sect. *Grandiflori* (Torr. & A. Gray) G.L. Nesom [= subsect. *Polyligulae* (Semple & Brouillet) G.L. Nesom] and sect. *Ericoidei* (Torr. & A. Gray) G.L. Nesom. Although the primary centre of diversity for this subgenus is eastern North America, particularly the eastern and southeastern United States (Brouillet *et al.* 2006, BONAP 2018), the subgenus also includes several species endemic to arctic and subarctic regions of the continent as well as widespread species of central and western North America. Many of the members of subg. *Virgulus* are characteristic of dry upland habitats, such as dry forests, grasslands, prairies, roadsides, and disturbed areas, although a few species (e.g., *S. falcatum*) are characteristic of wet habitats. British Columbia species of subg *Virgulus* range from diploid (*2n* = 10) to hexaploid (*2n* = 30). Hybridization within this subgenus is occasional [e.g., *S. campestre* × *S. ericoides* var. *pansum*; *S. ericoides* var. *pansum* × *S. falcatum* var. *falcatum*; *S. ericoides* var. *ericoides* × *S. novae-angliae*], with some of the resultant hybrids (e.g., *S. × amethystinum*) recognized as nothospecies. Inter-subgeneric hybridization between subg. *Virgulus* and members of subg. *Symphyotrichum* has produced subg. *Ascendentes* (Allen 1985, Allen & Eccleston 1998, Brouillet *et al.* 2006).

**ii. *Symphyotrichum* subg. *Ascendentes* (Ryd.) Semple**

This subgenus is the product of hybridization between members of *Symphyotrichum* subg. *Virgulus* (*n* = 5) and subg. *Symphyotrichum* (*n* = 8), and has a resulting base chromosome number of *n* = 13 (Allen 1985, Allen & Eccleston 1998, Brouillet *et al.* 2006). The subgenus is generally recognizing as comprising two species: the widespread western North American *S. ascendens*, which ranges north into British Columbia, and the localized Californian endemic *S. defoliatum* (Parish) G.L. Nesom (Brouillet *et al.* 2006). A third species (*S. × columbiaeanum*) is recognized in this treatment as belonging to subg. *Ascendentes* based on its apparent origin as an intra-subgeneric
hybrid between subg. *Virgulus* and subg. *Symphyotrichum*, although its sub-generic placement is somewhat speculative given the absence of ploidy information about the taxon.

### iii. *Symphyotrichum* subg. *Symphyotrichum*

*Symphyotrichum* subg. *Symphyotrichum*, with a base chromosome number of $n = 8$, is the largest subgenus in North America and comprises the vast majority of *Symphyotrichum* species in British Columbia. Three sections of the subgenus are recognized in this treatment as pertaining to British Columbia species: sect. *Conyzopsis* (2 native species in B.C.), sect. *Occidentales* (8 native species in B.C.), and sect. *Symphyotrichum* (6 native and 2 exotic species in B.C.). These are discussed individually below.

**Sect. *Conyzopsis* (Torr. & A. Gray) G.L. Nesom**

This section is well-differentiated morphologically, ecologically, and cytologically from other sections of subg. *Symphyotrichum*. It is a small section that is comprised of only three species, two of which (*S. ciliatum*, *S. frondosum*) occur in British Columbia. Members of sect. *Conyzopsis* are distinguished from other sections of subg. *Symphyotrichum* by their annual habit, filiform (or absent) ray florets that are arranged in 4-5 rows, typical association with saline or alkaline shoreline habitats, and a base chromosome number of $n = 7$ (vs. $n = 8$ in other sections). These considerable distinctions have sometimes resulted in the recognition of these species as belonging the separate genus *Brachyactis* Ledeb. or as *Aster* subg. *Conyzopsis* (Torr. & A. Gray) A. Gray, although phylogenetic studies (Xiang 1994, Semple *et al.* 2002) consistently place the group as nested within the larger clade that is here recognized as subg. *Symphyotrichum* and not in an isolated position relative to the rest of the clade.
Sect. *Occidentales* (Rydb.) G.L. Nesom

This section comprises 12 species of western North America, eight of which occur in British Columbia. Although consistently identified as deserving of infrageneric recognition, the exact nomenclature pertaining to the group varies among different authorities. For example, when placed in the genus *Aster*, this clade has been recognized as subg. *Dumosi* sect. *Foliacei* Torr. & A. Gray (e.g., Semple & Brouillet 1980) or as part of subg. *Symphyotrichum* sect. *Salicifolii* Torr. & A. Gray (e.g. Jones 1980). Conversely, when placed in the genus *Symphyotrichum*, this clade has alternatively been recognized as subg. *Symphyotrichum* sect. *Cordifolii* subsect. *Occidentales* ser. *Foliacei* (Rydb.) Semple (e.g. Semple et al. 2002). Although typically recognized as distinct from other sections of subg. *Symphyotrichum*, there are no consistent morphological synapomorphies that distinguish members of this subgenus from other related subgenera, although all species are united by their centre of distribution and abundance being in western North America.

Sect. *Symphyotrichum*

This large section of subg. *Symphyotrichum* represents a number of species with a primarily eastern North American centre of distribution, several of which also range westwards into areas of western North America. Even in wide-ranging species such as *S. laeve* and *S. lanceolatum*, however, the greatest morphological and cytological variation is commonly found in eastern North America, suggesting this region as the centre of diversity of the clade. Of the 36 species occurring in North America (Brouillet et al. 2006), eight members of this section occur in British Columbia, although two of these (*S. novi-belgii* var. *novi-belgii*, *S. pilosum* var. *pilosum*) occur only as established exotic species in the Georgia Depression. Members of this section with distinctly petiolate basal and proximal cauline leaves (i.e., *S. ciliolatum*, *S. laeve* subsp. *laeve*, *S. x maccallae*) are commonly separated as subsect. *Heterophylli* (Nees) Semple, as is done in this
treatment, although, as noted in Brouillet *et al.* 2006, the subsectional phylogeny of sect. *Symphyotrichum* is largely unresolved.

**Dichotomous Key to *Symphyotrichum* Species in British Columbia**

1a. Phyllaries slightly to densely stalked-glandular; peduncles, distal stems, and often distal cauline leaves usually moderately to densely stalked-glandular..............................2

2a. Phyllaries subequal, usually moderately to densely stalked-glandular; peduncles, upper stems, and often distal stem leaves moderately to densely stalked-glandular; stems never with lines of hairs proximal to the leaf bases; plants of upland grasslands and open forests .................................................................4. *S. campestre*

2b. Phyllaries moderately to strongly graduated, scarcely to sparsely stalked-glandular; peduncles, upper stems, and distal cauline leaves eglandular to very sparsely stalked-glandular; stems occasionally with lines of hairs proximal to the leaf bases; plants of valley-bottom wetlands, swales, and shorelines.........................8. *S. x columbianum*

1b. Plants eglandular throughout........................................................................3

3a. Plants annual (rarely short-lived perennial in *S. frondosum*); ray florets either absent or 90-110, filiform, and exceeding the involucre by 1.5-2 mm.................................4

4a. Ray florets absent; outer phyllaries linear-lanceolate to linear-oblanceolate, apices acuminate..................................................................................................................6. *S. ciliatum*

4b. Ray florets 90-110, whitish to pinkish, filiform, slightly exceeding the involucre; phyllaries narrowly oblanceolate, apices obtuse to acute or mucronate.......................14. *S. frondosum*

3b. Plants perennial; ray florets (10) 15-60, strap-shaped, exceeding the involucre by 3-18 mm ..........................................................................................................................5

5a. Stems glabrescent or uniformly pubescent, stem hairs not arranged in lines proximal to the leaf bases along mid- and distal stem.................................................................6

6a. Ray florets usually whitish, rarely faintly pinkish- or purple-tinged..................7
7a. Phyllary apices acute to acuminate, greenish-subulate; stems from a branched caudex, caudex not cormoid; peduncle bracts 7-25+; plants introduced, rare and local in sw BC [Vancouver].................................................................20. *S. pilosum*

7b. Phyllary apices minutely whitish-spinulose; caudex usually enlarged, woody, cormoid; peduncle bracts 0-4+; plants native, common throughout sc, se, and ne BC, rarely along lower Fraser River in sw BC (*S. falcatum*)......................................................8

8a. Capitulescence branches usually spreading to slightly recurved, capitulae moderately to strongly secund on branches; peduncles usually shorter than involucres; involucres 3-4 (5) mm; ray florets (8) 10-18 (20), laminae 3-8 mm; plants generally of dry upland habitats.....................................................11. *S. ericoides*

8b. Capitulescence branches usually ascending, generally terminated by a single capitulum and often with several smaller subterminal capitulae, capitulae not to slightly secund on branches; peduncles usually exceeding the involucres; involucres (3) 4-5 (8) mm; ray florets (15) 20-35, laminae 6-11 mm; plants generally of shorelines and other wet habitats.................................12. *S. falcatum*

6b. Ray florets generally pinkish, bluish, or purplish, occasionally whitish (usually as sporadic albino individuals in otherwise dark-rayed populations).................................9

9a. Stems glabrous to glabrescent; stems and leaves distinctly glaucous; leaves somewhat thick, fleshy.................................................................16. *S. laeve*

9b. Stems sparsely to densely pubescent; stems and leaves not glaucous, leaves not thickened or fleshy.................................................................10

10a. Basal and lower cauline leaves distinctly petiolate, blades ovate-lanceolate or ovate to deltate or strongly cordate, base of blade rounded or truncate to strongly cordate.................................................................7. *S. ciliolatum* [in part]

10b. Basal and lower cauline leaves petiolate or not, blades linear-lanceolate to broadly elliptic or obovate, base of blade cuneate to attenuate.................................11

11a. Phyllaries broad, rounded, strongly graduated; some phyllary apices usually minutely whitish-spinulose..................................................1. *S. ascendens*

11b. Phyllaries lanceolate to elliptic, apices acute to acuminate, subequal; phyllary
apices never minutely whitish-spinulose..................................................12

12a. Hairs of stem short, appressed..................................................3. *S. bracteolatum*
12b. Hairs of stem spreading, whitish, either soft and pilose or stiff and hirsute....13

13a. Hairs of stem whitish, pilose; plants of se BC [s Columbia Mts.]. ..............
...........................................................................................................9. *S. cusickii*
13b. Hairs of stem stiff, hirsute; plants of ne BC [east of the Rocky Mts.]. .......
...........................................................................................................21. *S. puniceum*

3a. Stem with hairs arranged in lines proximal to leaf bases, at least on mid-stem........14

14a. Basal and lower cauline leaves distinctly petiolate, blades ovate-lanceolate or deltate to strongly cordate, base of blade rounded or truncate to cordate...7. *S. ciliolatum* [in part]
14b. Basal and lower cauline leaves petiolate or not, blades linear-lanceolate to broadly elliptic or obovate, base of blade cuneate to attenuate.................................................................15

15a. Ray florets usually whitish, sometimes pinkish- or purplish tinged.................16

16a. Peduncles uniformly pubescent; leaves linear to linear-lanceolate; plants primarily of bogs, fens.................................................................2. *S. boreale*
16b. Peduncles with lines of spreading hairs, lines often reaching the base of the involucre; leaves linear to lanceolate or oblanceolate; plants primarily of shorelines.................................................................17. *S. lanceolatum* [in part]

15b. Ray florets pinkish, bluish, or purplish, rarely whitish (usually as sporadic albino individuals in otherwise dark-rayed populations).........................................................17

17a. Basal leaves usually persistent through anthesis.........................................18

18a. Involucre graduated, outer phyllaries linear-lanceolate and 1/5-1/3 the length of the inner phyllaries.................................................................22. *S. spathulatum*
18b. Involucres not graduated, outer phyllaries linear-lanceolate to broadly elliptic and usually 3/4+ the length of inner phyllaries........................................19

19a. Outer phyllaries largely or entirely foliaceous and lacking whitish hyaline bases, only inner phyllaries usually with whitish hyaline bases (these grade into
foliaceous outer phyllaries)..........................................................13. *S. frondeum*

19b. Outer phyllaries largely or entirely with extensive whitish hyaline bases……..20

20a. Lower cauline leaves long- to short-petiolate, blades broadly lanceolate to ovate-lanceolate; plants of sc and se BC...............................18. *S. x maccallae*

20b. Lower cauline leaves subsessile to short-petiolate, blades linear-lanceolate or elliptic-lanceolate or oblanceolate or narrowly obovate; plants of coastal BC...

..............................................................................................................21

21a. Middle and upper cauline leaves serrate, slightly thickened and fleshy;
phyllaries ascending or erect, occasionally spreading at the tips; plants of the central and northern coast.........................23. *S. subspicatum* [in part]

21b. Middle and upper cauline leaves entire, usually not thickened and fleshy;
phyllaries ascending to loosely spreading; plants of the south coast [Georgia Depression.................................................................19. *S. novi-belgii* [in part]

17b. Basal leaves usually withering prior to anthesis...........................................22

22a. Involucres strongly graduated, outer phyllaries < 1/2 length of inner phyllaries;
phyllary apices rounded to obtuse; plants primarily of coastal habitats in sw BC…

....................................................................................................................5. *S. chilense*

22b. Involucres not graduated, outer phyllaries 3/4+ length of inner phyllaries; phyllary apices acute to acuminate; plants widespread throughout s, c, and ne BC...........23

23a. Peduncles with lines of spreading hairs, lines often reaching the base of the involucre.................................................................17. *S. lanceolatum* [in part]

23b. Peduncles uniformly pubescent throughout.................................................24

24a. Cauline leaves linear to linear-lanceolate or linear-oblanceolate, bases not clasping or rarely subclasping.............................................10. *S. douglasii*

24b. Cauline leaves lanceolate or oblanceolate to broadly elliptic or obovate, bases distinctly clasping......................................................25

25a. Outer phyllaries largely or entirely foliaceous, whitish hyaline base (if present) usually < 1/3 total phyllary length; plants rare in se BC..............
15. *S. hendersonii*

25b. Outer phyllaries largely or entirely with extensive whitish hyaline bases; plants of coastal BC.................................................................26

26a. Middle and upper cauline leaves serrate, slightly thickened and fleshy; phyllaries ascending or erect, occasionally spreading at the tips; plants of the central and northern coast.........................23. *S. subspicatum* [in part]

26b. Middle and upper cauline leaves entire, usually not thickened and fleshy; phyllaries ascending to loosely spreading; plants of the south coast [Georgia Depression]...........................................19. *S. novi-belgii* [in part]

Monograph of *Symphyotrichum* Species in British Columbia

1. *Symphyotrichum ascendens* (Lindl.) G.L. Nesom

**WESTERN ASTER;** Long-leaved Aster; Longleaf Aster; Intermountain Aster; Western American-aster


*Aster denudatus* Nuttall (1841: 292). Type:—UNITED STATES. Wyoming (?): Lewis’ River, about latitude 42°, Rocky Mountains, no collection date reported, *Nuttall s.n.* (holotype BM!, isotypes PH!, GH!); *A. adscendens* Lindl. var *denudatus* Torrey & A.Gray (1841: 111).

*Aster denudatus* var. *ciliatifolius* Nuttall (1841: 293). Type:—UNITED STATES. Wyoming (?): Lewis’ River, Rocky Mountains, no collection date reported, *Nuttall s.n.* (holotype BM!); *A. adscendens* Lindl. var. *ciliatifolius* Torrey & A.Gray (1841: 111).

*Aster nuttallii* Torrey & A.Gray (1841: 126). Type:—UNITED STATES. Wyoming (?): plains of the Lewis River, near the Rocky Mountains, no collection date reported, *Nuttall
s.n. (lectotype [designated on specimen by A.G. Jones (1983)] PH!; isolecotyopes BM!, GH!, FI!).

*Aster adsurgens* Greene (1900: 212). Type:—UNITED STATES. Colorado: Cimarron, 30 August 1896, *Greene s.n.* (lectotype [designated on specimen by A.G. Jones (1982)] NDG!, isolecotyopes NDG!).

*Aster distichophyllus* Greene (1900: 213). Type:—UNITED STATES. Colorado: below Marshall Pass, 04 September 1896, *Greene s.n.* (holotype NDG!, isotypes NDG!).

*Aster pratincola* Greene (1900: 215). Type:—UNITED STATES. Colorado: Gunnison River, Gunnison, 01 September 1896, *Greene s.n.* (lectotype [designated on specimen by A.G. Jones (1984)] NDG!, isolecotyopes NDG!).

*Aster spithameus* Greene (1900: 215). Type:—UNITED STATES. Colorado: Gunnison Valley, 10 September 1890, *Greene s.n.* (holotype NDG!).


*Aster limoniifolius* Greene (1900: 222). Type:—UNITED STATES. Nevada: Pine Valley, 25 July 1896, *Greene s.n.* (holotype NDG!).

*Aster oxylepis* Greene (1900: 223). Type:—UNITED STATES. Nevada: Humboldt River, below Palisade, 24 August 1896, *Greene s.n.* (lectotype [designated on specimen by A.G. Jones (1984)] NDG!, isolecotyopes NDG!).

*Aster subracemosus* Rydberg (1900: 394). Type:—UNITED STATES. Montana: Helena, 08 September 1890, *Kelsey s.n.* (holotype NY!).


*Aster orthophyllus* Greene (1905: 146). Type:—UNITED STATES. Colorado: Gunnison, 23 July 1901, *C.F. Baker 570* (holotype NDG!, isotypes RM!, RSA!, Gi!).
Aster griseus Greene (1905: 147), auct. non Kuntze (1891), nom. illeg. Type:—UNITED STATES. Colorado: west of Denver, Bear Creek, near Sisty’s, 1875, Greene s.n. (holotype NDG!); A. subgriseus Rydberg (1917: 884).

Aster halophilus Greene (1909: 8). Type:—UNITED STATES. Utah: Beck’s Hot Springs, at 4500 ft., 06 September 1906, Garrett 2056 (holotype NDG!).

Aster leucopsis Greene (1909: 8). Type:—UNITED STATES. Utah: Salt Lake City, 4400 ft., 05 September 1905, Garrett 1694 (holotype NDG!, isotype NY!).

Aster deserticola Macbride (1918: 36). Type:—UNITED STATES. California: San Bernardino County, 3150 ft., 03 October 1917, Spencer 629 (holotype GH, isotypes NY!, BM!).

Plants perennial, long-rhizomatous, colonial. Stems usually not from a branched caudex, solitary to several, ascending to erect, simple to few-branched distally, sparsely to densely strigose (especially distally), sometimes becoming glabrescent proximally, greenish to greyish-green, 20-60 cm tall. Leaves basal and cauline, basal and proximal cauline withering prior to anthesis or persistent, little reduced distally, apices acute, margins entire and flat, usually minutely stiff-ciliate with antrorse hairs, faces glabrous to sparsely or moderately strigose; basal and proximal cauline leaves sessile to subpetiolate, linear-oblanceolate to oblanceolate, bases attenuate to cuneate, 5-15 cm; mid- and distal cauline sessile, leaves linear or linear-oblanceolate to narrowly lanceolate, bases cuneate to rounded, 30-70 (90) mm. Capitulescences generally open, narrow, often leafy, branches ascending; peduncle bracts 1-6 (8) per peduncle, linear to oblanceolate, often somewhat recurved, usually minutely spine-tipped with a whitish spine, distinct from phyllaries, (2) 3-10 (11) mm. Flowering heads few to numerous; involucres campanulate, (4) 5-7 mm; phyllaries unequal, in 3-5 series, erect to recurved, spreading-ciliate, faces glabrescent or sparsely to densely strigose, margins hyaline proximally, green zones obovate to elliptic and restricted to distal 1/3-1/2 (3/4); outer phyllaries oblanceolate to spatulate, apices usually rounded to obtuse and often subspinulose with a small whitish spine (especially outermost), 1-3 mm; inner phyllaries linear-
lanceolate to narrowly oblanceolate, apices acute to acuminate, 3-5 mm; ray florets (10) 15-40, bluish to violet, laminae 8-13 mm; disc florets 25-65 (80), yellowish to purple-tinged, lobes deltate, 4-6 mm. **Cypselae** cylindric to obovoid, not compressed, brownish, 3- to 5-nerved, densely short-hairy, 2-3.5 mm; pappus whitish to tawny, 4-7 mm.

Flowering (Jun) Jul-Oct. Moist to dry meadows, grasslands, open forests, shorelines, and disturbed areas, often on alkaline soils, in the steppe and lower montane zones; 750-850 m. Rare in southeast BC [Rocky Mountain Trench]. BC east to SK, south to CA, AZ, NM. $2n = 26, 32, 34, 36, 48, 52, 54 \ [2x-4x]$ (Allen 1985).

*Symphyotrichum ascendens* is widespread and common throughout much of the western United States, ranging north into the Canadian prairie provinces, but is decidedly rare and localized in British Columbia. It is known only from the southern Rocky Mountain Trench in B.C. (Figure 39), in an area that is known to support disjunct populations of several of other prairie species such as *Townsendia hookeri* and *Symphyotrichum falcatum* var. *commutatum*. It has previously been described or mapped as occurring more widely across the southern interior of British Columbia, as in Douglas (1995), Douglas et al. (1998), and Douglas et al. (2002b), but most or all records away from the Rocky Mountain Trench are here attributed to hybridization between *Symphyotrichum campestre* and *S. ericoides* var. *pansum* or to the apparently hybridogenous taxon that is here treated as *S. x columbianum*. The distinctly graduated involucres, in which the outer phyllaries are conspicuously shorter than the inner (Figure 36) are usually a reliable morphological indicator of *S. ascendens* within its range, and largely distinguish it from other co-occurring *Symphyotrichum* taxa. This character is also represented in both of the hybrids *S. campestre* x *S. ericoides* var. *pansum* and *S. x columbianum*, however, but these can be distinguished by the *ericoides*-like branching pattern and smaller, more numerous capitulae of the former, or the
presence of minute glands on the phyllaries and sometimes peduncles of the latter. Other distinctive morphological characteristics of *S. ascendens* include the typically rounded and minutely spine-tipped phyllary apices (Figure 36: B), the uniformly and often densely strigose stems and leaves (i.e., stem hairs not arranged in lines from the leaf bases) (Figure 37), the linear to narrowly lanceolate cauline leaves (Figure 38), and the overall grey-green appearance of the stems, leaves, and involucres.

*Symphyotrichum ascendens* has often been treated as a subspecies of *S. chilense* in the past (e.g., Cronquist 1943, Cronquist 1955, Hitchcock & Cronquist 1973), based solely on the shared character of graduated involucres (Allen 1985). These two taxa are otherwise very different morphologically, ecologically, and biogeographically, however, and are only distantly related, with *S. ascendens* being a stabilized allopolyploid derived from past hybridization (perhaps on multiple occasions) between *S. spathulatum* and *S. falcatum* (Allen 1985; Allen and Eccleston 1998). In contrast, *S. chilense* is part of a polyploid complex of the Pacific Northwest that also includes *S. douglasii*, *S. subspicatum*, *S. frondeum* [= *S. foliaceum*], and *S. spathulatum* (Cronquist 1943). As the parental species of *S. ascendens* are representative of different subgenera within *Symphyotrichum* (*S. spathulatum* = subg. *Symphyotrichum*; *S. falcatum* = subg. *Virgulus* [Raf.] G.L. Nesom), *S. ascendens*, as well as the related *S. defoliatum* (Parish) Nesom [= *Aster bernardianus* H.M. Hall] of California, have been assigned to the subgenus *Ascendentes* (Rydb.) Semple (Semple et al. 2002) or the genus *Virgulaster* Semple (Semple 1985). These names encompass taxa that have been derived from hybridization between subg. *Virgulus* and subg. *Symphyotrichum*.

The base chromosome number of *Symphyotrichum* subg. *Ascendentes* (*n* = 13) belies its hybrid origin, as it results from the hybridization between species with a base chromosome numbers of *n* = 8 (subg. *Symphyotrichum*) and *n* = 5 (subg. *Virgulus*) (Allen 1985, Allen &
Eccleston 1998). Although the cytotype of British Columbia populations is unknown, diploid and tetraploid populations are of different geographic distributions, with diploid [$2n = 26$] populations in the Great Basin and Sierra Nevada areas, and tetraploid [$2n = 56$] populations in the Rocky Mountains and on the Great Plains (Allen 1985). British Columbia populations, which are restricted to the southern Rocky Mountain Trench, are biogeographically more aligned with prairie elements rather than Great Basin elements, suggesting that these populations are most likely tetraploid; however, no B.C. collections were included in the cytological analyses of Dean (1966) or Allen (1985), and this conclusion remains speculative. There are no published morphological differences between diploid and tetraploid populations of *S. ascendens*, but there is pronounced morphological variation present across the species’ range that does not correspond with cytotype. This variation is primarily expressed in the shape and relative length of the phyllaries (ranging from rounded and strongly graduated to narrower and less clearly graduated) and the shape of the lower cauleine leaves (usually linear to oblanceolate, rarely more broadly oblanceolate, narrowly elliptic, or even spatulate). Furthermore, *S. ascendens* is known to backcross with both of its parental diploids (*S. spathulatum, S. falcatum*) as well as hybridize with *S. bracteolatum, S. ericoides* var. *pansum*, and representatives of the *S. subspicatum* complex (Allen 1985), resulting in additional morphological variation beyond that which is inherent within the species.

The specific epithet of *S. ascendens* often appears as ‘*adscendens*’ in many older taxonomic and floristic works. This is an orthographic variation that arose through a misspelling that appeared in A. P. de Candolle’s *Prodromus Systemis Naturalis Regni Vegetabilis* in 1836, following an earlier (1834) publication in J. W. Hooker’s *Flora Boreali-Americana* that established the spelling as ‘*ascendens*.’ The name ‘*adscendens*’ is now considered invalid (Dean and Chambers 1983) and the spelling ‘*ascendens*’ has been resurrected as the correct nomenclature for the species.
FIGURE 36. Variation in involucre and phyllary characteristics among B.C. specimens of *Symphyotrichum ascendens*. A = example with narrower and more acute phyllaries (*Lomer 8561*); B = example with broader and more rounded phyllaries (*Lomer 4601*).

FIGURE 37. Variation in the density of hairs on the distal stems and branches of *Symphyotrichum ascendens*. A = example of sparsely strigose stem (*Fodor 787b*); B = example of densely strigose stem (*Lomer 8561*). Note the uniformity of the hairs, which are not arranged in lines proximal to the leaf bases.
FIGURE 38. Example specimens of *Symphyotrichum ascendens* from British Columbia, showing overall habit and structure (A = Lomer 8561; B = Lomer 4601).

FIGURE 39. Distribution of British Columbia specimens of *Symphyotrichum ascendens* that were reviewed for this study (left), and approximate distribution of the species in northwestern North America (right).
2. *Symphyotrichum boreale* (Torr. & A. Gray) Á. Löve & D. Löve

**NORTHERN BOG ASTER;** Rush Aster; Common Rush Aster; Rush-like Aster; Slender White Aster

*Aster salicifolius* Richardson in Franklin (1823: 748), *auct. non* Lamarck (1783: 306), *nom. illeg.* Type:—not located.


*Aster franklinianus* Rydberg (1910a: 141). Type:—CANADA. Northwest Territories: Slave Lake, no collection date reported, *Richardson s.n.* (possible syntype K! [on mixed sheet, databased as *A. junceus*]).


**Plants** perennial, long-rhizomatous with very slender rhizomes, colonial. **Stems** not from a branched caudex, solitary to several, erect, usually simple to few-branched (sometimes much-branched distally), glabrescent proximally, sparsely to moderately pubescent distally, pubescence usually longer and arranged in lines from leaf bases on mid- and distal stem, (5.5) 13-30 (100) cm tall. **Leaves** basal and cauline, basal and proximal cauline withering prior to anthesis, not or little reduced distally, sessile, linear to linear-lanceolate, apices acute, bases subclasping, margins entire (rarely subserrulate) and revolute, minutely stiff-ciliate with antrorse hairs, faces glabrous, (20) 30-70 mm. **Capitulescences** open, narrow to somewhat broad and corymbiform, sometimes leafy, branches ascending; peduncle bracts 1-4 per peduncle, linear to linear-lanceolate, apices not minutely spine-tipped, distinct from phyllaries, (2) 4-15 mm. **Flowering heads** solitary to several; involucrees narrowly campanulate to somewhat turbinate, (4) 5-6 mm; phyllaries unequal to subequal, in 4-5 series, erect, eciliate to sparsely ciliate (especially proximally), faces glabrous, margins usually hyaline proximally (often reddish-tinged), green zones linear-lanceolate to
lanceolate and restricted to distal 1/2-2/3; outer phyllaries lanceolate to oblong-lanceolate, apices obtuse to acute, 3-4 mm; inner phyllaries linear to narrowly lanceolate, apices acute to acuminate, 4-5.5 mm; ray florets (15) 25-35 (41), whitish to pink-tinged (sometimes more strongly pinkish), laminae (7) 10-15 (20) mm; disc florets (15) 25-30 (40), pale yellowish (becoming pinkish or purplish in age), lobes deltate, 3.5-5 (6) mm. Cypselae obovoid, compressed, yellowish to purplish or brownish, 3- to 5-nerved, sparsely short-hairy, 0.5-2 mm; pappus whitish, 2.5-6.5 mm.

Flowering Jul-Sep (Oct). Moist to wet bogs, shorelines, streambanks, meadows, fens, and marsh edges, especially in areas of calcareous influence, in the montane and boreal zones; (350) 600-1200 m. Frequent in central and east-central BC [Coast Mts. east to Rocky Mts., north to Williston Lake, south to Shuswap Lake] and infrequent in northeast BC [Liard Basin, Fort Nelson lowlands]. AK east to NL, south to WA, ID, CO, WV, NJ. 2n = 16, 32, 48, 64 [2x-8x] (Semple et al. 2006).

This northern, wetland-associated aster is fairly common across the central interior of British Columbia, particularly through Fraser-Nechako Plateau and Cariboo-Chilcotin regions of the central interior, but is scarce and local in northern B.C. (Figure 42). Within its area of occupation in the province, S. boreale is typically associated with relatively cool boreal or sub-boreal wetlands such as bogs and fens, and is less frequent in warmer-water wetlands such as marshes. The geographic extent of the species in British Columbia has previously been overstated, with some publications (e.g., Douglas 1995; Douglas et al. 2002b) suggesting it to be widespread across southern parts of the province, south to the U.S. border; however, all reports from south of the South Thompson River and Yoho National Park appear to be the result of misidentifications of other narrow-leaved species such as S. lanceolatum subsp. hesperium, S. bracteolatum, and S. douglasii.
Symphyotrichum boreale is typically a rather small, gracile, slender-leaved species with long, very slender rhizomes (Figure 41: B); it is most likely to be confused with other similarly slender-leaved species such as S. bracteolatum and S. lanceolatum subsp. hesperium. It is usually distinguishable from both of these larger, more robust species, however, by the type and distribution of hairs on the stems and peduncles. In S. boreale, the peduncles, inflorescence branches, and distal stems are glabrescent or sparsely to densely, but uniformly, short-pubescent, with longer, spreading, whitish hairs arranged in lines proximal to the leaf bases on the mid-stem (Figure 40; Figure 41: A). In S. bracteolatum, which overlaps in distribution with S. boreale in the southern Chilcotin region and northern portions of the Columbia Mountains, the stem and peduncle pubescence is short and uniform throughout, without the presence of lines of longer pilose hairs. The stems of S. lanceolatum, in contrast, have conspicuous lines of pilose hairs along their entire length, including on the peduncles, with the areas between the lines of pubescence usually glabrous or nearly so. There are no areas of short, uniform pubescence on the stems of S. lanceolatum, except in some cases on the distalmost 1-2 mm of the peduncles (between the involucre and the distalmost peduncle bract). Other characters distinguishing these three species include the colour of the ray florets (S. boreale: white to pink-tinged; S. bracteolatum: usually pinkish, occasionally whitish; S. lanceolatum: whitish to bluish or pinkish), the typical shape of the capitulescence (S. boreale: corymbose to corymbose-paniculate; S. bracteolatum: racemose to racemose-paniculate; S. lanceolatum: narrowly to broadly paniculate), and, in S. lanceolatum, the presence on most heads of an enlarged, foliose peduncle bract immediately beneath the involucre that equals or exceeds the involucre. It should be noted that much of the literature on S. boreale suggests that the stems and peduncles are glabrous or nearly so (e.g., Brouillet et al. 2006); this is not representative of most British Columbia populations, which are consistently (though variably) pubescent, at least distally (Figure 41: A). Symphyotrichum boreale appears to hybridize rarely and locally with S.
*bracteolatum* and *S. falcatum var. falcatum* in the Chilcotin region of central British Columbia, as demonstrated by intermediate specimens from this region observed during this study. It is also known to hybridize with *S. puniceum var. puniceum* in central Canada, forming the hybrid *S. x longulum* (Sheld.) G.L. Nesom (Shinners 1942). Although the overlap in distribution between *boreale* and *puniceum* in British Columbia is minimal and restricted to the far northeast, such a hybrid may potentially occur in the province and should be considered when assessing specimens from areas that support both parental species.

The species presented here as *S. boreale* has passed under several names in the past, causing considerable confusion around the correct nomenclature for the taxon. It has often been treated as *Aster junciformis* in many floristic and taxonomic publications (e.g., Davis 1952, Hitchcock *et al.* 1955, Scoggan 1957, Moss 1959, Hultén 1968, Hitchcock & Cronquist 1973, Porsild & Cody 1980), based on type specimens collected in western Montana, but this name is now considered a junior synonym of *Aster borealis* (= *S. boreale*). Furthermore, based on annotations by A. G. Jones on at least one of the isotypes, *junciformis* is potentially representative of introgression from *Symphyotrichum lanceolatum* subsp. *hesperium* into *S. boreale* and thus may be better treated as a hybrid. The name *junciformis* is retained in *S. boreale* here, however, due to the lack of published evidence for its hybrid nature. The name *junceus* has also been attributed to this taxon in the past, but this name, which was based on a European garden-grown plant from northeastern North America, has subsequently been considered to represent a potential *S. boreale* x *S. novi-belgi* hybrid, or even a variation of *S. novi-belgii* itself (Shinners 1941, Semple *et al.* 2002). The name *junceus* is thus not presented here under synonymy for *S. boreale*, despite its occasional use in the past.

Some narrow-leaved aster populations from north-central Canada that have sometimes been recognized as the species *Aster franklinianus* (e.g., Rydberg 1910a, Porsild & Cody 1980)
are here treated as synonymous with *S. boreale*. These populations differ from typical *A. boreale* populations primarily in their larger size and more robust stature, as well their ‘bluish’ ray florets and subequal phyllaries with whitish margins at the base (Porsild & Cody 1980). Several of the published distinguishing characters, particularly those associated with the involucre and phyllaries, are within the range of variation of typical western *S. boreale*, however, while the differences in habit and ray floret colour may be attributable to either variation in *S. boreale* or hybridization between *S. boreale* and another species such as *S. lanceolatum* subsp. *hesperium*. As a thorough review of these plants, which occur outside of British Columbia, was beyond the scope of this study, the name is here included in synonymy with *A. boreale*, with which they are most consistent morphologically.

**FIGURE 40.** Variation in phyllary and involucre characteristics of *Symphyotrichum boreale*. A = Raup & Correll 11550; B = C.E. Thompson CT-73.
FIGURE 41. Morphological characteristics of *Symphyotrichum boreale*. A = typical stem vestiture, with hairs arranged in lines (C.E. Thompson CT-73); B = overall structure and habit (Björk 9685).

FIGURE 42. Distribution of British Columbia specimens of *Symphyotrichum boreale* that were reviewed for this study (left), and approximate distribution of the species in northwestern North America (right).
3. *Symphyotrichum bracteolatum* (Nutt.) G.L. Nesom

**EATON’S ASTER; Oregon Aster; Bracted Aster; Eaton’s American-aster**

*Aster bracteolatus* Nuttall (1841: 293). Type:—UNITED STATES. Wyoming (?): Lewis River, Rocky Mountains, no collection date reported, *Nuttall s.n.* (holotype BM!);


*Aster microlonchus* Greene (1902: 278). Type:—CANADA. British Columbia: Chilliwack Valley, 18 August 1901, *Macoun 26384* (lectotype [designated on specimen by Shinners (1946)] NDG!).


*Aster roseolus* Rydberg (1910a: 141). Type:—UNITED STATES. Montana: Melrose, 1895, *Rydberg 2817* (holotype NY!).

Plants perennial, usually short-rhizomatous, usually cespitose. Stems usually not from a branched caudex, solitary to several, erect, simple to much-branched distally, sparsely to moderately puberulent (sometimes glabrous or glabrescent, especially proximally), pubescence not arranged in lines from leaf bases, (20) 40-100 cm tall. Leaves basal and cauline, basal and proximal cauline withering prior to anthesis, little reduced distally, sessile, linear or lanceolate to narrowly oblong, apices obtuse to acute, bases cuneate and often subclasping or even auriculate (especially distally), margins usually entire (rarely serrulate) and slightly revolute, sometimes minutely stiff-ciliate with antrorse hairs, faces glabrous to sparsely puberulent, 20-70 (100) mm. Capitulescences dense to open, narrow, leafy, branches ascending; peduncle bracts 1-6, linear to lanceolate or narrowly oblanceolate, apices not minutely spine-tipped, distinct from phyllaries or distalmost sometimes grading into phyllaries, 5-20 mm. Flowering heads few to numerous; involucre shallowly campanulate, 5-8 mm; phyllaries subequal, in 3-5 series, often spreading (especially outer), eciliate to minutely ciliate, faces glabrous to sparsely puberulent.; outer phyllaries oblanceolate to oblong, apices acute to obtuse, often slightly enlarged and subfoliaceous, margins sometimes hyaline on proximal 1/2 or less, green zones oblanceolate to elliptic, 4-5 mm; inner phyllaries linear-lanceolate to narrowly oblanceolate, apices usually acute to acuminate, margins hyaline proximally, green zones oblanceolate and restricted to distal 1/2-2/3, 5-6 mm; ray florets 20-40, usually pinkish or pinkish-purple (sometimes whitish), laminae 7-15 mm; disc florets 35-60+, yellowish (becoming purplish in age), lobes deltate, 4.5-5 mm. Cypselae cylindric to ovoid, not compressed, brownish, 1- to 2-nerved, sparsely to densely short-hairy, 2.5-3.5 mm; pappus whitish, 5-6 mm.

Flowering (Jun) Jul-Sep. Moist to wet streambanks, meadows, shorelines, marshes, sloughs, ditches, and gravelly areas in the lowland, steppe, and montane zones; (30) 300-1000 (1450) m. Locally frequent in south-central and southeast BC [north to the Chilcotin region,
Cariboo Mountains, upper Fraser River watershed], rare in southwest BC [lower Fraser River]. BC east to SK, south to CA, AZ, NM. $2n = 16, 18, 32, 37, 48, 64$ [2x–8x] (Allen 1984).

*Symphyotrichum bracteolatum* is a relatively common and widespread aster of warm, valley-bottom wetlands and shorelines throughout the southern interior, but is decidedly rare in coastal areas of the province (Figure 45). It is a member of the taxonomically challenging sect. *Occidentales* of subg. *Symphyotrichum*, and has traditionally been poorly defined ecologically, morphologically, and biogeographically in the context of British Columbia due to its similarity to other members of this polyploid complex. Its status has been further clouded by occasional hybridization with other species of *Symphyotrichum*, which blurs the already poorly-defined morphological distinctions between the taxa. For example, putative hybrids between this species and *S. boreale*, *S. falcatum* var. *falcatum*, *S. laeve* subsp. *laeve*, *S. lanceolatum* subsp. *hesperium*, and *S. novi-belgii* var. *novi-belgii* have been collected from British Columbia and were reviewed as part of this study, as were examples of extralimital hybrids with *S. ascendens* (from Montana) and *S. chilense* (from California). Widespread hybridization with other taxa has also been reported by Allen (1984) [with *S. ascendens*] and Cronquist et al. (1994) [with members of the ‘*A. foliaceus*’ (= *S. frondeum*) and ‘*A. subspicatus*’ complexes].

Past taxonomic and floristic treatments dealing with this species in British Columbia (e.g., Douglas 1995, Douglas et al. 1998) have traditionally emphasized the pinkish ray florets, narrow leafy capitulescence with numerous capitulae, and narrow entire leaves (Figure 43) in its diagnosis, but all of these characteristics are at least occasionally, and sometimes commonly, expressed in other similar taxa. As these characters are challenging to use in practice, the stem vestiture is here recognized as the most effective means of distinguishing *S. bracteolatum* from these other similar taxa in the province, although the other characters mentioned may be considered supportive. The stem hairs of *S. bracteolatum* are short, appressed, and uniformly distributed throughout the
typically reddish stem, and do not occur in lines proximal to the leaf bases (Figure 44) as is characteristic of other species with which it could be confused such as *S. lanceolatum* subsp. *hesperium*, *S. douglasii*, *S. spathulatum*, *S. novi-belgii* var. *novi-belgii*, and *S. frondeum*. The use of stem vestiture in the identification of this species has been mentioned briefly in several taxonomic and floristic publications (e.g., Cronquist 1943, Hitchcock *et al.* 1955, Hitchcock and Cronquist 1973, Cronquist *et al.* 1994), but has not generally been emphasized as diagnostic. The specimens reviewed for this study, however, clearly demonstrated that this character is not only consistent among specimens of *S. bracteolatum* in B.C., but is not matched by any other provincial member of the genus; thus, it is here treated as the primary distinguishing feature of this species. From a cytological perspective, *S. bracteolatum* is further distinctive among related species in B.C. in being primarily diploid, including throughout its range in British Columbia, with polyploids (mostly tetraploid, rarely as high as octoploid) being infrequent and usually with narrowly defined or sporadic distributions outside of the province (Allen 1984). Other similar regional taxa, in contrast, are mostly polyploid, and range from tetraploid to duodecaploid (Allen 1984).

*Symphyotrichum bracteolatum* has long been treated under the specific epithet *eatonii* in floristic and taxonomic literature, but the name *Aster bracteolatus* is now confirmed to have nomenclatural priority (Brummitt 2011). Although *bracteolatus* has sometimes been attributed to this taxon previously (e.g., Dean & Chambers 1983, Allen 1984, Douglas *et al.* 1989, Douglas 1995), the name *eatonii* remained predominant through most of the 20th century due to confusion over the identification of the type specimen of *bracteolatus* and its potential hybrid origins. The type specimen of *Aster bracteolatus* is now known to have been correctly attributed to this taxon, and to not be of hybrid origin (Reveal *et al.* 2009), thus necessitating its nomenclatural adoption. Although Reveal *et al.* (2009) proposed that *bracteolatus* be rejected in favour of conserving the widely accepted epithet *eatonii*, despite the former’s nomenclatural priority, the name was
subsequently established as the definitive name for this species by the Nomenclature Committee for Vascular Plants (Brummitt 2011). As a result, most recent floristic and taxonomic publications, such as Baldwin et al. (2012), have subsequently restored the name *bracteolatum* for this taxon.

**FIGURE 43. Involucre and stem hair characteristics of *Symphyotrichum bracteolatum*.** *A* = phyllary and involucre characteristics; *B* = uniform, crisped hairs on reddish stem. Both images are of UBC V213912.
FIGURE 44. Example specimen of *Symphyotrichum bracteolatum* from British Columbia, showing overall habit and structure (*Eastham s.n.*).

FIGURE 45. Distribution of British Columbia specimens of *Symphyotrichum bracteolatum* that were reviewed for this study (left), and approximate distribution of the species elsewhere in northwestern North America (right).
4. *Symphyotrichum campestre* (Nutt.) G.L. Nesom

**WESTERN MEADOW ASTER**; Meadow Aster; Western Meadow American-aster


*Aster campestris* Nutt. var. *suksdorfii* Piper (1906: 572). Type:—UNITED STATES. Washington: along the Little Klickitat River, 05 October 1882, *Suksdorf 69* (holotype GH!).

**Plants** perennial, long-rhizomatous, cespitose to colonial. **Stems** often from a branched woody caudex, solitary to several, ascending to erect, simple to few-branched distally, glabrous to sparsely puberulent proximally, moderately to densely glandular-hairy distally (especially in capitulescence and on peduncles), 10-40 (70) cm tall. **Leaves** basal and cauline, basal and proximal cauline usually withering prior to anthesis, little reduced distally, sessile, linear-lanceolate to narrowly ob lanceolate, apices acute and usually mucronulate to subspinulose, bases cuneate to subclasping, margins entire and flat to slightly revolute, minutely stiff-ciliate with antrorse hairs, faces glabrous to sparsely strigose and stalked-glandular distally, 20-50 (80) mm. **Capitulescences** somewhat open, relatively narrow, somewhat leafy, branches spreading to ascending; peduncle bracts 2-4 (8), linear to narrowly lanceolate, apices minutely spine-tipped with a whitish spine, moderately to densely stalked-glandular, distinct from phyllaries, 3-8 mm. **Flowering heads** generally few;
involucres campanulate to cylindro-campanulate, 5.5-8 mm; phyllaries unequal to subequal, in 3-4 series, usually spreading to reflexed, eciliate to minutely ciliate, faces moderately to densely stalked-glandular; outer phyllaries narrowly lanceolate, apices acuminate and usually subspinulose with a whitish spine, margins usually hyaline on proximal 1/4-1/3, 3-5 (6) mm; inner phyllaries linear to linear-lanceolate, apices acuminate, margins hyaline on proximal 1/2-2/3, green zones oblanceolate to elliptic, 5-7 mm; ray florets 15-31, violet to purplish, laminae (5) 6-15 mm; disc florets 25-40, yellowish (becoming purplish in age), lobes deltate, 4.5-6 mm. **Cypselae** narrowly obovoid, somewhat compressed, pale brownish or reddish-brown, faintly 3- to 4-nerved, moderately to densely short-hairy, 2-2.5 mm; pappus tawny, 4-6 mm.

Flowering Jul-Sep (Oct). Dry grasslands, meadows, open forests, and disturbed areas in the steppe and montane zones; 600-1200 m. Common in south-central BC [north to the Chilcotin area, Shuswap Lake], locally frequent in southeast BC [southern Rocky Mountain Trench]. BC east to AB, south to CA, NV, CO. **2n = 10 [2x]** (Brouillet *et al.* 2006).

In a genus renowned for its taxonomic complexity and the difficulties associated with delimiting the boundaries of the component taxa, *Symphyotrichum campestre* stands apart as an unusually distinctive and well-defined species, both within the context of the British Columbia flora and beyond. It is an extensively glandular species, unlike any co-occurring member of the genus in the province, with the distal stems, leaves, peduncles, and phyllaries all moderately to densely stipitate-glandular (Figure 46: B). Within B.C., only *S. x columbianum* is also characterized by such glandularity, although in that species it is restricted to the peduncles and (especially) phyllaries. *Symphyotrichum x columbianum* is easily distinguished from *S. campestre*, however, by being only sparsely and inconspicuously glandular on the distal part of the plant (vs. conspicuously and densely glandular throughout the stems and phyllaries in *S. campestre*), having
more extensively glabrescent stems, and, most importantly, having strongly graduated phyllaries that are much more reminiscent of species such as *S. ascendens* or *S. chilense* than *S. campestre* (phyllaries somewhat unequal to subequal, but never strongly graduated, in *S. campestre* [Figure 46: A]). Although geographically sympatric, these two species are further distinguished ecologically, with *S. campestre* being a species of dry upland habitats (e.g., grasslands, open forests) and *S. x columbianum* being a species of wet, valley-bottom meadows, swales, lacustrine and fluvial shorelines, and wetland edges. The similarity of *S. campestre* and *S. x columbianum* is reflected in the presumption of the role of the former species in the hybrid origin of the latter (Brouillet *et al.* 2006).

Populations in the western United States with moderately strigose leaves have sometimes been segregated as *S. campestre* var. *bloomeri*, leaving British Columbia populations attributable to the nominate var. *campestre* (e.g., Hitchcock *et al.* 1955, Abrams & Ferris 1960, Hitchcock & Cronquist 1973, Douglas 1995, Douglas *et al.* 1998). This is a weakly defined variety, however, and has been relegated to synonymy with *campestre* by several recent authors (e.g., Cronquist *et al.* 1994, Brouillet *et al.* 2006). As the investigation of this variation, which occurs south of British Columbia, is beyond the scope of this treatment, and since some specimens within British Columbia approach the morphology associated with it, *bloomeri* is synonymized here with *campestre*. 
FIGURE 46. Phyllary and involucre characteristics (A) and densely stipitate-glandular peduncles (B) of *Symphyotrichum campestre* (McIntosh, Weston, Safford, & Bunge 2012_220).

FIGURE 47. Example specimen of *Symphyotrichum campestre* from British Columbia, showing overall habit and structure (McIntosh, Weston, Safford, & Bunge 2012_220).
FIGURE 48. Distribution of British Columbia specimens of *Symphyotrichum chilense* that were reviewed for this study (left), and approximate distribution of the species elsewhere in northwestern North America (right).

5. *Symphyotrichum chilense* (Nees) G.L. Nesom

**PACIFIC ASTER**, Common California Aster, California Aster, Coast Aster, Pacific American-aster


*Aster menziesii* Lindley in Hooker (1834b: 17). Type:—UNITED STATES. “north-west coast of America”, collection date not reported, *Menzies s.n.* (not located).

*Aster chamissonis* A. Gray in Wilkes (1874: 341). Type:—not located.


**Plants** perennial, long-rhizomatous, cespitose to colonial. **Stems** not from a branched caudex, usually solitary, erect, few- to much-branched distally, glabrous or glabrescent proximally,
sparsely to moderately hirsute distally, pubescence usually arranged in lines from leaf bases on mid- and distal stem, usually greenish to reddish-tinged, 40-100 (120) cm tall. **Leaves** basal and cauline, basal and proximal cauline usually withering prior to anthesis, little to moderately reduced distally, relatively thick and sometimes fleshy, margins entire to coarsely crenate-serrate and flat to slightly revolute, sometimes minutely stiff-ciliate with antrorse hairs, faces glabrous to sparsely puberulent, often somewhat fleshy; basal and proximal cauline leaves subpetiolate to short- or long-, lanceolate or oblanceolate to elliptic or spatulate, apices obtuse to acute, bases attenuate to cuneate, petioles narrowly- to broadly-winged, 50-150 (200) mm; mid- and distal cauline leaves sessile, lanceolate or ovate-lanceolate to ovate or elliptic, apices generally acute, bases attenuate to cuneate and not or only slightly clasping the stem, (10) 25-120 mm. **Capitulescences** compact to open, narrow to pyramidal, usually leafy, branches spreading to ascending; peduncle bracts 4-7, lanceolate to elliptic, apices not minutely spine-tipped, usually distinct from phyllaries, 5-35 mm. **Flowering heads** several to numerous; involucres campanulate, 5-8 mm; phyllaries unequal, in 3-5 series, usually erect (apices sometimes spreading), eciliate to minutely ciliate, faces usually glabrous; outer phyllaries oblanceolate to oblong, apices broadly acute to obtuse or rounded, sometimes enlarged and foliaceous, margins usually hyaline on basal 1/2 or less, green zones oblanceolate to obovate or nearly orbicular, 3-5 mm; inner phyllaries linear-oblong, apices acute to acuminate, margins hyaline on basal 1/2-3/4, green zones oblanceolate, 5-6 mm; ray florets 15-40, violet, laminae 9-15 mm; disc florets 35-60+, yellowish (becoming purplish in age), lobes deltate, 4-8 mm. **Cypselae** cylindric to obovoid, not compressed, brownish, 2- to 4-nerved, densely short-hairy, 3.5-4.5 mm; pappus whitish to tawny, 4-8 mm.

Flowering (Jul) Aug-Oct. Moist to wet beaches, salt marshes, estuaries, rocky headlands, islets, coastal bluffs, meadows, shorelines, and streambanks in the lowland zone; 0-30 (200) m. Locally frequent in southwest BC [Vancouver Island, Georgia Depression], rare north to west-
Symphyotrichum chilense is the characteristic aster of littoral habitats along the west coast of Vancouver Island, and also occurs widely (though more locally) throughout the Georgia Depression (Figure 51). It is rare along the coast of B.C. north of Vancouver, although it has been collected rarely on the islands of Haida Gwaii; it is largely replaced ecologically by S. subspicatum north of Vancouver Island. Although primarily a species of marine and brackish shorelines and near-shore habitats, it also ranges locally inland at low elevations along major rivers and lakeshores (e.g., Kennedy River, Cameron Lake, Fraser River).

This species is one of several high-polyplid asters of southern and coastal regions of British Columbia, and distinguishing among these species can often be problematic given the prevalence of hybridization, environmentally-induced phenotypic plasticity, and the overall morphologic similarity of the various taxa. These other similar taxa in the region include S. douglasii, S. frondem var. caurinum [= S. foliaceum var. foliaceum of other treatments], S. subspicatum, S. lanceolatum subsp. hesperium (rare), and the introduced S. novi-belgii, of which S. subspicatum and S. novi-belgii are the most similar morphologically and ecologically to S. chilense. Symphyotrichum chilense is best distinguished from these other taxa by its characteristically broad, rounded, and strongly graduated phyllaries (Figure 49: B); all similar taxa in the region are characterized by narrower and more distinctly pointed phyllaries that are not or only slightly graduated. The leaves of S. chilense are typically rather broad and fleshy relative to these other taxa, and often markedly so, although specimens collected from low elevation freshwater habitats tend to have narrower, thinner leaves that approach those of other taxa (Figure 50: A). Among the similar sympatric species, S. frondem var. caurinum and S. douglasii are distinguished by their phyllary and involucre characters (Figure 77 and Figure 65, respectively),
as well as their narrower (often linear or nearly so) leaves and, in the case of *S. frondeum* var. *caurinum*, its occurrence in high-elevation montane habitats ([150] 600-2100 [2400] m) that are above those occupied by the low-elevation *S. chilense* (0-30 [200] m). *Symphyotrichum novi-belgii* and *S. subspicatum* are both distinguished from the ecologically-similar *S. chilense* by the more conspicuously clasping bases of the cauline leaves, as well as their subequal phyllaries.

Many specimens of *Symphyotrichum* from coastal British Columbia reviewed for this study are suggestive of local hybridization between *S. chilense* and other similar taxa. These hybrids typically combine the distinctive phyllary and involucre characteristics of *S. chilense* with morphological characteristics (leaf shape, overall habit) that are otherwise indicative of the other taxa. Specifically, *S. chilense* appears to hybridize with *S. novi-belgii* around the mouth of the Fraser River and in brackish environments elsewhere in the Georgia Depression, and rarely with *S. subspicatum* on Haida Gwaii. Potential hybridization with *S. douglasii* and *S. frondeum* var. *caurinum* on Vancouver Island is also suggested by specimens reviewed for this study but is more difficult to ascertain based only on the herbarium material at hand.

**FIGURE 49.** Stem and involucre characteristics of *Symphyotrichum chilense*. A = conspicuous lines of spreading hairs along the stems proximal to the leaf bases (this character is also shown by many related species); B = blunt, strongly graduated phyllaries. Both images are of Calder & MacKay 31951.
FIGURE 50. Variation in overall habit and structure of *Symphyotrichum chilense*. A = narrower-leaved plant from freshwater environment (Calder & MacKay 31951); B = broader-leaved plant from brackish environment (van Dieren & van Dieren 141).

FIGURE 51. Distribution of British Columbia specimens of *Symphyotrichum chilense* that were reviewed for this study (left), and approximate distribution of the species elsewhere in northwestern North America (right).
6. **Symphyotrichum ciliatum** (Ledeb.) G.L. Nesom

**RAYLESS ALKALI ASTER;** Rayless Annual Aster; Rayless Aster; Rayless Annual American-aster; Alkali American-aster


*Crinitaria ? humilis* Hooker (1834b: 24). CANADA. Alberta: “on the banks of the Saskatchewan, between Carlton House and Edmonton House”, no collection date reported, *Drummond s.n.* (holotype not located; possibly the same holotype as *Tripolium angustum* [K!]); *Linosyris ? humilis* (Hook.) Torrey & A. Gray (1841: 234).

*Conyza altaica* de Candolle (1836: 380). Type:—collection locality unknown, 1834, *C.A.Meyer s.n.* (holotype GDC!).

*Aster brachyactis* S.F. Blake in Tidestrom (1925: 564). Type:—not designated.

**Plants** annual, taprooted. **Stems** not from a branched caudex, solitary, simple to much-branched throughout, decumbent to ascending or erect, bluish- to yellowish-green (often reddish-tinged), glabrous to glabrescent, 7-70+ cm tall. **Leaves** basal and cauline, basal and proximal cauline withering prior to anthesis, gradually reduced distally, sessile, linear to linear-oblancoceolate, apices acute to acuminate, bases slightly dilated and rounded to clasping, margins entire to minutely serrulate and flat, minutely stiff-ciliate with spreading to antrorse hairs, faces glabrous, (10) 30-80 (100) mm. **Capitulescences** dense to somewhat open, narrow to pyramidal, leafy, branches
spreading and decumbent (proximally) to ascending or erect (distally); peduncle bracts 0-6, linear to linear-lanceolate, apices often minutely spine-tipped, sometimes grading into phyllaries, 2-7 mm. **Flowering heads** usually numerous; involucre narrowly campanulate, 5-7 (11) mm; phyllaries usually subequal (outer sometimes exceeding inner), in 3-4 series, loosely spreading, margins eciliate to sparsely ciliate proximally, faces glabrous; outer phyllaries linear-lanceolate to linear-oblanceolate, apices acute to acuminate, wholly foliaceous or margins hyaline proximally, green zones oblanceolate and restricted to distal 2/3-3/4, 3-6 (12) mm; inner phyllaries linear-lanceolate, apices acuminate, margins hyaline proximally, green zones (when present) linear-oblanceolate to oblanceolate and restricted to distal 1/4-1/2, 4-7 mm; ray florets absent; disc florets 10-15, whitish to pinkish or yellowish, lobes narrowly deltate, 3.5-5 mm. **Cypselae** obovoid to oblong, somewhat compressed, grayish to brownish or purplish, faintly 2- to 4-nerved, densely short-hairy, 1.5-2.5 mm; pappus whitish to pink-tinged, 4-6 mm.

Flowering Jul-Oct. Moist to wet, saline or alkaline sloughs, marshes, pond edges, shorelines, meadows, and disturbed areas in the lowland, steppe, and lower montane zones; (10) 270-950 m. Locally frequent in south-central BC [north to the Chilcotin region], infrequent in southeast BC [southern Rocky Mountain Trench], rare in northeast [Peace River lowlands] and southwest [lower Fraser Valley (adventive)] BC. AK east to NB, south to WA, UT, OK, PA; Eurasia. \(2n = 14\) [2x] (Brouillet et al. 2006).

*Symphyotrichum ciliatum*, which has long been known as *Aster brachyactis* in floristic and taxonomic literature, is a fairly common annual species of saline and alkaline habitats in the dry grasslands of the south-central interior. It also occurs locally in similar habitats of the southern Rocky Mountain Trench and the Peace River area (Figure 54). It is a potentially weedy species and has been collected as a waif in landscaping and disturbed areas of the south coast (e.g., Lower
Mainland; it is also a widespread adventive weed in portions of eastern North America, where it has spread eastwards in association with winter road-salting activities (Brouillet et al. 2006). The specific or varietal epithet *angustum* has sometimes applied to North American populations to distinguish them from the nominate form in Eurasia, but this is not generally adopted in recent North American taxonomic literature.

This species is closely related to the provincially much rarer *S. frondosum*, and the two species may potentially hybridize along the shores of warm, valley-bottom water bodies in the southern Okanagan Valley of British Columbia; see the account of *S. frondosum* for a more detailed discussion of their separation and potential hybridization. These two species, along with the eastern Canadian endemic *S. laurentianum* [Fern.] G.L. Nesom, are generally recognized as the sect. *Conyzopsis* of *Symphyotrichum* subg. *Symphyotrichum* (Brouillet et al. 2006) in North America. The three species differ dramatically from other members of subg. *Symphyotrichum*, particularly in their annual life history, reduced and filiform ray florets that are sufficiently reduced in some species (e.g., *S. ciliatum*, *S. laurentianum*) so as to appear absent, long pappus bristles that conspicuously exceed the disc florets, and a base chromosome number of $x = 7$ (vs. $x = 8$ in other members of the subgenus). These morphological and cytological characteristics have been interpreted by many past authors as being sufficient for the recognition of these species as either members of a subgenus that is separate from subg. *Symphyotrichum* (as *Aster* subg. *Conyzopsis* [Torr. & A. Gray] A. Gray), or, in some cases, as a distinct genus unto themselves (as *Brachyactis* Ledeb.). However, both morphometric (Jones and Young 1983) and molecular (Xiang 1994) studies have now confirmed the placement of these three species within subg. *Symphyotrichum* as either sister to, or derived from, sect. *Occidentales* (Semple et al. 2002).
FIGURE 52. Variation in habit and structure of *Symphyotrichum ciliatum*. A = taller, slender plants (*Krajina s.n.*); B = smaller and low, spreading plants (*Lomer 99-254*).

FIGURE 53. Involucre and phyllary characteristics of *Symphyotrichum ciliatum* (*Krajina s.n.*).
7. *Symphyotrichum ciliolatum* (Lindl.) Á. Löve & D. Löve

**LINDLEY’S ASTER;** Fringed Aster; Fringed Blue Aster; Fringed Purple Aster; Ciliolate Aster; Lindley’s Heart-leaved Aster; Lindley’s American-aster


*Aster lindleyanus* Torrey & A. Gray (1841: 122). Type:—CANADA. Saskatchewan: no specific locality reported, no collection date reported, *Drummond s.n.* (lectotype [designated on specimen by A.G. Jones (1989) NY!).


**Plants** perennial, long-rhizomatous, cespitose to colonial. **Stems** sometimes from a branched caudex, solitary to several, erect, few- to much-branched distally, glabrous or glabrescent to sparsely hirsute or strigillose, usually sparsely to moderately white-villous distally (pubescence typically arranged in lines from leaf bases), (10) 20-120 cm tall. **Leaves** basal and cauline, basal and proximal cauline withering prior to anthesis or persistent, usually strongly reduced distally, apices acute to acuminate and often mucronulate, margins coarsely serrate to somewhat crenate (especially distally) and flat, minutely stiff-ciliate with antrorse hairs, faces glabrous to sparsely hirsute, midveins glabrous to densely white-villous abaxially; basal leaves long-petiolate, ovate, bases rounded or truncate to shallowly cordate, petioles winged and long-ciliate (especially proximally), (25) 40-120 (270) mm; proximal cauline leaves petiolate, lanceolate or oblanceolate to ovate, bases cuneate to subcordate, petioles winged and long-ciliate (especially proximally), (25) 60-150 mm; distal cauline leaves sessile or subsessile, linear or linear-lanceolate to elliptic, bases cuneate and sometimes somewhat clasping, 18-75 mm. **Capitulescences** open, pyramidal, usually not leafy, branches ascending; peduncle bracts 0-4, linear to linear-lanceolate, apices often minutely spine-tipped, usually distinct from phyllaries, 3.5-5 mm. **Flowering heads** usually numerous; involucres campanulate, (4) 5-6.5 mm; phyllaries unequal, in 4-5 series, erect, linear to linear-lanceolate or linear-oblanceolate, apices acuminate to long-acuminate, margins hyaline proximally, green zones oblanceolate to linear-oblanceolate and restricted to distal 1/4-1/3 (1/2), sparsely to moderately ciliate, faces glabrous or glabrescent; outer phyllaries 2-4 mm; inner phyllaries 4.5-6 mm; ray florets (12) 14-20, bluish to violet, laminae (8.5) 10-15 mm; disc florets 14-25 (30), yellowish (becoming reddish-purple in age), lobes narrowly deltate, 4.5-6.5 mm. **Cypselae** obovoid,
compressed, tan to brownish, 5- to 6-nerved, glabrous to sparsely (rarely moderately) short-hairy, 1-2 mm; pappus whitish to pink-tinged, 3-6 mm.

Flowering Jul-Oct. Moist to dry forests, thickets, forest edges, meadows, clearings, streambanks, shorelines, and disturbed areas in the lowland (rare), steppe (rare), montane, parkland, and boreal zones; (5) 350-1200 (1700) m. Common in south-central, southeast, central, and west-central BC, frequent in northeast BC, rare (primarily adventive) in southwest BC [Fraser Valley]. YT east to NL, south to WY, IL, CT. 2n = 48 [6x] (Brouillet et al. 2006).

This boreal aster is among the most abundant and widespread species of *Symphyotrichum* in British Columbia, ranging throughout most of the interior of the province, with the exception of the northwest (Figure 58). It is among the more characteristic species of the sub-boreal forests of the Cariboo-Chilcotin and Fraser-Nechako regions of the central interior, and is regularly encountered in all manner of habitats from aspen copses in dry, open grasslands to the margins of boreal wetlands and throughout a wide variety of forested habitats. Indeed, it is one of few British Columbia asters to regularly inhabit shady woodland interiors, especially where there is a significant proportion of deciduous trees in the canopy layer. It is very rare in coastal areas of the province, where it is known naturally only from the upper Fraser Valley and as a waif or adventive species in the Lower Mainland.

*Symphyotrichum ciliolatum* is the most widespread and abundant member of *Symphyotrichum* subg. *Symphyotrichum* subsect. *Heterophylli* (Nees) Semple in British Columbia. This is otherwise a group of primarily eastern North American taxa (Brouillet et al. 2006), with only *S. ciliolatum*, *S. laeve*, and the apparent allopolyploid *S. x maccallae* being represented in western Canada. Species in subsect. *Heterophylli* are characterized largely by the presence of distinctly petiolate, often deltate or cordate (occasionally broadly ovate-lanceolate, e.g., *S. x*
Symphyotrichum, S. laeve subsp. laeve) basal and lower cauline leaves (Semple et al. 2002, Brouillet et al. 2006) (Figure 55; Figure 57). Although generally distinctive within the context of the British Columbia flora, S. ciliolatum is considerably less distinctive than earlier sources (e.g., Douglas 1995, Brouillet et al. 2009) have suggested, due to both hybridization with other taxa (much of which is represented by S. x maccallae) and intraspecific variation. In its typical form, S. ciliolatum in British Columbia is easily distinguished by the morphology of the basal and lower cauline leaves, but in some regions of the southern interior (especially the Columbia and Rocky Mountains), the presence of S. x maccallae, itself of apparent hybrid origin between S. ciliolatum and S. laeve, can render these normally diagnostic morphological characters more difficult to apply. Symphyotrichum x maccallae is generally distinguishable from S. ciliolatum by the shape of the basal and lower cauline leaves, which are typically narrower (ovate-lanceolate to broadly lanceolate) and with the bases of the blade tapered to cuneate (vs. truncate or rounded to strongly cordate in S. ciliolatum). The leaves of S. x maccallae are typically somewhat thicker and flesher than in S. ciliolatum, presumably due to the influence of S. laeve in its parentage, and the species tends to occur primarily in open, naturally or artificially disturbed habitats (vs. S. ciliolatum commonly in wooded habitats). The other representative of subsect. Heterophylli in British Columbia, S. laeve subsp. laeve, has a basal and lower cauline leaf shape that is similar to S. x maccallae, but is also characteristically glabrous, glaucous, and with even thicker, leathery or somewhat fleshy leaves, as well as strongly clasping middle and upper cauline leaf bases, and is thus relatively easy to distinguish from S. ciliolatum under most circumstances.

Intraspecific variation within S. ciliolatum is more pronounced than generally has been described in past accounts of the species in British Columbia. Of particular note, Rydberg (1910a) recognized plants with strongly pilose stems, leaves, and petioles as the species Aster wilsonii Rydb., although he noted that the form graded into typical forms of S. ciliolatum. This form is best
exemplified by *Lomer 4253* [UBC] from the Peace River valley in northeastern B.C. (Figure 56: A) which is extensively whitish-pilose throughout most of the plant. However, as this study demonstrated that there do not appear to be any other characters that covary with pubescence type and, given that these forms are connected morphologically to less hairy populations through all manner of intermediate states, they are not recognized taxonomically here. Other variation present among specimens of *S. ciliolatum* in British Columbia involves the pubescence of the cypselae (ranging from glabrous to pubescent), the size and number of capitulae, and the shape of the blades of the basal and lower cauline leaves, with some of this variation having been recognized as taxonomically important by past authors (e.g. Rydberg 1910a). All of these characters vary extensively among the British Columbia specimens that were reviewed, however, with no indication of any geographic or ecological structuring or covariation with other characters, and they are thus not considered taxonomically informative here.

Most members of subsect. *Heterophylli* are known to hybridize frequently with other *Symphyotrichum* species in eastern North America (Semple *et al.* 2002), and *S. ciliolatum* is implicated in hybridization events with *S. laeve*, *S. lanceolatum*, and *S. novi-belgii*, as well as with other eastern North American species (Labrecque and Brouillet 1996, Semple *et al.* 2002, Brouillet *et al.* 2006). British Columbia specimens reviewed for this study suggest hybridization with *S. subspicatum s.s.* in west-central B.C. and the northern coast, with *S. lanceolatum* subsp. *hesperium* in the central and southern interior, and with *S. frondeum* var. *caurinum* in the central interior, as well as potential backcrosses with the allopolyloid *S. x maccallae* in the south-central and southeastern interior.
FIGURE 55. Variation in basal and lower cauline leaves of *Symphyotrichum ciliolatum*, for comparison with *S. x maccallae* [see Figure 94]. Note variation in overall blade shape (esp. width), marginal serrations, and outline of the base of the blade (rounded [C] to strongly cordate [A, B]). A = Straley 5659; B = Lomer 88-52; C = E. Wilson 638.

FIGURE 56. Variation in stem and leaf pubescence in *Symphyotrichum ciliolatum*. A = extensively whitish-pilose form corresponding to *Aster wilsonii* Rydb. (Lomer 4253); B = typical pubescence, with lines of sparser hairs interspersed by nearly glabrous areas (becoming wholly glabrescent on the proximal stem) (Bell s.n.).
FIGURE 57. Typical habit of *Symphyotrichum ciliolatum* (Straley 1696).

FIGURE 58. Distribution of British Columbia specimens of *Symphyotrichum ciliolatum* that were reviewed for this study (left), and approximate distribution of the species elsewhere in northwestern North America (right). Open circles denote introduced populations.
8. *Symphyotrichum x columbianum* (Piper) G.L. Nesom

**COLUMBIA ASTER**


**Plants** perennial, rhizomatous, colonial to cespitose. **Stems** solitary to several, sometimes from a branched caudex, decumbent to erect, usually branched distally, glabrate to sparsely strigose distally, 30-80 (120) cm tall. **Leaves** basal and cauline, basal and proximal cauline withering prior to anthesis or persistent, slightly reduced distally, margins entire and flat, minutely stiff-ciliate with antrorse hairs, faces glabrous to sparsely strigose; basal and proximal cauline leaves sessile, narrowly oblanceolate, apices obtuse to broadly acute and sometimes mucronulate, bases attenuate, 40-90 (110) mm; mid- and distal cauline leaves linear-lanceolate to linear-oblanceolate, apices acute and usually mucronulate (especially in capitulescence), bases rounded to slightly clasping, (10) 15-50 (60) mm. **Capitulescences** usually open, narrow to pyramidal, leafy, branches ascending; peduncle bracts 1-3+ per peduncle, oblong-lanceolate, sometimes slightly recurved, usually minutely spine-tipped with whitish spine, distinct from phyllaries, 2-5 mm. **Flowering heads** few to numerous; involucres campanulate to hemispheric, 4-6 mm; phyllaries unequal (rarely subequal), in 3-5 series, erect to recurved, spreading-ciliate, faces glabrescent to minutely glandular-hairy (especially inner), margins hyaline proximally, green zones elliptic or diamond-shaped to broadly oblanceolate and restricted to distal 1/4-1/2; outer phyllaries oblanceolate to spatulate, apices rounded or obtuse to acute and usually subspinulose with small whitish spine (especially outermost), 1.5-3 mm; inner phyllaries linear-lanceolate to linear-oblanceolate, apices obtuse to acute or acuminate, 4-5 mm; ray florets 20-35, pale bluish to pinkish or violet, laminae 5-15 mm; disc florets 20-30+, pale yellowish (becoming purplish in age), lobes deltate, 3-4 mm.
Cypselae obovoid, not compressed, tan to purplish or brownish, 7- to 9-nerved, densely short-hairy, 1.5-2 mm; pappus tawny to pink-tinged, 3.5-5.5 mm.

Flowering Jul-Oct. Moist to mesic sloughs, riverbanks, meadows, swales, shorelines, and disturbed areas in the steppe zone; 275-550 m. Infrequent in extreme south-central BC [southern Okanagan Valley, southern Similkameen Valley]. BC south to WA. 2n = ?

_Symphyotrichum x columbianum_ is locally distributed along shorelines and in wet meadows of the arid basins of the southern interior, ranging north along the Okanagan Valley to the Oliver area and along the Similkameen River to the Keremeos area (Figure 61). Additional collecting of asters in the southern interior may result in further populations to the west and north, however, based on the distribution of suitable habitats within this region. Similarly, further field and herbarium study of material in Washington and elsewhere in the Pacific Northwest, which was beyond the scope of this study, may better characterize its full distribution south of the U.S.–Canada border. It has long been overlooked as a component of the British Columbia aster flora, with specimens generally being attributed to the very similar _S. ascendens_ (Douglas 1995, Douglas _et al._ 2002b) or garden-derived cultivars of the hybrid _S. x amethystinum_ (≡ _S. ericoides_ var. _ericoides x S. novae-angliae_) (British Columbia Conservation Data Centre 2018). It is most similar morphologically to _S. ascendens_, with which it shares its distinctive uniform, strigose vestiture on the distal stems, strongly graduated phyllaries, and minutely spine-tipped outer phyllaries and distal peduncle bracts (Figure 59: A, B, E, F). It differs conspicuously from that species, however, in its glandular phyllaries and, on some plants, peduncles (Figure 59: C, D); this glandularity would not be expected within the allopolyploid _S. ascendens_, as neither of its parental species (_S. falcatum, S. spathulatum_ [Allen 1985]) are glandular. Indeed, the only glandular _Symphyotrichum_
in southern British Columbia is the otherwise distinctive *S. campestre* of upland habitats, which is thus hypothesized as one of the potential parental taxa of *S. x columbianum*.

*Symphyotrichum x columbianum* has not been previously recognized formally in any floristic or taxonomic studies of the Pacific Northwest aster flora. If discussed at all (e.g., Hitchcock *et al.* 1955, Abrams & Ferris 1960), it is generally mentioned only briefly and as an occasional and non-consequential hybrid. It is recognized in this treatment, however, based on: (i) its distinctive and stabilized morphology that differs discretely and consistently from any other related taxa; (ii) its well-defined ecological requirements and geographic distribution, which are distinct from any other sympatric members of the genus; (iii) its frequent occurrence within its limited geographic range; and (iv) the persistence of many populations over time, with some populations (e.g., Osoyoos Lake) having been collected repeatedly for nearly a century. Taken together, these factors indicate a frequently-occurring, reproductively viable, and persistent hybridogenous taxon that cannot be accommodated in any other species concept due to its distinctive morphology (particularly its glandularity), and which occupies a specific habitat range within a discrete geographic region.

*Symphyotrichum x columbianum* has been consistently suggested as representing a hybrid between *S. campestre* and *S. ericoides* var. *pansum* (Hitchcock *et al.* 1955, Abrams & Ferris 1960), both of which are upland members of *Symphyotrichum* subg. *Virgulus* that are widespread within areas that support *S. x columbianum*. The morphology of the plants that are here attributed to *S. x columbianum*, however, is not entirely consistent with such an origin, with certain morphological features (such as the overall habit of the plants [Figure 60]) suggesting the involvement of a member of *Symphyotrichum* subg. *Symphyotrichum*. Apparent hybrids between *S. campestre* and *S. ericoides*, which lack glandularity and bear smaller, more numerous capitula in a branching capitulescence that is reminiscent of *S. ericoides*, occur sporadically in British Columbia but are
not included in the concept of *S. x columbianum* presented here. Although it is difficult to ascribe parentage to this hybrid based solely on morphological considerations, few members of *Symphyotrichum* subg. *Symphyotrichum* co-occur with it in the same valley-bottom wetlands and moist meadows, limiting the number of potential parental taxa considerably. Specifically, only *S. bracteolatum* (frequent) and *S. lanceolatum* subsp. *hesperium* (rare) are sympatric geographically and ecologically with *S. x columbianum* and could potentially be involved in its origin. Conversely, the taxon may have had an origin in another geographic region, where additional taxa may be currently or historically present, followed by range expansion into British Columbia, perhaps with additional hybridization events during the expansion.

Based on the above rationale, three potential hypotheses are suggested to explain the origin of this taxon: (i) that it is an allopolyploid that is derived from hybridization between at least two representatives of *Symphyotrichum* subg. *Virgulus* (most likely *S. campestre* and *S. ericoides* var. *pansum*) and a third species that is a member of *Symphyotrichum* subg. *Symphyotrichum* (most likely *S. lanceolatum* subsp. *hesperium*); (ii) that it originated as a population of *S. ascendens*, which is itself a hybrid, that subsequently hybridized with the glandular *S. campestre*; or (iii) that it originated in another geographic region or at a historical time when there were different *Symphyotrichum* taxa present within its current distribution but which are no longer sympatric, and either spread into B.C. or persisted as the distribution of its parental taxa retracted from the province. Under all of these potential scenarios, this taxon would be placed within *Symphyotrichum* subg. *Ascendentes*, which was erected by Semple *et al.* (2002) to accommodate allopolyploid taxa originating from crosses between subg. *Virgulus* and subg. *Symphyotrichum*. It would join the other inter-subgeneric allopolyploids *S. ascendens* and the extralimital *S. defoliatum* in this subgenus (Brouillet *et al.* 2006).
FIGURE 59. Morphological characteristics of Symphyotrichum x columbianum. A, B = details of involucres and graduated phyllaries; C, D = glandular trichomes of the phyllaries (C) and peduncles (D); E = spinulose apices of outer phyllaries; F = uniformly sparsely strigose distal stems. A = G.W. Douglas 13082; B = Fenneman 2; C = Lomer 6711; D = Lomer 10942; E = Lomer 6711; F = Lomer 10902.
FIGURE 60. Overall habit of *Symphyotrichum x columbianum*. A = a plant of typical stature (*Lomer 14634*); B = a particularly large, robust, and heavily-branched plant (*Lomer 6711*).

FIGURE 61. Distribution of British Columbia specimens of *Symphyotrichum x columbianum* that were reviewed for this study (left), and approximate distribution of the species elsewhere in northwestern North America (right).
9. *Symphyotrichum cusickii* (A. Gray) G.L. Nesom

**CUSICK’S ASTER**


Plants perennial, long-rhizomatous, colonial to cespitose. Stems not from a branched caudex, solitary to several, ascending to erect, usually branched distally, sparsely to densely white-puberulent, pubescence usually uniform and only rarely arranged in lines from leaf bases, 40-100 cm tall. Leaves basal and cauline, basal and proximal cauline leaves usually withering prior to anthesis, slightly reduced distally, margins entire and flat, minutely stiff-ciliate with antrorse hairs, faces glabrescent to moderately (sometimes densely) soft-puberulent; basal leaves petiolate, obovate to broadly elliptic, apices acute, bases attenuate to cuneate, 5-200 mm; proximal cauline leaves sessile, oblanceolate to obovate, apices acute, bases strongly clasping and usually auriculate, 70-120 mm; distal cauline leaves sessile, lanceolate to broadly elliptic, apices obtuse to acute, bases truncate and usually auriculate, 30-110 mm. Capitulescences usually open, pyramidal, leafy or not, branches ascending; peduncle bracts 0 (1-3), lanceolate, apices acute to acuminate, usually distinct from the phyllaries, 8-15 (25) mm. Flowering heads solitary to several; involucres campanulate, 10-20 mm; phyllaries subequal or outer exceeding the inner, in 4-5 series, usually spreading, ciliate, faces glabrous to puberulent; outer phyllaries narrowly to broadly lanceolate or oblanceolate, apices acute to acuminate, often enlarged and foliaceous, margins sometimes hyaline on proximal 1/3 or less, green zones lanceolate to elliptic, (7) 9-16 mm; inner phyllaries linear to linear-lanceolate, apices acute to acuminate, margins hyaline proximally, green zones lanceolate to narrowly elliptic, 10-13 mm; ray florets 25-55, violet to purplish, laminae 10-18 mm; disc florets 60-150+, yellowish, lobes deltate, 2.5-4 mm. Cypselae cylindric to obovoid,
not compressed, brownish, 3- to 6-nerved, densely short-hairy, 3-3.5 mm; pappus whitish, 5-9 (11) mm.

Flowering Jul-Sep. Moist to dry meadows, open forests, streambanks, and shorelines in the montane zone; 1300-2000 m. Rare in southeast BC [southern Columbia Mts.]. BC south to OR, ID, MT. \(2n = 16, 32 \, [2x-4x] \) (Allen 1984).

*Symphyotrichum cusickii* is a rare, primarily diploid (rarely tetraploid) aster of montane habitats in southeastern British Columbia, where it occurs at several sites along the Canada-U.S. border between the Kettle River and the Rocky Mountain Trench (Figure 64). It was first reported in the province in 2014, based on a series of collections from the Boundary Lake area west of Creston, but the subsequent review of specimens associated with this study yielded an additional, older (1944) collection that had been overlooked. The inclusion of British Columbia within the described distribution of *S. cusickii* in Abrams & Ferris (1960) provides the only attribution of this species to the province prior to its ‘discovery’ in 2014, although it is unclear whether this conclusion was speculative or based on specimen evidence.

This taxon is part of the “*Aster foliaceus*” complex of species (Cronquist 1943), along with *S. frondeum* (formerly *S. foliaceum*) and *S. hendersonii*, and all of these taxa have traditionally been recognized as varieties of an expanded *Aster [= Symphyotrichum] foliaceus (= *S. frondeum* of this treatment) in the Pacific Northwest (e.g., Cronquist 1943; Hitchcock *et al.* 1955, Hitchcock & Cronquist 1973). *Symphyotrichum cusickii* is among the more distinctive of these species, however, and is characterized by its overall robust stature and large flowering heads, its large, leafy, and usually pyramidal capitulescence, its large, broad, and strongly auriculate-clasping cauline leaves that are little reduced within the capitulescence, its broad, usually foliaceous, subequal phyllaries, and its conspicuous shaggy, uniform, and often dense pubescence on the stems.
and occasionally leaves (Figure 6: A). In extreme forms (e.g. *Lomer 9676* [Figure 63: B]) the stems and leaves may be so densely and conspicuously hairy as to give the entire plant a canescent appearance. In contrast, other members of this species complex (and other similar, closely related species) are consistently less hairy and are never canescent, and the longer, whitish, pilose hairs along the stems of these species are arranged in longitudinal lines extending proximally from the leaf bases on at least the mid-stem (rarely shown by *S. cusickii*). *Symphyotrichum hendersonii*, which is restricted in British Columbia to the same areas that support *S. cusickii*, is particularly similar to this species, but can be distinguished by its smaller and narrower cauline leaves (especially within the capitulescence), smaller and more numerous capitulae, narrower phyllaries, and stem hairs that are more consistently and prominently arranged in lines from the leaf bases. Cronquist (1943) notes that this species grades morphologically into other members of the ‘*A. foliaceus*’ complex (e.g., *S. frondeum, S. hendersonii*), although the few specimens from British Columbia are distinct and provide no evidence of hybridization with other taxa.

**FIGURE 62.** Morphological characteristics of *Symphyotrichum cusickii*. A = densely and uniformly hairy stems (*Lomer 9679*); B = strongly clasping, auriculate cauline leaf bases (*Lomer 9680*); broad, foliaceous, subequal phyllaries (*Lomer 9679*).
FIGURE 63. Overall habit of *Symphyotricum cusickii*. A = Lomer 9679; B = Lomer 9676.

FIGURE 64. Distribution of British Columbia specimens of *Symphyotrichum cusickii* that were reviewed for this study (left), and approximate distribution of the species elsewhere in northwestern North America (right).

**DOUGLAS’ ASTER**

*Aster douglasii* Lindley in Hooker (1834b: 8). Type:—UNITED STATES. Washington (?): “common on the northwest coast near the confluence of the Columbia in open undulating grounds”, 1825, *Douglas s.n.* (holotype K!); *Symphyotrichum douglasii* (Lindl.) Fenneman, designated herein.


*Aster carterianus* J.K. Henry (1917: 57) [as ‘carteriana’]. Type:—CANADA. British Columbia: Cameron Lake, Vancouver Island, August 1916, *Henry 225* (syntype V!).

**Plants** perennial, long-rhizomatous, colonial. **Stems** not from a branched caudex, solitary to several, ascending to erect, usually branched distally, sparsely (to moderately) white-puberulent, pubescence arranged in lines from leaf bases, (15) 20-60 (100) cm tall. **Leaves** basal and cauline, basal and proximal cauline leaves usually withering prior to anthesis, only slightly reduced distally, margins entire to serrulate and flat, minutely stiff-ciliate with antrorse hairs, faces glabrous to glabrescent; basal and proximal cauline leaves petiolate, linear-lanceolate to narrowly oblanceolate, apices acuminat, bases long-attenuate, 70-210 mm; distal cauline leaves sessile, linear to lanceolate or narrowly oblanceolate, apices acute to acuminate, bases long-attenuate, (20) 30-100 (170) mm. **Capitulescences** usually open, corymbose-paniculate to pyramidal, branches ascending; peduncle bracts 2-4, linear to lanceolate, apices acute to acuminate, usually distinct from the phyllaries, 6-20 mm. **Flowering heads** usually several (occasionally solitary); involucres campanulate, 6-9 mm; phyllaries usually subequal (occasionally slightly graduated, or some outer phyllaries exceeding inner), in 3-4 series, erect to somewhat spreading, faces glabrous to glabrescent; outer phyllaries linear-lanceolate to lanceolate, apices acuminat, occasionally
somewhat enlarged and foliaceous, margins hyaline on proximal (1/3) 1/2-2/3, green zones lanceolate to elliptic, (3) 5-6 mm; inner phyllaries linear to linear-lanceolate, apices acuminate, margins hyaline proximally, green zones oblanceolate to narrowly elliptic, 5.5-7; ray florets 15-45, violet to purplish, laminae 10-16 (20) mm; disc florets 50-75, yellowish (becoming reddish or purplish in age), lobes lanceolate to deltate, 4-6 mm. Cypselae cylindric to obovoid, not compressed, tan to brownish, 3- to 6-nerved, glabrescent to moderately short-hairy, 2-4 mm; pappus whitish to tan, 4.5-8 mm.

Flowering (Jul) Aug-Sep (Oct). Moist to mesic shorelines, streambanks, meadows, thickets, and disturbed areas, especially on coarse or gravelly soils, in the lowland zone; 0-200 m. Locally frequent in southwest BC [Georgia Depression, western Vancouver Island]. BC south to CA. 2n = ?

*Symphyotrichum douglasii* is restricted in British Columbia to the southwestern coast of the province (Figure 67), where it is primarily a species of lacustrine and fluvial shorelines at low elevations of the Georgia Depression. It occurs most frequently along the southeastern coast of Vancouver Island, where it is the most common narrow-leaved *Symphyotrichum* away from areas of marine or estuarine influence, but is curiously absent from the extensive low elevation habitats of the lower Fraser River Valley; it is largely replaced in this latter area by the similar, introduced *S. novi-belgii* var. *novi-belgii*. The concept of *S. douglasii* presented here has long been subsumed within a broad concept of *Aster subspicatus (= Symphyotrichum subspicatum*) in floristic efforts dealing with the flora of the Pacific Northwest (e.g., Hitchcock *et al.* 1955, Abrams & Ferris 1960, Hitchcock & Cronquist 1973, Douglas *et al.* 1989, Douglas 1995, Douglas *et al.* 1998, Brouillet *et al.* 2006) and in studies concerned with the ‘*Aster occidentalis*’ complex of taxa (e.g., Allen 1984), obscuring its true status in the region. The concept of *subspicatum* presented in these earlier
efforts, however, appears to represent a taxonomic hodge-podge of different taxa and hybrids that are united primarily through their shared morphological characters of narrow, subequal phyllaries with extensive hyaline bases and narrow, usually serrate-marginated leaves. With the re-circumscription of *Symphyotrichum subspicatum* that is presented in this treatment (see that species), *S. douglasii* is resurrected as a distinct taxon due to its identifiable morphology, distinctive ecology, and well-defined geographic distribution.

*Aster douglasii* was originally described by Lindley from specimens collected by Dr. J. Scouler in 1825, who found it to be “common on the N.W. coast, near the confluence of the Columbia, in open undulating grounds.” It was recognized in most floristic studies of the Pacific Northwest through the early 20th century, although the concepts associated with the name varied somewhat between treatments. For example, Piper (1906), Henry (1915), Peck (1941b), Cronquist (1943), and Davis (1952) expanded the concept to include similar plants of eastern Washington and the southern interior of British Columbia that are here treated as representing *S. lanceolatum* subsp. *hesperium*, as well what are here treated as hybrids between other recognized taxa. In contrast, Howell (1900) presented a concept of the taxon that is morphologically, ecologically, and biogeographically consistent with the concept that is presented in this treatment, and noted its distribution as being along the coast from British Columbia to northern California. Further to this, Henry (1917) described populations from central Vancouver Island as a taxon distinct from *douglasii*, providing the name *Aster carterianus* to account for these plants. The type specimens and description of *carterianus* provided by Henry (1917) portray it as a single-headed plant of ‘lower habit’ (Henry 1917) than *douglasii*, with more thin-textured leaves, more commonly foliaceous outer phyllaries, and longer ray florets. During this study, a review of specimens pertaining to the same Vancouver Island populations that were cited by Henry (1917) as representing *A. carterianus* (e.g., Horne Lake, Cameron Lake) demonstrated that the
distinguishing characters cited by Henry (1917) were far more variable than was accounted for in the original description, and they were within the morphological variation that was present among other specimens that are here attributed to *S. douglasii*. As a result, *carterianus* is included in synonymy under *Symphyotrichum douglasii* in this treatment.

Species limits within the polyploid complex to which *S. douglasii* belongs have long presented an enormous challenge to interpret based on morphological considerations alone (see Cronquist 1943, Allen 1984). Despite these taxonomic complexities however, *Symphyotrichum douglasii* is generally recognizable within this complex through the combination of the following traits: (i) very narrow (generally linear to narrowly lanceolate), entire to occasionally sparsely serrate leaves (Figure 66); (ii) narrow, usually subequal phyllaries with extensive pale (often yellowish-tinged) hyaline bases (Figure 65); (iii) basal and lower cauline leaves that wither prior to anthesis (Figure 66); (iv) extensively rhizomatous habit and usually solitary stems (Figure 66); (v) subglabrous lower and mid-stems with lines of hairs below the leaf bases; (vi) extensively, and often uniformly, pubescent peduncles; and (vii) subcorymbose, relatively few-headed capitulescences with long-pedunculate capitulae (Figure 66). It is most similar to other narrow-leaved *Symphyotrichum* taxa of southern B.C. such as *S. lanceolatum* subsp. *hesperium*, *S. spathulatum* var. *intermedium*, *S. novi-belgii* subsp. *novi-belgii*, *S. chilense*, *S. frondeum* var. *caurinum*, and *S. bracteolatum*. *Symphyotrichum lanceolatum* subsp. *hesperium*, which is primarily a species of the southern interior of the province but which occurs rarely (introduced?) in the Georgia Depression, is distinguished from *S. douglasii* by the conspicuous lines of long, spreading, whitish hairs along its peduncles and the consistently serrate basal and cauline leaves (leaves usually entire in B.C. populations of *S. douglasii*). *Symphyotrichum spathulatum* var. *intermedium*, which is seemingly absent from the Georgia Depression, is distinguished by its persistent basal and lower cauline leaves and its consistently shorter outer phyllaries that result in
a graduated involucre (phyllaries usually subequal in *S. douglasii*). The introduced *Symphyotrichum novi-belgii* var. *novi-belgii* occurs sympatrically with *S. douglasii*, but is typically restricted to estuarine environments and is scarce in the freshwater shoreline habitats occupied by *S. douglasii*. It is often a much larger and more robust taxon, with more numerous heads in larger, leafier, usually paniculate or pyramidal capitulescences. It is further distinguished by its broader, usually loosely spreading (vs. erect to slightly spreading) phyllaries, and its often broader leaves with conspicuously clasping or subauriculate bases. *Symphyotrichum frondeum* var. *caurinum* is a species of higher elevations than *S. douglasii*, and is characteristic of montane environments of the south coast of British Columbia, but can be distinguished by its persistent basal and lower cauline leaves, its often broader cauline leaves with more conspicuous clasping bases, and its distinctive broad, often purple-tinged, and usually largely to entirely foliaceous outer phyllaries. *Symphyotrichum bracteolatum*, which is not known to occur sympatrically with *S. douglasii*, is easily distinguished by its uniformly short-hairy, usually reddish stems, while *S. chilense* of coastal estuaries and marine shorelines can be distinguished by its broad, rounded, strongly graduated phyllaries and usually broader, thicker-textured, coarsely serrate leaves. Putative hybrids between *S. douglasii* and several of these taxa (*S. novi-belgii* var. *novi-belgii*, *S. chilense*, *S. frondeum* var. *frondeum*) were noted among specimens that were reviewed as part of this study.
FIGURE 65. Variation in phyllary and involucre characteristics of Symphyotrichum douglasii. A = Darling s.n.; B = Janszen, Janszen, & Jamison 2867.

FIGURE 66. Variation in plant habit and overall structure of Symphyotrichum douglasii. A = larger, polycephalous plants (Lomer 8596); B = smaller, monocephalous plants (Crocker s.n.).
11. Symphyotrichum ericoides (L.) G.L. Nesom var. pansum (S.F. Blake) G.L. Nesom

HEATH ASTER; White Heath Aster; Tufted White Prairie Aster; Many-flowered Aster; Heath American-aster


Aster multiflorus Ait. var. pansus S.F. Blake (1928: 227). Type:—UNITED STATES. Washington: Ellensburg, 23 August 1897, Whited 853 (holotype US!, isotype OSC!); A.

**Plants** perennial, cespitose. **Stems** from a woody cormoid caudex, solitary to several, decumbent or arching to ascending or erect, usually branched distally, sparsely to densely strigose and/or hispid (sometimes glabrescent proximally), pubescence not arranged in lines from leaf bases, (3) 20-60 (100) cm tall. **Leaves** basal and cauline, basal and proximal cauline usually withering prior to anthesis, reduced distally (especially rameal leaves), margins entire and flat, not conspicuously ciliate to coarsely stiff-ciliate with spreading or antrorse hairs, faces usually sparsely to moderately strigose to hispid (occasionally glabrescent, especially on proximal leaves); basal leaves sessile, oblanceolate to oblong or spatulate, apices rounded to obtuse, bases attenuate, 10-50 mm; proximal cauline leaves sessile, linear or lanceolate to oblong, apices obtuse to acute, bases cuneate, 10-40 mm; distal cauline leaves sessile, ovate to oblong, apices acute, bases cuneate, 5-40 mm. **Capitulescences** open, racemose to pyramidal, not leafy, branches usually spreading to ascending; peduncle bracts 0-4, linear to lanceolate or narrowly oblong, apices minutely spine-tipped, usually grading into the phyllaries, 2-5 mm. **Flowering heads** usually numerous; involucres turbinate to campanulate, 2.5-4 (5) mm; phyllaries usually unequal (occasionally subequal), in 3-4 series, apices spine-tipped (at least on outer phyllaries), spreading to recurved, ciliate, faces sparsely to densely hispid; outer phyllaries oblong to spatulate, apices rounded to obtuse, margins broadly hyaline on proximal 1/2-2/3, green zones oblanceolate to elliptic or diamond-shaped, 1-2.5 mm; inner phyllaries linear to lanceolate, apices acuminate, margins hyaline on proximal 2/3-3/4, green zones oblanceolate, 3-4 mm; ray florets (8) 10-18 (20), whitish (rarely tinged with pink), laminae
3-8 mm; disc florets 6-25, yellowish (becoming brownish in age), lobes deltate, 2.5-4 mm. **Cypselae** obovoid to oblong-obovoid, not compressed, brownish to dark purplish, 7- to 9-nerved, moderately to densely short-hairy, 1-2 mm; pappus whitish, 3-4 mm.

Flowering Jul-Sep (Oct). Mesic to dry grasslands, sagebrush steppe, open forests, rocky slopes, meadows, and disturbed areas in the steppe and montane zones; 270-700 (950) m. Common in south-central BC [north to the Chilcotin], locally frequent in southeast [southern Rocky Mtn. Trench] and northeast [Peace River lowlands] BC. BC east to MN, north to NT, south to n Mexico. $2n = 10, 20$ [2x-4x] (Jones 1978b).

*Symphyotrichum ericoides* var. *pansum* is one of the dominant upland asters in the dry climates of the southern interior of British Columbia, where it is typically associated with open grasslands, grassy slopes, and dry, open forests. It often occurs alongside *S. campestre* in such habitats, and the two species occasionally hybridize to produce the hybrid *S. x columbianum* (treated as a distinct species in this treatment; see above). *Symphyotrichum ericoides* is very closely related to *S. falcatum*, and the two species together comprise *Symphyotrichum* subg. *Virgulus* sect. *Ericoidei* (A. Gray) G.L. Nesom [= *Aster* sect. *Multiflori* (A. Gray) R.A. Nelson]. Although very similar, *S. ericoides* var. *pansum* can usually be distinguished from *S. falcatum* by its distinctive capitulescence structure (with spreading to somewhat recurved branches [Figure 69]), smaller and more numerous capitulae that are usually strongly secund on the lateral branches, and densely spreading- or antrorsely-hairy stems (vs. usually sparsely to moderately appressed-strigose in *S. falcatum*) (Figure 68: B). The results of this study indicate that the differences in capitulum size that are often mentioned in the separation of these two species are not as pronounced in British Columbia material as has been suggested (such as in Jones 1978a, Jones 1978b, Brouillet *et al.* 2006). Moreover, differences in growth form (cormoid [*ericoides*] vs. rhizomatous [*falcatum*]) that
are cited by many authors as distinguishing the two species in the Pacific Northwest (e.g., Hitchcock et al. 1955, Hitchcock & Cronquist 1973, Douglas et al. 1989, Douglas 1995, Douglas et al. 1998) are based on the erroneous assumption that all populations of *S. falcatum* in the region are rhizomatous. As all populations of *S. ericoides* var. *pansum* and virtually all populations of *S. falcatum* in the region are cormoid, growth form cannot be used to identify these species; see *S. falcatum* (below) for more detail. Hybridization between these species is rare due to limited interfertility (Jones 1978b), although a small number of intermediate specimens from British Columbia reviewed for this study suggest that hybridization may occur at least occasionally throughout the widely sympatric distributions of the two species. Conversely, given the close similarity of these two species, some of these apparent hybrids may in fact represent variants of one or both species that overlap morphologically.

Included within the concept of var. *pansum* presented here is a morphotype that has been recognized as *Aster ericoides* subsp. *pansum* var. *stricticaulis* or *Symphyotrichum ericoides* var. *stricticaule*. This form, which is the dominant form east of the Rocky Mountains (Jones 1978a, 1978b), averages more slender overall than typical western forms of var. *pansum*, with less strongly secund capitulae, sparser and more commonly appressed-strigose stem vestiture, and less pronounced cormoid stem bases (Jones 1978a). In many ways, plants attributable to the *stricticaulis* morphology are intermediate between typical var. *pansum* (as it is expressed west of the Rocky Mountains) and *S. falcatum* var. *falcatus*, and this similarity may be one of the sources of identification difficulties within this pair of species. In reviewing specimens of *S. ericoides* var. *pansum* from British Columbia, however, few examples of the *stricticaulis* morphology were encountered and it is unclear to what extent is present in the province. If it does occur in British Columbia, this morphological varient is most likely to occur within the Peace River lowlands or the southern Rocky Mountain Trench based on its geographic association with prairie regions.
FIGURE 68. Morphological characteristics of Symphyotrichum ericoides var. pansum (both images of Anonymous s.n.). A = typical involucre and phyllaries; B = typical densely hairy stems, showing both spreading and antorse (ascending) hairs.

FIGURE 69. Typical plant habit and overall structure of Symphyotrichum ericoides var. pansum. A = McIntosh 2008_53; B = Eastham s.n.
FIGURE 70. Distribution of British Columbia specimens of *Symphyotrichum ericoides* var. *pansum* that were reviewed for this study (left), and approximate distribution of the species elsewhere in northwestern North America (right).

12. *Symphyotrichum falcatum* (Lindl.) G.L. Nesom

**WESTERN HEATH ASTER; Little Grey Aster; White Prairie Aster**


*Aster ramulosus* Lindl. in Hooker (1834b: 13). TYPE:—CANADA. Northwest Territories/Saskatchewan: “Fort Franklin and Cumberland House Fort”, no collection date reported, *Richardson s.n.* (holotype K!). [= *S. falcatum var. falcatum*]

*Aster ramulosus* Lindl. β *incanopilosus* Lindl. in Hooker (1834b: 13), *nomen nudum*; *A. incanopilosus* Sheldon (1893: 286); *A. multiflorus* Ait. var. *incanopilosus* (Lindl.) Rydberg (1895: 163). [= *S. falcatum var. commutatum*]


*Aster cordineri* A. Nelson (1905: 64). Type:—UNITED STATES. Colorado: Estes Park, 11 August 1904, *Cooper 151* (holotype RM!). [= *S. falcatum* var. *commutatum*]


**Plants** perennial, occasionally rhizomatous, cespitose to colonial. **Stems** usually from a woody cormoid caudex, solitary to several, ascending to erect, usually branched proximally and/or distally, moderately to densely strigose and/or hispid (sometimes glabrescent proximally), pubescence not arranged in lines from leaf bases, 10-60 (80) cm tall. **Leaves** basal and cauline, basal and proximal cauline usually withering prior to anthesis, usually reduced distally, margins entire and flat, not conspicuously ciliate to minutely stiff-ciliate with antrorse hairs, faces usually moderately to densely strigose to hispid (occasionally glabrescent, especially on proximal leaves); basal leaves sessile, oblanceolate, apices obtuse to acute, bases attenuate, 10-40 mm; proximal cauline leaves sessile, linear-oblanceolate to narrowly oblong, apices obtuse to acute, bases cuneate, 10-40 (60) mm; distal cauline leaves sessile, linear-lanceolate to linear-oblong, apices acute, bases cuneate, 5-45 mm. **Capitulescences** open, racemose to pyramidal, not leafy, branches ascending; peduncle bracts 1-4+, linear to lanceolate, apices minutely spine-tipped, usually grading into the phyllaries, 2-5 (7) mm. **Flowering heads** usually numerous; involucres
campanulate, (3) 4-5 (8) mm; phyllaries usually subequal or outer slightly exceeding the inner, in 3-4 series, apices spine-tipped (at least on outer phyllaries), usually recurved, ciliate, faces glabrous to moderately strigose or hispid; outer phyllaries oblongate to spatulate or narrowly oblong, apices obtuse to acute, margins usually broadly hyaline on proximal 1/3-2/3 (sometimes enlarged and foliaceous), green zones broadly elliptic to diamond-shaped, 2.5-5 mm; inner phyllaries linear-lanceolate, apices acuminate, margins hyaline on proximal 1/2-3/4, green zones narrowly oblongate to narrowly elliptic, 4-5 mm; ray florets (15) 20-35, whitish (rarely tinged with pink), laminae 6-11 mm; disc florets 5-25, yellowish (becoming brownish in age), lobes lanceolate to deltate, 2.5-4 mm. Cypselae obovoid, not compressed, dark brownish, 7- to 9-nerved, densely short-hairy, 1.5-2.5 mm; pappus whitish, 3-5 mm.

Flowering (Jun) Jul-Sep. Moist to mesic meadows, alkaline and saline flats, streambanks, shorelines, grasslands, open forests, and disturbed areas in the steppe, montane, and parkland zones. Locally frequent in south-central [north to the southern Chilcotin region] and southeast [southern Rocky Mtn. Trench] BC, infrequent in northeastern BC [Peace River lowlands]. AK east to ON, south to n Mexico. $2n = 10, 20, 30$ [2x-6x] (Jones 1978b).

*Symphyotrichum falcatum* is primarily a species of open grassland and shoreline habitats in the southern interior of British Columbia, but also occurs locally in northeastern parts of the province (Peace River area) (Figure 75). Although generally associated with the drier climates of the British Columbia interior, *S. falcatum* most commonly occurs in wet habitats within these regions, and is particularly frequent in areas of alkaline or saline influence (Jones 1978a, Douglas 1995). The centre of its distribution in the province is in the Thompson-Nicola and southern Chilcotin regions of the southern interior, where it is a frequent member of shoreline plant communities; populations in southeastern and northeastern British Columbia are more localized
and restricted in their extent. This is also one of several species of shoreline asters (along with *S. bracteolatum* and *S. lanceolatum* subsp. *hesperium*) that occur along the Fraser River in and west of the Coast-Cascade Mts., apparently due to the fluvial transport of seeds from interior populations and their subsequent germination in suitable shoreline habitats downstream. It is unclear if any of these populations along the lower Fraser River are persistent and established or, rather, are continuously augmented by the deposition of seeds from upstream.

*Symphyotrichum falcatum* is the northwesternmost representative of *Symphyotrichum* subg. *Virgulus* sect. *Ericoidei* (A. Gray) G.L. Nesom [= *Aster* sect. *Multiflori* (A. Gray) R.A. Nelson], but is less common in most areas of British Columbia than the other member of this section, *S. ericoides* var. *pansum*. These two taxa are often very similar, and considerable effort has been expended (see Jones 1978a, 1978b) in defining the taxonomic boundaries of the elements that here comprise these two species. They are best distinguished morphologically by the size of the capitulae (involucres (3) 4-5 (8) mm in *S. falcatum*, 3-4 (5) mm in *S. ericoides* var. *pansum*) and the branching pattern of the capitulescence. The size differential of the capitulae between the two species, at least in British Columbia, is not as pronounced as has been presented in Jones (1978b), who reported a size range of 5-8 mm for the involucres of *S. falcatum*. Although this size range appears consistent with collections of *S. falcatum* from the Canadian prairie provinces, as demonstrated by specimens in the UBC herbarium from that region, collections from British Columbia are consistently smaller-headed and thus less distinctive in this character when compared with *S. ericoides* var. *pansum*. With regard to the structure of the capitulescences, the branches of *S. falcatum* are typically ascending and either terminated by a single capitulum or with a larger terminal and subtending smaller, relatively long-peduncled subterminal or lateral capitulae that are not strongly secund (Figure 72). The capitulescence of most forms of *S. ericoides* var. *pansum*, in contrast, displays distinctively spreading or recurved branches with smaller, sessile to
short-pedunculate, moderately to strongly secund capitulae along most of their length. The differences in capitulescence structure are often more apparent in the field, wherein intrapopulational variation (often related to phenological stage) can be assessed, as opposed to in the herbarium, wherein there are limitations imposed by the amount of material available for study on each specimen. However, when considered alongside capitulum size, these species remain reasonably distinct even in the herbarium.

In addition to capitulum size and capitulescence structure, *S. falcatum* and *S. ericoides* var. *pansum* can further be distinguished by the type and extent of hairs on the stem, with *S. falcatum* generally sporting sparser, appressed, strigose hairs throughout (Figure 78: B), in contrast to the dense, spreading, pilose hairs of *S. ericoides* var. *pansum*. Some forms of *S. falcatum*, particularly var. *commutatum*, may show stem vestiture that is similar to *S. ericoides* var. *pansum* (see Jones 1978a, 1978b) (Figure 73), but such forms appear to be scarce among British Columbia specimens of *S. falcatum*. Conversely, forms of *S. ericoides* var. *pansum* with a capitulescence branching pattern and stem vestiture that are similar to *S. falcatum* (and which have been called *Aster ericoides* var. *stricticaulis* or *Symphyotrichum ericoides* var. *stricticaule*) are frequent on the Canadian prairies (Jones 1978a, 1978b) and may occur in northeastern or southeastern British Columbia. Such plants are best distinguished from *S. falcatum* by their smaller involucres, but not all plants may be easily placed into one or the other species. Ecological factors may further augment morphological characters in the diagnosis of these species, as *S. falcatum* is generally a species of wet or shoreline habitats, while *S. ericoides* var. *pansum* is closely associated with drier upland habitats such as grasslands and open forests, although the two species do often occur in close proximity where these habitats come into contact. Hybridization between *S. falcatum* and *S. ericoides* var. *pansum* appears to be rare, as demonstrated by Jones (1978b), and few collections from British Columbia are suggestive of such hybridization.
*Symphyotrichum falcatum* is implicated in the allopolyploid origin of the widespread western North American *S. ascendens*, which has been shown to have originated through hybridization between *S. falcatum* and *S. spathulatum* (Allen 1985, Allen & Eccleston 1998). Additionally, specimens reviewed for this study suggested hybridization in British Columbia between *S. falcatum* and *S. boreale, S. bracteolatum*, and potentially *S. ericoides* var. *pansum*, while Allen (1985) reports hybridization with *S. ascendens*. Jones (1978b) documented limited interfertility between *S. falcatum* and *S. ericoides*, and therefore some apparently intermediate plants observed during this study may be representative of intraspecific variation in one or the other species rather than true hybridization.

Two varieties of *S. falcatum* are present in British Columbia, and these may be distinguished as follows:

a. Plants cespitose; stems 1-5 (10) from a woody, cormoid caudex; stems usually sparsely to moderately appressed-strigose, rarely densely pubescent or spreading-hairy; phyllaries subequal, outer phyllaries often foliaceous, whitish hyaline bases usually 1/2 or less of phyllary length, apices usually not strongly recurved; peduncle bracts 1-5; plants throughout range in BC……………………………………………………………i. *S. falcatum* var. *falcatum*

aa. Plants rhizomatous, colonial; stems usually solitary, not from a woody, cormoid caudex; stems usually densely spreading-hairy, rarely appressed-strigose; phyllaries often unequal, outer not foliaceous and with pronounced whitish hyaline bases, apices usually strongly recurved; peduncle bracts 2-10+; plants rare in se and sc BC……………………………..……………………………………….ii. *S. falcatum* var. *commutatum*

i. *Symphyotrichum falcatum* var. *falcatum* is the most common and widespread variety of *S. falcatum* in British Columbia, and is found throughout the species’ range in the province (Figure 75). This variety represents the species in the northwestern component of its range (Jones 1978a), and is the only variety that ranges northward into northern Canada (Yukon, Northwest Territories) and Alaska. It is primarily distinguished from the more southerly var. *commutatum* by its strongly
cespitose growth form, in which the stems arise in clusters (occasionally singly) from a woody, cormoid stem base (Figure 72: A). Although critical in the identification of this variety, and pertaining to almost all populations in the Pacific Northwest, the growth form of this variety was misinterpreted in a number of regional floras in the past (e.g., Hitchcock et al. 1955, Hitchcock & Cronquist 1973, Douglas et al. 1989, Douglas 1995, Douglas et al. 1998), which has compromised its identification in the region. Specifically, these treatments have erroneously reported the growth form to be strongly rhizomatous, and thus differing from the strongly cormoid growth form of the similar *S. ericoides* var. *pansum*, with which this species often occurs. This confusion appears to be derived from the application of the concept of var. *commutatum* (which is rhizomatous) westward into the range of the cormoid var. *falcatum*, without an appreciation of the morphological differences between the two infraspecific taxa. This has resulted in most or all populations of *S. falcatum* from west of the Rocky Mountains being attributed to *S. ericoides* var. *pansum*, as in Hitchcock *et al.* (1955) and Hitchcock & Cronquist (1973), or otherwise scarcely differentiated from that taxon (e.g., Douglas *et al.* 1989, Douglas 1995, Douglas *et al.* 1998). Adoption here of the taxonomic concept of the variety presented in Jones (1978a, 1978b) has thus clarified its status in British Columbia and elsewhere in the Pacific Northwest.
ii. **Symphyotrichum falcatum** var. *falcatum* (Johns 645). A = typical involucre and phyllaries; B = typical appressed-strigose vestiture of the stems.

![Figure 7](image1.png)

**FIGURE 71.** Morphological characteristics of *Symphyotrichum falcatum* var. *falcatum*. A = typical involucre and phyllaries; B = typical appressed-strigose vestiture of the stems.

iii. **Symphyotrichum falcatum** var. *commutatum* is the most common and widespread variety of *S. falcatum* east of the Rocky Mountains, but is only rarely encountered in British Columbia.
The distribution of var. *commutatum* is widely sympatric with var. *falcatum* in the northern and western Great Plains (Jones 1978a), but there is only limited interfertility between the two varieties (Jones 1978b). This variety was detected quite recently in British Columbia, when it was identified in the southern Rocky Mountain Trench by F. Lomer in 2015; subsequent specimen review revealed several additional specimens of this variety from southern parts of the province (Figure 75). This variety is very similar to var. *falcatum*, particularly east of the Rocky Mountains where the two varieties are widely sympatric, but is characterized by its strongly rhizomatous habit and usually solitary, erect flowering stems (Figure 74). Jones (1978b) reported that the growth form (cespitose vs. rhizomatous) was apparently genetically fixed, thus reinforcing its taxonomic importance in this group. In addition to growth form, var. *commutatum* tends to be more densely hairy throughout the stems than var *falcatum*, with the hairs whitish and spreading (stems usually sparsely to moderately appressed-strigose in var. *falcatum*) (Figure 73: B), and averages larger capitulae with more extensively white-based phyllaries (Figure 73: A). Jones (1978a) suggests that var. *commutatum* is more characteristic of drier upland habitats than var. *falcatum*, although there is considerable ecological overlap between the two varieties.

![FIGURE 73. Morphological characteristics of Symphyotrichum falcatum var. commutatum (McCalla 10207). A = typical involucre and phyllaries; B = typical dense, spreading vestiture of the stems.](image)
FIGURE 74. Typical plant habit and overall structure of *Symphyotrichum falcatum* var. *commutatum*. Note the strongly rhizomatous habit. A = Lomer 9447; B = McCalla 12042.

FIGURE 75. Distribution of British Columbia specimens of *Symphyotrichum falcatum* that were reviewed for this study (left), and approximate distribution of the species elsewhere in northwestern North America (right).

**LEAFY-BRACTED ASTER;** Leafy Aster; Alpine Leafybract Aster; Parry’s Leafy Aster

[*= var. frondeum]*

*Aster foliaceus* Lindley in de Candolle (1836: 228), misappl. Type:—UNITED STATES. Alaska: Unalaschka (= Unalaska), no collection date reported, *Fischer s.n.* (holotype GDC!). [*= *S. frondeum var. caurinum* (misapplied)]


*Aster amplissimus* Greene (1895: 550). Type:—UNITED STATES. Washington: Mount Rainier, 21 August 1889, *Greene s.n.* (lectotype [designated on specimen by A.G. Jones (1992)] NDG!, isolectotype NDG!). [*= *S. frondeum var. frondeum*]

*Aster glastifolius* Greene (1900: 218). Type:—UNITED STATES. Wyoming: North Vermillion Creek, 17 July 1897, *A. Nelson 3555* (lectotype [designated on specimen by Shinners (1948)] NDG!, isolectotypes RM!, ILL!). [*= *S. frondeum var. frondeum*]

*Aster diabolicus* Piper (1902: 645). Type:—UNITED STATES. Oregon: Squaw Creek, Cook County, 17 July 1901, *Cusick 2670* (isotypes US!, E!, F!, P!, OSC!, NY!, G!, MIN!, NDG!RM!, K!, VT!, MSC!). [*= *S. frondeum var. frondeum*]

**Plants** perennial, long-rhizomatous, colonial. **Stems** not from a branched caudex, solitary to several, ascending to erect, simple to few-branched distally, sparsely to moderately white-
puberulent (especially distally), pubescence arranged in lines from leaf bases on mid-stem, (6) 10-50 (60) cm tall. **Leaves** basal and cauline, basal and proximal cauline leaves usually persistent, reduced distally, margins usually entire (rarely sparsely and minutely serrulate) and flat to slightly revolute, minutely stiff-ciliate with antrorse hairs, faces glabrous to sparsely soft-puberulent towards the apices; basal leaves petiolate, linear-oblanceolate or oblanceolate to obovate or spatulate, apices acute or obtuse to rounded, bases long-attenuate to cuneate, (20) 40-140 (200) mm; proximal cauline leaves petiolate to subsessile, linear-oblanceolate or oblanceolate to lance-elliptic, apices obtuse to acute, bases usually subclasping to auriculate, 40-100 (200) mm; distal cauline leaves sessile, lanceolate or oblanceolate to lance-oblong or oblong, apices rounded to acute, bases clasping and auriculate, (10) 20-110 mm. **Capitulescences** usually open, of solitary heads or subcorymbose, branches erect to ascending; peduncle bracts 0-3, lanceolate to narrowly oblong, apices obtuse to acute, usually grading into phyllaries, 4-25 mm. **Flowering heads** solitary to several (11+); involucres campanulate, 6-10 (15) mm; phyllaries subequal, in 4-6 series, usually spreading, ciliate, faces glabrous to puberulent; outer phyllaries linear or linear-lanceolate to broadly elliptic-oblanceolate, apices acute or acuminate to obtuse, 1 or more often enlarged and foliaceous, margins sometimes hyaline on proximal 1/3 or less, green zones broadly oblanceolate to elliptic, usually slightly to strongly purple-tinged (especially apically and along margins), 6-15 (-25) mm; inner phyllaries linear to narrowly lanceolate, apices acute to acuminate, margins hyaline proximally, green zones oblanceolate, 8-12 mm; ray florets 15-60, violet to purplish, laminae 8-18 (20) mm; disc florets 50-150, yellowish, lobes deltate, 5-8 mm. **Cypselae** cylindric to obovoid, not compressed, brownish, 3- to 4-nerved, densely short-hairy, 2.5-4 mm; pappus whitish to tan, 5-8 mm.

Flowering Jul-Sep (Oct). Moist to mesic meadows, streambanks, shorelines, thickets, openings, forest edges, talus slopes, and tundra in the montane, subalpine, and alpine zones; (150)
600-2100 (2400) m. Common in coastal BC [except absent from Haida Gwaii], frequent in south-central and southeast BC [north to the Chilcotin region, Yoho Nat. Park], and locally frequent in northwest [Boundary Ranges, Haines Triangle] and east-central [Rocky Mts., Cariboo Mts.] BC. AK and YT south to CA, AZ, NM and east to WY, CO. $2n = 16, 32, 48, 64, 80, 96 \ [2x-12x]$ (Allen 1984).

*Symphyotrichum frondeum* is the most common aster of montane and subalpine habitats in British Columbia, and is often the sole member of the genus inhabiting such areas of the province. It is typical of moist, usually open habitats such as streambanks, wet meadows, shorelines, and moist thickets at moderate to high elevations, although it also occurs in drier upland and disturbed habitats as well (particularly in the southern interior [= var. *frondeum*]). The species occurs widely across southern half of British Columbia (Figure 82), although it is scarce in the Columbia Mountains east of the Okanagan Valley and in the Fraser-Nechako Plateau of the central interior. Farther north, it is occasional along the Coast Mountains of northwestern B.C. in areas adjacent to the Alaska Panhandle, reaching its northernmost occurrences in the Haines Triangle of B.C., the extreme southwestern Yukon Territory (B. Bennett, *pers. comm.*), and the Seward Peninsula of Alaska (Figure 82). The species is characterized by the partially or completely foliaceous outer phyllaries that are subequal (i.e., not graduated) (Figure 77; Figure 79), as well as the usually persistent basal leaves, the entire and slightly to moderately clasping cauline leaves, and the few-headed capitulescences with long-pedunculate, relatively large capitulae. The clasping bases of the cauline leaves are much more consistent and pronounced than has often been recognized (as in, e.g., Brouillet *et al.* 2006) and can be considered a diagnostic feature of the species, at least within its British Columbia distribution and elevation range.

The name *Symphyotrichum frondeum* is proposed here as the correct nomenclature for the species that has previously been treated as *Symphyotrichum foliaceum* (or *Aster foliaceus*) in North
America. The holotype upon which the name *Aster foliaceus* de Candolle (1836) is based appears to represent the same taxonomic entity that is here treated as *Symphyotrichum subspicatum* [= *Aster subspicatus*] – which was published in 1832 (Nees von Essenbeck 1832) and thus has priority for that taxon – based on their similar morphology (lanceolate, clasping, serrate leaves; leafy capitulescences; short peduncles; subequal phyllaries with prominent pale bases) (Figure 76) along with phytogeographic considerations. The name *foliaceus* has thus been misapplied to the taxon that is here treated as *S. frondeum* since at least the early 20th century (e.g., Howell 1900, Piper 1906, Henry 1915), with only Hultén (1968) and Packer (1983) recognizing the conspecificity the type specimens of *foliaceus* and *subspicatus*. Neither of these later publications recognized the misapplication of the name *foliaceus* to a taxon that was not representative of the holotype, however, and the issue remained unresolved. Even in Cronquist (1943), which remains one of the most comprehensive taxonomic treatments of this and related species, the conspecificity of the names *foliaceus* and *subspicatus* was not recognized, with the author commenting that he had not reviewed the holotype of *foliaceus* during his work with the genus. Only A.G. Jones, who published extensively on the taxonomy of *Aster*, appears to have reviewed the holotypes of these names and recognized that they represented the same taxon, as indicated by her 1981 annotation to that effect on the holotype of *A. foliaceus*. The misapplication of the name *foliaceus* has thus persisted to the present day.
FIGURE 76. Comparison of holotypes of *Aster subspicatus* (left) and *Aster foliaceus* (right). These collections are proposed here to represent the same taxon, which is the only member of *Symphyotrichum* subg. *Symphyotrichum* sect. *Occidentales* present in most areas of south-coastal Alaska (where these collections were made). The conspecificity of these collections is reinforced by their morphology, as they share critical features of *S. subspicatum* such as serrate leaf margins, extensive pale bases to the narrow subequal phyllaries, and leafy capitulescences with relatively short-pedunculate capitulae.

The taxon to which the name *Symphyotrichum foliaceum* [= *Aster foliaceus*] has long been applied is treated under the specific epithet *frondeum* here, as this is one of the two oldest names available at the rank of species that could pertain to this complex. Although the name *Aster amplissimus* Greene (1895: 550) was published at species rank simultaneously with the first publication of the species-rank name *Aster frondeus* (A. Gray) Greene (1895: 551), rendering these as competing names at that rank, the specific epithet *frondeus* is selected here as the name for this
taxon in accordance with Article 11.5 of the Shenzhen Code of the International Association of Plant Taxonomists (2018). As the first author to unite the names *amplissimus* and *frondeus* (Cronquist 1943) did so by treating both as synonyms of the misapplied name *foliaceus* and did not indicate either as having priority, the decision to elevate one as the species name for this taxon was unresolved and available to be addressed in this study. The selection of the name *frondeus* [= *frondeum*] over *amplissimus* here maintains consistency with several prominent earlier publications (e.g., Cronquist 1943, Cronquist *et al.* 1994) wherein the name *frondeus* is familiar as an infraspecific epithet; the name *amplissimus* is treated as a synonym of *frondeus* to avoid the unnecessary introduction of an otherwise unfamiliar name.

Several varieties or subspecies have traditionally been recognized within *Aster foliaceus* [= *Symphyotrichum foliaceum*], and these infraspecific taxa are here moved to *S. frondeum*. Four infraspecific taxa have generally been recognized within *foliaceus* in North America, and these have typically been recognized at the varietal level as var. *foliaceus* (here designated var. *caurinum*), var. *parryi* (here designated var. *frondeum*), var. *apricus*, and var. *canbyi*. Two other taxa formerly recognized as varieties of *foliaceus* are here recognized as the species *Symphyotrichum cusickii* [= *Aster foliaceus* var. *cusickii*] and *S. hendersonii* [= *A. foliaceus* var. *lyallii*]. Among the four taxa that were treated as varieties of *Symphyotrichum foliaceum* in Brouillet *et al.* (2006), and which are moved to *S. frondeum* in this treatment, only var. *caurinum* [= var. *foliaceum* in Brouillet *et al.* (2006)] and var. *frondeum* [= var. *parryi* in Brouillet *et al.* (2006)] are recognized as being present within British Columbia. The var. *apricum* of the western United States has sometimes been recognized as occurring in the province (e.g., BC Conservation Data Centre 2018), but B.C. populations thus attributed do not differ meaningfully from typical var. *caurinum* with which they appear to intergrade completely, in any way other than their smaller stature and alpine habitat. Given the association of reduced plant size with increasing elevation,
and the absence of additional morphological characteristics supporting its recognition in British Columbia, populations formerly recognized as var. *apricum* in British Columbia (such as those from the Ilgachuz Mountains of west-central B.C.) are here recognized as var. *caurinum*; similar plants in the Rocky Mts. and Cascade Mts. may be attributable to var. *frondeum*. The status of var. *apricum* in the western United States is not further addressed here as it is considered beyond the geographic scope of the current study. The two varieties recognized as occurring in British Columbia appear to hybridize locally along the southern Coast Mountains and in the Cascade Mountains (Figure 81), where the ranges of the primarily coastal var. *caurinum* and var. *frondeum* of the southern interior meet. Typical examples of the varieties can be distinguished as follows:

**a.** Outer foliaceous phyllaries conspicuous, broadly lanceolate to ovate, apices obtuse to broadly acute and usually ascending to erect; capitulae commonly solitary; plants of wetter climates in coastal, c, and ec BC……………………………………i. *S. frondeum* var. *caurinum*

**aa.** Outer foliaceous phyllaries not conspicuous, linear to narrowly lanceolate, apices acute to acuminate and often spreading or somewhat squarrose; capitulae rarely solitary; plants of drier climates in sc and se BC……………………………………ii. *S. frondeum* var. *frondeum*

**i.** *Symphyotrichum frondeum* var. *caurinum* Fenneman, var. nov. Type:—CANADA. British Columbia: road up Windy Joe Mountain, Manning Park, 4800 ft., 04 August 1957, Beamish & Stone 7847 (UBC!). Figure 51:A.

[See Cronquist (1943) for morphological description of this taxon, where it was erroneously treated as *Aster foliaceus* var. *typicus.*]

The name *S. frondeum* var. *caurinum*, described here, is consistent with the taxon that has been treated as *S. foliaceum* var. *foliaceum* or *Aster foliaceus* var. *foliaceus* in other taxonomic and floristic publications. This variety represents the species in the wetter climates of British Columbia, both along the coast and the western slopes of the Coast-Cascade Mountains as well as across wetter portions of the central interior (south in the B.C. interior to the Cariboo Mountains). Although it is often reported to be primarily single-headed (e.g., Cronquist 1943, Hitchcock *et al.*
1955, Abrams & Ferris 1960, Brouillet et al. 2006), plants attributable to this variety range from single-headed (especially along the southern coast of the province) to polycephalous with as many as 6-7 (11) heads (especially in the Cariboo Mountains and elsewhere in the central interior) (Figure 78). The predominance of polycephalous populations in the interior of the province may be worthy of taxonomic recognition, although the occasional presence of such plants elsewhere in the species’ range and the lack of additional morphological discrepancies that correlate consistently with capitulum number suggests that these plants are better treated as part of the same, variable taxon at this time.

Plants of *S. frondeum* var. *caurinum* are reasonably distinctive, particularly those with solitary capitulae, but the taxon may be confused with *S. subspicatum* along the northern and central mainland coast, or with *S. douglasii* along the south coast. This taxon is best distinguished from *S. subspicatum* by its entire (vs. serrate), oblanceolate (vs. lanceolate to lance-elliptic) basal and cauline leaves, as well as its usually montane/subalpine habitat (vs. plants generally of coastal estuaries and maritime shorelines, rarely reaching 400 m elevation, in *S. subspicatum*). *Symphyotrichum douglasii* of the southern coast of the province is similarly of lower elevations than *S. frondeum* var. *caurinum*; however, there is some localized and limited elevational overlap between them, and hybridization between the two taxa may account for some *Symphyotrichum* populations from central Vancouver Island that have been recognized as ‘*Aster carterianus*’ in the past (here attributed to *S. douglasii*). The usually conspicuously broad and foliaceous outer phyllaries of *S. frondeum* var. *caurinum* as well as its commonly solitary capitulae and clasping leaf bases, should eliminate confusion with *S. douglasii* under most circumstances, especially when elevation and habitat are considered. In addition to hybridization with *S. frondeum* var. *frondeum* and potentially with *S. douglasii* on Vancouver Island, putative hybrids with *S. ciliolatum* have been collected rarely from the central interior of the province.
FIGURE 77. Variation in involucre and phyllary morphology in *Symphyotrichum frondeum* var. *caurinum*. A = example with broad, acute, extensively foliaceous outer phyllaries (*Brayshaw* & *Szczawinski* 27/9/54); B = example with narrower, less extensively foliaceous outer phyllaries that display limited pale, indurate bases (*Roemer* 317). Note the narrow purple phyllary margins in B, which are commonly expressed in this taxon.
FIGURE 78. Morphological variation in *Symphyotrichum frondeum* var. *caurinum*. A = example of broader-leaved morphotype (*Beamish & Stone 7847*; TYPE of *S. frondeum* var. *caurinum* Fenneman); B = example of narrow-leaved morphotype (*Krajina s.n.*); C = example of dwarf, alpine morphotype that has been attributed to var. apricum by some past authors (*R.L. Taylor, Beil, Marchant, & Oliver 3624*); D = example of polycephalous morphotype from the Cariboo Mountains of east-central BC (*McIntosh 2011_252*).
ii. *Symphyotrichum frondeum var. frondeum* is consistent with the taxon that has generally been treated as *S. foliaceum* var. *parryi* or *Aster foliaceus* var. *parryi*, and represents the species throughout the south-central and southeastern interior of British Columbia. It also occurs widely throughout the western United States, and is the most widespread and common representative of the *S. frondeum* complex throughout most of that region. This variety differs from var. *caurinum* primarily in its narrow, linear to linear-lanceolate phyllaries (Figure 79) and its more consistently polycephalous habit, and is most likely to be confused with forms of *S. spathulatum*, particularly the extralimital var. *spathulatum* which approaches the British Columbia border in Washington. It is best distinguished from *S. spathulatum* var. *spathulatum* by its subequal phyllaries and often broader basal and cauline leaves, which differ from the distinctly graduated phyllaries and generally narrower, often linear-lanceolate basal and lower cauline leaves of *S. spathulatum* var. *spathulatum*. These two forms intergrade widely across much of the United States, however, and their separation is not always straightforward. As a result, caution in identification is strongly recommended for any potential occurrences of *S. spathulatum* var. *spathulatum* in British Columbia.

**FIGURE 79.** Variation in involucre and phyllary morphology in *Symphyotrichum frondeum var. frondeum*. A = typical individual, with very narrow, extensively foliaceous, subequal outer phyllaries (*Lomer 7795*); B = capitulum with somewhat broader, wholly foliaceous phyllaries (right; note recurved apices of more typical capitulum on the left) (*Manton & J.Fenneman 299*).
FIGURE 80. Morphological variation in *Symphyotrichum frondeum* var. *frondeum*. A = example of broader-leaved morphotype (*E.R.Fenneman & J.D.Fenneman 28*); B = example of narrow-leaved morphotype (*Lomer 7795*). Note that many individuals are intermediate between these two extremes.

FIGURE 81. Collection locations (stars) for putative hybrids between *Symphyotrichum frondeum* var. *caurinum* (red) and var. *frondeum* (blue). The purple-dashed line indicates the approximate line of parapatry between these varieties.
FIGURE 82. Distribution of British Columbia specimens of *Symphyotrichum frondeum* that were reviewed for this study (left), and approximate distribution of the species elsewhere in northwestern North America (right).

14. *Symphyotrichum frondosum* (Nutt.) G.L. Nesom

**SHORT-RAYED ASTER;** Short-rayed Alkali Aster


*Brachyactis ciliata* (Ledeb.) Ledeb. var. *carnosula* Bentham (1876: 6). Type:—UNITED STATES. California: Sonora Pass, 1866, *Bolander 6160* (isosyntypes NY!, YU!).

**Plants** annual or sometimes perennial, taprooted. **Stems** not from a branched caudex, solitary to several, simple to much-branched throughout, decumbent to ascending or erect, glabrous, (2) 5-60 (140) cm tall. **Leaves** basal and cauline (basal and proximal cauline withering prior to anthesis), gradually reduced distally, sessile to subpetiolate, linear to oblanceolate, apices acute to obtuse
and sometimes mucronate, bases cuneate to attenuate, margins entire and minutely stiff-ciliate with antrorse hairs, faces glabrous, 10-50 (80) mm. **Capitulescences** dense to open, narrow and racemose to paniculate or pyramidal, usually leafy, branches spreading and decumbent (proximally) to ascending (distally); peduncle bracts 4-6, linear, apices often minutely spine-tipped, sometimes grading into phyllaries, 3-7 mm. **Flowering heads** few to numerous; involucres campanulate, 5-9 mm; phyllaries unequal to subequal (outer sometimes exceeding inner), in 3-4 series, loosely spreading, margins sparsely ciliate (especially proximally), faces glabrous; outer phyllaries narrowly oblanceolate, apices obtuse to acute and sometimes mucronate, wholly foliaceous or margins hyaline proximally, green zones oblanceolate to elliptic or oblong and restricted to distal 2/3-3/4, 3-7 mm; inner phyllaries linear-lanceolate to narrowly oblanceolate, apices obtuse to acuminate, margins hyaline proximally, green zones oblanceolate to elliptic or oblong and restricted to distal 1/2-2/3, 4-7.5 mm; ray florets 90-110, whitish to pinkish, laminae 1.5-2 mm; disc florets 30-45, yellow, lobes lanceolate, 4.5-5.5 mm. **Cypselae** obovoid, somewhat compressed, tan, 2- to 3-nerved, densely short-hairy, 2-2.5 mm; pappus whitish to tawny, 6.5-7.5 mm.

Flowering Jul-Oct. Moist to wet, often saline or alkaline shorelines and pond edges in the steppe zone; (40) 270-350 (700) m. Rare in south-central BC (southern Okanagan Valley). BC south to CA, AZ, NM; Mexico. \(2n = 14\ [2x]\) (Brouillet *et al.* 2006).

*Symphyotrichum frondosum* is a rare aster of exposed lacustrine shorelines in the arid southern Okanagan Valley (Figure 85), occurring north to Max Lake near Penticton (Sears *et al.* 2004, Symonds 2015). It was first collected in British Columbia at Osoyoos Lake in 1939 but was not observed again in the province for more than 50 years before being rediscovered at the same lake in 1992 (Sears *et al.* 2006). Outside of the Okanagan Valley, it has been reported as an
ephemeral introduction on sand dredgings along the lower Fraser River in southwestern B.C. (Sears et al. 2006), which has led to speculation that the species may occur undiscovered at sites upstream in the Fraser-Thompson Basin. Such speculation seems reasonable, given that a number of other species of similar habitats are disjunct between the southern Okanagan Valley and the Fraser-Thompson Basin (e.g., Rotala ramosior, Marsilea vestita, Eleocharis engelmannii). The species has not been collected in such habitats along the lower Fraser River since 1994, however, and the representative specimen (Lomer 94-228) appears to have been lost; this report thus remains somewhat enigmatic. In addition to this potentially natural occurrence, *S. frondosum* has also been collected as a non-established waif in landscaping in the Vancouver area (Lomer 6137 [UBC!], Lomer 6145 [UBC!]), perhaps originating as contamination in landscaping material arriving from the western United States (F. Lomer, pers. comm.).

*Symphyotrichum frondosum* is closely related to the much more common and widespread *S. ciliatum*, and the two species may hybridize locally in the southern Okanagan Valley based on reports of seemingly intermediate plants from this region (Symonds 2015; C. Björk, pers. comm.). ‘Intermediate’ plants corresponding with this supposed hybridization have been identified by their large, robust stature with generally erect stems, profusely-branched capitulescences with more numerous capitulae (Figure 84: B), and narrower phyllaries (Figure 83: B) (C. Björk, pers. comm.). ‘Typical’ plants of *S. frondosum*, in contrast, are generally defined by their small stature, often prostrate habit, relatively few capitulae, and broader phyllaries (C. Björk, pers. comm.). Plants corresponding to the ‘intermediate’ morphology appear to occur throughout the species range, however, even in areas beyond the known distribution of *S. ciliatum* (e.g., Nobs & S.G-Smith 1663 [UBC!]), and published descriptions of the species (e.g., Hitchcock et al. 1955, Abrams & Ferris 1960, Cronquist et al. 1994, Douglas et al. 1998, Brouillet et al. 2006) regularly incorporate such morphologies within the circumscription of *S. frondosum*. Indeed, type specimens of *Brachyactis*
angustus var. carnosula, which is recognized in synonymy under *S. frondosum* and is from beyond the range of *S. ciliatum* (i.e., California), are consistent with the morphology presented by such ‘intermediate’ plants in British Columbia. Furthermore, Houle (1988) found limited interfertility between the primarily selfing *S. ciliatum* and the primarily outcrossing *S. frondosum*, although there was some limited ability to produce hybrids between male *S. frondosum* and female *S. ciliatum* under artificial conditions (reciprocal crosses were unsuccessful). Thus, despite the rather pronounced morphological differences between the ‘typical’ and ‘intermediate’ morphologies, these may be better considered as ends of a morphological spectrum that is influenced more by environmental conditions than hybridization, as is typical of many annual species of shoreline habitats. However, the true status of these plants as hybrids may be better investigated through additional crossing and field studies than through morphological analysis of herbarium material.

**FIGURE 83. Variation in involucre and phyllary characteristics of *Symphyotrichum frondosum*.** A = typical involucre, with relatively broad, blunt outer phyllaries (*McIntosh 2007_38*); B = plant with narrower, more acute phyllaries, suggesting potential hybridization with *S. ciliatum* (*McIntosh & Hall 2007_77*).
FIGURE 84. Overall habit of Symphyotricum frondosum. A = morphology typical of plants from exposed shorelines, demonstrating diminutive stature and often procumbent stems (McIntosh 2008:68); B = larger, more robust plant of a morphology typical of sheltered, more stable, and more densely vegetated habitats, demonstrating extensive branching and erect stem (McIntosh & Hall 2007:45).

FIGURE 85. Distribution of British Columbia specimens of Symphyotrichum frondosum that were reviewed for this study (left), and approximate distribution of the species elsewhere in northwestern North America (right). Open circle denotes introduced waif.
15. *Symphyotrichum hendersonii* (Fern.) Nesom

**HENDERSON’S ASTER**

*Aster cusickii* A. Gray var. *lyallii* A. Gray (1884: 195) [as *lyalli*]. Type:—UNITED STATES. Washington: “between the Kootenay and Pend Oreille”, August 1861, Lyall s.n. (holotype K); *A. foliaceus* Lindl. in DC. var. *lyallii* (A. Gray) Cronquist (1943: 443).


*Aster eriocaulis* Rydberg (1910a: 143). Type:—UNITED STATES. Idaho: Traille River, Kootenai County, 09 August 1892, *Sandberg, MacDougal, & Heller* 877 (holotype NY!, isotypes GH!, CAS!, LE!, G!).

*Aster kootenayi* A. Nelson & Macbride (1913: 477). Type:—not designated.

**Plants** perennial, long-rhizomatous, colonial to cespitose. **Stems** not from a branched caudex, solitary to several, ascending to erect, usually branched distally, sparsely white-puberulent, pubescence arranged in lines from leaf bases, 40-100 cm tall. **Leaves** basal and cauline, basal and proximal cauline leaves usually withering prior to anthesis, slightly reduced distally, margins entire and flat, minutely stiff-ciliate with antrorse hairs, faces glabrescent to moderately (sometimes densely) soft-puberulent; basal leaves petiolate, obovate to broadly elliptic, apices acute, bases attenuate to cuneate, 5-200 mm; proximal cauline leaves sessile, oblanceolate to obovate, apices acute, bases strongly clasping and usually auriculate, 70-120 mm; distal cauline leaves sessile, lanceolate to broadly elliptic, apices obtuse to acute, bases truncate and usually auriculate, 30-110 mm. **Capitulescences** usually open, pyramidal, usually leafy, branches ascending; peduncle bracts 2-6, lanceolate, apices acute to acuminate, distinct from phyllaries or distalmost sometimes grading into phyllaries, 5-15 mm. **Flowering heads** several to numerous; involucres campanulate, 10-20 mm; phyllaries subequal or outer exceeding the inner, in 4-5 series,
usually spreading, sparsely ciliate (especially proximally), faces glabrous to puberulent; outer phyllaries narrowly to broadly lanceolate or oblanceolate, apices acute, often enlarged and foliaceous, margins sometimes hyaline on proximal 1/3 or less, green zones lanceolate to elliptic, 6-11 (15) mm; inner phyllaries linear to linear-lanceolate, apices acute to acuminate, margins hyaline proximally, green zones lanceolate, 6-10 (12) mm; ray florets 25-55, violet to purplish, laminae 10-18 mm; disc florets 60-150+, yellowish, lobes deltate, 2.5-4 mm. **Cypsela**e cylindric to ovoid, not compressed, brownish, 3- to 6-nerved, densely short-hairy, 3-3.5 mm; pappus whitish, 5-9 (11) mm.

Flowering Jul-Sep. Moist to dry meadows, open forests, rocky slopes, streambanks, and shorelines in the montane and subalpine zones. Rare in southeast BC [s Columbia Mts.]. BC south to CA, ID, MT. **2n** = 16, 32 [2x-4x] (Allen 1984).

*Symphyotrichum hendersonii* is among the rarest of British Columbia asters, being first detected in the province as recently as 2015 and currently known from only a single small area along the Canada-U.S. border west of Creston (Figure 87). A previous mention of the species occurring in British Columbia (as *Aster foliaceus* var. *lyallii*) in Cronquist (1943), based on a collected specimen from the Flathead region of the extreme southeastern corner of the province, is considered unlikely to have been correctly identified based on current understanding of the species’ distribution. However, as the specimen in question was not reviewed as part of this study, the veracity of its identification remains speculative.

This species is a primarily diploid member of the “*Aster foliaceus*” species complex (Cronquist 1943), where it has generally been recognized as a variety of *Aster [=Symphyotrichum] foliaceus* (= *S. frondeum* of this treatment), along with *parryi* (here treated as *S. frondeum* var. *frondeum*) and *cusickii* (Cronquist 1943, Hitchcock *et al.* 1955, Abrams & Ferris 1960, Hitchcock
& Cronquist 1973). It has rarely been treated as a variety (Gray 1884) or even synonym (Dean 1966) of *Aster [=Symphyotrichum] cusickii*. When treated taxonomically at the varietal level, this taxon has traditionally been recognized as var. *lyallii* (e.g., Cronquist 1943), based on the name *Aster cusickii* var. *lyallii* A. Gray (Gray 1884); however, the epithet *lyallii* is not available for use at the species level due to the publication of *Aster lyallii* Kuntze (1891: 316).

Within the ‘foliaceus’ complex of taxa, *S. hendersonii* is morphologically most similar to *S. cusickii*, with which it is fully sympatric in British Columbia. It is reliably distinguished from *S. cusickii* by a number of characters, however, including its narrower leaves with less prominently auriculate bases, its smaller and more numerous capitulae, its much narrower (usually linear-lanceolate) phyllaries (Figure 86: B), and the sparser, shorter, and less conspicuous pubescence on the stem and leaves, with that of the stem arranged in narrow, longitudinal lines proximal to the leaf bases. Although some plants of *S. cusickii* may approach *S. hendersonii* in the density of the stem hairs, *S. cusickii* can be reliably distinguished by the characteristic uniformity of its pubescence (the hairs not arranged in lines along the stem). *Symphyotrichum hendersonii* is further distinguished from other members of this complex, and from other sympatric species of *Symphyotrichum*, by the large, leafy, paniculate or corymbose-paniculate capitulescence with numerous sessile, auriculate-clasping, leafy capitulescence bracts that are only slightly reduced in size relative to the cauline leaves (Figure 86: A).
FIGURE 86. Morphological characteristics of *Symphyotrichum hendersonii* (Lomer 9696A). A = whole plant habit; B = detail of involucre/phyllaries.

FIGURE 87. Distribution of British Columbia specimens of *Symphyotrichum hendersonii* that were reviewed for this study (left), and approximate distribution of the species elsewhere in northwestern North America (right).
16. *Symphyotrichum laeve* (L.) Á. Löve & D. Löve subsp. *laeve*

**SMOOTH ASTER**; Smooth-leaved Aster; Smooth Blue Aster; Glaucous Aster; Smooth American-aster


*Aster brevibracteatus* Rydberg (1900: 392). Type:—UNITED STATES. Washington: Spokane County, 10 August 1889, *Suksdorf 928* (holotype NY!, isotypes WTU!, NDG!, US!).

*Aster scribneri* Rydberg (1900: 393). Type:—UNITED STATES. Montana: Birdtail Creek, 1883, *Scribner 91* (holotype NY!).


**Plants** perennial, short-rhizomatous, cespitose. **Stems** usually from a branched woody caudex, solitary to several, erect, few- to much-branched distally, glabrous to sparsely hirsute distally (pubescence, when present, often arranged in lines from leaf bases), greenish or sometimes reddish proximally, glaucous, (15) 20-70 (120) cm tall. **Leaves** basal and cauline, basal and proximal cauline usually withering prior to anthesis, reduced distally (especially in capitulescence), margins entire to coarsely crenate-serrate and usually revolute, sometimes minutely stiff-ciliate with antrorse hairs, faces glabrous, glaucous, somewhat fleshy; basal and proximal cauline leaves long-
petiolate, lanceolate or ovate to elliptic or spatulate, apices acute to obtuse or rounded, bases attenuate to cuneate, petioles narrowly to broadly winged, 30-200 mm; mid-cauline leaves sessile to short-petiolate, narrowly lanceolate to ovate or oblong, apices acute to obtuse, bases rounded to cuneate and often auriculate-clasping, petioles (when present) broadly winged, (20) 40-100 (180) mm; distal cauline leaves sessile, linear or lanceolate to lance-oblong, bases rounded and strongly auriculate-clasping, 7-45 mm. Capitulescences open, usually pyramidal, not leafy, branches spreading to ascending; peduncle bracts 3-6, linear to narrowly lanceolate, apices minutely spine-tipped, usually grading into the phyllaries, 2-5 mm. Flowering heads several to numerous; involucres campanulate to cylindro-campanulate, (4) 5-7 (8) mm; phyllaries usually unequal, in 4-6 series, erect, sparsely ciliate (especially proximally), faces glabrous, margins hyaline on basal (1/3) 2/3-3/4, green zones narrowly lanceolate to ob lanceolate; outer phyllaries lanceolate to oblong-lanceolate, apices acute to acuminate and often reddish- or purplish-mucronulate, 2-4 mm; inner phyllaries linear-lanceolate, apices acute to long-acuminate, 5-6 mm; ray florets (11) 13-23 (34), pinkish or violet to bluish (rarely whitish), laminae (6) 7-11 (14.5) mm; disc florets (17) 19-33 (43), yellowish (becoming reddish or purplish in age), lobes deltate, 3.5-6 mm. Cypselae oblong-obovoid, compressed, dark purplish or brownish, 4- to 5-nerved, glabrous or glabrate, 2-3.5 mm; pappus tawny to pink-tinged, 5-7 mm.

Flowering (Jun) Jul-Sep. Mesic to dry meadows, grasslands, open slopes, thickets, open forests, fields, clearings, agricultural areas, and disturbed areas in the steppe, montane, and parkland regions; (50) 400-1300 (1500) m. Frequent in northeast [Peace River lowlands] and southeast [southern Columbia Mts., Rocky Mountain Trench, Rocky Mountains] BC, rare and adventive in south-central [Okanagan Valley] and southwest [Lower Mainland] BC. BC east to NS, south to CA, AZ, TX, GA; disjunct north to YT. $2n = 48$ [6x] (Brouillet et al. 2006).
*Symphyotrichum laeve* subsp. *laeve* is a locally common, upland-associated aster in British Columbia, where it is restricted primarily to the Peace River area of the northeast and the East Kootenay region of the southeastern part of the province (Figure 90). Its true distribution in the province is considerably more restricted than has typically been shown in other regional floras (e.g., Douglas 1995, Douglas et al. 1998, Douglas et al. 2002b), with much of the confusion apparently stemming from misidentifications of herbarium material. Despite this more restricted distribution in British Columbia, *S. laeve* subsp. *laeve* can be rather common within the regions where it occurs; indeed, it is among the most common asters within the Peace River area. It is occasionally grown horticulturally, and has been collected as a non-persistent waif in the Lower Mainland area of the south coast (*Lomer 7506 [UBC!]*). Though native, this species readily occupies a variety of disturbed and agricultural environments; a roadside collection from the Okanagan Valley, which is otherwise disjunct from the species’ primary range in the province, is suspected of representing a non-native, adventive population whose spread and establishment has been facilitated by movement along roadways.

Although the distribution of *Symphyotrichum laeve* subsp. *laeve* in British Columbia has been clouded in the past by misidentifications, it is among the more distinctive *Symphyotrichum* species in the province. It is characterized by glabrous (or nearly so) stems, an overall glaucous colouration on the stems and leaves, somewhat thickened and fleshy leaves, broad and distinctly petiolate basal and lower cauline leaves, strongly auriculate-clasping cauline leaves, and greatly reduced leaves/bracts in the wide-branching capitulescence (Figure 88). It is most similar to the widespread and common *S. ciliolatum* of the British Columbia interior, but can best be distinguished by the shape of its basal and lower cauline leaves (strongly cordate in *S. ciliolatum*, generally lanceolate to ovate or elliptic in *S. laeve*), overall glabrous and glaucous herbage, and slightly thickened or fleshy leaves. Although there is considerable ecological overlap between
these two species, *S. ciliolatum* is typically associated with forested or woodland environments, whereas *S. laeve* is more closely associated with open, often disturbed habitats.

*Symphyotrichum laeve* subsp. *laeve* is capable of hybridizing with a wide range of other regional *Symphyotrichum* species. Indeed, despite its morphological distinctiveness and apparent biological isolation from most other *Symphyotrichum* species in the Pacific Northwest, Dean (1966) found this species to be among the most successful in producing hybrid offspring when crossed with other species. It has been reported as hybridizing readily with the relatively closely related *S. ciliolatum* (Brouillet 2006), and such a hybridization event has generally been implicated in the origin of the apparently allopolyploid *S. x maccallae* of southern B.C. and the Rocky Mountains (Jones 1984). *Symphyotrichum laeve* subsp. *laeve* (as var. *laeve*) has also been reported to hybridize with the widely sympatric *S. lanceolatum* in eastern North America (Semple et al. 2002, Brouillet 2006), and apparent hybrids with *S. bracteolatum* and *S. frondeum* var. *frondeum* in British Columbia were observed during this study. The apparent hybrids with *S. frondeum* var. *frondeum* closely resemble the holotype of *Aster umbachii* Rydb. (Holotype: UNITED STATES. Montana: Lake MacDonald, 20 August 1901, *Umbach 275* [NY!]), which may be an appropriate binomial for this hybrid combination if recognized taxonomically (i.e., as *S. x umbachii*). In addition, artificial garden-derived hybrids of *S. laeve* with other members of the genus are prevalent in the horticultural industry, and one of these (*S. x versicolor* Willd. [= *S. laeve* subsp. *laeve* x *S. novi-belgii* var. *novi-belgi*]) has escaped and become locally established in Europe (Tutin et al. 1976, Brouillet et al. 2006, Botanical Society of Britain & Ireland 2018). *Symphyotrichum x versicolor* has been collected from a single site in the Similkameen River area of south-central B.C., and thus this hybrid may be expected to occur as an occasional introduction in the region; however, it is excluded here as part of the provincial flora pending additional collections and evidence of establishment.
Western North American populations of *S. laeve* have commonly been recognized as distinct from those of eastern North America, usually as var. *geyeri* or subsp. *geyeri* (Hitchcock *et al.* 1955, Abrams & Ferris 1960, Hitchcock & Cronquist 1973, Douglas 1995, Douglas *et al.* 1998, Brouillet *et al.* 2006); two additional varieties occur in southeastern North America (Brouillet *et al.* 2006). The two varieties differ only in their phyllaries and involucres, with the western ‘*geyeri*’ exhibiting relatively longer outer phyllaries that often approach the length of the inner, as well as narrower lanceolate green zones near the phyllary apices (Brouillet *et al.* 2006). The eastern ‘*laeve*’, in contrast, has a more strongly graduated involucre (outer phyllaries conspicuously shorter than the inner) and shorter, broader, diamond-shaped green zones near the phyllary apices (Brouillet *et al.* 2006). These characters, though distinct at their extremes, and reasonably well aligned geographically, intergrade widely across much of central North America, and even away from this region it is not infrequent that some plants of one variety (assigned based on geographic considerations) are essentially indistinguishable from the other variety (Hitchcock *et al.* 1955, Cronquist *et al.* 1994). Even within British Columbia, although most specimens are relatively easy to assign to the ‘*geyeri*’ morphology, some collections are morphologically intermediate between the two varieties or are actually more consistent with the ‘*laeve*’ morphology (Figure 89). The morphological ambiguity between the two varieties has occasionally received mention in floristic and monographic treatments of the group (e.g., Hitchcock *et al.* 1955, Cronquist *et al.* 1994, Semple *et al.* 2002, Brouillet *et al.* 2006), even when they are maintained as distinct. For example, Brouillet *et al.* (2006) recognizes the two varieties, but proposes either combining them into a single subsp. *laeve*, itself with two varieties, or recognizing *geyeri* as a synonym of *laeve*. As a result of the morphological overlap between these two forms, and the inability to assign a varietal name to a great many specimens from both B.C. and elsewhere across North America, they are treated as synonymous in this treatment, as per the latter suggestion in Brouillet *et al.* (2006).
FIGURE 88. Overall habit and structure (A) and auriculate leaf bases (B) of *Symphyotrichum laeve* subsp. *laeve* (Straley 6191).

FIGURE 89. Variation in phyllary and involucre morphology of *Symphyotrichum laeve* subsp. *laeve* specimens from British Columbia. A = involucre and phyllaries of typical ‘var. geyeri’ morphology (Straley 6191); B = involucre and phyllaries approaching ‘var. laeve’ morphology (Fodor 246).


Aster hesperius A. Gray var. wootonii Greene (1898: 119). Type:—UNITED STATES. New Mexico: White Mountains, Lincoln County, 12 August 1897, Wooton 329 (holotype NDG!, isotypes NY!, G!, US!, MIN!, P!, MO!, VT!, RM!); A. wootonii (Greene) Greene (1905: 146); A. coerulescens DC. var. wootonii (Greene) Wiegand (1933: 28).


Aster exsul Greene (1900: 221). Type:—UNITED STATES. Nevada: Humboldt River meadows, near Deeth, 05 August 1895, Greene s.n. (holotype NDG!).

Aster limosus Greene (1900: 222). Type:—UNITED STATES. Nevada: near Palisade, 24 August 1896, Greene s.n. (lectotype [designated on specimen by A.G. Jones (1984)] NDG!, isolectotypes NDG!).

Aster osterhoutii Rydberg (1904: 654). Type:—UNITED STATES. Colorado: New Windsor, Weld County, 25 September 1896, Osterhout 2506 (holotype NY, isotypes RM!).

Aster fluvialis Osterhout (1905: 611). Type:—UNITED STATES. Colorado: Cache la Poudre [= Cache la Pudre] River, New Windsor, Weld County, 11 September 1904, Osterhout 2941 (holotype RM!).

Plants perennial, long-rhizomatous, colonial. Stems not from a branched woody caudex, solitary, erect, few- to much-branched distally, glabrescent with prominent lines of long whitish hairs (especially distally), lines not restricted to areas proximal to leaf bases, (20) 35-100 (150) cm tall. Leaves basal and cauline, basal and proximal cauline withering prior to anthesis, slightly reduced distally, apices acute to acuminate and mucronulate, margins entire to moderately serrate and flat, minutely stiff-ciliate with antrorse hairs, faces glabrous to sparsely scabrous; basal leaves petiolate, elliptic-ob lanceolate to obovate, bases cuneate to attenuate, petioles winged and ciliate, 10-80 mm; proximal cauline leaves sessile to subpetiolate, linear to oblanceolate or lanceolate, bases cuneate to attenuate, (40) 60-140 (150) mm; distal cauline leaves sessile, linear to lanceolate or
oblanceolate, bases cuneate to subclasping or sometimes auriculate, 30-100 (140) mm. **Capitulescences** open, racemose-paniculate to subcorymbose or pyramidal, leafy, branches usually ascending; peduncle bracts 1-3 (5), linear to linear-lanceolate, not minutely spine-tipped, usually distinct from phyllaries, distalmost usually enlarged and equalling to slightly exceeding the involucre, 3-25 mm. **Flowering heads** usually numerous; involucres campanulate, 3-8 mm; phyllaries usually subequal (sometimes unequal), in 3-6 series, erect, linear-lanceolate to lanceolate, apices acute to acuminate, margins hyaline proximally (outermost sometimes wholly green), green zones linear-oblanceolate to narrowly elliptic and restricted to distal (1/3) 1/2 (2/3), sparsely to densely ciliate, faces glabrous to sparsely pubescent (adaxially); outer phyllaries 3-5 mm; inner phyllaries 4-7 mm; ray florets 16-50, whitish to pinkish or bluish-pink, laminae 4-10 (14) mm; disc florets 15-50, yellowish (becoming reddish or purplish in age), lobes lanceolate to deltate, 3-6 mm. **Cypselae** obovoid, tan to brownish, sparsely to densely short-hairy, 4- to 5-nerved, 1.5-2 mm; pappus whitish to tawny, equalling to exceeding the disc florets by (0.3) 0.5-1 mm, 5.5-6 mm.

Flowering Jul-Sep (Oct). Wet to moist meadows, streambanks, marsh edges, ditches, shorelines, and occasionally disturbed areas in the steppe, montane, and parkland zones; (5) 50-700 (1200) m. Locally frequent in south-central, southeast, and northeast [Peace River lowlands] BC, and rare in central [Fraser-Nechako Plateau] and southwest BC [Georgia Depression]. BC east to QC, north to NT, south to n Mexico. \(2n = 48, 64 \) \([6x-8x]\) (Semple et al. 1983).

*Symphyotrichum lanceolatum* is a common, widespread, and well-known aster of eastern North America, but is relatively less well-known in western areas of the continent, particularly in western Canada. It has long been included in floristic studies of British Columbia and elsewhere in the Pacific Northwest (e.g., Hitchcock et al. 1955, Abrams and Ferris 1960, Douglas et al. 1989,
Douglas 1995, Douglas et al. 1998), often under the name Aster hesperius, but has generally been poorly defined morphologically, biogeographically, and ecologically in the region. Based on specimens reviewed for this study, S. lanceolatum is primarily a species of lakeshores and riverbanks in the Pacific Northwest, but also occurs in ditches, wetland margins, wet meadows, and even disturbed areas. It is closely associated with the shorelines of several major river systems in British Columbia such as the Peace, Fraser, and Thompson (both North and South) Rivers (Figure 93), and is often one of the dominant asters (along with S. bracteolatum) in such habitats of the southern interior. Although primarily a species from east of the Coast-Cascade Mountains in B.C., it also occurs locally in the Georgia Depression of southwestern B.C., especially along the shores of the lower Fraser River where seeds washed downstream from the interior are able to germinate in suitable shoreline habitats. The origin of other populations in the Georgia Depression, particularly on Vancouver Island, is less certain, and some or all of these may be non-native. This species is well known to have weedy tendencies within its native range (Chmielewski and Semple 2001) and is present in the horticultural trade (Cullen et al. 2011). In Europe, it has spread from gardens and become invasive across central and western regions of the continent (Tutin et al. 1976). However, these south-coastal populations are treated as native here due to the lack of definitive evidence of any non-native status.

This species has traditionally proven difficult to distinguish from the multitude of very similar species that occur throughout British Columbia, and its true status in the province has long remained elusive as a result. Floristic references that pertain specifically to British Columbia have described this species as either rare (Douglas et al. 1998) or infrequent (Douglas et al. 1989, Douglas 1995), and as either restricted to the southeastern part of the province (Douglas et al. 1989) or more widespread across southern B.C. (Douglas 1995, Douglas et al. 1998). To further complicate our understanding of the species in B.C., mapped distributions in these publications
include very few records that do not necessarily correspond with the written descriptions of the distributions, as can be seen in Douglas (1995). As well, the presence of the species in the Peace River region, which is one of its primary centres of distribution in the province, was not reported in Douglas et al. (1989), Douglas (1995), Douglas et al. (1998), or Douglas et al. (2002b). Other studies that have addressed the taxonomy and distribution of the lanceolatus complex (Semple et al. 1983, Semple and Chmielewski 1987, Chmielewski and Semple 2001) have included few or no specimens from British Columbia in their analyses, resulting in limited insight into its range in the province. Based on the published literature available, the review of Symphyotrichum lanceolatum presented herein is the most exhaustive and comprehensive for the British Columbia portion of its range to date.

Identification of this species in British Columbia is inherently challenging due to its close morphological similarity to several other regional taxa, particularly S. douglasii, S. spathulatum var. intermedium, and S. bracteolatum. Although S. douglasii occurs strictly in the Georgia Depression and S. lanceolatum subsp. hesperium is primarily a species of interior B.C., the occasional presence of S. lanceolatum subsp. hesperium in the Georgia Depression (Figure 93) brings the two species into local sympatry. Although S. lanceolatum subsp. hesperium can generally be distinguished from S. douglasii by its slightly broader lanceolate and more conspicuously and consistently serrate cauline leaves (leaves narrower, often linear, and usually entire in S. douglasii), it is best identified by the characteristic lines of long, spreading hairs interspersed by glabrous or short-pubescent areas on the peduncles, with the lines of hairs usually reaching the base of the involucre. Symphyotrichum douglasii, in contrast, has uniformly pubescent peduncles, with lines of hairs generally apparent only on the mid- (and sometimes distal) parts of the stem. Symphyotrichum spathulatum var. intermedium, which is both geographically and ecologically sympatric with S. lanceolatum subsp. hesperium in British Columbia, has
similarly uniform pubescence on the peduncles, and is further distinguished from most forms of *S. lanceolatum* subsp. *hesperium* by its more conspicuously graduated phyllaries, smaller capitulae, and open capitulescence with reduced, bract-like leaves throughout the capitulescence branches. *Symphyotrichum bracteolatum*, which often occurs in abundance alongside *S. lanceolatum* subsp. *hesperium* in the southern interior, is easily distinguished by the more conspicuously reddish stems and, especially, its distinctively and uniformly short-hairy stems and peduncles without any indication of longer hairs arranged in lines. Indeed, the presence of such lines of hairs along the peduncles of *S. lanceolatum* is considered the morphological character that most consistently distinguishes the species from the various other similar species in the province. It should be noted, however, that this character is subject to considerable individual variation within *S. lanceolatum* subsp. *hesperium* populations in B.C., some of which may be related to hybridization with other species of *Symphyotrichum*, and thus the identification of this species should be based on the entirety of morphological, biogeographic, and ecological information available.

*Symphyotrichum lanceolatum* in North America is represented primarily by two wide-ranging, but widely intergrading, subspecies: subsp. *lanceolatum* in eastern North America (itself with several varieties [Semple & Chmielewski 1987]) and subsp. *hesperium* (= *Aster hesperius* A. Gray) in western North America (Semple & Chmielewski 1987, Brouillet et al. 2006). These subspecies differ primarily in features of the involucres and phyllaries, with the eastern subsp. *lanceolatum* possessing narrower, unequal phyllaries and subsp. *hesperium* possessing broader, subequal phyllaries and often having a prominent, enlarged, leafy bract beneath the capitulum that equals or exceeds the length of the involucre (Semple & Chmielewski 1987, Brouillet et al. 2006) (Figure 92: A). All populations in British Columbia are here attributed to the western subsp. *hesperium*, but the structure of the morphological variation present among B.C. populations suggests that there may be two morphologically and biogeographically distinct entities in the
province. Populations of subsp. *hesperium* from northeastern B.C. (Peace River lowlands), as well as some populations in the central interior, are characterized by often whitish or pinkish (occasionally bluish or purplish) ray florets, more commonly entire leaf margins, and more conspicuously clasping leaf bases. In contrast, populations from southern B.C. have consistently bluish or purplish ray florets, more consistently serrate leaf margins, and non-clasping to subclasping leaf bases. Representatives of both morphologies occur in the central interior of B.C. (e.g., Cariboo-Chilcotin region, Fraser-Nechako Plateau), indicating potential sympatry between them. Southern populations are in many ways intermediate between typical *S. lanceolatum* subsp. *hesperium* (as represented by populations in northeastern B.C., Alberta, and the parkland regions of central Canada) and members of the western North American *Symphyotrichum* subg. *Symphyotrichum* sect. *Occidentales*, particularly the coastal *S. douglasii*. These are here included within *S. lanceolatum* subsp. *hesperium*, however, due primarily to presence of lines of hairs along the peduncles and the overall similarities in habit and ecology. Additional research on these plants in the northwestern United States (particularly Washington, Idaho, Montana), which was geographically outside of the scope of this study, is recommended to better understand the relationship of these southern populations to both typical *S. lanceolatum* subsp. *hesperium* (as occurs in central Canada and the Rocky Mountain region of the United States) as well as other northwestern North American asters.
FIGURE 91. Morphological variation in *Symphyotrichum lanceolatum* subsp. *hesperium*. A, B = typical morphotype of southern British Columbia (A = McIntosh, Fenneman, McCulloch, & Ross 2011_368; B = McIntosh & Dunster 2011_420); C = extremely narrow-leaved morphotype from southern British Columbia (Ceska & Ogilvie 23067); D = typical morphotype from northeastern British Columbia (McCalla 10233).
FIGURE 92. Variation in phyllary and involucre characteristics in *Symphyotrichum lanceolatum* subsp. *hesperium*. A = example with broader, more extensively foliaceous phyllaries and a characteristic peduncle bract subtending the involucre that exceeds the length of the phyllaries, typical of northeast BC populations (*McCalla s.n.*); B = example with narrower phyllaries and lacking the subtending peduncle bract, typical of southern BC populations (*McIntosh & Joya 2011_409*).

FIGURE 93. Distribution of British Columbia specimens of *Symphyotrichum laeve* subsp. *laeve* that were reviewed for this study (left), and approximate distribution of the species elsewhere in northwestern North America (right).

**McCALLA’S ASTER**


*Aster butleri* Rydberg (1910a: 139). Type:—UNITED STATES. Montana: Gateway, 16 August 1908, Butler 443 (holotype NY!).

*Aster subcaudatus* Rydberg (1910a: 144). Type:—CANADA. Alberta: Laggan, Lake Louise region, 23 August 1902, Rosendahl 1089 (holotype NY!).

**Plants** perennial, long-rhizomatous, cespitose to colonial. **Stems** not from a branched woody caudex, usually solitary, erect, few- to much-branched distally, glabrous to sparsely white-villous (especially distally), the pubescence typically arranged in lines proximal to the leaf bases on midstem, (12) 20-80 (100) cm tall. **Leaves** basal and cauline, basal and proximal cauline withering prior to anthesis or persistent, slightly to strongly reduced distally, apices acute to acuminate and often mucronulate, margins moderately to coarsely serrate and flat, minutely stiff-ciliate with antrorse hairs, faces glabrous to sparsely hirsute, midveins glabrous to sparsely white-villous abaxially; basal leaves long-petiolate, broadly lanceolate to ovate-lanceolate, bases cuneate to rounded, petioles winged and often long-ciliate (at least proximally), (40) 50-110 (120) mm; proximal cauline leaves long- to short-petiolate, broadly lanceolate to ovate-lanceolate, bases cuneate to rounded, petioles winged and long-ciliate (at least proximally), (35) 60-120 (140) mm; distal cauline leaves sessile to subsessile, linear-lanceolate to narrowly lanceolate, bases cuneate to rounded and usually somewhat clasping, (15) 20-90 mm. **Capitulescences** usually open, racemose-paniculate to pyramidal, sometimes leafy, branches usually ascending (rarely...
spreading); peduncle bracts 0-4, linear to linear-lanceolate, apices often minutely spine-tipped, usually distinct from phyllaries, 3-4.5 mm. **Flowering heads** usually numerous; involucres campanulate, 5-7 (9) mm; phyllaries usually subequal (sometimes unequal), in 3-5 series, erect, lanceolate to linear-lanceolate, apices acute to acuminate, margins hyaline proximally, green zones linear-oblanceolate to narrowly elliptic and restricted to distal 1/3-1/2 (3/4), usually sparsely ciliate, face glabrous to glabrescent; outer phyllaries 3-5 mm; inner phyllaries 5-6 mm; ray florets 15-30, bluish to violet, laminae 8-15 mm; disc florets 20-60, yellowish (becoming reddish-purple in age), lobes lanceolate to deltate, 5-6.5 mm. **Cypselae** obovoid, tan to brownish, glabrous to moderately short-hairy, 5- to 6-nerved, 1.5-3 mm; pappus whitish to tawny, 4-6 mm.

Flowering Jul-Sep. Moist to mesic shorelines, streambanks, forest edges, meadows, thickets, and disturbed areas, especially on coarse or gravelly substrates, in the steppe and montane zones; 400-1500 (1800) m. Frequent in southeast BC, locally frequent in south-central BC [north to Shuswap Lake, North Thompson River]. BC east to AB, south to MT. 2n = ?

*Symphyotrichum x maccallae* is a rather common aster of the southern interior of British Columbia, and is among the more common members of the genus in the Rocky Mountains and West Kootenay regions of the province (Figure 96). It also occurs in adjacent areas of southern Alberta, where it is restricted to the Rocky Mountain region of the province, and collections reviewed for this study suggest a wider distribution in that province than has been presented in the past (e.g., Packer 1983). This is primarily a species of open, often somewhat disturbed (naturally or otherwise) habitats such as shorelines, riverbanks, riparian thickets, alluvial flats, clearings, roadsides, and rocky outcrops, especially on coarse or gravelly soils, and it rarely occurs in heavily forested habitats. It is most similar to the widespread and common *S. ciliolatum*, and can best be distinguished from that species by the generally narrower blades of the basal and proximal cauline
leaves and their distinctly tapered or cuneate bases (Figure 94), unlike the characteristically truncate or cordate leaf bases of *S. ciliolatum*. The leaves of *S. x maccallae* also tend to be thicker and slightly coriaceous relative to the thinner, more herbaceous leaves of *S. ciliolatum*.

The concept of *Symphyotrichum x maccallae* presented herein represents an apparently hybridogenous taxon that is centred around *S. ciliolatum*, with which it is widely sympatric in southern portions of that species’ range in the province. This species was originally recognized by P.A. Rydberg as *Aster maccallae* (Rydberg 1910a), who based his description on collections from the Rocky Mountains of Alberta and British Columbia. Another species described in the same publication, *Aster butleri*, is also an apparent hybrid involving the same parental taxa (perhaps backcrossed with *S. ciliolatum*) and was similarly based on collections from the Rocky Mountains (in that case, Montana). The characters mentioned in Rydberg (1910a) for distinguishing *maccallae* and *butleri*, such as the number and size of the flowering heads and the hairiness of the cypselae, are not at all consistent in the manner portrayed in that publication, with the larger number of specimens available for review during this study demonstrating that these characters are much more variable and the morphological discontinuities much less conspicuous; as a result, these names are treated as synonymous here. *As maccallae* (inc. *butleri*) is a widespread, common, ecologically distinct, and morphologically consistent hybrid taxon relative to many other hybrids, particularly those within *Symphyotrichum*, it is afforded species status in this treatment despite its hybrid origin.

*Symphyotrichum x maccallae* has often been subsumed within a very broad concept of *S. subspicatum* (or *Aster subspicatus*) in recent floristic and taxonomic studies (e.g., Brouillet et al. 2006) due to its often serrate leaves and prominent pale bases to the phyllaries, but it is clearly misplaced there given the apparent role of *S. ciliolatum* in its origins. Only Packer (1983) has recognized the species in a way that is consistent with the approach taken here. Contrary to its
treatment by Jones (1984), it is not recognized as an infraspecific taxon of *S. ciliolatum* due to its apparent hybrid origin. Jones (1980) originally treated *S. x maccallae* as a hybrid species (*= ciliolatum x subspicatum*), before later (Jones 1984) suggesting that it is not of hybrid origin and is instead better treated at the varietal level under *S. ciliolatum*. However, in the same paragraph the author suggested the introgression of *S. laeve* in the taxon, thereby seeming to refute the non-hybrid origin suggested several sentences earlier. The review of specimens associated with the present study supports the view that the taxon is likely hybridogenous in origin, based on the variation present among the specimens and the morphological similarity of much of this variation to other *Symphyotrichum* taxa (e.g. *S. laeve* subsp. *laeve*, *S. frondeum var. frondeum* [Figure 95]).

Furthermore, *S. x maccallae* and *S. ciliolatum* tend to occupy distinct habitats where they are sympatric, with *S. x maccallae* occurring in open, often disturbed habitats and *S. ciliolatum* being primarily a species of forests and woodlands; the taxa largely maintain their morphological integrity under such conditions of sympatry. In central and northern British Columbia, where *S. x maccallae* is absent and only *S. ciliolatum* is present, the latter species may occur in a wider range of habitats, including those that would normally be occupied by *S. x maccallae* in more southerly areas. Thus, *S. x maccallae* is recognized as specifically distinct from *S. ciliolatum*, despite the apparent role of that species in its hybrid origins.

Although *S. ciliolatum* and *S. laeve* subsp. *laeve* are clearly the most dominant species involved in the hybrid origin of this species (based on morphological considerations), variation within the species suggests that additional taxa may contribute genetically, at least in some regions of the province. For example, populations in southeastern British Columbia, particularly in the Rocky Mountains, often have less conspicuously serrate leaf margins, fewer and larger flowering heads, and a capitulescence structure that is reminiscent of *S. frondeum var. frondeum* (Figure 95), while those from the central interior, Cariboo-Chilcotin region, North and South Thompson
Rivers, and the Shuswap Lake region often have narrower leaves and an involucre morphology that is suggestive of the potential influence of *S. lanceolatum* subsp. *hesperium* or even *S. bracteolatum*. Jones (1984) suggested the influence of *S. puniceum* in the parentage of at least a portion of what is here presented as *S. x maccallae*, but, as there appears to be little or no morphological justification for such a hypothesis and essentially no extant sympatry between *puniceum* and *maccallae*, this seems to be an unlikely scenario. Jones (1984) also proposed *S. subspicatum* in the parentage of *S. x maccallae* but, with the dissolution of earlier concepts of *S. subspicatum* (see the treatments of *S. subspicatum* and *S. douglasii* herein), it is unclear to what taxon Jones was referring. Her suggestion of “*Aster foliaceus*” in the parentage of *S. x maccalae* in Jones (1977) suggests that she was perhaps referring to *S. frondeum* var. *frondeum*; this would be consistent with the interpretation of the taxon’s parentage presented here.

**FIGURE 94.** Typical basal leaves of *Symphyotrichum x maccallae*, showing strongly tapering/cuneate bases to lanceolate blades. Photo: *Bush Arm, Kinbasket Lake, 09 July 2016, J. Fenneman.*
FIGURE 95. Overall habit and structure of *Symphyotrichum x maccallae*. These plants are typical of many Rocky Mountain populations, which show possible introgression of *S. frondeum* var. *frondeum*. A = Eastham s.n.; B = McCalla 9312.

FIGURE 96. Distribution of British Columbia specimens of *Symphyotrichum x maccallae* that were reviewed for this study (left), and approximate distribution of the species elsewhere in northwestern North America (right).
19. *Symphyotrichum novi-belgii* (L.) G.L. Nesom var. *novi-belgii*

**NEW YORK ASTER;** New York American-aster; Michaelmas Daisy; Traditional Michaelmas Daisy; Confused Michaelmas-Daisy


**Plants** perennial, long-rhizomatous, colonial to cespitose. **Stems** not from a branched woody caudex, solitary to several, erect, few- to much-branched distally, sparsely white-puberulent, pubescence arranged in lines from leaf bases, greenish to reddish or purplish, 17-100 (150) cm tall. **Leaves** basal and cauline, basal and proximal cauline leaves withering prior to anthesis, slightly reduced distally, margins entire to sparsely serrulate and often slightly revolute, minutely stfficiliate with antrorse hairs, faces glabrous to sparsely scabrous, often somewhat thickened or coriaceous; basal leaves petiolate, lanceolate to ovate, apices acute to acuminate, bases attenuate to cuneate, petioles winged, 17-60+ mm; proximal cauline leaves sessile to petiolate with broadly-
winged petioles, linear-lanceolate or oblong-lanceolate to narrowly obovate or elliptic, apices acute to acuminate, bases usually cuneate, 40-200+ mm; mid- and distal cauline leaves sessile, linear-lanceolate or lanceolate to lance-elliptic or oblong-lanceolate, apices acute to acuminate, bases cuneate to rounded and subclasping to auriculate, 13-60+ mm. **Capitulescences** usually open, racemose or paniculate to pyramidal or subcorymbose, leafy or not, branches usually ascending; peduncle bracts 1-3, linear-oblong-lanceolate or lanceolate to ovate, sometimes grading into the phyllaries, distalmost often enlarged and equalling to exceeding the involucre, 3-10 (20) mm. **Flowering heads** several to numerous; involucres campanulate, 6-9 mm; phyllaries somewhat unequal to subequal, in 3-4 series, spreading to somewhat squarrose, sparsely short-ciliate, faces glabrous to sparsely pubescent, margins hyaline on basal (1/5) 1/3-1/2 (2/3) or the outermost often wholly foliaceous, green zones lanceolate or oblong-lanceolate to narrowly or broadly elliptic; outer phyllaries oblong-oblong-lanceolate to spatulate, apices obtuse to acute, 3.5-7 mm; inner phyllaries linear or linear-lanceolate to oblong-lanceolate, apices generally acute, 5.5-8 mm; ray florets 15-35, bluish to purplish, laminae (6) 10-19 mm; disc florets 28-68, yellowish (becoming reddish or purplish in age), lobes lanceolate, 4-7.5 mm. **Cypselae** obovoid, tan to brownish, 4- to 6-nerved, glabrate to sparsely short-hairy, 2-4 mm; pappus tawny to yellowish, 4-6 mm.

Flowering Jul-Oct. Moist to mesic estuaries, brackish wetlands, marshes, ditches, shorelines, and disturbed areas in the lowland zone; 0-30 (120) m. Introduced; locally frequent in southwest BC [Georgia Depression]. Native to eastern North America; also introduced in Mexico, Europe, Australia. $2n = 48$ [6x] (Labrecque & Brouillet 1996).

The eastern North American *Symphyotrichum novi-belgii* var. *novi-belgii* has not previously been reported from the Pacific Northwest, but is presented here as being well established as an exotic species at low elevations around the Georgia Depression of southwest
British Columbia (Figure 101). It is fairly common within this limited area, and is the most commonly encountered *Symphyotrichum* species in the Vancouver area and adjacent Fraser Valley. It occurs primarily in brackish estuarine marshes, wet meadows, along roadsides, and in other disturbed areas, but may also be encountered locally in freshwater marshes, ditches, and along lacustrine and fluvial shorelines. Even when occurring in freshwater habitats, however, occurrences of *S. novi-belgii* in B.C. have rarely been documented far from areas of tidal influence. Outside of British Columbia, *S. novi-belgii* is also established as an exotic species in Mexico and Australia (Brouillet et al. 2006), as well as throughout much of Europe, where it and several of its garden-derived hybrids have become aggressive and invasive weeds (Tutin et al. 1976, Jedlička & Prach 2006, Sell & Murrell 2006, Verloove 2018). The earliest British Columbia specimens observed during this study were collected in the late 19th century, suggesting that *S. novi-belgii* was among a group of weeds that became established in the region shortly after the arrival of settlers from Europe and eastern North America. As the species has been known in gardens of the UK and elsewhere in Europe since the early 18th century, and has been established in Europe as an exotic weed since the mid-19th century (Botanical Society of Britain & Ireland 2018, Old Court Nurseries 2018), such an early arrival in the region is not particularly unexpected. Indeed, many of the common urban weeds of southwestern British Columbia (e.g., *Taraxacum officinale*, *Plantago major*) are represented by provincial specimens dating from the late 19th century, suggesting that a number of exotic species were well established in the region by that time.

The close morphological similarity of this species to several western North American taxa of *Symphyotrichum* subg. *Symphyotrichum* sect. *Occidentales* has long hindered detection of this species in the Pacific Northwest. Specimens of *S. novi-belgii* from British Columbia have traditionally been assigned to *S. subspicatum* s.l. (e.g. Cronquist 1943, Hitchcock et al. 1955, Hitchcock & Cronquist 1973, Allen 1984, Douglas 1995, Douglas et al. 1998) due to their narrow,
usually lanceolate leaves and prominent pale, scarious bases of the subequal phyllaries. The broad concept of *S. subspicatum* that incorporated this taxon, however, represented a disparate collection of taxa that are here treated separately as *S. novi-belgii* var. *novi-belgii*, *S. douglasii*, *S. subspicatum* s.s., *S. x maccallae*, *S. lanceolatum* subsp. *hesperium* (in part), and a variety of hybrids. In addition to its overall morphological similarity to these other taxa, *S. novi-belgii* is also exceedingly morphologically variable itself (Labrecque & Brouillet 1996), with the patterns of variation often related to local environmental conditions (Labrecque & Brouillet 1996) and mirroring those of the native Pacific Northwest taxa with which it has been confused. Thus, discrete morphological characteristics by which the species can be consistently distinguished from the native taxa are few and difficult to apply, particularly to herbarium collections wherein any intrapopulation variation is generally not detectable. The presence of escaped and sometimes established garden-derived cultivars of *S. novi-belgii* in the region (Figure 100), many of which represent hybrids with other taxa such as *S. dumosum*, *S. laeve* subsp. *laeve*, *S. cordifolium*, *S. ericoides* var. *ericoides*, *S. lateriflorum*, and *S. lanceolatum* subsp. *lanceolatum* (Tutin et al. 1976, Brouillet 2006, Old Court Nurseries 2018), has further decreased the morphological homogeneity of the taxon in the region, as has apparent hybridization with several similar native species such as *S. bracteolatum*, *S. chilense*, and *S. douglasii* (as determined by the presence of putative hybrids reviewed during this study). The above combination of factors (morphological similarity to native taxa, inherent morphological variability, hybridization with local taxa, and the presence of escaped garden-derived hybrids and cultivars) is proposed here as an explanation for the lack of detection of this species around the Georgia Depression and, potentially, elsewhere in the Pacific Northwest for more than a century.

Despite its morphological similarity to several native taxa, and the pronounced variation within both this species and its native look-alikes, the morphology presented by *S. novi-belgii*
represents a unique combination of characters that should allow for identification under most circumstances, particularly when ecology and biogeography are considered. The primary characters of importance for its identification include the narrow, entire to serrate leaves with weakly to strongly clasping bases (Figure 98: A), the typically pale cypselae, and the subequal, usually loosely spreading phyllaries in which the outermost are often somewhat enlarged and foliaceous or, if exhibiting whitish hyaline bases, these are generally restricted to the basal 1/2 or less (Figure 97). It is most likely to be confused with *S. douglasii*, which is similarly frequent around the Georgia Depression but is primarily a species of Vancouver Island and is absent from the lower Fraser Valley where *S. novi-belgii* is most abundant. *Symphyotrichum douglasii* can be distinguished by its narrower (usually linear or linear-lanceolate, less commonly lanceolate) and usually entire leaves that lack clasping bases, its darker brownish cypselae, and its narrower and more erect (less spreading) phyllaries that are more extensively whitish-hyaline at the base (usually on the basal 1/2-3/4) and rarely enlarged and foliaceous. *Symphyotrichum chilense*, which is locally sympatric with *S. novi-belgii* in the estuaries of the Georgia Depression, is best distinguished from *S. novi-belgii* by its characteristically broad, rounded, and strongly graduated phyllaries, its often broader and more consistently serrate leaves that do not clasp the stem at the base, and its darker brownish cypselae. The distribution of *Symphyotrichum subspicatum* s.s. scarcely overlaps that of *S. novi-belgii*, but it can be distinguished most easily from *S. novi-belgii* by its conspicuously serrate leaves and darker, brownish cypselae. *Symphyotrichum bracteolatum*, which is rare in the Georgia Depression and confined primarily to the lower Fraser River, is best distinguished by its uniformly short-hairy, more consistently reddish stems (stem hairs not arranged in lines) and narrower capitulescences. Finally, *S. lanceolatum* subsp. *hesperium*, which is also rare (and perhaps introduced) in the Georgia Depression, is easily distinguished by the
distinct lines of spreading hairs along the peduncles which extend to the bases of the involucre
(peduncles uniformly hairy on *S. novi-belgii* var. *novi-belgii*).

Plants assigned to *S. novi-belgii* in British Columbia are here attributed to the nominate
var. *novi-belgii* of Atlantic Canada and the northeastern United States, but some plants with
narrower, less conspicuously clasping leaves approach or match the morphology of var. *elodes* of
the mid-Atlantic coast of the United States. These narrow-leaved plants are retained within var.
*novi-belgii* here, however, as they appear to represent either environmentally-influenced or
otherwise natural variation within var. *novi-belgii* (as has been documented by Labrecque &
Brouillet 1996) or demonstrate characteristics that suggest that they may be of hybrid origin, either
with native species or as garden-derived horticultural cultivars. *Symphyotrichum novi-belgii* is
among the most popular asters in the horticultural industry, and a great number of cultivars are
available for the garden (Semple *et al.* 2002, Hawke 2013, Old Court Nursery 2018), some of
which are capable of escaping and establishing wild populations. For example, invasive
populations of *Symphyotrichum* in Europe that have traditionally been treated as *S. novi-belgii* are
now recognized as being largely comprised of garden-derived hybrids with other species,
particularly *S. lanceolatum* subsp. *lanceolatum* (= *S. x salignum* Willd.) and *S. laeve* subsp. *laeve*
(= *S. x versicolor* Willd.) (Tutin *et al.* 1976, Botanical Society of Britain & Ireland 2018, Verloove
2018). Specimens that are attributable to *S. x versicolor* have been collected from a single wild
population in the southern interior of British Columbia (see *S. laeve* subsp. *laeve*, above), while
other specimens from the south coast show suggestions of the influence of *S. lanceolatum* subsp.
lanceolatum (e.g., narrower and graduated phyllaries, narrower and less conspicuously clasping
leaves) and may be attributable to *S. x salignum*. The potential presence of these garden escapes
should be considered when attempting to identify problematic or otherwise atypical asters,
particularly on the south coast.
FIGURE 97. Variation in phyllary and involucre characteristics of Symphyotrichum novi-belgii var. novi-belgii from British Columbia. A = Bayly 23; B = Eastham s.n.

FIGURE 98. Clasping, auriculate upper leaf bases (A) and lanceolate, somewhat serrate lower leaves (B) of Symphyotrichum novi-belgii var. novi-belgii. A = Lomer 4660; B = Manton, van der Linde, & Ross 1710.
FIGURE 99. Examples of garden-derived cultivars and hybrids of Symphyotrichum novi-belgii var. novi-belgii collected as non-established waifs in southwestern British Columbia. A = Lomer 6471; B = Lomer 6529; C = Lomer 9101; D = Lomer 9108.
FIGURE 100. Variation in overall habit and structure among naturalized *Symphyotrichum novi-belgii* var. *novi-belgii* specimens from British Columbia. A = Eastham s.n.; B = W. Taylor s.n.

FIGURE 101. Distribution of British Columbia specimens of *Symphyotrichum novi-belgii* var. *novi-belgii* that were reviewed for this study (left), and approximate distribution of the species elsewhere in northwestern North America (right). Open circles denote introduced populations.
20. *Symphyotrichum pilosum* (Willd.) G.L. Nesom var. *pilosum*


Plants perennial, occasionally rhizomatous, cespitose. Stems often from a branched caudex, solitary to several, ascending to erect, branched distally, sparsely to densely hirsute or pilose, pubescence uniform or sometimes arranged in lines from leaf bases, greenish to reddish, (5) 20-120 (150) cm tall. Leaves basal and cauline, basal and usually proximal cauline leaves withering prior to anthesis, slightly reduced distally, margins entire to serrulate and flat, minutely soft-ciliate with antrorse hairs, faces glabrous to hirsute; basal leaves subpetiolar to petiolate, oblanceolate to obovate or spatulate, apices obtuse to rounded, bases attenuate, petioles winged, 10-60 mm; proximal cauline leaves subpetiolar or petiolar to nearly sessile, linear-lanceolate or -oblanceolate to elliptic-oblanceolate, apices acute to acuminate and mucronate, bases attenuate to cuneate, petioles (when present) winged, usually with axillary clusters of reduced leaves, 40-100 mm; distal cauline leaves sessile, linear or linear-lanceolate to lance-oblong, apices acute to acuminate, bases cuneate, 10-60 (100) mm. Capitulescences open, paniculate to pyramidal, leafy or not, branches spreading to ascending; peduncle bracts 7-25+, linear to subulate, minutely spine-tipped, usually distinct from the phyllaries, 3-12 mm. Flowering heads numerous; involucres campanulate to cylindro-campanulate, (2.5) 3.5-5 (6.5) mm; phyllaries usually unequal, in 4-6 series, erect to slightly spreading, linear-lanceolate to oblong-lanceolate, apices acute to acuminate and often inrolled (‘awl-shaped’), not minutely whitish-spinulose, sparsely ciliate (especially proximally), faces glabrous or glabrate, margins hyaline on basal 1/3-2/3, green zones oblanceolate
to narrowly elliptic, 2.5-4 (5) mm; ray florets 12-20, whitish (rarely pink-tinged), laminae 5-8 mm; disc florets 10-25, creamy-white to yellowish (becoming pinkish or reddish in age), lobes lanceolate, (2.5) 3-4.5 mm. **Cypselae** obovoid, somewhat compressed, grayish to tan, faintly 4- to 5-nerved, sparsely short-hairy, 1-2 mm; pappus whitish, 2.5-3.5 mm.

Flowering Sep-Nov. Dry roadsides, railway lines, vacant lots, and disturbed areas in the lowland zone; 0-30 m. Introduced; rare in sw BC [Vancouver area]. Native to eastern North America. $2n = 32, 40, 48$ [4x-6x] (Chmielewski & Semple 2001).

**Symphyotrichum pilosum** var. **pilosum** is a rare and locally-established exotic taxon in British Columbia, where it has been collected occasionally in the Vancouver area (east at least to Coquitlam) (Figure 103). This late-flowering aster is most commonly collected in association with railway lines in British Columbia, suggesting that this may be the primary mode of introduction of the species. It is often weedy, even within its native eastern North American range (Chmielewski & Semple 2001), and is occasionally reported as a non-native introduction elsewhere in North America, such as in New Brunswick and Nova Scotia (Brouillet et al. 2006) and in Whatcom County, Washington (Hitchcock et al. 1955). It was also recently re-collected as an introduction in Washington (mouth of Lower Crab Creek, Columbia River, Grant County, 07 October 2002, Zika 18070 [WTU!]), where it had not been observed in the state since the first collections in Whatcom County in 1943 (Hitchcock et al. 1955). All collections of this species in British Columbia are from small populations, often of only single plants, and all were made during a brief period from 1990-1993 (despite increased collection effort in the region since 1993). It is thus unclear how well established this taxon is in British Columbia, although the presence of a substantial population at the site of the most recent (2002) collection in Washington, as indicated
on the specimen label, suggests that the species is capable of developing robust populations in the Pacific Northwest.

The identification of *Symphyotrichum pilosum* presents few identification problems within the context of the provincial *Symphyotrichum* flora, although it may potentially be confused with two other native white-rayed taxa: *S. ericoides* var. *pansum* and *S. falcatum* var. *falcatum*. Neither of these two species occurs within the limited range occupied by *S. pilosum* var. *pilosum*, although *S. falcatum* var. *falcatum* occurs along the lower Fraser River west at least to Agassiz and may be encountered farther downstream in association with the main river stem. *Symphyotrichum pilosum* var. *pilosum* should be immediately distinguishable from those species, however, by its characteristic inrolled or ‘awl-shaped’ phyllary apices. The species otherwise presents an intermediate morphology in many ways between these native taxa, with the branching pattern of the capitulescence resembling *S. ericoides* var. *pansum*, but the capitulum size resembling *S. falcatum* var. *falcatum*.

Most collections of *Symphyotrichum pilosum* var. *pilosum* in British Columbia are typical of the tetraploid to hexaploid *S. pilosum* var. *pilosum*, which is characterized by its moderately to densely hirsute to pilose stems (Figure 102: B), but a single collection (*Lomer 91-306*), with the stems bearing lines of spreading whitish hairs proximal to the leaf bases, is intermediate between var. *pilosum* and the hexaploid, glabrous-stemmed *S. pilosum* var. *pringlei* (A. Gray) G.L. Nesom. This plant may be attributable to var. *pilosum*, as the hairiness of the stems has been shown to be under at least some environmental control (Semple 1978); conversely, it may be representative of one of numerous cultivars of *S. pilosum*, many of which resemble the glabrous-stemmed var. *pringlei* (Semple et al. 2002). It is included here within var. *pilosum*, although it is recognized as morphologically divergent from other provincial collections.
FIGURE 102. Morphological characteristics of *Symphyotrichum pilosum* var. *pilosum*. A = whole plant habit, demonstrating the small flowering heads and branching pattern of the capitulescence (Lomer 93-315); B = uniformly pilose stems (Lomer 90-170); C = involucre and phyllaries (Lomer 93-328).

FIGURE 103. Distribution of British Columbia specimens of *Symphyotrichum pilosum* var. *pilosum* that were reviewed for this study (left), and approximate distribution of the species elsewhere in northwestern North America (right). Open circles denote introduced populations.
21. *Symphyotrichum puniceum* (L.) Á. Löve & D. Löve var. *puniceum*

**PURPLE-STEMMED ASTER,** Purplestem Aster, Swamp Aster, Red-stemmed Aster, Purple-stemmed American-aster


*Aster puniceus* L. var. *compactus* Fernald (1899b: 189). Type:—not located.

*Aster puniceus* L. var. *oligocephalus* Fernald in Fernald & Sornberger (1899: 105). Type:—not located.

*Aster puniceus* L. var. *perlongus* Fernald (1915: 17). Type:—CANADA. Quebec: Table-top Mountain, Gaspé County, 14 August 1906, *Fernald & Collins 737* (holotype GH, isotypes NY!, US!).


**Plants** perennial, short-rhizomatous, sometimes weakly cespitose. **Stems** from a branched caudex or stout rhizome, solitary to several, erect, usually branched distally, sparsely to densely hirsute or hispid, pubescence uniform (not arranged in lines), often glabrate proximally, greenish to reddish or purplish, (7) 50-150 (200) cm tall. **Leaves** basal and cauline, basal and lower cauline withering prior to anthesis, not or slightly reduced distally, apices mucronulate, margins entire to sparsely serrate and flat to slightly revolute, minutely stiff-ciliate with antrorse hairs, faces glabrate to scabrous, midvein sparsely to densely white-villous abaxially; basal leaves subpetiolate to petiolate, oblanceolate to spatulate, apices rounded to acute or acuminate, bases cuneate to attenuate, petioles winged and dilated, 30-110+ mm; proximal cauline leaves subpetiolate or petiolate to nearly sessile, lanceolate or oblanceolate to elliptic or oblong, apices acute to
acuminate, bases cuneate or attenuate to clasping or auriculate, petioles (when present) winged, (55) 70-200 (220) mm; distal cauline leaves sessile, lanceolate or oblanceolate to oblong, apices acute to acuminate, bases strongly auriculate, 8-160 mm. **Capitulescences** open, pyramidal to subcorymbose, leafy, branches spreading to ascending; peduncle bracts 0-3, linear to lanceolate, not minutely spine-tipped, sometimes grading into phyllaries, 10-20 mm. **Flowering heads** usually numerous; involucres campanulate, (6) 8-12 (15) mm; phyllaries subequal, in 4-6 series, erect to spreading, linear to linear-lanceolate, apices long-acuminate, margins usually narrowly hyaline proximally (at least on inner phyllaries), green zones linear-oblanceolate and restricted to distal 1/2-4/5, outer phyllaries sometimes enlarged and foliaceous, sparsely to moderately ciliate distally, faces glabrous to hispid, 7-12 mm; ray florets 20-60, bluish to purplish, laminae (7) 12-18 (21) mm; disc florets 30-50 (90), yellowish (becoming purplish in age), lobes deltate, (4) 5-6.5 mm. **Cypselae** oblanceoloid to obconic, compressed, tan to dark brownish or purplish-brown, 3- to 4-nerved, glabrous to sparsely short-hairy, (2) 2.5-3.5 (4) mm; pappus whitish, 4-6 mm.

Flowering Jul-Sep. Moist to wet meadows, marshes, ditches, fens, swamps, open forests, streambanks, and shorelines in the boreal and parkland zones; (350) 600-1000 m. Locally frequent in northeast BC [Peace River lowlands, Fort Nelson lowlands, Liard Basin]. BC east to NL, south to NE, AB, GA. $2n = 16$, 32 [2x-4x] (Brouillet et al. 2006).

*Symphyotrichum puniceum* var. *puniceum* is among the more distinctive members of the genus in British Columbia as a result of its overall large size and robust stature, large flowering heads, strongly auriculate cauline leaves, and, especially, its coarsely and uniformly spreading-hairy stems (Figure 104). It is unlikely to be mistaken for any other regional *Symphyotrichum*, particularly considering its restricted distribution in northeastern portions of the province where it is sympatric with relatively few other members of the genus. It is of frequent occurrence within
this limited area of distribution, where it is strongly associated with wet, open habitats such as roadside ditches, wet meadows, and marshy lakeshores. The centre of its distribution in the province is in the Peace River lowlands, with lower densities northwards through the Fort Nelson lowlands and Liard Basin (Figure 105). Despite its abundance within this region, the species was first reported in the province only as recently as 1997, when it was collected near the Yukon border by T. McIntosh (T. McIntosh, pers. comm.); however, subsequent herbarium research resulted in the discovery of several previously-collected specimens that had been overlooked due to misidentification. The species was considered a rare taxon in the province for most of the following two decades (Douglas et al. 2002a), but after increased sampling of the mid- to late season flora of northeastern B.C. the species was shown to be widespread and common east of the Rocky Mountains. It was removed as a species of provincial conservation concern in 2016 (British Columbia Conservation Data Centre 2018) due to this increase in newly-reported populations.

This species is known to hybridize with *S. lanceolatum* subsp. *hesperium* (Semple et al. 2002, Brouillet 2006), with which it is sympatric in the Peace River area of B.C.; several putative hybrids between these two species have been collected from this region (see Hybrids, below). The hybrids largely resemble *S. lanceolatum* subsp. *hesperium*, but differ in their more strongly purplish ray florets (ray florets typically whitish or purplish-tinged in *S. lanceolatum* subsp. *hesperium*), darker reddish or purplish stems, and uniformly spreading-hairy stems (stem hairs arranged in conspicuous lines in *S. lanceolatum* subsp. *hesperium*).
FIGURE 104. Morphological characteristics of *Symphyotrichum puniceum* var. *puniceum*. A = overall plant structure and plant habit, showing the robust structure, leafy pyramidal capitulescence, and large flowering heads (*Lomer 4226*); B = distinctive coarse, spreading, uniform stem hairs and reddish/purplish stems (*Lomer 4226*); C = lanceolate, subequal, somewhat foliaceous phyllaries (*Krichbaum & Krichbaum eaglecap15135*).

FIGURE 105. Distribution of British Columbia specimens of *Symphyotrichum puniceum* var. *puniceum* that were reviewed for this study (left), and approximate distribution of the species elsewhere in northwestern North America (right).

**WESTERN MOUNTAIN ASTER**; Western Aster

*Aster spathulatus* Lindl. in Hooker (1834b: 8). Type:—CANADA. Northwest Territories: Bear Lake and Fort Franklin, on the Mackenzie River, no collection date reported, *Richardson s.n.* (holotype CGE, isotypes GH!, K!).


**Plants** perennial, long-rhizomatous, colonial. **Stems** occasionally from a branched caudex, solitary to several, erect, usually branched distally, glabrous or glabrescent proximally, sparsely to moderately hirsute distally, pubescence usually arranged in lines from leaf bases on mid- and distal stem, greenish to reddish-tinged, (20) 40-80 (100) cm tall. **Leaves** basal and cauline, basal and lower cauline usually persistent, moderately to strongly reduced distally (especially in capitulescence), margins usually entire and flat, minutely stiff-ciliate with antrorse hairs, faces glabrous to sparsely puberulent; basal and proximal cauline leaves petiolate, linear-lanceolate or lanceolate to oblanceolate or narrowly elliptic (rarely narrowly obovate), apices acute to acuminate, bases cuneate to attenuate, petioles narrowly winged, 50-150 mm; mid-cauline leaves sessile to subpetiolate, linear to linear-lanceolate or narrowly oblanceolate, apices acute, bases cuneate to rounded and often subclasping, 30-60 mm; distal cauline leaves sessile, linear, apices
acute to acuminate, bases rounded to attenuate, 8-30 (50) mm. **Capitulescences** open, corymbiform to paniculate or pyramidal, not leafy, branches ascending; peduncle bracts 0-3+, linear, minutely spine-tipped, not grading into phyllaries, 2-8 (12) mm. **Flowering heads** few to numerous; involucres campanulate, 5-10 mm; phyllaries unequal, in 3-5 series, erect, linear to narrowly oblong, apices usually acute, margins hyaline proximally, green zones lanceolate to narrowly elliptic and restricted to distal 1/3-2/3 (4/5), often sparsely ciliate distally, faces glabrous to puberulent, 3-7 mm; ray florets 15-40, bluish to purplish, laminae 9-15 mm; disc florets 30-80 (100), yellowish (becoming reddish or purplish in age), lobes deltate, 4.5-6 mm. **Cypselae** cylindric to obovoid, not compressed, yellowish or tan to brownish, 3- to 4-nerved, short-hairy, 2.5-3.5 mm; pappus whitish, 5-7 mm.

Flowering Jul-Oct. Wet to moist shorelines, riverbanks, and marshy fens in the montane zone; 340-550 m. Rare in south-central [Shuswap region] and southeast [Kootenay Lake] BC; south to ID, NV, CA. \(2n = 32, 48, 64\) [4x-8x] (Brouillet et al. 2006).

This widespread aster of the western United States, which has long been treated as *Aster occidentalis* in regional floras (e.g., Hitchcock et al. 1955, Abrams & Ferris 1960, Hitchcock & Cronquist 1973, Douglas et al. 1989, Douglas 1995, Douglas et al. 1998), extends locally northward along shoreline habitats into south-central and southeastern British Columbia (Figure 107). It appears to be considerably rarer in the province than has been described in other floristic and taxonomic publications from British Columbia such as Douglas (1995) and Douglas et al. (1989, 1998, 2002b), presumably due to confusion with other narrow-leaved asters of the region. Based on specimen analysis associated with this study, mapped occurrences of this species from the southern coast of the province appear to largely pertain to populations that are here treated as *S. douglasii*, while widespread occurrences across the southern and central portions of the B.C.
interior appear to pertain primarily to misidentified material of *S. frondéum* var. *frondéum* and *S. lanceolatum* subsp. *hesperium*. In addition, although only var. *intermedium* is reported here for British Columbia, previous regional floras have also recognized the nominate var. *spathulatum* (as *Aster occidentalis* var. *occidentalis*) as occurring across southern British Columbia (Douglas 1995, Douglas et al. 1998, 2002b). This variety is distinguished from var. *intermedium* primarily by its smaller stature, fewer flowering heads, and more compact capitulescences (Hitchcock et al. 1955, Brouillet 2006). No specimens were encountered during the course of this study that conformed to the morphology of var. *spathulatum*, and those that had been identified as such (based on herbarium label and annotation data) appeared to be misidentifications of other taxa. As a result, this variety has been excluded as part of the British Columbia *Symphyotrichum* flora in this treatment (see Excluded Species, below).

*Symphyotrichum spathulatum* var. *intermedium* is most likely to be confused in British Columbia with narrow-leaved examples of the much more widespread *S. frondéum* var. *frondéum*, although it largely occurs in areas of the province and at elevations where *S. frondéum* is scarce or absent. These two taxa share several morphological characteristics, such as persistent basal and lower cauline leaves, but *S. spathulatum* var. *intermedium* can be distinguished by its conspicuously shorter outer phyllaries (phyllaries subequal in *S. frondéum* var. *frondéum*), more extensively hyaline phyllary bases, smaller and more numerous flowering heads in a more open and branching capitulescence, numerous small, linear peduncle bracts, and its generally narrower leaves (Figure 106). *Symphyotrichum lanceolatum* subsp. *hesperium*, which is the most likely similar species to occur sympatrically (both geographically and ecologically) with *S. spathulatum* var. *intermedium*, is distinguished by its subequal phyllaries, its often foliaceous outer phyllaries, and the more prominent lines of spreading, whitish hairs along the peduncles (peduncles uniformly hairy in *S. spathulatum* var. *intermedium*). The coastal *S. douglasii*, which does not appear to occur
sympatrically with *S. spathulatum* var. *intermedium*, has subequal phyllaries and basal and lower cauline leaves that usually wither prior to anthesis. *Symphyotrichum spathulatum* has been reported to hybridize with several other similar species in the western United States, such as *S. bracteolatum*, *S. frondeum* var. *frondeum* (as *S. foliaceum* var. *parryi*), and *S. hendersonii* (Brouillet *et al.* 2006), although no examples of such hybrids were encountered during this study. Apparent hybrids with *S. lanceolatum* subsp. *hesperium* have been collected from Mara Lake in south-central B.C. and, although collections of pure *S. spathulatum* var. *intermedium* are not known from that particular location, its presence at the site (either extant or historical) can be inferred by the presence of these putative hybrids.

This taxon is treated as ‘*S. spathulatum*’ (Lindl. in Hook.) G.L. Nesom’ in this treatment, but may be better treated under the specific epithet ‘*occidentalis* Nutt.,’ as was the tradition through most of the 20th century. This approach was in following with Cronquist (1943), who recognized *Aster spathulatus* in synonymy under *A. occidentalis* due to the mistaken assumption that the earlier-published name *spathulatus* Lindl. in Hook. (1834) was an illegitimate later homonym of *Aster spathulatus* Lag. (1816) (Cronquist *et al.* 1994). The name *Aster spathulatus* Lag. was never validly published, however, which renders *Aster spathulatus* Lindl. in Hook. as available and, ultimately, the name with nomenclatural priority for this taxon (Cronquist *et al.* 1994). As such, it is adopted in this treatment as the correct name for the taxon in question.

Although *spathulatus* is recognized as the correct name for this taxon if the type specimens of *spathulatus* and *occidentalis* are considered to represent the same taxon, there is some evidence to suggest that they may not be conspecific. Of primary interest is that the geographic distributions of the morphologies that correspond to these names are disjunct by over 1000 km between southern British Columbia (= ‘*occidentalis*’) and the Mackenzie River of the Northwest Territories (= ‘*spathulatus*’). While disjunctions of comparable distance are certainly not rare among vascular
plants in North America, the specific disjunction of a taxon (or even related taxa) between the western United States and Northwest Territories is extremely unusual, if not unprecedented. Furthermore, as noted in Cronquist et al. (1994), there are subtle differences in the pubescence of the stems, leaves, and phyllaries of these two populations (with northern ‘spathulatus’ populations more conspicuously and consistently pubescent), although overlap in this character reportedly makes it difficult to apply consistently. Thus, the unusual geographic disjunction of these populations, coupled with subtle morphological distinctions between them, suggests that two taxa may be involved. If so, the name ‘occidentalis’ could be reinstated for western United States and British Columbia material, and the name ‘spathulatus’ retained for the populations from the Mackenzie River area. These latter populations may represent a separate, taxonomically significant northern taxon that is related to western United States populations, or, conversely, may pertain to plants of hybrid origin between several northern aster species that result in a morphology that is similar. As this question is beyond the scope of this study, however, the name ‘occidentalis’ is included here as a synonym of ‘spathulatum,’ as has been standard practice in North American floras in recent years.
FIGURE 106. Morphological characteristics of *Symphyotrichum spathulatum* var. *intermedium*. A = overall habit and structure (*Straley 1695*); B, C = variation in involucre and phyllary characters (B = *Straley 1695*; C = *Anonymous s.n.*).

FIGURE 107. Distribution of British Columbia specimens of *Symphyotrichum spathulatum* var. *intermedium* that were reviewed for this study (left), and approximate distribution of the species elsewhere in northwestern North America (right).
23. *Symphyotrichum subspicatum* (Nees) G.L. Nesom

**ALASKA ASTER**


**Plants** perennial, long-rhizomatous, colonial. **Stems** not from a branched woody caudex, solitary to several, erect, usually few-branched distally, sparsely white-puberulent distally, pubescence arranged in lines on mid-stem, (10) 20-80 (120) cm tall. **Leaves** basal and cauline, basal and proximal cauline leaves withering prior to anthesis, slightly reduced distally, apices acute, margins usually sparsely to moderately serrate and flat to slightly revolute, minutely stiff-hairy with antrorse hairs, faces glabrous to sparsely scabrous; basal leaves petiolate, lanceolate to oblanceolate, bases attenuate to cuneate, petioles narrowly winged, 10-60+ mm; proximal cauline leaves subsessile to petiolate with broadly winged petioles, lanceolate to lance-elliptic, bases attenuate to cuneate and often subclasping, (50) 70-120 mm; distal cauline leaves sessile to subsessile, linear-lanceolate or lanceolate to narrowly oblong or elliptic, bases rounded to cuneate and usually clasping or auriculate, 20-60 (80) mm. **Capitulescences** dense to moderately open, racemose to subcorymbose, usually leafy, branches ascending; peduncle bracts 0-2, linear to lanceolate, not grading into the phyllaries, distalmost sometimes enlarged and foliaceous, (2) 5-10 mm. **Flowering heads** usually few to several (occasionally solitary); involucres campanulate, 7-9 mm; phyllaries subequal, in 3-5 series, erect to slightly spreading, apices acute, margins hyaline proximally (outermost sometimes wholly green), green zones oblanceolate to narrowly elliptic and restricted to distally 1/2-1/3, often purple-tinged (especially margins), ciliate, faces glabrous to
sparsely pubescent (within); outer phyllaries lanceolate to lance-elliptic, outermost sometimes enlarged and foliaceous, 4-7 (12) mm; inner phyllaries linear to lanceolate, 6-7 mm; ray florets 15-60, violet to purplish, laminae 10-20 mm; disc florets 50-150, yellowish (becoming reddish or purplish in age), lobes deltate, 5-8 mm. Cypselae cylindric to obovoid, not compressed, yellowish to brownish, 3- to 4-nerved, moderately to densely short-hairy, 2.5-4 mm; pappus whitish to tan, 5-8 mm.

Flowering Jul-Sep. Moist to wet beaches, brackish estuaries, salt marshes, coastal headlands, islets, meadows, shorelines, cliffs, and open slopes in the lowland and lower montane (rare) zones; 0-30 (400) m. Frequent in west-central [Haida Gwaii, north/central coast], infrequent in southwest BC [n Vancouver Island]; north to AK. 2n = ?

Symphyotrichum subspicatum is the most common aster of coastal habitats from northern Vancouver Island north through south-coastal Alaska (Figure 110). It occurs primarily along maritime coastlines, in salt marshes, and in brackish estuaries, occasionally extending inland in wet habitats to at least 400 m elevation. It is ecologically similar to the native S. chilense and the introduced S. novi-belgii var. novi-belgii of southwestern B.C., and largely replaces the former species along the northern and central coast of the province. It is morphologically similar to both of these species, but can be distinguished from S. chilense by its longer, acute to acuminate, subequal (or nearly so), often somewhat foliaceous outer phyllaries (vs. phyllaries broader, rounded to obtuse at the apices, strongly graduated, and never foliaceous in S. chilense) (Figure 108), more conspicuously clasping leaf bases, and more consistently and coarsely serrate leaf margins. It can best be distinguished from S. novi-belgii var. novi-belgii, which is restricted in B.C. to the Georgia Depression and is not known to occur sympatrically with S. subspicatum, by its consistently and coarsely serrate leaf margins and somewhat thicker, flesher leaves, as well as its
more ascending/erect (vs. often loosely spreading, at least at the tips) phyllaries. Putative hybrids between *S. subspicatum* and *S. chilense* from the west coast of Haida Gwaii were detected during this study, suggesting occasional hybridization between these species in their narrow region of overlap; additional putative hybrids between *S. subspicatum* and *S. ciliolatum* have been collected from west-central BC [Skeena-Bulkley region].

The concept of *Symphyotrichum subspicatum* presented in this treatment differs dramatically from the concept that has traditionally been used in the floristic and taxonomic literature, but is consistent with the taxon that is represented by the holotype of the species. Hitchcock *et al.* (1955) first applied the name *Aster subspicatus* to the taxon that had previously been recognized as *Aster douglasii* by Cronquist (1943), and which represented a taxon of northwestern North America that was distinguished primarily by its narrow (usually lanceolate), generally serrate leaves and relatively narrow, acute to acuminate, subequal phyllaries with prominent pale or yellowish, scarious bases (Hitchcock *et al.* 1955). This concept was subsequently adopted by most taxonomic and floristic studies, including Abrams & Ferris (1960), Hultén (1968), Hitchcock and Cronquist (1973), Scoggan (1979), Douglas (1995), Douglas *et al.* (1998), Brouillet *et al.* (2006), but the taxon was noted as extremely variable and difficult to define by virtually all authors. This intraspecific variability has traditionally been attributed primarily to hybridization with other members of sect. *Occidentales*, which are well-known to be highly interfertile (Allen *et al.* 1983), but the proposed extent of this hybridization did not permit the identification of a definable central morphology that could represent the taxon. The structure of the variation present within this traditional concept is also not consistent with such an explanation, as there are clear biogeographic and morphological patterns that suggest the presence of multiple taxa within *S. subspicatum* s.l.
This traditional, broad concept of *S. subspicatum s.l.* is here recognized as including both native and introduced species-level taxa as well as a variety of hybrids. It is interpreted as a classic taxonomic ‘trash can’ or ‘dust bin’ taxon (Davis & Heywood 1963) that amalgamates a rather disparate and unnatural assortment of entities which are united by what are inherently variable and poorly-defined morphological synapomorphies. Within British Columbia, this traditional concept has included what are here recognized as *S. x maccallae* (an allopolyplloid hybrid between *S. ciliolatum* and *S. laeve* subsp. *laeve*), *S. douglasii*, elements of *S. lanceolatum* subsp. *hesperium*, the introduced *S. novi-belgii* var. *novi-belgii*, and a variety of occasional, unstabilized hybrids, as well as *S. subspicatum s.s.* as it is presented here. South of British Columbia, entities that have been subsumed within *S. subspicatum* but which do not appear to be applicable to the taxon include *Aster okanoganus* Piper and *A. elmeri* Greene from northeastern Washington (which appear to represent the same taxon), with their broad and coarsely serrate leaves and strongly graduated involucres, as well as the extensively pubescent, entire-leaved *A. grayi* Suksd. from the lower Columbia River of southern Washington; however, as these populations are outside of the geographic scope of this study they are not treated further here. The various taxa and hybrids mentioned here, though largely sharing the leaf and involucre characters that have previously defined *S. subspicatum s.l.*, vary considerably in most other characters, and even the supposedly diagnostic characters of *S. subspicatum s.l.* are often poorly expressed and/or much more variable among these entities than has generally been appreciated. With the removal of these taxa and hybrids from the concept of *S. subspicatum*, what remains is a morphologically and ecologically coherent coastal taxon of south-central and southeastern Alaska and the northern/central coast of British Columbia that is consistent with the holotype of *Aster subspicatus*; this is the concept of *S. subspicatum* that is adopted in this treatment.
In addition to the narrowed circumscription of *S. subspicatum* that is presented here, the name *Aster foliaceus* Lindl. (= *Symphyotrichum foliaceum* [Lindl.] G.L. Nesom) is also placed within its synonymy. The holotypes of *A. subspicatus* and *A. foliaceus*, both of which are from coastal Alaska, clearly represent the same taxon based on morphological, phytogeographic, and ecological considerations, and their synonymy is supported by the near absence of other similar *Symphyotrichum* taxa within the region from which they were collected. The name *Aster foliaceus* (and later *Symphyotrichum foliaceum*) has long been applied erroneously to a common taxon of montane habitats of the Pacific Northwest that is here afforded the name *Symphyotrichum frondeum*; see the treatment of *S. frondeum* (above) for a more detailed discussion of the renaming of that taxon.

**FIGURE 108.** Variation in involucre and phyllary characteristics in *Symphyotrichum subspicatum*. A = typical involucre (Griffith s.n.); B = specimen with enlarged and foliaceous outer phyllaries (Björk & Kohler 16092); C = specimen with slightly broader, purple-tinged phyllaries (Pinder-Moss 1287).
FIGURE 109. Variation in overall habit and structure of *Symphyotrichum subspicatum*. Note the consistently lanceolate, coarsely serrate leaves and leafy capitulescences. A = Krajina s.n.; B = Calder & R.L. Taylor 23522; C = Björk & Kohler 16092; D = Pinder-Moss 1287.
Putative *Symphyotrichum* Hybrids Involving British Columbia Taxa

Hybridization among *Symphyotrichum* species is widespread and frequent throughout North America (Allen 1985), including in British Columbia (Figure 111). The following list of putative hybrids that pertain to British Columbia *Symphyotrichum* taxa was compiled based on specimens reviewed for this study as well as a review of the applicable literature. Hybrids reported from elsewhere in North America, but involving species present within British Columbia, are included so as to highlight potential hybridization that may be occur within the province but has not yet been documented. Of the following 30 hybrids involving British Columbia *Symphyotrichum* species, twenty of these have been documented as potentially occurring within the province and are represented by specimens reviewed during this study. Such putative hybrids identified as occurring in British Columbia are denoted by an asterisk (*).
FIGURE 111. Hybridization among *Symphyotrichum* taxa occurring in British Columbia. Heavy lines denote hybridization that has been documented as occurring in British Columbia; narrow lines denote extralimital hybridization involving species present in B.C. The diagram includes two taxa of hybrid origin (*S. x columbianum* [triangle]; *S. x maccallae* [square]), with their hypothesized origins identified. ASC = *S. ascendens*; BOR = *S. boreale*; BRA = *S. bracteolatum*; CAM = *S. campestre*; FRO CAU = *S. frondeum* var. *caurinum*; FRO FRO = *S. frondeum* var. *frondeum*; CHI = *S. chilense*; CILIA = *S. ciliatum*; CILIO = *S. ciliolatum*; CUS = *S. cusickii*; DOU = *S. douglasii*; ERI = *S. ericoides* var. *pansum*; FAL = *S. falcatum* (both var.); FRO = *S. frondosum*; HEN = *S. hendersonii*; LAE = *S. laeve* subsp. *laeve*; LAN = *S. lanceolatum* var. *hesperium*; NOV = *S. novi-belgii* var. *novi-belgii*; PIL = *S. pilosum* var. *pilosum*; PUN = *S. puniceum* var. *puniceum*; SPA = *S. spathulatum* var. *intermedium*; SUB = *S. subspicatum*. 
i. *Symphyotrichum ascendens* x *S. bracteolatum*

This hybrid is represented by a single extralimital (Montana) specimen that was reviewed during this study. The distributions of the parental taxa are sympatric in southeastern British Columbia (e.g., southern Rocky Mountain Trench) and this hybrid combination may be expected in that region.

ii. *Symphyotrichum ascendens* x *S. ericoides* var. *pansum*

Hybridization between these two species has been reported by Allen (1985), based on specimens from Utah. The two taxa occur sympatrically in the southern Rocky Mountain Trench of southeastern British Columbia, and thus such a hybrid may be expected in that region. Although the variety of *S. ericoides* involved in the hybridization was not specified in Allen (1985), it may be inferred to be var. *pansum* based on geographic considerations.

iii. *Symphyotrichum ascendens* x *S. falcatum*

*Symphyotrichum falcatum* is one of the parental taxa involved in the origin of the allopolyloid *S. ascendens*, and Allen (1985) notes occasional backcrossing between the two taxa. No putative hybrids between these species from British Columbia were noted during this study, but the species are locally sympatric in the southern Rocky Mountain Trench of southeastern B.C. and hybridization may be expected to occur in that region. Although the variety of *S. falcatum* involved in these backcrosses is not specified, it is most likely to be var. *commutatum* given the extensive geographic overlap between that variety and *S. ascendens*.

iv. *Symphyotrichum ascendens* x *S. frondeum*

This hybrid combination was reported from the western United States (Idaho, Utah) by Allen (1985). Although the name *S. 'foliaceum'* was used in Allen (1985), this would pertain to the taxon treated here as *S. frondeum*, although it is unclear to what variety of that taxon is involved.
in the reported hybridization. Of the three varieties of *S. foliaceum* [= *S. frondeum* of this treatment] present within the area of reported hybridization, only one (var. *frondeum*) is known to occur northward into British Columbia, where it occurs sympatrically with *S. ascendens* in the southeastern part of the province.

v. *Symphyotrichum ascendens* x *S. spathulatum*

As with *S. falcatum* (above), *Symphyotrichum spathulatum* is one of the parental taxa involved in the origin of the allopolyploid *S. ascendens*, and Allen (1985) reports occasional backcrossing between the taxa. No specimens pertaining to this hybrid from British Columbia were reviewed as part of this study, and the rarity of both taxa in the province along with little or no geographic sympatry between them suggests that such a hybrid combination would be unlikely to occur. The variety of *S. spathulatum* involved in the hybridization with *S. ascendens* was not specified in Allen (1985).

vi. *Symphyotrichum boreale* x *S. bracteolatum* (*)

Several examples of this apparent hybrid were documented from the southern interior of British Columbia during this study. The distributions of the two parental taxa overlap locally in the Chilcotin region, northern Columbia Mountains, and upper Fraser River watershed.

vii. *Symphyotrichum boreale* x *S. falcatum var. falcatum* (*

This hybrid combination is represented in British Columbia by a single apparent specimen from the southern Chilcotin region of the south-central interior, where the distributions of these two taxa are locally sympatric.
viii. *Symphyotrichum boreale* x *S. puniceum* var. *puniceum* [= *S. longulum* (Sheld.) G.L. Nesom]

This hybrid occurs across central Canada and the northern United States (Brouillet *et al.* 2006), where the distributions of the two parental taxa are widely sympatric, but has not been documented from British Columbia. Although there is only limited geographic overlap between *S. boreale* and *S. puniceum* in B.C., such a hybrid may be anticipated in northeastern parts of the province (i.e., Peace River lowlands, Fort Nelson lowlands, Liard Basin) where the two species co-occur.

ix. *Symphyotrichum bracteolatum* x *S. chilense*

A single extralimital (California) specimen that appears to pertain to this hybrid combination was reviewed for this study. These two species barely occur sympatrically in British Columbia (lower Fraser River), and thus such a hybrid is not anticipated to occur with any regularity in the province.

x. *Symphyotrichum bracteolatum* x *S. falcatum* var. *falcatum* (*)

This putative hybrid has been collected from the southern Rocky Mountain Trench of southeastern British Columbia. The distributions of the two parental taxa overlap widely across south-central and southeastern parts of the province, and they may hybridize more widely than the single voucher specimen suggests.

xi. *Symphyotrichum bracteolatum* x *S. laeve* subsp. *laeve* (*)

The ranges of these two species overlap locally in southeastern British Columbia, although they tend to occupy discrete habitats within this region (*S. bracteolatum* along shorelines and in wetlands, *S. laeve* in dry uplands and disturbed habitats). Hybrids are recognizable due to the
combination of the distinctive stem pubescence of \textit{S. bracteolatum} and distinctive leaf shape of \textit{S. laeve}.

\textbf{xii. Symphyotrichum bracteolatum x S. lanceolatum subsp. hesperium (*)}

These two species overlap extensively in both distribution and habitat throughout the southern interior of the province, with both being among the dominant asters of lacustrine and riverine shorelines in that region. Despite this, however, few examples of putative hybrids between the species were documented during the course of this study. Although similar in overall gross morphology (i.e., tall, narrow-leaved species), the two species differ discretely in characters such as stem pubescence and, often, leaf serration, rendering hybrids relatively easily identifiable.

\textbf{xiii. Symphyotrichum bracteolatum x S. novi-belgii var. novi-belgii (*)}

Potential hybridization between the native \textit{S. bracteolatum} and the introduced \textit{S. novi-belgii var. novi-belgii} is supported by the presence of an intermediate specimen from the lower Fraser River valley in southwestern British Columbia. There are likely limited opportunities for these two species to hybridize given the scarcity of \textit{S. bracteolatum} on the south coast.

\textbf{xiv. Symphyotrichum campestre x S. ericoides var. pansum (*)}

This hybrid combination has been proposed as producing the hybrid \textit{S. x columbianum} (Hitchcock \textit{et al.} 1955, Abrams & Ferris 1960), but here that name is restricted to a somewhat glandular taxon that is consistent with the holotype specimen (see \textit{S. x columbianum}, above). Apparent hybrids between \textit{S. campestre} and \textit{S. ericoides var. pansum}, as they are recognized here, tend to maintain the spreading-arching branching, spreading whitish pubescence, and sometimes the secund capitulae of \textit{S. ericoides}, but have larger capitulae and purplish ray florets, the latter being representative of \textit{S. campestre} parentage. Such plants have been collected from scattered
locations across south-central and southeastern British Columbia, where the distributions of the parental taxa are widely sympatric.

xv. *Symphyotrichum frondeum var. caurinum* x *S. frondeum var. frondeum* (*)

The two varieties of *S. frondeum*, which have long been attributed to *S. foliaceum*, are primarily parapatric where their distributions meet in British Columbia. They appear to intergrade regularly along the Coast-Cascade Mountains and occasionally in the Cariboo Mountains (see Figure 54).

xvi. *S. frondeum var. caurinum* x *S. ciliolatum* (*)

Specimens pertaining to this hybrid have been collected from scattered locations across central British Columbia where the distributions of the two parental species are sympatric. This hybrid may occur more widely across central B.C. than the few collections suggest given the extensive sympatry of the parental taxa, and may expected to occur most frequently in the Cariboo Mountains where *S. frondeum var. caurinum* is particularly common.

xvii. *Symphyotrichum frondeum var. caurinum* x *S. douglasii* (*)

The two parental species involved in this hybridization are geographically sympatric in southwestern British Columbia, primarily on Vancouver Island, but are typically separated elevationally, with *S. douglasii* occurring primarily below 200 m and *S. frondeum var. caurinum* occurring above 600 m. Nonetheless, apparent hybridization was detected on central Vancouver Island during this study, and morphological considerations suggest the potential influence of *S. frondeum var. caurinum* in some central Vancouver Island populations of *S. douglasii* that were described by Henry (1917) as representing the species *Aster carterianus*. 
xviii. **Symphyotrichum frondeum var. frondeum x S. laeve subsp. laeve (**) 

This hybrid is occasional in the Rocky Mountains of southeastern British Columbia and southwestern Alberta, where the distributions of the two parental taxa are locally sympatric. Many collections of *S. x maccallae* from this region also suggest the potential introgression of *S. frondeum* var. *frondeum* into that taxon, which is otherwise representative of hybridization between *S. ciliolatum* and *S. laeve* subsp. *laeve*. Collections attributed to this hybrid combination are morphologically similar to the holotype of *Aster umbachii* Rydb., and may represent the same entity.

xix. **Symphyotrichum frondeum var. frondeum x S. lanceolatum var. hesperium (**) 

The distributions of *S. frondeum* var. *frondeum* and *S. lanceolatum* var. *hesperium* are locally sympatric across the southern interior of British Columbia, but the two species are generally separated both elevationally and ecologically. *Symphyotrichum frondeum* var. *frondeum* is most commonly a species of moderate and high elevations, and commonly occurs in dry upland habitats, while *Symphyotrichum lanceolatum* var. *hesperium* is primarily a species of shorelines and wetlands. The single apparent hybrid between these two species in British Columbia is from the Shuswap region of the southern interior.

xx. **Symphyotrichum ciliolatum x S. lanceolatum var. hesperium (**) 

The two parental species involved in this apparent hybridization are widely sympatric across the boreal forests of Canada, including much of southern and northeastern (Peace River lowlands) British Columbia. Hybridization between *S. ciliolatum* and *S. lanceolatum* var. *hesperium* is suggested by the presence of intermediate specimens from scattered locations across the area of sympatry in the province, and may be more widespread than the few collections would indicate.
xxi. *Symphyotrichum ciliolatum* x *S. novi-belgii* var. *novi-belgii* [= *S. subgeminatum* (Fern.) G.L. Nesom]

*Symphyotrichum ciliolatum* hybridizes locally with *S. novi-belgii* var. *novi-belgii* in the Gulf of St. Lawrence area of eastern Canada (Labrecque & Brouillet 1996, Brouillet *et al.* 2006), where both parental taxa are native. The distributions of the two parental taxa barely overlap in the lower Fraser Valley area of southwestern British Columbia, where *S. novi-belgii* var. *novi-belgii* is an established exotic species and *S. ciliolatum* is a rare native species at the periphery of its natural range, and thus such a hybridization event is expected to be, at best, exceedingly rare in the province.

xxii. *Symphyotrichum ciliolatum* x *S. subspicatum* (*)

Specimens attributed to this hybrid combination have been collected from areas of west-central British Columbia (Skeena River, Bulkley Valley). The apparent hybrid from Moricetown Canyon is considerably removed from the established distribution of *S. subspicatum* in British Columbia, which is otherwise confined to coastal and near-coastal environments, and thus its involvement in this inland hybridization event is only tentatively accepted here based on the morphological intermediacy of the applicable specimen.

xxiii. *Symphyotrichum chilense* x *S. douglasii*

Although both parental taxa are relatively common on the south coast of British Columbia, no provincial specimens were reviewed during this study that could convincingly suggest hybridization between them; however, a specimen from Oregon was deemed to be a potential hybrid between the two taxa. Such a hybrid may be expected to occur north into Canada,
particularly on central Vancouver Island where there may be extensive hybridization occurring between these and other polyploid species of sect. *Occidentales*.

**xxiv. *Symphyotrichum chilense* x *S. novi-belgii var. novi-belgii* (*)

The native *Symphyotrichum chilense* and the introduced *S. novi-belgii var. novi-belgii* are ecologically similar taxa that are largely restricted to marine and estuarine shorelines or occasionally near-coastal freshwater habitats. They occur sympatrically near the mouth of the Fraser River and on southeastern Vancouver Island in southwestern British Columbia, where a number of intermediate specimens suggest ongoing hybridization between them in this region.

**xxv. *Symphyotrichum chilense* x *S. subspicatum* (*)

*Symphyotrichum subspicatum* largely replaces *S. chilense* as the primary aster of marine and estuarine shorelines along the British Columbia coast, but there remains localized sympatry between the two species on northern Vancouver Island and Haida Gwaii (where *S. chilense* is rare). A single specimen from Haida Gwaii that was reviewed for this study was determined to be morphologically intermediate between these two parental taxa and is proposed here to represent hybridization between them. Such a hybrid may also be expected on northern Vancouver Island.

**xxvi. *Symphyotrichum douglasii* x *S. novi-belgii var. novi-belgii* (*)

A single specimen from central Vancouver Island with intermediate morphology is proposed here as a hybrid between the native *S. douglasii* and the introduced *S. novi-belgii var. novi-belgii*. Although *S. novi-belgii* is primarily a species of estuarine and coastal habitats, both in its native range in eastern North America and in British Columbia where it is introduced, it also occurs sporadically in low elevation freshwater habitats of the Georgia Depression where *S. douglasii* is otherwise the dominant aster. Thus, hybridization between these species may be more
prevalent than the single specimens suggests, although hybridization between these two similar and variable species would be difficult to verify.

**xxvii. Symphyotrichum ericoides var. pansum x S. falcatum var. falcatum (*)**

The two parental taxa of this hybrid have limited interfertility (Jones 1978b), but some intermediate specimens from their extensive area of sympatry in southern and northeastern British Columbia suggest the occurrence of occasional hybridization. Both parental taxa are somewhat variable, with much of this variability related to growth form and thus poorly represented on many herbarium specimens, but intermediate characteristics present on some specimens are here attributed to hybridization rather than strictly to intraspecific variation in one or the other parental taxon. Given the extent of sympatry between *S. ericoides var. pansum* and *S. falcatum* in British Columbia, relatively few examples of potential hybridization were detected during the course of this study.

**xxviii. Symphyotrichum lanceolatum x S. laeve subsp. laeve**

This hybrid was reported by Semple *et al.* (2002) and Brouillet *et al.* (2006), based (at least in part) on hybrid specimens from Ontario (Semple *et al.* 2002). The hybridization events described by Semple *et al.* (2002) and Brouillet *et al.* (2006) pertain to the eastern var. *lanceolatum* rather than the western var. *hesperium*, but these two varieties are similar and closely related. As *S. lanceolatum* (as var. *hesperium*) and *S. laeve* subsp. *laeve* are sympatric in the Peace River lowlands of northeastern British Columbia, which represents the provincial centre of abundance of both species, such a hybrid combination may be expected in that region.

**xxvix. Symphyotrichum lanceolatum subsp. hesperium x S. puniceum var. puniceum (*)**

Hybridization between these two species in British Columbia is suggested by the presence of intermediate specimens from the Peace River lowlands in northeastern regions of the province,
where their distributions are locally sympatric. Hybridization between these species has also been noted in Brouillet et al. (2006) from eastern North America. Proposed hybrids combine the overall structure and morphology of *S. lanceolatum* var. *hesperium* with the spreading, uniform stem hairs of *S. puniceum* var. *puniceum*.

**xxx. Symphyotrichum lanceolatum subsp. hesperium x S. spathulatum var. intermedium (†)**

*Symphyotrichum spathulatum* var. *intermedium* is a rare aster of shoreline habitats in the southeastern and south-central (Shuswap region) British Columbia, occurring sympatrically with the much more common, and ecologically similar, *S. lanceolatum* var. *hesperium* in both areas. A single potential example of hybridization between these two species was detected from the Shuswap region (Mara Lake). Given the rarity of *S. spathulatum* var. *intermedium* in the province, hybridization between these two taxa is likely very rare in British Columbia.

**Symphyotrichum Species Excluded from the British Columbia Flora**

The following *Symphyotrichum* taxa have been reported as occurring within British Columbia, but are either unsupported by any voucher specimens or photographic evidence or are known only as non-established or otherwise non-persistent populations (i.e., waifs). These taxa are thus excluded from the provincial flora pending additional evidence of their occurrence or establishment.

i. **Symphyotrichum x amethystinum** (Nutt.) G.L. Nesom

**AMETHYST ASTER**

This hybridogenous species [= *S. ericoides* var. *ericoides* x *S. novae-angliae*] has been reported as introduced into the province by the British Columbia Conservation Data Centre (2018); however, the application of this name is based on misidentification of plants that are here referred
to *S. x cumbrianum*. True *S. x amethystinum* occurs sporadically in eastern North America where the ranges of the two parental taxa are sympatric (Benke 1931, Semple et al. 2002, Brouillet et al. 2006), and is also present in the horticultural trade (Semple et al. 2002). It should be noted that horticultural varieties of *S. x amethystinum* (also known as *Aster ‘Kylie’*), which were created artificially in European gardens and are not based on collection of wild material (Cullen et al. 2011), and are not morphologically identical to the natural hybrids. Specifically, horticultural varieties differ from their wild counterparts in their sparser glandularity and pubescence and more prominently spinulose phylary apices (Cullen et al. 2011). Were it to occur as an exotic waif or established introduced species in the Pacific Northwest, such horticultural varieties of *S. x amethystinum* would be the likely source of the introduction.

ii. *Symphyotrichum cordifolium* (L.) G.L. Nesom

**HEART-LEAVED ASTER**

This eastern North American aster is closely related to, and very similar to, the widespread native *S. ciliolatum*. A specimen consistent with the morphology of this species was collected as a non-established waif from railyards near Vancouver in 1993 (*F. Lomer, pers. comm.*)) but the species has not been collected since and is not known to have any established populations in British Columbia. It is distinguished from *S. ciliolatum* by the more deeply cordate bases of the basal and lower cauline leaves (although some specimens of *S. ciliolatum* approach this feature), conspicuously shorter outer phyllaries with smaller green zones, and slightly shorter ray florets (Semple et al. 2002).

iii. *Symphyotrichum foliaceum* (Lindl.) DC. var. *apricum* (A.Gray) G.L. Nesom

**ALPINE LEAFY ASTER**
This infraspecific taxon would be placed within the species that is here treated as *Symphyotrichum frondeum* but, as its distribution is outside of the geographic scope of this study, no nomenclatural changes are proposed herein. This variety represents a dwarf, stunted, alpine form of *S. frondeum* that is widespread throughout the western United States and has been reported as occurring in British Columbia (British Columbia Conservation Data Centre 2018). It differs from the lower-elevation *S. frondeum* var. *frondeum*, with which it is widely sympatric, in its more diminutive stature, fewer flowering heads, and more uniformly greenish (vs. purplish) phyllaries (Brouillet *et al.* 2006). In assessing British Columbia specimens of *S. frondeum* for this study, numerous examples of diminutive alpine collections were observed, but all were otherwise indistinguishable from larger, lower-elevation collections except for their reduced size. Furthermore, a complete continuum in size was apparent between these extremes, suggesting that the smaller size of alpine populations was more attributable to environmental influences than to anything of taxonomic significance. As a result, British Columbia populations previously attributed to var. *apricum* are here attributed to *S. frondeum* var. *caurinum*. The taxonomic significance of *apricum* populations from outside of British Columbia is not otherwise assessed, as it is beyond the geographic scope of this study.

iv. *Symphyotrichum hallii* (A. Gray) G.L. Nesom

**HALL’S ASTER**

This rare white-rayed aster is endemic to the southern Puget Sound lowlands of Washington and the Willamette Valley of Oregon. It was reported for British Columbia (as *Aster chilensis* var. *hallii*) by Taylor & MacBryde (1977), but no voucher specimens confirming its presence in the province were located during this study. Similarly, other floristic studies of British Columbia Asteraceae (Douglas *et al.* 1989, Douglas 1995, and Douglas *et al.* 1998) have reported an absence
of documentation of this species in the province. As a result, this species is excluded from consideration as part of British Columbia’s flora.

v. *Symphyotrichum lanceolatum* (Willd.) G.L. Nesom subsp. *lanceolatum*

**LINED ASTER**

Populations of *S. lanceolatum* from the Peace River region of northeastern British Columbia, which differ morphologically from populations in southern parts of the province (see the account of *S. lanceolatum*, above), have sometimes been attributed to the eastern subsp. *lanceolatum* by the British Columbia Conservation Data Centre (2018). This highly variable taxon is widespread, and often weedy, throughout its range in eastern North America, and occurs as an invasive species in Europe, but is not generally reported from western North America. It differs from the western North American subsp. *hesperium* primarily in its strongly graduated involucres and the lack of an elongate peduncle bract beneath the involucre, although the two forms intergrade across parts of central North America (Semple et al. 2002, Brouillet et al. 2006). Despite the occasional attribution of northeastern B.C. populations to subsp. *lanceolatum*, the morphology of these populations is clearly aligned with subsp. *hesperium* and, in fact, it is populations from southern British Columbia that are actually morphologically out-of-place within the current taxonomy of the *S. lanceolatum* complex; these latter populations may in fact be worthy of taxonomic recognition themselves. Interestingly, both the cytological and biogeographic patterns within *S. lanceolatum* (Semple et al. 1983) suggest a closer association of western boreal populations (including those from the Peace River region) with the eastern subsp. *lanceolatum* than with typical subsp. *hesperium* of the western United States, but these patterns are not mirrored in the morphology of the plants. Given the morphological discrepancies between western boreal populations and those from eastern North America (= subsp. *lanceolatum*), the former are here included within subsp. *hesperium*. This is consistent with how the group has been treated in other
taxonomic and floristic studies of the *S. lanceolatum* complex (e.g., Semple *et al.* 1983, Semple & Chmielewski 1987, Semple *et al.* 2002, Brouillet *et al.* 2006). Apparent collections of true var. *lanceolatum* from the Vancouver area of southwestern B.C. (*F. Lomer,* pers. comm.) refer to non-established waifs and garden escapes and are thus not appropriate for inclusion in this treatment.

vi. *Symphyotrichum lateriflorum* (L.) Löve & Löve

**CALICO ASTER**

This widespread, and often weedy, eastern North American aster has been collected once in British Columbia as a non-established waif along railway lines in New Westminster (*F. Lomer,* pers. comm.). Among native and established *Symphyotrichum* species in British Columbia, *S. lateriflorum* most closely resembles *S. pilosum* var. *pilosum* in its overall form and structure (e.g., capitulescence branching, small capitulae); it is best distinguished by the lack of subulate apices on the phyllaries and the more deeply lobed corollas of the disk florets.

vii. *Symphyotrichum novae-angliae* (L.) G.L. Nesom

**NEW ENGLAND ASTER**

This species is a very common, and very weedy, native aster throughout much of North America (*Brouillet et al.* 2006) and has been collected sporadically as a non-established waif in the Vancouver area of British Columbia (*F. Lomer,* pers. comm.). It is established locally as an exotic species in western North America, such as in Montana, Oregon, Utah, Washington, and Wyoming (*Brouillet et al.* 2006), although all British Columbia collections appear to pertain to non-established garden escapes. It is a robust and highly distinctive species of aster, with the stems and leaves densely spreading pubescent, the peduncles and phyllaries densely stipitate-glandular, and the large, showy capitulae sporting deep rose-purple ray florets; it is unlikely to be mistaken
for any other native or introduced species of *Symphyotrichum* in British Columbia. One of the provincial collections is representative of a double-flowered horticultural hybrid rather than the natural morphotype (*F. Lomer, pers. comm.*).

viii. *Symphyotrichum praetaltum* (Poir.) G.L. Nesom

**WILLOW-LEAVED ASTER**

This widespread aster of eastern North America was reported for British Columbia by Taylor & MacBryde (1977), but no voucher specimens documenting its presence in B.C. were located during this study or during any previous studies of the province’s Asteraceae flora (e.g., Douglas *et al.* 1989, Douglas 1995, Douglas *et al.* 1998). It is morphologically very similar to many other native and introduced species of *Symphyotrichum* in the region, and its reported presence is attributed to specimen misidentification. It is thus excluded here as part of the province’s aster flora.

xiv. *Symphyotrichum spathulatum* (Lindl.) G.L. Nesom var. *spathulatum*

**WESTERN MOUNTAIN ASTER**

This is a widespread aster throughout much of the western United States, and has been reported as occurring north into southern British Columbia in most floristic and taxonomic studies of the region. Indeed, some authors (e.g., Douglas 1995, Douglas *et al.* 1998, Douglas *et al.* 2002b) have noted it to be widespread, if rare, across much of the southern and central portions of the province, ranging as far north as Prince Rupert and the Prince George region (Douglas 1995). It is similar to *S. spathulatum* var. *intermedium*, which occurs rarely in the southern interior of the province, but is an overall smaller plant with fewer capitulae in a more compact capitulescence. It is also very similar to the widespread *S. frondeum* var. *frondeum*, but differs in its smaller
capitulae, narrower basal leaves, and, especially, its distinctly graduated involucre. Despite the
frequent reference to its occurring in British Columbia, no specimens of this taxon were noted
during the course of this study, and all specimens that had been identified as such were found to
be misidentifications of other narrow-leaved taxa (e.g., *S. frondeum* var. *frondeum*, *S. lanceolatum*
subsp. *hesperium*, *S. douglasii*). As its distribution approaches the southern border of the province,
particularly along the Cascade Mountains of Washington, it may yet be documented in British
Columbia; however, as no documentation of its presence has yet been presented, it is excluded
from further consideration as part of the province’s flora.
CHAPTER FOUR:

PERSPECTIVES ON ACADEMIA AND THE TAXONOMIC IMPEDIMENT

“Taxonomy (the science of classification) is often undervalued as a glorified form of filing—with each species in its folder, like a stamp in its prescribed place in an album; but taxonomy is a fundamental and dynamic science, dedicated to exploring the causes of relationships and similarities among organisms. Classifications are theories about the basis of natural order, not dull catalogues compiled only to avoid chaos.” Stephen Jay Gould, *Wonderful Life* (1989)

4.1 Introduction

The field of taxonomy\(^3\) has long been seen as a discipline in decline. This has been largely attributed to the rise of molecular biology (including molecular systematics) and shifts in hiring and funding priorities. The challenges facing taxonomy have now been well documented by a number of authors (e.g., Scotland *et al.* 2003, Tautz *et al.* 2003, Wheeler 2004, Wilson 2004, Agnarsson & Kuntner 2007, Wheeler 2008a, Wheeler 2008b, Coleman 2015, Bik 2017), particularly those with a taxonomic background or who undertake taxonomically-related research themselves. Its decline, especially as it relates to the insufficient taxonomic expertise available to address the world’s remaining undescribed species, has come to be known as the ‘Taxonomic Impediment’ (Coleman 2015) and, while the importance of overcoming the Taxonomic Impediment has been widely discussed (see Godfray 2002, Hebert 2003, Tautz *et al.* 2003, Wheeler 2004, Wilson 2004, Agnarsson & Kuntner 2007, Godfray 2007, Wheeler 2008a, Wheeler 2008b), perspectives on how best to address the issue have varied among contributors to this discussion. Among the many perspectives that have been put forth, few have commented specifically on the role of the academic system in this decline, and fewer still have recognized the impacts of the Taxonomic Impediment on taxonomic end-users outside of the academic system.

\(^3\) The use of the term ‘taxonomy’ in this paper corresponds with the notion of ‘alpha-taxonomy,’ which seeks to describe and define the units of biodiversity (species) through the publication of monographs, floras, and regional natural history summaries.
This essay will explore these aspects of the Taxonomic Impediment to contribute additional perspectives on the issue. Of central importance to this discussion is the recognition that, although taxonomy has been ill-served by the academic system for decades, this same academic system can nonetheless be an important and influential force in addressing the Taxonomic Impediment. Partnership between taxonomists and other biologists whose work incorporates taxonomic themes could promote the establishment of a novel model for the training of taxonomists along with promoting a better appreciation of the science within academia itself. Such a reinvigoration of taxonomy would be of considerable benefit to biologists within and outside of the academic system.

4.2  A Brief History of the Taxonomic Impediment

The Taxonomic Impediment is the result of decades of instability in the relationship between taxonomy and the rest of the biological sciences, and is therefore best understood through the lens of history. Taxonomy has existed in more or less its current form for c. 250 years, beginning with the publication of Linnaeus’ (1753) seminal *Species Plantarum* and, later, *Systema Naturae* (Linnaeus 1758). These publications not only established the binomial system of biological nomenclature for plants and animals, respectively – for which they are justifiably lionized – but also provided the basis for how scientists view and interpret the elements (species) of what is today known as biodiversity (Wilson 1988). During the 150 years following the publication of *Species Plantarum* and *Systema Naturae*, taxonomy led to the biological discovery that exploded around the world in association with exploration and colonial conquest. The concepts and nomenclatural systems defined by Linnaeus (1753, 1758) were applied by biologists to the discoveries made during excursions to newly studied regions of the globe, resulting in a multitude of new species being described during this time. Many revolutionary monographic and floristic treatises were produced during this period by zoologists and botanists alike. From a
botanical perspective, it was during this period that such influential botanists as Asa Gray [1810-1888], Thomas J. Howell [1842-1912], and John Torrey [1796-1873] explored North America and described hundreds of new species of plants, resulting in many comprehensive taxonomic works that synthesized the existing knowledge of the continent’s flora. It was an age of biological discovery, and taxonomy was a critical component of that discovery process.

During this first century-and-a-half, and extending into the early 20th century, taxonomy was largely characterized by traditional specimen-based research. It was inherently descriptive in many of its aims, and relied heavily on the interpretation of morphological variation among museum specimens by the practicing taxonomist. The resulting taxonomic treatments were largely seen as comprising a framework of hypotheses about the species described, their morphological and ecological attributes, and their relationships to other taxa. That these hypotheses have, in many cases, withstood a century or more of further inquiry underscores the potential strength inherent in the taxonomist’s interpretation. By the 1940s, the Modern Evolutionary Synthesis (Huxley 1942) contributed to enhancing the taxonomists’ ‘toolbox’ with new methods and approaches such as population genetics and cytogenetics that could explore the role of microevolutionary processes in defining species. These advances were later joined by molecular phylogenetics, and together these new tools provided the opportunity for exciting new insights into the world’s biodiversity. Although they were of considerable benefit to taxonomy, however, the addition of these new tools rapidly shifted the focus away from organismal and biodiversity studies and towards understanding the evolutionary processes responsible for that diversity (Wheeler 2008a). This shift, which was relatively subtle on its surface, was ultimately the genesis for the large-scale abandonment of baseline taxonomic research in favour of the expansion of research into the evolutionary processes responsible for producing biodiversity. The justification for this shift rested largely on the notion that the ‘patterns’ observed in biodiversity could be accounted for simply by understanding of the
evolutionary ‘processes’ underlying them (Wheeler 2008a), and that a taxonomic scheme would inevitably emerge from the study of these evolutionary processes. In such a world, of what use was the seemingly redundant study of pattern? Of what use was the ‘old-fashioned’ (Dobzhansky 1966) field of taxonomy when the future belonged to new tools that could approximate the same taxonomic system while simultaneously investigating the evolutionary history of the component elements – particularly when these new tools were among the most cutting-edge and modern scientific advancements of the day?

Huxley (1940) was among the first to redefine taxonomy. He argued for the importance of taxonomy, but stressed that the future belonged to the study of evolutionary processes (his ‘New Systematics’) rather than the ‘old’ discipline of taxonomy. This sentiment is well captured by the closing paragraph of Huxley (1940), in which the author states:

“[The New Systematics] will in some ways doubtless help classical taxonomy in its practical pigeon-holing functions4; it will give a much more detailed picture of the actual facts of the diversity of organic nature and its distribution in groups and in character-gradients over the globe; it will reveal many facts and principles of great importance to general biology; and through it taxonomy will become the field of major interest for all those concerned with the study of evolution at work.”

In other words, the path to successful taxonomy runs directly through the application of Huxley’s ‘New Systematics.’ Inadvertent as any negative repercussions may have been, Huxley’s position was highly influential in propelling the early abandonment of traditional taxonomy by others within the biological sciences. His position was echoed at nearly the same time by Ernst Mayr (1942) – among the most influential biologists of the past century – who conveyed a decidedly more antagonistic view of traditional taxonomy. His view of taxonomy was

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4 This view of taxonomists as providing little more than ‘pigeon-holing’ functions would persist throughout the rest of the 20th century and beyond, and would colour impressions of taxonomy throughout that period.
contemptuous on its face, as he lamented that “the major problems [of old systematics (= taxonomy)] are those of a cataloguer or bibliographer, rather than those of a biologist” (pg.6), and that “…the new systematist tends to approach his material more as a biologist and less as a museum cataloguer” (pg.7). He further denigrated the science by proclaiming that those pursuing the new, ‘modern’ fields of the New Systematics showed a “deeper interest in the formulation of generalizations…and consider[ed] the describing and naming of a species only as a preliminary step of a far-reaching investigation” (pg.7). The contributions of Huxley and Mayr during the 20th century were unassailably important and influential, and thus their dismissive views of taxonomy were rapidly incorporated into the zeitgeist of the biological community. Taxonomists have been fighting an uphill battle for recognition ever since.

By the 1960s, biologists such as Hennig (1966) were beginning to question the marginalization of taxonomy within the biological sciences, and were arguing strongly on its behalf. In particular, Hennig (1966) argued that taxonomy should be ‘holomorphologic,’ which he defined as an integrated taxonomy informed by all relevant sources of evidence (Wheeler 2008b) – a concept that would much later be resurrected as ‘integrative’ (Will et al. 2005) or ‘iterative’ (Yeates et al. 2011) taxonomy. His goal was to re-focus taxonomy back onto the patterns of biodiversity, with the molecular-genetic, cytological, and population-genetic evidence included among multiple evidentiary lines that should be assessed to explain those patterns. Despite the brief resurgence of taxonomic research that resulted from Hennig’s arguments (Wheeler 2008a), the continuous emergence of new technological and theoretical advancements proved far too enticing for the biological community to resist, for, as noted in Wheeler (2008a), “new money in any science has a tendency to follow new methods and ideas.” The proclamations of Hennig (1966) were thus unable to permanently shift the marginalization of taxonomy, which continued throughout the rest of the 20th century and into the early years of the 21st. As evident from the
introductory quote from Gould (1989), above, there remained a general sense within academic biology at the end of the 20th century that taxonomy was (and is) simply a mundane and rather dull process of cataloguing names in databases and checklists, and is often derided as ‘simply’ a descriptive science…if it is considered a science at all (as per Mayr [1942]). As noted by Wheeler (2004), descriptive taxonomy is now widely considered ‘passé’ within the academic system, and has suffered all of the consequences to funding, career opportunities, and, ultimately, scientific discovery that would be expected with such a designation. This is now the landscape within which the field sits, despite more than 70 years and a multitude of papers arguing for its importance. The Taxonomic Impediment has now become firmly entrenched.

4.3 The Importance of Taxonomy in the Biological Sciences

The universal shift in organismal biology toward the study of evolutionary processes has left much of academic biology unfamiliar with the science of taxonomy, and unaware of its importance throughout the biological sciences. The roles that taxonomy plays within biology are numerous, and capture some of the most critical aspects of the discipline, but these important contributions are often overlooked within the academic system. I here recognize four specific roles that taxonomy plays within biology, within which it can be seen: (i) as a language; (ii) as context; (iii) as a hypothesis generator; and, ultimately, (iv) as a knowledge system.

Taxonomy as a Language

Taxonomy provides the linguistic tools for biologists and non-biologists alike to discuss and understand biodiversity. Within the field of floristics, for example, the taxonomic names associated with the plants that are present within a given region allow for the presentation and discussion of the unique elements (species) that comprise the region’s flora. The use of this standard taxonomic ‘language’ allows for these discussions to extend beyond the specialists and to reach others who will require this information, such as conservationists, ecologists, and natural
historians. This ‘language’ has rules, as does any traditional language, which permits the dissemination of concepts among interested parties. In much the same way as a visitor to a foreign land may come to discover, those who are fluent in the ‘language’ of taxonomy and biodiversity are rewarded with considerable clarity in an otherwise chaotic and confusing landscape.

Taxonomy as Context

Taxonomy provides the context within which the entirety of our understanding of the biological world sits. This context emerges as a result of the copious amount of information about the natural world that is captured by, housed in, and disseminated through the taxonomic system. Taxonomy defines the units for all manner of biological subdisciplines to investigate and compare, whether they deal specifically with questions of biodiversity or not. The context provided by taxonomy extends far beyond the ecologists, conservationists, and others who require discrete entities to understand biodiversity. Even for the cell biologist or medical researcher, understanding the taxonomic placement of their study organism (including *Homo sapiens*) provides invaluable context by which to understand its physiology, anatomy, or behaviour. Without the ability to catalogue and manage this wealth of information, the entire enterprise of biology would soon become so overburdened by dissociated facts that the effective use of this information to develop and investigate new hypotheses would be greatly diminished. As a building might be supported by steel girders to ensure its stability and integrity, the concepts and classifications of taxonomy provide the contextual support for the entirety of the biological sciences. And as the structural integrity of the building would suffer without consideration of the importance of this support system, so too would the biological sciences suffer dramatically from a failure to maintain a strong and vibrant field of taxonomy.
**Taxonomy as a Hypothesis Generator**

Taxonomy has a direct relationship with many other elements of the biological sciences through its emphasis on the formulation of hypotheses that can be addressed by other biological subdisciplines. In many ways, this is among its most important contributions, as any proposed taxonomic scheme is inherently a hypothesis unto itself. For example, the species delineations proposed in Chapters 2 and 3 of this thesis lead to predications that can be evaluated with additional evidence. Even the concept of a particular species (including its ecology, distribution, morphological diagnosis, and phylogenetic relationships) is considered a hypothesis, being open to repeated testing and refinement. Any subsequent taxonomic revisions are then informed by additional data from experimental and observational sources. The synthesis of evidence and subsequent proposal of hypotheses that characterizes (alpha-) taxonomy, and which is largely descriptive, is thus intimately connected to the experimental investigation of these hypotheses, particularly as it relates to the study of higher-order relationships among clades (beta-taxonomy [e.g., biosystematics]) (Figure 112). As hypotheses are generated by (alpha-) taxonomy, these are made available to experimental biologists to help direct investigation toward unanswered questions and other ambiguities, with the results of these investigations then informing subsequent taxonomic revisions. To borrow language from the realm of physics, one may see fit to label (alpha-) taxonomy as ‘Theoretical Taxonomy’ and beta-taxonomy as ‘Experimental Taxonomy,’ with the relationship between them mirroring the relationship between ‘Theoretical Physics’ and ‘Experimental Physics.’ And, as in physics, neither strand can be successful without the support of the other.
Taxonomy as a Knowledge System

Taxonomy represents a knowledge system that incorporates the accumulated information and data from countless experiments and discoveries, made over hundreds of years. The information is made accessible through the role of taxonomy as a data management system, and this knowledge provides invaluable context across all of the subdisciplines of biology. New insights and information are incorporated into this knowledge system, and over time the system grows and develops to better reflect the synthesis of new information. Although many of the more recently-developed strands within the field of biology provide important data and information to contribute to our cumulative knowledge of biodiversity, this information must be expressed in a taxonomic framework. Thus, in the absence of effective taxonomy, our understanding of biodiversity would be limited to dissociated datapoints without any overarching epistemological basis.
4.4 **Taxonomy in the Academic System**

Despite its foundational position and critical importance across the subdisciplines of biology, the many challenges that taxonomy has faced within the academic system have in large part produced the Taxonomic Impediment that the field now faces. The term ‘academic system’ here refers to the interconnected network of universities and associated research facilities and research scientists, along with the journals and funding organizations that collectively support and disseminate the vast majority of biological research. This academic system has traditionally had an important role to play in supporting taxonomic research. Excluded from this definition of the academic system are museums and other research collections which, although they currently employ many taxonomists, are not involved in degree confirmation. Academic institutions, as they are defined here, are in contrast to non-governmental organizations (NGOs), consulting biologists, conservation organizations, restoration ecologists, biodiversity data repositories (such as the British Columbia Conservation Data Centre), invasive species councils, parks (federal, provincial, and municipal), and natural history groups who depend directly on the accurate application of the taxonomic concepts devised, published, and tested by those working within or trained by the academic system. It is oftentimes these non-academic end-users of taxonomic information who have been at the forefront of recognizing the effects of the Taxonomic Impediment, as they have had to struggle to apply a taxonomic system that has not been able to keep pace with new discoveries, or with new challenges to previous taxonomies.

**Taxonomy and the ‘Ivory Tower’**

The term ‘Ivory Tower’ has been used to describe universities and academics for nearly a century, although the use of the term in other contexts far predates that time (Shapin 2012). Among the many variations on the current definition of the idiom, the concept behind it is well-captured by the following definition, as taken from the Wiktionary (2018) page on the term:
Ivory Tower (n): “a sheltered, overly-academic existence or perspective, implying a disconnection or lack of awareness of reality or practical considerations.”

Although the term is typically used in a pejorative fashion, at times unfairly, the notion underlying it speaks to a culture within academia that enables, or even encourages, such a disconnect, if perhaps inadvertently. Although provocative, this term seems relevant to the relationship between the biological sciences (as represented within the academic system) and the non-academic end-users of taxonomic concepts and information. At a minimum, it seems fair to claim that taxonomy as a discipline has been largely abandoned as a priority by academia.

The end-users of taxonomy are many and varied, ranging from the amateur to the professional, and often operate in arenas where accurate taxonomy is either useful or necessary. Those whose interests intersect with taxonomy are from a wide variety of research streams within the life science subdisciplines of academia itself. For example, the products of taxonomic research inform the ecologist studying changes in soil microbial communities in the boreal forest, the population geneticist studying changing allele frequencies within a complex of interbreeding plant populations, and the phylogeneticist attempting to resolve the interrelationships amongst clades of fish. For these researchers, an understanding of the evolutionary units (= species) being investigated, and the boundaries between them, is crucial if one is to be confident in the results and conclusions of the study. However, as the role of taxonomy has been reinterpreted within academia to be an outgrowth of the study of evolutionary processes (as per Wheeler 2008a), prioritization has trended away from taxonomic elements of research to the point of its near-exclusion from most studies. This contributes to a further decline in the awareness within academic biology of the fundamental role of taxonomy (Gould 1989, Wilson 2004), even when it is demonstrably critical to an individual’s particular research field. This in turn further reduces the
ability of academia to respond effectively to the decline of taxonomy and its potential long-term ramifications.

A great number of individuals and organizations who are dependent on the application of accurate taxonomic concepts, and who are here recognized as critical end-users of taxonomic information, reside outside the academic system. This includes biodiversity data repositories such as the British Columbia Conservation Data Centre (https://www2.gov.bc.ca/gov/content/environment/plants-animals-ecosystems/conservation-data-centre) and the Alberta Native Plant Council (https://anpc.ab.ca/), who are instrumental in tracking and monitoring endangered species within their respective jurisdictions. It includes consulting and industry biologists who survey and document native species, including threatened and endangered species, and provide mitigation strategies to protect them during industrial development. It also includes the multitude of local and regional natural history organizations and amateur naturalists who have become increasingly important in documenting biodiversity through online ‘Citizen Science’ portals such as eBird (https://ebird.org/) and BugGuide (https://bugguide.net). With the exception of providing distributional datapoints, these end-users of taxonomic information are rarely involved in the production of the taxonomic systems they use. Rather, they rely on the products of academically-trained taxonomists to inform their application of species concepts. The marginalization of taxonomy within the academic system, however, has failed to train sufficient numbers of taxonomists, and has essentially left untended a discipline that is of central importance to both these non-academic end-users and many academic biologists alike. The link between the producers of taxonomy and those who rely most on the products has broken, much to the detriment of these conservationists, consulting biologists, biodiversity data repositories, and natural history organizations.
A Shifting Landscape

The metrics by which success is assessed within academia, and the resulting prioritization of research areas, present considerable challenges for the field of taxonomy within the academic environment. At the time of the Modern Evolutionary Synthesis, taxonomy was far more integrated into the biological sciences, both within the academic system and in associated public and private research institutions. This is evidenced by the frequency and magnitude of primary taxonomic publications (especially monographs) that were produced during this period, many of which remain highly relevant to the current understanding of the taxa to which they pertain. Within the genera included in my doctoral research, for example, critical taxonomic publications such as Cronquist (1943) (for *Symphyotrichum*) and Porsild (1950) (for *Antennaria*) were produced during this period, when taxonomy held court next to the emerging theoretical and technological advances of the time. But as the priorities within academia shifted towards experimental and molecular biology, the landscape of the biological sciences became increasingly inhospitable to baseline taxonomic research. Funding for taxonomic research and collections management, especially in universities, declined sharply, along with a pronounced decline in the number of academic positions for taxonomists. Over time, museums became the primary refugia for taxonomic activity.

Taxonomic research is very different from the experimental and molecular research that currently dominates university biology departments across North America. Taxonomy is a relatively slow and methodical science, requiring time for specimens to be consulted and analyzed, and the various available lines of evidence to be considered before proposing any taxonomic hypotheses. Much of the taxonomist’s insight into the organizational structure of the group being investigated is borne from extensive individual experience with the component species over years of careful study in the field and museum. It is a holistic discipline that seeks evidence from a wide diversity of different fields to inform decisions, and the strength of a taxonomic publication is
often dependent on the success of its application by the community of practicing taxonomists. It can thus be challenging to evaluate the impact of taxonomic publications over short time intervals, particularly by those who are unfamiliar with the methods and goals of the field.

The landscape within which taxonomy succeeds stands in contrast to the shorter-term impact that is favoured by the current academic system. University research today is often expected to be of high impact, as is reflected by journal ‘Impact Factors’ (McDade et al. 2011). Nonetheless, these immediate impacts have now become a key currency for hiring, promotion, and funding decisions. As taxonomic publications tend not to yield many citations outside of the (shrinking) field of taxonomy itself, and a high proportion of taxonomic citations fall outside of the two-year window for calculating Impact Factors (Krell 2002), this has resulted in the limited ability of taxonomic publications to compete under this metric. Taxonomic studies are often published in highly specialized and relatively poorly accessible journals and other publications (Krell 2002), reducing their availability to both taxonomists and non-taxonomists alike. Original species descriptions and associated nomenclature, which are among taxonomy’s most important contributions, have very modest ‘impact,’ in part because of the absence of a requisite for the citation of original species descriptions in almost all journals (Agnarrson & Kuntner 2007). This occurs despite the universal use of these published names and species concepts across all realms of the biological sciences, and therefore grossly undervalues their impact. As a result of these factors and others, there are few high-impact journals wherein taxonomy can find opportunities for publication, which then negatively affects access to funding and departmental support for taxonomic research. Taxonomy has subsequently become orphaned from much of the structural support that the academic system provides for scientific inquiry and training, as it is now evaluated by metrics that are largely incompatible with its goals and techniques. The landscape has shifted beneath taxonomy, and taxonomy has struggled to adapt.
The Next Generation

The declining representation of taxonomy in academic programs has undermined the training of the next generation of taxonomists, exacerbating the already challenging environment within which taxonomy now operates. Many students still enter the undergraduate system with a strong curiosity in taxonomy and natural history, which I have directly observed on many occasions during my time as an instructor of undergraduate biology students within the university setting. However, cultural and systemic biases against taxonomy within the biological sciences are not compatible with the interests of such students, and I have not yet observed an example of a taxonomically-inclined undergraduate student being able to translate that interest into graduate work or, ultimately, a career in a taxonomically-related field. Graduate training (especially at the doctoral level) has traditionally focused on training the next generation of academic researchers, so this shift in direction is fueled by shifts in hiring priorities for researchers. If the aim is to train academics, what good is it to train someone in a field with limited academic opportunities? But such a notion fails to recognize the opportunities for employment outside of academia in fields that depend on the application of good taxonomy to be effective. It therefore also fails to recognize the contributions that such students can make outside of the academic system using the skills and knowledge developed over the course of a doctoral degree that incorporates taxonomy. Without advocacy for these non-academic opportunities by academics, and absent the mentorship and training in taxonomy that would have historically been provided by the university system, undergraduate biology students with an interest in taxonomy are left both unaware of such opportunities and unprepared to pursue them.

Kehm (2006) summarized many of the challenges facing doctoral education in North America and Europe. Among six criticisms of doctoral programs, this study found that doctoral students were widely seen to be “educated and trained too narrowly” and “ill-informed about
opportunities outside of academia.” These criticisms thus relate directly to the myopia of the academic system that is relevant to the devaluing of training in taxonomy. Despite attempts to address this narrow focus (such as UBC’s Public Scholar’s Initiative [PSI], discussed below), the insular nature of academia remains an unresolved challenge within the university system that has likely contributed to the diversion of potential students away from taxonomy. This loss of university graduates with formal taxonomic training or even an appreciation of taxonomy, including at the undergraduate level, has subsequently impacted the downstream disciplines that rely on trained taxonomists to both develop and apply the knowledge systems that underpin our understanding of biodiversity. The result has been conservation organizations, consulting and industry biologists, and other groups that are increasingly populated by biologists who are less prepared to operate effectively in areas where biodiversity literacy is required. As these individuals and organizations typically operate at the interface between the academic pursuit of taxonomy and its application in the assessment and conservation of biodiversity, they are critical partners through which the results of taxonomic research can be applied to affect positive change. With biodiversity under siege globally, their contributions are more important now than they have ever been.

This loss of skilled practitioners has impacted biodiversity management across British Columbia. In my capacity as a consulting biologist who works extensively with species at risk, I have often observed poorly-equipped field biologists who have failed to document species at risk or, conversely, have mistakenly drawn upon limited conservation resources due to the misidentification of common species as rare species. In both types of circumstances, familiarity with taxonomy and species identification could have prevented such errors. Fewer and fewer biologists emerge from their academic programs with the capacity to effectively document or survey for biodiversity, particularly when more than a few taxa are included within the scope of the survey. In response to these challenges, the B.C. Conservation Data Centre recently revised
the provincial ‘best practices’ for plant and lichen surveys in British Columbia to address the declining taxonomic and biodiversity literacy among practicing biologists (Ministry of Environment and Climate Change Strategy 2018). This revised document, to which I contributed, aimed to re-prioritize the quality of the data collected (which is based on taxonomic skills of the biologists) over increasing the rates of data collection and dissemination, as well as standardize the required qualifications for biodiversity management in the province. Ultimately, meeting these new targets will require academia, which is tasked with training the next generation of biologists, to reconsider the importance of such skills and knowledge. Without such intervention, the collective understanding of the structure of biodiversity of both professional biologists and amateur naturalists is likely to continue to decline.

4.5 Technological Taxonomy

A trend has emerged among recent proposed solutions to the Taxonomic Impediment in which technological innovation is encouraged as a potential remedy (e.g., Godfray 2002, Hebert et al. 2003, Tautz et al. 2003, Blaxter 2004, Schindel & Miller 2005, Godfray 2007, Bik 2017), especially as it relates to species circumscription and identification. Of particular importance has been the potential for technology to increase the rate at which taxonomic data can be acquired and disseminated, as well as the potential for automating the process of identification and classification. Advances such as DNA barcoding (Hebert et al. 2003) have been interpreted as a remedy for the declining capacity of biologists to identify and document biodiversity. The suggestion that such an advancement can address the loss of taxonomic knowledge among practicing biologists was described above. Concurrent to this view, however, has been an alternative view (e.g., Seberg et al. 2003, Wheeler 2004, Ebach & Holdrege 2005a, Ebach & Holdrege 2005b, Will et al. 2005) that these approaches may actually harm the field by diverting resources, as well as by the lack of quality control and inherent limitations in their application.
These opposing points of view are representative of a conversation that taxonomists have been having within the academic arena for many decades – that of the circumscription of taxonomic research, its relationship to the other biological subdisciplines, and the importance of technology as a part of its methodology. As the academic system has generally been an important voice in promoting technological advancements as a response to the Taxonomic Impediment (e.g., Hebert et al. 2003), the application of such advancements to this problem requires at least some discussion when considering the relationship between taxonomy and academia.

Taxonomy is not an inherently technological enterprise itself, although it does benefit from the incorporation of information derived from diverse methods and tools. Unfortunately, the incorporation of technology to taxonomy has likely contributed to its marginalization within the current scientific environment. Godfray (2002, 2007), Hebert et al. (2003), Tautz et al. (2003), Blaxter (2004), Schindel & Miller (2005), Bik (2017), and others have argued that what is needed for taxonomy to regain its traditional prominence within biology is for the field to adapt to rapid-output, highly technological methodology that is common elsewhere in the biological sciences. Such an approach would focus on using recent advances such as enhanced cyber-infrastructure and DNA barcoding to increase the rate at which new species can be detected, reduce the time and expertise needed to survey for biodiversity, increase the availability of biodiversity data, and extend the means of identification beyond the specialist to anyone with access to the technology. This perspective restricts the role of taxonomy to that of a provider of data and does not acknowledge the depth and richness of scientific inquiry inherent within the field. It also shifts the focus of taxonomy away from the formulation of solid taxonomic hypotheses and towards the rapid production and dissemination of taxonomic information, irrespective of the quality of that information. It is no surprise, then, that such proposals have been met with a robust.
The response of taxonomists to many technological solutions proposed to address the Taxonomic Impediment centre around the following four critiques: (i) that technological applications are often unnecessary for good taxonomic research, and their introduction may be more problematic than helpful in many instances (e.g., Seberg et al. 2003); (ii) that such solutions (especially DNA barcoding) provide little to no biodiversity context or knowledge system within which to place these data (e.g., Ebach & Holdrege 2005a, 2005b); (iii) that resources are diverted towards technological fads that propose to replace traditional taxonomy (e.g., Ebach & Holdrege 2005a, Will et al. 2005); and (iv) that error rates in species identification stemming from the use of technological identification tools are greater than those of traditional taxonomists, and provide less recourse for correction (e.g., Lehmann et al. 2017). Speaking to this concern, Scotland et al. (2003) noted that “added technology, rather than the continued or enhanced investment in taxonomic expertise, does not necessarily result in increased taxonomic productivity.” This sentiment captures the concern of many taxonomists, myself included, over attempts to replace traditional taxonomy with high-output technological solutions. However, although many of these concerns have been expressed for decades, the implementation of technological solutions does not appear to have been sufficient to address them, and the demand for identification skills and accurate biodiversity knowledge has only increased during the intervening years.

There is no single technological advance that can supplant the contributions of traditional taxonomy, but many of these provide critical information to be incorporated into any taxonomic interpretation of biodiversity. In many instances, however, the most successful taxonomy rests upon careful interpretation of biological patterns (whether they be morphological, ecological, or biogeographical) by a practicing taxonomist, and is not contingent on the incorporation of a pre-specified tool or method. Molecular data are but one piece of evidence consulted during the formulation of taxonomic hypotheses, at least those at the species or infraspecies levels. For
example, estimates of phylogenetic relationships provide extraordinary insight into the relationships between and among species and higher clades, and are a critical piece of data for the taxonomist to use to understand the structure of biodiversity. However, phylogenetic hypotheses cannot entirely replace other evidence that a taxonomist must consider when proposing taxonomic hypotheses, and the DNA sequences required for phylogenetic reconstruction should be corroborated by these other pieces of evidence, and vice versa, to achieve a truly ‘integrative’ (Will et al. 2005) taxonomy. The reduction of species to mere short strands of DNA – devoid of much context – may be sufficient for some purposes, but does little for disciplines where the accumulated taxonomic knowledge of the species is important. Data is the backbone of scientific enterprise but it is of little utility unless it can be synthesized and placed into context, and so the prioritization of data over context ultimately results in the compromising of one of the most important contributions of taxonomy.

4.6 Addressing the Taxonomic Impediment

The challenges facing taxonomy have been widely discussed in both the popular and scientific literature since at least the observations of Hennig (1966), yet the Taxonomic Impediment continues to be of considerable concern to biologists into the early 21st century. As the landscape of scientific inquiry has shifted away from taxonomy, many potential solutions to combat the declining fortunes of the field have been put forward (e.g., Tautz et al. 2003, Blaxter 2004, Agnarsson & Kuntner 2007, Wheeler 2008a, Bik 2017). Although I have expressed some skepticism about the potential for technological tools such as DNA barcoding to ‘solve’ Taxonomic Impediment, there are ample additional opportunities to address the problem, and in my view, they are most likely to succeed if done in a collaborative fashion. Indeed, it appears as though the only realistic solutions will need to involve biologists within the university system and those in non-academic positions working in a mutually-beneficial relationship to help rebuild the
reputation and capacity of the field. This would help to ensure that taxonomy is able to fulfill its original mandate of describing and providing context to the world’s biodiversity.

**Taxonomy in the University**

Although the academic system has contributed to the Taxonomic Impediment, it should be seen as a critical partner in any attempt to reinvigorate the field. Specifically, universities can play an integral role in the promotion of taxonomic and natural history sciences, and must be a partner in the training of the next generation of biologists. As already stated, many students of biology enter the university system with an inherent interest in taxonomy, natural history, and other organismal streams, but are dissuaded (implicitly, or at times explicitly) away from these fields and toward the fields that are well-represented in the academic environment. The result has been a major ‘brain drain’ away from taxonomy. This contribution to the Taxonomic Impediment, however, could be relatively easily addressed through the simple inclusion of taxonomy back into the purview of undergraduate and graduate biology programs, both as an increased component of course material as well as a topic of discussion between students and faculty at the university level. Although courses that survey the diversity of various organismal groups are still offered at many major universities (though certainly not all), these are often focused more on exploring the evolutionary history of organisms within a particular clade without ever expressly discussing what taxonomy is, why it’s important, and how it is done. The result is that students may not be sufficiently exposed to taxonomic philosophy or the mechanics of how taxonomy operates, and are thus unprepared to appreciate its role within the biological sciences. An increase in the quality and quantity of interaction between biology students and museum collections, which are present on many campuses, could also contribute much to the students’ understanding and appreciation of biodiversity. These collections represent, in some cases, hundreds of years of detailed study and documentation of the world’s flora and fauna, and should be seen as an invaluable component of
the teaching of biology. A more ambitious, but likely more effective, means of improving the understanding of taxonomy within the university system would be the creation of courses that are specifically designed to address the philosophy and methodology of taxonomy and the natural history of organisms. If such a course was a requirement within certain streams of undergraduate biology, or if there were more opportunities for attending guest lectures from taxonomic researchers, students would graduate with a better understanding of the theory, practice, and importance of taxonomy and its relevance to the rest of the biological sciences. The combination of increased incorporation of taxonomic themes into undergraduate courses, increased exposure to museum collections, and, potentially, specifically designed courses on taxonomic theory would result in a student body that is more intimately familiar with the field.

In addition to increasing the exposure of students to taxonomic material in courses, university biology programs can raise awareness of the availability of taxonomically-related careers that exist outside of academia. It is not particularly desirable to promote taxonomy to students who will ultimately feel that there are no real career prospects within the field, so advocacy of non-academic career paths that employ taxonomic theory or biodiversity literacy should be included alongside the existing promotion of academic opportunities. If a new generation of taxonomists is to be inspired to pursue employment within the field, it would seem that capturing the interest of talented undergraduate students and presenting them with viable career options that would capitalize on that interest would be a role that the academic system would be uniquely well-positioned to provide. This was the environment that the University of British Columbia’s Public Scholar’s Initiative (PSI) sought to encourage when it was created in 2015 with a mandate to “assist PhD students as they rise to address complex challenges in new, collaborative, and engaged ways” (Public Scholar’s Initiative 2018). The landscape that the PSI program aims to address is one that extends far beyond the realms of taxonomy, and, rather, reflects a systemic
issue within academia – that of a university system that needs to shift away from using doctoral education solely to ‘regenerate the professoriate’ (Public Scholars Initiative 2018) and instead highlight the importance of supporting the ‘diverse forms of collaborative scholarship’ that promote careers outside of the academy. In other words, it is a recognition that those who inhabit the ‘Ivory Tower’ have become too narrow in their interpretation of what should and should not qualify as suitable doctoral education, and have left graduates unprepared to operate in the non-academic arenas within which a great many of them will ultimately find themselves. Given the preponderance of taxonomically-related positions outside academia, taxonomy has been particularly hard hit by this myopia. It was through this program that I was afforded the opportunity to work with the provincial Conservation Data Centre (CDC), which is the central repository for B.C.’s biodiversity data, to improve the efficacy of the process by which taxonomic changes are incorporated into their understanding of British Columbia’s flora. Thus, this program, and my experiences with it, is an example of the type of program that universities could provide to promote taxonomic research. Providing opportunities for the pursuit of research outside academia would allow those with taxonomic ambitions to explore these possibilities without being constrained by narrow definitions of scholarship.

A Partnership to Support Taxonomy

Although it may seem intuitive to suggest that increasing the funding and opportunities available for taxonomic research within the academic system would be the primary tool to address the Taxonomic Impediment, such a notion would fail to acknowledge the depth and complexity of the structural biases against the field that have led to the decline of taxonomy within academia over the past half-century. As taxonomy has fallen to the wayside in the biological sciences, resources that could have been made available for its support and promotion have been diverted to other streams, leaving taxonomists without the support needed to operate effectively. These
shifts in priority, which led to shifts in funding, which led to shifts in opportunities, have created a feedback loop that has disadvantaged taxonomy to such a degree that there seems little use in attempting to fit the ‘square peg’ of taxonomy back into the ‘round hole’ of an academic landscape that has shifted so markedly. Thus, for taxonomy to be allowed to flourish in a way that reflects its fundamental importance to the rest of biology, it may be best to consider partnerships between academia and taxonomists working outside of the academic system. Such partnerships would combine the accreditation, collections, resources, and students offered by the academic setting with the taxonomy-specific training, mentorship, and career opportunities available outside of academia. Furthermore, such partnerships could be beneficial in reintroducing taxonomic theory into the university setting, where so many researchers are either unfamiliar with the field or, at least, unprepared to provide training in it.

Perhaps one of the clearest examples of such an organization is the Botanical Research Institute of Texas (BRIT) ([www.brit.org](http://www.brit.org)), which has emerged as an influential force through its combined priorities of taxonomic and biodiversity research, collection and curation of specimens, education, and conservation. Incorporated as a non-profit organization in 1987, BRIT has emerged as a leading force in the production and dissemination of floristic and taxonomic research, and has operated entirely outside of the academic system. Their peer-reviewed Journal of the Botanical Institute of Texas (JBRIT) publishes high-quality taxonomic and floristic studies from around the world, providing a platform for the types of research that are excluded from ‘mainstream’ journals. Funding sources, in particular the Partnerships for Enhancing Expertise in Taxonomy (PEET) program of the U.S National Science Foundation (NSF), have emerged to provide funding to research programs irrespective of their association with a university, and are therefore a resource that is far less constrained by the associations of the applicants. In the United Kingdom, the House of Lords (2002) found that virtually all taxonomic research there is now done outside of the
universities, although only three institutions (Natural History Museum, Royal Botanic Gardens Edinburgh, and Royal Botanic Gardens Kew), along with interested parataxonomists, are now responsible for the vast majority of that research. Although presented as an unfortunate development in the report, this may ultimately be the direction in which taxonomy must turn if it is to regain any of the foothold that it has lost over the past 50-70 years. Both BRIT and this ‘British model’ should thus be recognized as part of a global rethink about the relationship between taxonomy and the academic system, and the successes or failures of these initiatives should be evaluated to best promote their effective partnership.

4.7 Conclusions

In 1972, Duane Isely at Iowa State University produced the dystopian essay ‘The Disappearance,’ which envisioned a world in which the entirety of taxonomic knowledge had been instantaneously purged from the biological sciences. It made clear the potentially severe ramifications of such an occurrence, and provided both an alarm bell about the status of taxonomy in the early 1970s, as well as a cautionary tale of the disaster that would unfold if such a drastic situation were to continue. In the year 2018, nearly a full half-century after his impassioned plea for the importance of the field, it has become clear that his concerns have largely gone unheeded. Taxonomists have become an ‘endangered species’ within biology, where they must now contend with a system that often regards their contributions as unimportant or, at times, unsophisticated. The academic system that was of such critical importance in the growth and development of taxonomy over the 250 years following Linnaeus’ Systema Naturae has moved away from one of the most foundational subdisciplines of biology in the pursuit of the next technological or analytical advance that has the potential to bring biology ‘into the 21st century.’ Taxonomists are often caricatured as stuffy and ‘old-fashioned,’ and the pursuit of the field considered ‘passé.’ And as such biases have come to dominate the research sphere, the important linguistic, contextual,
organizational, and epistemological contributions that taxonomy has gifted to the rest of biology have been systematically degraded. As taxonomists, we now find ourselves in something approaching the dystopia that Isely (1972) so clearly warned us about.

The future of taxonomy, then, appears as though it would require a rather radical intervention if its contributions are to be preserved as part of the landscape of the biological sciences. As it no longer appears feasible for taxonomy to continue to operate effectively when confined to its traditional academic home, taxonomists should continue to build upon developments such as BRIT and the ‘British Model’ that have begun the process of moving taxonomy outside of the university. As the landscape has shifted beneath the feet of the taxonomists over the past 50-70 years, it is clear that the systemic and cultural biases against the field within academia are now so deeply entrenched as to be unlikely to respond to efforts to manipulate them for the benefit of taxonomy. Academic biology should still be seen as having a crucial role to play in any future reinvigoration of taxonomy, such as through advocacy for the field to undergraduate and graduate students, encouraging an awareness of the career opportunities that exist for taxonomists outside of the academic setting, and partnering with non-academic taxonomists for the benefit of researchers in both environments. It must be the purview of the taxonomists themselves, however, to take the reins of taxonomy’s resurgence and take meaningful steps towards its. With the catastrophic environmental degradation that the human species will shortly come to endure, and as we launch into the post-biodiversity world that will come to define the latter parts of the 21st century and beyond, it seems that this may be the last, best chance for the taxonomists and other biodiversity scientists to capture the essence of what will soon be a lost world.
CHAPTER FIVE: CONCLUDING REMARKS

This thesis presents a detailed, region-specific revision of the taxonomy of two large genera in the family Asteraceae in British Columbia – Antennaria (the pussytoes) and Symphyotrichum (the American asters). Both genera have a long history of presenting challenges for taxonomists interested in untangling their relationships and species limits, and many aspects of their taxonomy have remained unresolved or ambiguous as a result. The well-defined regional focus of this study allowed for an opportunity to address shortcomings in the representation of British Columbian material in most of the earlier taxonomic studies, and to test existing taxonomic approaches against specimens that had not previously been considered during the formulation of those approaches. The methodology employed for this study was that of a traditional specimen-based alpha-taxonomic study that included a detailed morphological review of herbarium specimens, the repeated testing of specimens against existing taxonomic approaches, the development of novel taxonomic approaches when necessary, an assessment and update of morphological circumscriptions of the taxa, a comprehensive nomenclatural review of the accepted taxa (including reviews of type specimens of all nomenclatural synonyms), a revision of the geographic distributions of the taxa based on the specimens that were included in the study, and the development of new tools (dichotomous keys) to aid in the diagnosis of the taxa. The resulting regional monographs represent the most comprehensive and detailed assessment of the taxonomy of either genus in the Pacific Northwest to date, and provide enhanced tools to aid in the identification of provincial specimens by botanists.

The alpha-taxonomic methodology of this study was widely adopted by biologists throughout much of the 19th and early 20th centuries, and was instrumental in laying the foundations of our current understanding of biodiversity. This study demonstrates the extent to
which taxonomic uncertainties still remain – even in conspicuous species of temperate ecosystems (let alone poorly studied groups and in hyper-diverse tropical ecosystems) – as well as how baseline taxonomic research can used to both identify and address those uncertainties. The ability to compare competing taxonomic approaches, a major aspect of the study of *Antennaria* here, can be considered a powerful tool in alpha-taxonomy as it allows for the incorporation of diverse perspectives on the group’s taxonomy, as well as the identification of ambiguities that remain unaddressed by other approaches. The systematic review of the circumscriptions of the taxa in both genera provides a stronger foundation for studies that require the application of these taxonomic concepts, such as in ecology, conservation science, and phylogenetics, and to make the component taxa better defined, more easily diagnosable, and more reflective of the breadth of taxonomically-relevant information that is available.

As with any taxonomic treatment, the classification scheme and species circumscriptions provided here are best viewed as a series of hypotheses that are open to future review and revision by other taxonomists. The various hypotheses presented are intended to provide a framework that best represents the taxonomic elements present within British Columbia, but the incorporation of new insights into the morphological or molecular circumscriptions of the taxa, as well as differing perspectives on the interpretation of the existing circumscriptions, are all considered an important component of the ongoing taxonomic ‘dialogue.’ These monographic treatments should be viewed as a critical step in furthering this dialogue regarding the taxonomy of *Antennaria* and *Symphyotrichum* in British Columbia, as they provide a comprehensive synopsis of current knowledge as well as a launching pad for the investigation of uncertainties that are highlighted in the treatments. It is through this continual process of information synthesis (alpha-taxonomy) followed by experimental investigation (beta-taxonomy) that the foundations of our understanding of the structure of biodiversity are continually tested and strengthened. The interplay between these
two aspects of taxonomic inquiry thus represents one of the major strengths of taxonomy, and is one of the most important contributions that it gifts to the remaining biological sciences.

As important as it is, the science of alpha-taxonomy has faced something of a crisis over the past 50-70 years. This has occurred as the landscape of the biological sciences has shifted away from the support of baseline taxonomic research and towards the pursuit of new and exciting advances in molecular research, genomics, bioinformatics, and advanced analytical and statistical techniques, yet the importance of the descriptive science of alpha-taxonomy has not declined in concert. Indeed, as ecosystems around the world face unprecedented pressure from human overpopulation and climate change, the comprehensive accounting of the world’s biodiversity that is the goal of taxonomy has perhaps never been more important. Added to this concern is the enormous, and ever-increasing, volume of data and information being produced in ecology and evolution that require a solid taxonomic system within which to reside if they are to effectively contribute to the cumulative knowledge of the planet’s biodiversity. Studies such as that presented here can contribute markedly by providing this taxonomic system for the biological sciences and ensuring that biological data and information remain anchored within a framework that represents our best current understanding of the world’s biodiversity.


Greene, E.L. (1908) Novitates boreali-Americanae. II. Repertorium Specierum Novarum Regni Vegetabilis 5: 241-244.


Nuttall, T. (1841) Descriptions of new species and genera of plants in the natural order of the Compositae, collected in a tour across the continent to the Pacific, a residence in Oregon, and a visit to the Sandwich Islands and upper California, during the years 1834 and 1835. *Transactions of the American Philosophical Society, new series* 7: 283-453.


APPENDIX A:

MAP OF BIOGEOCLIMATIC ZONES OF BRITISH COLUMBIA

From Meidinger & Pojar (1991)
APPENDIX B:

ANTENNARIA SPECIMENS REVIEWED DURING THIS STUDY

Antennaria anaphaloides

CANADA. Alberta: Waterton Lakes National Park, interpretive building hill, 4400 ft., 49°06' N, 113°52' W, 11 June 1969, Nagy & Blais 997 (UBC!); MacLeod District, north of Waterton Lakes National Park, 5 miles sw of Twin Butte, 01 August 1950, Dore & Breitung 12230 & 12231 (UBC!); Waterton Lakes National Park, park entrance, 4200 ft., 49°07' N, 113°51' W, 15 June 1969, Blais 1019 (UBC!). British Columbia: Kootenay-Boundary Regional District, Kelowna area, Beaverdell, 01 August 1972, Carson s.n. (UBC!); Sorenson Lake, 16 June 1955, Marrion 55042 (UBC!); Larkin, 24 May 1906, E. Wilson 857 (UBC!); Armstrong, 29 May 1905, E. Wilson 496 (UBC!); Larkin, 24 May 1906, E. Wilson s.n. (UBC!); North Okanagan Regional District, Vernon, Coldstream Ranch, 21 May 1917, Warren 74-7 (UBC!); Cariboo Road, 15 July 1906, E. Wilson s.n. (UBC!); Armstrong, 29 May 1905, E. Wilson 496 (UBC!); Flagstone, Mt. Cavend, 6300 ft., August 1944, Peterson s.n. (UBC!); northwest side of Stump Lake, 25 miles northeast of Merritt on highway to Kamloops, 3000 ft., 27 May 1956, Calder, Parmalee, & R.L. Taylor 16745 (UBC!); Canal Flats, 12 July 1947, Eastham s.n. (UBC!); upper Kootenay River valley, on gravel bed of river about 10 miles from Canal Flats, 14 July 1947, Eastham s.n. (UBC!); Monte Creek, 12 June 1940, Eastham s.n. (UBC!); Cariboo, Flying U Ranch, 22 June 1944, Eastham s.n. (UBC!); Elko, 26 June 1948, Eastham s.n. (UBC!); Penticton area, 15 July 1937, Stonor s.n. (UBC!); Osoyoos area, southwest of town, west of Inkaneep Vineyard, 675 m, 49°02' N, 119°27' W, Goward 90-742 (UBC!); Kamloops, Tod Mountain, 09 July 1963; Taylor & Szczawinski 771 (UBC!); Guichon Valley, 3500 ft., 06 June 1958, Brayshaw 48144 (UBC!); Thompson-Nicola Regional District, near Kamloops, Tranquille Range, 3500 ft., June 1936, Brink s.n. (UBC!); Kamloops, Scotty Valley, 2800 ft., 18 May 1961, Arlidge & Tusko 26 (UBC!); Chilcotin District, Chilko River, 02 June 1914, Newcombe s.n. (UBC!); Grand Forks, at junction of Kettle and Granby Rivers, 21 May 1978, Rose 78216 (UBC!); Chilcotin, plot no. 88, 3650 ft., 51°43' N, 122°55' W, July 1968, Beil 68-7-10 (UBC!); Mount Turnbull-Fording River, site 6, 7040 ft., 28 July 1971, Morrison s.n. (UBC!); Penticton, Horne Lake, 28 May 1937, Stonor s.n. (UBC!); upper Hat Creek, Cairn Peak, 7600 ft, 29 August 1949, Brink 49-511 (UBC!); upper Hat Creek, Harmona Lake, 07 July 1950, Brink s.n. (UBC!); Kootenay District, Wolf Creek drainage, 20 June 1975, Ng s.n. (UBC!); Skuo-ach [sic], 1915, Davidson s.n. (UBC!); near Ashcroft, Three Sisters Valley, 16 May 1915, Davidson s.n. (UBC!); Chilcotin, north end of Callanan Lake, 1015 m, 18 June 1975, Jenkins 10091 (UBC!); Thompson-Nicola Regional District, Botanie Valley, Forest Lookout Trail, 4800 ft., 24 May 1958, Beamish, Vrugtman, & Sperrings 8225 (UBC!); East Kootenay Regional District, Kimberley, 07 June 1957, Oseko 40 (UBC!); north end of Okanagan Lake, Adventure Bay Mountain, 50°14' N, 119°24' W, 29 May 1977, Wright s.n. (UBC!); mountainside above confluence of Chilcotin and Fraser Rivers, 1158 m, 19 June 1972, Jones 201 (UBC!); Thompson-Nicola Regional District, Hat Creek, 3800 ft., 50°46' N, 121°36' W, 06 August 1972, Lemon 3-047 (UBC!); Moore Peak, 2164 m, 50°42' N, 121°44' W, 09 July 1978, Johns 556 (UBC!); Elko, 15 June 1948, Eastham s.n. (UBC!); ca. 5 miles from Oliver on Cawston Road, 2700 ft., 17 May 1969; Beamish & Vrugtman 60447 (UBC!); Similkameen, 1894, Allison s.n. (UBC!); Pavilion Lake, 900 m, 50°50' N, 121°40' W, Taylor & Lewis 166 (UBC!); Merritt, 02 June 1949, T.M.C. Taylor 2067 (UBC!); 6 miles south of Merritt, Mount Nicola, 3400 ft., 50°05' N, 120°38' W, Krajina 650623169 (UBC!); 1 to 5 miles north of Princeton, 2300 ft., 49°25' N, 120°33' W, 24 June 1965, Krajina 65062402 (UBC!); south of Princeton, 3100 ft., 49°20' N, 120°35' W, 24 June 1965, Krajina 65062481 (UBC!); East Kootenay Regional District, about 4
miles east of Cranbrook, 28 May 1947, *McCalla 9520 (UBC!); North Okanagan Regional District, near Vernon, Kalamalka Lake Park, 50°12’ N, 119°15’ W, 23 May 1984, Ceska & Ogilvie s.n. (UBC!); Thompson Uplands, Salmo River crest, 50°21.95’ N, 119°52.5 W, 19 July 2005, Björk 11551 (UBC!); Princeton, Whipsaw Creek, 3000 ft., 03 July 1952, Brayshaw & Ogilvie s.n. (UBC!); Thompson-Okanagan, Princeton, Willyview Farm Road, north of the city, 49°27’30” N, 120°30’30” W, 16 May 1976, Ceska & Ceska s.n. (UBC!); Anarchist Mountain, 500 m southwest of summit, 7 km due east of Osoyoos, 1420 m, 49°02’05” N, 119°20’20” W, 13 June 2000, Lomer 3798 (UBC!); Princeton, Whipsaw Creek, 3000 ft., 03 July 1952, Brayshaw & Ogilvie s.n. (UBC!); Thompson-Nicola Regional District, road to Cornwall Hills Provincial Park, 1285 m, 50.6593° N, 121.47998° W, 09 July 2011, Mosquin 2011.0002 (UBC!); Okanagan-Similkameen Regional District, Red Creek Forest Service Road, 898 m, 49.56385° N, 120.4097° W, 14 July 2011, Manton, McGrath, & Shiller 689 (UBC!); Kelowna, 13 May 1915, Holman s.n. (UBC!); Canal Flats, 1500 ft., 50°09’ N, 115°45’ W, 21 May 1977, Rose 77-524A (UBC!); Similkameen District, Hedley, 518 m, 49.23° N, 119.06° W, 11 July 1981, Rose 81258 (UBC!); Anarchist Mountain, 1.7 km due north of Highway 3, 1265 m, 49°01’20” N, 119°20’25” W, 09 July 2013, Lomer 8437 (UBC!); west of Osoyoos, Kruger Mountain Road, 49.061495° N, 119.557614° W, June 2004, J. Fenneman 48 (UBC!).

**Antennaria anaphaloides x lanata**

**CANADA.** British Columbia: Mount Kobau, outcrop near summit area, 1800 m, 49°07’ N, 119°38’ W, 05 June 1990, Goward 90-877; Kootenay, Limestone Ridge, saddle north of the main peak and slopes on southeast side, 49°27’ N, 114°43’ W, 30 June 1983, Ceska & Ogilvie 15769 (UBC!).

**Antennaria borealis**

Beamish, Krause, & Luitjens 681821 (UBC!); Vancouver Island, Forbidden Plateau, 1936, Fowle s.n. (UBC!); Stikine Regional District, Atlin Provincial Park, Teresa Island, Birch Mountain, southeast slope north of knoll, 5100 ft., 59°25′ N, 133°45′ W, 09 July 1974, Buttrick 484 (UBC!); Hudson Bay Mountain, above Smithers, 6000 ft., 54°48′ N, 127°20′ W, 09 August 1973, Krajina s.n. (UBC!); Bonney Lake vicinity, upper valley of the Kwinageese River, which flows west into the Nass River, 56° N, 128° W, 11 July 1973, Krajina, Anna, McMinn, & Klinka s.n. (UBC!); forest lookout below Nanika Mountain and above Morice Lake, 5500 ft., 54° N, 127° W, August 1973, Krajina s.n. (UBC!); Two Sisters Mountain, 10 miles north of Barkerville, 6500 ft., 53° N, 121° W, 13 August 1974, Pojar & Krajina s.n. (UBC!); Vancouver Island, Strathcona Park, Burman Lake, 5000-6000 ft., 49°36′ N, 125°36′ W, 10 August 1968, Krajna, Bednar, & Kojima 68081011 (UBC!); Coast District, Bulkley Range, on ridge between Legate Creek (flows into Skeena River) and Red Canyon Creek (flows into Zymoetz River), 5000 ft., 54° N, 128° W, Krajina s.n. (UBC!); northwest of Tumber Ridge, near summit of Bull Moose Mountain, ca. 2000 m, 55°10′ N, 121°30′ W, 28 July 1991, Straley & Nicholls 6895 (UBC!); Smithers, Hudson Bay Mountain, above upper ski lift, ca. 2000 m, 54°45′ N, 127°20′ W, 25 July 1990, Straley & Nicholls 6155 (UBC!); on saddle between Mount Pierce and Mcfarlane, 5800 ft., 49°94′ N, 121°37′ W, 08 September 1974, Pinder-Moss & Pojar 1039a (UBC!); Cassiar District, south Trout Line Creek, 1200 m, 59°15′ N, 129°45′ W, 19 June 1956, C.E.Jones s.n. (UBC!); northeastern British Columbia, Saxon Mountain mine site, 1830 m, 54°20′ N, 120°03′ W, 13 August 1976, C.E.Jones s.n. (UBC!); northeastern British Columbia, Quintette Mountain mine site, 1740 m, 54°55′ N, 120°55′ W, 25 July 1976, C.E.Jones s.n. (UBC!); northeastern British Columbia, Quintette Mountain mine site, 1640 m, 54°55′ N, 120°55′ W, 26 July 1976, C.E.Jones s.n. (UBC!); northeastern British Columbia, Saxon Mountain mine site, 1995 m, 54°20′ N, 120°03′ W, 12 August 1976, C.E.Jones s.n. (UBC!); Peace River District, Saxon Mountain mine site, 1680 m, 54°55′ N, 120°55′ W, 26 July 1976, C.E.Jones s.n. (UBC!); northeastern British Columbia, Saxon Mountain mine site, 1540 m, 58° N, 128° W, 06 July 1981, Donovan & Sienes 179 (UBC!); Cassiar District, north-northeast shore of lake at foot of Glacial Mountain, 1540 m, 58° N, 128° W, 16 August 1981, Donovan & Sienes 1005 (UBC!); Blusky Mountain, 2256 m, 50°36′ N, 123°02′ W, Revel s.n. (UBC!); northeastern British Columbia, Saxon Mountain mine site, 1540 m, 58° N, 129° W, 15-25 August 1972, R.L.Taylor, Beil, Marchant, & Oliver 5610 (UBC!); Blusky Mountain, 2325 m, 50°36′ N, 123°02′ W, Revel s.n. (UBC!); Cassiar District, north of Hudson Bay Mountain, 3000 ft., 59°30′ N, 136°30′ W, 08 July 1956, T.M.C.Taylor, Szczawinski, & Bell 1138 (UBC!); Cassiar District, southwest of Hudson Bay Mountain, 3000 ft., 59°30′ N, 136°30′ W, 28 June 1915, Skilton 003 (UBC!); Ilgachuz Mountains, Festuca Creek, 5350-5500 ft., 52°45′ N, 125°15′ W, 15-25 August 1972, R.L.Taylor, Beil, Marchant, & Oliver 6026 (UBC!); Ilgachuz Mountains, Festuca Creek, 5350-5500 ft., 52°45′ N, 125°15′ W, 15-25 August 1972, R.L.Taylor, Beil, Marchant, & Oliver 5610 (UBC!); Cassiar District, Williston Lake, 1554-1676 m, 55°26′ N, 123°02′ W, Revel s.n. (UBC!); Cassiar District, 5000 ft., 12 August 1912, Davidson s.n. (UBC!); Coast area, Garibaldi, Black Tusk, 6500 ft., 12 August 1912, Davidson s.n. (UBC!); Panorama Ridge, 06 August 1913, Baggs s.n. (UBC!); Garibaldi Park, Little Diamond Head, Cheekye Ridge, 49°49′ N, 123°01′ W, 20 September 1964, Krajina & Brooke 64092025 (UBC!); Haines Road, mile 60, 1200 m, 59°30′ N, 136°30′ W, no date provided, T.M.C.Taylor & Szczawinski 1223 (UBC!); Garibaldi Park, Warren Glacier foreland, 5000 ft., 16 August 1966, Fraser s.n. (UBC!); Peace River District, Saxon Mountain mine site, 1540 m, 58° N, 129° W, 16 August 1981, Donovan & Sienes 1005 (UBC!); Blusky Mountain, 2256 m, 50°36′ N, 123°02′ W, Revel s.n. (UBC!); Cassiar District, south of Haines Road, 1200 m, 59°30′ N, 136°30′ W, 08 July 1956, T.M.C.Taylor, Szczawinski, & Bell 472 (UBC!); Garibaldi Park, Senitinel Glacier foreland, 5000 ft., 12 August 1966, Fraser s.n. (UBC!); Garibaldi Park, Panorama Ridge, 06 August 1913, Baggs s.n. (UBC!); Garibaldi Park, Panorama Ridge, 06 August 1913, Baggs s.n. (UBC!); Garibaldi Park, Little Diamond Head, Cheekye Ridge, 49°49′ N, 123°01′ W, 20 September 1964, Krajina & Brooke 64092025 (UBC!); Haines Road, mile 60, 1200 m, 59°30′ N, 136°30′ W, no date provided, T.M.C.Taylor & Szczawinski 1223 (UBC!); on northeast slope of Tundra Mountain, 6700-7200 ft., 52°45′ N, 125°15′ W, 15-25 August 1972, R.L.Taylor, Beil, Marchant, & Oliver 6026 (UBC!); Ilgachuz Mountains, Festuca Creek, 5350-5500 ft., 52°45′ N, 125°15′ W, 15-25 August 1972, R.L.Taylor, Beil, Marchant, & Oliver 5610 (UBC!); Smithers, foot of Hudson Bay Mountain, 3000 ft., 31 July 1960, Szczawinski s.n. (UBC!); head of basin north of Pipe Organ Peak, 6800 ft., 52°45′ N, 125°15′ W, 15-25 August 1972, R.L.Taylor, Beil, Marchant, & Oliver 5840 (UBC!); Haines Triangle, Samuel Glacier Trail, 1050 m, 59°41′16.254″ N, 136°37′05.466″ W, 28 June 1915, Skilton 003-9 (UBC!); Telkwa area, Winfield Creek Road, 1487 m, 54°39′54.474″ N, 127°23′44.454″ W, 23 July 2015, Skilton 003-15 (UBC!); along the trail between Gladys Lake


Antennaria dimorpha

CANADA. British Columbia: Vaseux Lake, 1600 ft., 27 May 1972, Carson s.n. (UBC!); 1 mile northeast of Kaledon, Okanagan Game Farm, 1800 ft., 49°26’ N, 119°39’ W, 19 May 1977, Wikeem & Gale s.n. (UBC!); Westwick Lake, 24 May 1955, Marrion 55015 (UBC!); Thompson-Nicola Regional District, near Kamloops, Tranquille Range, 07 April 1919, Tisdale s.n. (UBC!); Thompson-Nicola Regional District, Tranquille, 14 April 1943, Fodor 5 (UBC!); Summerland, 04 April 1940, Wooliams s.n. (UBC!); Princeton, May 1920, Copley s.n. (UBC!); Kamloops, 17 April 1914, Wattie s.n. (UBC!); Pentiction, 07 June 1938, Eastham s.n. (UBC!); Pentiction, 03 May 1939, Eastham s.n. (UBC!); Pentiction, Apex Road, 2800 ft., 01 May 1968, Beamish, Luitjens, & Krause 680056 (UBC!); Mount Douglas, near Victoria, Vancouver Island, 200 m, 48°28’ N, 123°18’ W, 18 May 1950, Krajina & Spilsbury s.n. (UBC!); south of Elko, 0.7 miles southwest of Flagstone, 16 May 1958, R.L. Taylor & Ferguson 527 (UBC!); northwest of Kelowna, on west side of Okanagan Lake, 3 miles north of Westside Road, 366-579 m, 49°56’ N, 119°31’ W, 07 May 1973, R.L. Taylor 6224 (UBC!); Pavilion Lake, 50°50’ N, 121°40’ W, 12 June 1952, T.M.C. Taylor & Lewis 153 (UBC!); Oliver, 2 miles east, 1100 ft., 26 May 1952, Brayshaw & Krajina s.n. (UBC!); Vaseux Lake, 2 km east of lake near Irrigation Creek, 600 m, 49°17’ N, 119°31’ W, 07 May 1991, Goward 91-103 (UBC!); Thompson-Nicola Regional District, Nicola Valley, Quilchena Creek, 2500 ft, 19 May 1941, Brink s.n. (UBC!); Knutsford, 2 miles northwest, 20 May 1952, Krajina s.n. (UBC!); Vernon, 29 April 1913, Brittain 8978 (UBC!); Chilcotin, plot no. 71, 3250 ft., 51°42’ N, 121°28’ W, 20 May 1968, Beil 68-5-20 (UBC!); near Kamloops, Tranquille Range, 488 m, April-May 1937, Tisdale & Brink 40-787 (UBC!); Thompson-Nicola Regional District, Botanie Road near Lytton, 1800 ft., 50°22’ N, 121°34’ W, 18 May 1974, Pinder-Moss & Pojar 653 (UBC!); White Lake Road out of Oliver, 2500 ft., 30 April 1968, Beamish, Luitjens, & Krause 680038 (UBC!); Hope-Princeton (Hwy), ca. 5 miles east of Whipsaw, 2800 ft., 01 May 1960, Beamish & Vrugtman 60020 (UBC!); 5 miles south of Merritt, 3450 ft., 02 May 1960, Beamish & Vrugtman 60260 (UBC!); Pentiction, East Bench, 12 April 1937, Stonor s.n. (UBC!); 30 km south of Ashcroft, west off Highway 1, 100 m east of Venables Valeay Road, near Oregon Jack Hill, 50°34’ N, 121°19’ W, 17 April 1999, Bandringa 67 (UBC!); west of Goose Lake, 3300 ft., 50°43’ N, 121°36’ W, Scagel 77-0-60 (UBC!); Okanagan-Similkameen Regional District, near Summerland, Trout Creek Ecological Reserve, 49°33’ N, 119°42’ W, Larmour & Ng s.n. (UBC!).

UNITED STATES. Oregon: Redmond, 21 May 1947, T.M.C. Taylor s.n. (UBC!).


Antennaria flagellaris

CANADA. British Columbia: Whipsaw Creek, ca. 590 m northeast of Stevenson Lake, west side of Highway 3, 880 m, 49°24’49.6’’ N, 120°34’0.5’’ W, 25 June 2002, Douglas, Lomer, & Penny 13613 (UBC!); Princeton, 5.3 km due south-southwest of, 1.1 km south of Wrights Road, ca. 100 m west of Highway 3, 600 m northeast of Stevenson Lake, 2850 ft., 49°24’50” N, 120°34’00’’ W, 11 October 1996, Lomer 96-178 (UBC!); Cascade Lee, 18 km south-southwest of Princeton, Friday Mountain, northeast slope, 500 m due north of junction of Highway 3 and Friday Creek Forest Service Road, 1343 m, 49°18’16” N, 120°35’04” W, 11 July 2009, Lomer 7025 (UBC!); Princeton, 8 km south-southwest of, 1.5 km west of Highway 3, 250 m south of Tracey Lake, 900 m, 49°23’15.4’’ N, 120°35’02.4’’ W, 17 June 2003, Lomer 4878 (UBC!); Princeton, 5 km south-southwest of, 250 m east of Stevenson Lake, 920 m, 49°24’40” N, 120°34’10’’ W, 18 June 2003, Lomer 4890 (UBC!); southwest of Princeton, 907 m, 10U 676301 5473561 (NAD83), 07 June 2011, McIntosh, Sadler, Dyer, Safford, & Robinson 2011_44_1 (UBC!); southwest of Princeton, 908 m, 10U 676304 5473566 (NAD83), 07 June 2011, McIntosh, Sadler, Dyer, Safford, & Robinson 2011_44_2 (UBC!); southwest of Princeton, 904 m, 10U 676283 5473546 (NAD83), 07 June 2011, McIntosh, Sadler, Dyer, Safford, & Robinson 2011_46_1 (UBC!); southwest of Princeton, 908 m, 10U 676295 5473565 (NAD83), 07 June 2011, McIntosh, Sadler, Dyer, Safford, & Robinson 2011_46_2 (UBC!); southwest of Princeton, 905 m, 10U 676282 5473547 (NAD83), 29 September 2009, McIntosh 2009_114 (UBC!).

UNITED STATES. Washington: Yakima Co., 20 miles north of Yakima, Clemen Mt., 4000 ft., 27 May 1940, J.W.Thompson 14580 (UBC!).

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Antennaria howellii subsp. howellii

Chilco Range, 51° N, 123° W, 25 June 1972, Beil 137 (UBC!); Falls Lake exit along Coquihalla Highway, west of Merritt, 1179 m, 10U 640817 5497177 (NAD83), 16 July 2011, McIntosh & Hanna 2011-177 (UBC!); Cordillera Natural Region, Kootenay River Valley, north side of Highway 3, 2 km northwest of Jaffray, 49°23’01” N, 115°18’45” W, 10 July 2013, MacDonald 130710b8 (UBC!); south of Nakusp, McDonald Creek Provincial Park, 440 m, 50.17° N, 117.79° W, 13 May 2014, Fenneman 2014-31 (UBC!); Vancouver Island, Comox Lake, 200 m, 49°38’ N, 125°06’ W, 25 April 1998, Fenneman V40 (UBC!).

Ontario: Bruce Co., Lion’s Head, 20 June 1935, Krotkov 9938 (UBC!); Algoma District, right bank of Michipicoten River, T. 30, R. 23, 47°56’ N, 84°54’ W, 07 July 1971, Garton et al. 14325 (UBC!); Petawawa, Forestry Research Station, 500 ft., 18 May 1962, Brayshaw & Merillees 6244 (UBC!); Thunder Bay District, Sibley Provincial Park, Thunder Cape, Breast of Sleeping Giant, 48°21’ N, 88°54’ W, 04 June 1972, Garton 14895 (UBC!).

Saskatchewan: Cypress Hills Park, 4100 ft., 01 July 1947, Breitung 4196 (UBC!).

UNITED STATES. Oregon: Jefferson and Deschutes Cos., northwest of Sisters, Black Butte, 3300 ft., 01 July 1944, Johnson 451 (UBC!).

Antennaria howellii subsp. neodioica

CANADA. Alberta: 1/4 mile south of Fort Saskatchewan, 04 June 1944, Turner 4020 (UBC!).

British Columbia: 6 miles south of Creston, 15 May 1953, Calder & Savile 7799 (UBC!); Creston, east slope of Goat Mountain, 12 June 1947, Eastham s.n. (UBC!); east of Slocan Lake, 0.5 miles north of Kane Creek from New Denver-Kaslo Road, 2500-2900 ft, 12 July 1975, Beamish 750175 (UBC!); Fraser-Cheam Regional District, Elk Mountain, north of Chilliwack River, ca. 4500 ft., 49°07’ N, 121°48’ W, 15 July 1973, T.M.Taylor s.n. (UBC!); Thompson-Nicola Regional District, Botanie Valley, 22 August 1949, Krajina s.n. (UBC!); East Kootenay Regional District, few miles south of Moyie, south of Cranbrook, 08 June 1944, McCalla 8167 (UBC!); Beaver Lake, 25 August 1935, Clemens s.n. (UBC!); Yale, 17 August 1950, Krajina s.n. (UBC!); Silver King Basin, 5000 ft., 06 August 1955, Ashford 23 (UBC!); alpine valley northwest of Mount Sampson on Lillooet Road, 5800 ft., 50°31’ N, 123°10’ W, 26 August 1973, Pinder-Moss & Pojar 600 (UBC!);

Fraser-Cheam Regional District, Mount Thurston, north of Chilliwack River, 5500 ft., 20 July 1974, Pinder-Moss 828 (UBC!); Edgewood, Lower Arrow Lake, 25 June 1951, Ridewood 51 (UBC!); Galena, 21 June 1962, T.M.C.Taylor & Szczawinski 485 (UBC!); Chilcotin, Meldrum Lake, 16 July 1950, Cottle 183 (UBC!); Fraser-Cheam Regional District, Skagit River floodplain within 5 miles of Ross Lake, ca. 1000 ft., 12 June 1974, Beamish, Pinder-Moss, Selby, Pojar, & Perkins 74031 (UBC!); Monashee Road, east of Wauchope Creek, 3800 ft., 08 June 1957, Beamish & Gilmartin 7172 (UBC!); Kootenay Bay, May 1963, Borysowich s.n. (UBC!); Columbia River basin, Trout Lake, August 1904, E.Wilson 448 (UBC!); between Redstone and Chelquoit Lake, 26 July 1944, Eastham s.n. (UBC!); Vancouver Island, Capital Regional District, Sooke, 05 May 1938, Eastham s.n. (UBC!); Thompson-Nicola Regional District, Lytton, 175-500 m, 50°14’ N, 121°34’ W, 18 August 1949, Krajina 1194 (UBC!); Wells Gray Park, near Dawson and Helmeck Falls, Murtle River, 51°57’ N, 120°07’ W, 02 June 1977, Goward 81-109 (UBC!); Central Okanagan Regional District, east of Kelowna, 20 June 1951, Brink s.n. (UBC!); Vancouver Island, Green Mountain, 1200 m, 49°03’ N, 124°19’ W, 23 July 1950, Krajina, Spilsbury, & Szczawinski s.n. (UBC!); Skagit River valley, 2800 ft., 49°13’ N, 121°00’ W, 24 June 1965, Krajina 650624118 (UBC!); Whistler-Squamish Road, Highway 99, 4.2 km north of Brandwyine Falls Provincial Park lake, 400 m, 50°04’ N, 123°05’ W, 15 June 2001, Kennedy & Ganders 5426 (UBC!); Alex Fraser Research Forest, approx. 5 km south of 150 Mile House, Knife Creek, 980 m, 52°02’ N, 121°50’ W, 13 June 1996, Hanel 9 (UBC!); Fraser Valley, Deroche, 2 km east of, north side of Highway 7, 400 m east of Brooks Road, ca. 100 m north of Nicomen Slough, 27 m, 49°11’55” N,

Manitoba: Riverton, 24 June 1956, Krivda R-71 (UBC!).

New Brunswick: York Co., Keswick, above Fredericton, 07 June 1945, Dore & Gorham 45-78 (UBC!).

Ontario: Norfolk Co., Turkey Point, 24 May 1937, Brown 5471 (UBC!); Bowesville Road, 21 May 1935, Forward s.n. (UBC!); Algoma District, Batchawana River, 47°00' N, 84°45' W, 28 August 1935, T.M.C. Taylor et al. 1566 (UBC!); Algoma District, Mamainse Point, 47°00' N, 84°45' W, 02 September 1935, T.M.C. Taylor et al. 1564 (UBC!); Kingston, 09 June 1902, Fowler s.n. (UBC!); Thunder Bay District, Strange Twp., Round Lake, 25 July 1950, Garton & Campbell 1212 (UBC!); Algoma District, Hwy. 17, 49.4 miles north of Michipicoten River, T. 32B, R. 27, 24 July 1971, 48°26' N, 85°07' W, Garton et al. 17659 (UBC!); Thunder Bay District, Mattawin Road, mile 40, just south of Nelson Lake, 48°26' N, 90°32' W, 04 June 1981, Garton et al. 19971 (UBC!); Thunder Bay District, bridge over Weikwabinonaw River, just below Buda Lake access road, 48°22' N, 90°37' W, 18 June 1981, Garton 20077 (UBC!).


Washington: Pierce Co., along Route 5H, northeast of Roy, 20 May 1954, Dress 4211 (UBC!).

Antennaria lanata


British Columbia: Mount Baldy, “Chua Chua” (=Chu Chua), 7000 ft., August 1936, Tisdale s.n. (UBC!); Okanagan, Armstrong, 29 May 1905, E. Wilson 496 (UBC!); Mount Cheam, 7500 ft., no collection date, Henry s.n. (UBC!); south side of Quinsinco Lake in the Ashnola Range, 6850 ft., 49°04' N, 120°12' W, 02 August 1956, Calder, Parmelee, & R.L. Taylor 19628 (UBC!); Blackwell Peak north of ranger station on Hope-Princeton highway, 6000 ft., 15 July 1953, Calder & Savile 10507 (UBC!); southwest of Penticton, Mount Apex, 18 July 1953, Calder & Savile 10707 (UBC!).

Revelstoke National Park, along road to Heather Lodge, 5400 ft., 22 July
Antennarua luzuloides subsp. luzuloides

**CANADA.** British Columbia: Cascade, 2 miles west along highway to Grand Forks, 29 May 1962, **Calder & Spicer 32979** (UBC!); Creston, east slope of Goat Mountain, 12 June 1947, **Eastham s.n.** (UBC!); Kamloops, Tod Mountain, 1800 m, 09 July 1963, **T.M.C.Taylor & Szczawinski 795** (UBC!); Rossland, Little Sheep Creek trail, 05 July 1942, **Eastham s.n.** (UBC!); Nelson, Silver King Mine, 6000 ft., 07 July 1940, **Eastham s.n.** (UBC!); Grand Forks, ca. 6 km north of, 2.15 km due northeast of junction of Granby River and Sand Creek Forest Service Road, 790 m, 49°05’09” N, 118°25’30” W, 20 June 2002, **Lomer 4404** (UBC!); Purcell Mountains, Mount Kitchener, southwest slope, 2 km north of the town of Kitchener, 990 m, 49°10’26” N, 116°19’49” W, 16 June 2007, **Lomer 6242** (UBC!); Anarchist Mountain, 1.6 km southwest of summit, 7 km due east of Osoyoos, 1350 m, 49°01’39” N, 119°21’00” W, 13 June 2000, **Lomer 3790** (UBC!); Grand Forks, 5.5 km due north of, 3 km east on Sand Creek Forest Service Road from Granby River Road junction, 810 m, 49°05’13” N, 118°25’31” W, 16 May 2001, **Lomer 3998** (UBC!); Kootenay-Boundary Regional District, Gilpin Grasslands Provincial Park, 517 m, 49.01118° N, 118.31162° W, 13 June 2012, **Manton & van der Linde 1446** (UBC!); Anarchist Mountain, 2 km north of Anarchist Mountain Rest Stop on Highway 3, 1400 m, 49°01’50” N, 119°20’45” W, 09 July 2013, **Lomer 8436** (UBC!); south of Christina Lake, upper Santa Rosa Road, 1540 m, 49°04’ N, 118.09’ W, 30 June 2016, **J.Fenneman 2016-271** (UBC!); Flathead Valley, La Coulette Ridge, south end slope, 1 km up drainage creek from Sage Creek Road, 1890 m, 49°09’26.7” N, 114°16’56.4” W, 06 July 2015, **Lomer, Penny, Roemer, & Batten 9526** (UBC!); Flathead Valley, base of Sunkist Mountain, 50 m north of creek, 1450 m, 49°08’32.1” N, 114°20’38.5” W, 10 July 2015, **Lomer, Roemer, & Batten 9601** (UBC!); Selkirk Mountains, 80 m north of Maryland Creek Forest Service Road, 1.8 km northwest of Priest River Falls, 30 km due west of Creston, 1405 m, 49°01’41.8” N, 116°56’46.2” W, 20 August 2015, **Lomer 9674** (UBC!). **UNITED STATES.** Montana: Iwingston, 24 June 1947, **Brink s.n.** (UBC!); Gallatin Co., Wallrock Basin, ca. 12 miles northwest of Wilsall, 08 July 1921, **Suksdorf 356** (UBC!); Lincoln Co., northern Salish Mountains, ca. 3 km east of Sheep Mountain, just south of Grimm Creek, 48°33’ N, 115°04’ W, 12 June 1995, **Spribille 3529** (UBC!); Missoula, 21 June 1939, **McCalla 5687** (UBC!). Utah: Cache Co., Logan, Logan Canyon, 23 May 1939, **Muenscher, Muenscher, &**
Antennaria media

site, 1600 m, 54°55' N, 120°55' W, 28 July 1976, C.E.Jones s.n. (UBC!); Quintette Mountain Mine site, 1840 m, 54°55' N, 120°55' W, 04 August 1976, C.E. Jones s.n. (UBC!); Quintette Mountain Mine site, 1750 m, 54°55' N, 120°55' W, 03 August 1976, C.E. Jones s.n. (UBC!); Vancouver Island, Roger’s Ridge, 4000-5500 ft., 10 August 1969, Kojima s.n. (UBC!); Cariboo District, Marble Mountains, Lime Ridge North, 600 m northwest of summit of northernmost ridge, 2125 m, 51°08'30”’ N, 121°52'07”’ W, 05 August 2013, Lomer 8490 (UBC!); Germansen Landing, 55 miles northwest, Kennco Mining Camp, 5500-6000 ft., 18 August 1949, Eastham s.n. (UBC!); Taseko Lake area, Tchaikazan Valley, 6850 ft., 10 August 1969, Beamish & Pinder-Moss 690050 (UBC!); Cariboo District, near Kluane Lake, Sheep Mountain, 6000-6300 ft., 61°00’ N, 138°34’ W, 18 July 1970, Krajina & Hoefs s.n. (UBC!); Mount McIntyre, road near summit, 1558 m, 60°37’19.998”’ N, 135°09’00.438”’ W, 19 June 2015, Skilton 003-5 (UBC!); Mount McIntyre, near end of road near summit, 1570 m, 60°37’10.248”’ N, 135°08’39.22”’ W, 19 June 2015, Skilton 003-4 (UBC!).

UNITED STATES. Colorado: no location specified, summer 1891, Penard s.n. (UBC!); no location specified, summer 1891, Penard s.n. (UBC!).

Antennaria microphylla

CANADA. Alberta: Henry House, 3348 ft., 17 July 1949, Krajina 28 (UBC!); Jasper Park lodge, 3470 ft., 17 July 1949, Krajina 63 (UBC!); Calgary, above Sunnyside, 13 July 1945, McCalla 8780 (UBC!); North Clover Bar, Glenbrook Farm, 30 June 1948, McCalla 10089 (UBC!); 1/4 mile southwest of Fort Saskatchewan, 05 July 1943, Turner 3529 (UBC!); Calgary, corner of 10th St. NW and 13th Ave. NW, 08 July 1943, McCalla 7594a (UBC!); 2 miles northeast of Fort Saskatchewan, 14 July 1943, Turner 3558 (UBC!); Calgary, valley north of King George School, 20 July 1945, McCalla 8825 (UBC!); valley north of King George School, 22 July 1945, McCalla 8824 (UBC!); 1 mile west of Fort Saskatchewan, 10 June 1943, Turner 3396 (UBC!); fair grounds, Fort Saskatchewan, 07 June 1943, Turner 3376 (UBC!); 2 miles northeast of Fort Saskatchewan, 18 June 1943, Turner 3370 (UBC!); 1/4 mile southwest of Fort Saskatchewan, 26 June 1943, Turner 3466 (UBC!); 1/4 mile south of Fort Saskatchewan, 30 June 1943, Turner 3493 (UBC!); cemetery 1/4 mile south of Fort Saskatchewan, 15 June 1943, Turner 3418 (UBC!); fair grounds, Fort Saskatchewan, 25 June 1943, Turner 3443 (UBC!); 2 miles northeast of Fort Saskatchewan, 06 June 1943, Turner 3370 (UBC!); Calgary, above 10th St. NW, on east side south of 11th Ave., 05 July 1952, McCalla 11703 & 11704 (UBC!); Jasper National Park, 3000 ft., 53° N, 118° W, 15 August 1953, collector illegible (UBC!); Calgary, 08 July (year unknown), McCalla 6595A (UBC!); Calgary, above Sunnyside, 04 July 1953, McCalla 11896 (UBC!); Calgary, above
Antennaria monocephala subsp. angustata


Antennaria monocephala subsp. monocephala

Antennaria neglecta

Antennaria parvifolia


**Antennaria pulcherrima subsp. pulcherrima**

Crum 7554 (UBC!); Kluane Lake, Slim River slough, 03 July 1943, **Brink 7-43-7-2 (UBC!)**; Kluane Lake, vicinity of Burwash, 61°22’ N, 138°59’ W, 06 September 1948, **Raup, Drury, & Raup 14003 (UBC!)**.

**Antennaria pulvinata**


**Antennaria pulvinata**

7600 ft., 12 August 1968, Eady s.n. (UBC!); Okanagan Highland, Big White Mountain, 7600 ft.,
01 August 1968, Eady s.n. (UBC!). UNITED STATES. Montana: Carbon Co., 23 miles southwest
of Red Lodge, northeast of Quad Creek, 9500 ft., 07 August 1955, Cronquist 8092 (UBC!).
Washington: Twin Lakes, 6000 ft., 01 July 1946, Rattenbury s.n. (UBC!).

Antennaria racemosa

CANADA. Alberta: Banff National Park, Larch Valley, 7100 ft., 51°20' N, 116°10' W, September
1962, Vrugtman 620115 (UBC!); Banff National Park, Moraine Lake, 09 July 1936, McCalla 4542
(UBC!); Waterton Lakes National Park, upper Twin Lake, 6500 ft., 49°08' N, 114°09' W, 16 July
1969, Blais 1936 (UBC!); Waterton Lakes National Park, above Red Rock Canyon, 04 June 1952,
McCalla 11675 (UBC!); Waterton Lakes National Park, below Carthew Ridge, 7800 ft., 07 August
1951, T.M.C. Taylor 8647 (UBC!); Banff National Park, Consolation Valley, 6200 ft.,
02 August 1962, Beamish & Vrugtman 620160 (UBC!); Banff National Park, Larch Valley, 7200
ft., 51°20’ N, 116°10’ W, 31 July 1962, Vrugtman 620112 (UBC!); Banff National Park,
Consolation Valley, 6200 ft., 02 August 1962, Beamish & Vrugtman 620161 (UBC!); Banff
(UBC!). British Columbia: Mount Robson Provincial Park, 200 m south of Yellowhead Lake, near
Mount Fitzwilliam trailhead, 1138 m, 52°51'22.9" N, 118°32'31.2'' W, 18 June 2015, Lomer
9345 (UBC!); Strathcona Provincial Park, Marble Meadows, 1280 m, 49°40' N, 125°35' W, 25
July 2000, J.Fenneman 1090 (UBC!); Tranquille Range, near Kamloops, 3500 ft., July 1937, Tisdale 40-804 (UBC!); Swansee
Mountain, west of Armstrong, 12 May 1904, E.Wilson 72 (UBC!); Thompson-Nicola Regional
District, Botanie Valley, July 1917, Ferry s.n. (UBC!); East Kootenay Regional District,
Kimberley, Mark Creek, 02 May 1967, Fodor 460 (UBC!); East Kootenay Regional District,
Kimberley, 30 May 1943, Fodor 79 (UBC!); Cassiar, Pelly Creek, Moose or Goat Mountain,
56°55’ N, 126°15’ W, Copley 98 (UBC!); Kootenay Lake, Crawford Bay, 24 May 1947, Murray
s.n. (UBC!); Lillooet area, Sunday Summit, 2 miles west on Highway 3, 07 June 1969, Maze,
Muhlenbacher, & Schofield 555 (UBC!); about 8 miles southwest of Okanagan Falls, 4700 ft., 01
July 1953, Calder & Savile 9942 (UBC!); 15 miles west-northwest of Ootsa Lake village along
Ootsa Lake, 24 July 1954, Calder, Savile & Ferguson 13484 (UBC!); East Kootenay Regional
District, just north of Moyie along east side of Moyie Lake, Cranbrook-Creston Highway, 3100
ft., 16 June 1953, Calder & Savile 9238 (UBC!); along trail to summit of Mount McLean at
Lillooet, 5000-6000 ft., Penticton, Mount Apex, 4000 ft., 14 July 1939, Eastham s.n. (UBC!);
Penticton, Mount Brent, 4000-6000 ft., Eastham s.n. (UBC!); Fairmont Hot Springs, along
Fairmont Creek, 17 July 1947, Eastham s.n. (UBC!); Rossland-Grand Forks Highway, 21 July
1939, Eastham s.n. (UBC!); Fort St. James, Mount Pope, 23 July 1945, Eastham s.n. (UBC!); west
end of Ootsa Lake, 07 July 1944, Eastham s.n. (UBC!); Nelson, Athabasca Mill, 4000 ft., 19 June
1938, Eastham s.n. (UBC!); Rossland-Cascade Highway, 5000 ft., 25 June 1938, Eastham s.n. (UBC!);
Nelson, Venus mine, 4000 ft., 25 June 1940, Eastham s.n. (UBC!); East Kootenay Regional
District, Kimberley, St. Mary’s Lake, 30 June 1947, Eastham s.n. (UBC!); between Salmo and Fruitvale, 07 June 1947, Eastham s.n. (UBC!); Monashee Pass, 4000 ft., 23 June 1937,
McTaggart-Cowan 10237 (UBC!); Ilgachuz Mountains, north of Anahim Lake, Carnick
Mountain, below Carnlick Lake, 6200-6500 ft., 52°45’ N, 125°15’ W, 15 August 1972,
R.L. Taylor, Beil, Marchant, & Oliver 54328 (UBC!); Ilgachuz Mountains, Festuca Pass, 6200-
6400 ft., 52°45’ N, 125°15’ W, 15 August 1972, R.L. Taylor, Beil, Marchant, & Oliver 5686
(UBC!); Ilgachuz Mountains, north of Anahim Lake, Festuca Pass, 5800 ft., 52°45’ N, 125°15’
W, 15 August 1972, R.L.Taylor, Beil, Marchant, & Oliver 5901 (UBC!); along highway by
Kootenay Lake, Alkali Creek, 3 miles north of Sanca, 03 June 1958, R.L.Taylor & Ferguson 1124
(UBC!); Tetana Lake, 55° N, 126° W, 01 July 1938, Fletcher 11119 (UBC!); East Kootenay
Regional District, ca. 5 km west of Crowsnest Pass, near Erickson Creek, 1350 m, 49°37’ N,
114°44’ W, 03 August 1981, Goward 81-1716B (UBC!); Merritt, Spius Creek valley, 975 m,
50.09° N, 120.35° W, 21 May 1952, Brayshaw B1 (UBC!); below Bolean Lake, 3700 ft., 50°30’
N, 119°30’ W, 25 July 1952, Krajina 739 (UBC!); Kamloops, Falkland, 2400 ft., 01 June 1961,
Arlidge & Tusko 142 (UBC!); Kootenay Lake, Gray Creek, 12 May 1947, McCalla 9429 (UBC!);
Kootenay, Crawford Bay, 30 May 1918, Kidman s.n (UBC!); Pemberton, Tenquille Lake, Copper
Mountain, August 1946, W.Taylor s.n. (UBC!); Fort St. James, ca. 12 km northwest, next to
Darbour Hg Group west, 12 June 1982, Kruckeberg 225 (UBC!); Pope Mountain, 54°30’ N,
124°20’ W, 11 July 1981, Kruckeberg 128 (UBC!); Takla Bralorne mine site, 55°34’ N, 125°23
W, 24 July 1981, Kruckeberg 172 (UBC!); Windy Joe Mountain, 5987 ft., 49°03’ N, 120°46’ W,
24 July 1973, Chuang 761 (UBC!); mountain north of Gibson Pass, 5500 ft., 49°04’ N, 120°53.5’
W, 04 July 1973, Chuang 405 (UBC!); McLeese Lake, 3000 ft., 52°27’ N, 122°10’ W, no date
provided, Beil 67 (UBC!); on south-facing slope above Relay Creek cabin, 1865 m, 51°11’ N,
122°58’ W, 23 August 1977, Selby s.n.. (UBC!); Central Okanagan Regional District, Kelowna
District, 13 June 1951, Lok s.n. (UBC!); Manning Park, Lightning Lake, 09 August 1945, Hardy
19070 (UBC!); Manning Park, F.B. cabin, 24 July 1945, Hardy 19076 (UBC!); Tenquille Lake
area, Crown Mountain, 6000-6500 ft., no date provided, Beamish, Tisdale, & Vrugtman 60946
(UBC!); Kitimat-Stikine Regional District, Cassiar District, upper Kwinageese River valley,
Banney Lake vicinity, 56° N, 128° W, 11 July 1973, Krajina, McMinn, Annas, & Klinka s.n.
(UBC!); Kamloops, Falkland, 2400 ft., 29 May 1961, Arlidge & Tusko s.n. (UBC!); south of
Tumbler Ridge, Herman Mountain, 1600 m, 54°55’ N, 120°55’ W, 27 July 1991, Straley &
Nicholls 6834 (UBC!); Central Kootenay Regional District, southeast of New Denver, Idaho Peak,
49°58’ N, 117°10’ W, 20 July 1958, Krajina s.n. (UBC!); Adventure Bay Mountain, 50°14’ N,
119°24 W, 29 May 1977, Wright s.n. (UBC!); Kootenay Lake, Deanshaven, 08 May 1916, Holman
25 (UBC!); lower Skookum Valley, Skoonka Creek, 12 June 1914, Davidson s.n. (UBC!); upper
Botanie Valley, Botanie Lake, 14 June 1914, Davidson s.n. (UBC!); upper Skookum Valley,
Skoonka Creek, 15 June 1914, Davidson s.n. (UBC!); east side of Slocan Lake, just below lookout
on Mount Idaho, 6800-7000 ft., 11 July 1975, Beamish, Luitjens, & Carey 750109 (UBC!);
Jackson Basin on Stenson Creek, 7000 ft., 49°59’ N, 117°10’ W, 19 July 1972, Pinder-Moss 42
(UBC!); near Penticton, Goodchap Mountain, 7500 ft., 27 July 1950, Martin s.n. (UBC!); East
Kootenay Regional District, Kimberley, 07 June 1966, Fodor 371 (UBC!); Nelson, Silver King
Mine, 6000 ft., 30 June 1940, Eastham s.n. (UBC!); Hazelton, crags east of Skeena River, Rocher
de Boule District, 5000 ft., July-August 1952, Harrison s.n. (UBC!); Manning Park, 10 July 1951,
Allen 75 (UBC!); Flathead Road, mile 14, 4900 ft., 15 July 1957, Bell & Davidson 50 (UBC!);
Flathead Road, mile 19, 6800 ft., 16 July 1957, Bell & Davidson 163 (UBC!); Monashee
Mountains, 19 km west of Needles on Highway 6, 20 June 1960, Ridewood 41 (UBC!); Penticton,
May-July 1937, Stonor s.n. (UBC!); Manning Park, Three Brothers area, Valley View Mountain,
4200-5800 ft., 10 July 1951, Allen, Burroughs, & Howe 75 (UBC!); Kamloops, Tod Mountain,
1800 m, 09 July 1963, T.M.C.Taylor & Szczawinski 779 (UBC!); Gerrard, 700 m, 22 June 1962,
T.M.C.Taylor & Szczawinski 536 (UBC!); Noaxe Lake, 04 August 1957, Brink s.n. (UBC!); Noaxe
Lake, 05 August 1957, Brink s.n. (UBC!); Vancouver Island, Cameron Lake, 07 June 1917, Carter
170a (UBC!); Hope area, May 1956, Sheppe s.n. (UBC!); East Kootenay Regional District,
Kimberley, 19 May 1957, Oseko 37 (UBC!); East Kootenay Regional District, Kimberley, Mark
Creek, 20 July 1967, Fodor 460 (UBC!); Manning Park, Windy Joe Mountain, 5000 ft., 49°02’ N,
120°45’ W, 01 July 1956, Vrugtman 258 (UBC!); Sunday Creek, 18 miles west of Princeton, 24

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July 1964, Lowther s.n. (UBC!); Manning Park, Hope-Princeton Highway, north of mile 126, 3400 ft., 01 July 1957, Beamish, Stone, & Vrugtman 7636 (UBC!); Manning Park, Black Wall, 6400 ft., 14 July 1960, Beamish & Vrugtman 60852 (UBC!); Kishinena Valley, 4000-5000 ft., 22 July 1970, Beamish, Bell, & Anderson 770 (UBC!); northwest of Lillooet, Yalakom River basin, Elizabeth Mine Road, 6100 ft., 28 July 1961, Beamish & Vrugtman 610629 (UBC!); Monashee Road, east of Wauchope Creek, 3800 ft., 06 June 1957, Beamish & Gilmartin 7171 (UBC!); Monashee Road, about 5 miles east of Kettle River, 07 June 1957, Beamish & Gilmartin 7238 (UBC!); 8 miles west of Princeton, 11 June 1959, Holm 298a (UBC!); North Okanagan Regional District, Silver Star Mountain (Aberdeen Mountain), 12 miles northeast of Vernon, 4000 ft., 50°22' N, 119°04' W, 07 June 1949, Ross s.n. (UBC!); Lardeau, 2000 ft., 25 August 1959, Bell s.n. (UBC!); middle of ridge above confluence of Chilcotin and Fraser Rivers, 1372 m, 51° N, 122° W, 19 June 1972, Jones 197 (UBC!); Manning Park, trail to Windy Joe Mountain, June 1965, Williams s.n. (UBC!); central Okanagan Regional District, Klo Creek, south of McCulloch Road bridge, ca. 7 miles southeast of Kelowna, 1850-2400 ft., 49°49' N, 119°22' W, 10 May 1973, R.L. Taylor 6272 (UBC!); 4 miles south of Tacheeda Lake, 2000-2500 ft., 22 August 1968, Revel s.n. (UBC!); Otter Valley, 05 June 1900, Hill s.n. (UBC!); Wells, 1800 m, 04 August 1949, T.M.C. Taylor 9087 (UBC!); Wall Lake, 6000 ft., 49° N, 114° W, 08 August 1951, T.M.C. Taylor 8926 (UBC!); Thompson-Nicola Regional District, Botanie Valley, 22 August 1949, Krajina s.n. (UBC!); Lower Battle Mountain, 914 m, 51°58' N, 119°52' W, 25 June 1977, Goward & Fafard 81-124 (UBC!); Spaa Hills, Bolean Lake-Arthur Lake, 4750 ft., 07 August 1951, Krajina & Arlidge 7025 (UBC!); Princeton-Manning Park, Friday Summit, 4100 ft., 49°18' N, 120°34' W, 24 June 1965, Krajina 65062487 (UBC!); beside Isintok Lake, about 30 km west of Summerland, 1000 m, 14 May 1987, Whiting 9 (UBC!); Allsion Lake Provincial Park, 49° N, 120° W, 07 June 1969, Schofield, Maze, & Mehlbacher s.n. (UBC!); Allsion Lake Provincial Park, 49°41’ N, 120°36’ W, 08 June 1969, Schofield, Maze, & Mehlbacher 969 (UBC!); Grizzly Bear Lake, north end of Shulaps Range, 6500 ft., 05 August 1957, Bird 3409 (UBC!); Gray Creek, 27 June 1944, McCalla 8305 (UBC!); Gray Creek, woods above Kootenay Lake, 12 May 1947, McCalla s.n. (UBC!); Gray Creek, 17 May 1947, McCalla 9458 (UBC!); Gray Creek, 23 May 1947, McCalla 9500 (UBC!); East Kootenay Regional District, Hosmer, Wheeler Creek mine site, 1067 m, 49°40' N, 114°58' W, 07 July 1976, McLachlin s.n. (UBC!); Peace River Regional District, Quintette Mountain mine site, 1690 m, 54°55’ N, 120°55’ W, 25 July 1976, C.E. Jones s.n. (UBC!); Peace River Regional District, Saxon Mountain mine site, 1945 m, 54°20’ N, 120°03’ W, 12 August 1976, C.E. Jones s.n. (UBC!); southeastern British Columbia, Hosmer-Wheeler mine site, 49°40’ N, 114°58’ W, 02 June 1976, McLachlin s.n. (UBC!); northeastern British Columbia, Quintette mine site, 1740 m, 54°55’ N, 120°55’ W, 28 July 1976, C.E. Jones s.n. (UBC!); Tulameen area, Tulameen Ultramafic Complex, Grasshopper Mountain, 1434 m, 49°32’32.5'' N, 120°53’53” W, 08 July 2002, Lewis & Ingram 25 (UBC!); Tulameen area, Tulameen Ultramafic Complex, Grasshopper Mountain, 1457 m, 49°32’57.7” N, 120°52’51.7” W, 20 June 2002, Lewis & Ingram 25 (UBC!); 40 km southeast of Cranbrook, near Lake Koocanusa, Twin Lakes, 1040 m, 49°13 N, 115°21’ W, 13 July 1996, Hanel 104 (UBC!); Vancouver Island, Mount Cokely, north foothills, 49°14’00” N, 124°35’30” W, 09 August 1976, Ceska & Ceska s.n. (UBC!); Rocky Mountain foothills, ca. 6.5 km west of Alberta border, lower peak ca. 2.2 km northeast of Ptarmigan Mountain, 1970 m, 54°24’15” N, 120°06’10” W, 22 June 2001, Lomer & Petherbridge 4072 (UBC!); Okanagan-Similkameen Regional District, Chute Lake Road, near Naramata, 1192 m, 49.69150° N, 119.53574° W, 21 May 2011, Manton & McGrath 377 (UBC!); Kootenay-Boundary Regional District, Gilpin Grasslands Provincial Park, 517 m, 49.01118° N, 118.31162° W, 13 June 2012, Manton & van der Linde 1447 (UBC!); Okanagan-Similkameen Regional

**Antennaria rosea**

16 August 1965, Fraser s.n. (UBC!); Stikine Regional District, Cassiar, 28 June 1956, Scrimger 11 (UBC!); Stikine Regional District, Cassiar, 28 June 1956, Scrimger 2 (UBC!); Terrace, 22 May 1940, King s.n. (UBC!); junction of Peace and Pouce Coupe Road, 20 June 1943, Crickmay s.n. (UBC!); near Penticon, Goodchap Mountain, 27 June 1957, Martin s.n. (UBC!); North Okanagan Regional District, Silver Star Mountain (Aberdeen Mountain), 12 miles northeast of Vernon, 5000 ft., 50°22 N, 119°04' W, 15 July 1951, Ross & Jones s.n. (UBC!); Sorenson Lake, 16 June 1955, Marrion s.n. (UBC!); North Thompson, Vavenby, 22 July 1914, Heywood s.n. (UBC!); near Lumby, 1000 ft., 12 July 1932, Hume 673 (UBC!); Atlin Lake area, 2000-3000 ft., July-August 1913, Wilkinson s.n. (UBC!); Thompson-Nicola Regional District, Tranquille Range, near Kamloops, 3800 ft., June 1935, Tisdale s.n. (UBC!); Cariboo Road, Fraser, 14 July 1906, E.Wilson 704 (UBC!); Cariboo Regional District, 150 Mile House, 16 July 1906, E.Wilson 719 (UBC!);

East Kootenay Regional District, Kimberley, 17 July 1967, Fodor 462 (UBC!); Wasa, 05 June 1956, Fodor 373 (UBC!); East Kootenay Regional District, Cranbrook, 29 May 1967, Fodor s.n. (UBC!); Hope-Princeton Highway, mile 46, Manning Park, 4000 ft., 49°02’ N 120°34’ W, 30 June 1956, Vrugtman 289 (UBC!); Manning Park, F.B. cabin, 22 July 1945, Hardy 19088 (UBC!); Lac la Hache, 30 June 1942, Hardy s.n. (UBC!); Ingenika River, 671 m, 56°46’ N, 126°25’ W, 18 June 1914, Copley 128 (UBC!); Cassiar, Ingenika River, 2200 ft., 56°46’ N, 126°25’ W, 18 June 1914, Copley s.n. (UBC!); Allen Grove, west slope, 2750 ft., 28 June 1919, Copley 11 (UBC!); Lundbom Commons, south, 3250 ft., 08 June 1918, Copley 6-14 (UBC!); mouth of Ingenika River, 2150-2350 ft., 56°45’ N, 125°10’ W, 09 June 1914, Copley 92 (UBC!); Kootenay River, Crawford Bay, 1947, Murray s.n. (UBC!); Garibaldi District, Panorama Ridge, 6000 ft., 03 August 1903, Sampson s.n. (UBC!); Rocky Mountains, vicinity of Summit Pass, 58°31’ N, 124°34’ W, 13 July 1943, Raup & Correll 10500 (UBC!); Rocky Mountains, vicinity of Summit Pass, 58°31’ N, 124°34’ W, 16 July 1943, Raup & Correll 10609 (UBC!); mountains near Hedley, 6000 ft., Buckland s.n. (UBC!); Barkerville, Cunningham Creek, 4200 ft., 21 July 1954, Grant s.n. (UBC!); Dease Lake, 1912, Teit 21 (UBC!); Spences Bridge, upper Skoonka Valley, 13 June 1914, Wattie s.n. (UBC!); Kamloops, Penanton Lake, 24 May 1914, Wattie s.n. (UBC!); Skagway Quad, lower Llewellyn Glacier, camp 26 and Marble Mountain nunataks, 1500-1800 m, 59°10’ N, 134°20’ W, 16 August 1978, Anderson 3632 (UBC!); Okanagan Landing, July 1911, Henry s.n. (UBC!); Sunday Creek, 18 miles west of Princeton, 24 July 1964, Lowther s.n. (UBC!); Stikine Regional District, Spatsizi Provincial Park, Gladys Lake, 4200 ft., 57°35’ N, 128°47’ W, 18 July 1975, Pajar s.n. (UBC!); Garibaldi, Sentinel Ridge (Sentinel Glacier), 02 August 1914, Davidson s.n. (UBC!); Coast area, Garibaldi, Corrie Ridge, 6000 ft., 03 August 1913, Davidson s.n. (UBC!); Tenquille Valley (Tenquille Lake), 30 July 1931, Davidson s.n. (UBC!); upper Skoonka Valley (Skoonka Creek), 13 June 1914, Davidson s.n. (UBC!); Jackson Basin on Stenson Creek, 7000 ft., 49°59’ N, 117°10’ W, 19 July 1972, Pinder-Moss 47 (UBC!); East Kootenay Regional District, old Cranbrook-Moyrie Road, 06 August 1943, Eastham s.n. (UBC!); Grand Forks-Rossland Highway, near summit, 5400 ft., 21 July 1939, Eastham s.n. (UBC!); Kootenay Lake, Procter, 07 July 1937, Eastham s.n. (UBC!); Creston, East Camp Lister, 11 June 1947, Eastham s.n. (UBC!); Cariboo, Flying U Ranch, 22 June 1944, Eastham s.n. (UBC!); East Kootenay Regional District, Kimberley, St. Mary’s Lake, 30 June 1947, Eastham s.n. (UBC!); between Salmo and Fruitvale, 07 June 1947, Eastham s.n. (UBC!); Garibaldi Park, Garibaldi Lake, 4816 ft., 28 July 1951, Cottle 361 (UBC!); Oliver area, Sawmill Lake, 03 August 1961, Milroy s.n. (UBC!); Powell River, 05 July 1957, Roller s.n. (UBC!); Babine Lake, 05 July 1959, Roller s.n. (UBC!); Taseko Lake, Tchaikazan Valley, 5800 ft., 51°10’ N, 123°43’ W, 05 August 1969, Beamish & Pinder-Moss 690138 (UBC!); Hope-Princeton (Highway), north of mile 126, 1097 m, 01 July 1957, Beamish, Stone, & Vrugtman 7606 (UBC!); Hope-Princeton (Highway), north of mile 126, Manning Park, 4800 ft., 01 July 1957, Beamish, Stone, & Vrugtman 7617 (UBC!); Manning Park, Lightning Lake,
southwest end, 4000 ft., 13 July 1960, Beamish & Vrugtman 60784 (UBC!); Wells area, Bowron Lake Road, 4300 ft., 23 July 1958, Beamish, Vrugtman, & Campbell 8503 (UBC!); Lillooet District, above Relay Creek, 4500 ft., 25 July 1965, Beamish 650037 (UBC!); overlooking Good Hope Lake on Stewart-Watson Lake Road, 2500 ft., 59° N, 126° W, 04 July 1973, Beamish, Pajar, & Wade 730190 (UBC!); 33 miles north of Cassiar cutoff on Stewart-Watson Lake Road, 2500 ft., 59° N, 129° W, 07 July 1973, Beamish, Pajar, & Wade 730299 (UBC!); Monashee Road, 15 miles west of Edgewood, 2450 ft., June 1957, Beamish & Gilmartin 7225 (UBC!); Lumby area, Shuswap Falls, 1600 ft., 13 June 1957, Beamish & Gilmartin 7429 (UBC!); Monashee Road, east of Wauchope Creek, 3850 ft., June 1957, Beamish & Gilmartin 7166 (UBC!); Kamloops, Dewdrop Flats, 01 June 1949, Sieburth s.n. (UBC!); Manning Park, 10 July 1951, Allen 73 (UBC!); Flathead Road, mile 14, 4900 ft., 15 July 1957, Bell & Davidson 5 1 (UBC!); Flathead Road, mile 14, 4900 ft., 15 July 1957, Bell & Davidson 76 (UBC!); Monashee Mountains, 19 km west of Needles on Hwy.6, 20 June 1960, Ridewood 44 (UBC!); Summerland, 06 June 1937, Stonor s.n. (UBC!); Manning Park, Three Brothers area, Valley View Mountain, 4200-5800 ft., 10 July 1961, Allen, Burroughs, & Howe 73 (UBC!); Tulameen River, Taylor Lake, June 1950, Jackson s.n. (UBC!); Moberly, 01 July 1930, Graham 289 (UBC!); Lake Quinsoncoe, 12 August 1976, Hainault 8016 (UBC!); half mile south of Quesnel, 12 June 1949, Stace-Smith (UBC!); Baldy Mountain, east of Oliver, 2500 ft., 08 June 1952, Ogilvie s.n. (UBC!); Brandywine Falls, 0.5 miles southwest down railway line from where it crosses Hwy.99, 19 May 1977, Gornall 20 (UBC!); north of Chuchi Lake, 2000-2500 ft., 25 July 1968, Revel s.n. (UBC!); Smithers, experimental farm, 07 June 1956, Ashford 63 (UBC!); Ilgachuz Mountains, north of Animah Lake, northeast flank of Phacelia Peak, 6200 ft., 52°45’ N, 125°15’ W, 15 August 1972, R.L.Taylor, Beil, Marchant, & Oliver 5421 (UBC!); Ilgachuz Mountains, north of Animah Lake, above Camlack Creek, 5700 ft., 52°45’ N, 125°15’ W, 15 August 1972, R.L.Taylor, Beil, Marchant, & Oliver 57478 (UBC!); Ilgachuz Mountains, north of Animah Lake, trail from Festuca Pass to Camlack Creek, 5500-6100 ft., 52°45’ N, 125°15’ W, 15 August 1972, R.L.Taylor, Beil, Marchant, & Oliver 5928 (UBC!); Okanagan-Similkameen Regional District, Trout Creek Ecological Reserve, near Summerland, 49°33’ N, 119°42’ W, 25 July 1974, Larmour & Ng s.n. (UBC!); Summit Lake, Teapot Mountain, 600 m, 54° N, 122° W, 25 July 1953, Florian 105 (UBC!); 9 km south of Mamit Lake on Logan Lake Road, 1000 m, 50°19’ N, 120°47’ W, 27 June 1981, Goward 81-1245B (UBC!); Ashnola District, Cathedral Lakes, 6500 ft., 49°00’ N, 120°15’ W, 14 July 1951, T.M.C.Taylor 1305 (UBC!); Wells, 1700 m, 14 July 1951, T.M.C.Taylor 9102 (UBC!); Kamloops, Tod Mountain, 1800 m, 09 July 1963, T.M.C.Taylor & Szczawinski 789 (UBC!); Thompson-Nicola Regional District, Tranquille, 50°N, 120° W, 900 m, 01 June 1949, T.M.C.Taylor 2042 (UBC!); Thompson-Nicola Regional District, Tranquille, 50° N, 120° W, 01 June 1949, T.M.C.Taylor 2043 (UBC!); Pavilion Lake, 800 m, 50°50’ N, 121° 40’ W, 12 June 1952, T.M.C.Taylor & Lewis 157 (UBC!); near Princeton, Copper Mountains, 1000 m, 17 June 1957, T.M.C.Taylor & Szczawinski 31 (UBC!); Priestley, 700 m, 54°10’ N, 125°20’ W, 21 June 1952, T.M.C.Taylor & Lewis 372 (UBC!); Perow, 700 m, 54°30’ N, 126°25’ W, 23 June 1952, T.M.C.Taylor and Lewis 433 (UBC!); Stikine Regional District, Cassiar, 1600 m, 59°15’ N, 129°45’ W, 23 June 1956, T.M.C.Taylor, Szczawinski, & Bell 641 (UBC!); Cariboo-Chilcotin, China Flats, lower Alkali Creek, 680 m, 51°43’ N, 122°20’ W, 13 June 1994, Goward & Roberts 94-76 (UBC!); Old Baldy-Rancheria River, 01 August 1943, Brink s.n. (UBC!); Cariboo-Jesmond Road, 15 August 1953, Brink s.n. (UBC!); Cassiar Mountains, Baldy Mountain, Rancheria Road, August 1943, Brink s.n. (UBC!); Noaxa Lake, 05 August 1957, Brink s.n. (UBC!); Tranquille, Thompson River valley, Pass Lake, 1/8 mile north of the lake, 3200 ft., 20 July 1939, Brink s.n. (UBC!); Takysie District, July-August 1943, Brink s.n. (UBC!); upper Hat Creek, Hammond Lake (Langlie Lake), 07 July 1950, Brink s.n. (UBC!); Point St. John, east of town between Beatton and Peace River, 19 June 1943, Brink
s.n. (UBC!); east of Kelowna, 27 June 1951, Brink s.n. (UBC!); Michel, 30 June 1947, Brink s.n. (UBC!); Thompson-Nicola Regional District, Lytton, Stein River valley, 800-1200 m, 50°16' N, 121°55' W, Krajina 1655 (UBC!); Thompson-Nicola Regional District, Lytton, 20 August 1949, Krajina s.n. (UBC!); north-central BC, Hyland Post, near junction of Spatsizi and Ross Rivers, 3300 ft., 57°37' N, 128°09' W, 14 July 1975, Krajina s.n. (UBC!); near a small lake 9 miles south of Kamloops, 860 m, 50°30' N, 120°21' W, 21 June 1965, Krajina 65062376 (UBC!); Mount Nicola, 6 miles south of Merritt, 3400 ft., 50°05' N, 120°36' W, 23 June 1965, Krajina 650623170 (UBC!); 1.5 miles north of Princeton, 2300 ft., 49°25' N, 120°33' W, 24 June 1965, Krajina 65062444 (UBC!); south of Princeton, 3100 ft., 49°20' N, 120°35' W, 24 June 1965, Krajina 65062480 (UBC!); Similkameen River valley, 1700 ft., 24 May 1964, Krajina & Fraser 645-96 (UBC!); Kamloops, 12 miles southwest, Falkland, 1900 ft., 27 May 1961, Aridge & Tusko 64 (UBC!); Yoho National Park, Mount Stephen, 25 July 1945, McCalla 7716 (UBC!); Grey Creek, 10 June 1944, McCalla 8192 (UBC!); Garibaldi, July 1913, W. Taylor s.n. (UBC!); Quesnel, July 1933, W. Taylor s.n. (UBC!); Mount Waddington, 4000 ft., July 1937, W. Taylor s.n. (UBC!); Chilcotin District, no date provided, Newcombe 39 (UBC!); Lac la Hache, 14 June 1949, Cottle 37 (UBC!); Chilcotin, Meldrum Lake, 16 June 1950, Cottle 193 (UBC!); Stikine River area, west side of Klappan River, just south of BCR access road, 769-780 m, 57°00' N, 128°30' W, 10 July 1979, Gorman 1078 (UBC!); north side of Stikine River, 25 km east of Klappan River, 763-767 m, 57°00' N, 128°30' W, 25 June 1979, Gorman 1261 (UBC!); Bulkley-Nechako Regional District, Darbar Hg Group west, ca. 12 km northwest of Fort St. James, 12 June 1982, Kruckeberg 224 (UBC!); Kamloops, Lac du Bois, 3000 ft., 30 June 1974, Wilkinson s.n. (UBC!); Invermere, Paradise Mountain, 2440 m, 50°30' N, 116°10' W, Rose 79666 (UBC!); Peace River District, Pink Mountain, 1786 m, 57.03° N, 122.57° W, 07 July 1982, Rose 227 (UBC!); Topley, 54° N, 126° W, 18 July 1956, MacDonald 393 (UBC!); Pope Mountain, 54°30’ N, 124°20’ W, 13 July 1981, Kruckeberg 112 (UBC!); Manning Park, nature house area, 3900 ft., 49°04’ N, 120°48’ W, 07 July 1973, Chuang 477 (UBC!); Okanagan-Similkameen Regional District, Manning Park, Similkameen River, 3800-3900 ft., 49°04’ N, 120°45.5’ W, 22 June 1973, Chuang 92 (UBC!); above Salmon Lake, 50°17.5’ N, 119°56’ W, 12 July 1972, Beil 201 (UBC!); Farwell Creek, 51° N, 122° W, 19 July 1972, Beil 279 (UBC!); on the way to the Chilco, about 1 mile above turnoff, 54° N, 123° W, 21 July 1972, Beil 301 (UBC!); above Prentice Lake, trail overlooking Relay Creek, 51’11’ N, 122°54’ W, 24 July 1977, Selby 564 (UBC!); near Regan Lake, 1180 m, 51°46’ N, 123°27’ W, 19 July 1978, C.E. Jones 1-2c-1 (UBC!); 1.5 miles north of Fletcher Lake, 1120 m, 51°47’ N, 123°02’ W, 29 June 1978, C.E. Jones cj-48 (UBC!); above Relay Creek cabin, 1830 m, 51°11’ N, 122°58’ W, 17 July 1978, Selby 265 (UBC!); southwest of Kamloops, Lac le Jeune, south slope, 4000 ft., 03 July 1957, Gilmartin 502 (UBC!); Bennett, 13 July 1949, Mitchell 151 (UBC!); Mount Cheam, 05 September 1916, Hutchinson s.n. (UBC!); East Kootenay Regional District, Kimberley, 31 May 1964, Fodor 462 (UBC!); Ootsa Lake, 09 July 1944, Eastham s.n. (UBC!); Moberly, 14 July 1930, Graham 41 (UBC!); upper Hat Creek, Cairn Peak, 29 August 1949, Brink 49-510 (UBC!); upper Hat Creek, Hammond Lake (Langlie Lake), 07 July 1950, Brink s.n. (UBC!); northwest slope above eastern end of Nicola Lake, 40 miles south of Kamloops, 1900 ft., 50°14’ N, 120°25’ W, 23 June 1965, Krajina 650623129 (UBC!); northwestern BC, ca. 5 km southeast of Atlin, above Atlin Lake, Monarch Mountain, 59°30’ N, 133°40’ W, 24 July 1989, Straley & Nicholls 5734 (UBC!); Thompson-Nicola Regional District, Paradise Lake Road at head of Quilchena Creek, 49° N, 120° W, 01 July 1975, Krause s.n. (UBC!); Kootenay District, Wolf Creek drainage, 49° N, 115° W, 20 June 1975, Ng s.n. (UBC!); Black Fox Lake, 4000 ft., 57° N, 128° W, 27 August 1959, Szczawinski 30 (UBC!); Peace River Regional District, vicinity of Beatton River, 57°05’ N, 122°35’ W, 29 June 1943, Raupt & Correll 10327 (UBC!); Pine Pass, Steven Creek, 4 miles northwest of Azouzetta Lake on Hart Highway, 06 July 1954, Calder,
Savile, & Ferguson 12538 (UBC!); I. R. Summerland, 06 June 1937, Stonor s.n. (UBC!); Thompson-Nicola Regional District, Tranquille, 900 m, 50° N, 120° W, 01 June 1949, T.M.C. Taylor 2042 (UBC!); upper Hat Creek, Blustry Mountain, 7500 ft., 29 August 1949, Brink 49-512 (UBC!); just below lookout on Mount Idaho, east side of Slocan Lake, 6800-7000 ft., 49° N, 117° W, 11 July 1975, Beamish, Luitjens, Carey, & Campbell 750128a (UBC!); Chilcotin, 0.5 miles from Fish Lake, 611 m, 51° N, 122.5° W, 08 July 1975, Jenkins 10125 (UBC!); overlooking Meager Creek, about 1 mile from its junction with Lillooet River, 01 July 1973, Pinder-Moss 461 (UBC!); Fraser-Cheam Regional District, Mount Thurston, north of Chilliwack River, 5500 ft., 49° N, 121° W, 20 July 1974, Pinder-Moss 829 (UBC!); just below lookout on Mount Idaho, east side of Slocan Lake, 6800-7000 ft., 49° N, 120° W, 11 July 1975, Beamish, Luitjens, Carey, & Campbell 750091 (UBC!); above mile 60 of the Stewart-Cassiar Highway as measured from Alaska Highway, 20 July 1976, no collection date provided, McComb-Watson s.n. (UBC!); Haines Road, mile 98, 700 m, 59°30' N, 136°30' W, 07 July 1956, T.M.C. Taylor, Szczawinski, & Bell 1004 (UBC!); Fraser-Cheam Regional District, Skagit River floodplain, within 5 miles of Ross Lake, 1000 ft., 49° N, 121° W, 12 June 1974, Beamish, Vrugtman, & Sperrings 8423 (UBC!); Wells area, 6 miles up Bowron Lake Road, 4300 ft., 1958, Beamish, Vrugtman, & Sperrings 8441 (UBC!); Wells area, Lowhee Ditch, 4900 ft., 1958, Beamish, Vrugtman, & Sperrings 8655 (UBC!); lookout on Idaho Mountain, east side, 7460 ft., 49° N, 117° W, 11 July 1975, Beamish, Luitjens, Carey, & Campbell 750091 (UBC!); Chilcotin, 52° N, 124° W, June 1977, Maze 1270 (UBC!); Toad Mountain, mile 422 of Alaska Highway, 06 July 1980, Gilmore 40 (UBC!); Cassiar District, at foot of Glacial Mountain, northwest part of lake known locally as Glacial Lake, 1600 m, 58° N, 129° W, 10 August 1981, Donovan & Sienes 884 (UBC!); Cassiar District, at foot of Glacial Mountain, southwest side of lake known locally as Glacial Lake, 1600 m, 58° N, 129° W, 19 July 1981, Donovan & Sienes 566 (UBC!); above Gang Ranch Road, 1158 m, 51° N, 122° W, 01 August 1972, Jones 387 (UBC!); ridge of and to west of confluence of Chilcotin and Fraser River, 1372 m, 51° N, 122° W, 19 June 1972, Jones 198 (UBC!); west of Goose Lake, 1006 m, 50°43' N, 121°36' W, 12 June 1977, Scagel 77-0-62 (UBC!); Stikine Regional District, Atlin Provincial Park, Teresa Island, Birch Mountain, east ravine, 4800 ft., 59°25' N, 133°45' W, 02 August 1974, Buttrick 587 (UBC!); Pemberton Meadows, Miller Creek, north of North Fork, 1829 m, 50°24' N, 122°58' W, July-September 1979, Chaney 02 (UBC!); Osoyoos area, mountain just south of Richter Pass, 920 m, 49°05' N, 119°35' W, 14 May 1990, Goward & Lea 90-599 (UBC!); Wells Gray Park, south end of Clearwater Lake, 640 m, 52°09' N, 120°11' W, 02 July 1977, Goward 81-134 (UBC!); Wells Gray Park, Ray Farm, 11 km south of Clearwater Lake, 52°03' N, 120°10' W, 12 June 1980, Goward 81-555 (UBC!); Wells Gray Park, south gate near youth crew camp, 51°57' N, 120°07' W, 21 June 1977, Goward 81-118 (UBC!); Wells Gray Park, Ray Farm, 11 km south of Clearwater Lake, 52°03' N, 120°10' W, 21 June 1979, Goward 81-330 (UBC!); Stikine River at junction with Cullivan Creek, 808-833 m, 57° N, 129° W, 12 July 1980, Gorman 3135 (UBC!); Whistler-Squamish Road, Highway 99, 4.2 km north of Brandywine Falls Provincial Park lake, adjacent to pond across from Cal Creek confluence, BC recreation site, 400 m, 50°04' N, 123°05' W, 15 June 2001, Kennedy & Ganders 5427 (UBC!); Kamloops, north of South Thompson River, 880 m, 50°48’ N, 120°28’ W, 20 August 1999, Warman 1 (UBC!); East Kootenay Regional District, Line Creek mine site, 1249 m, 49°54’ N, 114°50’ W, 07 July 1976, E.E. Jones s.n. (UBC!); East Kootenay Regional District, Hosmer, Wheeler Creek mine site, 1067 m, 49°40’ N, 114°58’ W, 13 July 1976, McLachlin s.n. (UBC!); East Kootenay Regional District, Hosmer, Wheeler Creek mine
site, 1067 m, 49°40’ N, 114°58’ W, 09 July 1976, McLachlin s.n. (UBC!); southeastern British Columbia, Hosmer-Wheeler mine site, 1067 m, 49°40’ N, 114°58’ W, 10 July 1976, McLachlin s.n. (UBC!); northeastern British Columbia, Quintette Mountain mine site, 1265 m, 54°55’ N, 120°55’ W, 28 July 1976, C.E.Jones s.n. (UBC!); southeastern British Columbia, Line Creek mine site, 49°54’ N, 114°50’ W, 15 July 1976, C.E.Jones s.n. (UBC!); southeastern British Columbia, Hosmer-Wheeler mine site, 08 July 1976, C.E.Jones s.n. (UBC!); Wells Gray Provincial Park, Vavenby limestone, 51°35’ N, 119°44’ W, 04 July 2005, Björk & Goward 11377 (UBC!); East Kootenays, Albert River, East Kootenays Trail, 50°40’ N, 115°35’ W, 30 July 2005, Björk & Spribille 11993 (UBC!); Hope, north end of Ross Lake, Chittenden Meadow, 22 June 2003, Smith 18 (UBC!); southeastern British Columbia, Hosmer-Wheeler mine site, 49°40’ N, 114°58’ W, 1976, McLachlin s.n. (UBC!); Tulameen area, Tulameen Ultramafic Complex, Grasshopper Mountain, 1471 m, 49°33’03.7” N, 120°53’0.9” W, 18 July 2002, Lewis & Ingram 28 (UBC!); Tulameen area, Tulameen Ultramafic Complex, Grasshopper Mountain, 1433 m, 49°32’53.9” N, 120°53’02.5” W, 25 July 2002, Lewis & Ingram 28 (UBC!); BC side of Alberta border, 6 km north of Wapiti River, 860 m, 54°47’25’’ N, 120°00’0.5’’ W, 16 July 1998, Lomer & Lancaster 98-294 (UBC!); Okanagan-Similkameen Regional District, Tulameen Forest Service Road, campsite along Tulameen River, 1196 m, 49.43427° N, 121.01277° W, 14 July 2012, Manton & J.Fenneman 239 (UBC!); Okanagan-Similkameen Regional District, Manning Provincial Park, Mule Deer campground, 1080 m, 49.09094° N, 120.68001° W, 06 August 2013, E.Fenneman & J.Fenneman 33 (UBC!); East Kootenay Regional District, near Invermere, Panorama Road, 1096 m, 50.4841° N, 116.19668° W, 12 June 2012, Manton & Shiller 1572 (UBC!); Kootenay-Boundary Regional District, Granby-Burrell Forest Recreation Site, 625 m, 49.36758° N, 118.46054° W, 12 June 2012, Manton & van der Linde 1437 (UBC!); Kootenay-Boundary Regional District, Mount Baldy ski area, 1733 m, 49.15285° N, 119.23613° W, 14 August 2011, Manton & McGrath 1028 (UBC!); North Okanagan, Mara, 23 May 1921, Stewart s.n. (UBC!); Cariboo, Flying U Ranch, 22 June 1944, Eastham s.n. (UBC!); Nevis Creek, 20 July 1969, Luckhurst F59 (UBC!); Cold Fish Lake area, 1959, Szczawinski 33 (UBC!); Kootenay District, Jumbo Creek, 2440 m, 50.30° N, 116.1° W, 21 August 1981, Rose aar81669 (UBC!); Chilcotin, Gang Ranch south of Farwell Creek, 15 July 1967, Krajina & Beil 67-07-15-122 (UBC!); Parsnip River, Tutu Creek, 700 m, 03 July 1963, T.M.C.Taylor & Szczawinski s.n. (UBC!); Spatsizi Plateau, Cold Fish Lake, 4000 ft., 57° N, 128° W, 23 July 1959, Szczawinski 134 (UBC!); Kootenay Lake, Riondel, 13 June 1916, Holman s.n. (UBC!); Ashnola River District, draining into Ewart Creek, on the slopes of Flatiron Mountain, 49° N, 119° W, 01 July 1968, Morrison s.n. (UBC!); Otter Valley, 05 June 1900, Hill s.n. (UBC!); Spatsizi Plateau, 4000 ft., 57° N, 128° W, 23 July 1959, Szczawinski 121 (UBC!); Salmon River, 1082 m, 50°17.5’ N, 120°56’ W, 11 July 1972, Beil 184 (UBC!); Metro Vancouver, Burnaby, north side of Marine Way, 100 m west of Glenlyon Parkway, 50 m east of overpass walkway, 6 m, 49°12’19.8’’ N, 123°00’42.3’’ W, 20 May 2014, Lomer 8720 (UBC!); west of Merritt, Coquihalla Highway, Falls Lake exit, 1179 m, 10U 640821 5497174 (NAD83), 16 July 2011, McIntosh & Hanna 2011_178 (UBC!); northwest of Kamloops, Lac du Bois grasslands, 900 m, 10U 680512 5627992 (NAD83), 24 May 2009, McIntosh, Harcombe, Ballin, & Mackenzie 2009_142 (UBC!); northwest of Kamloops, Lac du Bois grasslands, 749 m, 10U 684462 5627142 (NAD83), 06 June 2009, McIntosh & Punnett 2009_22 (UBC!); Stewart-Cassiar Highway, just north of Dease Lake, 897 m, 58°34’19.2’’ N, 130°00’30.48’’ W, 18 July 2015, Skilton 003-13 (UBC!); trail by Skihist Provincial Park, 50°15’08.124’’ N, 121°30’56.832’’ W, 06 June 2015, Skilton 003-165 (UBC!); Rocky Mountain Trench, Jackman Flats, northwest of ecological reserve.
parking lot, 5 km southeast of Tete Jaune Cache, 790 m, 52°56'00'' N, 119°22'23.5'' W, 19 June 2015, Lomer 9361 (UBC!). Northwest Territories: District of Mackenzie, Mackenzie Mountains, vicinity of Brin nell Lake, Red Mountain, 62°05' N, 127°35' W, 21 June 1939, Raup & Soper 9215 (UBC!); District of Mackenzie, vicinity of Fort Simpson, west of Mackenzie River, 62°51' N, 121°23' W, 24 August 1939, Raup & Soper 9910 (UBC!); Mackenzie District, Yellowknife, 13 July 1949, Cody & McCanse 2593 (UBC!); Mackenzie District, Dome Lake, 62°45' N, 113°15'' W, 01 August 1949, Cody 3172 (UBC!); Mackenzie District, Yellowknife, road to airstrip, 06 August 1949, Cody & McCanse 3258 (UBC!); Mackenzie District, Fort Smith, 60°00' N, 111°53' W, 18 July 1950, Cody & Loan 4357 (UBC!); Mackenzie District, lower Hay River, 60°51' N, 115°42' W, 23 July 1951, Lewis 883 (UBC!); 4 miles east of Trout River on Mackenzie River, Browning’s farm, 60°17' N, 119°47' W, 30 June 1961, Cody & Spicer 11400 (UBC!); Nahanni National Park, Caribou River, Caribou Spring, 1000 m, 61.03802° N, 126.78642° W, 09 August 2012, Bennett, McLennan, McKillop, & Tate 12-0373 (UBC!). Yukon: Dawson, 23 July 1935, Berton 290 (UBC!); Dawson, Midnight Dome, 20 July 1935, Berton 251 (UBC!); Whitehorse, 1903, Hill s.n. (UBC!); south shore of Kluane Lake near its eastern end, Alaska Hwy., Mile 1064-1065, 61°03' N, 138°31' W, Raup & Raup 12203 (UBC!); vicinity of Whitehorse, 60°43' N, 135°03' W, Raup & Correll 11163 (UBC!); Johnson’s Crossing, 2250 ft., 60°29' N, 133°10' W, 09 July 1947, M.P.Porsild 433 & 434 (UBC!); Johnson’s Crossing, 2250 ft., 60°29' N, 133°10' W, 09 July 1947, E.Porsild 436 (UBC!); ca. 1 mile east of Haines Road junction, valley of Alsek River, 60°46' N, 137°30' W, 26 June 1944, Raup & Raup 11954 (UBC!); along Alaska Hwy., Mile 1019, vicinity of Pine Creek, 60°47' N, 137°35' W, 16 June 1944, Raup & Raup 11752 (UBC!); ca. 1 mile east of Little Atlin Lake, 60°29' N, 133°25' W, 17 August 1943, Brink s.n. (UBC!); 24 miles east of Little Atlin Lake, 60°22' N, 133°51' W, 13 August 1943, Raup & Raup 11360 (UBC!); Alaska Hwy., Mile 1022, 01 July 1957, Schofield & Crum 7418 (UBC!); vicinity of Mackintosh, Alaska Hwy., Mile 1022, near Summit Creek, 04 July 1957, Schofield & Crum 7535 (UBC!); vicinity of Mackintosh, Alaska Hwy., Mile 1022, ca. 5 km southeast of Watson Lake, 60°28' N, 128°34' W, 16 June 1958, Sheeter & Stone 3089 (UBC!); vicinity of Mackintosh, Watson Lake, 60°28' N, 128°35' W, 29 June 1959, Hoefs s.n. (UBC!); Watson Lake, Ross River Road, Mile 220, 2500 ft., 18 June 1968, Beamish, Krause, & Luitjens 681231 (UBC!); Haines Road, Dezadeash Lake, 2500 ft., 60°23' N, 137°00' W, 16 July 1968, Beamish, Krause, & Luitjens 681919 (UBC!); Ross River, 2200 ft., 23 June 1968, Beamish, Krause, & Luitjens 681279 (UBC!); near Whitehorse, Haeckel Hill Road, 1314 m, 60°44’41.940’’ N, 135°13’23.712’’ W, 20 June 2015, Skilton 003-14 (UBC!); near Whitehorse, Mount McIntyre Road, 1318 m, 60°38’49.2’’ N, 135°11’03.48’’ W, 19 June 2015, Skilton 003-8 (UBC!); Million Dollar Falls road, 739 m,
Antennaria umbrinella


British Columbia: Farwell Canyon, south side, 19 May 1968, Beil 68-5-19 (UBC!); Nicomen Valley, 29 July 1946, Rattenbury s.n. (UBC!); Spences Bridge, no collection date provided, J.A.T. s.n. (UBC!); about 15 miles west of Windermere, Paradise Mine, 8000 ft., 01 August 1953, Calder & Savile 11316 (UBC!); Pemberton Meadows, Finch Ridge, 27 July 1931, Davidsson s.n. (UBC!); Wasa Lake campsite, 2500 ft., 09 May 1960, Beamish & Vrugtman 60182 (UBC!); Chelquito Lake, 3 km north of, 1200 m, 51°45’ N, 124°11’ W, 15 July 1981, Goward 81-1511B (UBC!); 8 km southwest of Merritt, Coldwater Creek NTT, 650 m, 50°04’ N, 120°47’ W, 26 June 1981, Goward 81-1238d (UBC!); 10 km north of Lower Nicola, Logan Lake Road, 950 m, 50°14’ N, 120°51’ W, 27 June 1981, Goward 81-1239c (UBC!); 12 km east-southeast of Logan Lake, Lac la Jeune Road, 1200 m, 50°30’ N, 120°40’ W, 27 June 1981, Goward 81-1250c (UBC!); Osoyoos area, Haynes Lease ecoreserve, 49°01.5’ N, 119°41.5’ W, 12 May 1990, Goward 90-959 (UBC!); Osoyoos area, mountain just south of Richter Pass, 920 m, 49°05’ N, 119°35’ W, 14 May 1990, Goward 90-603 (UBC!); Osoyoos area, mountain just south of Richter Pass, 920 m, 49°05’ N, 119°35’ W, 14 May 1990, Goward 90-959 (UBC!); Osoyoos area, west side of Similkameen River, near USA border, 450 m, 49°01’ N, 119°43.5’ W, 17 May 1990, Goward 90-982 (UBC!); Pavilion Lake, 800 m, 50°50’ N, 121°40’ W, 12 June 1952, T.M.C. Taylor & Lewis 155B (UBC!); Macalister, 500 m, 52°20’ N, 122°30’ W, 18 June 1952, T.M.C. Taylor & Lewis 288 (UBC!); North...
Okanagan Regional District, Baldie, Vernon, 3500 ft, 23 August 1949, Brashaw 49416 (UBC!); Princeton, 3500 ft, 18 August 1950, Krajina s.n. (UBC!); road between Dease Lake and Telegraph Creek, 58° N, 130° W, 17 July 1973, Krajina, McMinn, Klinka, & Annas s.n. (UBC!); Bulkley-Nechako Regional District, Telkwa, area, ridge above the Bulkley River and Hwy.16, ca. 4 miles southeast of Telkwa, 1800-2200 ft., 54°30' N, 127°00' W, 07 July 1974, Krajina, Pajar, & Parsons s.n. (UBC!); between Quesnel and Williams Lake, 19 June 1965, Krajina s.n. (UBC!); Indian reserve outside Oliver, 1100 ft., 23 May 1964, Krajina & Fraser 645-45 (UBC!); East Kootenay Regional District, Cranbrook, above airport, 28 May 1947, McCalla 9332 (UBC!); East Kootenay Regional District, Cranbrook, above airport, 06 May 1947, McCalla 9406 (UBC!); Chilko, 31 May 1914, Newcombe 52 (UBC!); Thompson-Nicola Regional District, Tranquille Range, near Kamloops, 2800 ft, June 1936, Tisdale s.n. (UBC!); Salmon River, stand #4, 1082 m, 50°17.5' N, 119°56' W, 11 July 1972, Beil 184 (UBC!); Gaspard Creek valley, 1067 m, 51° N, 121° W, 22 July 1972, Beil 336 (UBC!); outside of Hanceville, Big Creek Road, 51° N, 123° W, 25 June 1972, Beil 119 (UBC!); east end of Two Lakes Basin, 1600 m, 51°12' N, 123°04' W, 13 July 1977, Selby 135 (UBC!); Relay Creek valley, just below saddle & east of rocks, 2125 m, 51°11' N, 122°58' W, 31 July 1931, Selby 707 (UBC!); Chilcotin, Gang Ranch, south of Farwell Creek, 15 July 1967, Krajina & Beil 87-07-15-123 (UBC!); west side of main creek and south side of Dash Plateau, 15°12' N, 123°00' W, 18 August 1977, Selby s.n. (UBC!); ca. 2 km southwest of Kilpoola Lake, 907 m, 49°01' N, 119°36' W, 12 June 1991, G.W. Douglas 12532 (UBC!); Okanagan-Similkameen Regional District, near Summerland, Trout Creek Ecological Reserve, 49°33' N, 119°42' W, 19 May 1974, Larmour & Ng s.n. (UBC!); Mount Whistler, 6500 ft., 13 August 1967, Krajina s.n. (UBC!); Whipsaw Creek, 49°22' N, 120°34' W, 02 September 1968, Krajina & Bednar 68090206 (UBC!); Garibaldi, Cinder Cone, 25 July 1958, Brink s.n. (UBC!); Summerland, 15 June 1913, Hill s.n. (UBC!); Knutsford, 2 miles northwest, 2200 ft., 20 May 1952, Anonymous s.n. (UBC!); 1 mile northeast of Kaledon, Okanagan Game Farm, 1800 ft., 49°26' N, 119°39' W, 19 May 1977, Wikeem & Gale s.n. (UBC!); Big Bank, 19 May 1915, Bertrand s.n. (UBC!); Farwell Canyon, 19 May 1968, Beil 68-5-19 (UBC!); Kamloops, Rose Hill, 2600 ft., May 1940, Tisdale s.n. (UBC!); near Kamloops, Tranquille Range, 1400 ft., 31 May 1937, Tisdale s.n. (UBC!); Okanagan, Larkin, 24 May 1906, E. Wilson 859 (UBC!); Flagstone, Mount Caven, 6300 ft., August 1944, Peterson s.n. (UBC!); Thompson-Nicola Regional District, Hat Creek, 50°44 N, 121°36' W, 3350 ft., 18 May 1976, Forrest 3-007 (UBC!); Kamloops, 12 May 1914, Wattie s.n. (UBC!); Osoyoos, southeast of town along Hwy. 3, 2000 ft., 13 June 1972, Pojar 336 (UBC!); Vancouver, North Shore, Black Mountain summit, 12 July 1912, Davidson s.n. (UBC!); Thompson-Nicola Regional District, near Lytton, Botanie Road, 1800 ft., 50° N, 121° W, 18 May 1974, Pinder-Moss & Pojar 654 (UBC!); Thompson-Nicola Regional District, Lytton, 11 June 1940, Eastham s.n. (UBC!); Penticton, Mount Munson, 03 May 1939, Eastham s.n. (UBC!); Penticton, 06 May 1939, Eastham s.n. (UBC!); east of Grand Forks, 2400 ft., 15 May 1960, Beamish & Vrugtman 60362 (UBC!); Okanagan-Similkameen Regional District, 5 miles east of Hedley, 2000 ft., 03 May 1960, Beamish & Vrugtman 60284 (UBC!); Indian Reserve east of Oliver, 1600 ft., 04 May 1960, Beamish & Vrugtman 60113 (UBC!); Kamloops area, Dewdrop Flats, 01 June 1949, Sieburth 49-128 (UBC!); Summerland, June 1937, Stonor s.n. (UBC!); Central Okanagan Regional District, Kelowna, 23 April 1915, Holm 46 (UBC!); south of Kamloops, 19 May 1952, Ogilvie s.n. (UBC!); Thompson-Nicola Regional District, Tranquille, 800 m, 49° N, 120° W, 01 June 1949, T.M.C. Taylor 2043 (UBC!); Pavilion Lake, 800 m, 50°50’ N, 121°40’ W, 12 June 1952, T.M.C. Taylor & Lewis 155 (UBC!); Copper Mountain, near Princeton, 1000 m, 17 June 1957, T.M.C. Taylor & Szczawinski 33 (UBC!); Merritt, 50° N, 120° W, 02 June 1949, T.M.C. Taylor 2071 (UBC!); Princeton, 24 June 1962, T.M.C. Taylor & Szczawinski 670 (UBC!); east of Kelowna, 13 June 1951, Brink s.n. (UBC!); Thompson-Nicola
Regional District, Lytton, 175-500 m, 50°14' N, 121°34' W, 18 August 1949, Krajina 1175 (UBC!); Princeton, 19 August 1950, Krajina s.n. (UBC!); south of Kamloops, between Shumway and Trapp Lakes, 2300 ft., 50°25' N, 120°15' W, 23 June 1965, Krajina 650623107 (UBC!); Mount Nicola, 6 miles south of Merritt, 3400 ft., 50°05' N, 120°03' W, 23 June 1965, Krajina 650623171 (UBC!); 9 miles south of Kamloops, 2860 ft., 50°30' N, 120°20' W, 23 June 1965, Krajina 65062355 (UBC!); 1 to 5 miles south of Princeton, 2300 ft., 49°25' N, 120°33' W, 24 June 1965, Krajina 65062424 (UBC!); Princeton, 2 to 7 miles southwest, 2930 ft., 49°23' N, 120°35' W, 24 June 1965, Krajina 65062474 (UBC!); Princeton, 3 miles west, 2170 ft., 22 May 1964, Krajina & Fraser 645-15 (UBC!); Okanagan-Similkameen Regional District, Similkameen River valley, northeast slope, 3 miles west of Keremeos, 1600 ft., 24 May 1964, Krajina & Fraser 645-76 (UBC!); Kamloops, Falkland, Pillar Lake, 3600 ft., 03 June 1961, Aslidge & Tusko s.n. (UBC!); on saddle between Mount Pierce and McFarlane, 5800 ft., 49°04' N, 121°37' W, 08 September 1974, Pinder-Moss & Pojar 1011 (UBC!); Miller Creek which flows east and southeast into Lillooet River near Pemberton, 50° N, 122° W, 13 September 1973, Brink s.n. (UBC!); East Kootenay Regional District, 7 miles north of Kimberley, 11 September 1951, Rogers s.n. (UBC!); Hope, Mount Holy Cross, 6500 ft., 02 September 1941, Brink s.n. (UBC!); East Kootenay Regional District, Kimberley, 14 May 1957, Oseko 41 (UBC!); East Kootenay Regional District, Kimberley, 15 May 1957, Oseko 52 (UBC!); Telegraph Creek, 305 m, 57°55' N, 131°10' W, 30 June 1980, Albright 31 (UBC!); Anarchist Mountain, 8 miles west of summit, in stopping area on Highway 3, 49°01’ N, 119°23’ W, 06 June 1979, McComb-Watson 79-84, 79-85 (UBC!); junction of Chilcotin and Fraser Rivers, 671 m, 51° N, 122° W, 18 June 1972, Ralston 9 (UBC!); near junction of Chilcotin and Fraser Rivers, 457 m, 51° N, 122° W, 01 August 1972, Jones 291 (UBC!); near junction of Chilcotin and Fraser Rivers, 914 m, 51° N, 122° W, 01 August 1972, Jones 307 (UBC!); 2 miles south of confluence of Chilcotin River and Fraser River, on west bank of Fraser River, 853 m, 51° N, 122° W, 15 June 1972, Jones 125 (UBC!); 30 km south of Ashcroft, west of Hwy. 1, 100 m east of Venables Valley Road, near Oregon Jack Hill, 50°34’ N, 121°19’ W, 15 May 1999, Bandringa 114 (UBC!); west of Goose Lake, 3300 ft., 50°43’ N, 121°36’ W, 12 June 1977, Scagel 77-0-61 (UBC!); Darke Lake Provincial Park, above Okanagan Lake, south of Peachland, 49°43’ N, 121°37’ W, 08 September 1974, Pinder-Moss & Pojar 1011 (UBC!); Miller Creek which flows east and southeast into Lillooet River near Pemberton, 50° N, 122° W, 13 September 1973, Brink s.n. (UBC!); East Kootenay Regional District, 7 miles north of Kimberley, 11 September 1951, Rogers s.n. (UBC!); Hope, Mount Holy Cross, 6500 ft., 02 September 1941, Brink s.n. (UBC!); East Kootenay Regional District, Kimberley, 14 May 1957, Oseko 41 (UBC!); East Kootenay Regional District, Kimberley, 15 May 1957, Oseko 52 (UBC!); Telegraph Creek, 305 m, 57°55’ N, 131°10’ W, 30 June 1980, Albright 31 (UBC!); Anarchist Mountain, 8 miles west of summit, in stopping area on Highway 3, 49°01’ N, 119°23’ W, 06 June 1979, McComb-Watson 79-84, 79-85 (UBC!); junction of Chilcotin and Fraser Rivers, 671 m, 51° N, 122° W, 18 June 1972, Ralston 9 (UBC!); near junction of Chilcotin and Fraser Rivers, 457 m, 51° N, 122° W, 01 August 1972, Jones 291 (UBC!); near junction of Chilcotin and Fraser Rivers, 914 m, 51° N, 122° W, 01 August 1972, Jones 307 (UBC!); 2 miles south of confluence of Chilcotin River and Fraser River, on west bank of Fraser River, 853 m, 51° N, 122° W, 15 June 1972, Jones 125 (UBC!); 30 km south of Ashcroft, west of Hwy. 1, 100 m east of Venables Valley Road, near Oregon Jack Hill, 50°34’ N, 121°19’ W, 15 May 1999, Bandringa 114 (UBC!); west of Goose Lake, 3300 ft., 50°43’ N, 121°36’ W, 12 June 1977, Scagel 77-0-61 (UBC!); Darke Lake Provincial Park, above Okanagan Lake, south of Peachland, 49°43’ N, 121°37’ W, 08 September 1974, Pinder-Moss & Pojar 1011 (UBC!); Okanagan Center, 14 May 1924, Hare s.n. (UBC!); Brunswick Mountain, 29 June 1914, Perry s.n. (UBC!); Kaledon, 17 May 1921, Milley s.n. (UBC!); Osoyoos area, along Similkameen River, near USA border, 500 m, 49°01’ N, 119°29’ W, 12 May 1990, Goward & Lea 90-571 (UBC!); Osoyoos area, mountain just south of Richter Pass, 920 m, 49°05’ N, 119°35’ W, 14 May 1990, Goward and Lea 90-598 (UBC!); Garibaldi Park, Little Diamond Head, Cheekye Ridge, 6250 ft., 20 September 1964, Krajina & Brooke 64092024 (UBC!); Bulkley-Nechako Regional District, ridge above Bulkley River and Hwy. 18, ca. 4 miles southeast of Telkwa, 1800-2200 ft., 54°30’ N, 127°00’ W, 07 July 1974, Krajina, Pojar, & Parsons s.n. (UBC!); Thompson-Nicola Regional District, Highland Valley, headwaters of Pukaist Creek, northwest of Spences Bridge, Bethlehem Mine site, 50°25’ N, 121°03’ W, 20 June 1972, Morrison s.n. (UBC!); East Kootenay Regional District, Fording River, Eagle Mountain, 7450-7700 ft., 50°14’ N, 114°50’ W, 30 September 1970, Morrison s.n. (UBC!); Princeton, Mitchell’s farm, 49°27’30’’ N, 120°30’30’’ W, 16 May 1976, Ceska & Ceska s.n. (UBC!); Cascade Mountains, Skagit Range, ca. 13 km northwest of north end of Chilliwack Lake, Foley Peak, south slope, 1900 m, 49°09’20’’ N, 121°35’40’’ W, 21 September 1999, Lomer 99-198 (UBC!); Summerland, August 1913, F.G.H. s.n. (UBC!); Okanagan-Similkameen Regional District, Chute Lake Road, near Naramata, 1192 m, 49.69150° N, 119.53574° W, 21 May 2011, Manton & McGrath 382 (UBC!); Kootenay-Boundary Regional District, Conkle Lake Provincial Park, 1089 m, 49.18175° N, 119.09125° W, 13 August 2011, Manton & McGrath 989 (UBC!); Okanagan-Similkameen Regional District, South Okanagan
APPENDIX C:

ANTENNARIA SPECIES IN BRITISH COLUMBIA AND THEIR SYNONYMS

1. *Antennaria anaphaloides* Rydb.
   *Antennaria pulcherrima* (Hook.) Greene subsp. *anaphaloides* (Rydb.) W.A. Weber
   *Antennaria pulcherrima* (Hook.) Greene var. *anaphaloides* (Rydb.) G.W. Dougl.

2. *Antennaria borealis* Greene
   *Antennaria isolepis* Greene
   *Antennaria maculata* Greene
   *Antennaria manicouagana* Landry
   *Antennaria pallida* E.E. Nelson
   *Antennaria pedunculata* A.E. Porsild
   *Antennaria rousseauii* A.E. Porsild

3. *Antennaria dimorpha* (Nutt.) Torr. & A. Gray
   *Antennaria dimorpha* (Nutt.) Torr. & A. Gray var. *integra* L.F. Henderson
   *Antennaria dimorpha* (Nutt.) Torr. & A. Gray var. *macrocephala* D.C. Eaton
   *Antennaria dimorpha* (Nutt.) Torr. & A. Gray var. *nuttallii* D.C. Eaton
   *Antennaria latisquama* Piper
   *Antennaria macrocephala* (D.C. Eaton) Rydb.
   *Gnaphalium dimorphum* Nutt.

4. *Antennaria flagellaris* (A. Gray) A. Gray
   *Antennaria dimorpha* (Nutt.) Torr. & A. Gray var. *flagellaris* A. Gray

5. *Antennaria howellii* Greene
   5a. subsp. *howellii*
   *Antennaria appendiculata* Fern.
   *Antennaria canadensis* Greene
   *Antennaria canadensis* Greene var. *randii* Fern.
   *Antennaria canadensis* Greene var. *spathulata* Fern.
   *Antennaria eximia* Greene
   *Antennaria howellii* Greene subsp. *canadensis* (Greene) Bayer
   *Antennaria neglecta* Greene subsp. *howellii* (Greene) Hult.
Antennaria neglecta Greene var. howellii (Greene) Cronq.
Antennaria neglecta Greene var. randii (Fern.) Cronq.
Antennaria neodioica Greene subsp. canadensis (Greene) Bayer & Stebbins
Antennaria neodioica Greene subsp. howellii (Greene) Bayer
Antennaria neodioica Greene var. randii (Fern.) Boiv.
Antennaria petasites Greene
Antennaria spathulata (Fern.) Fern.

5b. subsp. neodioica (Greene) Bayer
Antennaria callilepis Greene
Antennaria campestris Rydb. var. neodioica (Greene) Cronq.
Antennaria concolor Piper
Antennaria howellii Greene subsp. neodioica (Greene) Bayer
Antennaria howellii Greene subsp. petaloidea (Fern.) Bayer
Antennaria grandis (Fern.) House
Antennaria lanulosa Greene
Antennaria neglecta Greene var. attenuata (Fern.) Cronq.
Antennaria neglecta Greene var. petaloidea (Fern.) Cronq.
Antennaria neodioica Greene
Antennaria neodioica Greene subsp. petaloidea (Fern.) Bayer & Stebbins
Antennaria neodioica Greene var. attenuata Fern.
Antennaria neodioica Greene var. chlorophylla Fern.
Antennaria neodioica Greene var. grandis Fern.
Antennaria neodioica Greene var. interjecta Fern.
Antennaria neodioica Greene var. petaloidea Fern.
Antennaria neodioica Greene var. rupicola (Fern.) Fern.
Antennaria obovata E.E. Nelson
Antennaria pedicellata Greene
Antennaria petaloidea (Fern.) Fern.
Antennaria rupicola Fern.
Antennaria stenolepis Greene

6. Antennaria lanata (Hook.) Greene
Antennaria carpatica (Wahlenb.) Bluff & Fingerh. var. lanata Hook.
7. *Antennaria luzuloides* Torr. & A. Gray subsp. *luzuloides*

*Antennaria luzuloides* Torr. & A. Gray var. *oblanceolata* (Rydb.) Peck

*Antennaria oblanceolata* Rydb.

8. *Antennaria media* Greene

*Antennaria acuta* Rydb.

*Antennaria alpina* (L.) Gaertn. var. *media* (Greene) Jeps.

*Antennaria alpina* (L.) Gaertn. var. *scabra* (Greene) Jeps.

*Antennaria atriceps* Fern.

*Antennaria austromontana* E.E. Nelson

*Antennaria candida* Greene

*Antennaria chlorantha* Greene

*Antennaria densa* Greene

*Antennaria fusca* E.E. Nelson

*Antennaria gormanii* St. John

*Antennaria media* Greene subsp. *ciliata* E.E. Nelson


*Antennaria media* Greene subsp. *pulchella* (Greene) Chmiel.

*Antennaria modesta* Greene

*Antennaria mucronata* E.E. Nelson

*Antennaria pulchella* Greene

*Antennaria scabra* Greene

*Antennaria stolonifera* A.E. Porsild

*Antennaria tomentella* Greene


*Antennaria bracteosa* Rydb.

*Antennaria foliacea* Greene

*Antennaria microphylla* Rydb. var. *solstitialis* (Lunell) Lunell

*Antennaria nitida* Greene

*Antennaria parvifolia* Nutt. var. *bracteosa* (Rydb.) A. Nelson

*Antennaria rosea* Greene var. *nitida* (Greene) Breitung

*Antennaria solstitialis* Lunell
10. *Antennaria monocephala* DC.

10a. subsp. *angustata* (Greene) Hult.

*Antennaria alpina* (L.) Gaertn. var. *megacephala* (Fern.) S.L. Welsh
*Antennaria angustata* Greene
*Antennaria burwellensis* Malte
*Antennaria congesta* Malte
*Antennaria fernaldiana* Polunin
*Antennaria hudsonica* Malte
*Antennaria megacephala* Fern.
*Antennaria nitens* Greene
*Antennaria pygmaea* Fern.
*Antennaria tansleyi* Polunin
*Antennaria tweedsmuirii* Polunin

10b. subsp. *monocephala*

*Antennaria alpina* (L.) Gaertn. var. *monocephala* (DC.) Torr. & A. Gray
*Antennaria exilis* Greene
*Antennaria monocephala* DC. var. *exilis* (Greene) Hult.
*Antennaria philonipha* A.E. Porsild
*Antennaria shumaginensis* A.E. Porsild

11. *Antennaria neglecta* Greene

*Antennaria athabascensis* Greene
*Antennaria campestris* Rydb.
*Antennaria campestris* Rydb. var. *athabascensis* (Greene) Boivin
*Antennaria chelonica* Lunell
*Antennaria erosa* Greene
*Antennaria howellii* Greene var. *athabascensis* (Greene) Boivin
*Antennaria howellii* Greene var. *campestris* (Rydb.) Boivin
*Antennaria longifolia* Greene
*Antennaria lunellii* Greene
*Antennaria neglecta* Greene var. *athabascensis* (Greene) Tayl. & MacBr.
*Antennaria neglecta* Greene var. *campestris* (Greene) Steyerm.
Antennaria parvula Greene
Antennaria wilsonii Greene

12. **Antennaria parvifolia** Nutt.
    Antennaria aprica Greene
    Antennaria aprica Greene var. aureola (Lunell) J.W. Moore
    Antennaria aprica Greene var. minuscula (Boivin) Boivin
    Antennaria aprica Greene var. rosea Lunell
    Antennaria aureola Lunell
    Antennaria aureola Lunell var. rosea (Lunell) Lunell
    Antennaria dioica (L.) Gaertn. var. parvifolia (Nutt.) Torr. & A. Gray
    Antennaria holmii Greene
    Antennaria minuscula Boivin
    Antennaria obtusata Greene
    Antennaria parvifolia Nutt. var. aureola (Lunell) Chmiel.
    Antennaria recurva Greene
    Antennaria rhodantha Suksd.

13. **Antennaria pulcherrima** (Hook.) Greene subsp. *pulcherrima*
    Antennaria carpatica (Wahlenb.) Bluff & Fingerh. var. pulcherrima Hook.
    Antennaria pulcherrima (Hook.) Greene var. angustisquama A.E. Porsild
    Antennaria pulcherrima (Hook.) Greene var. sordida Boivin

14. **Antennaria pulvinata** Greene
    Antennaria albescens (E.E. Nelson) Rydb.
    Antennaria alpina (L.) Gaertn. var. cana Fern. & Wieg.
    Antennaria aromatica Evert
    Antennaria bayardii Fern.
    Antennaria brunnescens Fern.
    Antennaria cana (Fern. & Wieg.) Fern.
    Antennaria columnaris Fern.
    Antennaria confusa Fern.
    Antennaria foggii Fern.
    Antennaria pulvinata Greene subsp. albescens E.E. Nelson
    Antennaria rosea Greene subsp. pulvinata (Greene) Bayer
Antennaria sedoides Greene
Antennaria vexillifera Fern.

15. **Antennaria racemosa** Hook.
Antennaria piperi Rydb.

16. **Antennaria rosea** Greene
Antennaria acuminata Greene
Antennaria alborosea M.P. Porsild
Antennaria angustifolia Rydb.
Antennaria arida E.E. Nelson
Antennaria arida E.E. Nelson subsp. viscidula E.E. Nelson
Antennaria breitungii A.E. Porsild
Antennaria concinna E.E. Nelson
Antennaria confinis Greene
Antennaria elegans A.E. Porsild
Antennaria foliacea Greene var. *humilis* Rydb.
Antennaria formosa Greene
Antennaria howellii Greene subsp. *gaspensis* (Fern.) Chmiel.
Antennaria imbricata E.E. Nelson
Antennaria incarnata A.E. Porsild
Antennaria laingii A.E. Porsild
Antennaria leontopodioides Cody
Antennaria leuchippii M.P. Porsild
Antennaria neglecta Greene var. *gaspensis* (Fern.) Cronq.
Antennaria neodioica Greene var. *gaspensis* Fern.
Antennaria oxyphylla Greene
Antennaria peasei Fern.
Antennaria polyphylla Greene, *nom. nud.*
Antennaria rosea Greene subsp. *arida* (E.E. Nelson) Bayer
Antennaria rosea Greene subsp. *confinis* (Greene) Bayer
Antennaria rosea Greene subsp. *divaricata* E.E. Nelson
Antennaria rosea Greene var. *angustifolia* (Rydb.) E.E. Nelson
Antennaria sansonii Greene
Antennaria scariosa E.E. Nelson
Antennaria sordida Greene, nom. illeg.
Antennaria straminea Fern.
Antennaria subviscosa Fern.
Antennaria viscidula (E.E. Nelson) A. Nelson

17. Antennaria umbrinella Rydb.
Antennaria aizoides Greene
Antennaria dioica (L.) Gaertn. var. kernensis Jeps.
Antennaria hendersonii Piper
Antennaria speciosa E.E. Nelson
APPENDIX D:

NOMENCLATURAL CROSS-REFERENCE FOR ACCEPTED ANTENNARIA TAXA AND THEIR SYNONYMS

acuminata [= A. rosea]
acuta [= A. media]
aizoides [= A. umbrinella]
albescens [= A. pulvinata]
alborosea [= A. rosea]
anaphaloides
angustata
angustisquama [= A. pulcherrima subsp. pulcherrima]
appendiculata [= A. howellii subsp. howellii]
aprica [= A. parvifolia]
arida [= A. rosea]
aromatica [= A. pulvinata]
athabascensis [= A. neglecta]
attenuata [= A. howellii subsp. neodioica]
atriceps [= A. media]
aureola [= A. parvifolia]
austromontana [= A. media]
bayardii [= A. pulvinata]
bo realis
bracteosa [= A. microphylla]
breitungii [= A. rosea]
brunnescens [= A. pulvinata]
burwellensis [= A. monocephala subsp. angustata]
callilepis [= A. howellii subsp. neodioica]
campestris [= A. neglecta]
cana [= A. pulvinata]
canadensis [= A. howellii subsp. howellii]
candida [= A. media]
chloranthera [= A. media]
chlorophylla [= A. howellii subsp. neodioica]
ciliata [= A. media]
columnaris [= A. pulvinata]
concinna [= A. rosea]
concolor [= A. howellii subsp. neodioica]
confinis [= A. rosea]
confusa [= A. pulvinata]
congesta [= A. monocephala subsp. angustata]
densa [= A. media]
dimorpha
divaricata [= A. rosea]
elegans [= A. rosea]
erigeroides [= A. racemosa x A. rosea]
exilis [= A. monocephala subsp. monocephala]
eximia [= A. howellii subsp. howellii]
feraldiana [= A. monocephala subsp. angustata]
dimorpha
foggi [A. pulvinata]
foliacea [= A. microphylla]
formosa [= A. rosea]
fusca [= A. media]
gaspensis [= A. rosea]
gormanii [= A. media]
grandis [= A. howellii subsp. neodioica]
hendersonii [= A. umbrinella]
holmii [= A. parvifolia]
howellii
hudsonica [= A. monocephala subsp. angustata]
humilis [= A. rosea]
imbricata [= A. rosea]
incarnata [= A. rosea]
totem [= A. dimorpha]
interjecta [= A. howellii subsp. neodioica]
islepis [= A. borealis]
kernensis [= A. umbrinella]
laingii [= A. rosea]
lanata
lanulosa [= A. howellii subsp. neodioica]
latisquama* [= A. dimorpha] (nom. Illeg.)
leontopodioides [= A. rosea]
leuchippii [= A. rosea]
luzuloides
macounii [= A. media x A. umbrinella]
macrocephala [= A. dimorpha]
maculata [= A. borealis]
manicouaganana [= A. borealis]
media
megacephala [= A. monocephala subsp. angustata]
microphylla
minuscula [= A. parvifolia]
modesta [= A. media]
monocephala
mucronata [= A. media]
neglecta
neodioica
nitens [= A. monocephala subsp. angustata]
nitida [= A. microphylla]
nuttallii [= A. dimorpha]
oblanceolata [= A. luzuloides subsp. luzuloides]
oblancifolia [= A. racemosa x A. umbrinella]
obovata [= A. howellii subsp. neodioica]
obtusata [= A. parvifolia]
oxiphylla [= A. rosea]
pallida [= A. borealis]
parvifolia
peasei [= A. rosea]
pedicellata [= A. howellii subsp. neodioica]
pedunculata [= A. borealis]
petaloidea [= A. howellii subsp. neodioica]
petasites [= A. howellii subsp. howellii]
philonipha [= A. monocephala subsp. monocephala]
piperi [= A. racemosa]
polyphylla* [= A. rosea] (nomen nudum)
pulchella [= A. media]
pulcherrima
pulvinata
pygmaea [= A. monocephala subsp. monocephala]
racemosa
randii [= A. howellii subsp. howellii]
recursa [= A. parvifolia]
rhodantha [= A. parvifolia]
rosea
rosea (var.) [= A. parvifolia]
rousseauii [= A. borealis]
rupticola [= A. howellii subsp. neodioica]
sansonii [= A. rosea]
sabra [= A. media]
sariosa [= A. rosea]
sedoides [= A. pulvina]
shumaginensis [= A. monocephala subsp. monocephala]
solstitialis [= A. microphylla]
sordida [= A. pulcherrima subsp. pulcherrima]
sordida* [= A. rosea] (nom. Illeg.)
spathulata [= A. howellii subsp. howellii]
speciosa [= A. umbrinella]
stenolepis [= A. howellii subsp. neodioica]
stolonifera [= A. media]
straminea [= A. rosea]
subvisscosa [= A. rosea]
tansleyi [= A. monocephala subsp. angustata]
tomentella [= A. media]
tweedsmuirii [= A. monocephala subsp. angustata]

**umbrinella**

vexillifera [= A. pulvinata]

viscidula [= A. rosea]
### APPENDIX E: REPORTED CHROMOSOME COUNTS FOR BRITISH COLUMBIA *ANTENNARIA*

<table>
<thead>
<tr>
<th>Species</th>
<th>Chromosome Count</th>
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<sup>5</sup> Species of *Antennaria* with 2n = 28 (x = 14) are treated as diploid in current literature, although Bayer and Stebbins (1987) argue that these plants are in fact paleotetraploids that have “re-diploidized.”

<sup>6</sup> Reported as *A. pallida* (synonym)

<sup>7</sup> Reported as *A. isolepis* (synonym)

<sup>8</sup> Reported as *A. pedunculata* (synonym)

<sup>9</sup> Reported as *A. howellii* [= subsp. *howellii*], but presumed to be attributable to *A. howellii* subsp. *neodioica*

<sup>10</sup> Likely pertains to *A. howellii* subsp. *howellii* based on the collection locations
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11 Reported as *A. media*, but all cited specimens are from within the range of the sexual populations (*= pulchella*) in OR and CA.
12 Reported as *A. pulchella* (synonym)
13 Reported as *A. atriceps* (synonym)
14 Reported as *A. stolonifera* (synonym)
15 Reported as *A. alpina*; referred here to *A. media* based on biogeographic and morphological considerations
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[16] Reported as *A. aromatica* (synonym)
[17] Refers only to sexual populations in MT, which are commonly treated as “A. aromatica”
[18] Reported as *A. sedoides* (synonym)
[19] Includes both sexual and apomictic populations
This is an unexpected diploid count from *A. rosea*, and is likely erroneous; likely refers to *A. microphylla*

28 + 1B 2x Chinnappa (1986)
Bayer and Stebbins (1987)

28 + 3B 2x Chinnappa (1986)

28 2x Chmielewski and Chinnappa (1990)\(^{20}\)
Chmielewski and Chinnappa (1990)\(^{21}\)

42 3x Bayer and Stebbins (1987)
Chmielewski and Chinnappa (1988)

### *Antennaria rosea*

56 4x Bayer (1984)
Chinnappa (1984)
Chinnappa (1986)
Chmielewski and Chinnappa (1988)
Chmielewski and Chinnappa (1988)\(^{22}\)
Chmielewski and Chinnappa (1988)\(^{23}\)
Chmielewski and Chinnappa (1990)
Chmielewski and Chinnappa (1990)\(^{24}\)
Chmielewski and Chinnappa (1990)\(^{25}\)
Chmielewski and Chinnappa (1990)\(^{26}\)
Chmielewski and Chinnappa (1990)\(^{27}\)
Chmielewski (1995)\(^{26}\)
Chmielewski (2006)

60 ca. 4x Chmielewski and Chinnappa (1988)

ca. 62 ca. 5x Chinnappa (1986)

ca. 68 ca. 5x Morton (1981)

70 5x Bayer (1984)
Chinnappa (1986)
Chmielewski and Chinnappa (1988)
Chmielewski and Chinnappa (1990)

ca. 72 ca. 5x Chinnappa (1986)

28 2x Bayer (1984)
Chinnappa (1986)
Chmielewski and Chinnappa (1988)

### *Antennaria umbrinella*

56 4x Bayer (1984)
Chinnappa (1986)
Chmielewski and Chinnappa (1988)
Chmielewski and Chinnappa (1990)

---

\(^{20}\) This is an unexpected diploid count from *A. rosea*, and is likely erroneous; likely refers to *A. microphylla*

\(^{21}\) Reported as *A. elegans* (synonym); an unexpected diploid count in *A. rosea*, and may be erroneous

\(^{22}\) Reported as *A. alborosea* (synonym)

\(^{23}\) Reported as *A. laingii* (synonym)

\(^{24}\) Reported as *A. breitungii* (synonym)

\(^{25}\) Reported as *A. incarnata* (synonym)

\(^{26}\) Reported as *A. oxyphylla* (synonym)

\(^{27}\) Reported as *A. straminea* (synonym)
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28 Specimen collected from slightly outside of the known distribution of *A. umbrinella*, and likely an erroneous identification given its unusual chromosome count.
**APPENDIX F:**

**SYMPHYOTRICHUM SPECIMENS REVIEWED DURING THIS STUDY**

*Symphyotrichum ascendens*

**CANADA.** Alberta: near Medicine Hat, 25 August 1954, *E.H.Moss 10661* (UBC!). British Columbia: Rocky Mountain Trench, 26 km due north northwest of Golden, 1 km east of Waitabit Creek confluence with Columbia River, 780 m, 51°30'04.6" N, 117°10'57.4" W, 20 August 2013, *Lomer 8561* (UBC!); Columbia River Valley, 5.2 km north of Fairmont Hot Springs, 170 m west of Hwy 93/95, 835 m, 50°22'50" N, 115°53'03" W, 22 September 2002, *Lomer 4601* (UBC!); Bummer’s Flat, Fort Steele, 49°42' N, 115°42' W, 11 August 1972, *Fodor 787b* (UBC!); 6.5 km south-southeast of Windermere Lake, 3 km due northwest of Fairmont Hot Springs, 813 m, 50°21'03.5" N, 115°53'25.5" W, 16 August 2014, *Lomer 8898* (UBC!).

*Symphyotrichum boreale*


**Symphyotrichum bracteolatum**

**CANADA.** Alberta: below upper hot springs, Banff, 23 August 1948, McCalla 10254 (UBC!); below Cave and Basin, Banff, 23 August 1948, McCalla 10261 (UBC!); south of Elkwater Lake, Cypress Hills, 4200 ft., 14 August 1947, Breitung 5566 (UBC!); along stream below Cave and Basin, Banff, 31 August 1934, McCalla 3935 (UBC!); Banff, 31 August 1934, McCalla 3934 (UBC!); north of Cave and Basin, Banff, 09 August 1949, Mair 222 (UBC!). British Columbia: Old Cranbrook, Mogie (= Moyie) Road, 06 August 1943, Eastham s.n. (UBC!); Trout Lake, Columbia basin, 20 June 1905, E.Wilson 453 (UBC!); Armstrong, Okanagan basin, August 1913, E. Wilson s.n. (UBC!); Hedley, 1700 ft., September 1913, Cornish 81 (UBC!); Jacko Lake outlet, Thompson Plateau, 50°36’ N, 120°27’ W, 04 August 2007, Björk 14922 (UBC!); Marl Lake, Flathead Valley, 4800 ft., 04 August 1957, Eastham 801 (UBC!); Armstrong, Okanagan basin, 15 August 1904, E.Wilson 391 (UBC!); Salmon River, Fraser basin, 01 September 1905, E.Wilson 647 (UBC!); Paul Lake, Kamloops, 28 August 1950, Krajina s.n. (UBC!); Fraser River, between Fraser Surrey docks and Pattullo Bridge, Surrey, 24 September 1991, Lomer 91-348 (UBC!); U.S. border, Flathead, 4600 ft., 27 July 1957, Bell & Davidson 582 (UBC!); Tranquille Range, Kamloops, 3200 ft., July 1936, Tisdale s.n. (UBC!); Swiftcurrent Creek, Mount Robson Park, 1058-1067 m, 53°05’ N, 119°20’ W, 30 July 1975, Chuang 75/214 (UBC!); Penticton, 29 July 1937, Stonor s.n. (UBC!); Clearwater Lake, Wells Gray Park, 52°09’ N, 120°11’ W, 25 September 1979, Goward 81-527 (UBC!); Azure Lake, Wells Gray Park, 640 m, 52°23’ N, 120°05’ W, 06 August 1980, Goward 81-692 (UBC!); Hells Gate, 26 August 1915, Newcombe 256 (UBC!); west of road in Dog Creek valley, Dog Creek area, Cariboo-Chilcotin, 51°34’ N, 122°15’ W, 22 July 1994, Goward & Clement 94-625 (UBC!); banks of the Columbia River, Revelstoke, 23 September 1917, Davidson s.n. (UBC!); 1.5 miles southeast of Lumberton on Creston-Cranbrook highway, 04 August 1953, Calder & Savile 11418 (UBC!); Kimberley, 1961, Fodor s.n. (UBC!); Marl Lake, Flathead Valley, 4800 ft., 04 August 1957, Eastham 807 (UBC!); Old Cranbrook-Moyie Road, 06 August 1943, Eastham s.n. (UBC!); Coyle-Merritt, 28 August 1950, Krajina s.n. (UBC!); Trout Lake City, 12 August 1904, Scheuber 122 (UBC!); Pitt Ponder, ca. 100 ft., 49° N, 123° W, 02 September 1975, Sullivan s.n. (UBC!); Botanie Valley, 21 August 1949, Krajina s.n. (UBC!); Kettle River, north bank, 270 m west of Cleghorn Street, town of Midway, 573 m, 49°00’22.8” N, 118°47’05” W, 08 September 2010, Lomer 7502 (UBC!); Similkameen River,
300 m north of Hwy.3 bridge, east shore, town of Princeton, 632 m, 49°27'43'' N, 120°30'11.5'' W, 08 September 2010, Lomer 7505 (UBC!); Penticton, 12 July 1937, Stonor s.n. (UBC!); Bush Arm causeway, Kinbasket Lake, 755 m, 51.809865° N, 117.366841° W, 11 July 2015, J.Fenneman 2015-350 (UBC!); Beaver Valley fen, adjacent to Hwy.1 (west side of highway), Glacier National Park, 830 m, 51.401124° N, 117.465448° W, 10 July 2017, Fenneman & Miller 2017-65 (UBC!); Princeton, Similkameen River, east bank, 300 m south of Hwy.3 bridge, 638 m, 49°27'21'' N, 120°30'18'' W, 17 August 2015, Lomer 9649 (UBC!); Kettle River, 2.4 km due south of Christina Lake, 430 m downstream from Highway 393 bridge, 445 m, 49°01'22'' N, 118°12'43'' W, 23 August 2015, Lomer 9698 (UBC!); Princeton, Similkameen River, east shore, 230 m south of Hwy.3 bridge, 640 m, 49°27'23.5'' N, 120°30'16.2'' W, 29 September 2015, Lomer 9740 (UBC!).

UNITED STATES. Idaho: at north fork of Slate Creek, along road to Adams G.S. from Slate Creek, Idaho County, 18 August 1966, Sutherland & Spellenberg 1243 (UBC!).

Montana: Wallrock Basin, about 12 miles northwest of Wilsall, Gallatin County, 08 September 1921, Suksdorf 962 (UBC!).

Oregon: Coast Range at Walker Flat, ca. 11.5 miles west of Carlton, Yamhill County, 552 m, 26 August 1985, Halse 3231 (UBC!); Walker Flat, on Walker Creek in upper drainage of Nestucca River, 1840 ft., 24 August 1984, Chambers s.n. (UBC!).

Symphyotrichum campestre


**Symphyotrichum chilense**


**Symphyotrichum ciliatum**


**Symphyotrichum ciliolatum**

**CANADA.** Alberta: approx. 80 km west of Manning, along existing ROW on Chinchaga Road, 738 m, 11V 414320 6349198 (NAD83), 13 August 2011, *Shaben & Brown Stanton61 CRP06* (UBC!); Bow River Forest Reserve, 09 July 1946, *MacDonald s.n.* (UBC!); bank of Fish Creek, west of Midnapore, 18 August 1953, *McCalla 12036* (UBC!); near Bremner, 29 August 1954, *McCalla 12326* (UBC!); below Cave & Basin, Banff, 07 August 1941, *McCalla 6792* (UBC!); Lynx Creek, west of ranger station, Crowsnest area, 4800 ft., 21 July 1960, *Ogilvie s.n.* (UBC!); below Cave and Basin, Banff, 23 August 1948, *McCalla 10262* (UBC!); Lynx Creek ranger
station, Crowsnest area, 4450 ft., 16 July 1960, Ogilvie s.n. (UBC!); lower slope of Sulphur Mountain, near upper swimming pool, Banff, 23 August 1948, McCalla 10256 (UBC!); Rocky Mountain foothills, 13 km west of Sundre, 1130 m, 51°48’ N, 114°45’ W, 04 August 1978, Lahringer 14 (UBC!). British Columbia: Okanagan Mission, Kelowna, no collection date reported, Kerr s.n. (UBC!); Kelowna, Okanagan, no collection date reported, Kerr s.n. (UBC!); Hell’s Gate, 11 August 1915, Newcombe 259 (UBC!); Armstrong, Okanagan, 04 October 1913, E.Wilson a.n. (UBC!); Okanagan, no collection date reported, E.Wilson 648 (UBC!); Armstrong, Okanagan, 16 September 1905, E.Wilson 640 (UBC!); Armstrong, Okanagan, 16 September 1905, E.Wilson 640 (UBC!); Marl Lake, Flathead Road, Kootenay District, 457 m, 49.09° N, 114.30° W, 22 August 1981, Rose aar81475 (UBC!); Pinchi Mine, 54°38’ N, 124°26’ W, 16 July 1981, Kruckeberg 72 (UBC!); south gate, Wells Gray Park, 51°56’ N, 120°02’ W, 24 October 1980, Goward 81-949 (UBC!); prison camp, 20 km north of Clearwater village, 52°50’ N, 120°02’ W, 08 September 1980, Goward 81-823 (UBC!); 7.3 km west of Penticton on road to Apex Mountain, 49°25’ N, 119°40’ W, 06 August 1986, Staley 3771 (UBC!); south shore of False Creek, near Manitoba Street, Vancouver, 04 July 1988, Lomer 88-052 (UBC!); along Hwy.16 in New Hazelton, 55°20’ N, 127°30’ W, 19 July 1989, Staley & Nicholls 5659 (UBC!); Roberts Bank coal terminal, 29 July 1991, Lomer 91-179 (UBC!); Fertilizer Mountain, Moose Pond, 49° N, 117° W, 06 July 1980, Gilmore 21 (UBC!); Canyon Creek (Quesnel-Prince George), 01 August 1946, Eastham s.n. (UBC!); Barnston Island, Surrey, 17 September 1993, Lomer 93-254 (UBC!); Knife Creek, Alex Fraser Research Forest, approx. 5 km south of 150 Mile House, 980 m, 52°02’ W, 120°10’ W, 26 July 1996, Hanel 151 (UBC!); CP yards, Surrey, 07 August 1991, Lomer 91-192 (UBC!); Taylor, ca. 27 km southeast of Fort St. John, 700 m north of golf course, 200 m east of Spruce Street, 560 m, 56°10'17'' N, 120°41'15'' W, 28 August 2001, Lomer 4253 (UBC!); Hwy.97, 1.5 km north of Stickle Road, southeast side of Swan Lake, Vernon, 398 m, 50°18’ N, 119°14’55” W, 12 August 2008, Lomer 6740 (UBC!); Hull Dr. & Springfield Rd., Lavington, east of Vernon, 530 m, 50°14’ N, 119°05’29” W, 20 September 2003, Lomer 5080 (UBC!); Penticton, 23 September 1939, Eastham s.n. (UBC!); Penticton, 28 September 1939, Eastham s.n. (UBC!); Penticton, 05 September 1937, Stonor s.n. (UBC!); Columbia Valley, 3 miles south of Fairmont, 23 July 1939, Eastham s.n. (UBC!); Revelstoke, 1932, Clemens s.n. (UBC!); Canoe Creek, Cariboo, 2800 ft., 30 August 1937, Tisdale s.n. (UBC!); I.R. Summerland, 05 August 1937, Stonor s.n. (UBC!); base of Battle Mountain, Wells Gray Park, 762-975 m, 51°57’ N, 119°53’ W, 24 July 1980, Goward 81-652 (UBC!); south end of Clearwater Lake, 52°09’ N, 120°11’ W, 22 September 1979, Goward 81-526 (UBC!); Sorrento Centre, Shuswap Lake, 50°55’ N, 119°30’ W, 29 September 1979, Watson s.n. (UBC!); Riske Creek, Cariboo, 28 August 1936, Tisdale s.n. (UBC!); Bailey’s Chutes, 11 km south of Clearwater Lake, Wells Gray Park, 52°03’ N, 120°10’ W, 06 August 1979, Goward 81-427 (UBC!); Williams Lake, August 1979, Eriderg s.n. (UBC!); Mcalure Lake (Tyhee Lake), near Telkwa, 54°43’ N, 127°01’ W, 27 July 1979, Franko 79087 (UBC!); Mcalure Lake (Tyhee Lake), near Telkwa, 54°43’ N, 127°01’ W, 27 July 1979, Franko 79075a (UBC!); White Horse bluffs area, southern Wells Gray Park, 51° N, 120° W, 25 July 1979, Goward 81-363 (UBC!); Dog Creek Reserve, Chilcotin, 975 m, 51° N, 122.5° W, 01 August 1975, Jenkins 10203 (UBC!); Yellowhead gravel pit, Mount Robson Park, 1158 m, 52°53’ N, 118°30’ W, 16 August 1975, Chuang 75/497 (UBC!); Frolek Ranch on Merritt Highway, 50° N, 120° W, 16 August 1975, Brink s.n. (UBC!); near Ray farm, south of Clearwater Lake, the Horseshoe, 52°03’ N, 120°10’ W, 31 July 1977, Goward 81-147 (UBC!); below wst part of Red Cliffs, ca. 2 miles east of Relay Creek cabin, 51°11’ N, 122.58’ W, 21 August 1977, Selby s.n. (UBC!); Armstrong Point, Shuswap Lake, ca. 29 km northwest of Rte.1, north of Salmon Arm, 10 October 1977, Staley 1696 (UBC!); airport road, Nakusp, 512 m, 50°16’ N, 117°48’ W, 01 September 1978, Papov s.n. (UBC!); Anderson Creek, upper Hat Creek valley, 1219 m, 50°43’ N, 121°42’ W, 13 August 1978, Johns 647 (UBC!);
New Denver-Kaslo Road, a few miles east and west of Whitewater Creek, Slocan, 3500 ft., 49° N, 117° W, 15 July 1975, Beamish, Luitjens, Carey, & Campbell 750282 (UBC); south of Penticton, east of road just south of Mahoney Lake, 481 m, 11U 312013 5462002 (NAD83), 01 September 2011, McIntosh 2011_290 (UBC); Smithers, 10 August 1945, Preston s.n. (UBC); 2 miles east of Fletcher Lake, 1120 m, 51°46’ N, 123°20’ W, 06 August 1978, C.E.Thompson CT-119 (UBC!); Prince George, 20 July 1946, Eastham s.n. (UBC!); near Seymour Lake, Smithers, 26 July 1946, Eastham s.n. (UBC!); along road to Duthie Mine, Smithers, 27 July 1946, Eastham s.n. (UBC!); Quesnel, 01 August 1946, Eastham s.n. (UBC!); bank of Sullivan River, Big Bend Highway, Kinbasket, 01 August 1947, Eastham s.n. (UBC!); Anahim Lake, 3500 ft., 24 July 1948, Brooks 28 (UBC!); Paul Lake, Kamloops, 20 August 1948, Clemens s.n. (UBC!); Soda Creek, 02 August 1949, T.M.C.Taylor 9030 (UBC!); Kaslo-New Denver Highway, 12 July 1940, Eastham s.n. (UBC!); Waitabit Creek, 14.5 miles west of Golden, 31 July 1947, Eastham s.n. (UBC!); Kaslo, 11 July 1941, Eastham s.n. (UBC!); about 25 miles east of Summit Pass, Alaska Highway, 27 August 1943, Raup & Correll 11558 (UBC!); vicinity of Buckinghorse River, Alaska Highway, 57°23’ N, 122°48’ W, 31 August 1943, Raup & Correll 11576 (UBC!); Houston, 15 July 1944, Eastham s.n. (UBC!); Cottonwood Creek, Quesnel, 18 July 1944, Eastham s.n. (UBC!); Gerrard, 3050 ft., 14 August 1959, Bell s.n. (UBC!); south of Kuzkwa River, on Leo Creek Rd., 16 July 1982, Kruckeberg 357 (UBC!); Vernon, 22 August 1950, Krajina s.n. (UBC!); Paul Lake, Kamloops, 28 August 1950, Krajina s.n. (UBC!); Mabel Lake, 24 August 1950, Krajina s.n. (UBC!); North Thompson River, near Kamloops, 26 August 1950, Krajina s.n. (UBC!); Thompson River, Kamloops, 26 August 1950, Krajina s.n. (UBC!); Paul Lake, 27 August 1950, Krajina s.n. (UBC!); Trapp Lake, 27 August 1950, Krajina s.n. (UBC!); Eagle River, 28 August 1950, Krajina s.n. (UBC!); against Liberty Creek, Columbia River valley, 17 July 1953, Krajina s.n. (UBC!); Mabel Lake, 23 August 1950, Krajina s.n. (UBC!); six miles east of Smithers, 14 August 1957, Ashford 146 (UBC!); Nakusp, 1450 ft., 20 July 1959, Bell s.n. (UBC!); Caribou Creek, 2490 ft., 16 July 1959, Bell s.n. (UBC!); Whatshan Lake, 28 August 1958, Bell s.n. (UBC!); east of Crown Lake, 05 August 1958, T.M.C.Taylor, Krajina, Tusko 3 (UBC!); Arrow Park, 09 July 1958, Bell s.n. (UBC!); Westwick Lake, 06 September 1955, Marrison 55083 (UBC!); Gardner Island, near Agassiz, Fraser River Valley, 49°20’ N, 121°40’ W, 15 September 1955, Krajina s.n. (UBC!); Prince George, 600 m, 54° N, 122° W, 01 August 1953, Florian 150 (UBC!); Arrow Park, 1400 ft., 09 July 1958, Bell s.n. (UBC!); Penticton, 23 September 1939, Eastham s.n. (UBC!); Prince George, 29 July 1935, Newton s.n. (UBC!); Kamloops, 1200 ft., 28 August 1936, Tisdale s.n. (UBC!); 7 miles southeast of Smithers on Highway 16, 01 September 1955, Ashford 34 (UBC!); Merritt, 2000 ft., 28 August 1920, Copley s.n. (UBC!); Horsefly area, 30 July 1967, Luitjens & Williams 125 (UBC!); McLeod Lake, 2250 ft., 19 July 1967, Krajina & Revel s.n. (UBC!); Crawford (= Crawford) Bay, May 1963, Borysowich s.n. (UBC!); Edgewood, Lower Arrow Lake, 04 August 1960, Ridwood 64 (UBC!); plot no.10, Chilocotin, 3700 ft., 51°41’ N, 123°03’ W, August 1968, Beil 68-8-17 (UBC!); near Okanagan Helicopter Pad, Smithers, 1650 ft., 25 July 1974, Krajina, Pojar, & Parsons s.n. (UBC!); Portage Brûlé Hot Springs on the Liard River near Mile 532 of the Alaska Highway, 59°37’ N, 126°55’ W, 24 July 1974, Annas s.n. (UBC!); between New Hazelton and Smithers, 15-20 miles south of New Hazelton, 1250 ft., 55° N, 127° W, 07 August 1973, Krajina s.n. (UBC!); 10.3 miles north of Alkali Lake P.O. on road to Williams Lake, 27 August 1972, Marchant & T.M.C.Taylor RLT6182 (UBC!); Cameron River area, August 1963, McWilliams 17 (UBC!); Carbon Creek mine site, northeastern British Columbia, 56°00’ N, 122°40’ W, August 1971, Morrison s.n. (UBC!); road above Wells camp, 963 m, 51° N, 122° W, 01 August 1972, Jones 393 (UBC!); 10.4 miles west of Kleena Kleene P.O. on Hwy.20, 26 August 1972, Marchant & T.M.C.Taylor RLT6163 (UBC!); 9.5 miles west of Riske Creek on Hwy.20, Cariboo region, 13 August 1972, R.L.Taylor, Beil, Marchant, & Oliver
Symphyotrichum x columbianum

**CANADA.** British Columbia: Osoyoos, 27 September 1939, *Eastham s.n.* (UBC!); Osoyoos Lake, southwest shore, Haynes Point Provincial Park, lagoon spit ca. 200 m south of Picnic area, 50 m north of interpretive trail sign, 278 m, 49°00'48" N, 119°27'16" W, 25 September 2002, *Lomer 4634* (UBC!); Osoyoos, 29 September 1939, *Eastham s.n.* (UBC!); Keremeos, Similkameen River channel east of town, 160 m due south of Willis Ranch Road, 406 m, 49°12'07" N, 119°48'33" W.
Symphyotrichum cusickii

British Columbia: Mount Caven, Flagstone, 6300 ft., August 1944, *Peterson s.n.* (UBC!); 4 km northwest of Boundary Lake, Maryland Forest Service Road, Selkirk Mountains, 1360 m, 49°02'28.3'' N, 116°55'23.4'' W, 08 July 2013, *Lomer 8409a* (UBC!); Selkirk Mountains, Priest River, 700 m north of falls, 1285 m, 49°01'12.2'' N, 116°55'54.4'' W, 21 August 2015, *Lomer 9680* (UBC!); Selkirk Mountains, 50 m north of Maryland Creek Forest Service Road, 4 km northwest of Boundary Lake, 1.7 km due northwest of Priest River Falls, 1370 m, 49°01'40.9'' N, 116°56'39.2'' W, 20 August 2015, *Lomer 9679* (UBC!); Selkirk Mountains, 80 m north of Maryland Forest Service Road, 1.8 km northwest of Priest River Falls, 30 km west of Creston, 1405 m, 49°01'41.8'' N, 116°56'46.2'' W, 20 August 2015, *Lomer 9676* (UBC!); Selkirk Mountains, 80 m north of Maryland Forest Service Road, 1.5 km north of Priest River Falls, 30 km due west of Creston, 1337 m, 49°01'39.7'' N, 116°56'01.7'' W, 20 August 2015, *Lomer 9672* (UBC!); Selkirk Mountains, Maryland Creek Forest Service Road, 5.7 km due north-northwest of Boundary Lake, 1470 m, 49°03'22.0'' N, 116°55'33.2'' W, 20 August 2015, *Lomer 9667* (UBC!); Selkirk Mountains, Maryland Creek Forest Service Road, 6 km due north-northwest of Boundary Lake, 1510 m, 49°03'42.9'' N, 116°55'21.7'' W, 20 August 2015, *Lomer 9665* (UBC!).

Symphyotrichum douglasii

1938, Newton s.n. (UBC!); Kennedy Lake, wester Vancouver Island, 31 July 1914, Darling s.n. (UBC!); Cowichan Lake, Vancouver Island, 27 August 1939, Buckland s.n. (UBC!); Cameron Lake, south shore, Beaufort Picnic Site, Vancouver Island, 190 m, 49°17'23'' N, 124°37'22'' W, 24 September 2013, Lomer 8596 (UBC!); head of Booth Canal, Saltspring Island, 11 September 1955, Ashlee s.n. (UBC!); Duck Lake, Powell River, 550 ft., 03 September 1956, Crocker s.n. (UBC!); Horne Lake, Vancouver Island, 120 m, 49°20' N, 124°44' W, 14 July 1998, Fenneman V465 (UBC!); Marble River, ca. 3 miles from Marble River Park, northwest Vancouver Island, 46 m, 50°33' N, 127°30' W, 22 July 1979, McComb-Watson 79-23 (UBC!); Victoria Lake, near Port Alice, northern Vancouver Island, 50° N, 127° W, 05 August 1977, McComb & Watson s.n. (UBC!); Victoria Lake, near Port Alice, northern Vancouver Island, 50° N, 127° W, 05 August 1977, McComb & Watson s.n. (UBC!).

UNITED STATES. Oregon: bank of the Willamette River, Jasper, Lane County, 05 November 1974, Mason 10018 (UBC!).

Symphyotrichum ericoides var. pansum

Symphyotrichum falcatum var. falcatum

CANADA. Alberta: Craigmyle District, 18 August 1948, Brinkman 5310 (UBC!); Banff, 17 July 1941, Eastham s.n. (UBC!); Normal School grounds, Calgary, 11 August 1945, McCalla 8903 (UBC!); about a mile west of Lake Chestermere, 03 September 1953, McCalla 12067 (UBC!); Craigmyle District, 08 August 1942, Brinkman 5301 (UBC!); road south of Glenbrook Farm, Bremner, 30 August 1954, McCalla 12329 (UBC!); near Edmonton, 25 August 1938, Moss 4481 (UBC!); North Hill, Calgary, 23 August 1942, McCalla 7284 (UBC!); few miles northeast of Calgary airport, 11 September 1954, McCalla 12336 (UBC!); few miles northeast of Calgary airport, 11 September 1954, McCalla 12337 (UBC!); below Normal Road Road, Calgary, 28 August 1941, McCalla 6801 (UBC!); Normal School grounds, Calgary, 18 August 1945, McCalla 8953 (UBC!); road south of Glenbrook Farm, Bremner, 30 August 1954, McCalla 12328 (UBC!); valley of Elbow River, beyond Elboya Bridge, Calgary, 28 August 1947, McCalla 9769 (UBC!); few miles northwest of Calgary, north of Banff Highway, 25 August 1953, McCalla 12040 (UBC!); North Hill, Calgary, 05 August 1940, McCalla 6437 (UBC!); about 7 miles northwest of Calgary on Banff Road, 29 August 1953, McCalla 12051 (UBC!); Craigmyle District, 11 August 1942, Brinkman 5305 (UBC!). British Columbia: Yoho National Park, ca. 100 m upriver from Highway 1 bridge, 1092 m, 51°13′12″ N, 116°34′34.4″ W, 15 August 2014, Lomer 8891 (UBC!); 3.5 miles east of Tatla Lake P.O. on road to Chilanko Forks, Chilcotin area, 27 August 1956, Calder, Parmelee, & R.L. Taylor 20482 (UBC!); Three Mile Lake, a few miles south of Clinton along highway to Cache Creek, 12 August 1956, Calder, Parmelee, & R.L. Taylor 20058 (UBC!); Dryas Island (in Fraser opposite Hope), 08 August 1914, Thacker s.n. (UBC!); Westwick Lake, 52° N, 122° W, 07 September 1955, Marrion 55096 (UBC!); old smelter, Grand Forks, 20 July 1939, Eastham s.n. (UBC!); Alces Lake, ca. 1 km northwest of mouth, 412 m, 56°07′40″ N, 120°02′10″ W, 26 July 1995, G.W. Douglas & Djan-Checker 13057 (UBC!); Fraser Valley, island in Fraser 6 km due west of Agassiz, 380 m due south of Limbert Rd. dyke, 12 m, 49°13′46.8″ N, 121°50′50.1″ W, 11 August 2010, Lomer 7412 (UBC!); Fairmont, Columbia Valley, 23 July 1939, Eastham s.n. (UBC!); 12 km southwest of 70 Mile House, 1100 m, 51°15′ N, 121°31′ W, 02 September 1981, Goward & Djan-Checker 92193 (UBC!); Chilcotin District, 27 June 1915, Newcombe 101 (UBC!); Summerland, Okanagan basin, 10 July 1910, Foek 48 (UBC!); Drummond Lake-east end, Chilcotin Plateau, 3300 ft., 52°02′ N, 122°32′ W, 08 September 1971, P. Jones 14 (UBC!); Heffley Creek, North Thompson, 11 August 1947, Eastham s.n. (UBC!); Kootenay, along Hwy.3 ca. 5 km east of Grand Forks, 49°02′ N, 118°26′ W, 30 August 1987, Ceska & Ogilvie 23038 (UBC!); Rolla, 15 km due northeast of Dawson Creek, 404 Avenue, 685 m, 55°33′58″ N, 120°08′25″ W, 27 August 2001, Lomer 4229 (UBC!); 2 miles east of Fletcher Lake, 1125 m, 51°46′ N, 123°20′
Sympotrichum falcatum var. commutatum

Symphyotrichum frondeum var. caurinum

CANADA. British Columbia: Cariboo Hudson Mine, above Cunningham Lake, Wells area, 5700 ft., 07 August 1958, Beamish, Vrugtman, & Sperrings 8893 (UBC!); Rocky Mountain foothills, 5 km northwest of Stony Lake, ca. 44 km southeast of Tumbler Ridge, 1130 m, 54°52’02’’ N, 120°38’47’’ W, 21 August 2001, Lomer & Petherbridge 4155 (UBC!); 10 miles west of Wells along Hwy.26, 12 July 1993, McCutcheon s.n. (UBC!); Court House Road, Wells area, 4350 ft., 23 July 1958, Beamish, Vrugtman, & Sperrings 8469 (UBC!); Mile 46, Haines Road, 200 m, 15 July 1956, T.M.C.Taylor, Szczawinski, & Bell 1424 (UBC!); Trophy Mountain, south of Wells Gray Park, 1935 m, 51°58’ N, 119°53’ W, 11 October 1979, Goward 81-538 (UBC!); west of Woss Lake, Vancouver Island, 500 ft., 03 September 1972, Pajar & Pinder-Moss 84 (UBC!); upper end of Claud Elliot Lake, Tsitika watershed, Vancouver Island, 1000 ft., 50°17’ N, 126°34’ W, July 1973, Roemer 317 (UBC!); junction of Sedum Creek and Festuca Creek, Ilgachuz Mountains, north of Anahim Lake, 5300 ft., 52°45’ N, 125°15’ W, 15-25 August 1972, R.L.Taylor, Beil, Marchant, & Oliver 5583 (UBC!); Murtle Lake, Fairyslipper Island, Wells Gray Park, 1067 m, 52°08’ N, 119°48’ W, 17 September 1979, Goward 81-515 (UBC!); south-facing slope above Relay Creek cabin, 1865 m, 51°11’ N, 122°58’ W, 23 August 1977, Selby s.n. (UBC!); Black Tusk Meadow, Garibaldi Park, 7000 ft., 49°51’ N, 123°48’ W, 29 August 1951, Cottle 403 (UBC!); Miller Creek which flows east and southeast into Lillooet River near Pemberton, 50° N, 122° W, 13 September 1973, Brink s.n. (UBC!); Hooper Mountain, 49°00’48’’ N, 124°28’00’’ W, 25 July 1986, A.Ceska 20539 (UBC!); Noaxe Lake slough, 07 August 1957, Brink s.n. (UBC!); Itcha Mountains, 26 miles northeast of Anahim Lake, 6200 ft., 52°43’ N, 124°54’ W, 18 August 1956, Calder, Parmelee, & R.L.Taylor 20300 (UBC!); Garibaldi, cinder cone, no collection date reported, Brink 250758 (UBC!); just east of Two Lakes Basin, Relay Creek area, 51°12’ N, 123°04’ W, 11 August 1977, Selby s.n. (UBC!); Elisabeth Mine, up Blue Creek, Lillooet area, 6250 ft., 26 July 1961, Beamish & Vrugtman 610516 (UBC!); next to W. Kwanika Creek, near
confluence with Kwanka Creek, 55°34' N, 125°23' W, 25 July 1981, Kruckeberg 191 (UBC!); Mount Moor, Noaxe Lake, north end of Shulaps Range, 6200 ft., 07 August 1957, Bird 3398 (UBC!); Sunny Point, 15.5 miles northwest of Smithers, 3500 ft., 06 August 1955, Ashford 14 (UBC!); Warren Glacier foreland, Garibaldi Park, 5000 ft., 14 August 1965, Fraser s.n. (UBC!); Vancouver Island, Jordan Ridge, plateau 7.8 km northwest of mouth of Jordan River, 1.8 km south of Loss Creek, 2200 ft., 48°29' N, 124°06' W, 17 September 2000, Roemer HR0103 (UBC!); Garibaldi, 12 August 1938, Eastham s.n. (UBC!); Forbidden Plateau, 1936, Fowle s.n. (UBC!); Mount Becher, Vancouver Island, 11 September 1967, Beder, Bednar, Kojima, & Krajina s.n. (UBC!); on road to Silver King Basin, 21 miles northwest of Smithers, 5000 ft., 05 September 1955, Ashford 55 (UBC!); Noaxe Lake, 05 September 1957, Brink s.n. (UBC!); Carbon Creek mine site, northeastern British Columbia, 56°00' N, 122°40' W, 20 August 1971, Morrison s.n. (UBC!); Garibaldi, 09 August 1938, Eastham s.n. (UBC!); Capilano Creek muskeg, 30 July 1959, Krajina s.n. (UBC!); Lihumitson Mountain, 4500 ft., 49° N, 121° W, 04 September 1950, Elvidge s.n. (UBC!); Chipiun Mountain in Hat Creek drainage, 2134 m, 50°44' N, 121°44' W, 04 September 1978, Fras 70 (UBC!); road up Windy Joe Mountain, Manning Park, 4800 ft., 04 August 1957, Beamish & Stone 7847 (UBC!); Mt. Three Brothers area, 2225 m, 49°10’ N, 122°48’ W, 04 August 1954, Brayshaw & Szczawinski 279/54 (UBC!); south-southeast slope above Carnlick Creek, Ilgachuz Mountains, ca. 5700 ft., 52°45’ N, 125°15’ W, 15-25 August 1972, R.L. Taylor, Beil, Marchant, & Oliver 5991 (UBC!); along Taylor Creek, Black Tuske Meadows, Garibaldi Park, 7000 ft., 49°51’ N, 122°48’ W, 04 August 1951, Cottle 396 (UBC!); Mount Cheam, 6000 ft., 05 September 1954, Eastham s.n. (UBC!); south-southeast slope above Carnlick Creek, Ilgachuz Mountains, 6000-6300 ft., 52°45’ N, 125°15’ W, 15-25 August 1972, R.L. Taylor, Beil, Marchant, & Oliver 5736 (UBC!); Mount Washington, Vancover Island, 900 m, 49°44’ N, 125°15’ W, 17 July 1998, Fenneman V504 (UBC!); east of Quesnel, Wells, 1209 m, 10U 592168 5881936 (NAD83), 12 August 2011, McIntosh 2011_252 (UBC!); Haines Road, km 139, 930 m, 59.941157° N, 136.799201° W, 10 August 2015, Fenneman & Hersh 2015-341 (UBC!). UNITED STATES. Alaska: Divide, Kenai Peninsula, 60°15’ N, 149°21’ W, 20 August 1951, Calder 6865 (UBC!); about 3 miles north of Lower Summit Lake, Kenai Peninsula, 60°43’ N, 149°28’ W, 18 August 1951, Calder 6843 (UBC!).

Symphyotrichum frondeum var. frondeum

CANADA. Alberta: Banff, 27 August 1907, Fletcher & Anderson 1013 (UBC!); Highwood Summit, Kananaskis Highway, 2377 m, 50°35’ N, 115°00’ W, 16 September 1975, Fodor 791 (UBC!); Kananaskis Valley, Marmot Creek, ca. 6000 ft., 13 August 1963, Ogilvie s.n. (UBC!). British Columbia: North Fork Flathead Valley Road, 1 km west of of Flathead townsite, 1485 m, 49°21'30.2'' N, 114°37'56.2'' W, 08 July 2015, Lomer, Penny, Roemer, & Batten 9545 (UBC!); Mount Brent, 4500 ft., 16 July 1939, Eastham s.n. (UBC!); Orchid Meadow, 2 miles east of ranger station, Manning Park, 1128 m, 49°51’ N, 122°48’ W, 31 July 1973, Chuang 876 (UBC!); Mount Washington, Vancouver Island, 900 m, 49°44’ N, 125°15’ W, 17 July 1998, Fenneman V504 (UBC!); east of Quesnel, Wells, 1209 m, 10U 592168 5881936 (NAD83), 12 August 2011, McIntosh 2011_252 (UBC!); Haines Road, km 139, 930 m, 59.941157° N, 136.799201° W, 10 August 2015, Fenneman & Hersh 2015-341 (UBC!).
Thompson-Okanagan, Quilchena, commonage above Quilchena, 3500 ft., 50°05' N, 120°28’ W, 11 September 1989, Pavlick 98-162 (UBC!); on road to Mount Apex, 4000 ft., 49° N, 119° W, 14 September 1974, Anonymous s.n. (UBC!); Thompson-Okanagan, Cornwall Hills, along Cornwall Hills Road, 6200 ft., 50°42’30” N, 121°27’30” W, 13 September 1989, Pavlick 89-233 (UBC!); Beaver Pond, Manning Park, 1189 m, 49°04’ N, 120°46’ W, 18 July 1974, Anonymous s.n. (UBC!); Thompson-Okanagan, Cornwall Hills, along Cornwall Hills Road, 6200 ft., 50°42’30” N, 121°27’30” W, 13 September 1989, Pavlick 89-233 (UBC!); Snow Mountain, Penticton, 03 September 1989, Pavlick 98-162 (UBC!); on road to Mount Apex, 4000 ft., 49° N, 119° W, 14 September 1974, Anonymous s.n. (UBC!); Thompson-Okanagan, Cornwall Hills, along Cornwall Hills Road, 6200 ft., 50°42’30” N, 121°27’30” W, 13 September 1989, Pavlick 89-233 (UBC!); Beaver Pond, Manning Park, 1189 m, 49°04’ N, 120°46’ W, 18 July 1974, Anonymous s.n. (UBC!); Thompson-Okanagan, Cornwall Hills, along Cornwall Hills Road, 6200 ft., 50°42’30” N, 121°27’30” W, 13 September 1989, Pavlick 89-233 (UBC!); Snow Mountain, Penticton, 03 September 1937, Stonor s.n. (UBC!); Beaver Pond, Manning Park, 1189 m, 49°04’ N, 120°46’ W, 18 July 1973, Chuang 685 (UBC!); Thompson-Okanagan, Cornwall Hills, along Cornwall Hills Road, 6200 ft., 50°42’30” N, 121°27’30” W, 13 September 1989, Pavlick 89-233 (UBC!); Snow Mountain, Penticton, 03 September 1937, Stonor s.n. (UBC!); slopes of Flatiron Mountain draining into Ewart Creek in Ashnola River District, 49° N, 119° W, 13 August 1969, Morrison s.n. (UBC!); Mile 35, Flathead Road, 4800 ft., 07 August 1957, Bell & Davidson 815 (UBC!); Mount Caven, Flagstone, 6300 ft., August 1944, Peterson s.n. (UBC!); Anahim Lake, Chilcotin, August 1944, Cornwall s.n. (UBC!); along Lussier River at White-Lussier Forest Development Road crossing, 27 August 1970, Maze s.n. (UBC!); Princeton, 05 August 1906, E.Wilson 759 (UBC!); between nature house and amphitheatre, Manning Provincial Park, Mule Deer Campground, 1080 m, 49.09094° N, 120.68001° W, 06 August 2013, E.Fenneman & J.Fenneman 28 (UBC!); Glacier National Park, Beaver River, near East Gate, 300 m west of Hwy.1, 822 m, 51°24’52.4’’ N, 117°28’35.5’’ W, 03 October 2011, Lomer 7795 (UBC!); 8 km east of Siwash Lake, about 50 km northwest of Summerland, 5200 ft., 49°50’ N, 119°33’ W, 30 July 1987, Whiting 21 (UBC!); Saint Mary River, 300 m south of confluence with Kootenay River, 1.5 km due northwest of Fort Steele, 772 m, 49°37’25’’ N, 115°38’51’’ W, 28 June 2015, Lomer 9399 (UBC!).

UNITED STATES. Colorado: no location reported, summer 1891, Penard s.n. (UBC!). Montana: Suksdorf’s Gulch, 9 miles northwest of Wilsall, 25 August 1921, Suksdorf 853 (UBC!). Oregon: near summit of Mount Ashland, 03 September 1985, Straley 3320 (UBC!); 75 yards east of Marsh Creek Bridge, 1 mile east of Umlil., Klamath County, 4750 ft., 17 September 1956, Steward & Head 7244 (UBC!). Washington: above and below trail to Frozen Lake, Yakima Peak, Mount Rainier, 6500-6800 ft., 19 August 1938, McCalla 5203 (UBC!). Wyoming: just below Holly Lake, ca. 9000 ft., Grand Teton National Park, Teton County, 20 August 1963, Rossbach 5605 (UBC!).

Symphyotrichum frondosum

CANADA. British Columbia: north of Osoyoos, east side of Osoyoos Lake, 276 m, 11U 320015 5436398 (NAD83), 19 September 2007, McIntosh & Hall 2007_43 (UBC!); north of Osoyoos, east side of Osoyoos Lake, 276 m, 11U 320015 5436398 (NAD83), 19 September 2007, McIntosh & Hall 2007_44 (UBC!); south of Okanagan Falls, northeast end of Vaseux Lake, 328 m, 11U 315921 5464149 (NAD83), 18 September 2007, McIntosh 2007_38 (UBC!); north of Osoyoos, east side of Osoyoos Lake, 276 m, 11U 320015 5436398 (NAD83), 19 September 2007, McIntosh & Hall 2007_45 (UBC!); north of Osoyoos, east side of Osoyoos Lake, 276 m, 11U 320015 5436398 (NAD83), 19 September 2007, McIntosh & Hall 2007_46 (UBC!); southeast of Oliver, 673 m, 11U 320877 5446686 (NAD83), 05 October 2007, McIntosh & Hall 2007_76 (UBC!); north of Osoyoos, east side of Osoyoos Lake, 276 m, 11U 320015 5436398 (NAD83), 19 September 2007, McIntosh & Hall 2007_41 (UBC!);
north of Osoyoos, east side of Osoyoos Lake, 276 m, 11U 320015 5436398 (NAD83), 19 September 2007, McIntosh & Hall 2007_42 (UBC!); New Westminster, McBride Blvd. and Royal Ave., northwest corner, 46 m, 49°12′44.2″ N, 122°53′56.3″ W, 21 September 2006, Lomer 6145 (UBC!); New Westminster, McBride Blvd. and Royal Ave., northwest corner, 46 m, 49°12′44.2″ N, 122°53′56.3″ W, 11 September 2006, Lomer 6137 (UBC!); Okanagan Valley, Vaseux Lake Provincial Park, ca. 5.5 km south of Okanagan Falls, Christie Memorial Provincial Park, 338 m, 49°20′51.7″ N, 119°34′25″ W, 14 October 1999, Lomer 99-263 (UBC!); Okanagan Valley, Vaseux Lake Provincial Park, ca. 5.5 km south of Okanagan Falls, 326 m, 49°17′55″ N, 119°31′52″ W, 14 October 1999, Lomer 99-260 (UBC!); Inkaneep Indian Reservation, northeast shore of Osoyoos Lake, 29 September 1993, Lomer 93-281 (UBC!); edge of Osoyoos Lake, 28 July 1939, Eastham s.n. [in part] (UBC!); Osoyoos, ca. 400 m southwest of Indian Reserve border, Cottonwood Park at the pumping station, 276 m, 49°01′55″ N, 119°26′54″ W, 21 September 2000, Lomer 3908 (UBC!); Osoyoos Lake, east side, on a spit ca. 1 km southeast of Mica Creek, 279 m, 49°03′10″ N, 119°27′50″ W, 15 August 1995, G.W.Douglas 13081 (UBC!); southeast of Oliver, 673 m, 11U 320877 5446686 (NAD83), 05 October 2007, McIntosh & Hall 2007_77 (UBC!).

**Symphyotrichum hendersonii**

**CANADA.** British Columbia: Selkirk Mountains, 1.5 km north of Priest River Falls, 1375 m, 49°01′40.9″ N, 116°55′51.3″ W, 21 August 2015, Lomer 9683 (UBC!); Selkirk Mountains, 6.2 km due north-northwest of Boundary Lake, 7.1 km north of Idaho border, 26 m east of Maryland Creek Forest Service Road, 1512 m, 49°03′51″ N, 116°54′47″ W, 22 August 2015, Lomer 9696A (UBC!); Selkirk Mountains, 440 m north of Maryland Creek Forest Service Road, 1.7 km due north of Priest River Falls, 1445 m, 49°01′45″ N, 116°55′49″ W, 21 August 2015, Lomer 9689 (UBC!).

**Symphyotrichum laeve subsp. laeve**

**CANADA.** Alberta: Craigmyle District, south of S.W.27.32.16.W.4, 27 August 1942, Brinkman 5325 (UBC!); Craigmyle District, south of S.E.29.32.16.W.4, 19 August 1942, Brinkman 5313 (UBC!); North Hill, Calgary, 23 August 1942, McCalla 7286 (UBC!); Prince’s Island, Calgary, 19 August 1950, McCalla 11307 (UBC!); prov. Govt. property, 10th Street N.W., Calgary, 19 August 1950, McCalla 11301 (UBC!); North Hill, Calgary, 16 August 1948, McCalla 10225 (UBC!); old mixing ground, Banff road, 8 miles west of Calgary, 06 August 1945, McCalla 8886 (UBC!); St. Patrick’s Island, Calgary, 31 August 1945, McCalla 9012 (UBC!); near Fish Creek, west of Midnapore, 18 August 1953, McCalla 12037 (UBC!); bank of Elbow River, near Calgary, 27 August 1948, McCalla 10276 (UBC!); North Hill, Calgary, 30 August 1953, McCalla 12053 (UBC!); mixing ground on Banff road, 8 miles west of Calgary, 06 August 1945, McCalla 8890 (UBC!); east of Edmonton International Airport, at corner of 4th Street and 11th Avenue, Nisku, 19 August 1987, Straley 4371 (UBC!); Crownsnest area, Lynx Creek, west of ranger station, 4800 ft., 21 July 1960, Ogilvie s.n. (UBC!); Waterton Lakes National Park, Red Rock Canyon Road, 2 miles east of warden station, 4900 ft., 03 August 1961, Ogilvie s.n. (UBC!); Spray River Cabin horse grounds, Banff National Park, 22 June 1949, Mair 24b (UBC!); Grand Valley, 3 miles north and 1 mile west of Banff Highway, 17 August 1949, McCalla 10570 (UBC!); low bank of Bow River, south edge of St. George’s Island, Calgary, 20 August 1948, McCalla 10241 (UBC!); valley of Elbow River beyond Elboya Bridge, Calgary, 28 August 1947, McCalla 9768 (UBC!); south
end of Astoten Lake, Elk Island National Park, Lamont, 22 August 1939, O'Connor 17-6 (UBC!); southwest of Calgary, August 1987, Black 100 (UBC!); Banff, 05 August 1902, R.Watson s.n. (UBC!); 27 miles from Calgary centre, 17 August 1947, McCalla 9709 (UBC!); along west side of Red Deer River east of Delburne, 12 August 1984, Straley 3075 (UBC!). British Columbia: along Rte.29, ca. 23.5 km southwest of junction with Alaska Highway, near bridge over Cache Creek, west of Fort St. John, 56°20' N, 121°15' W, 28 July 1990, Straley 6191 (UBC!); Premier Lake, Kimberley, 14 July 1946, Fodor 93 (UBC!); Goat Mountain, Erickson, just above Holder’s ranch, 04 August 1943, Eastham s.n. (UBC!); Edgewater, 04 September 1950, Brink 50-12 (UBC!); junction of Peace and Pouce Coupé Rivers, B.C. side, June-July 1943, Crickmay s.n. (UBC!); Waldo, 10 September 1950, Brink s.n. (UBC!); S. Peace River, SW 2 80 18 6, 08 July 1958, Shearer s.n. (UBC!); along Rte.29, ca. 23.5 km southwest of junction with Alaska Highway, near bridge over Cache Creek, west of Fort St. John, 56°20' N, 121°15' W, 28 July 1990, Straley 6191 (UBC!); Creston, 26 September 1964, Fodor 245 (UBC!); Peace River area, Pouce Coupé, 23 September 1929, Travis 2 (UBC!); Cranbrook, September 1917, Davidson s.n. (UBC!); side of Okanagan Landing Road, 49°39' N, 114°51' W, 10 August 1977, Wright s.n. (UBC!); Canal Flats, 22 July 1938, Eastham s.n. (UBC!); Sparwood area, Michael pile, side of Hwy.3, across from Westar Mine security gate, 49°39' N, 114°51' W, 10 August 1991, Lee 226 (UBC!); 5 km east of Crownsnest Pass on Hwy.3, 1390 m, 49°37' N, 114°35' W, 02 August 1981, Goward 81-1695B (UBC!); roadside rest area at Lost Creek, along Rt.3, east of junction with Rt.6, south of Salmo, 49°05' N, 117°10' W, 24 August 1984, Straley 3092 (UBC!); between Jaffray and Elko, 13 August 1943, Eastham s.n. (UBC!); Fairmont Hot Springs, 10 August 1943, Eastham s.n. (UBC!); Creston, 26 September 1964, Fodor 246 (UBC!); New Westminster, 100 m east of McBride Blvd., 200 m south of Memorial Drive, 50 m, 49°12’51'' N, 122°53,59’ W, 16 September 2010, Lomer 7506 (UBC!); off Baldonnel Road, above Beatton River, southeast of Fort St. John, 580 m, 56.158376° N, 120.434973° W, 25 August 2017, Fenneman & McIntosh 2017-61 (UBC!); Fort St. John, 10N 671997 6246650 (NAD83), 03 July 2012, Decker 7689 (UBC!). Manitoba: The Pas, 40 miles south of Winnipeg Highway, 12 August 1956, Krivda 1786 (UBC!); Graham Bay, Algoma District, 47°00’ N, 84°45’ W, 18 September 1935, T.M.C.Taylor et al. 1483 (UBC!); CNR tracks at northwest corner of Russell, Russell Township, 26 August 1972, Garton 15247 (UBC!). Saskatchewan: Rabbit, Prince Albert National Park, 11 September 1958, Pearson s.n. (UBC!); Spruce River Camp, Prince Albert National Park, 21 August 1958, Pearson 7 (UBC!); Coulee, south of Swift Current, 13 August 1959, Buchanan s.n. (UBC!); Rt.7, 2 miles east of Moosomin, 17 August 1969, Wiehler 6977 (UBC!). United States. Colorado: Boulder, Boulder County, 30 August 1962, G.N.Jones 34839 (UBC!). Massachusetts: Tyngsboro, 09 September 1927, Beattie s.n. (UBC!); North Easton, 18 September 1901, Blomberg s.n. (UBC!). Montana: Game Range Flats, entrance road, Lewis & Clark County, 31 July 1977, Harvey 77257 (UBC!); Glacier National Park, 18 August 1969, Langford s.n. (UBC!). New Hampshire: Pelham, 13 September 1927, Beattie s.n. (UBC!). New York: 1 mile south of junction of Rts.22 & 71 on Rte.22 (Green River), 18 September 1967, Ahles 70008 (UBC!). South Dakota: along Indian Creek, ca. 20 miles north of Belle Fourche, Butte County, 23 August 1963, G.N.Jones 36345 (UBC!). Wisconsin: west side of Madison, 04 October 1941, Shimmers 4127 (UBC!).

**Symphyotrichum lanceolatum subsp. lanceolatum**

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British Columbia: Dawson Creek, north of railroad track, 670 m, 55°47’ N, 120°14’ W, 26 July 1976, Chuang 228 (UBC!); Meier’s Lodge on northwest side of Cluculz Lake between Prince George and Vanderhoof, 03 September 1954, Calder, Savile, & Ferguson 15353 (UBC!); Rolla, 15 km due northeast of Dawson Creek, 404 Ave. across from church, 685 m, 55°53’58” N, 120°08’25” W, 27 August 2001, Lomer 4228 (UBC!); Jim Meadow, Chilcotin, 358 m, 51° N, 124° W, July 1979, Selby & Roberts 1 (UBC!); Cowichan Lake, Vancouver Island, 27 August 1939, Buckland s.n. (UBC!); Bear Flats, Peace River, west of Fort St. John, 425 m, 56.260460° N, 121.240907° W, 18 July 2017, Fenneman & McIntosh 2017-64 (UBC!); Beatton River, east of Fort St. John, south of Cecil Lake, 430 m, 56.27° N, 120.68° W, Fenneman & McIntosh 2016-59 (UBC!); Rolla, Pouce Coupé River, Landry Road bridge crossing, 590 m, 55.87° N, 120.03° W, 15 August 2016, Fenneman & McIntosh 2016-60 (UBC!); Peace Island Park, Taylor, 420 m, 56.14° N, 120.70° W, 18 August 2016, Fenneman & McIntosh 2016-47 (UBC!); Powell River area, Sliammon Lake, 140 m, 49.925728° N, 124.589773° W, 18 August 2015, Fenneman 2015-342 (UBC!); north of Hope, Yale Garry Oak Ecological Reserve, 51 m, 11U 615796 5491782 (NAD83), 03 October 2011, McIntosh & Joya 2011_409 (UBC!); Sicamous, marshy edge of Shuswap Lake, 23 July 1941, Eastham s.n. (UBC!); Kootenay Landing, Kootenay Lake, 25 September 1917, Davidson s.n. (UBC!); Osoyoos, 27 September 1939, Eastham s.n. (UBC!); Creston Flats, 26 July 1939, Eastham s.n. (UBC!); Indian Hay Meadow, Kamloops area, 24 July 1939, Davidson s.n. (UBC!); Kootenay, Christina Lake Provincial Park, Christina Lake, east shore north of Texas Point, 49°03’ N, 118°13 W, 14 August 1981, Ceska & Ceska 7140 (UBC!); South Nakusp, 13 July 1940, Eastham s.n. (UBC!); Kootenay, Christina Lake, east shore at the end of White Road, 49°07’ N, 118°15’ W, 30 August 1987, Ceska & Ogilvie 23067 (UBC!); Fraser Canyon, Boston Bar, bridge over Fraser to North Bend, west bank north of bridge, 106 m, 49°52’40” N, 121°26’40” W, 29 August 2004, Lomer 5425 (UBC!); Gray Creek, Kootenay Lake, 12 July 1941, Eastham s.n. (UBC!); Longbeach, Kootenay Lake, 21 July 1937, Eastham s.n. (UBC!); Lightning Peak Road, Monashee, 4000 ft., 14 July 1940, Eastham s.n. (UBC!); near Doukbr. Wharf, rocks above Kootenay Lake, 08 September 1947, Murray s.n. (UBC!); Kaslo, 11 July 1941, Eastham s.n. (UBC!); Kokanee Creek area, 1000 m, 49°40’ N, 117°07’ W, 30 July 1981, Goward 81-1648B (UBC!); Mirror Lake, 08 July 1940, Eastham s.n. (UBC!); Yale, on Fraser River gravel bar, 09 September 1972, Pinder-Moss s.n. (UBC!); Chilliwack, 15 August 1939, Eastham s.n. (UBC!); Sumas, 02 August 1940, Eastham s.n. (UBC!); Chilliwack, 15 August 1939, Eastham s.n. (UBC!); Hatzic, 5 m, 49°09’ N, 122°15’ W, 02 August

**Canada**.


**Symphyotrichum x maccalae**


**UNITED STATES.** Montana: Shields River, north of Wilsall, Park County, 17 August 1921, *Suksdorf 798* (UBC!).

**Symphyotrichum novi-belgii var. novi-belgii**

of the Kearney exit, Clay County, 21 September 1972, Lomer 9108 (UBC!); 300 m north of Hwy.7, 1.2 km east of Pitt River bridge, Pitt Meadows, 2 m, 49°14’30”’ N, 122°42’37”’ W, 16 October 2002, Lomer 4660 (UBC!); 70 m east of King Edward Street, in back of 1101 United Blvd., Coquitlam, 5 m, 49°13’54”’ N, 122°57’38”’ W, 13 September 2003, Lomer 5069 (UBC!); Broadway & Duthie Ave., northwest lot, Burnaby, 65 m, 49°15’41”’ N, 122°57’13”’ W, 05 November 2007, Lomer 6529 (UBC!); Trent River estuary, Royston, 1 m, 49°38’ N, 124°55’ W, 19 August 1999, Fenneman V948 (UBC!); Iona Island, Vancouver, 1 m, 49.21° N, 123.20° W, 23 August 2013, Fenneman 2013-150 (UBC!); Terra Nova, off River Road, Richmond, 0 m, 49.17° N, 123.20° W, 07 September 2016, Fenneman 2016-27 (UBC!); Terra Nova, off River Road, Richmond, 0 m, 49.17° N, 123.20° W, 07 September 2016, Fenneman 2016-26 (UBC!); Southlands, trail off end of Celtic Ave., south Vancouver, 0 m, 49.21° N, 123.16° W, 07 September 2016, Fenneman 2016-22 (UBC!); Iona Island causeway, Vancouver, 1 m, 49.21° N, 123.20° W, 07 September 2016, Fenneman 2016-19 (UBC!); Iona Island causeway, Vancouver, 1 m, 49.21° N, 123.16° W, 07 September 2016, Fenneman 2016-18 (UBC!). Nova Scotia: Cow Bay, 21 August 1930, Forward s.n. (UBC!); Lawrencetown, 24 August 1903, Forward s.n. (UBC!). Quebec: Ruisseau Bleu, Canton Randin, 48°32’ N, 65°05’ W, 22 July 1963, Lemieux s.n. (UBC!); Pointe-aux-Outardes, Côté Saguenay, 30 July 1963, Cinq-Mars, Rousseau, & Bonneau 63-875 (UBC!); Coleraine, canton de Coleraine, comté de Mégantic, 11 August 1965, Blais, Deshaies, & Forest 10723 (UBC!); Lac Aylmer, canton de Coleraine, comté de Wolfe, Baie du Pansu, 02 August 1967, Brisson & Hamel 12812 (UBC!); Lac Aylmer, canton de Coleraine, comté de Wolfe, Baie du Disraeli, 28 August 1967, Hamel 13127 (UBC!); Black Lake, nord-ouest de Reed Hill, canton de Coleraine, comté de Mégantic, 26 August 1965, Blais, Brisson, Deshaies, & Forest 10776 (UBC!); Trou de Fées, St-Jacques, comté de Montcalm, 18 August 1933, Louis-Marie s.n. (UBC!); Rivièrè Ste-Marguerite, canton Labrosse, cté Chicoutimi, 48°24’ N, 70°07’ W, 12 August 1964, Coyouette & Brisson 64706 (UBC!); Parc des Laurentides, aux Portes d’Enfer, comté de Montmorency, 13 August 1959, Louise-Marie, Gervais, & Lavigne s.n. (UBC!); Black Lake, canton d’Ireland, comté de Mégantic, 24 August 1965, Blais, Brisson, Deshaies, & Forest 10756 (UBC!); Lac Aylmer, canton de Garthby, comté de Wolfe, Baie Moose ouest, 03 September 1967, Brisson 13182 (UBC!); Canton Garnier, cté Lac-St-Jean, 14 August 1963, Cinq-Mars, v.d.Hende, Rousseau, & Bonneau 63-1150 (UBC!). UNITED STATES, Massachusetts: Newburyport, 1903, Eaton & Robinson s.n. (UBC!); North Easton, 26 September 1901, Eaton s.n. (UBC!). New York: Greenport, Suffolk County, 16 October 1939, Latham 8356 (UBC!); Greenport, Suffolk County, 22 September 1939, Latham 8851 (UBC!). North Carolina: 1.8 miles north-northwest of Garland on NC.411, 12 October 1957, Ahles 36791 (UBC!). Washington: Point Roberts, 24 September 1916, Perry s.n. (UBC!).

**Symphyotrichum pilosum var. pilosum**

Gulch, 09 August 1950, *Krajima s.n.* (UBC!). *South Carolina*: Camden, Kershaw County, 06 October 1957, *Radford 29945* (UBC!); at corner of Wheat and Pickens St., Richland County, 10 October 1994, *Drakeford 42* (UBC!).

**Symphyotrichum puniceum var. puniceum**

**CANADA.** *Alberta*: Hwy.16, west of Seba, 28 August 1954, *McCalla 12315* (UBC!); 6 km east of BC border, 990 m, 54°47’20” N, 119°54’00” W, 14 July 1998, *Lomer & Lancaster 98-274* (UBC!); Hwy.16, west of Seba, 28 August 1954, *McCalla 12316* (UBC!); Acheson Bog, west of Edmonton, 16 September 1956, *Moss 10858* (UBC!); Bruderheim, 29 July 1938, *Moss 4443* (UBC!); northeast of Gibbons, north of Edmonton, 07 September 1942, *Moss 6417* (UBC!). *British Columbia*: approximately 150 km east of Fort Nelson, along existing Ekwan pipeline ROW, 370 m, 10V 635715 6504583 (NAD83), 23 July 2011, *Kershaw & Shaben Stantec004_T06* (UBC!); Taylor, 800 m, 10V 657868 6209670 (NAD83), 31 July 2015, *Anderson s.n.* (UBC!); approximately 150 km east of Fort Nelson, along existing Ekwan pipeline ROW, ~370 m, 10V 632766 6503463 (NAD83), 23 July 2011, *Kershaw & Shaben Stantec004_T06* (UBC!); Peace River Regional District, north of Chetwynd, south of the Peace River, on both sides of the 400 Road, 657 m, 56.1071° N, 121.0721° W, 06 August 2011, *R.Krichbaum & M.Krichbaum eaglecap15135* (UBC!); Peace River Regional District, north of Chetwynd, near Monias Lake Road, 686 m, 56.0564° N, 121.2489° W, 08 August 2011, *R.Krichbaum & M.Krichbaum eaglecap15136* (UBC!); Peace River Regional District, south of Hudson’s Hope, approximately 7.5 km east of Hwy.29, 722 m, 55.9668° N, 121.8675° W, 23 September 2011, *R.Krichbaum & M.Krichbaum eaglecap15137* (UBC!); Peace River Regional District, north of Moberly Lake, approximately 3 km west of Medicine Woman Road, 753 m, 55.9816° N, 121.7385° W, 24 September 2011, *R.Krichbaum & M.Krichbaum eaglecap15138* (UBC!); Peace River Regional District, north of Moberly Lake, approximately 5.5 km east of Medicine Woman Road, 722 m, 55.9966° N, 121.6007° W, *R.Krichbaum & M.Krichbaum eaglecap15139* (UBC!); Peace River Regional District, north of Moberly Lake, approximately 3.3 km east of Medicine Woman Road, 717 m, 55.9926° N, 121.6373° W, 25 September 2011, *R.Krichbaum & M.Krichbaum eaglecap15140* (UBC!); Peace River Regional District, north of Chetwynd, approximately 9 km west of Jackfish Road, 681 m, 56.0082° N, 121.5175° W, 26 September 2011, *R.Krichbaum & M.Krichbaum eaglecap15141* (UBC!); Peace River Regional District, south of Hudson’s Hope, approximately 4 km east of Hwy.29, 723 m, 55.9648° N, 121.9082° W, 27 September 2011, *R.Krichbaum & M.Krichbaum eaglecap15143* (UBC!); Peace River Regional District, Hudson’s Hope, north of the airport, 684 m, 56.0542° N, 121.9889° W, 18 July 2012, *R.Krichbaum & M.Krichbaum eaglecap15163* (UBC!); Peace River Regional District, north of Chetwynd, south of the Peace River, along the 400 Road north of the railroad tracks, 652 m, 56.1174° N, 121.0972° W, 16 August 2012, *R.Krichbaum & M.Krichbaum eaglecap15165* (UBC!); Peace River Regional District, south of Fort St.John, south of the Peace River, 640 m, 56.1638° N, 120.9222° W, 23 July 2011, *R.Krichbaum & M.Krichbaum eaglecap15132* (UBC!); Peace River Regional District, north of Chetwynd, south of the Peace River, north of Ice Bridge Road, 656 m, 56.1285° N, 120.9938° W, 04 August 2011, *R.Krichbaum & M.Krichbaum eaglecap15133* (UBC!); Peace River Regional District, north of Chetwynd, south of the Peace River, 647 m, 56.1343° N, 120.9738° W, 05 August 2011, *R.Krichbaum & M.Krichbaum eaglecap15134* (UBC!); near Redwillow Creek recreation area, 35 km south of Kelly Lake, 930 m, 10U 688200 6088949 (NAD83), 28 August 2007, *Ottenbreit & Yakimchuk s.n.* (UBC!); west on Hwy.97 from Dawson Creek, south on Hwy.52, Upper Cutbank Road, 825 m, 10U 659393 6160794 (NAD83), 16 August 2008, *Golinski & Griffiths s.n.* (UBC!); west on Hwy.97 from Dawson Creek, south on Hwy.52, adjacent to Upper
Cutbank Road (east of Fellers Heights), 825 m, 10U 656592 6165351 (NAD83), 18 August 2008, Golinski & Griffiths s.n. (UBC!); ca. 500 m south of Tupper Creek, Hwy. 2 ca. 2.4 km west of Alberta border, 736 m, 55°39'21"' N, 120°02'16"' W, 27 August 2001, Lomer 4226 (UBC!); ca. 25 km north-northeast of Dawson Creek, ca. 1.5 km south of town of Doe River, 640 m, 55°59'13"' N, 120°05'24"' W, 27 August 2001, Lomer 4231 (UBC!); near the Komie Road, northeast of Fort Nelson, 10V 598924 6509869 (NAD83), 21 July 2010, Beechey & Ottenbreit s.n. (UBC!); Hwy. 97, south of Taylor, 745 m, 56.05° N, 120.64° W, 15 August 2016, Fenneman & McIntosh 2016-48 (UBC!); Stewart Lake, 64 km northwest of Dawson Creek, 890 m, 55.96° N, 121.17° W, 18 August 2016, Fenneman & McIntosh 2016-57 (UBC!); east of Fort St. John, Cecil Lake area (north of lake), 250 Road, 725 m, 56.36° N, 120.63° W, 18 August 2016, Fenneman & McIntosh 2016-58 (UBC!); west of Fort St. John, Upper Cache Creek Road, 640 m, 56.25° N, 121.44° W, 14 August 2016, Fenneman & McIntosh 2016-61 (UBC!).

Manitoba: Moon Lake Nature Trail, Riding Mountain National Park, 50°52.8' N, 100°03.2° W, 06 August 1979, Wojtas, Wojtas, & Allan- Wojtas 959 (UBC!); Dump Road, The Pas, 15 August 1956, Krivda 1841 (UBC!).

Newfoundland & Labrador: Goose Bay, 53°17' N, 60°30' W, 01 August 1950, Gillett & Findlay 5551 (UBC!); Goose Bay, 53°18' N, 60°25' W, 26 August 1950, Gillett & Findlay 5896 (UBC!).

Northwest Territories: Pine Point mine site, 600 m, 60°1’ N, 114°15’ W, 22 August 1976, C.E.Jones s.n. (UBC!).

Nova Scotia: Lawrencetown, 05 September 1930, Forward s.n. (UBC!).

Ontario: Angler, Thunder Bay District, 48°45' N, 86°15' W, 05 August 1939, T.M.C.Taylor, Bannan, & Harrison 357 (UBC!); by railway track, Angler, Thunder Bay District, 48°45' N, 86°15' W, 05 August 1939, T.M.C.Taylor, Bannan, & Harrison 339 (UBC!); Big Lake, Thunder Bay District, 48°45' N, 86°15' W, 09 August 1939, T.M.C.Taylor, Bannan, & Harrison 334 (UBC!); beside railway, Melgund, Thunder Bay District, 48°45' N, 86°15' W, 26 July 1939, T.M.C.Taylor, Bannan, & Harrison 338 (UBC!); Plevna, 15 August 1902, Fowler s.n. (UBC!); near Heart Lake, Snelgrove, Peel County, 12 October 1935, Brown 5044 (UBC!); 1/2 mile south of Hwy. 61, Neebing-Blake townline, Thunder Bay District, 09 September 1950, Garton & Campbell 1350 (UBC!); 1 mile east of shipyard crossing, CPR tracks, Current River, Port Arthur, Thunder Bay District, 24 September 1950, Garton 1372 (UBC!); Port Coldwell, Thunder Bay District, 48°45' N, 86°15' W, 05 August 1939, T.M.C.Taylor, Bannan, & Harrison 333 (UBC!); Big Lake, Thunder Bay District, 48°45' N, 86°15' W, 09 August 1939, T.M.C.Taylor, Bannan, & Harrison 334 (UBC!); beside railway, Melgund, Thunder Bay District, 48°45' N, 86°15' W, 26 July 1939, T.M.C.Taylor, Bannan, & Harrison 338 (UBC!); Plevna, 15 August 1902, Fowler s.n. (UBC!); near Heart Lake, Snelgrove, Peel County, 12 October 1935, Brown 5044 (UBC!); 1/2 mile south of Hwy. 61, Neebing-Blake townline, Thunder Bay District, 09 September 1950, Garton & Campbell 1350 (UBC!); 1 mile east of shipyard crossing, CPR tracks, Current River, Port Arthur, Thunder Bay District, 24 September 1950, Garton 1372 (UBC!); Port Coldwell, Thunder Bay District, 48°45' N, 86°15' W, 05 August 1939, T.M.C.Taylor, Bannan, & Harrison 333 (UBC!); 14.4 miles northeast of Hwy. 17, off Mission Road, Algoma District, 47°54' N, 84°40' W, 12 August 1971, Garton et al. 14733 (UBC!); south bank of Little Pine River, 1 mile west of mouth, Crooke Township, Thunder Bay District, 16 August 1952, Garton 2150 (UBC!); Rockliffe, 15 September 1935, Forward s.n. (UBC!); Rockland, 28 August 1935, Forward s.n. (UBC!); Buda Lake access road, 1 km south of Weikwabinonaw River bridge, Thunder Bay District, 48°22' N, 90°38' W, 10 August 1981, Garton 20470 (UBC!); Lake Nipigon Provincial Park at CNR crossing of park road, Kilkenny Township, Thunder Bay District, 19 August 1983, Garton 23087 (UBC!); Muskrat River, just as it emerges from Muskrat Lake, 5 miles south-southwest of Black Sturgeon Research Station, Thunder Bay District, 49°19' N, 88°48' W, 11 August 1969, Garton 12429 (UBC!); vicinity of Rainy River town, Atwood Township, Rainy River District, September 1961, Martinsen 9515 (UBC!); behind Riverside Cemetery, Oliver Road, Thunder Bay City, 48°21' N, 89°19' W, 04 September 1969, Garton 12586 (UBC!); Chalk River, 15 August 1962, Merrilees & Brayshaw s.n. (UBC!).


**Symphyotrichum spathulatum var. intermedium**


**Symphyotrichum subspicatum**


**PUTATIVE HYBRIDS**

**Symphyotrichum ascendens x S. bracteolatum**

**UNITED STATES.** Montana: Jackrabbit Gulch, 9 miles northwest of Wilsall, Park County, 20 August 1921, *Suksdorf 807* (UBC!).

**Symphyotrichum boreale x S. bracteolatum**

**CANADA.** British Columbia: small fen aside highway between Revelstoke and Shelter Bay ferry, West Kootenays, 50°43’ N, 118°00’ W, 02 June 2005, *Björk 22018* (UBC!); shore of Madden Lake, 20 miles north of Riske Creek, Chilcotin, 31 July 1950, *Cottle 286* (UBC!).

**Symphyotrichum boreale x S. falcatum var. falcatum**

**CANADA.** British Columbia: unnamed lake above the junction of the Big Creek and Gang Ranch Roads, 1158 m, 51° N, 122° W, 01 August 1972, *P.Jones 402* (UBC!).

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Symphyotrichum boreale x S. puniceum var. puniceum [= S. x longulum]

Canada. Alberta: Craigmyle District, 26 August 1942, Brinkman 5321 (UBC!).

Symphyotrichum bracteolatum x S. chilense

United States. California: St. Lawrence, 20 September 1982, M.E. Jones 2743 (UBC!).

Symphyotrichum bracteolatum x S. falcatum var. falcatum

Canada. British Columbia: 7.5 km south-southeast of Windermere Lake, 2 km west of Fairmont Hot Springs resort, 810 m, 50°20’40” N, 115°53’05” W, 16 August 2014, Lomer 8904 (UBC!).

Symphyotrichum bracteolatum x S. laeve subsp. laeve


Symphyotrichum bracteolatum x S. lanceolatum subsp. hesperium

Canada. British Columbia: Nicola Lake, 2000 ft., 50°10’ N, 120°40’ W, 08 August 1951, Dickens 111 (UBC!); Mara Meadows Ecological Reserve, north of Enderby, west of Mara Lake, 671 m, 08 August 1971, Beamish & Revel 710031a (UBC!).

Symphyotrichum bracteolatum x S. novi-belgii var. novi-belgii

Canada. British Columbia: 1/2 mile northwest of Langley Prairie, 29 July 1954, Faris, Jr. 225 (UBC!).

Symphyotrichum campestre x S. ericoides var. pansom

Canada. British Columbia: Rocky Mountain Trench, Fairmont Hot Springs, 900 m, 50°19’53” N, 115°51’00” W, 24 September 2003, Lomer 5109 (UBC!); 400 m north of Quad F-5, Hat Creek, 3850 ft., 50°40’ N, 121°36’ W, 22 July 1976, Beirne, Burnard, & Boulding 1-054 (UBC!); Kamloops area, Dufferin, south of Hwy.1, 2 km east of Lac le Jeune Road, 300 m east of Copperhead Dr. & Hugh Allen Rd., 760 m, 50°39’14” N, 120°23’38” W, 22 September 2004, Lomer 5486 (UBC!).

Symphyotrichum ciliolatum x S. lanceolatum subsp. hesperium

Canada. Alberta: ca. 80 km west of Manning, Alberta, along existing ROW on Chinchaga Road, 809 m, 11V 405026 6354415 (NAD83), 13 August 2011, Shaben & Brown Stantec033 CRP05 (UBC!). British Columbia: Red Rocks, 600 m, 54° N, 122° W, 06 September 1953, S.F.F. 159 (UBC!); 2 miles from Agassiz on south side of Fraser, 02 September 1912, W. Taylor s.n. (UBC!); near Cambie, 06 August 1958, T.M.C. Taylor, Krajina, & Tusko 14 (UBC!); Cottonwood Island Park, Prince George, 560 m, 53°55’ N, 122°43’ W, 20 September 1998, Fenneman V661 (UBC!).
Symphyotrichum ciliolatum x S. novi-belgii var. novi-belgii [= S. x subgeminatum]

CANADA. Quebec: Mont Ste-Anne, côte Gaspé, 20 August 1935, Colpron s.n. (UBC!).

Symphyotrichum ciliolatum x S. subspicatum

CANADA. British Columbia: Moricetown Canyon, 1500 ft., 13 July 1974, Krajina, Pojar, & Parsons s.n. (UBC!); Inshipsan (?) Point, Skeena River valley, 120 ft., 28 July 1973, Krajina s.n. (UBC!).

Symphyotrichum chilense x S. douglasii

UNITED STATES. Oregon: Applegate River, on Palmer Creek Road, 1.4 km from junction with Applegate Road, south of Ruch, 11 September 1994, Straley 8070 (UBC!).

Symphyotrichum chilense x S. novi-belgii var. novi-belgii

CANADA. British Columbia: Fraser Mills, 21 September 1913, Henry s.n. (UBC!); Canoe Pass, 07 August 1958, Eastham 4199 (UBC!); Ganges, 06 September 1959, Ashlee 17 (UBC!); Greater Vancouver, Surrey, Timberland Road, 1 km south of Pattullo Bridge, 3 m, 06 September 2003, Lomer 5044 (UBC!); islands below Sapperton, New Westminster, 17 September 1994, Lomer 94-205 (UBC!); edge of Fraser River, Gladstone Riverfront Park, foot of Portside Drive, off SE Marine Drive, 01 October 1989, Straley 5913 (UBC!); Somass River delta, Port Alberni, 0 m, 15 August 1972, Pojar 359 (UBC!); Sproat Falls, Alberni, Vancouver Island, 09 August 1941, Eastham s.n. (UBC!); Captain’s Cove, 49° N, 123° W, 16 October 1971, McLaren s.n. (UBC!).

Symphyotrichum chilense x S. subspicatum

CANADA. British Columbia: Cape St. James, St. James Island, Queen Charlotte Islands, 51°56’ N, 131°01’ W, 18 August 1978, Veale s.n. (UBC!).

Symphyotrichum douglasii x S. novi-belgii var. novi-belgii

CANADA. British Columbia: Quinsam Lake, Vancouver Island, 20 June 1951, Bendell s.n. (UBC!).

Symphyotrichum ericoides var. pensus x S. falcatum var. falcatum

Symphyotrichum frondeum var. caurinum x S. frondeum var. frondeum

CANADA. British Columbia: Grouse Mountain, July 1958, Roller s.n. (UBC!); Tchaikazan Valley, Taseko Lake area, 6000 ft., 51°10’ N, 123°45’ W, 04 August 1969, Beamish & Pinder-Moss 690117 (UBC!); Festuca Creek, Ilgachuz Mountains, 5350-5500 ft., 52°45’ N, 125°15’ W, 15-25 August 1972, R.L. Taylor, Beil, Marchant, & Oliver 5636 (UBC!); Garibaldi, August 1940, McTavish s.n. (UBC!); Lightning Ridge, Manning Park, 16 August 1970, Fisher s.n. (UBC!); Boss-Crooked Lake, 30 July 1967, Luitjens & Williams 111 (UBC!); Anaheim (= Anahim) Lake, 1220 m, 49°06’15” N, 120°50’ W, 27 August 1974, Chuang 1288 (UBC!); Fraser Valley, Elk Mountain, south slope, ca. 1.5 km east of summit, ridge below trail to Mount Thurston, ca. 10 km southeast of Chilliwack, 1500 m, 49°06’15” N, 121°46’50” W, 22 September 1999, Lomer 99-219 (UBC!); between Gibson Pass and Strawberry Flats, Manning Park, 1372 m, 49°04’ N, 120°53’ W, 25 July 1973, Chuang 786 (UBC!); Barrier Lake, Garibaldi Park, 01 August 1951, Jackson s.n. (UBC!).

Symphyotrichum frondeum var. caurinum x S. ciliolatum

CANADA. British Columbia: Topley, 54° N, 126° W, 31 July 1956, MacDonald 397 (UBC!); 6 miles up Bowron Lakes Road, Wells area, 4300 ft., 22 July 1958, Beamish, Vrugtman, & Sperrings 8417 (UBC!).

Symphyotrichum frondeum var. caurinum x S. douglasii

CANADA. British Columbia: Cameron Lake, Vancouver Island, 21 August 1917, McBey s.n. (UBC!).

Symphyotrichum frondeum var. frondeum x S. laeve subsp. laeve

Specimens Reviewed: CANADA. Alberta: Kananaskis Valley, lower Marmot Creek, 5300 ft., 12 August 1963, Ogilvie s.n. (UBC!). British Columbia: Mile 35, Flathead Road, 4800 ft., 07 August 1957, Bell & Davidson 814 (UBC!); Emkay Mine, Elk River, Mount Bleasdell, 50°20’ N, 114°57’ W, 10 August 1972, Morrison s.n. (UBC!).

Symphyotrichum frondeum var. frondeum x S. lanceolatum subsp. hesperium

CANADA. British Columbia: Mabel Lake, 1300 ft., 24 August 1950, Krajina s.n. (UBC!).

Symphyotrichum lanceolatum subsp. hesperium x S. puniceum var. puniceum

CANADA. British Columbia: Pine River, southwest of Taylor, 455 m, 56.035430° N, 121.184759° W, 27 August 2017, Fenneman & McIntosh 2017-63 (UBC!); Peace River Regional District, Hudson’s Hope, north of the airport, 687 m, 56.0535° N, 121.9815° W, 15 August 2012, R.Krichbaum & M.Krichbaum eaglecap15164 (UBC!).

Symphyotrichum lanceolatum subsp. hesperium x S. spathulatum var. intermedium

CANADA. British Columbia: Mara Lake, 28 August 1950, Krajina s.n. (UBC!).