

## A Taxonomic Revision of the Genus *Antennaria* (Asteraceae: Inuleae: Gnaphaliinae) of Alaska and Yukon Territory, Northwestern North America

Randall J. Bayer

University of Alberta, Department of Botany, Edmonton, Alberta T6G 2E9, Canada.

### Abstract

Keys to all species of *Antennaria* of Alaska and Yukon Territory are presented. The number of taxa acknowledged in the current treatment is 17, including 10 species with several subspecies circumscribed within some of the more diverse species. A synopsis enumerating all the recognized taxa provides their correct name, relevant synonyms, basionym, type locality, key morphological features, chromosome numbers and assorted taxonomic notes. Maps of each taxon are provided.

### Introduction

*Antennaria*, commonly known as “pussytoes,” is a genus of dioecious, perennial herbs distributed throughout temperate to arctic regions of the Northern Hemisphere. The center of diversity for *Antennaria* is western North America. The genus is taxonomically complex because agamospermy (asexual seed production) has led to the evolution of numerous microspecies, which have been recognized by many taxonomists as distinct species. Most of the previous floristic treatments of the genus were based exclusively on herbarium studies, whereas the current one is based on extensive field, in addition to laboratory and herbarium, studies and is a much more evolutionary classification than previous typological ones. This treatment was prompted by William J. Cody, who is currently completing his “Flora of the Yukon,” and David F. Murray, who convinced me that the revision might be expanded easily to include Alaska. An abridged version of this revision of *Antennaria* will appear in the “Flora of the Yukon.” I have made detailed studies of the systematics of most of the taxa over the past 15 yr; however, a couple problematical taxa, such as the *A. alpina* complex, are still in need of much more detailed investigation. Their taxonomy must still be considered provisional at this time.

### HISTORY OF THE MAJOR TREATMENTS OF WESTERN ARCTIC ANTENNARIA

*Antennaria* is a genus that is infamous for its taxonomic complexity and the *Antennaria* of Alaska and Yukon are no exception. The first comprehensive treatment for *Antennaria* of the region was Malte's (1934) revision of arctic *Antennaria*. This was followed by A. E. Porsild's revisions in Hultén's “Flora of Alaska and Yukon” (Hultén, 1949) and his revision for northwestern Canada (Porsild, 1950). Porsild's taxonomic concepts in *Antennaria* were also the basis of the treatment of *Antennaria* in Anderson's flora of Alaska and adjacent Canada (Anderson, 1959). Although these early treatments do accentuate the large diversity of apomictic microspecies in the Arctic, they are mostly impractical as the keys tend to use qualitative characters that are not well defined or have overlapping features.

In his *Flora of Alaska and Neighboring Territories*, Hultén (1968) was the first to produce a truly practicable classification of arctic *Antennaria*. He achieved this by combining numerous apomictic microspecies into taxa that were more broadly circumscribed. In recognizing fewer numbers of taxa than previous

treatments, Hultén's classification (1968), is more in accordance with my current thoughts as to the ultimate number of species that should be recognized for the Yukon Territory and Alaska. Welsh's revision of Anderson's flora (Welsh, 1974) takes a similar approach to Hultén, but in recognizing only eight species for the entire region much of the variation is left unrepresented. My current treatment is based on Hultén (1968), except I have united several taxa that he recognized.

### THE REVISED CLASSIFICATION

The number of taxa recognized in the current treatment is 17, including 10 species and several subspecies within several those species. This treatment is based on some of my taxonomic and evolutionary work to date on the genus (Bayer, 1984, 1987a, 1987b, 1988, 1989a, 1989b, 1989c, 1989d, 1989e, 1990a, 1990b, 1990c, 1991; Bayer and Stebbins 1981, 1982, 1983, 1987; Bayer, et al., 1991), as well as extensive field experience with this genus throughout North America including the summer of 1989 in Yukon and Alaska. Although the number of recognized species is a conservative one, many of the taxa are still difficult to identify because of tremendous amounts of morphological variability within some of the polyploid species complexes. Morphological descriptions and keys are based on measurements of at least 30 specimens of each taxon. The key I present below is mostly artificial and consequently phylogenetic relationships of taxa should not be inferred from it. Chromosome number reports are taken from Bayer and Stebbins (1981, 1987), Bayer (1984), as well as unpublished additional counts (Bayer, unpubl.). Maps of the taxa (Fig. 1) are based on specimens from ALA, ALTA, CAN, DAO, GH, and NY.

### Keys to Success in Identifying *Antennaria*

Several details must be kept in mind when collecting and trying to identify species of *Antennaria*. Unfortunately, one of the most determinative features of keys relies on a character that may not be readily identified on herbarium specimens, that being whether the populations are gynoecious (i.e., consisting entirely of pistillate plants) or dioecious (i.e., consisting of both staminate and pistillate plants). Dioecious populations are generally regarded as sexually reproducing, whereas the all pistillate (gynoecious) ones are usually regarded as agamosperous, reproducing exclusively by asexual seed production. This character is

readily determined in the field by simple gender ratios, however, on herbarium specimens absence of staminate could mean that they were not collected or that they were actually absent from the population. This character is especially important in separating the subspecies in *A. monocephala* and *A. friesiana*. Since the sexual dioecious and asexual gynoeious populations represent different evolutionary lineages and often have different geographic distributions, it is an important distinction. Specimens containing both staminate and pistillate individuals present no difficulty in determination to the subspecific level. However, entirely pistillate specimens can only be determined to the species level if information on the gender ratio can not be determined. Since the sexual and asexual subspecies of these two taxa have more or less distinct geographic ranges (Bayer, 1991), collection locality can often be of use in determining the "all pistillate" herbarium material of these taxa. It is imperative that both genders be sought and gathered when making collections of *Antennaria*. Absence of staminate plants should be noted when preparing herbarium specimen labels.

Another feature of importance in the taxonomy of *Antennaria* is the presence or absence of well-developed stolons that root at their tips. Some *Antennaria*, such as *A. pulcherrima* or *A. friesiana* subsp. *friesiana* produce short erect stolons that do not root at the tips and these should not be confused with typical stolons that are more elongate and horizontal, rooting at the tips.

The final feature of great taxonomic importance in *Antennaria* is the presence or absence of flags on the upper and middle cauline leaves. These are flat, linear, scarious, tips that are similar to the tips of the phyllaries, not to be confused with ordinary subulate or blunt leaf tips that are essentially green and herbaecous.

### ***Antennaria* Gaertner**

Perennial, caespitose or stoloniferous, or stems solitary; plants dioecious or gynoeious. Stems 1–65 cm. Leaves basal and cauline, the basal 1–3-nerved, alternate, simple, entire, ± tomentose. Inflorescence: heads discoid or disciform, solitary or in cymes, panicle-like or raceme-like clusters; phyllaries many, overlapping in several series, papery or membranous, those of staminate heads relatively broad and conspicuous, those of pistillate heads narrower, more acute, less conspicuous; receptacle naked. Staminate florets 2–5 mm; corollas narrowly funnel-shaped or tubular, white, yellow, or red in color; ovary much reduced, pappus bristles in most species enlarged at tip. Pistillate flowers 2–10 mm; corollas narrowly tubular, minutely lobed, white, yellow or red in color; pappus bristles numerous, soft and slender, weakly barbed. Fruit elliptic to ovoid, 0.5 to 3.5 mm long. Many species or races reproduce by apomixis, their populations consisting entirely of pistillate plants.

### **Key to *Antennaria* of Alaska and the Yukon Territory**

- 1 Basal leaves prominently 3 to 5-nerved and similar in outline to lower cauline leaves, pistillate plants usually 30–65 cm tall ..... *A. pulcherrima*
- 1 Basal leaves 1-nerved (sometimes with two obscure lateral veins), cauline leaves usually reduced and of a different outline than basal leaves, pistillate plants usually less than 30 cm tall (sometimes *A. howellii* can be greater than 30 cm) ..... 2
  - 2 Flowering stalks monocephalous ..... (*A. monocephala* s.l.) ... 3
    - 3 Plants gynoeious; staminate plants absent from populations ..... *A. monocephala* subsp. *angustata*
    - 3 Plants dioecious; staminate and pistillate plants present in equal frequency in populations ..... *A. monocephala* subsp. *monocephala*
  - 2 Flowering stalks few (2–5) headed (paucicephalous) or many headed (polycephalous) ..... 4
    - 4 Largest basal leaves greater than 6.0 mm wide and greater than 20 mm long; phyllary tips white, ivory, to light brown never pink, red, dark brown, dark green or black (*A. howellii* complex) ..... 5
      - 5 Basal leaves 1–3 nerved, greater than 9.0 mm wide, phyllaries tips light brown, flags usually absent from upper cauline leaves ..... *A. howellii* subsp. *howellii*
      - 5 Basal leaves 1-nerved, less than 9.0 mm wide, phyllaries tips whitish, flags present on upper cauline leaves ..... *A. howellii* subsp. *canadensis*
    - 4 Largest basal leaves less than 6.0 mm wide and less than 20 mm long, or if greater than 20 mm long then less than 6.5 mm wide, or if greater than 6.5 mm wide then less than 20 mm long; phyllary tips white, ivory, pink, red, light to dark brown, dark green or black ..... 6
      - 6 Plant tufted or caespitose, not mat-forming, with crowded sessile or subsessile rosettes from short rhizomatous caudices, upper cauline stem always beset with glandular hairs ..... 7
        - 7 Plants gynoeious; staminate plants absent from populations; pistillate involucre bracts dark, olive or black, and relatively narrow ..... *A. friesiana* subsp. *friesiana*
        - 7 Plants dioecious; staminate and pistillate plants present in equal frequency in populations; pistillate involucre bracts usually lighter often dark brown or whitish and relatively wide ..... *A. friesiana* subsp. *alaskana*
  - 6 Plant loosely caespitose, mat-forming, with rosettes borne at the ends of well developed prostrate or ascending leafy stolons, upper cauline stem either beset with glandular hairs or without glandular hairs ..... 8
    - 8 Basal leaves cuneate to cuneate spatulate, less than two times longer than wide, densely caespitose and arising from short prostrate stolons, plants endemic to limestone talus ..... *A. densifolia*
    - 8 Basal leaves narrowly spatulate or oblanceolate, more than two times longer than wide, caespitose with well developed prostrate stolons, plants of habitats other than limestone talus ..... 9
      - 9 Scarious portion of phyllaries green-black or black ..... 10
        - 10 Flowering stem and leaves beset with glandular hairs; plants dioecious; staminate and pistillate plants present in equal frequency in populations ..... *A. friesiana* subsp. *neolaskana*
        - 10 Flowering stem and leaves without glandular hairs; plants gynoeious; staminate plants absent from populations ..... 11

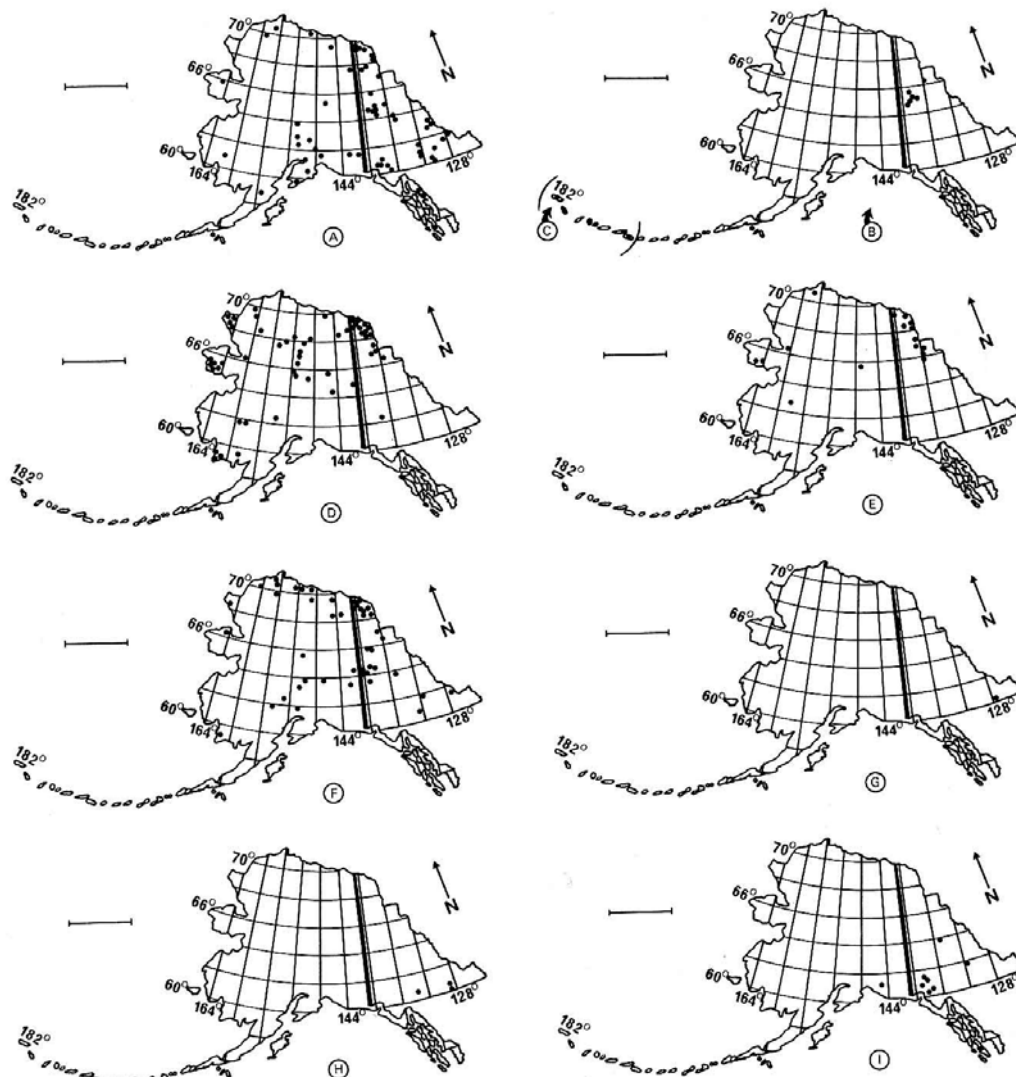


FIGURE 1. Distribution of Alaska and Yukon species of *Antennaria*. A. *A. alpina*, B. *A. densifolia*, C. *A. dioica*, D. *A. friesiana* subsp. *alaskana*, E. *A. friesiana* subsp. *nealaskana*, F. *A. friesiana* subsp. *friesiana*, G. *A. howellii* subsp. *canadensis*, H. *A. howellii* subsp. *howellii*, I. *A. media*, J. *A. microphylla*, K. *A. monocephala* subsp. *angustata*, L. *A. monocephala* subsp. *monocephala*, M. *A. rosea* subsp. *arida*, N. *A. rosea* subsp. *confinis*, O. *A. rosea* subsp. *pulvinata*, P. *A. rosea* subsp. *rosea*, Q. *A. pulcherrima*. Bars = 500 km. Each dot may represent more than one collection.

- 11 Upper and middle cauline leaves with a flat, linear, scarious, tip (flag), similar to the tips of the phyllaries ..... *A. alpina*
- 11 Upper and middle cauline leaves blunt or with subulate or subulate-aristate tips (only those about the corymb with flags) ..... *A. media*
- 9 Scarious portion of phyllaries zoned combinations of white, pink, rose, sanguine, or light brown ..... 12
- 12 Plants dioecious (staminate and pistillate plants present in equal frequency in populations), scarious portion of phyllaries white or pink tipped with green at base, upper stem either beset with glandular hairs or without glandular hairs,
- 13 Basal leaves bright-green glabrous above, pubescent below, upper stem without glandular hairs, known only from the western Aleutian Islands ..... *A. dioica*

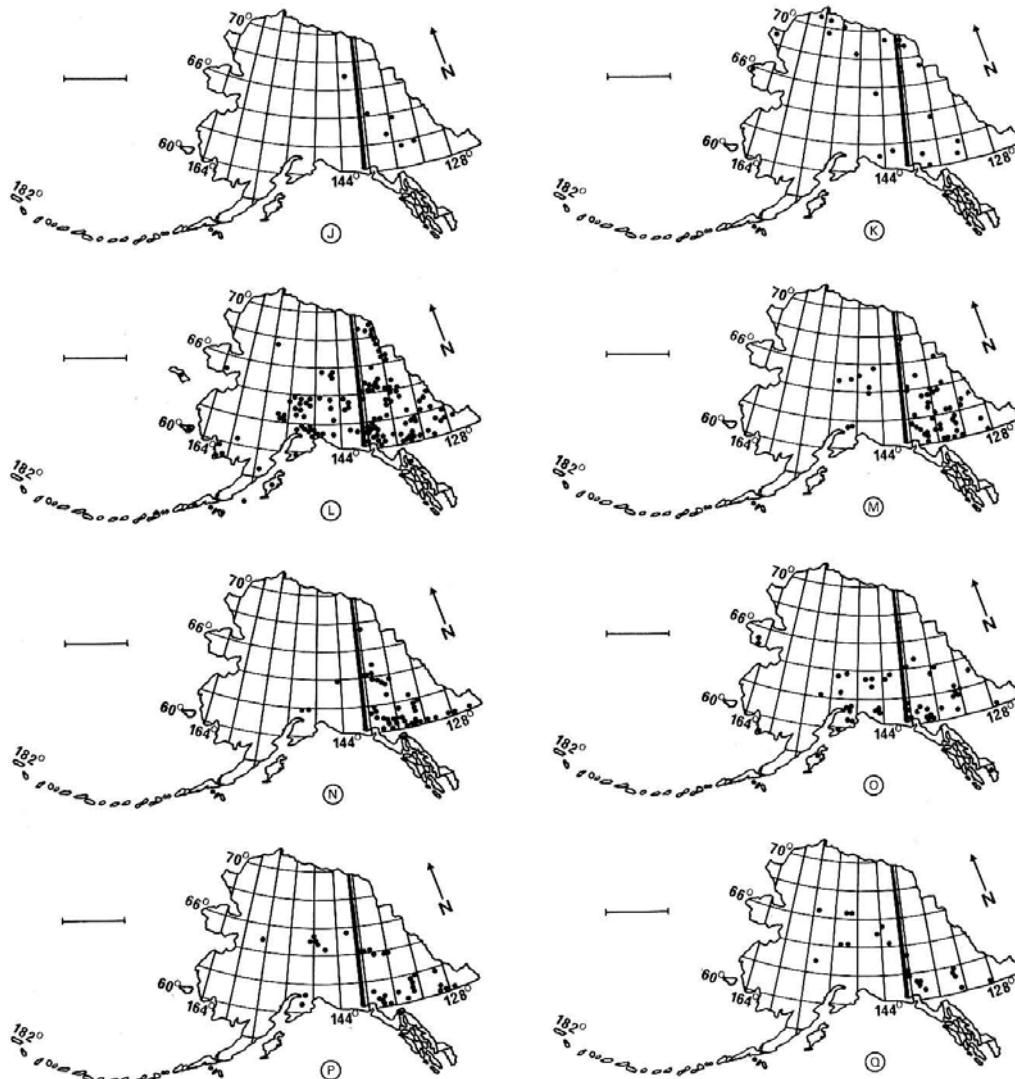


FIGURE 1. (cont.)

- 13 Basal leaves silvery-gray pubescent both above and below, upper stem beset with glandular hairs, known from east-central Alaska and central Yukon ..... *A. microphylla*
- 12 Plants gynoeceous (staminate plants absent from populations), scarios portion of phyllaries zoned combinations of white, pink, rose, sanguine, or light brown, upper stem without glandular hairs (*A. rosea* complex) ..... 14
- 14 Longest leaves of flowering rosettes 20.0 mm more in length; phyllaries shades of white, pink, green, or red, but usually *not* brown ..... *A. rosea* subsp. *rosea*
- 14 Longest leaves of flowering rosettes less than 20.0 mm in length; phyllaries of various shades of white, pink, green, red, and light brown ..... 15
- 15 Involucre less than 6.5 mm in length, corolla 3.5 mm or less in length, pappus usually 5.0 mm or less in length, cauline leaves tapering to a slender, subulate tip; phyllaries usually various shades of brown ..... *A. rosea* subsp. *confinis*
- 15 Involucre 6.5 mm or greater in length, corolla greater than 3.5 mm in length, pappus usually greater than 5.0 mm long, cauline leaves sometimes tipped with a flat, lanceolate scarios appendage; phyllaries of various colors ..... 16

- 16 Flowering stalks greater than 17 cm high; lowermost cauline leaves usually greater than 19 mm long; heads usually 6–12 in number ..... *A. rosea* subsp. *arida*  
 16 Flowering stalks less than 17 cm high; lowermost cauline leaves usually 19 mm or less in length; heads usually 3–5 in number ..... *A. rosea* subsp. *pulvinata*

### Enumeration of Taxa

The following section gives the correct name, relevant synonyms, the type locality, description, chromosome numbers, key morphological features and taxonomic notes for each of the taxa. If the correct name is not the basionym, then the basionym is also provided.

- 1) *A. alpina* (L.) Gaertn., De fructibus et seminibus plantarum 2: 410. 1791.

Basionym: *Gnaphalium alpinum* L. Sp. Pl. 850. 1753.  
 (= *A. atriceps* Fern., *A. Böcheriana* A. E. Pors., *A. canescens* var. *pseudoporsildii* Böcher, *A. ungvagensis* (Fern.) Malte, *A. glabrata* (J. Vahl) E. L. Greene, *A. porsildii* Ekman, *A. canescens* (Lge.) Malte, *A. compacta* Malte, *A. sornborgeri* Fern., *A. brevistyla* E. L. Greene, *A. arenicola* Malte, *A. vexillifera* Fern., *A. wiegandii* Fern.)

Type locality: Lapland.

Gynoeceous, staminate plant very rare in Alaska and Yukon (only one specimen seen from Yukon: DAO sheet # 579801). Flowering stems 3–18 cm high. Stolons 1–7 cm long. Basal leaves 6–25 mm, 2–7 mm wide, spoon-shaped to oblanceolate, tips mucronate, 1-nerved, green glabrescent to gray pubescent above, tomentose below; cauline leaves 5–20 mm, linear, with prominent flags on upper, middle, and often lower cauline leaves. Heads (1)2–5 in a cymose cluster; pistillate involucre 4–7(10) mm, pubescent at base; phyllaries narrow, acute, upper scarious part dark brown, black or olivaceous; corollas 3.5–5 mm; pappus capillary 4.5–6 mm; fruits 1–1.8 mm, sparingly papillose. Staminate involucre 5–6 mm, pubescent at base; corollas 3–3.5 mm; pappus clavate 3.5–4 mm.  $2n = 84$ . Distribution map: Fig. 1.A.

This circumpolar species complex is one of the most morphologically variable of all the agamic complexes in the genus. Some taxonomists have argued that true *A. alpina* does not occur in North America (Malte, 1934), this based on the fact that none of the North American material exactly matches the type of *A. alpina*, which is from Lapland and is deposited in the herbarium of the Linnaean Society (Malte, 1934; Porsild, 1965). If one uses a strict typological species concept then this is true, but I recognize that this species complex is composed of innumerable apomictic clones and am circumscribing a broad species concept for *A. alpina*. The list of synonyms presented above is still tentative and a revision of this complex is forthcoming. It is likely that infraspecific categories will be recognized to describe major subspecific groups in *A. alpina*, similar to what has been done for the other large polyploid complexes such as *A. howellii* and *A. rosea*. The species in North America is gynoeceous and characterized by its dark green to black phyllaries and conspicuous flags on the upper and middle cauline leaves. The basal leaves vary from glabrous, as in the type material, to pubescent.

- 2) *A. densifolia* A. E. Pors., Bull. Nat. Mus. Canad. #101. 1945.

(= *A. ellyae* A. E. Pors.)

Type locality: District of MacKenzie, Northwest Territories.

Dioecious, both staminate and pistillate plants equally common in most populations. Flowering stems 3.5–16 cm high. Stolons 1–2 cm long. Basal leaves 3–7 mm, 2–5 mm wide, spoon-shaped to wedge-shaped, tips mucronate, 1-nerved, both sides gray tomentose; cauline leaves 2–13 mm, linear, the upper cauline leaves tipped with flags. Heads 2–5 in a cymose cluster; pistillate involucre 4.5–7.5 mm, pubescent at base; phyllaries narrow, acute, upper scarious part light brown, dark brown, or black; corollas 2.5–4.5 mm; pappus capillary 2.5–3.5 mm; fruits .8–1.5 mm, glabrous. Staminate involucre 3–6.5 mm, pubescent at base; corollas 2–3.5 mm; pappus clavate 2.5–3.5 mm.  $2n = 28$ . Distribution map: Fig. 1.B.

This narrow endemic is found on limestone talus below the treeline. It is found in the MacKenzie, Richardson, and Ogilvie Mountains of the District of MacKenzie and Yukon (Bayer, 1989c). One disjunct population of *A. densifolia* was recently found in Granite Co., Montana (Bayer, 1989c). A detailed taxonomic treatment of *A. densifolia* with complete distribution maps is found in Bayer (1989c).

- 3) *A. dioica* (L.) Gaertn., De fructibus et seminibus plantarum 2: 410. 1791.

Basionym: *Gnaphalium dioicum* L. Sp. Pl. 850. 1753.

(= *A. insularis* E. L. Greene, *A. hyperborea* D. Don)

Type locality: "Habitat in Europae apricis aridis."

Dioecious, both staminate and pistillate plants equally common in most populations. Flowering stems 3–10 cm high. Stolons 2–5 cm long. Basal leaves 3–18 mm, 3–6 mm wide, spoon-shaped, tips mucronate, 1-nerved, green above, gray tomentose below; cauline leaves 7–13 mm, linear, acute at apex. Heads 3–7 in a cymose cluster; pistillate involucre 5–7 mm, pubescent at base; phyllaries narrow, acute, upper scarious part dark pink to light pink or white; corollas 4–5 mm; pappus capillary 5–6 mm; fruits 0.5–1.0 mm, papillose. Staminate involucre 5–6.5 mm, pubescent at base; corollas 3–4 mm; pappus clavate 3.5–4.5 mm.  $2n = 28$ . Distribution map: Fig. 1.C.

*Antennaria dioica* is widely distributed across Eurasia from the British Isles to Japan and its range extends east into North America only in the Aleutian Islands. It is characterized by having glabrous upper leaf surfaces and pink or white bracts. The circumscription of *A. dioica* in North America has long been a topic of debate, as *A. marginata* Greene (syn. = *A. dioica* var. *marginata* (Greene) Jepson) of the southwestern states bears a remarkable similarity to *A. dioica*. The two species differ by the fact that the upper flowering stem lacks glandular hairs and the surface of the stolons are pubescent, but not densely woolly, in *A. dioi-*

ca; whereas in *A. marginata* the upper flowering stem is usually beset with purple glandular hairs and the stolon surface is densely woolly and obscures the surface of the stolon. It seems best to recognize these two strongly allopatric taxa as distinct species.

- 4a) *A. friesiana* (Trautv.) Ekman subsp. *alaskana* (Malte) Hult., Ark. Bot. 7: 134. 1968.

Basionym: *A. alaskana* Malte, Rhodora 36: 107. 1934.

Type locality: "Near, Port Clarence", Alaska.

Dioecious, both staminate and pistillate plants equally common in most populations. Flowering stems 7.5–14 cm high and beset with glandular hairs. Stolons .5–1 cm long. Basal leaves 11–30 mm, 2–4 mm wide, narrowly spoon-shaped to oblanceolate, tips mucronate, 1-nerved, green glabrescent to gray pubescent above, tomentose below; cauline leaves 4–20 mm, linear, with prominent flags on upper and lower stem leaves. Heads 2–6 in a cymose cluster; pistillate involucre 5.5–7 mm, pubescent at base; phyllaries narrow, acute, upper scarious part light brown, dark brown, black or olivaceous; corollas 3–4.5 mm; pappus capillary 3.5–5 mm; fruits 1.2–1.8 mm, glabrous or slightly papillose. Staminate involucre 4–6.5 mm, pubescent at base; corollas 2.5–3 mm; pappus clavate 3–4 mm.  $2n=28, 56$ . Distribution map: Fig. 1.D.

The *A. friesiana* complex consists of *A. friesiana* subsp. *alaskana*, *A. friesiana* subsp. *nealaskana*, and *A. friesiana* subsp. *friesiana*, the former two being the dioecious (sexual) phase of the later gynoeious (asexual) form. The sexual populations (subsp. *alaskana* and subsp. *nealaskana*) are restricted to Alaska and cordilleran areas of northern Yukon and adjacent Northwest Territories (Bayer, 1991). The apomictic phase (subsp. *friesiana*) is almost circumpolar, occurring from the central and eastern Siberian plateau eastward across the North American arctic to Greenland (Bayer, 1991). Hultén circumscribed a third subspecies within *A. friesiana* s.l., *A. friesiana* subsp. *compacta* (Malte) Hultén. After studying its morphology, both in the field and in the herbarium, it is apparent that Hultén's taxon contains at least three incongruous entities. These are probably not at all related to the other two subspecies of *A. friesiana*. Hultén's circumscription of *A. friesiana* subsp. *compacta* included *A. densifolia*, *A. nealaskana* Porsild, which I recognize as distinct taxa, and *A. crymophila* Porsild as taxonomic synonyms. *Antennaria compacta* Malte s. str. and *A. crymophila* are perhaps hybrid apomicts and are included as synonyms under *A. alpina* (see Bayer, 1991 for details).

- 4b) *A. friesiana* (Trautv.) Ekman subsp. *nealaskana* (A. E. Pors.) Bayer and Stebbins, in ed. Canad. J. Bot.

Basionym: *A. nealaskana* A. E. Pors. Sargentia 4: 71. 1943.

Type locality: Northwest Territories.

Description as for the typical variety except stolons well developed 1–4 cm long forming extensive mats. Staminate and pistillate involucre slightly larger than the typical variety, the former 6–7 mm, the later 7–8 mm high. Staminate phyllaries light brown.  $2n=56$ . Distribution map: Fig. 1.E.

Subspecies *nealaskana* occurs from eastern Alaska, to the Richardson Mountains and into the central

MacKenzie Mountains, on the Yukon–Northwest Territories boundary (Bayer, 1991). Its habitat is arctic fell fields or gravelly frost boils (Bayer, 1991). Hultén included this taxon in synonymy under his *A. friesiana* subsp. *compacta*, but that taxon contains at least three discrete taxa (see notes under *A. friesiana*). This subspecies of *A. friesiana* can be separated from other arctic members of *Antennaria* because it is dioecious, paucicephalous (few-headed), and has well-developed elongate stolons forming extensive mats.

- 4c) *A. friesiana* (Trautv.) Ekman subsp. *friesiana*, Ark. Bot. 7: 134. 1968.

Basionym: *A. alpina* (L.) Gaertn. var. *friesiana* Trautv., Trudy Imp. S. Peterburgsk. Bot. Sada. 6:24. 1878.

(= *A. ekmaniana* A. E. Pors., *A. angustifolia* Ekman)

Type locality: Siberia.

Gynoeious, staminate plant unknown in Alaska and Yukon. Flowering stems 3.5–12.5 cm high and beset with glandular hairs. Stolons .5–1 cm long. Basal leaves 10–30 mm, 2–4 mm wide, narrowly spoon-shaped to oblanceolate, tips mucronate, 1-nerved, glabrescent green to gray pubescent above, tomentose below; cauline leaves 7–14 mm, linear, with prominent flags on upper and lower stem leaves. Heads 2–4 in a cymose cluster; pistillate involucre 6–7 mm, pubescent at base; phyllaries narrow, acute, upper scarious part light brown, dark brown, black or olivaceous; corollas 3.5–4 mm; pappus capillary 4–4.5 mm; fruits 1–2 mm, glabrous to slightly papillose.  $2n=56, 63, 100+$ . Distribution map: Fig. 1.F.

See above discussion under *A. friesiana* subsp. *alaskana*.

- 5a) *A. howellii* E. L. Greene subsp. *canadensis* (E. L. Greene) Bayer, Brittonia 41: 397. 1989d.

Basionym: *A. canadensis* E. L. Greene, Pittonia 3: 275. 1898.

(= *A. neodioica* E. L. Greene subsp. *canadensis* (E. L. Greene) Bayer and Stebbins, *A. canadensis* var. *randii* Fern., *A. neglecta* E. L. Greene var. *randii* (Fern.) Cronq., *A. neglecta* E. L. Greene var. *canadensis* (E. L. Greene) Cronq., *A. spathulata*)

Type locality: "Rocky places, Campbellton", New Brunswick.

Gynoeious, staminate plant unknown in the area covered by this revision. Flowering stems 15–35 cm high. Stolons 3–8 cm long. Basal leaves 20–40 mm, 6–9 mm wide, spoon-shaped to oblanceolate, tips mucronate, 1-nerved, green glabrous above, tomentose below; cauline leaves 12–30 mm, linear, with prominent flags on upper stem leaves. Heads 3–7 in a cymose cluster; pistillate involucre 7–10 mm, pubescent at base; phyllaries narrow, acute, upper scarious part white or cream sometimes rose at the base; corollas 4–6.5 mm; pappus capillary 7–9 mm; fruits 1–1.5 mm, notably papillose.  $2n=56, 84$ . Distribution map: Fig. 1.G.

The *A. howellii* species complex is highly variable morphologically and four more or less distinct subspecies can be recognized within it. The species is entirely gynoeious and its range extends from the Appalachians and Atlantic seaboard across boreal Canada to the Pacific coast. The two subspecies occur in southern Yukon, but are unknown from Alaska.

Subspecies *canadensis* is almost exclusively restricted to the eastern half of North America. Cronquist (Cronquist, 1945; Gleason and Cronquist, 1991) included members of this complex as synonyms of *A. neglecta*, but I maintain that, since these apomicts are of hybrid polyploid origin from among many sexual progenitors, they are best not included under the circumscription of any one sexual progenitor (for detailed discussion of this debate see Bayer, 1989d, page 397.). This subspecies is probably most closely related to *A. racemosa* of the northern Rockies and *A. neglecta* of the Great Plains. (See Bayer (1985) for a complete discussion of the origins of the complex).

- 5b) *A. howellii* E. L. Greene subsp. *howellii*, Brittonia 41: 396. 1989d.

Basionym: *A. howellii* E. L. Greene, Pittonia 3: 174. 1897. (= *A. neodioica* E. L. Greene subsp. *howellii* (E. L. Greene) Bayer, *A. neglecta* var. *h.* (E. L. Greene) Cronq., *A. neglecta* subsp. *h.* (E. L. Greene) Hult.).

Type locality: St. Helens, Oregon.

Gynoecious, staminate plant unknown in the area covered by this revision. Flowering stems 15–30 cm high. Stolons 1–4 cm long. Basal leaves 25–40 mm, 9–12 mm wide, spoon-shaped to oblanceolate, tips mucronate, 1–3-nerved, green above, tomentose below; cauline leaves 20–40 mm, linear, acute at apex. Heads 5–12 in a cymose clusters; pistillate involucre 6–7.5 mm, pubescent at base; phyllaries narrow, acute, upper part light brown to white; corollas 5–6 mm; pappus capillary 6–8 mm; fruits 1.5–2 mm, papillose.  $2n=56,84,140$ . Distribution map: Fig. 1.H.

Subspecies *howellii* is most common in the western half of the range of *A. howellii*. Based on morphology, it is obvious that this group of apomicts is closely related to *A. racemosa* of the northern Rockies (Bayer, 1985).

- 6) *A. media* E. L. Greene, Pittonia 3: 286. 1898. (= *A. alpina* (L.) Gaertn. var. *media* (E. L. Greene) Jepson, *A. austromontana* E. Nels., *A. modesta* E. L. Greene, *A. densa* E. L. Greene, *A. candida* E. L. Greene) Type locality: "Mts. above Coldstream", Placer Co., California.

Gynoecious, staminate plant unknown in Alaska and Yukon. Flowering stems 5–13 cm high. Stolons 1–4 cm long. Basal leaves 6–19 mm, 2.5–6 mm wide, spoon-shaped to oblanceolate, tips mucronate, 1-nerved, both sides gray pubescent; cauline leaves 5–20 mm, linear, acute at apex. Heads 2–7 in a cymose cluster; pistillate involucre 4–8 mm, pubescent at base; phyllaries narrow, acute, upper scarious part dark brown, black or olivaceous; corollas 3–4.5 mm; pappus capillary 4.5–5 mm; fruits .6–1.6 mm, glabrous or papillose.  $2n=56, 98, 112$ . Distribution map: Fig. 1.I.

*Antennaria media* occurs throughout western North America from Arizona and New Mexico to Alaska and both dioecious and gynoeccious populations are encountered (Bayer and Stebbins, 1987). It is rare in Yukon and Alaska. The dioecious (sexual) populations are restricted primarily to California and Oregon (Bayer et al., 1990). The main distinction between *A. media* and *A. alpina* is the presence of flat, scarious, tips

(flags), at the ends of the upper cauline leaves in *A. alpina*, which are mostly absent in *A. media* (Bayer, 1989e, 1990c). Additionally, the phyllaries of the pistillate plants in *A. alpina* tend to be quite acute, whereas they are blunter in *A. media*. Considerable overlap seems to exist between the two taxa and it may be more reasonable to follow the lead of Jepson (1925) and some later authors and recognize *A. media* as a subspecific variant of *A. alpina*. Further investigation on this problem is needed before a final decision is made (see additional comments under *A. alpina*).

- 7) *A. microphylla* Rydb., Bull. Torr. Bot. Club 24: 303. 1897. (= *A. nitida* E. L. Greene, *A. solstitialis* Lunell)

Type locality: "Manhattan", Montana.

Dioecious, both staminate and pistillate plants equally common in most populations. Flowering stems 9–30 cm high. Stolons 1–5 cm long. Basal leaves 6–16 mm, 2–6 mm wide, spoon-shaped, tips mucronate, 1-nerved, both sides silvery-white pubescent; cauline leaves 5–25 mm, linear, acute at apex. Heads 6–13 in a cymose cluster; pistillate involucre 5.5–7 mm, pubescent at base; phyllaries narrow, acute, upper scarious part bright white to light yellow; corollas 3–4.3 mm; pappus capillary 3–5 mm; fruits .7–1.2 mm, glabrous or sparingly papillose. Staminate involucre 5–6.5 mm, pubescent at base; corollas 2.5–3 mm; pappus clavate 3–4 mm.  $2n=28$ . Distribution map: Fig. 1.J.

The range of *A. microphylla* extends from New Mexico to Yukon Territory in the Rockies and west to east-central Alaska and east to Minnesota and Northern Ontario (Bayer and Stebbins, 1987; Bayer et al., 1991). Cronquist (1955) preferred to include *A. rosea* within his circumscription of *A. microphylla*, but the two are really quite distinct. *Antennaria microphylla* is always dioecious, whereas *A. rosea* is always gynoeccious. Additionally, *A. microphylla* always has white phyllaries, whereas *A. rosea* only occasionally has white phyllaries. Weber's keen observation (Weber, 1987) that *A. microphylla* has numerous glandular hairs on the upper stem, whereas *A. rosea* does not, is also a convenient key character difference. Several authors have recognized *A. nitida* as a distinct species of *Antennaria*, but comparisons of the types of the two species shows that they are identical, therefore the older name, *A. microphylla*, is the correct one.

- 8a) *A. monocephala* DC. subsp. *angustata* (E. L. Greene) Hult., Ark. Bot. 7: 135. 1968.

Basionym: *A. angustata* E. L. Greene, Pittonia 3: 284. 1898.

(= *A. burwellensis* Malte, *A. congesta* Malte, *A. hudsonica* Malte, *A. nitens* E. L. Greene, *A. tansleyi* Polunin, *A. tweedsmuirii* Polunin, *A. fernaldiana* Polunin)

Type locality: Coast of Hudson's Strait, Northwest Territories.

Gynoecious, staminate plant unknown in Alaska and Yukon. Flowering stems 5–13 cm high and usually beset with glandular hairs. Stolons 2–4 cm long. Basal leaves 9–18 mm, 2–4 mm wide, spoon-shaped to oblanceolate, tips mucronate, 1-nerved, green glabrescent above, tomentose below; or more often both sides gray pubescent;

cauline leaves 4–11 mm, linear, with prominent flags on both upper and lower stem leaves. Heads solitary (rarely 2 or 3 in some individuals); pistillate involucre 5–8 mm, pubescent at base; phyllaries narrow, acute, upper scarious part brown, dark brown, black or olivaceous; corollas 3.5–4 mm; pappus capillary 4–5 mm; fruits 1–1.3 mm, usually glabrous.  $2n=56,70$ . Distribution map: Fig. 1.K.

It seems reasonable partly to follow Hultén's broad concept of *A. monocephala* (Bayer, 1991). Hultén (1968) circumscribed *A. monocephala* as containing three subspecies. The sexual phase of *A. monocephala* (i.e. subsp. *monocephala* and subsp. *philonipha*) is confined to southern Alaska, south of the Brooks Range and to southern Yukon Territory and areas of the Northwest Territories immediately adjacent to it (Hultén, 1968; Bayer pers. obs.). Within his concept of *A. monocephala* s.l., Hultén also circumscribed the apomictic form of the species as *A. monocephala* subsp. *angustata* extending the range of the species to northern Yukon and Alaska and across the Canadian arctic into Greenland and down the western Cordillera into Montana and Wyoming. *Antennaria monocephala* s.l. is most often found on the disturbed margins of solifluction lobes or on unstable, moist, gravelly sloping tundra (Bayer, 1991).

- 8b) *A. monocephala* DC. subsp. *monocephala*, Ark. Bot. 7: 135. 1968.

Basionym: *A. monocephala* DC, Prodrum 6: 269. 1837. (= *A. philonipha* A. E. Pors., *A. exilis* E. L. Greene, *A. monocephala* subsp. *philonipha* (A. E. Pors.) Hult., *A. monocephala* subsp. *monocephala* var. *exilis* (E. L. Greene) Hult.)

Type locality: Port Clarence, Alaska.

Dioecious, both staminate and pistillate plants equally common in most populations. Flowering stems 5–13 cm high and beset with glandular hairs. Stolons 2–4 cm long. Basal leaves 9–18 mm, 2–4 mm wide, spoon-shaped to oblanceolate, tips mucronate, 1-nerved, mostly green glabrous to glabrescent above, tomentose below; or sometimes both sides gray pubescent; cauline leaves 4–11 mm, linear, with prominent flags on both upper and lower stem leaves. Heads solitary (rarely 2 or 3 in some individuals); pistillate involucre 5–8 mm, pubescent at base; phyllaries narrow, acute, upper scarious part brown, dark brown, black or olivaceous; corollas 3.5–4 mm; pappus capillary 4–5 mm; fruits 1–1.3 mm, usually glabrous. Staminate involucre 5–7 mm, pubescent at base; corollas 2.5–3.5 mm; pappus clavate 3–4 mm.  $2n=28$ . Distribution map: Fig. 1.L.

Hultén's (1968) key distinctions between *A. monocephala* subsp. *monocephala* and *A. monocephala* subsp. *philonipha* are obscure and seemingly arbitrary, therefore subsp. *philonipha* has been subsumed into subsp. *monocephala* (Bayer, 1991). *Antennaria exilis* is a pubescent form of *A. monocephala* subsp. *monocephala*, but there is intergradation between between this form and the typical glabrous form. Therefore, it does not seem warranted to give taxonomic recognition to the two forms. See additional notes above under subsp. *angustata*.

- 9) *A. pulcherrima* (Hook.) E. L. Greene, Pittonia 3: 176. 1897. Basionym: *A. carpatica* var. *pulcherrima* Hook., Fl. Bor. Amer. 1: 329. 1834.

(= *A. pulcherrima* var. *sordida* Boivin, *A. pulcherrima* var. *angustisquama* A. E. Pors.)

Type locality: Rocky Mountains.

Dioecious, both staminate and pistillate plants equally common in most populations. Flowering stems (15) 30–65 cm high. Stolons .5–1 cm long. Basal leaves 5–20 cm, 4–25 mm wide, spoon-shaped to oblanceolate, tips mucronate, 3–5-nerved, both sides gray pubescent; cauline leaves 8–140 mm, linear, with prominent flags on upper stem leaves. Heads 3–30 in a cymose to paniculate cluster; pistillate involucre 7–12 mm, pubescent at base; phyllaries narrow, acute, upper scarious part light brown, dark brown, black or olivaceous; corollas 4–6 mm; pappus capillary (7)8–10 mm; fruits 1–1.5 mm, glabrous. Staminate involucre 5–8 mm, pubescent at base; corollas 3.5–5 mm; pappus clavate 4–6 mm.  $2n=28, 56$ . Distribution map: Fig. 1.Q.

The species is indigenous of the northern Rocky Mountains, but is also widespread across boreal and subarctic North America from Quebec to Alaska and is characterized by whitish phyllaries with a large black spot at their base (Bayer and Stebbins, 1987).

- 10a) *A. rosea* E. L. Greene subsp. *arida* (E. Nels.) Bayer, Brittonia 41: 57. 1989e.

Basionym: *A. arida* E. Nels., Bot. Gaz. 27:210. 1899.

(= *A. scariosa* E. Nels., *A. arida* subsp. *viscidula* E. Nels.)

Type locality: "Tipton, S.W. Wyoming".

Gynoeceous, staminate plant unknown in Alaska and Yukon. Flowering stems 19–30 cm high. Stolons 1.5–4.5 cm long. Basal leaves 10–20 mm, 2–10 mm wide, spoon-shaped to narrowly wedge-shaped, tips mucronate, 1-nerved, both sides gray pubescent; cauline leaves 9–26 mm, linear, acute at apex. Heads 6–12 in a cymose cluster; pistillate involucre 6.5–8 mm, pubescent at base; phyllaries narrow, acute, upper scarious part white, pink, green, red, or brown; corollas 3.5–6 mm; pappus capillary 5–6 mm; fruits .7–1.8 mm, glabrous or papillose.  $2n=42, 56, (70)$ . Distribution map: Fig. 1.M.

The *A. rosea* polyploid agamic complex is one of the most morphologically diverse and widespread complexes of North American *Antennaria*. It occurs from the western cordillera of North America from southern California, Arizona and New Mexico north to the Arctic from Alaska east to the shores of Hudson and James Bay. Additionally, *A. rosea* occurs disjunctly in the Canadian maritime provinces, eastern Quebec, and immediately north of and adjacent to Lake Superior (Bayer and Stebbins, 1987; Bayer et al., 1991). The group is taxonomically confusing because of numerous agamospermous microspecies, having been recognized as distinct species. Morphometric and isozyme analyses have demonstrated that the primary source of morphological variability in the complex derives from six sexually reproducing progenitors, *A. aromatica*, *A. corymbosa*, *A. pulchella*, *A. microphylla*, *A. racemosa*, and *A. umbrinella* (Bayer, 1989b, 1990a). Additionally, two other sexually reproducing species, *A. marginata* and *A. rosulata*, may have contributed to the genetic complexity of the *A. rosea* com-



plex (Bayer, 1990a). Four reasonably distinct subspecies can be recognized within the complex all differing from each other by the characters of the key. Subspecies *arida* is most closely related to *A. microphylla* of the Rocky Mountains (Bayer, 1989e) as is shown by their similar morphology.

- 10b) *A. rosea* E. L. Greene subsp. *confinis* (E. L. Greene) Bayer, *Brittonia* 41: 57. 1989e.

Basionym: *A. confinis* E. L. Greene, *Pittonia* 4: 40. 1899. (= *A. sordida* E. L. Greene, *A. angustifolia* Rydb., *A. rosea* E. L. Greene var. *angustifolia* (Rydb.) E. Nels., *A. foliacea* E. L. Greene var. *humilis* Rydb., *A. arida* E. Nels. *humilis* (Rydb.) E. Nels., *A. tomentella* E. Nels., *A. concinna* E. Nels., *A. sedoides* E. L. Greene, *A. dioica* (L.) Gaertn. var. *kernensis* Jepson, *A. laingii* A. E. Pors., *A. leuchippi* M. T. Pors., *A. elegans* A. E. Pors., *A. breitungii* A. E. Pors., *A. incarnata* A. E. Pors., *A. leontopodioides* Cody)

Type locality: "Santa Catalina Mountains", Arizona.

Gynoeceous, staminate plant unknown in Alaska and Yukon. Flowering stems 9–25 cm high. Stolons 1.5–4.5 cm long. Basal leaves 10–20 mm, 2–10 mm wide, spoon-shaped to wedge-shaped, tips mucronate, 1-nerved, both sides gray pubescent; cauline leaves 6–20 mm, linear, acute at apex. Heads 4–11 in a cymose cluster; pistillate involucre 4–6.5 mm, pubescent at base; phyllaries narrow, acute, upper scarious part cream, pale yellow, grayish or light brown; corollas 2.5–4 mm; pappus capillary 3.5–5 mm; fruits .7–1.8 mm, glabrous or papillose.  $2n=42$ , 56, 70. Distribution map: Fig. 1.N.

Subspecies *confinis* is most closely related to *A. pulchella* of the Sierra Nevada and *A. umbrinella* of the northern Rockies (Bayer, 1989e), as is shown by its relatively small basal leaves and smallish heads that usually have dark phyllaries. For additional comments on the *A. rosea* complex see above under *A. rosea* subsp. *arida*.

- 10c) *A. rosea* E. L. Greene subsp. *pulvinata* (E. L. Greene) Bayer, *Brittonia* 41: 59. 1989e.

Basionym: *A. pulvinata* E. L. Greene, *Pittonia* 3: 287. 1898. (= *A. pulvinata* E. L. Greene subsp. *albescens* E. Nels., *A. albescens* (E. Nels.) Rydb., *A. sansonii* E. L. Greene, *A. maculata* E. L. Greene, *A. neodioica* E. L. Greene var. *gaspensis* Fern., *A. gaspensis* (Fern.) Fern., *A. isolepis* E. L. Greene, *A. manicouagana* Landry)

Type locality: "Moose Mt., Elbow River, Alta., Mountain slope, Alt. 6,200–7,000", Alberta.

Gynoeceous, staminate plant unknown in Alaska and Yukon. Flowering stems 4–17 cm high. Stolons 1–6 cm long. Basal leaves 8–18 mm, 2–10 mm wide, spoon-shaped to wedge-shaped, tips mucronate, 1-nerved, both sides gray pubescent; cauline leaves 6–19 mm, linear, acute at apex. Heads 3–5 in a cymose cluster; pistillate involucre 6.5–10 mm, pubescent at base; phyllaries narrow, acute, upper scarious part white, pink, green, red, or brown; corollas 3.5–5.0 mm; pappus capillary 5–6.5 mm; fruits .7–1.8 mm, glabrous or papillose.  $2n=42$ , 56. Distribution map: Fig. 1.O.

*Antennaria aromatica* of is undoubtedly one of the sexual progenitors of *A. rosea* subsp. *pulvinata* (Bayer, 1989e, 1989c), as is evidenced its comparatively short stature and relatively low number of large heads. For

additional comments on the *A. rosea* complex see above under *A. rosea* subsp. *arida*.

- 10d) *A. rosea* E. L. Greene subsp. *rosea*, *Brittonia* 41: 56. 1989e.

Basionym: *A. rosea* E. L. Greene, *Pittonia* 3: 281. 1898. (= *A. imbricata* E. Nels., *A. bracteosa* Rydb., *A. oxyphylla* E. L. Greene, *A. speciosa* E. Nels., *A. rosea* E. L. Greene subsp. *divaricata* E. Nels., *A. hendersoni* Piper, *A. acuminata* E. L. Greene, *A. chlorantha* E. L. Greene, *A. lanulosa* E. L. Greene, *A. formosa* E. L. Greene, *A. alborosea* A. E. Pors.)

Type locality: "Mountain Meadows, Kootenai Co., Idaho".

Gynoeceous, staminate plant unknown in Alaska and Yukon. Flowering stems 10–40 cm high. Stolons 2–7 cm long. Basal leaves 20–40 mm, 2–10 mm wide, spoon-shaped, oblanceolate, or wedge-shaped, tips mucronate, 1-nerved, infrequently green above, tomentose below; or more often both sides gray pubescent; cauline leaves 8–36 mm, linear, acute at apex. Heads 6–20 in a cymose cluster; pistillate involucre 5–8 mm, pubescent at base; phyllaries narrow, acute, upper scarious part white, pink, green, red, or brown; corollas 3–4.5 mm; pappus capillary 4–6 mm; fruits .7–1.8 mm, glabrous or papillose.  $2n=42$ , 56. Distribution map: Fig. 1.P.

The typical subspecies is most closely related to two northern Rockies species, *A. corymbosa* and *A. racemosa* (Bayer, 1989e), as is shown by its long basal leaves that range from pubescent to glabrous. For additional comments on the *A. rosea* complex see above under *A. rosea* subsp. *arida*.

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