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THE TAXONOMY OF ASTER SECTION MULTIFLORI (ASTERACEAE) I. NOMENCLATURAL REVIEW AND FORMAL PRESENTATION OF TAXA

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Aster sect. *Multiflora* A. Gray (1884) is one of the more stable and well delimited groups in this highly variable and polymorphic genus. Nevertheless, the entities included within this group have posed problems for virtually every floristic botanist who has had to deal with them. Asters are notorious for their high degree of interspecific compatibility and, in the view of several authors, hybridization is one of the major causes of confusion of taxa in the field (Burgess, 1906; Cronquist, 1952a; Shinnars, 1941; Wiegand, 1928). The genus is characterized by nearly complete self-sterility and obligatory out-crossing. The resulting heterozygosity and a ready phenotypic response to environmental fluctuations find expression in a wide range of structural variability, as well as extensive geographic ranges for most species.

A difficulty confronting the monographer who relies principally on herbarium material is the inadequacy of many specimens, particularly of older collections, including many types. They often lack underground parts or consist of single branches that fail to display some very diagnostic characteristics of the plants, e.g., habit of stems and rhizomes. Habitat data are frequently lacking on specimen labels, although these data can provide critical information for the identification and characterization of *Aster* species (Jones, 1978).

The views presented in previous taxonomic treatments of *Aster* sect. *Multiflora* vary considerably. At one extreme, seven species are recognized (Rydberg, 1917), and at the other only one (Boivin, 1962). However, none of the previous investigators has studied the

group over its entire geographic range. The taxa under consideration are widely distributed, ranging from New England to Washington, north to Alaska, and south to Mexico. The plants are absent in the southeastern United States, California, and Nevada.

This treatment recognizes two species, *Aster ericoides* Linnaeus and *A. falcatus* Lindley, on the basis of morphology, cytology, and the presence of a strong reproductive barrier. In each species, the major morphological variants are treated at the subspecific level, while several less well defined entities are given varietal rank. The conclusions are based, in part, on the examination of over 7,000 herbarium specimens from about 40 herbaria. Experimental, cytological, phytogeographical, and statistical data in support of this interpretation will be presented in the sequel to this paper.

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NOMENCLATURAL REVIEW

Nomenclatural problems connected with *Aster* sect. *Multiflori* are quite formidable. A list of 48 names and combinations has been compiled, and several names must be excluded altogether. The oldest names date back to Linnaeus (1753), Aiton (1789), Muhlenberg ex Willdenow (1804), Persoon (1807), Lindley (in Hooker, 1834, and in DeCandolle, 1836), and to Torrey and Gray (1841).

Aster ericoides Linnaeus is the oldest name for a species in sect. *Multiflori*. Linnaeus (1753) based the description of this species not on a specimen but on three references, the first from Gronovius (1739), the second from Royen (1740), and the third from Dillenius (1732). The specimen underlying the Gronovius citation is *John Clayton 194* (BM!); it has been marked "type," but I do not know by whom. Royen merely referred to Dillenius' diagnosis and illustration. The Dillenius reference provides the name-bringing citation and a drawing based on a plant cultivated by James Sherard.

Great confusion was caused when, sometime after 1755, a specimen from the Uppsala Botanic Garden was included in the Linnaean herbarium. It was labeled *Aster ericoides* but was, in reality, a plant of the taxon we now call *A. pilosus* Willdenow. Solander (in Aiton's *Hortus Kewensis*, 1789) used this specimen for the diagnosis of *A. ericoides*. The Dillenius (1732) reference under *A. ericoides* L. in *Species Plantarum* and a specimen from a cultivated plant, designated as type and annotated: "Sol. in Hort. Kew. iii: 203" (BM!), were used to define *A. multiflorus* Aiton. Later authors followed the interpretation given in *Hortus Kewensis*, but in the citation of range, the confusion was quite apparent. Hooker (1834), for example, cited Drummond's collection from "Saskatchewan and toward the Rocky Mountains" and Douglas' "Red River" [Canada] collection for *A. ericoides* sensu Aiton, which cannot possibly apply as *A. pilosus* does not extend that far west. Nees (1833) cited Pursh's collection "*a Canada ad Carolinam usque*" for *A. multiflorus* Aiton, which can apply only in part because this species, except for one doubtful record, does not occur in the Carolinas. Persoon (1807) placed *A. multiflorus* as a variety under *A. ericoides* sensu Aiton, which possibly accounts for the conflicting geographic information. The locality for *Clayton 194*, i.e., the type for *A. ericoides* in the proper Linnaean sense, is "Virginia." Only one authentic herbarium collection from Virginia was found among those examined (*Allard 12196*, US), but geographic information for very early collections from North America is often not very precise. Lamarck (1783) used the epithet *ericoides* in the correct Linnaean sense, and Michaux (1803) and Schkuhr (1808) applied the name to plants that were only varietally separable from the Linnaean species.

The error in application of the epithet *ericoides* persisted in the

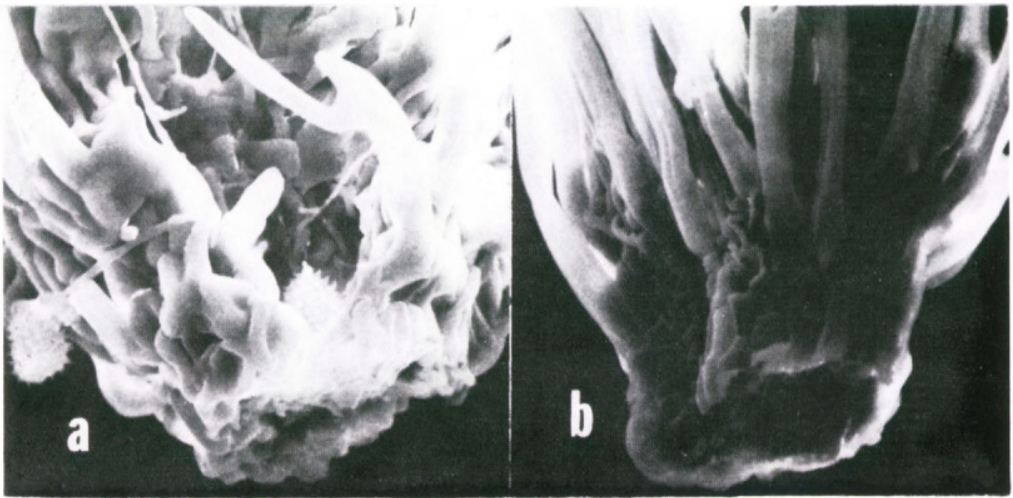


Figure 1. Scanning electron micrographs of achene bases. a, *Aster ericoides* ssp. *ericoides*; voucher 905 (ILL); b, *Aster falcatus* ssp. *commutatus*; Raup 963 (DAO).

literature until Mackenzie (1926) clarified the nomenclatural situation. He pointed out that Gray (1882) recognized the misapplication but did not correct it. The story was summarized by Blake (1930) who stated that the correct name for *Aster ericoides* sensu Aiton is *A. pilosus* Willdenow. Ten varietal names of *A. ericoides* sensu authors belong in synonymy under *A. pilosus* and related taxa. As many of the older manuals are still extensively used, and many collectors are unaware of the nomenclatural confusion surrounding these taxa, herbaria abound with specimens for which the name *A. ericoides* was misapplied.

The name *Ericoidei* Nees (1833) cannot be used for the section of *Aster* that includes *A. ericoides* Linnaeus. Nees and all subsequent authors based this infra-generic epithet on *A. ericoides* sensu Aiton (1789) and on the misidentified specimen in the Linnaean herbarium, i.e., on a different "type." Torrey and Gray (1841) included *A. multiflorus* Aiton and *A. falcatus* Lindley in *Ericoidei*, but A. Gray (1884) segregated these species from that section and placed them, for the first time, in their proper conspectus under sect. *Multiflori*.

In *Flora of North America*, Torrey and Gray (1841) recognized under *Aster multiflorus* the varieties β *stricticaulis* and γ *commutatus*. The type for β *stricticaulis* is a Drummond collection from "Saskatchewan and toward the Rocky Mountains" (K!). There is a second Drummond collection on the type sheet of *A. ramulosus* Lindley (K!), which was marked by Asa Gray as var. " β " and probably is a syntype of var. *stricticaulis* but, erroneously, was cited

by Torrey and Gray under var. γ *commutatus*. The type citation for the epithet *commutatus* [= *A. falcatus* ssp. *commutatus* in this interpretation] is "Upper Missouri [River] Dr. James (NY!). One of the Richardson collections (Ft. Franklin) mounted on the type sheet for *A. ramulosus* was marked " γ " by Asa Gray and cited for var. *commutatus* in *Flora of North America*.

In *Synoptical Flora of North America*, A. Gray (1884) elevated var. *commutatus* to the rank of species. Under *Aster multiflorus*, he cited as synonyms *A. scoparius* [sensu] DeCandolle (1836) [not *A. scoparius* Nees (1818)], and *A. hebecladus* DeCandolle. These two taxa were recognized as good species by Torrey and Gray and based on Berlandier collections from Texas. Examination of isotypes and microfiche photographs of the types from the DeCandolle herbarium proved Gray's interpretation correct; the plants are *A. ericoides* Linnaeus. Type material of *A. scoparius* appears to have somewhat larger heads than typical *A. ericoides*. This was noted by Rydberg (1906a) when he reinstated the species under the name *A. polycephalus*.

There has been little doubt about the name *Aster falcatus* Lindley. The type citation, as given in Hooker's (1834) *Flora Boreali-americana*, is "Arctic America, Dr. Richardson." The type specimen (K!) and two of the five different plants on the type sheet of *A. ramulosus* Lindley, also collected by Dr. Richardson, are identical. Date and place of original publication are the same for both names. *Aster ramulosus* was placed in synonymy under *A. falcatus* by Torrey and Gray (1841).

The name *Aster ciliatus* Muhlenberg ex Willdenow (1804) also created nomenclatural confusion. As it is a later homonym of *A. ciliatus* Walter (1788), the epithet is unavailable. The Muhlenberg collection is a plant of *A. ericoides* with spreading stem pubescence. Fernald (1899) placed the name *ciliatus* in synonymy under his *A. multiflorus* var. *exiguus*, which represents a slender-stemmed plant with few heads, and was subsequently reduced to forma status by the author himself (1949). It was on the basis of the Muhlenberg specimen, however, that Rydberg (1901) chose the name *exiguus* to recognize, at the rank of species, plants allied to *A. multiflorus* but with hirsute stem pubescence. Rydberg's choice created a nomen ambiguum, but the name was introduced, with his interpretation, into several floristic works, some of which are still widely used.



TYPES AND AUTHENTIC SPECIMENS
(From Herb. Clayt., Brit. Mus.,)

Type of
Aster ericoides L.

Figure 2. Type of *Aster ericoides* L.; Clayton 194 (BM). (Photograph courtesy of B. Boivin).

Since the species cannot be upheld taxonomically, the nomenclatural problem will resolve itself. The earliest name available for the variety of *A. ericoides* ssp. *ericoides* with spreading stem pubescence is *A. multiflorus* β *prostratus* Kuntze (1891).

The epithet *pansus* was coined by Blake (1928) to replace the untenable epithet *exiguus* sensu Rydberg. At the time, Blake felt that Kuntze's varietal epithet *prostratus* also did not apply to plants with spreading stem pubescence, since Kuntze did not interpret his variety in that particular sense. As the type for *Aster multiflorus* var. *pansus*, Blake designated a collection from Washington: *Whited* 853 (US!). When the article by Mackenzie (1926) on the status of *A. ericoides* had come to his attention, Blake placed var. *pansus* in synonymy under *A. ericoides* var. *prostratus*. Cronquist (1950) noted the distinctness in habit of the small-headed western populations of sect. *Multiflori*, and he elevated var. *pansus* to specific rank. In this interpretation, these populations are recognized as *A. ericoides* ssp. *pansus*.

Rydberg elevated all the morphological entities he could recognize to the rank of species, and in his *Flora of the Rocky Mountains* (1917), he placed seven species in sect. *Multiflori*. Six of these are based on previously named taxa; the seventh is *Aster crassulus* Rydberg, described in 1901 as a plant with stoloniferous rootstock, erect or ascending stems, and densely hirsute indument. In this interpretation, this taxon is reduced to varietal rank under *A. falcatus* ssp. *commutatus*.

Basionyms in sect. *Multiflori* not discussed so far include: *Aster cordineri* A. Nelson (1905), a plant with exceptionally large heads, to be placed in synonymy under *A. falcatus* ssp. *commutatus*; *A. elegantulus* Porsild (1950), the type (CAN!) of which is a perfect match to that of typical *A. falcatus*; and *Aster incanopilosus* (Lindley in Hooker) Sheldon (1893), which is a nomen nudum based on *A. ramulosus* β *incanopilosus*. According to Rydberg (1901), the term "*incanopilosus*" was used by Lindley in a descriptive sense, not as a varietal epithet. The name belongs, at least in the sense of Sheldon's authentic collections [Battle Lake, Otter Tail County, Minnesota, Aug. 1892 (WS, UC, RM)] in synonymy under *A. falcatus* ssp. *commutatus*.

Aster Section Multiflori A. Gray, Synopt. Fl. N. Am. **1**(2): 185. 1884.

Aster [subseries] *Densiflori* Nees von Esenbeck, Gen. et Sp. Ast., 110. 1833. — In part. — DeCandolle (1836) 242, as section, in part.

Aster sect. *Leucanthi* sensu DeCandolle, Prodrum **5**: 239. 1936. — In part, not Nees von Esenbeck (1833).

Aster sect. *Ericoidei* Torrey & Gray, Fl. N. Am. **2**: 123. 1841. — In part, not Nees von Esenbeck (1833), nor A. Gray (1884).

Aster sect. *Multiflori* A. Gray, Synopt. Fl. N. Am. **1**(2): 185. 1884. — Rydberg (1917) 880, in part, (1932) 804; R. A. Nelson (1933) **35**: 323–327.

Aster sect. *Squarrosa* Sheldon, Bull. Torrey Bot. Club **20**: 286. 1893.

Aster subsect. *Dumosi* House, Annot. List Pl. N. Y. 706. 1924. — In part.

Diagnostic Characteristics of the Section. Rhizomatous perennial herbs of variable habit. Stem pubescence uniformly distributed, not in lines, often scabrous, or glabrescent toward the base. Rosette leaves linear to somewhat spatulate, 2–6(–8) cm long, usually not more than 1 cm wide, with an entire, ciliolate margin, a mucronate apex, and a somewhat sheathing base. Cauline leaves in 3–4 size classes, linear to linear-lanceolate, sessile, entire, except for the ciliolate and often scabrous margin, the apex acute or obtuse, always armed with a slender bristle, the base often clasping or dilated; midrib prominent but lateral veins obscure or lacking; rameal leaves much reduced in size. Leaf pubescence uniform on both surfaces, usually more copious on cauline than on basal leaves. Inflorescence variable, depending on the species, but usually paniculate, never corymbiform. Heads radiate. Phyllaries in 3–4 series which may be subequal in height, or more commonly are imbricated; outer phyllaries linear or somewhat spatulate, with a ciliolate or fimbriolate margin and an obtuse or acute, mucronate apex, at least somewhat squarrose, pubescent on the outside and often also on the inside; inner phyllaries linear to linear-lanceolate, acute to attenuate, with an erose upper margin, somewhat pubescent or glabrous. Head size variable, depending on the species, ranging from 1–2 cm in diameter and from 20–60 florets per head. Ligules white, or occasionally slightly lavender. Disk florets yellow when young, turning purple after anthesis; corolla-tubes widening gradually, not distinctly differentiated into tube and limb portions. Pappus of white or somewhat discolored but never tawny capillary bristles, about as long as the disk corolla. Mature achenes purple or chocolate brown, 1.2–2.5 mm long, plump, strigillose, with 7 ribs.

Polien grains with a spinulose exine. TYPE SPECIES: *Aster ericoides* Linnaeus. Sp. Pl. 2: 875. 1753.

ANALYTICAL KEY

1. Heads small, the involucre 2.5–4.5 mm high; phyllaries strongly imbricated and graduated, the outer 2–3(–3.5) mm long; ligules 10–18(–20), typically less than 6.5 mm long; inflorescence compound-racemiform, the numerous crowded heads usually secund on arching branches. 2.
2. Habit colonial, the plants with erect stems; rhizome system stoloniferous, typically lacking cormoid portions; rosette shoots formed mostly some distance removed from old stems; involucre in fresh material cylindrical-campanulate. 1a. *Aster ericoides* ssp. *ericoides*.
 - i. Stem pubescence sparse, strigose or ascending. var. *ericoides*.
 - ii. Stem pubescence copious, divaricate-hirsute. var. *prostratus*.
2. Habit caespitose, the plants forming clusters of erect or ascending stems; rhizomes cormoid, not strongly stoloniferous; rosette shoots mostly ascending from or near the base of old stems; involucre in fresh material broadly campanulate. 1b. *Aster ericoides* ssp. *pansus*.
 - i. Plants forming many-stemmed clumps, the stems erect, sturdy, typically with copious spreading indument. var. *pansus*.
 - ii. Plants forming few-stemmed clusters, the stems decumbent or ascending, slender; indument typically sparse and appressed-strigose. var. *stricticaulis*.
1. Heads larger, the involucre 5–8 mm high; outer phyllaries (3–)4–7 mm long; ligules 22–35, 7 mm long or longer; inflorescence variable, but heads typically not secund. 3.
3. Habit caespitose, the plants forming few-stemmed clusters; rhizomes cormoid; rosette shoots and buds arising nearly vertically at or near the base of old stems; inflorescence with heads terminally disposed on long, slender, few-bracted peduncles; phyllaries not strongly squarrose, subequal in length, or the outer ones longest, largely herbaceous; plants sparsely pubescent, mostly appressed-strigose. 2a. *Aster falcatus* ssp. *falcatus*.
3. Habit scattered colonial, or plants forming sod-like patches; rhizomes tangled, strongly stoloniferous; rosette shoots formed some distance removed from the old stems; peduncles stout, often relatively short and with many bracts; phyllaries strongly squarrose, at least somewhat imbricated, with a conspicuous indurate basal portion; plants usually copiously pubescent. 2b. *Aster falcatus* ssp. *commutatus*.
 - i. Stems decumbent or ascending, usually branched from near the base; inflorescence diffuse-paniculate, or sometimes a simple raceme; heads rarely secund, usually with 40–50(–60) florets. var. *commutatus*.
 - ii. Stems erect, usually divaricately branched near the middle; inflorescence compound-racemiform; heads often somewhat secund, with 35–40(–45) florets. var. *crassulus*.

SYNONYMY AND DESCRIPTION OF TAXA

1. **Aster ericoides** Linnaeus, Sp. Pl. 2: 875. 1753. TYPE: "Virginia," *John Clayton 194* (BM!). Figure 2.

Lamarck (1783) 1: 304; Michaux (1803) 2: 113; Schkuhr (1808) 105, *pl.* 245; Poiret (1823) 492; Hooker (1834) 2: 12 [exclusive of description and synonyms; applicable only to the collections cited]; Mackenzie (1926) 65; Blake (1930) 138; Rydberg (1932) 809; R. A. Nelson (1933) 325; Small (1933) 1389; Raup (1934) 204; Palmer & Steyermark (1935) 663; Raup (1935) 166, (1936) 320; Benke (1936) 121; Cory & Parks (1937) 101; Dole (1937) 257; Reeves & Bain (1947) 255; St. John (1937) 426; Deam (1940) 943; Gates (1940) 241, (1941) 238; Kittell (1941) 406; Tidestrom & Kittell (1941) 406; G. N. Jones (1945) 254; Norton & Brown (1945) 41; Tatnall (1946) 262; Breitung (1947) 97; Cronquist (1947) 144; Hanes & Hanes (1947) 250; Ogden, et al. (1948) 63; W. C. Stevens (1948) 403; Hodgdon & Friedlander (1949) 112; Rosendahl & Cronquist (1949) 511; Turner (1949) 25; Fernald (1950) 1432; G. N. Jones (1950) 276; O. A. Stevens (1950) 278; Cronquist in Gleason (1952) 3: 464; Weber (1953) 181; Harrington (1954) 576; Evers (1955) 439; Jones & Fuller (1955) 468; St. John (1956) 426; Guldner (1960) 187; Massey (1961) 197; Weber (1961) 181; Boivin (1962) 66; Waterfall (1962) 214; Gleason & Cronquist (1963) 730; G. N. Jones (1963) 251; St. John (1963) 463; Steyermark (1963) 1518; Lakela (1965) 364; Rickett (1966) 1(2): 578, *pl.* 157; Boivin (1967) 1032; Cormack (1967) 355; Barkley (1968) 341; Porsild & Cody (1968) 96; Seymour (1969) 353; Correll & Johnston (1970) 1597; Klein (1970) *f.* 720; Van Faasen (1971) 100; Waterfall (1972) 214; Weber (1972) 121; Jones & Bell (1974) 22; Swink (1974) 47; Mohlenbrock (1975) 429. — not sensu Aiton (1789).

Characters of the Species. Plants up to one meter tall, the stems usually branched above the middle. Rosette leaves mostly 2–5 cm long; stem leaves reduced in size, the larger and medium ones withered and deciduous at flowering time; ultimate rameal leaves typically phyllary-like, squarrose, stiff, intergrading with the involucre. Inflorescence racemiform, many-flowered, with heads on densely bracteate short peduncles, or sessile and crowded, mostly secund on arching or ascending branches. Heads 1 cm or less in diameter; receptacle conspicuously alveolate; involucre 2.5–4.5(–5) mm high, strongly imbricated, the outer phyllaries squarrose, firm, 1.2–2.5(–3) mm long, with a spatulate herbaceous portion covering about 60% of the area, the basal portion chartaceous and indurate; inner phyllaries longer and narrower, and more flexible. Ligules 10–18(–20), about 4–6.5 mm long, including the corolla-tube; disk florets 6–12(–20), the corolla about 2.5–4 mm long. Pappus of 30–40 bristles. Achenes purple, or brown when weathered, 1.2–1.8(–2.0) mm long, and about 0.4–0.5 mm in diameter, lacking a conspicuous callus base (Figure 1a).

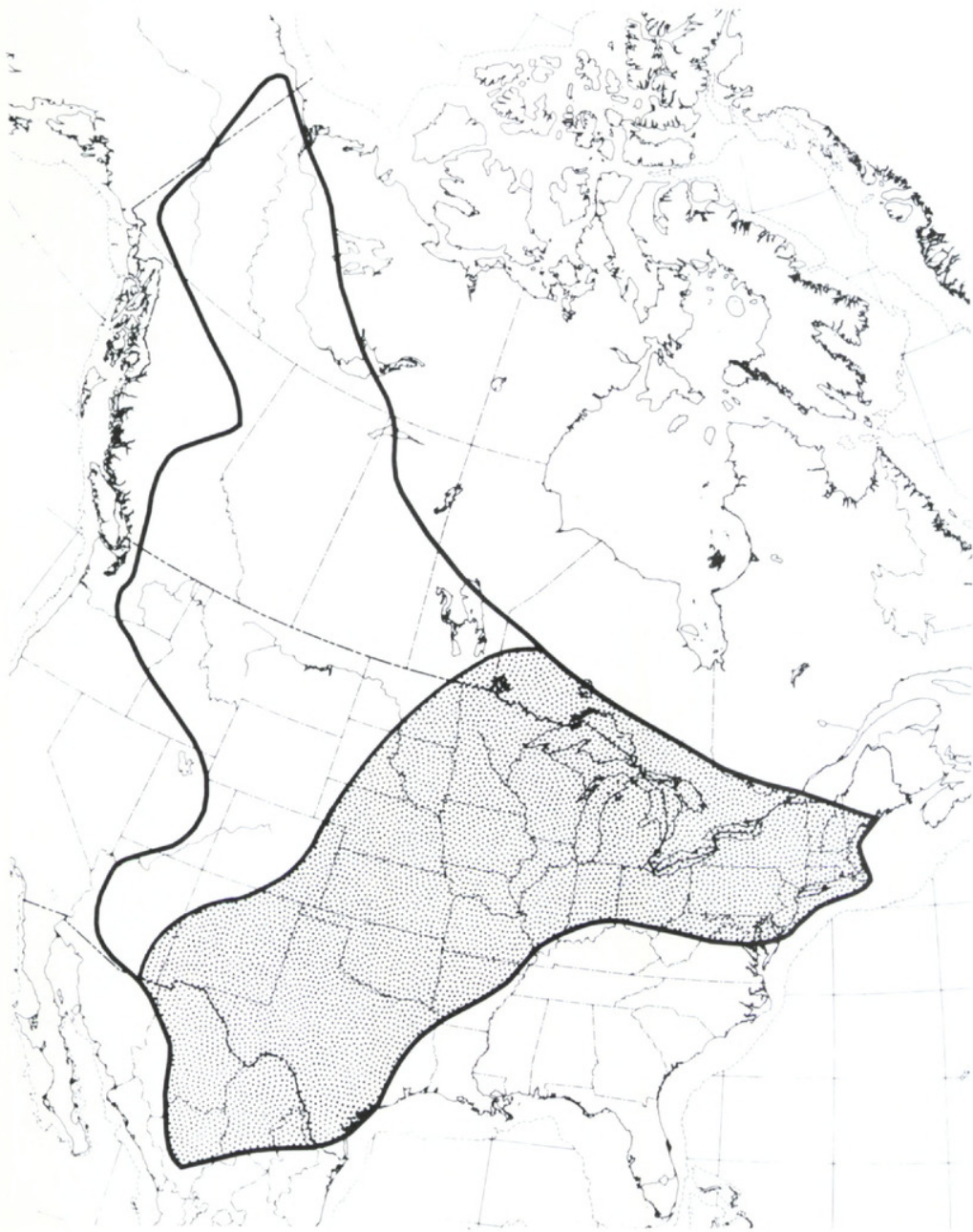


Figure 3. Range of *Aster ericoides* ssp. *ericoides*.

1a. *Aster ericoides* Linnaeus ssp. *ericoides*

Aster multiflorus Aiton, Hort. Kew., Ed. 1, 3: 203. 1789. – [Based on Dillenius (1732) cited by Linnaeus (1753) as one of the references for *A. ericoides*]. – Willdenow (1804) 2027; Muhlenberg (1813) 74; Pursh (1814) 2: 546; Hornemann (1815) 2: 813; Nuttall (1818) 2: 155; Barton (1818) 117; Nees von Esenbeck (1818) 31; Link (1822) 2: 331; Sprengel (1826) 531; Link (1829) 1: 740; Nees von Esenbeck (1833) 116; Hooker (1834) 2: 13; DeCandolle (1836) 5: 243; Torrey & Gray (1841) 124; Torrey (1843) 341; Gray (1848) 201, (1850) 90; Chapman (1860) 202; Darby (1860) 3641; Lesquereux (1861) 367; Porter & Coulter (1874) 56; Gray (1882) 165; Watson (1883) 103; Gray (1884) 1(2): 185; Macoun (1884) 223; J. M. Coulter (1885) 161, in part; Brendel (1887) 50; Britton (1889) 138; Gray (1889) 260; Watson & Coulter (1890) 260; Kuntze (1891) 1: 313; J. M. Coulter (1892) 195; MacMillan (1892) 520; Porter (1894) 325; Rydberg (1895) 163; Britton & Brown (1898) 3: 381; Porter (1898) 493; S. Coulter (1899) 976; Britton (1901) 964; Mohr (1901) 783; Porter & Small (1903) 326; Rydberg (1906b) 355, in part; Robinson & Fernald (1908) 811; G. T. Stevens (1910) 666; Petersen (1912) 176; Small (1913) 1224; Monroe (1913) 99; Brainerd (1915) 251; Hegi (1915) 6(1): 420; Wooton & Standley (1915) 685; Rydberg (1917) 885; Lowe (1921) 278; Rydberg (1922) 885; Britton & Brown (1923) 3: 427; House (1924) 707; Pepoon (1927) 501; Schaffner (1928) 535; Pammel & King (1930) 3851; Peattie (1930a) 376, (1930b) 141; Harned (1931) 554; Benner (1932) 293; Over (1932) 139; Zenkert (1934) 256; Stemen & Myers (1937) 563; Madison (1938) 150, f. 734; Harper (1944) 225; Taylor (1955) 520; Voss & Eifert (1967) 235. – *Aster ericoides* L. * *multiflorus* (Ait.) Persoon, Synops. Sp. Pl. 2: 443. 1807. TYPE: cult. "Sol. Hort. Kew. iii: 203" (BM!); photograph of type, ILL.

Aster ciliatus sensu Muhlenberg ex Willdenow, Sp. Pl. 3: 2027. 1804. – Persoon (1807) 2: 443; Pursh (1814) 2: 546; Nees von Esenbeck (1818) 30; Poiret (1823) 1: 492. — *Aster multiflorus* Ait. [var.] *ciliatus* (Muhl. ex. Willd.) Barton, Compend. Fl. Philad. 2: 117. 1818. – Nees von Esenbeck (1833) 117. — Not *A. ciliatus* Walter (1788). TYPE CITATION: "*Muhlenberg in litt. Habitat in America boreali.*"

[A specimen, presumably from Muhlenberg's type, sent to Asa Gray by Nees von Esenbeck (GH!) was annotated by Fernald: "*A. multiflorus* Ait., var. *exiguus* Fernald, n. var.", and the name *A. ciliatus* was placed in synonymy under Fernald's (1899) var. *exiguus*. Rydberg's (1901) choice of the name *exiguus* for plants with divaricate pubescence was based on this specimen, not on Fernald's type].

Aster hebecladus DeCandolle, Prodr. 5: 242. 1836. — Torrey & Gray (1841) 146; Coulter & Nelson (1909) 515, in part; Wooton & Standley (1915) 685; Cory & Parks (1937) 101. TYPE: "In Mexican prov. Texas". *Berlandier* 2085 (Holotype, G; Isotype, GH!) — Jones (1973) *pl.* 3a.

Aster scoparius sensu DeCandolle, Prodr. 5: 242. 1836. — Torrey & Gray (1841) 146. — Not Nees von Esenbeck (1818, 1833). TYPES: "Comancheros orientalis, Texas". *Berlandier* 1868, 1871, 1894 (Lectotype designated herein = *Berlandier* 1871, G; Isolectotypes, GH!, MO!, WIS!) — Jones (1973) *pl.* 3c.



Figure 4. Holotype of *Aster multiflorus* Ait. var. *pansus* Blake (= *A. ericoides* ssp. *pansus*); Whited 853 (US).

Aster multiflorus Aiton α *normalis* Kuntze, Rev. Gen. Pl. **1**: 313. 1891.

Aster multiflorus Aiton β *prostratus* Kuntze, Rev. Gen. Pl. **1**: 313. 1891.

[This is the basionym of *A. ericoides* L. ssp. *ericoides* var. *prostratus* (Kuntze) Blake.] — *Aster ericoides* L. var. *prostratus* (Kuntze) Blake, Rhodora **32**: 138. 1930. — Palmer & Steyermark (1935) 663; Gates (1940) 241; Hanes & Hanes (1947) 250; Fernald (1950) 1432; Cronquist in Gleason (1952) **3**: 464; Gleason & Cronquist (1963) 730; Mohlenbrock (1975) 429. — *Aster ericoides* L. f. *prostratus* (Kuntze) Fernald, Rhodora **51**: 96. 1949. — Steyermark (1963) 1518. TYPE: Nebraska, O. Kuntze, Sept. 1874 (Holotype, NY!) — Jones (1973) *pl.* 4b.

Aster multiflorus Aiton var. *exiguus* Fernald, Rhodora **1**: 187. 1899. — Robinson & Fernald (1908) 811; House (1924) 707. — *Aster ericoides* L. f. *exiguus* (Fernald) Fernald, Rhodora **51**: 96. 1949. — Fernald (1950) 1433. — Not *A. exiguus* Rydberg (1901). TYPE: Dedham, Massachusetts, C. E. Faxon (Holotype, GH!) — Jones (1973) *pl.* 5e. [The name was applied to specimens of delicate and slender habit].

Aster exiguus Rydberg, Bull. Torrey Bot. Club **28**: 505. 1901. — In part. — [Based on *A. multiflorus* Ait. var. *exiguus* Fernald only as to name-bringing synonym, not as to type]. — Britton (1901) 964; Mackenzie & Bush (1902) 196; Rydberg (1906b) 355, in part; Daniels (1911) 233; Petersen (1912) 177; Small (1913) 1224; Rydberg (1917) 884, in part, (1922) 884, in part, (1932) 808; Deam (1940) 943; G. N. Jones (1945) 254; Reeves & Bain (1947) 255; G. N. Jones (1950) 275; Jones & Fuller (1955) 468; Mohlenbrock & Voigt (1959) 346; Guldner (1960) 187; G. N. Jones (1963) 251. [This epithet belongs in synonymy under *A. ericoides* L. ssp. *ericoides* var. *prostratus* (Kuntze) Blake].

Aster polycephalus Rydberg, Bull. Torrey Bot. Club **33**: 153. 1906.

[This name is based on the type of *A. scoparius* sensu DeCandolle (1836), which is a later homonym of *A. scoparius* Nees (1818). As to the interpretation of authors, including Rydberg, the name belongs in synonymy under *A. falcatus* ssp. *commutatus*].

Aster multiflorus Aiton var. *caeruleus* Benke, Rhodora **30**: 78. 1928. — *Aster ericoides* L. f. *caeruleus* (Benke) Blake, Rhodora **32**: 139. 1930. — Fernald (1950) 1433; Steyermark (1963) 1518. TYPE: Illinois [near Bushnell], H. C. Benke 4373 (Holotype, FM).

[This is a form with blue or purplish rays, possibly the result of introgressive hybridization].

Aster Batesii Rydberg, Brittonia **1**: 102. 1931. — *Aster ericoides* L. [var.] *Batesii* (Rydb.) Gates, Trans. Kansas Acad. Sci. **42**: 138. 1939. — Gates (1940) 241. — at least in part. TYPE: Nebraska, St. Paul, J. M. Bates 5440 (Holotype, NY!).

[This is a slightly glandular form with lavender rays, possibly the result of introgressive hybridization].

Aster ericoides Linnaeus f. *gramsii* Benke, Am. Midl. Nat. **13**: 326. 1932 — Fernald (1950) 1433; Guldner (1960) 187. TYPE: Illinois. Cook County, Schiller Park, H. C. Benke 4948 (Holotype, FM).

[A form with rose-red ligules, possibly the result of introgressive hybridization].

Illustrations in Literature: Dillenius (1732) *t.* 36, *f.* 40; Schkuhr (1808) *pl.* 245; Bois (1896) *t.* 136 [as *multiflorus*]; Robinson & Fernald (1908) *f.* 952 [as *multiflorus*]; G. T. Stevens (1910) 666, *pl.* 183 [as *multiflorus*]; Hegi (1915) VI(1):420 [as *multiflorus*]; Britton & Brown (1923) 3: *f.* 4337 [as *multiflorus*]; Pammel & King (1930) *f.* 384, 385 [as *multiflorus*]; Madison (1938) *f.* 734 [as *multiflorus*]; Gates (1941) *f.* 346; W. C. Stevens (1948) *f.* 702 [not *f.* 701, which may be *A. simplex*]; Fernald (1950) *f.* 1660; O. A. Stevens (1950) *f.* 305; Gleason (1952) 3: 465; Steyermark (1963) *pl.* 360, *f.* 5; Rickett (1966) 1(2): *pl.* 157; Klein (1970) *f.* 720.

Distinctive Characteristics of the Subspecies. Plants colonial, the stems erect, 50–100 cm tall, typically only one emerging at any point, rhizome system horizontal, lacking distinct cormoid portions, strongly stoloniferous; winter rosettes produced at tips of elongate stolons some distance removed from the old stems; only the ultimate rameal leaves persisting at flowering time, these linear, not dilated at the base, and not strongly clasping. Involucre mostly short-cylindric (turbinate in dry specimens); disk florets usually less than 12, up to 14 in populations of the southern or western part of the range.

Two varieties are recognized, mainly on the basis of pubescence characteristics, var. *ericoides* with indument relatively sparse, appressed to ascending, var. *prostratus* (Kuntze) Blake (1930) with copious spreading, often scabrous pubescence. Heads and number of florets average somewhat smaller in var. *prostratus* than in var. *ericoides* (Jones, 1974).

FLOWERING PERIOD. Late August to October (to November in the South).

HABITAT. Dry ground, roadsides, railroad sidings, prairies, open ranges, grassy hillsides, glades, and dunes.

RANGE. Southern Maine, northern Virginia, Ohio, Illinois, Arkansas, Oklahoma, Texas, northern Mexico, Arizona, eastern Colorado, Nebraska, eastern Dakotas, southeastern Manitoba, southern Ontario, and perhaps southwestern Quebec (Figure 3).

REPRESENTATIVE SPECIMENS. **Arizona:** GILA CO., Payson, *R. E. Collom* 183 (GH, MICH, MO, NY). **Arkansas:** WASHINGTON CO., Fayetteville, *F. L. Harvey* 37 (ILL, MICH, MO, NY). **Colorado:** BACA CO., Pritchett, *C. M. Rogers* 6422 (COLO, MICH, TEX, US). **Connecticut:** LITCHFIELD CO., South Canaan, *J. M. Greenman* 41 (MO). **Illinois:**

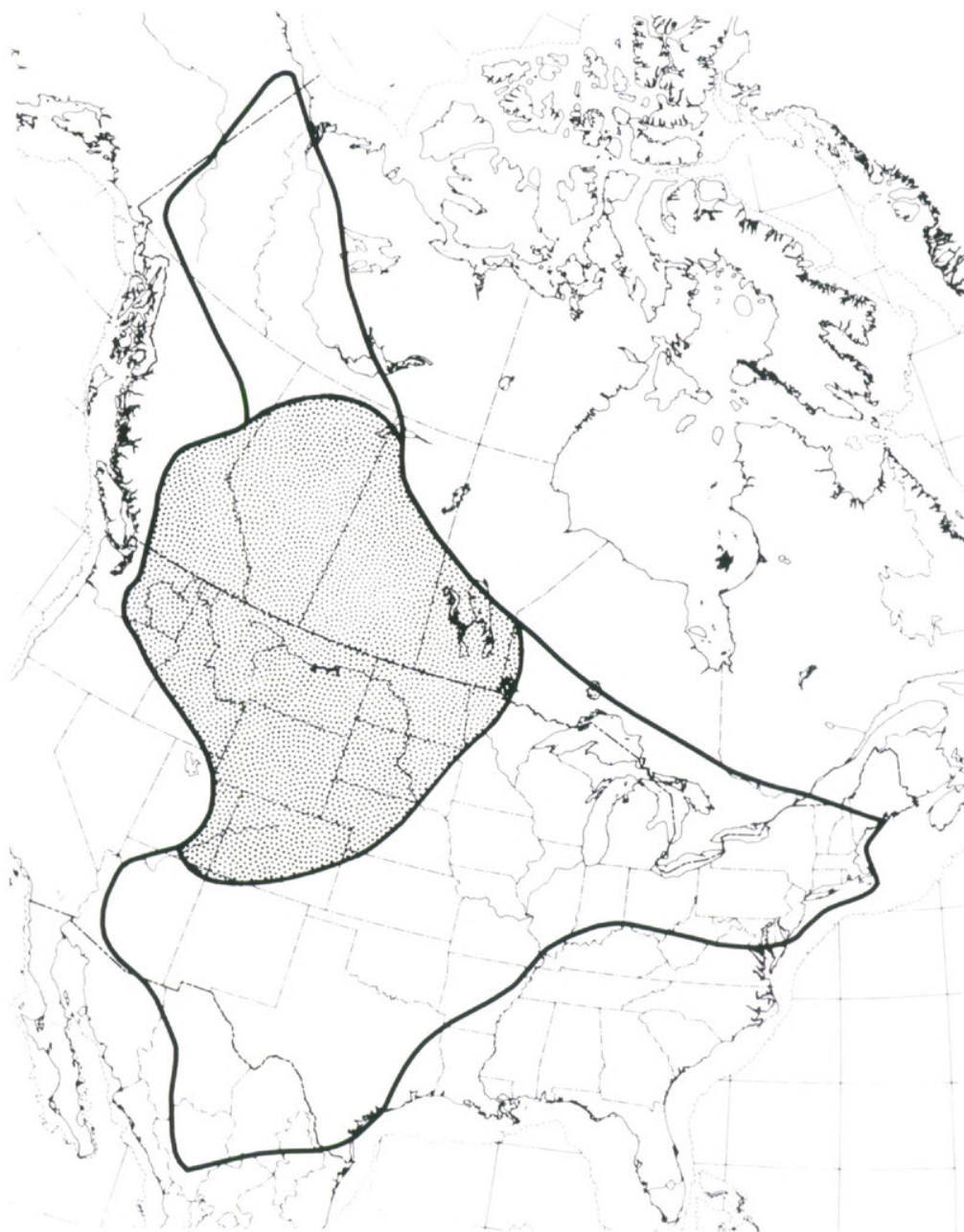


Figure 5. Range of *Aster ericoides* ssp. *pansus*.

CHAMPAIGN CO., Urbana, *G. N. Jones* 16312 (ILL). **Indiana:** BENTON CO., Fowler, *C. C. Deam* 32718 (IND). **Iowa:** ADAMS CO., Washington Twp., *M. J. Fay* 5700 (TEX). **Kansas:** SALINE CO., Bavaria, *K. L. Johnson* 1729 (NCU, NDA). **Maine:** LINCOLN CO., Monhegan, *N. C. Fassett* 21558 (MO, WIS). **Massachusetts:** MIDDLESEX CO., Woburn, *A. R. Hodgdon & M. Hopkins*, s.n. (COLO, DAO, GA, GH, ILL, ISC, KY, MAINE, MO, MSC, NY, OSU, PH, RM, TEX, UBC, UC, US, WIS, WS). **Michigan:** WASHTENAW CO., Dixboro, *F. J. Herman* 7348 (GH, MICH, MO, MSC, NY, PH). **Minnesota:** CLEARWATER CO., Squaw Lake, Itasca Park, *M. L. Grant* 6776 (ISC, WIS). **Missouri:** PUTNAM CO., Livonia, *B. F. Bush* 7747 (GH, ILL, MO, NDA, NY). **Nebraska:** RICHARDSON CO., Humboldt, *H. C. Reynolds* 2607 (WIS). **New Hampshire:** STRAFFORD CO., Durham, *C. H. Knowlton*, s.n. (NCU, PH). **New Jersey:** CAPE MAY CO., Wildwood, *H. M. Moldenke* 4030 (NY). **New Mexico:** GRANT CO., Silver City, *O. B. Metcalfe* 781 (GH, ILL, MO, NY, RM). **New York:** ALBANY CO., Loudonville, *H. D. House* 27073 (ILL, OKL). **North Dakota:** GRAND FORKS CO., Larimore, *P. Bates* 676 (NDA, WIS). **Ohio:** ASHTABULA CO., West Jefferson, *E. C. Leonard* 2035 (US). **Oklahoma:** MAYES CO., Locust Grove, *J. G. Brown* 13 (OKL, TEX). **Pennsylvania:** NORTHAMPTON CO., Easton, *T. C. Porter* 16808 (MO). **Rhode Island:** PROVIDENCE CO., Diamond Hill, *E. J. Palmer* 46580 (NEBC). **South Dakota:** SPINK CO., Redfield, *A. E. Ricksecker* 140 (ILL). **Texas:** BEXAR CO., San Antonio, *F. Lindheimer* 876 (MO, NY, OKL, TEX, UC, US). **Virginia:** FAUQUIER CO., *H. A. Allard* 12196 (TEX, US, WIS). **Wisconsin:** IOWA CO., Ridgeway, *H. H. Iltis* 19395 (WIS). **Manitoba:** Winnipeg, *G. N. Jones* 23566 (ILL). **Ontario:** YORK CO., Toronto, *H. H. Brown* 1432 (DAO), 5035 (UBC). **Mexico:** Coahuila, Parras, *E. Palmer* 439 (MO, UC, US).

1b. *Aster ericoides* Linnaeus ssp. *pansus* (Blake) A. G. Jones, stat. nov.

Aster multiflorus sensu authors. – J. M. Coulter (1885) 161; A. Nelson (1896) 127; Rydberg (1900) 393; Piper & Beattie (1901) 186; Piper (1906) 572; Rydberg (1906b) 355, in part; Coulter & Nelson (1909) 515; Piper & Beattie (1914) 270; Henry (1915) 293; Clements & Clements (1945) 259. — Not Aiton (1789).

Aster multiflorus β *stricticaulis* Torrey and Gray, Fl. N. Am. 2: 125. 1841. – [This is the basionym for *A. ericoides* L. ssp. *pansus* (Blake) A. G. Jones var. *stricticaulis* (Torr. & Gray) Gates]. – Macoun (1884) 223; Rydberg (1895) 163. – *Aster stricticaulis* (Torr. & Gray) Rydberg, Fl. Rocky Mountains, p. 885. 1917. – Rydberg (1922) 885, (1932) 809. — *Aster ericoides* L. [var.] *stricticaulis* (Torr. & Gray) Gates, Trans. Kansas Acad. Sci. 42: 138. 1939. – Gates (1940) 241. TYPE: "Saskatchewan, and towards the Rocky Mountains". *Drummond* (Lectotype, designated herein, κ !).

[The type material is mounted on two sheets, each consisting of several different collections: Jones (1973) *pl.* 2c = lectotype, *pl.* 1c = *Drummond* 584 (syntype or isolectotype) on the type sheet of *A. ramulosus* (κ !). The individual specimens have been annotated by Asa Gray].

Aster exiguus Rydberg, Bull. Torrey Bot. Club 28: 505. 1901. – In part. – Rydberg (1906b) 355, (1917) 884, in part; Standley (1921) 424. – Not *A. multiflorus* Ait. var. *exiguus* Fernald (1899).



Figure 6. Holotype of *Aster falcatus* Lindl. in Hook.; Dr. Richardson (κ). (Photograph courtesy of B. Boivin).

Aster multiflorus Aiton var. *pansus* Blake, *Rhodora* **30**: 227. 1928. – [This is the basionym of *A. ericoides* L. ssp. *pansus* (Blake) A. G. Jones]. – *Aster pansus* (Blake) Cronquist, Leaflets West. Bot. **6**: 45. 1950. – Cronquist in Davis, et al. (1952) 705; Breitung (1954) 89, 92; Cronquist in Hitchcock, et al. (1955) **5**: 91; Scoggan (1957) 526; Moss (1959) 457; Abrams & Ferris (1960) **4**: 322, f. 5546; Peck (1961) 781; Thieret (1961) 120; Hitchcock & Cronquist (1973) 492. – *Aster ericoides* L. var. *pansus* (Blake) Boivin, *Nat. Canad.* **89**: 70. 1962. TYPE: Washington, Kittitas County, Ellensburg, K. *Whited* 853 [Holotype (Figure 4), US!; Isotypes OSU!, WS!].

Aster ericoides Linnaeus var. *commutatus* sensu Boivin, *Nat. Canad.* **89**: 67. 1962. – In part. – Boivin (1967) 1032, (1972) 32, in part. – Not *A. multiflorus* γ *commutatus* Torrey and Gray (1841).

Illustrations in Literature: Hitchcock, et. al. (1955) **5**: 96; Abrams & Ferris (1960) **4**: 323, f. 5546.

Distinctive Characteristics of the Subspecies. Plants forming distinct caespitose clusters or many-stemmed clumps, with several stems arising from a cormoid rhizome portion. Several clumps often interconnected by horizontal strands, but these produced only at times of little moisture stress in early spring. Winter rosettes formed at or near the base of old stems, not at the tips of elongate stolons; leaves of larger size often persistent at flowering time in addition to the numerous rameal leaves; smaller leaves usually somewhat dilated or clasping at the base. Involucre campanulate or turbinate; disk florets 10–20; achenes similar to those of the typical subspecies, but often somewhat paler purple.

Two varieties are recognized which appear to be well separated geographically. Variety *pansus* (Blake) Boivin (1962) is distinct by forming sturdy, many-stemmed clumps, the stems erect, up to 100 cm tall at maturity, mostly densely spreading pubescent; heads strongly secund. Variety *stricticaulis* (Torrey & Gray) Gates (1939) is more delicate and slender in every respect. Stems decumbent or ascending, the cormoid rhizome portions more widely spaced; stem pubescence mostly appressed-strigose; heads not strongly secund.

FLOWERING PERIOD. Mid-July to end of September, rarely into October.

HABITAT. Dry or well-drained sandy or gravelly soil, lake shores, salt flats, open ranges, hillsides, river banks and sandbars.

RANGE. Variety *pansus*: British Columbia, Washington, Oregon, and Idaho, with slight representation in adjacent regions east of the

Continental Divide; variety *stricticaulis*: Alberta, Saskatchewan, southern Manitoba, Dakotas, Nebraska, Kansas, Colorado, Utah, Wyoming, and Montana, with slight representation in adjacent regions (Figure 5).

REPRESENTATIVE SPECIMENS. **Colorado**: JEFFERSON CO., Arvada, *I. W. Clokey* 3908 (GH, ILL, ISC, MICH, MO, RM, UC, US, WS). **Idaho**: LATAH CO., Moscow, *L. T. Henderson* 2804 (GH, US). **Minnesota**: GRANT CO., Sanford Twp., *J. W. & M. F. Moore* 10126 (ILL, ISC). **Montana**: JEFFERSON CO., Helena, *M. A. Carleton* 224 (ILL, KSC). **Nebraska**: CUSTER CO., Arnold, *K. L. Johnson* 2879 (NDA). **North Dakota**: STARK CO., Dickinson, *O. A. Stevens* 1506 (NDA). **Oregon**: MORROW CO., Rhea Creek, *J. B. Leiber* 896 (MO, US). **South Dakota**: HARDING CO., Table Mountain, *S. S. Visser* 342 (RM). **Utah**: SAN JUAN CO., Lost Canyon, *S. L. Welsh, G. Moore, & M. Olsen* 3770 (BRY). **Washington**: ASOTIN CO., Asotin, *A. Cronquist & S. Preece* 6816 (DAO, OSU, US, WS). **Wyoming**: FREMONT CO., Jeffrey City, *G. N. Jones* 35187 (ILL). **Alberta**: ACADIA D., Craigmyle, *A. H. Brinkman* 293 (DAO), 788 (ALTA, US). **British Columbia**: EAST KOOTENAY D., Windermere, *J. A. Calder & D. B. O. Savile* 11180 (DAO). **Manitoba**: PORTAGE LA PRAIRIE D., Langruth, *A. & D. Löve* 5662 (DAO). **Ontario**: RAINY RIVER D., 10 miles below Rainy River, *C. E. Garton* 9424 (DAO, UC). **Saskatchewan**: LAKE CENTRE D., Watrous, *H. A. Senn* 2947 (DAO).

2. ***Aster falcatus*** Lindley in Hooker, *Fl. Bor.-Am.* 2: 12. 1834.
TYPE: "Arctic America," *Dr. Richardson* (Holotype, K!, Isotype, GH!). Figure 6.

DeCandolle (1836) 5: 241; Torrey & Gray (1841) 125; Porter & Coulter (1874) 56; Gray (1884) 185; Macoun (1884) 223; Rydberg (1896) 506, (1906b) 355; Henry (1915) 293; Rydberg (1917) 885, (1922) 885; R. A. Nelson (1933) 326; Raup (1936) 303; Cronquist (1947) 144; Rosendahl & Cronquist (1949) 511; Hultén (1950) 1492; Cronquist in Gleason (1952) 3: 464; Cronquist in Davis, et al. (1952) 702; Weber (1953) 181; Harrington (1954) 576; Cronquist in Hitchcock, et al. (1955) 5: 82; Scoggan (1957) 527; Moss (1959) 456; Cody (1960) 97; Weber (1961) 181; Gleason & Cronquist (1963) 730; Barkley (1968) 341; Porsild & Cody (1968) 96; Weber (1972) 121; Hitchcock & Cronquist (1973) 492.

Specific Characteristics. Habit of plants variable, the stems mostly branched below the middle. Rosette leaves 3–8 cm long; stem leaves in 3–4 size classes, mostly with somewhat clasping base, usually only the midrib strongly expressed, but sometimes lateral veins present in larger leaves. Inflorescence diffuse-paniculate or compound-racemiform, or sometimes a simple raceme. Heads not crowded, usually single or few at tips of branches, not secund, 1–1.5(–2) cm in diameter, the receptacle not as strongly alveolate as in *Aster ericoides*. Involucre 5–8 mm long; outer phyllaries 3–8 mm long,

usually at least somewhat squarrose; inner phyllaries 4–7 mm long, more slender. Ligules 20–35, 7–10 mm long, including the corollatube; disk florets (16–)18–30, the corolla (3.5–)4–5.5 mm long. Pappus of 40–55 bristles. Achenes chocolate brown, or sometimes pale purple, 2–2.5 mm long, with a short callus base (Figure 1b).

2a. *Aster falcatus* Lindley in Hooker ssp. *falcatus*

Aster ramulosus Lindley in Hooker, Fl. Bor.-Am. **2**: 13. 1834. — DeCandolle (1836) **5**: 243; Nuttall (1841) 293; Macoun (1884) 223. TYPE: "Fort Franklin, and Cumberland House Fort", *Dr. Richardson* (K!); Jones (1973) *pl. 1c*.

[The type sheet consists of five different plants from three localities. Asa Gray annotated the specimens and determined that the Richardson collections are identical with *A. falcatus*].

Aster elegantulus Porsild, Canad. Field-Nat. **64**: 43. 1950. TYPE: Yukon Territory, Whitehorse, *A. E. Porsild & A. J. Breitung 10703* (Holotype, CAN!) — Jones (1973) *pl. 2a*.

Aster ericoides Linnaeus var. *commutatus* sensu Boivin, Nat. Canad. **89**: 67. 1962. — In part. — Boivin (1967) 1032, (1972) 32, in part. — Not *A. multiflorus* γ *commutatus* Torrey and Gray (1841).

Illustration in Literature: Gleason (1952) **3**: 465.

Distinctive Characteristics of the Subspecies. Plants in distinct cespitose clusters, with several stems arising from a cormoid rhizome portion; connecting horizontal strands formed mostly in spring. Winter rosettes arising at a steep angle from or near the base of old stems, often not emerging until spring. Stems usually ascending, not erect, typically with sparse appressed pubescence, or sometimes thinly hirsute. Cauline leaves of all sizes usually persistent at flowering time, the smaller leaves dilated and often clasping at the base; rameal leaves flexible, not phyllary-like. Inflorescence typically diffuse-paniculate, with heads single or few at ends of branchlets, usually on long, slender peduncles with few, distant, flexible bracts. Terminal heads conspicuously larger than lateral heads. Involucre hemispherical, or broadly turbinate when pressed, not strongly imbricated, and not strongly squarrose, the phyllaries subequal in length, or often the outer ones longer than the inner ones. Outer phyllaries thinly appressed pubescent to nearly glabrous, sparingly ciliolate, spatulate, largely herbaceous, the indurate base covering less than 30% of the area; disk florets typically more than 20, the total number of florets 40 or more per head.

FLOWERING PERIOD. End of July to mid-September.

HABITAT. In well-drained soil; river banks and slopes; edges of alkali lakes and flats; prairies and plains; in the southern part of the range in the montane zone up to 8,000 feet elevation, mostly in somewhat more mesic situations, as compared to the subspecies *commutatus*.

RANGE. Alaska, Yukon D., southwestern Mackenzie D., British Columbia, Utah, Arizona, New Mexico, Colorado, western Dakotas, western Manitoba, and Alberta. The plants are more commonly found in the northern than in the southern part of range (Figure 7).

REPRESENTATIVE SPECIMENS. **Alaska:** Ft. Yukon, *O. S. Bates*, 1888 (US). **Arizona:** COCONINO CO., Flagstaff, *G. A. Pearson* 307 (US). **Colorado:** GUNNISON CO., Gunnison, *I. W. Clokey* 2973, 2975 (ILL, RM, UC, US, WIS). **Montana:** GLACIER CO., Babb, *D. Lynch* 6696 (WS). **New Mexico:** SIERRA CO., Kingston, *O. B. Metcalfe* 1406 (MO, UC, US). **North Dakota:** BILLINGS CO., Medora, *N. Zaczkowski* 1492, 4293, 6177 (NDA). **South Dakota:** PENNINGTON CO., Black Hills Nat. For., *A. S. & B. Tomb* 576 (TEX). **Utah:** DAGGETT CO., Sheep Creek, south of Manila, *L. L. Welsh & G. Moore* 6736 (BRY). **Wyoming:** ALBANY CO., Centennial, *A. Nelson* 8792 (NY). **Alberta:** VEGREVILLE D., Fort Saskatchewan, *G. H. Turner* 2747, 6492, 7395, 7421, 8623, & 8628 (ALTA), 2809 (DAO, ALTA, WIS). **British Columbia:** CARIBOO D., Chilcotin, *W. A. Newcombe* 101 (UBC). **Manitoba:** CHURCHILL D., The Pas, *W. Krivda* 2104 (COLO, DAO, WIS). **Northwest Territories:** MACKENZIE D., Fort Liard, *W. J. Cody & K. W. Spicer* 11749 (UBC); YUKON D., Haines Junction, *J. A. Calder & I. Kukkonen* 28250 (ALTA, COLO, UC, WS). **Saskatchewan:** MAPLE CREEK D., Cypress Hills, *A. J. Breitung* 5673 (DAO, MO).

2b. *Aster falcatus* Lindley ssp. *commutatus* (Torrey & Gray) A. G. Jones, stat. & comb. nov.

Aster ramulosus β *incanopilosus* Lindley in Hooker, Fl. Bor.-Am. 2: 13. 1834.
– Nomen nudum. — DeCandolle (1836) 5: 243. — *Aster incanopilosus* (Lindl.) Sheldon, Bull. Torrey Bot. Club 20: 286. 1893. — Porter (1894) 323; Britton & Brown (1893) 3: 381, f. 3803; Rydberg (1900) 393. [Authentic specimens: Battle Lake, Otter Tail County, Minnesota, Aug. 1892, *E. P. Sheldon* (RM!, UC!, WS!)].
Aster multiflorus Ait. [var.] *incanopilosus* (Lindl.) Rydberg, Fl. Sand Hills, Nebraska. Contr. U.S. Nat. Herb. 3: 163. 1895. — Nomen. — Rydberg (1896) 506.

Aster multiflorus Aiton γ *commutatus* Torrey and Gray, Fl. N. Am. 2: 125. 1841.
– [This is the basionym for *A. falcatus* Lindl. in Hook. ssp. *commutatus* (Torr. & Gray) A. G. Jones]. — Macoun (1884) 223. — *Aster commutatus* (Torr. & Gray) A. Gray, Synopt. Fl. N. Am. 1(2): 185. 1884. — J. M. Coulter (1885) 161; Williams (1892) 192; A. Nelson (1896) 126; Howell (1897) 308; Britton (1901) 965; Henshaw (1906) 68, pl. 21; Rydberg (1906b) 355; Robinson & Fernald (1908) 811; Coulter & Nelson (1909) 515; Daniels (1911) 234; Pétersen (1912) 177; Henry

(1915) 293; Wooton & Standley (1915) 685; Rydberg (1917) 885, (1922) 885; Britton & Brown (1923) 3: 427; Tidestrom (1925) 559; Rydberg (1932) 809; Ashton (1933) 122; R. A. Nelson (1933) 326; Palmer & Steyermark (1935) 664; Cory & Parks (1937) 101; Gates (1940) 241; Kittell (1941) 406; Shinnars (1941) 416; Tidestrom & Kittell (1941) 406; Kearney & Peebles (1942) 918; Cronquist (1947) 144; Turner (1949) 25; Fernald (1950) 1433; O. A. Stevens (1950) 278; Kearney & Peebles (1951) 871; Harrington (1954) 576; Steyermark (1963) 1519, *pl.* 360; Barrell (1969) 94. — *Aster ericoides* L. var. *commutatus* (Torr. & Gray) Boivin, Nat. Canad. **89**: 67. 1962. — In part. — Boivin (1967) 1032, (1972) 32, in part. TYPE: "Upper Missouri". Long's Expedition, Dr. James (Holotype, NY!) — Jones (1973) *pl.* 5c.

Aster adsurgens sensu authors. — R. A. Nelson (1933) 325; Peck (1941) 724. — Not E. L. Greene (1900).

[The status of this species is the subject of a separate publication (Jones, 1975)].

Aster crassulus Rydberg, Bull. Torrey Bot. Club **28**: 504. 1901. — [This is the basionym for *A. falcatus* Lindl. in Hook. ssp. *commutatus* (Torr. & Gray) A. G. Jones var. *crassulus* (Rydb.) Cronquist]. — Rydberg (1906b) 355; Daniels (1911) 234; Wooton & Standley (1915) 685; Rydberg (1917) 884; Standley (1921) 424; Rydberg (1922) 884, (1932) 809. — *Aster commutatus* (Torr. & Gray) A. Gray, var. *crassulus* (Rydb.) Blake, in Tidestrom, Fl. Utah and Nevada. Contr. U. S. Nat. Herb. **25**: 560. 1925. — Blake (1940) 470; Kittell (1941) 406; Tidestrom & Kittell (1941) 407; Kearney & Peebles (1942) 918, (1951) 871; Shields (1951) 63; Harrington (1954) 576. — *Aster falcatus* Lindl. in Hook. var. *crassulus* (Rydb.) Cronquist, Bull. Torrey Bot. Club **74**: 144. 1947. — Cronquist in Gleason (1952) 3: 464; Breitung (1954) 88, 92; Cronquist in Hitchcock, et al. (1955) 5: 82; Moss (1959) 456; Abrams & Ferris (1960) 4: 322, *f.* 5545. TYPE: Colorado, La Veta, F. K. Vreeland 690a [Holotype, NY! (Figure 8); Possible Isotype, RM!, misnumbered as Vreeland 190a].

Aster cordineri A. Nelson, Bot. Gaz. **40**: 64. 1905. — Coulter & Nelson (1909) 515. TYPE: Colorado, Estes Park, W. S. Cooper 151 (Holotype, RM!) — Jones (1973) *pl.* 5d.

[This specimen has very large heads and traits, generally, somewhat intermediate between typical *A. falcatus* and ssp. *commutatus*].

Aster polycephalus Rydberg, Bull. Torrey Bot. Club **33**: 153. 1906. — In part, not including the type, which is that of *A. scoparius* DC. — Rydberg (1906b) 355; Daniels (1911) 234; Petersen (1912) 177; Rydberg (1917) 885; Standley (1921) 424; Rydberg (1922) 885, (1932) 809. — *Aster commutatus* (Torr. & Gray) A. Gray var. *polycephalus* (Rydb.) Blake, in Tidestrom, Fl. Utah and Nevada. Contr. U. S. Nat. Herb. **25**: 560. 1925. — Blake (1940) 470; Kittell (1941) 406; Tidestrom & Kittell (1941) 407; Kearney & Peebles (1942) 918, (1951) 871; Harrington (1954) 576. — *Aster ericoides* L. [var.] *polycephalus* (Rydb.) Gates, Trans. Kansas Acad. Sci. **42**: 138. 1939. — Gates (1940) 241.

Aster hebecladus sensu Coulter & Nelson, Man. C. Rocky Mts., p. 515. 1909. — In part. — Not DeCandolle (1836).

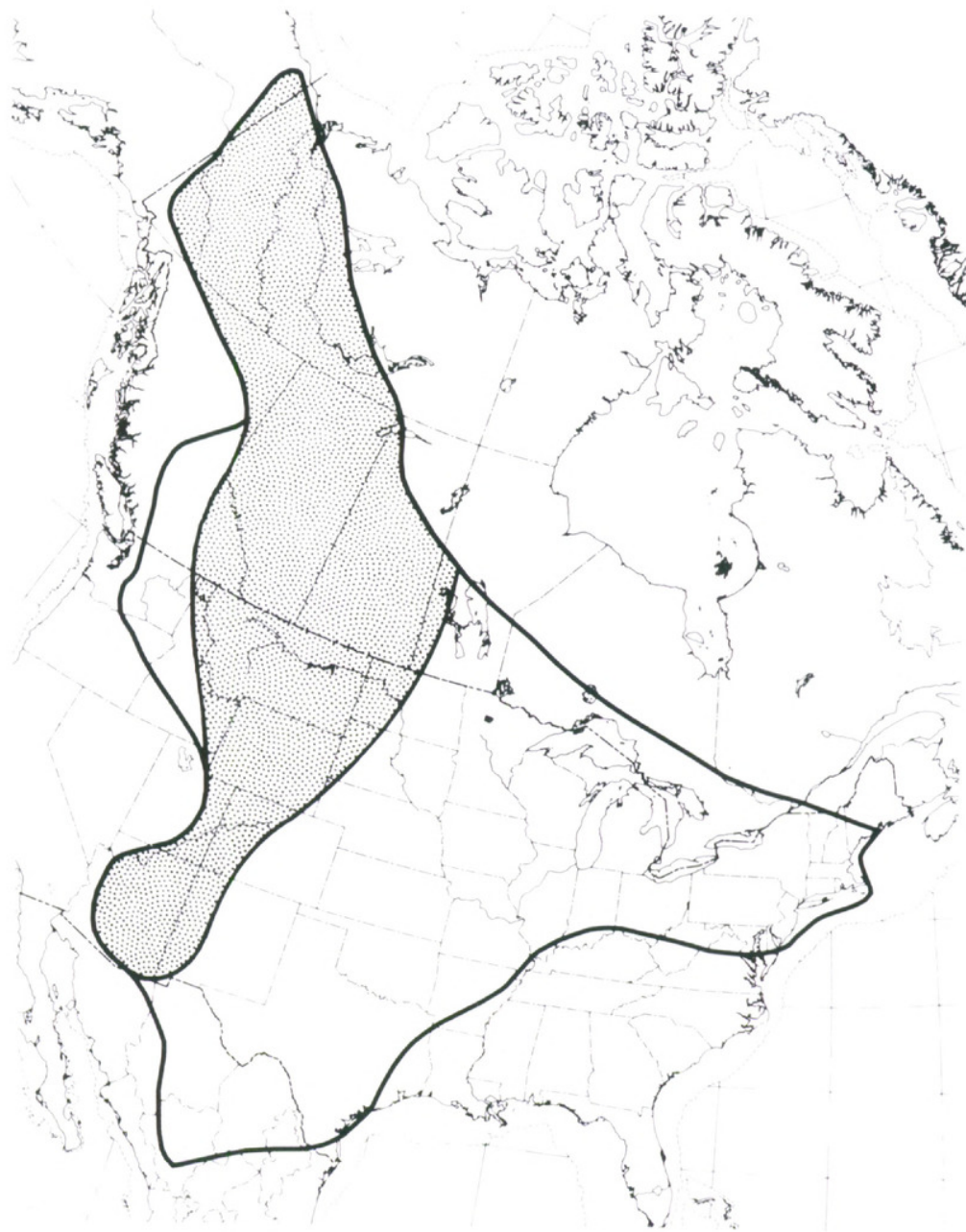


Figure 7. Range of *Aster falcatus* ssp. *falcatus*.

Illustrations in Literature: Britton & Brown (1898) 3: f. 3803 [as *incanopilosus*]; Henshaw (1906) 65. pl. 21; Britton & Brown (1923) 3: f. 4338; Hitchcock, et al. (1955) 5: 85 [as *falcatus*]; Abrams & Ferris (1960) 4: f. 5545 [as var. *crassulus*]; Steyermark (1963) pl. 360, f. 2.

Distinctive Characteristics of the Subspecies. Plants forming sod-like patches or colonies, the stems typically single or few from each point of emergence, erect, or more commonly ascending; height of stems variable, depending on the variety, as well as the habitat; rhizomes creeping or densely tangled, horizontal, lacking distinct cormoid portions. Winter rosettes produced at the tips of elongate stolons, some distance removed from the old stems. Pubescence generally copious, appressed or spreading; leaves of all sizes often persistent at flowering time; rameal leaves usually not conspicuously dilated or clasping. Inflorescence diffuse-paniculate or compound-racemiform or, in pastured habitats, a simple raceme. Heads uniform in size; peduncles often densely bracteate and the bracts stiff, intergrading with the phyllaries; involucre hemispherical, typically strongly imbricated, the outer phyllaries shorter than the inner ones, copiously pubescent on the back, squarrose, obtuse or acute, the chartaceous indurate basal portion covering 35% or more of the area.

Two varieties are distinguished, mainly on characteristics of habit. Variety *commutatus* forms bushy or sprawling plants, about 20–60 cm high, with stems usually decumbent or ascending, branched near the base; inflorescence typically diffuse-paniculate, the heads mostly terminal, not secund, large, with more than 20 disk florets, the total number of florets 40–50(–60). Variety *crassulus* (Rydberg) Cronquist (1947) has stems erect, 60–100 cm tall, usually branched near the middle; inflorescence compound-racemiform, usually with strongly divaricate branches; heads often somewhat secund, with (14–)18–20 disk florets, the total number of florets 35–40(–45).

FLOWERING PERIOD. August–October (or November in the southern part of range).

HABITAT. Dry soil; plains, hills, river banks, prairies, roadsides, and railroad sidings.



Figure 8. Holotype of *Aster crassulus* Rydberg (= *A. falcatus* ssp. *commutatus* var. *crassulus*); Vreeland 690a (NY).

RANGE. Southern Alberta, Montana, Wyoming, Colorado, Arizona, Mexico, Texas, Oklahoma, Kansas, Nebraska, Dakotas, Manitoba, and Saskatchewan (Figure 9).

REPRESENTATIVE SPECIMENS. **Arizona:** COCONINO CO., south of Flagstaff, *O. M. Clark* 12152 (GH, OKL). **Colorado:** PUEBLO CO., Rye, *I. W. Clokey* 4344 (MICH, MO, NY, RM, UC, US, WS). **Kansas:** BARTON CO., Claflin, *H. C. Benke* 6211 (KSC, TEX). **Minnesota:** OTTER TAIL CO., Battle Lake, *E. P. Sheldon*, s. n. (RM, UC, WS). **Montana:** MADISON CO., Montana Valley, *A. & E. Nelson* 6839 (ILL, ISC, NY, RM, US). **Nebraska:** SHERIDAN CO., Hay Springs, *E. S. Nixon* 241, 242 (RM). **New Mexico:** RIO ARIBACO CO., Tank Canyon, Santa Fe Nat. For., *H. W. Springfield* 418 (TEX). **North Dakota:** CASS CO., Fargo, *O. A. Stevens* 299 (DAO, GA, NDA, OKL, UC, US, WIS). **Oklahoma:** WOODS CO., Alva, *G. W. Stevens* 2857 (ILL, MO, OKL). **South Dakota:** CUSTER CO., Custer, *S. Stevens* 45432 (NY). **Texas:** YOUNG CO., Graham, *J. Reverchon* 3316 (MO). **Wyoming:** SHERIDAN CO., Sheridan, *S. S. Sharp* 233 (RM). **Alberta:** CALGARY D., Calgary, *W. C. McCalla* 9028, 10207 (ALTA, UBC). **Manitoba:** BRANDON D., Brandon, *G. A. Stevenson* 497, 1046, 1059, 1626, & 1972 (DAO). **Saskatchewan:** MAPLE CREEK D., *A. J. Breitung* 5680 (DAO, US). QU'APPELLE D., north of Regina, *A. J. Breitung* 3893 (DAO, MO, RM). **Mexico:** Chihuahua, Villa Ahumada, *H. Le Sueur* 365 (MO, TEX).

REPORTED HYBRIDS

Aster × **amethystinus** Nuttall, (*pro sp.*), Trans. Am. Phil. Soc. 2(7): 294. 1841. (*Aster ericoides* Linnaeus × *novae-angliae* Linnaeus). TYPE: "Hab. In Massachusetts, near Cambridge and Salem; rare" Nuttall (BM!).

[Nuttall's paper was read before the American Philosophical Society on April 4, 1837]. — Torrey & Gray (1841) 2: 144; Gray (1884) 1(2): 185, (1889) 260; Porter (1894) 322; Porter & Small (1903) 323; Robinson & Fernald (1908) 810; Monroe (1913) 99; Britton & Brown (1923) 418; House (1924) 703; Knowlton (1930) 185; Peattie (1930a) 375; Benner (1932) 293; Rydberg (1932) 809; Palmer & Steyermark (1935) 664; Shinnars (1941) 417; G. N. Jones (1945) 225, (1950) 275; Fernald (1950) 1432; G. N. Jones (1963) 251; Boivin (1967) 1032; Seymour (1969) 353; Van Faasen (1971) 100.

Aster bostoniensis Hort. ex Baker, in Gard. Chron. 2: 744. 1884. [Type unknown; the name was applied to a plant cultivated in Europe].

Aster multiflorus Aiton × *novae-angliae* Linnaeus, *H. C. Benke*, Rhodora 32: 1-3, pl. 192. 1930. TYPE: Wisconsin, Kaukauna, *H. C. Benke* 767 (Holotype, MIL).

Aster amethystinus Nuttall f. *leucerythros* Bemis, Rhodora 32: 3. 1930. TYPE: Massachusetts, Worcester, *E. W. Bemis*, Oct. 5, 1924 (Holotype, GH!). [A rose-rayed form].

Aster amethystinus Nuttall f. *leucos* Bemis, *Rhodora* 33: 63. 1931. TYPE: Massachusetts, Worcester, E. W. Bemis, Sept. 24, 1930 (Holotype, GH!). [A white-rayed form].

Benke (1930) was the first to present circumstantial evidence for the hybrid nature of these plants, noting that they were rare, and were always found in conjunction with the putative parent species. Hybrid status was experimentally verified by Wetmore and Delisle (1939) and confirmed by my own work (Jones, 1973).

Diagnostic Characteristics. Perennials with stoloniferous rhizomes; stems erect, 30 cm high or more, with ascending branches and densely hirsute pubescence. Cauline leaves linear, entire with ciliate margins, sessile and somewhat auriculate-clasping, hirsutulous on both sides, the apex acute or nearly obtuse, armed with a bristle. Inflorescence racemiform or somewhat corymbiform, the heads on leafy branches. Involucre campanulate, about 4–5 mm high, the outer phyllaries linear to oblanceolate, squarrose, mucronate, hispidulous and somewhat glandular on the back. Receptacle alveolate; florets about 60, the ligules 20–30, 6–8 mm long, typically purple; pappus tawny; achenes brown, strigillose and somewhat glandular-punctulate.

FLOWERING PERIOD. Late August to early October.

HABITAT. The same as the parent species: dry soil; in prairie vegetation along roads and railroads.

REPRESENTATIVE SPECIMENS. **Connecticut:** HARTFORD CO., Stony Brook, H. A. Ahles 65409 (NCU). **Illinois:** COOK CO., Palatine, H. C. Benke 5943 (UC). **Iowa:** CLAY CO., Ruthven, A. Hayden 11137, 11134 (ISC). **Massachusetts:** BERKSHIRE CO., Williamstown, C. H. Knowlton, s.n. (KY). **Michigan:** WAYNE CO., River Rouge, O. A. Farwell 8800, 8784, & 8804 (MICH). **Rhode Island:** PROVIDENCE CO., Providence, F. Collins, s.n. (GH). **Wisconsin:** RACINE CO., Racine, S. C. Wadmond, s.n. (KSC). **Ontario:** WENTWORTH CO., Hopkins Creek area, J. S. Pringle 639 (WIS).

Aster × **Batesii** Rydberg, (*pro sp.*), *Brittonia* 1: 102. 1931. (*Aster ericoides* Linnaeus × *?oblongifolius* Nuttall). TYPE: Nebraska, St. Paul, J. M. Bates 5440 (Holotype, NY!).

Aster ericoides L. [var.] *Batesii* (Rydb.) Gates, Trans. Kansas Acad. Sci. 42: 138. 1939. — Gates (1940) 241. — Perhaps, in part.

This hybrid has not been experimentally verified. In the original publication, Rydberg suggests: "mistaken for *A. amethystinus* Nutt. Perhaps a hybrid, *A. ericoides* × *Kumleini*." *Aster kumleini* is a synonym for *A. oblongifolius*. The type and other specimens labeled *A. batesii* resemble plants of *A. ericoides*, but leaf margins are slightly glandular scabrous and ligules lavender. Introgression may be involved, but the proposed parentage of *A. oblongifolius* is questionable. My own experimental work does not lend support to Rydberg's suggestion, and I have listed *A. batesii* in synonymy under *A. ericoides* ssp. *ericoides*.

Aster × **columbianus** Piper, (*pro sp.*), Contr. U.S. Nat. Herb. **16** (5): 210. 1913. (*Aster ericoides* Linnaeus × *campestris* Nuttall). TYPE: Washington, Waitsburg, *Horner 559* [Holotype, US, apparently lost (Blake, 1928); Isotype, WS! (Jones, 1973, *pl. 4d*)].

Piper & Beattie (1914) 270; Cronquist in Hitchcock et al. (1955) **5**: 91; St. John (1956) 424; Abrams & Ferris (1960) 322; St. John (1963) 461. — *Aster multiflorus* Ait. var. *columbianus* (Piper) Blake, *Rhodora* **30**: 227–228. 1928.

Aster amethystinus sensu authors. — Piper & Beattie (1901) 186; Piper (1906) 572. — Not Nuttall (1841).

This hybrid has not been experimentally verified. The isotype and two other collections from Washington that I have seen [Whitman Co., *H. St. John 9265* (WS); Okanogan River, *S. Watson 191* (GH)] do have characteristics intermediate between the putative parent species. The plants resemble those of *Aster ericoides* ssp. *pansus*, but ligules are purple; phyllaries, leaf margins, and peduncles somewhat glandular; pappus sordid; achenes canescent.

Aster exiguus Rydberg × **pilosus** Willdenow, Ahles ex Jones & Fuller, Vasc. Pl. Illinois. 468. 1955. — Nomen nudum. (*Aster ericoides* Linnaeus × *pilosus* Willdenow) TYPE: Illinois, Cook Co., Palatine, *V. H. Chase 9105* (Holotype, ILL!; Isotype, ILLS).

This hybrid has not been experimentally verified. Specimens from Illinois cited in addition to the type are: Champaign Co., Rantoul, *H. A. Gleason, s.n.* (ILL); Normal Park, *E. J. Hill, s.n.*; Du Page Co., Wheaton, *W. S. Moffatt 462*. I have seen only the type and the Gleason collection, and they are somewhat atypical

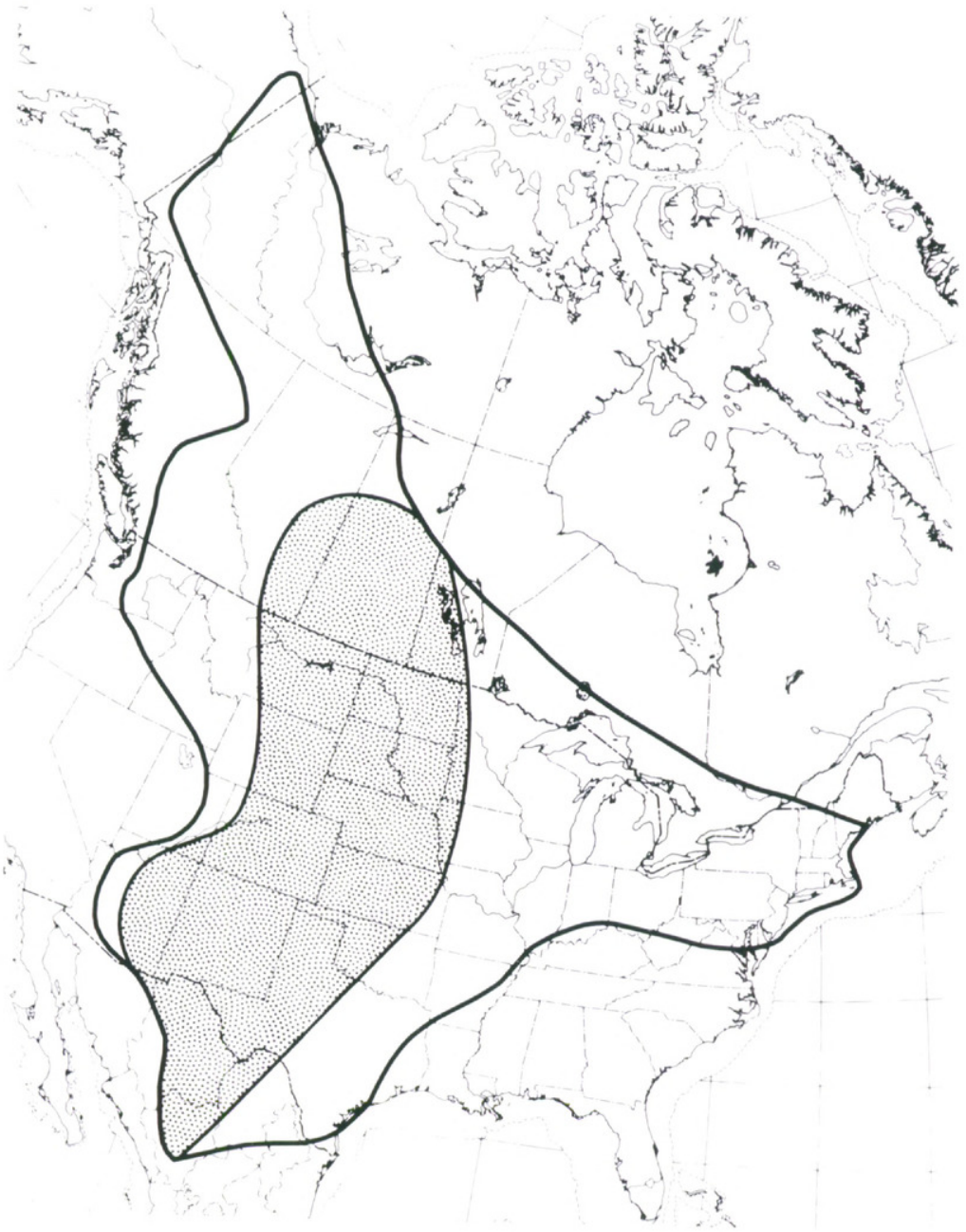


Figure 9. Range of *Aster falcatus* ssp. *commutatus*.

late-season specimens of *Aster ericoides* ssp. *ericoides* var. *prostratus*. Plants of this kind, characterized by stems with relatively soft spreading pubescence, a leafy inflorescence with heads not conspicuously secund, and leaves with long soft bristles, can often be found on mowed roadsides. They are usually still in flower when adjacent undisturbed stands have finished. The only speci-

men that looks somewhat like an intermediate between the two putative parent species is a collection from dry sandy soil, Mason County, Illinois, *R. T. Rexroat 1255* (ISM).

EXCLUDED NAMES

The following is a list of names that have been applied to *Aster ericoides* but properly belong in synonymy under taxa unrelated to sect. *Multiflori*.

Synonyms of ***Aster pilosus*** Willdenow, or varieties of that species:

Aster ericoides var. *pilosus* (Willdenow) Porter, Mem. Torrey Bot. Club **5**: 323. 1894.

Aster ericoides γ *platyphyllus* Torrey & Gray, Fl. N. Am. **2**: 125. 1841.

Aster ericoides var. *Pringlei* A. Gray, Synopt. Fl. N. Am. **1**(2): 184. 1884.

Aster ericoides var. *Randii* Britton in Britton & Brown, Ill. Fl. **3**: 379. 1898.

Aster ericoides var. *Reevesii* A. Gray, Synopt. Fl. N. Am. **1**(2): 184. 1884.

Aster ericoides var. *strictus* Porter, in Porter & Coulter, Synops. Fl. Colorado, 56. 1874.

Aster ericoides β *villosus* (Michaux) Torrey & Gray, Fl. N. Am. **2**: 124, 503. 1841.

Synonyms of ***Aster parviceps*** Mackenzie & Bush:

Aster ericoides var. *parviceps* Burgess, in Britton & Brown, Ill. Fl. **3**: 379. 1898.

Aster ericoides var. *pusillus* A. Gray, Synopt. Fl. N. Am. **1**(2): 184. 1884.

Synonym of ***Aster depauperatus*** (Porter) Fernald:

Aster ericoides var. *depauperatus* Porter, Mem. Torrey Bot. Club **5**: 323. 1894.

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