The biosystematics of *Arnica fulgens* and *A. sororia* (Asteraceae)

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Arnica fulgens Pursh and *A. sororia* Greene are sympatric throughout most of their ranges in northwestern United States and adjacent southwestern Canada. These taxa were previously recognized as two morphologically overlapping varieties or not very well separated species. A study of their floral and vegetative morphology, using TAXMAP cluster analyses, foliar flavonoid chemistry, reproductive biology, and ecology indicates that they are distinct species. Studies of reproductive behaviour reveal them to be amphimictic ($2n = 38$) and self-incompatible. Artificial hybridization experiments between the two species were unsuccessful.

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Le *Arnica fulgens* Pursh et le *A. sororia* Greene sont sympatriques dans presque toutes leurs régions au nord-ouest des États-Unis et au sud-ouest canadien limitrophe. Ces taxons étaient auparavant reconnus comme deux variétés qui se chevauchent morphologiquement ou comme espèces pas très distinctes. Une étude de leur morphologie florale et végétative à l'aide de groupements TAXMAP, la chimie des flavanoïdes, la biologie de la reproduction et l'écologie, indique qu'il s'agit d'espèces distinctes. Des études du comportement reproductif les a révélé comme étant amphimictiques ($2n = 38$) et auto-incompatibles. Des expériences d'hybridation artificielle entre les deux espèces ont échoué.

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Introduction

Arnica (Asteraceae), a genus of about 28 species, is predominantly confined to the boreal and montane regions of the northern hemisphere, with most species occurring in the western cordillera of North America (Maguire 1943). These rhizomatous perennial herbs are characterized by simple stems bearing opposite leaves and large, single or cymose heads of yellow flowers.

Two species of *Arnica*, *A. fulgens* Pursh and *A. sororia* Greene, are essentially sympatric throughout their ranges in northwestern United States and adjacent southwestern Canada. In the northernmost part of their ranges these taxa occur in prairies and grasslands (a habitat unique to the genus); in the southernmost areas they occupy montane habitats. *Arnica fulgens* is widely distributed from British Columbia to Manitoba, south to Colorado, and west to northern California; *A. sororia* does not extend as far south or north nor does it enter into Saskatchewan or Manitoba (Maguire 1943; White and Johnson 1980; Douglas 1982; Packer 1983).

Arnica fulgens and *A. sororia* are very similar in vegetative and reproductive features with only the presence of septate hairs scattered among the stipitate-glandular hairs of the disc corolla and dense axillary tufts of brown woolly hairs in the persistent leaf bases traditionally used to separate them (Maguire 1943; Ediger and Barkley 1978). The possibility that these two taxa are not well separated has been suggested by Packer (1983). Douglas and Ruyle-Douglas (1978) observed that the diagnostic features used to separate the two species, with the exception of disc corolla pubescence, are unsatisfactory and that all other characters overlap to such an extent that separation at the specific level does not appear warranted. They therefore treated *A. sororia* as a variant of *A. fulgens*.

Because of the presence of extensive sympatry, numerous taxonomic synonyms, morphological overlap, difficult taxonomic circumscription, and the potential for hybridization, *A. fulgens* and *A. sororia* were in need of a thorough biosystematic investigation.

Arnica fulgens was first described by Pursh (1814) in his *Flora Americae Septentrionalis*. Not recognizing the true identity of Pursh's *A. fulgens*, Rydberg proposed two species, *A. pedunculata* (Rydberg 1897) and *A. monocephala* (Rydberg 1900), for various forms of *A. fulgens*. *Arnica monocephala* was later reduced by Rydberg (1917) and others to *A. pedunculata* and then ultimately transferred under synonymy to *A. fulgens* (Rydberg 1927). The taxonomy of *A. sororia* has not been as complex, but it is still intriguing. This name was originally proposed by Greene in 1910. It was later interpreted as *A. fulgens* sensu Rydberg (Rydberg 1917), which added considerable confusion to the true identity of these taxa. Included here was *A. stricta* Greene, a taxon similar to *A. sororia* but much larger and with many capitula. A full account of the taxonomy of these two species is given in the taxonomy section of this paper.

Interestingly, the apparent close morphological similarity between *A. fulgens* and *A. sororia* is not reflected in Maguire's (1943) proposed phylogeny of the subgenus containing these two taxa. Maguire (1943) suggests that *A. fulgens* has closest affinities with *A. angustifolia* Vahl ssp. *angustifolia* as a result of a similarity in periclinium pubescence and the presence of only one capitulum. *Arnica sororia*, on the other hand, superficially resembles *A. lonchophylla* Greene and probably has closest affinities with this species or, as illustrated in his phylogenetic interpretation, may have also originated from *A. frigida* Meyer ex Iljin (Maguire 1943). In the original description of *A. sororia* by Greene (1910), he notes the close affinity with *A. lonchophylla* but also is aware of the close similarity to *A. fulgens*. Needless to say, the delineation of taxa within this complex has been at best speculative.

Emasculation techniques have been utilized to determine the presence or absence of apomictic reproduction. In an investigation into the embryology of the polyploid complex *A. angustifolia* ssp. *angustifolia* from Greenland, Engell (1970) observed that emasculation had no influence on embryo development, indicative of an apomictic mode of reproduction. The embryo in these emasculated plants developed without fertilization and the emasculated capitula produced the same number of achenes as on the intact, normal capitula

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TABLE 1. Previously reported chromosome numbers in *Arnica fulgens* and *A. sororia*

Taxon	*n*	2*n*	Locality	Reference
A. fulgens	19		Idaho, Lewis County	Ornduff *et al.* 1967
	19		Washington, Kittitas County, Ellensburg	Barker 1967
		38	Wyoming, Crook Country, ca. 19 km west Sundance	Straley 1979
		38	British Columbia, Grasmere	Taylor and Brockman 1966
		52–57	Saskatchewan, Cypress Hills Provincial Park	Taylor and Brockman 1966
A. sororia	19		Washington, Kittitas County, Ellensburg	Barker 1967
	19		Washington, Douglas County	Ornduff *et al.* 1967
		38	Oregon, Union County, southeast LeGrande	Straley 1979

TABLE 2. Collections used in TAXMAP, flavonoid analysis (*), and diploid chromosome number determination (+)

OTU no.	OTU code	OTU description
1	A-548+	Alberta, N. Calgary near Balzac off Hwy. 566, *Downie 548* (ALTA)
2	A-549	Alberta, W. Cochrane, Hwy. 1A, *Downie 549* (ALTA)
3	A-551	Alberta, S.W. Pincher Creek near Beauvais Lake Prov. Park, *Downie 551* (ALTA)
4	A-552+	Alberta, N. Police Outpost Prov. Park near Lee Creek crossing, *Downie 552* (ALTA)
5	A-554*	Alberta, S. junction Hwys. 36 and 9 near Hanna, *Downie 554* (ALTA)
6	A-555+	Alberta, Hwy. 36, S.E. Hanna, *Downie 555* (ALTA)
7	A-559*+	Alberta, S. Junction Hwys. 1 and 41 near Medicine Hat, *Downie 559* (ALTA)
8	A-562*+	Alberta, S. Cypress Hills, *Downie 562* (ALTA)
9	A-563*	Alberta, 0.5 km N. Bare Creek, Hwy. 41, *Downie 563* (ALTA)
10	A-564	Alberta, Bare Creek Road, 3 km off Hwy. 41, *Downie 564* (ALTA)
11	A-565*+	Alberta, Bare Creek Reservoir, *Downie 565* (ALTA)
12	A-566	Alberta, Bare Creek Reservoir, *Downie 566* (ALTA)
13	A-571F*+	Alberta, Hwy. 880, N. Aden, *Downie 571F* (ALTA)
14	WY-697+	Wyoming, Big Horn Co., Milepost 38 Hwy. 14A, Big Horn Natl. Forest, *Downie 697* (ALTA)
15	WY-698*	Wyoming, Big Horn Co., E. Medicine Wheel Archeological Site Rd., Big Horn Natl. Forest, *Downie 698* (ALTA)
16	WY-699*+	Wyoming, Johnson Co., S.W. Buffalo, *Downie 699* (ALTA)
17	WY-700+	Wyoming, Campbell Co., N. Savageton, *Downie 700* (ALTA)
18	WA-109	Washington, Asotin Co., Big Butte, *Downe 109* (ALTA)
19	MO-310	Montana, Gallatin Co., Bozeman, *Blankinship 310* (MT)
20	MO-709+	Montana, Toole Co., 2 km W. Sweetgrass, *Downie 709* (ALTA)
21	MO-710*+	Montana, Toole Co., 15 km W. Sweetgrass, *Downie 710* (ALTA)
22	MO-711	Montana, Liberty Co., N. Whitlash, *Downie 711* (ALTA)
23	MO-712*+	Montana, Liberty Co., near Port of Whitlash border crossing, *Downie 712* (ALTA)
24	MO-713*+	Montana, Pondera Co., S.W. Conrad on Hwy. 219, *Downie 713* (ALTA)
25	MO-714*+	Montana, Judith Basin Co., junction Hwys. 80 & 87, *Downie 714* (ALTA)
26	MO-719	Montana, Sweetgrass Co., S. Harlowton, E. Porcupine Butte, *Downie 719* (ALTA)
27	MO-1497	Montana, Missoula Co., N. Missoula, *Straley 1497* (UBC)
28	ND-95776	North Dakota, Rolette Co., Dunsieth, *Lunell s.n.* (PH)
29	ID-1939	Idaho, Idaho Co., White Bird, *Constance 1939* (PH)
30	A-11648	Alberta, 10 miles N. Elkwater Lake, *McCalla 11648* (UBC)
31	A-161927	Alberta, Scotfield, S.E. Hanna, *Brink s.n.* (UBC)
32	A-16903	Alberta, Kananaskis, *Aikenhead s.n.* (ALTA)
33	WY-1841	Wyoming, Crook Co., W. Sundance, *Straley 1841* (UBC)
34	CO-1463	Colorado, Larimer Co., N. Virginia Dale, *Straley 1463* (UBC)
35	CO-4382	Colorado, Boulder Co., Boulder, *Bethel & Clokey 4382* (PH)
36	OR-744	Oregon, Harney Co., Steens Mtns., *Hansen 744* (NY)
37	S-4312	Saskatchewan, Cypress Hills Prov. Park, *Breitung 4312* (ALTA)
38	BC-530	British Columbia, Harry Lake, Hat Creek, *Johns 530* (UBC)
39	M-11040	Manitoba, 30 miles W. Brandon, *Scoggan 11040* (ALTA)
40	A-11866	Alberta, N.E. Cochrane, *McCalla 11866* (ALTA)
41	A-2749	Alberta, E. Banff, *Straley 2749* (UBC)
42	A-1174	Alberta, Seven Persons, *Klar 1174* (ALTA)
43	A-557*+	Alberta, Hwy. 1, 2 km E. Suffield, *Downie 557* (ALTA)
44	A-558*+	Alberta, Hwy. 41, E. Medicine Hat, *Downie 558* (ALTA)
45	A-568*+	Alberta, Manyberries, *Downie 568* (ALTA)
46	A-569*+	Alberta, Pendant Orielle, *Downie 569* (ALTA)
47	A-570*	Alberta, W. Pendant Orielle, *Downie 570* (ALTA)

TABLE 2. (*Concluded*)

OTU no.	OTU code	OTU description
48	A-571S*+	Alberta, Hwy. 880, N. Aden, *Downie 571S* (ALTA)
49	A-572*	Alberta, W. McNab, N.W. Warner, *Downie 572* (ALTA)
50	A-573*+	Alberta, S. side Milk River Ridge Reservoir, *Downie 573* (ALTA)
51	A-574	Alberta, Milk River Ridge Reservoir, *Downie 574* (ALTA)
52	UT-588	Utah, Rich Co., N.W. Sage Creek Junction, *Snyder & Hawkins 588* (NY)
53	UT-13815	Utah, Cache Co., W. Spring Hollow, *Maguire et al. 13815* (UC)
54	NE-13460	Nevada, Elko Co., E. Angel Lake, *Raven & Solbrig 13460* (NY)
55	ID-717	Idaho, Latah Co., Moscow, *Abrams 717* (UC)
56	ID-4765	Idaho, Clark Co., Monida Pass, *Maguire 4765* (ALTA)
57	ID-3293	Idaho, Nez Perces Co., Lake Wawa, *A. A. & E. G. Heller 3293* (UC)
58	ID-26659	Idaho, Owyhee Co., between Silver City and War Eagle Mtn., *Maguire & Holmgren 26659* (UC)
59	CA-866	California, Lassen Co., Madeline Plains, *Applegate 866* (US)
60	CA-1788	California, Lassen Co., N. Madeline, *Babcock & Stebbins 1788* (UC)
61	WY-58727	Wyoming, No Locality Information, *Tweedy s.n.* (US)
62	OR-1929	Oregon, No Locality Information, *Cusick 1929* (US)
63	OR-2387	Oregon, Harney Co., Steens Mtns., *Leiberg 2387* (ALTA)
64	MO-715+	Montana, Wheatland Co., Judith Gap, N. Harlowton, *Downie 715* (ALTA)
65	MO-716*+	Montana, Wheatland Co., 12 miles W. Harlowton, Hwy. 12, *Downie 716* (ALTA)
66	MO-717*+	Montana, Wheatland Co., 0.5 miles E. Shawmut, Hwy. 12, *Downie 717* (ALTA)
67	MO-718	Montana, Golden Valley Co., Junction Hwys. 3 & 12, *Downie 718* (ALTA)
68	MO-4743	Montana, Clark Co., S. Helena, *McCalla 4743* (ALTA)
69	MO-4510	Montana, Glacier Co., Glacier Natl. Park, *McCalla 4510* (ALTA)
70	MO-11499	Montana, Missoula Co., W. Greenough, *Hitchcock & Muhlick 11499* (UC)
71	WA-4461	Washington, Lincoln Co., Davenport, *Maguire 4461* (ALTA)
72	WA-551	Washington, Ferry Co., Northport, *Rogers 551* (UC)
73	OR-7360	Oregon, Grant Co., Dayville, *Cronquist 7360* (UC)
74	WA-8064	Washington: No Locality Information, *Sheldon 8064* (US)
75	A-15768	Alberta, Waterton Lakes Natl. Park, *Breitung 15768* (ALTA)
76	A-16893	Alberta, Castle River Region, *Cormack s.n.* (ALTA)
77	BC-702	British Columbia, S. Fairmont Hot Springs, *Downie 702* (ALTA)
78	BC-703*+	British Columbia, Wasa, N. Cranbrook, *Downie 703* (ALTA)
79	BC-705	British Columbia, Osoyoos Lake, *Downie 705* (ALTA)
80	BC-706	British Columbia, N. Osoyoos on way to Oliver, Hwy. 97, *Downie 706* (ALTA)
81	BC-707*+	British Columbia, S. Kamloops on Hwy. 5, *Downie 707* (ALTA)
82	BC-708*+	British Columbia, near Tranquille, N.W. Kamloops, *Downie 708* (ALTA)
83	BC-8157	British Columbia, 35 miles N. Cranbrook, *McCalla 8157* (ALTA)
84	BC-9552	British Columbia, S. Canal Flat, *McCalla 9552* (ALTA)
85	BC-9519	British Columbia, E. Cranbrook, *McCalla 9519* (ALTA)
86	BC-11565	British Columbia, Cariboo, *Eastham 11565* (CAN)
87	NT-3416	Northwest Territories, Fort Norman, *Hume(?) s.n.* (CAN)
88	A-14723	Alberta, Devil's Lake, *Macoun 14723* (CAN)
89	NT-7081	Northwest Territories, Mile 96.8 Mackenzie River – Yellowknife Hwy., *Thieret & Reich 7081* (NY)
90	A-426	Alberta, Prospect Mtn., S.W. Cadomin, *Mortimer 426* (ALTA)
91	NT-140	Northwest Territories, E. Tuktoyaktuk harbour, *Haag 140* (ALTA)
92	BC-7015	British Columbia, Natural Bridge, Yoho National Park, *McCalla 7015* (ALTA)

NOTE: OTU nos. 1 to 42, *Arnica fulgens*; 43 to 86, *A. sororia*; 87 to 89, *A. lonchophylla* ssp. *lonchophylla*; 90 to 92, *A. angustifolia* ssp. *angustifolia*.

(Engell 1970). In contrast, no embryos were found in the emasculated heads of *A. fulgens* and *A. sororia* (Barker 1966). When the plants were permitted to self-pollinate or when the disc florets were removed and the ray florets permitted to develop, seedless achenes were produced. Barker (1966) considered both *A. fulgens* and *A. sororia* to be amphimictic and self-incompatible. Using pollen quality as an alternative indicator of reproductive mode in *Arnica*, Barker (1966) found amphimictic populations had better than 90% stainability in lactophenol – cotton blue and apomictic populations showed varying degrees of pollen deformity and less than 80% stainability. A strong correlation was also found to exist between ploidy level and method of reproduction. All known amphimicts were diploid and most known apomicts polyploid (Barker 1966). In an estimation of pollen quality in 27 collections of *A. fulgens* and 10 collections of *A. sororia*, both species examined had better than 90% stainability and both were determined to be wholly amphimictic (Barker 1966). However, Barker could only provide a somewhat cursory overview of the genus because of the wide scope of his study and the limited availability of material. It is possible that a more thorough investigation might reveal apomictic elements.

The basic chromosome number for *Arnica* was shown by Böcher and Larsen (1950) and Ornduff *et al.* (1967) to be $x = 19$, with chromosome races of $2n = 38$, 57, 76, and 95 being reported. Previously reported chromosome numbers for *A. fulgens* and *A. sororia* are summarized in Table 1. A count of $2n =$ ca. 97 for *A. fulgens*, incorrectly referenced by Barker

(1966) from Ornduff *et al.* (1967), is in error and omitted. The count of $2n = 52-57$ for *A. fulgens* from Cypress Hills Provincial Park, Saskatchewan (Taylor and Brockman 1966), is presumably triploid ($2n = 57$) and is the only report of polyploidy in these two species.

Flavonoids have been used extensively to support taxonomic revisions, to infer phylogenetic relationships, and to document changes in chemical complexity as a result of hybridization, polyploidy, geographical isolation, or plant migrations. Although phytochemical investigations in *Arnica* are numerous (Borkowski *et al.* 1966; Saner and Leupin 1966; Willuhn *et al.* 1983; Merfort 1984, 1985; Wolf 1981; Downie and Denford 1986*b*), this is a first report on the flavonoids within *A. fulgens* and *A. sororia*.

Materials and methods

Field collections of *A. fulgens* and *A. sororia* were made during the summers of 1984 and 1985 throughout northwestern North America. Materials for morphological, flavonoid, and experimental analyses were collected from 43 populations. Live plant material was transplanted directly from the field and transported to the University of Alberta Phytotron for cultivation. Voucher specimens are deposited at ALTA. In addition, a study of specimens from throughout the range of the complex comprising approximately 500 specimens involved material from, or visitations to, the following herbaria: ALTA, BYU, C, CAN, MONT, MT, NY, PH, RM, SASK, UBC, UC, US, UT, and RENO. This information, in addition to the information obtained from literature (Maguire 1943; White and Johnson 1980; Douglas 1982; Packer 1983), was used in the plotting of distribution maps.

Phenetic analysis

Eighty-six representative specimens of *A. fulgens* and *A. sororia* (Table 2) were scored or measured for 26 floral and 17 vegetative attributes (Table 3). Each operational taxonomic unit (OTU) was assigned an OTU code indicating where the specimen was collected (e.g., A, Alberta; MO, Montana; CO, Colorado) and the number of the collector or the herbarium accession number. Each quantitative character represented a mean of 3 to 10 measurements, the total being dependent upon the number of plants per herbarium sheet. The characters chosen were selected from previous authors' treatments (Rydberg 1927; Maguire 1943; Ediger and Barkley 1978) and our experience in the field and greenhouse. Cluster analysis was performed using the TAXMAP classification program developed by Carmichael and Sneath (1969). The information obtained is readily amenable to a two-dimensional diagrammatic representation (taxometric map) drawn with the aid of the Calcomp plotter at the University of Alberta. The clustering procedure is outlined in detail in Carmichael *et al.* (1968) and has been recently used to delimit taxa in the *Arnica frigida–louiseana* complex (Downie and Denford 1986*a*).

Three specimens each of *A. lonchophylla* ssp. *lonchophylla* and *A. angustifolia* ssp. *angustifolia* have been included in the phenetic analysis in an effort to elucidate the morphological relations among the two taxa. Locality information for these six OTUs has also been included in Table 2.

Flavonoid analysis

Foliar flavonoid constituents within *A. fulgens* and *A. sororia* were determined using the modified procedures of Mabry *et al.* (1970), Ribéreau-Gayon (1972), and Markham (1982). Precise methodology for the isolation and identification of *Arnica* flavonoids can be found in Downie and Denford (1986*b*) and Wolf (1981).

Experimental analyses

Pollen grain viability was determined by staining pollen in a drop of lactophenol – cotton blue stain for 24 h. Pollen grains were considered viable if they took up the stain and appeared a dark blue colour. Viability was estimated on the percentage of stained grains in the 500 to 600 grains examined per specimen.

Acetocarmine root-tip squashes were based upon a modification of the Chambers (1955) technique. Actively growing root tips were removed from greenhouse-propagated material, prefixed in a 0.002 *M* 8-hydroxyquinoline solution for 2–2.5 h at 13–16°C, and then fixed in 3 absolute ethanol – glacial acetic acid (3:1, v/v). Squashes were made using the conventional acetocarmine technique. Voucher specimens of material used in cytological studies are filed in the University of Alberta Vascular Plant Herbarium.

Reproductive behaviour in *A. fulgens* and *A. sororia* was assessed using the procedures of Raunkiaer (1903), Barker (1966), and Heyn and Joel (1983). Both emasculation and crossing experiments were carried out in an insect-free growth room. In an effort to determine if the ovaries would produce seed without pollination, the entire capitulum was excised with a razor blade to remove effectively the stamens, corolla, stigma, and part of the style of each floret, leaving only the epigynous ovary and a style remnant. Disc florets which had already reached anthesis were removed prior to emasculation. As an alternative technique, all the disc florets were removed leaving only the peripheral rays. This was done prior to the opening of the capitulum, thus the capitulum had to be cut on one side to reach the disc florets. The plants were left to mature and monitored for achene formation.

Crosses were made between the species and within the same species but from different localities. Ray florets from emasculated plants were pollinated upon stigma emersion by transferring a clump of pollen onto the stigma by using tweezers or by rubbing the pollen directly from a disc floret. Each head was pollinated only once. Control was by artificial pollination of the ray florets in emasculated heads with the pollen from two flowers of the same plant. Fertility was estimated in two ways: pollen stainability in lactophenol – cotton blue and (or) the percentage of viable achenes produced. To differentiate between genetic and environmentally induced traits, plants from all collections were grown under identical environmental conditions in the controlled-environment facilities at the University of Alberta. Germinability of achenes was enhanced by placing them in a freezer 5–9 days prior to sowing.

Results

Herbarium studies

An initial examination of herbarium specimens was carried out to gain an overall view of the morphological variability encountered within the species. The high degree of uniformity within each species and the close similarity of *A. fulgens* to *A. sororia* was immediately obvious. Considerable confusion was found with respect to plant identification. In many instances *A. sororia* specimens were misidentified as *A. fulgens*. A list of representative specimens, too numerous to be included in this paper, can be supplied by the authors upon request.

Phenetic analysis

TAXMAP recognizes 3 clusters and 8 isolated OTUs, or single-member clusters. The resulting taxometric map appears in Fig. 1. All attributes were equally weighted to minimize subjectivity. Evident from the taxometric map is the separation of *A. fulgens* and *A. sororia* into discrete clusters and the close similarity of these two taxa with *A. angustifolia* ssp. *angustifolia*. The clusters can be described as follows. Cluster 1 contains 27 OTUs of *A. fulgens*. Cluster 2 contains all 34 OTUs of *A. sororia*. Cluster 3 is most closely related to cluster 1 and contains two anomalous specimens of *A. fulgens* which are characterized by a very tall habit and a long leaf length. Isolated clusters 4 and 5 are most closely related to *A. fulgens*. Cluster 4 represents a plant with a low number of large ligulate florets and large involucral bracts. The OTU in cluster 5 is a tall plant bearing wide leaves and a rather large capitulum.

TABLE 3. Attributes used in TAXMAP analysis

No.	Attribute	Mode of assessment
1	Habit	0, stem unbranched; 1, stem branched
2	Stem pubescence	0, glabrous to sparse; 1, moderate; 2, dense
3	Stem glandularity	0, absent or inconspicuous; 1, abundant
4	Leaf margin	0, entire; 1, entire to occasionally denticulate; 2, denticulate to occasionally dentate; 3, dentate
5	Leaf pubescence	0, glabrous to sparse; 1, moderate; 2, dense
6	Leaf glandularity	0, absent or inconspicuous; 1, abundant
7	Basal leaf petiole	0, sessile (or subsessile) or very short and broad winged; 1, narrow or broad winged and shorter than blade; 2, slender winged and approximately equaling the blade
8	Basal leaf apex	0, acute or acuminate; 1, obtuse
9	Basal leaf shape	0, linear to narrowly lanceolate; 1, narrowly to broadly lanceolate; 2, broadly lanceolate (to sometimes ovate); 3, narrowly oblong to oblanceolate; 4, oblanceolate to spathulate
10	Capitula position	0, erect; 1, nodding
11	Periclinium colour	0, white; 1, yellow to yellowish gold
12	Periclinium pubescence	0, glabrous to sparse; 1, moderate; 2, dense
13	Periclinium glandularity	0, absent or inconspicuous; 1, abundant
14	Achene pubescence	0, sparsely hirsute above middle, glabrous below; 1, sparse hirsute throughout; 2, dense hirsute throughout
15	Achene glandularity	0, absent or inconspicuous; 1, abundant
16	Involucral bract pubescence	0, sparingly pilose, otherwise glabrous; 1, pilose at base, glabrous above; 2, pilose throughout; 3, dense woolly–villous
17	Involucral bract shape	0, narrowly lanceolate; 1, broadly lanceolate; 2, oblanceolate
18	Involucral bract glandularity	0, absent or inconspicuous; 1, abundant
19	Ligule margin	0, entire to minutely denticulate; 1, prominently dentate
20	Disc corolla pubescence	0, glabrous to sparse; 1, moderate; 2, dense
21	Disc corolla glandularity	0, absent or inconspicuous; 1, abundant
22	Dense tufts in axils basal leaves	0, absent; 1, present
23	Capitula shape	1, broadly hemispheric; 2, campanulate–turbinate
24	Capitula number (per stem)	
25	Cauline leaves, number of pairs	
26	Plant height	Centimetres
27	Basal leaf length	Centimetres
28	Basal leaf width	Centimetres
29	Basal leaf length/width ratio	
30	Capitula width	Millimetres
31	Capitula height	Millimetres
32	Achene length	Millimetres
33	Involucral bract length	Millimetres
34	Involucral bract width	Millimetres
35	Involucral bract length/width ratio	
36	Ligule tooth length	Millimetres
37	Ligule length	Millimetres
38	Ligule width	Millimetres
39	Ligule length/width ratio	
40	Ligule number (per capitulum)	
41	Disc corolla length	Millimetres
42	Disc corolla length	Millimetres
43	Number major veins per leaf	

Isolated clusters 6, 7, and 8 and 9, 10, and 11 represent the six OTUs of *A. lonchophylla* ssp. *lonchophylla* and *A. angustifolia* ssp. *angustifolia*, respectively. Both these taxa are extremely polymorphic with respect to quite a number of attributes (S. R. Downie, unpublished).

Flavonoid analysis

Five flavonoid glycosides (three flavonols and two flavones) and one flavone aglycone were isolated from *A. fulgens* and *A. sororia* (Table 4). The 25 collections used in the flavonoid analyses are indicated in Table 2. Quercetin 3-O-galactoside, kaempferol 3-O-glucoside, quercetin 3-O-diglucoside, and luteolin 7-O-glucoside were ubiquitous. Luteolin 6-methoxy 7-O-glucoside and the aglycone apigenin were found only in the collections of *A. fulgens* and the former in only two collections of *A. sororia* (557 and 568). With the exception of these

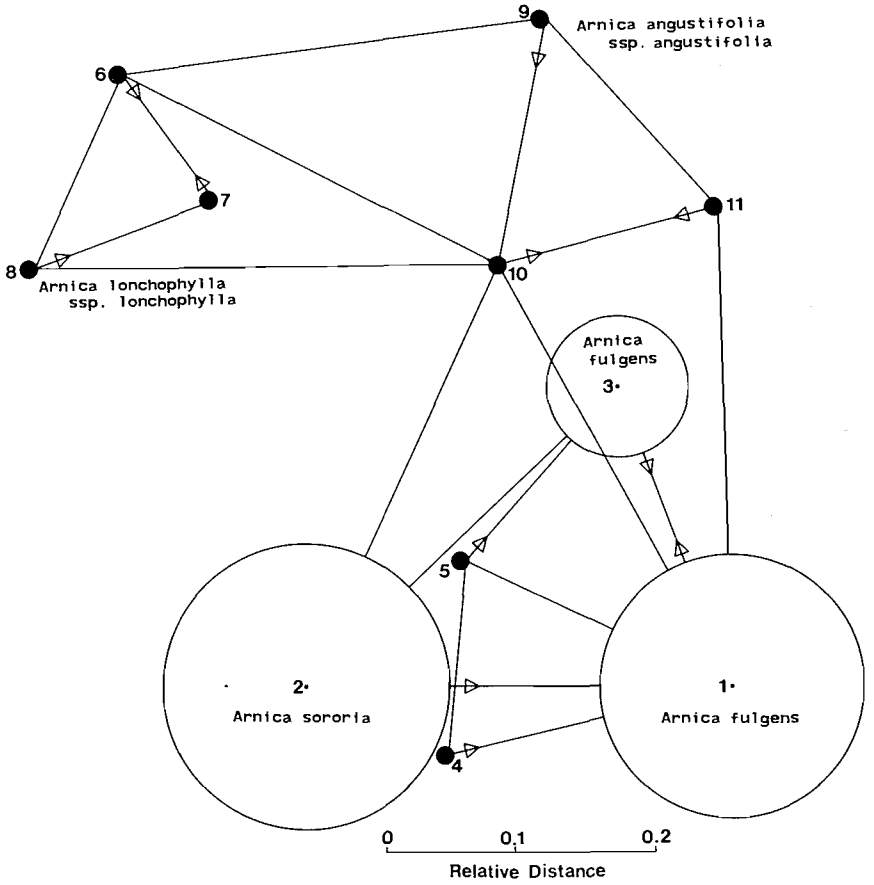

FIG. 1. Taxometric map showing the relations between *Arnica fulgens* (42 OTUs), *A. sororia* (44 OTUs), *A. angustifolia* (3 OTUs), and *A. lonchophylla* (3 OTUs), based on morphological data. The diameter of the circles represents the maximum distance between any pair of OTUs included in the cluster. The lines connecting the margins of the circles represent the undistorted phenetic distance between the nearest neighbours in the two clusters. The arrows indicate the nearest neighbour to each cluster. Two arrows facing each other indicate the clusters are equidistant from each other.

TABLE 4. Distribution of flavonoids in 25 specimens of *Arnica fulgens* and *A. sororia*

	Flavonoid[a]					
	1	2	3	4	5	6
Arnica fulgens (12 specimens)	+	+	+	+	+	+
Arnica sororia (11 specimens)	+	+	+	+		
Arnica sororia (collection nos. 557, 568)	+	+	+	+	+	+

[a]Flavonoid type: 1, quercetin 3-O-galactoside; 2, kaempferol 3-O-glucoside; 3, quercetin 3-O-diglucoside; 4, luteolin 7-O-glucoside; 5, luteolin 6-methoxy 7-O-glucoside; 6, apigenin.

two collections of *A. sororia*, the flavonoid profiles were unvarying and species specific.

Pollen viability

The pollen quality of 191 specimens, representing 43 field collections and 148 herbarium specimens, was determined. Herbarium specimens were chosen to represent collections from throughout the entire range of the complex. Within *A. fulgens*, 29 of 86 collections (34%) exhibited pollen viability less than 90% and 9 collections (10%) less than 75% viability. Within *A. sororia*, 36 of 105 collections (34%) exhibited pollen viability less than 90%, with only 13 collections (12%) less than 75%. All unstainable pollen in *A. fulgens* and *A. sororia* maintained its normal size and shape, unlike *A. frigida*, in which pollen grains exhibiting less than 80% stainability showed varying degrees of deformity (Downie and Denford 1986*a*). This report of low pollen stainability, suggestive of apomictic elements in *A. fulgens* and *A. sororia*, is in contrast to Barker's (1966) study in which all pollen was found to be greater than 90% viable.

Cytology

Fifteen collections of *Arnica fulgens* and 12 collections of *A. sororia* were all found to possess chromosome numbers of $2n = 38$ (Table 2), corroborating Barker's (1966) hypothesis that these taxa are wholly amphimictic. Pollen viability ranged from 21 to 100% for these collections.

Reproductive behaviour

Five capitula from *A. fulgens* and four from *A. sororia* were emasculated and the epigynous ovaries permitted to mature. In all instances no seeds were found within the small, fragile achenes. Similar results were obtained when the disc florets were removed and the ligulate florets allowed to develop. The achenes from the ligulate florets of two collections each of *A. fulgens* (571F, 559) and *A. sororia* (571S, 703) were found to be devoid of seeds. No evidence of agamospermy was found.

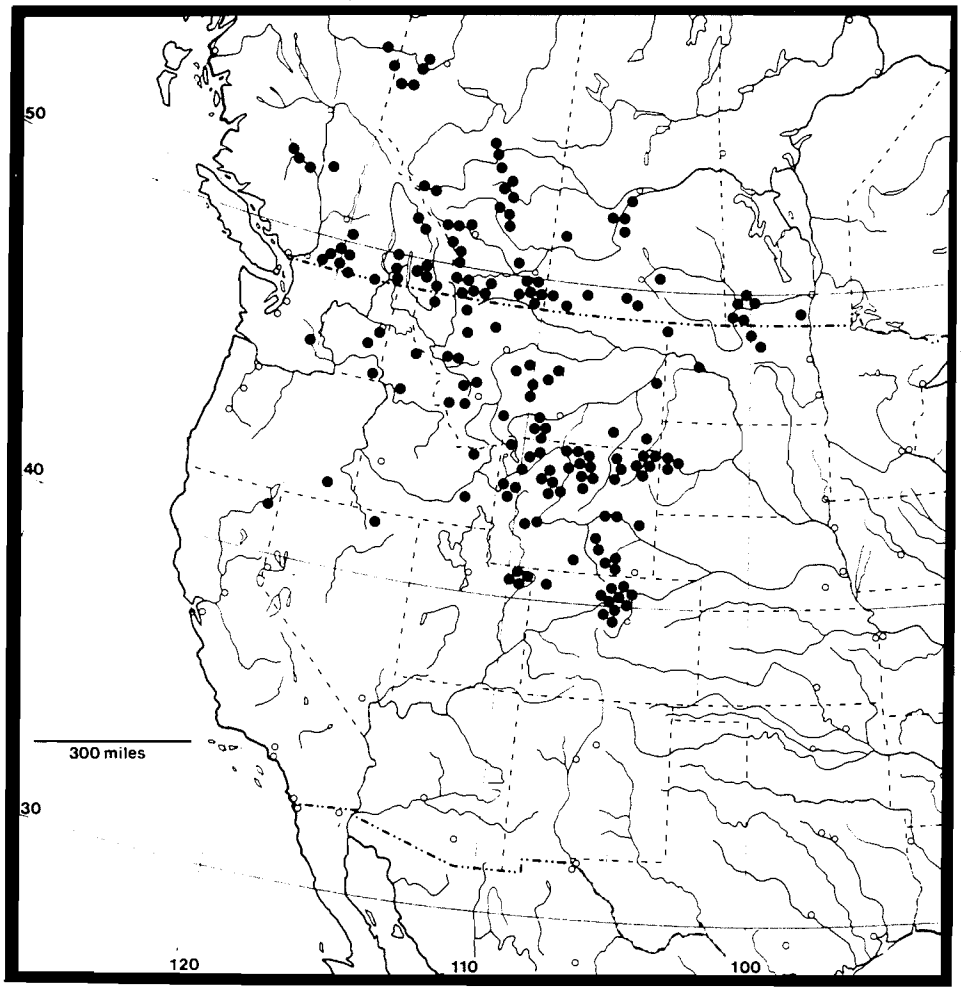

FIG. 2. Distribution of *Arnica fulgens* Pursh in western North America.

A limited number of artificial hybridization experiments were attempted. Nonsynchronous flowering periods between the two species and even between populations of the same species made it difficult to allow for immediate pollen transfer. Interpopulational crosses of *A. fulgens* (571F × 712, 559 × 562, 554 × 697) and *A. sororia* (573 × 570, 703 × 571S) were usually successful with the percentage of viable achenes between 65 and 85%. Unsuccessful intraspecific crosses (555 × 571F, 569 × 570) may be due to inviable pollen or to incomplete fertilization. Five interspecific crosses were attempted, but no viable achenes resulted (571F × 571S, 558 × 559, 699 × 558, 699 × 703, 554 × 703).

Field and greenhouse observations

Subtle differences in the ecology of these two species were noted, but these differences were obvious when both species were growing in the same locality. *Arnica fulgens* characteristically occurs in slightly moist to mesic depressions in the prairie. The more moisture that was available, the taller and more robust were the plants. All populations of *A. fulgens* were generally quite large and formed dense rhizomatous clumps. Associated species included *Zigadenus venenosus* S. Wats. var. *gramineus* (Rydb.) Walsh, *Geum triflorum* Pursh, *Cerastium arvense* L., *Dodecatheon conjugens* Greene, and *Thermopsis rhombifolia* (Nutt.) Richards. On the higher and drier portions of the prairie *A. sororia* was common. At one locality *A. sororia* was observed to be common around a depressed moister area containing *A. fulgens*. Populations of *A. sororia* were not as dense as *A. fulgens* and were very widely scattered. Associated species typically included *Selaginella densa* Rydb., *Artemisia frigida* Willd., *Allium textile* Nels. & Macbr., *Sphaeralcea coccinea* (Pursh) Rydb., and *Stipa comata* Trin & Rupr. var. *comata*. With respect to phenology, *A. fulgens* generally produces buds, flowers, and fruits before *A. sororia*, the timing being dependent upon the local environmental conditions.

Greenhouse-propagated plants were generally more branched (possessing numerous axillary capitula) and shorter than their naturally occurring parents. Both *A. fulgens* and *A. sororia*, however, maintained their differentiating morphological and chemical differences in the greenhouse. Unlike other *Arnica* species, in which flowering often occurs after a short 2- to 3-week period of vegetative growth (S. R. Downie, unpublished), both *A. fulgens* and *A. sororia* maintained their vegetative condition 2 to 3 months prior to flowering. This may reflect the longer growing season within the prairies as opposed to that in the typical *Arnica* habitat, arctic or alpine, or the cool greenhouse conditions.

Discussion

The present investigation of *Arnica fulgens* and *A. sororia* supports the recognition of two distinct taxa. *Arnica fulgens* is a densely rhizomatous species occupying mesic to moist habi-

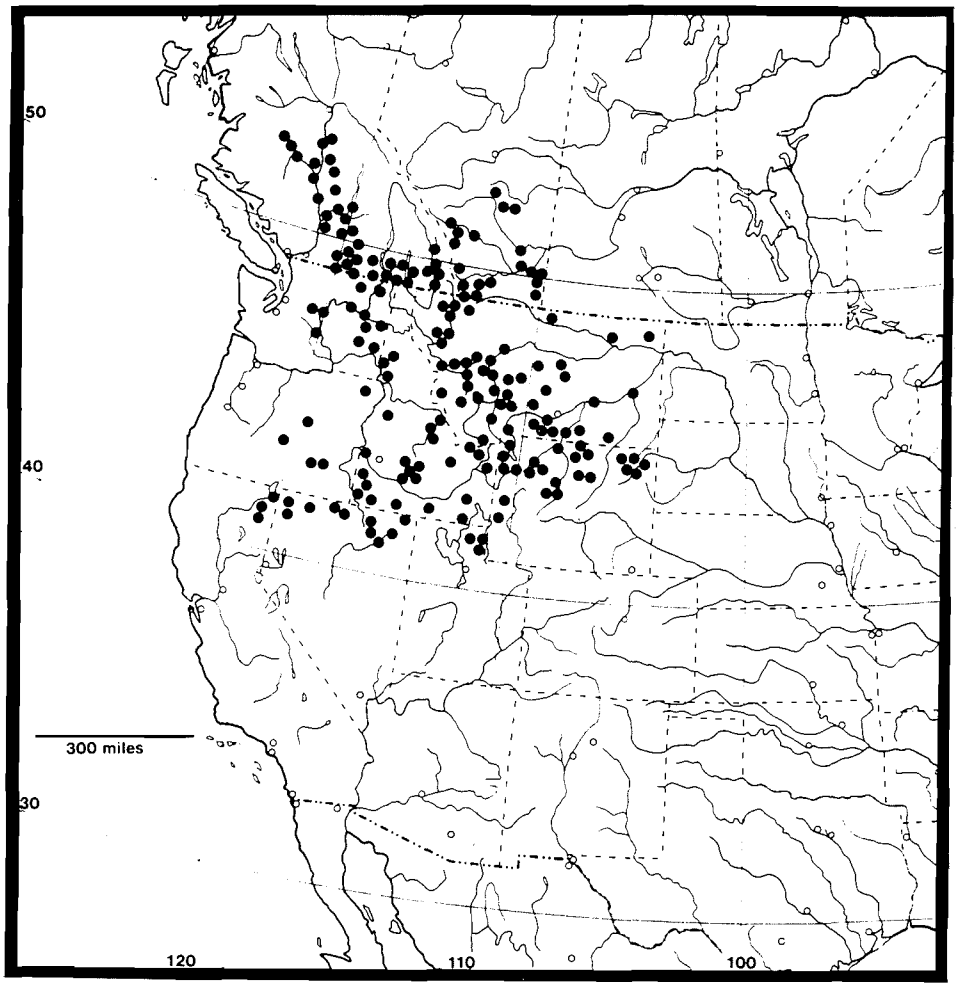

FIG. 3. Distribution of *Arnica sororia* Greene in western North America.

tats and is widely distributed throughout northwestern United States and adjacent southwestern Canada. It is distinguished by dense axillary tufts of brown woolly hair at the base of the plant, glandless hairs on the disc corollas, and the presence of luteolin 6-methoxy 7-O-glucoside and apigenin. Populations of *Arnica sororia* are not as dense as *A. fulgens* and are found on the drier portions of the prairie. Its leaves are generally much shorter and narrower, the plant is smaller, and the species are not as widely distributed as *A. fulgens*. Unsuccessful attempts at hybridizing the two taxa suggest that they are incompatible.

Davis and Heywood (1963) have described varieties to be "local facies of species (apparently comprising a few biotypes)." A variety differs morphologically and may also be found to differ cytologically, ecologically, or geographically, but it is restricted to small, localized areas. These entities lack a sufficient degree of morphological differentiation to be treated as species or are not widely enough distributed to be treated as subspecies (Davis and Heywood 1963). We accept this usage and reject Douglas' and Ruyle-Douglas' (1978) treatment of *A. sororia* as a variety of *A. fulgens*. The data from morphology, phytochemistry, ecology, plant distribution, and hybridization studies indicate that *Arnica fulgens* and *A. sororia* are separated by a number of good, discontinuous, independent character differences and we feel that they are both good taxonomic and biological species.

Considering the distribution of chromosome races in *Arnica*, Barker (1966) showed that no well-developed sexual species ($2n = 38$) occurs in a glaciated area and no well-developed polyploid series occurs in an unglaciated area. This has been shown to be particularly evident in *A. frigida* (Downie and Denford 1986*a*). Both *A. fulgens* and *A. sororia* occupy the greater part of their ranges outside the limits of continental glaciation and thus today remain as well-developed sexual species (Barker 1966). The previously reported chromosome count of $2n = 57$ for *A. fulgens* (Taylor and Brockman 1966) from Cypress Hills Provincial Park, Saskatchewan, is not corroborated by this study. Without further evidence, the existence of polyploidy in this complex is indeed a rare phenomenon, if indeed it exists at all.

Apomixis has also been shown to exist in plants having a high altitudinal or north latitudinal distribution (Gustafsson 1947). The distribution of *A. fulgens* and *A. sororia* is predominantly prairie with *A. fulgens* becoming low montane in the southern part of its range. The presence of sexual elements in these areas is correlated with the fact that these habitats would have been largely free of glaciation (Barker 1966).

In contrast to *A. frigida*, in which we see high pollen grain viability correlated closely with nonglaciated areas (Downie and Denford 1986*a*), there is no such correlation in *A. fulgens* and *A. sororia*. In both taxa, plants found producing unstainable grains were scattered throughout the whole range of the

species. In an estimation of pollen quality, 34% of the 191 collections examined exhibited less than 90% stainability and of these, 12% exhibited less than 75% stainability. The presence of low pollen stainability suggests that *A. fulgens* and *A. sororia* may be partially apomictic. However, chromosome counts obtained for two collections having low pollen stainability (555 and 569) were $2n = 38$. Barker (1966) has observed that all apomictic collections showed varying degrees of pollen deformity, whereas amphimictic collections had well-formed pollen. All collections of *A. fulgens* and *A. sororia* exhibiting low pollen viability had well-formed, normal-sized grains. As Barker (1966) suggests, determination of reproductive mode based on pollen quality estimates cannot be considered infallible, particularly when pollen stainability is between 70 and 89%. Barker (1966) has shown the existence of diploid apomicts in *A. amplexicaulis*. The existence of diploid apomicts in *A. fulgens* and *A. sororia* is subject to further investigation.

In wide-ranging species one would expect high flavonoid diversity, especially if the taxon occurs in a number of different habitat types (Mears 1980; Wolf and Denford 1984; Downie and Denford 1986*b*). However, in *Arnica fulgens* and *A. sororia*, the presence of one chromosome race, a restricted habitat specificity, and little morphological variation are reflected in little or no variation in the flavonoid profile, although differences are apparent between the species. The presence of luteolin 6-methoxy 7-O-glucoside and apigenin in two collections of *A. sororia* is significant and poses interesting questions. However, a more thorough examination of the flavonoids in this taxon is required before phylogenies can be resolved.

Morphologically, *A. fulgens* and *A. sororia* are more similar to *A. angustifolia* than to *A. lonchophylla*. The large solitary hemispheric capitula, entire to irregularly dentate leaves, and the short, narrow or broad-winged petioles of *A. fulgens*, *A. sororia*, and *A. angustifolia* are in contrast to the numerous small campanulate-turbinate capitula and the long petiolate, regularly dentate leaves of *A. lonchophylla*. The high degree of morphological similarity between *A. fulgens* and *A. sororia* suggests that they may be best treated as sister groups, arising from *A. angustifolia* or an ancestor resembling *A. angustifolia*.

Studies of reproductive behaviour indicate that both taxa are completely amphimictic and self-incompatible, corroborating the studies of Barker (1966). In the field, numerous pollinating vectors were observed on the flowers. These included bees, flies, spiders, and butterflies, with no apparent insect specificity. Artificial hybridization experiments between the two species were unsuccessful. Very rarely were both species found growing in the same proximity. The allotopic distribution and slightly different flowering periods would preclude much cross-pollination. Both taxa appear to be good biological species.

Taxonomy

Key to *Arnica fulgens* and *A. sororia*

Base of stem with dense tufts of brown woolly hair in axils of old leaves; disc corollas with spreading stipitate-glandular and glandless hairs ..... *A. fulgens*

Base of stem lacking axillary tufts of brown hair, occasionally with few whitish hairs; disc corollas stipitate-glandular only with no spreading septate glandless hairs ..... *A. sororia*

Arnica fulgens Pursh, Fl. Am. Sept. 527. 1814. *A. montana* var. *fulgens* (Pursh) Nutt., Gen. N. Am. Plts. 2: 164. 1818

TYPE: "On the banks of the Missouri" (Pursh 1814). (HOLOTYPE indicated by Maguire (1943) to be in BM was not found by staff. ISOTYPE, without locality, PH! PHOTO CAN!)

A. pedunculata Rydb., Bull. Torrey Club, 24: 297. 1897

TYPE: "Flora of Central Montana, Spanish Basin, Madison Range. July 11, 1896. *J. H. Flodman 899.*" (HOLOTYPE NY!)

A. monocephala Rydb., Mem. N.Y. Bot. Gard. 1: 435. 1900. *A. pedunculata* var. *monocephala* (Rydb.) Lunell, Am. Midl. Nat. 5: 241. 1918. *A. pedunculata* forma *monocephala* (Rydb.) Cockerell, Torreya, 18: 183. 1918

TYPE: "Exploration of Montana and Yellowstone Park. Bridger Mountains, Mont. 14 June 1897. *P. A. Rydberg and E. A. Bessey 5221.*" (HOLOTYPE NY!, ISOTYPE CAN!)

A. pedunculata var. *tubularis* Cockerell, J. Hered. 7: 428. 1916

TYPE: "Boulder, Colorado. June 1915. *W. P. Cockerell s.n.*" (HOLOTYPE GH!)

Plants 1.0–7.2 dm high; *stems* simple, stout, moderately puberulent becoming increasingly pubescent upwards, stipitate-glandular; *leaves* 3–5 pairs; *upper cauline leaves* sessile and reduced; *basal leaves* 4.5–20.0 cm long, 0.6–2.5 cm broad, apex obtuse, narrowly oblong to oblanceolate, rarely broadly spathulate or oval, the petioles narrow or broad-winged and shorter than the blade, margins entire to rarely remotely denticulate, moderately uniformly pubescent, stipitate-glandular, 3- to 5-nerved; *capitula* erect, solitary to occasionally 3, broadly hemispheric, 14.0–30.0 mm broad, 11.0–17.0 mm high; *periclinium* moderately to densely white pilose, stipitate-glandular; *involucral bracts* 13–21, 10.0–15.5 mm long, 1.5–4.5 mm broad, narrowly to broadly lanceolate to elliptic–oblong, apex obtuse to occasionally acute, uniformly pilose throughout, the tips pilose within, stipitate-glandular; *ligulate florets* 8–16, dark orange–yellow, 16–32 mm long, 2.9–8.0 mm broad, 3-toothed, the lobes 0.3–2.1 mm long; *disc florets* 6.0–9.1 mm long, goblet-shaped, stipitate-glandular, densely pilose, the tube 2.5–5.0 mm long; *achenes* 3.5–7.0 mm long, densely hirsute throughout, occasionally sparingly glandular; *pappus* white, occasionally tawny, barbellate; *rhizomes* short, densely scaly, thick, conspicuous dense tufts of long brown woolly hair in axils of basal leaves and persistent leaf bases, *chromosome number* $2n = 38, 57$.

DISTRIBUTION AND HABITAT: Plants widely distributed throughout interior British Columbia and southern Alberta, extending north into the Peace River drainage area, southern Saskatchewan, southwestern Manitoba, and as far south as northern California, northern Nevada, northern Utah, northern

FIG. 4. Illustrations of *Arnica fulgens* and *A. sororia*. (A) Habit of *A. fulgens* (slightly modified from *Downie 554* (ALTA)); (B) habit of *A. sororia* (based on *McCalla 4510* (ALTA)); and (C and D) disc florets (with pappus removed) of *A. fulgens* and *A. sororia*, respectively.

Colorado, and east to western North and South Dakota (Fig. 2). Plants of the prairies and grasslands at low elevations in the northern part of its range to montane plants up to 9800 ft (1 ft = 0.3048 m) in Wyoming and Colorado. Plants commonly found in moist depressed areas, often growing in dense clumps.

In 1818, Nuttall reduced *A. fulgens* Pursh to *A. montana* var. *fulgens* and later, recognizing its affinity with *A. angustifolia* Vahl, transferred it to the latter in 1841 (Nuttall 1841). *Arnica fulgens* was maintained under *A. angustifolia* in the North American floras of Torrey and Gray (1843) and Gray (1884). It would not regain its specific status until Rydberg's

North American Flora.

Arnica pedunculata Rydb. was proposed in 1897 for those plants similar to *A. angustifolia* but with axillary tufts of brown hair, a long-peduncled solitary head, and fine pubescence (Rydberg 1897). Three years later, Rydberg (1900) proposed the name *A. monocephala* Rydb. for a plant resembling *A. pedunculata* but much smaller and with broader leaves. The type specimens of both *A. pedunculata* and *A. monocephala* are typical *A. fulgens*.

In his *Flora of the Rocky Mountains*, Rydberg (1917) included *A. monocephala* in *A. pedunculata* and treated *A. sororia* Greene as *A. fulgens*. In 1927, however, Rydberg properly interpreted the plants with the dense axillary tufts as *A. fulgens* and placed both *A. pedunculata* and *A. monocephala* in synonymy. *Arnica sororia* was recognized as its true form. The close similarity between *A. pedunculata* and *A. monocephala* must have been apparent to others for in 1918 both Cockerell and Lunell treated *A. monocephala* as a forma and variety of *A. pedunculata*, respectively. It is presumed that they had not yet seen the work of Rydberg (1917).

The type and only specimen of *A. pedunculata* var. *tubularis*, consisting of only peduncle and capitulum, is an aberration of *A. fulgens* in which the ligulate florets are tubular.

Arnica sororia Greene, Ottawa Nat. 23: 213. 1910. *A. fulgens* var. *sororia* (Greene) G. W. Dougl. and G. Ruyle-Dougl. in Taylor and MacBryde, Can. J. Bot. 56: 185. 1978

TYPE: "Near International Boundary between Kettle and Columbia rivers. Cascade, B.C. June 30, 1902. *J. M. Macoun (Geol. Surv. Can. No. 64987).*" (HOLOTYPE ND!, ISOTYPES CAN!, GH!, PHOTOS CAN!, UC!)

A. stricta Greene non Nels., Ottawa Nat. 23: 214. 1910. *A. trinervata* Rydb., N. Am. Fl. 34: 344. 1927

TYPE: "Near International Boundary between Kettle and Columbia rivers. June 30, 1902. *J. M. Macoun (Geol. Surv. Can. No. 64979).* On Isotypes: "W. of Cascade, B.C." (HOLOTYPE ND!, ISOTYPES CAN!, NY, PHOTOS CAN!, UC!)

Plants 1.5–5.0 dm high; *stems* simple to branched, slender, moderately puberulent below becoming increasingly pubescent upwards, stipitate-glandular; *leaves* 3–6 pairs; *upper cauline leaves* sessile and reduced; *basal leaves* 3.5–14.5 cm long; 0.6–2.4 cm broad (usually narrower than *A. fulgens*), apex obtuse, narrowly oblong to oblanceolate, the petioles narrow-winged and shorter than the blade, margins entire to rarely remotely denticulate, moderately uniformly pubescent, short-stipitate glandular, 3- to 5-nerved; *capitula* erect, 1–5 (rarely more), broadly hemispheric, 11.0–27.0 mm broad, 9.0–17.0 mm high; *periclinium* moderately to densely white pilose, stipitate-glandular; *involucral bracts* 13–20, 9.5–14.2 mm long, 1.2–3.1 mm broad, narrowly to occasionally broadly lanceolate, apex acute, uniformly pilose throughout, tips not at all pilose within, glandular; *ligulate florets* 9–17, dark orange–yellow, 15.0–31.0 mm long, 2.5–7.5 mm broad, 3-toothed, the lobes 0.2–1.8 mm long; *disc florets* 6.9–10.0 mm long, goblet-shaped, uniformly stipitate-glandular, not at all pubescent, the tube 3.0–5.5 mm long; *achenes* 3.0–5.5 mm long, densely hirsute throughout, occasionally sparingly glandular; *pappus* white or nearly so, barbellate; *rhizomes* short, less scaly than *A. fulgens*, slender, hair tufts in axils of old basal leaves sparse and white, or absent; *chromosome number* $2n = 38$.

DISTRIBUTION AND HABITAT: Widely distributed throughout the interior of southern British Columbia, southern Alberta, and as far south as northern California, northern Nevada, northern Utah and east to north and western Wyoming and eastern Montana (Fig. 3). Plants of the prairies and grasslands at low elevations particularly in very dry areas. Plants in less dense populations, in drier habitats, and at lower elevations than *A. fulgens*.

The rejection and subsequent transfer of *A. stricta* Greene to *A. trinervata* Rydb. by Rydberg (1927) was due to the former being a later homonym of *A. stricta* Nels. (1901), now a synonym of *A. chamissonis* Less. ssp. *foliosa* (Nutt.) Maguire. *Arnica stricta* Greene was based on a single collection of J. M. Macoun (Geol. Surv. Can. No. 64979) from British Columbia. These tall, coarse, broad-leaved plants with numerous axillary capitula are somewhat anomalous in *A. sororia*. However, as first indicated by Maguire (1943), these specimens appear to be only morphological extremes in a comparatively unvariable species. We are in agreement with Maguire's (1943) inclusion of *A. trinervata* as a synonym of *A. sororia*.

The recognition of *A. sororia* as a variety of *A. fulgens* (Douglas and Ruyle-Douglas 1978) was influenced by the strong morphological similarity between these two taxa, with the only differentiating character being the presence or absence of disc corolla pubescence. The long axillary tufts of dense brown woolly hairs in *A. fulgens* were not observed to comprise a consistent character (Douglas and Ruyle-Douglas 1978). It is presumed that this misunderstanding occurred because of the frequent misidentification of these taxa and the inclusion of many members of *A. sororia* with *A. fulgens* herbarium specimens. We find that these axillary tufts furnish an excellent character to delimit the taxa.

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