Contributions to the Taxonomy of *Chrysothamnus viscidiflorus* (Astereae Compositae) and Other *Chrysothamnus* Species Using Paper Chromatography

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Highlight: Chromatographic patterns of phenolic compounds were determined for each of the common subspecies of the widespread range shrub *Chrysothamnus viscidiflorus* (low rabbitbrush), some other *Chrysothamnus* taxa, and some related Compositae genera. Each subspecies of *C. viscidiflorus* exhibited variation across its geographical range, but within sites the patterns were consistent. Chromatographic pattern distributions suggest a predominance of self-pollination in *C. viscidiflorus*; however, the limited outcrossing has important genetic implications. Analysis of the chromatographic spot patterns revealed three groups or clusters within *C. viscidiflorus*. Surprisingly, *C. greenei* clustered more closely to some *C. viscidiflorus* subspecies than these subspecies clustered with other *C. viscidiflorus* subspecies. *C. greenei* clustered with ssp. *lanceolatus* and *stenophyllus*. Ssp. *viscidiflorus* clustered s > 0.70 with ssp. *latifolius* and a group of collections intermediate in morphology between *viscidiflorus* and *lanceolatus*. It shares some intense spots with these taxa. Subspecies *puberulus* did not cluster at s = > 70 with any other taxon. Chromatographic data supported the independent species status of *C. linifolius* and the internal integrity of the three large species complexes in *Chrysothamnus—C. viscidiflorus*, *C. nauseosus*, and *C. parryi*. The genus *Petradoria* had high s values with *Chrysothamnus*, as did *Haplopappus bloomeri*. Other shrubby Compositae (*Xanthocephalum sarothrae* and *Lepidospartum latisquamum*) had much lower s values with *Chrysothamnus*. Chromatography complements morphology in delimiting taxonomic rank. Each *Chrysothamnus* taxon should be evaluated on its merits.

The *Chrysothamnus viscidiflorus* (Hook.) Nutt. (low rabbitbrush) complex is a natural and widespread component of the Great Basin and surrounding arid regions of the western United States. The genus *Chrysothamnus* is a member of the tribe Astereae, family Compositae. The *C. viscidiflorus* complex grows principally in dry, open places in the valleys, plains, foothills, and the mountains throughout this region (Cronquist 1955; Ferris 1960; Munz 1974). However, the plant group is not highly salt tolerant; consequently, it is not usually found in pockets with poor drainage where pH and salinity are high (Hall and Clements 1923).

The importance of this species is largely unrecognized and controversial at the present time (USDA Forest Service 1937; Holmgren and Hutchings 1972; Evans et al 1973; Young and Evans 1974). As a forage shrub, its usefulness has not been throughly documented. However, its heavy utilization by deer and livestock during periods of stress and the occasional use of some subspecies during spring and summer months have frequently been observed (USDA Forest Service 1937; Cook et al 1954; Kufeld et al 1973). Hall and Clements (1923) related the preference for this shrub to the relative abundance of other forage plants; they noted that where more common forage is scarce, utilization of *C. viscidiflorus* subspecies is often quite heavy. Its value as browse may be greatly underestimated in areas where, due to shallow and rocky soil, difficulty may be encountered in encouraging the growth of other more desirable plants. In such areas, this species may become an important segment of the vegetation (Cook et al. 1954).

The most significant characteristic of *C. viscidiflorus*, however, may be its ability to become quickly established in areas of soil disturbance. The natural pioneering capacity of this shrub is obvious from its early appearance in rights-of-way and other similarly disturbed areas. Its early growth and establishment make it valuable for revegetating areas where, due to strip mining, road construction, and other disturbances, early and rapid plant growth under adverse circumstances is desirable (Plummer 1977).

Taxonomic Treatment

The number of subspecies that should be included in this species is not clear. Hall and Clements (1923) listed nine: *lanceolatus*, *viscidiflorus*, *latifolius*, *linifolius*, *pumilis*, *elegans*, *puberulus*, *stenophyllus*, and *humilis*. Anderson (1970b) recognized all except *humilis* and *linifolius*, which, following earlier works, he reinstated to the ranks of species.

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In a later publication, Anderson (1971) stated that "plants named *pumilis* are only environmentally modified variants" of ssp. *viscidiflorus*. Hall and Clements (1923) and Cronquist (1955) suggested a similar close relationship between ssp. *latifolius* and ssp. *viscidiflorus*; however, each retains the former as a valid subspecies. Anderson (1964) also described a new subspecies, *planifolius*, a narrow endemic, known only from Coconino County, Ariz. Anderson (personal communication, May 17, 1976) recently examined the type specimen of subspecies *elegans*. He stated " . . . it is a narrow leaved form of *C. viscidiflorus* ssp. *lanceolatus*."

Common Subspecies

The subspecies most abundant in the Great Basin are *viscidiflorus*, *stenophyllus*, *lanceolatus*, and *puberulus*. Their distribution overlaps and there is some intergradation (Ferris 1960). A number of intermediates have been located during our field studies.

The leaves and upper stems of subspecies *viscidiflorus* and *stenophyllus* are essentially glabrous, although the leaf margins are often ciliate to scabrous and the stems are sometimes sparsely puberulent. Subspecies *viscidiflorus* normally has the largest leaves, ranging from 1 to 5 mm in width and 2 to 5 cm in length. It is taller than ssp. *stenophyllus*, often over 5 dm high when mature. This subspecies is widely distributed throughout western North America. Subspecies *stenophyllus* is usually under 5 dm in height. It has filiform (threadlike) leaves 1 mm or less in width. The ssp. *stenophyllus* is more common in the southern portion of the Intermountain area. The bark of the younger twigs of ssp. *stenophyllus* is usually white. This coloration may occur in the other subspecies, but is not as pronounced as in ssp. *stenophyllus*.

The leaves and upper stems of subspecies *lanceolatus* and *puberulus* are pubescent, often densely so. Subspecies *lanceolatus* has larger leaves than subspecies *puberulus*. Its leaves range from 2.5 to 6 mm in width and 1.5 to 4 cm in length and are usually flat. This subspecies occurs at middle to high elevations 1,525 to 3,200 m (5,000 to 10,500 ft) in the central and northern portions of the Intermountain region. The leaves of ssp. *puberulus* are often strongly twisted. They range in width from less than 1 to 2 mm. Individual plants and even whole populations of *puberulus* have involucral bracts, each of which has a thickened greenish spot near its tip. This characteristic is occasionally found on other subspecies. The green spotted tip has been considered to be a diagnostic feature of ssp. *elegans* (Hall and Clements 1923). However, the type specimen for ssp. *elegans* is a collection of ssp. *lanceolatus* (Anderson, personal communication) and has no such spot. We have noted populations of ssp. *puberulus* with green spotted involucral bracts being heavily browsed by sheep and deer. Subspecies *puberulus* is concentrated mainly in Utah and Nevada at lower and intermediate elevations—below 2,130 m (7,000 ft).

Other C. viscidiflorus Complex Species

Chrysothamnus linifolius Greene and *C. greenei* (Gray) Greene are believed to be a part of the *C. viscidiflorus* complex (Hall and Clements 1923; Anderson 1964). *Chrysothamnus linifolius* is a tall rabbitbrush (up to 2.5 m) with relatively broad leaves. Because it profusely root sprouts, it has value as a stabilizer of disturbed soils (McArthur et al. 1974; Plummer 1977). It occurs in alkaline areas in the Upper Colorado River Basin. *Chrysothamnus greenei* is morphologically similar to *C. viscidiflorus*; its most obvious difference is its sharply tipped or attenuate involucral bracts (Hall and Clements 1923). *C. greenei* usually occurs on valley floors in the eastern half of the Great Basin and of the Upper Colorado River Basin.

Chromatography as a Taxonomic Aid

Classification of the *C. viscidiflorus* complex depends heavily on nonfloral characters, such as shrub size, pubescence, leaf width, leaf length, and number of midveins (Hall and Clements 1923; Anderson 1964). Unfortunately, these morphological traits are often not sufficiently reliable for the positive identification of field collections. The variable and overlapping nature of these characters has been recognized (Hall and Clements 1923; Cronquist 1955). Anderson 1964; Hall and Clements (1923) considered this condition as evidence of the "extreme plasticity" within *C. viscidiflorus*. To aid in the clarification of the systematic problems so evident in the complex there have been a number of recent studies by Anderson and his colleagues (Anderson 1964, 1966, 1970a, 1970b, 1971; Anderson and Fisher 1970; Anderson et al. 1974) using floral anatomy, embryology, and cytology in an effort to clarify the taxonomy of this species.

The usefulness of chemical analysis to supplement morphological criteria in the classification of plants has become widely established in recent years (Harborne 1973; Bendz and Santesson 1974). Our previous studies (Hanks et al. 1971, 1973, and 1975; Hanks and Jorgensen 1973; Stevens and McArthur 1974) have demonstrated that chromatographic methods are useful in taxonomic identification and potentially useful in selection and breeding programs of sagebrush and rubber rabbitbrush. Because of the obvious need of additional characteristics to supplement those already used in the study of *C. viscidiflorus*, we felt that a similar approach would supply information that could contribute significantly toward understanding the *C. viscidiflorus* complex.

Materials and Methods

Approximately 300 specimens of *C. viscidiflorus* were collected from diverse locations in Utah, Nevada, Wyoming, and California (Fig. 1). Additionally, 100 specimens of other species [*C. greenei*, *C. parryi* (Gray) Greene, *C. linifolius*, and *C. depressus* Nutt.] were collected. A few collections of other Astereae [*Petradoria discoida* L. C. Anderson, *P. pumila*, (Nutt.) Greene, *Xanthocephalum sarothrae* Shinners, and *Haplopappus bloomer*, Gray] were also made. We also collected *Lepidospartum latisquamum* S. Wats. of the tribe Senecioneae. This species resembles *Chrysothamnus* in several respects, most notably its imbricated involucral bracts. These species grow sympatrically with *Chrysothamnus* species at various locations on collection transects of Figure 1.

Extracts were prepared by suspending 0.5 g of dried, pulverized foliage in 10 ml absolute methanol for 48 hours. The liquid was

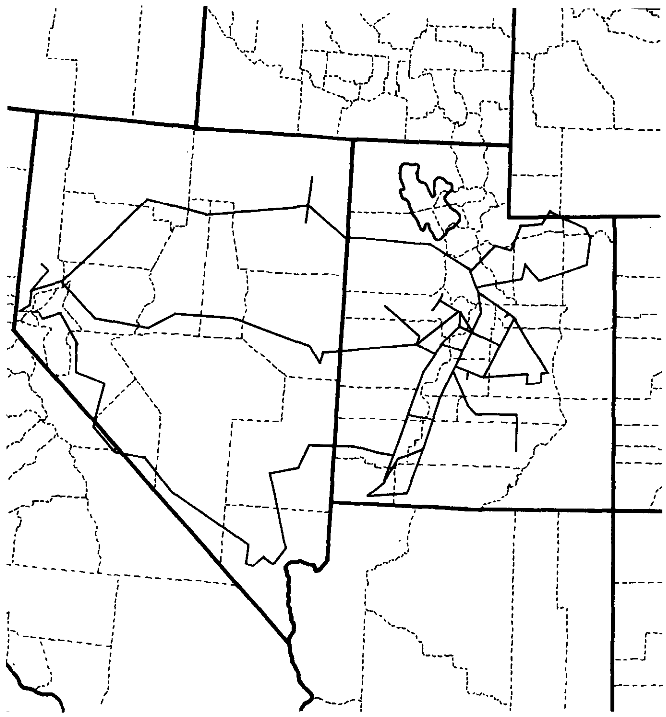

Fig. 1. *Map with lines showing collection transects for* Chrysothamnus *populations studied.*

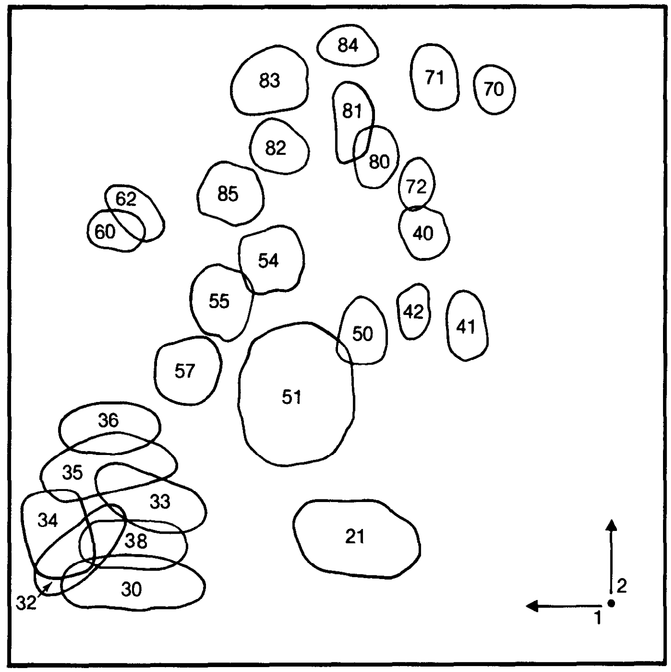

Fig. 2. *Composite two-dimensional chromatogram of methanol-soluble extracts from the leaves of the subspecies of* Chrysomthamnus viscidiflorus *and other* Chrysothamnus *taxa. Spots are shown in relative size and position.*

carefully decanted and concentrated by evaporation using a Rinco[1] flash evaporator to a final volume of 2.0 ml. Chromatograms were prepared and developed according to the procedures previously described (Hanks et al. 1975). Chromatograms were observed under longwave ultraviolet light and the spots were characterized according to R_f values (R_{f1} = first dimension, R_{f2} = second dimension) and color before and after exposure to ammonia vapor. Each finished chromatogram, following exposure to ammonia, was photographed under ultraviolet light using a 35-mm camera equipped with an ultraviolet filter and using ASA 25 film. The developed 35-mm slides were studied in a slide viewer to estimate the relative color intensity and spot size. Also, they were compared with traced copies of chromatograms and notes recorded from the original chromatograms. The numbering of spots was organized by dividing the chromatogram into nine equal rectangular divisions in three horizontal series. Beginning at the origin in the lower right hand division, and moving from right to left across the lower, middle, and upper series, spots within each division were numbered successively by tens (that is, 10 to 19, 20 to 29 . . . 90 to 99). The phenolic compounds represented by the spots were not identified. However, Urbatsch et al. (1975) identified 10 flavonoids (a class of phenolic compounds) from a northern Arizona collection of *C. viscidiflorus.*

Percentage similarity values (Cox 1973) were used to express levels of chromatographic similarity among species and subspecies. These values were calculated using the formula: s = number of common spots divided by the total number of different spots of the taxa being compared. A spot was counted for a taxon if it was detectable on at least half of the chromatograms. A dendrogram was constructed using a cluster analysis technique (Sokal and Sneath 1963). Stems in the dendrogram were tied together in descending order according to s values. Stems representing multiple taxa were joined together at the average s value for all taxa being united above each union.

C. viscidiflorus Chromatographic Patterns

R_f values, spot distribution frequency for *C. viscidiflorus,* and color characteristic of each spot are included in Table 1. Table 2 and Hanks et al. (1975) give the spot frequencies for other species and subspecies of *Chrysothamnus* and provide a comparison of spot frequency. The percent similarity of each *Chrysothamnus* taxon to each other taxon studied is given in Table 3.

A representative Chromatogram of *C. viscidiflorus* subspecies is illustrated in Figure 2.

Three spots, 40, 51, 81, were observed in virtually all *Chrysothamnus* chromatograms. A species specific pattern for *C. viscidiflorus* was found to include 34, 40, 50, 51, 70, 72, 80, and 81 since these were common to all *C. viscidiflorus* subspecies. Other spots provided distinction for each subspecies (Table 1) and were used to establish patterns of chemical relationship between them (Fig. 3).

Subspecies within geographical areas gave noticeably consistent chemical patterns. These patterns remained relatively consistent within given areas even though two or more subspecies were growing together. Looking at the overall study, however, single spots or combinations of spots normally associated with a given subspecies were occasionally found in chromatograms of other subspecies (and species) and vice versa. Subspecies patterns varied slightly in different areas (Table 4). Similar variations were noted among subspecies of *Chrysothamnus nauseosus* (Pallas) Britt. in a previous study (Hanks et al. 1975).

Breeding System

The distribution of chemical patterns within and among subspecies suggests that *C. viscidiflorus* is largely self-pollinating but that outcrossing is possible and occasionally occurs. In effect, this occasional outcrossing often would be much like self-pollination since neighboring plants are often of similar genotypes.

The small amount of effective outcrossing could be

[1] Use of trade or firm names is for reader information only, and does not constitute endorsement by the U.S. Department of Agriculture of any commercial product or service.

Table 1. Chromatographic spot properties and occurrence for the subspecies of *Chrysothamnus viscidiflorus*.

Spot no.	R_{f1} (x100)[1]	R_{f2} (x100)[2]	Color: Ultraviolet light	Color: Ultraviolet light + ammonia vapor	Color: Visible light + ammonia vapor	Frequency of occurrence[3]: Chvi^{v}	Chvi^{v-l}	Chvi^{l2}	Chvi^{l}	Chvi^{s}	Chvi^{p}
21	41	10	blue	blue	—	0.07	0.04	0.00	0.03	0.58	0.60
30	72	05	gold	gold	—	.78	.73	.89	.82	.58	.27
32	90	13	—	blue green	—	.27	.42	.00	.13	.42	.01
33	76	16	gold	gold	—	.52	.42	.78	.53	.79	.85
34	86	12	violet	brown	yellow	.96	.92	.78	.95	.89	.98
35	83	20	—	light blue	—	.21	.08	.33	.08	.42	.93
36	88	30	orange	tan	—	.14	.11	.11	.03	.42	.54
38	73	07	blue	blue	—	.11	.08	.11	.10	.21	.37
40	28	55	pink	pink	—	1.00	1.00	1.00	1.00	.89	.94
41	13	48	violet	gold	yellow	.11	.00	.11	.15	.68	.54
42	34	50	violet	gold	yellow	.01	.00	.00	.00	.00	.01
50	37	39	violet	gold	yellow	.93	.85	.89	.92	.94	.96
51	49	32	blue	yellow green	grey	1.00	1.00	1.00	.97	1.00	.98
54	50	59	violet	gold	?	.03	.04	.00	.02	.00	.00
55	59	57	violet	gold	?	.00	.00	.67	.03	.11	.00
57	65	38	violet	gold	?	.10	.15	.00	.06	.05	.01
60	80	58	blue	blue	—	.87	.69	.78	.26	.21	.30
62	79	63	blue	blue	—	.00	.00	.00	.00	.00	.00
70	15	80	—	blue	—	.72	.73	.78	.50	1.00	.91
71	21	86	—	blue	—	.63	.50	.44	.39	.05	.10
72	26	65	grey blue	grey blue	—	.62	.85	1.00	.92	.95	.87
80	34	73	blue	yellow green	yellow brown	.92	.96	1.00	.98	1.00	.98
81	44	76	blue	blue green	—	.97	.96	1.00	1.00	1.00	.94
82	52	69	blue	blue	—	.29	.38	.22	.37	.26	.04
83	54	82	blue	blue	—	.81	.62	.78	.11	.11	.10
84	46	89	—	blue	—	.57	.42	.11	.31	.00	.06
85	63	58	blue	blue	—	.02	.00	.00	.00	.00	.00

[1] N-butanol:acetone:water, 4:1:3 (v/v/v).
[2] 15% acetic acid.
[3] Abbreviation for *Chrysothamnus viscidiflorus* subspecies: Chvi^{v} = *viscidiflorus* (113 samples); Chvi^{v-l} = *viscidiflorus* introgressed by *lanceolatus* (26 samples); Chvi^{l2} = *latifolius* (9 samples); Chvi^{l} = *lanceolatus* (62 samples); Chvi^{s} = *stenophyllus* (19 samples); Chvi^{p} = *puberulus* (67 samples).

Table 2. Chromatographic spot properties and occurrence for *Chrysothamnus* taxa other than *C. viscidiflorus*[1].

Spot no.	R_{f1} (x100)[2]	R_{f2} (x100)[3]	Color: Ultraviolet light	Color: Ultraviolet light + ammonia vapor	Color: Visible light + ammonia vapor	Frequency of occurrence[4]: Chgr^{g}	Chgr^{f}	Chli	Chpa^{m}	Chpa^{n}	Chpa^{a}	Chpa^{h}	Chpa^{a2}	Chde
21	41	10	blue	blue	—	0.35	0.11	0.00	0.00	0.00	0.00	0.00	0.00	0.00
30	72	05	gold	gold	—	.92	.89	.25	.00	1.00	.00	.41	.14	.00
32	90	13	—	blue green	—	.21	.11	.00	.00	.00	.00	.00	.00	.00
33	76	16	gold	gold	—	1.00	.84	.62	.00	.00	.00	.38	.14	.00
34	86	12	violet	brown	yellow	1.00	.84	.50	.00	1.00	.00	.77	.85	.00
35	83	20	—	light blue	—	.00	.00	.12	.00	.67	.00	.69	.42	.00
36	88	30	orange	tan	—	.07	.05	.62	.00	.00	.00	.38	.00	.00
38	73	07	blue	blue	—	.85	.52	.12	.00	.00	.00	.00	.00	.00
40	28	55	pink	pink	—	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
41	13	48	violet	gold	yellow	.28	.11	.00	.00	.00	.00	.00	.00	.00
42	34	50	violet	gold	yellow	.28	.34	.25	.00	.00	.00	.00	.00	.00
50	37	39	violet	gold	yellow	1.00	1.00	1.00	.00	.00	.25	.69	.00	1.00
51	49	32	blue	yellow green	grey	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
54	50	59	violet	gold	?	.00	.17	.20	.00	.00	.00	.00	.00	.00
55	59	57	violet	gold	?	.00	.00	.50	1.00	.67	1.00	.54	1.00	.00
57	65	38	violet	gold	?	.21	.17	.25	.00	.00	.00	.00	.00	.00
60	80	58	blue	blue	—	.46	.34	.37	.25	1.00	.12	.62	.85	.00
62	79	63	blue	blue	—	.00	.00	.62	.00	.00	.00	.00	.00	.00
70	15	80	—	blue	—	1.00	.78	.00	.00	.25	.00	.69	.28	.75
71	21	86	—	blue	—	.53	.05	.62	1.00	1.00	1.00	1.00	1.00	.00
72	26	65	grey blue	grey blue	—	1.00	.68	.62	.00	.00	.00	.00	.00	.00
80	34	73	blue	yellow green	yellow brown	.93	.89	.62	.00	.25	.67	.84	1.00	1.00
81	44	76	blue	blue green	—	1.00	.95	1.00	1.00	1.00	1.00	.92	1.00	1.00
82	52	69	blue	blue	—	.33	.47	.87	1.00	.67	1.00	.62	.00	.75
83	54	82	blue	blue	—	.00	.00	.62	.25	1.00	1.00	.69	1.00	.00
84	46	89	—	blue	—	.00	.17	.00	.75	1.00	.00	.92	.42	.25
85	63	58	blue	blue	—	.00	.00	.62	.00	.00	.00	.00	.00	.00

[1] The data for *C. nauseosus* may be found in Hanks et al. 1975.
[2] N-butanol:acetone:water, 4:1:3 (v/v/v).
[3] 15% acetic acid.
[4] Abbreviations for *Chrysothamnus* taxa other than *C. viscidiflorus*: Chgr^{g} = *C. greenei* ssp. *greenei* (15 samples); Chgr^{f} = *C. greenei* ssp. *filifolius* (19 samples); Chli = *C. linifolius* (8 samples); Chpa^{m} = *C. parryi* ssp. *monocephalus* (4 samples); Chpa^{n} = *C. parryi* ssp. *nevadensis* (8 samples); Chpa^{a} = *C. parryi* ssp. *asper* (12 samples); Chpa^{h} = *C. parryi* ssp. *howardi* (13 samples); Chpa^{a2} = *C. parryi* ssp. *attenuatus* (7 samples); Chde = *C. depressus* (4 samples).

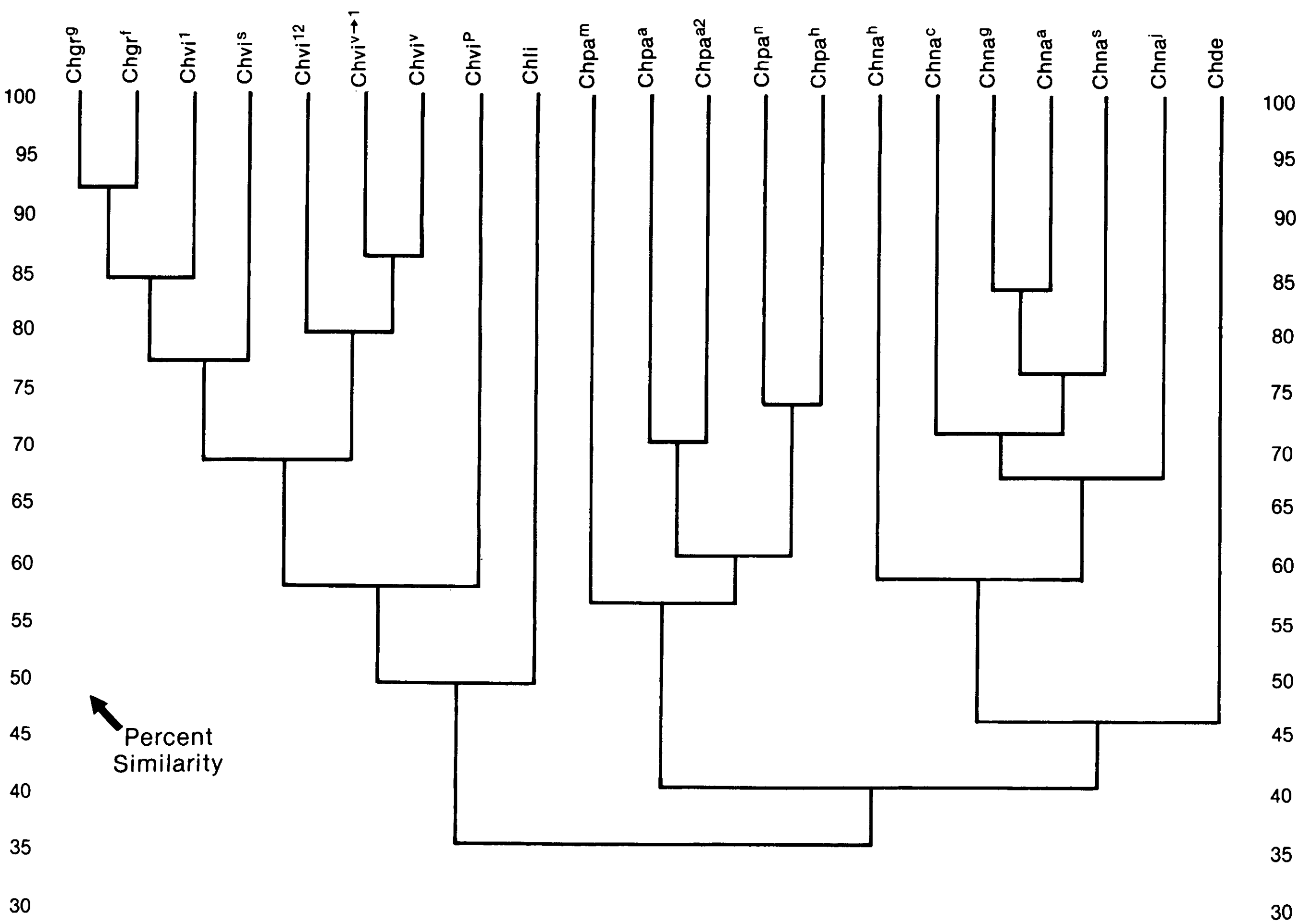

Fig. 3. *Dendrogram of* Chrysothamnus *taxa based on* s *values, Taxa symbols are: Chgr*^{g} = C. greenei: *ssp.* greenei, *Chgr*^{f} C. greenei *ssp.* filifolius, *Chvi*^{l} = *C.* viscidiflorus *ssp.* lanceolatus, *Chvi*^{s} = C. viscidiflorus *ssp.* stenophyllus, *Chvi*^{12} = C. viscidiflorus *ssp.* latifolius, *Chvi*^{lv} = C. viscidiflorus *ssp.* viscidiflorus *introgressed by* C. viscidiflorus *ssp.* lanceolatus, *Chvi*^{v} = C. viscidiflorus *ssp.* viscidiflorus, *Chvi*$_{P}$ = C. viscidiflorus *ssp.* puberulus, *Chli* = C. linifolius *Chpa*^{m} = C. parryi *ssp.* monocephalus, *Chpa*^{a} = C. parryi *ssp.* asper, *Chpa*^{a2} = C. parryi *ssp.* attentuatus, *Chpa*^{n} = C. parryi *ssp.* nevadensis; *Chpa*^{h} = *C.* parryi *ssp.* howardi; *Chna*^{h} = C. nauseosus *ssp.* hololeucus, *Chna*^{c} = C. nauseosus *ssp.* consimilis, *Chna*^{g} = C. nauseosus *ssp.* graveolens, *Chna*^{a} = C. nauseosus *ssp.* albicaulis, *Chna*^{s} = C. nauseosus *ssp.* salicifolius, *Chna*^{j} = C. nauseosus *ssp.* junceus, *and Chde* = C. depressus.

important since it leads to new genetic combinations. *Chrysothamnus viscidiflorus* is a vigorous colonizer of disturbed sites. According to Young et al. (1972), it is one of a few native plants with the ability to invade dense stands of the alien weed, cheatgrass brome (*Bromus tectorum* L.). The *C. viscidiflorus* complex has several characteristics of ideal colonizing species (Baker 1965). We suggest that it is successful as a colonizer and invader because (1) its successful genotypes are self-perpetuating by way of self-pollination and (2) occasional outcrossing provides new genotypes of fill newly exposed niches. The new genotypes might exhibit heterosis and hence be more vigorous and competitive. Young et al. (1972) attributed part of the success of the highly competitive introductions, cheatgrass brome, and medusahead [*Taeniatherum asperum* (Sim.) Nevski], to predominantly self-pollinating but occasional outcrossing breeding systems.

C. greenei Clusters with *C. viscidiflorus*

The *C. viscidiflorus* complex includes three clusters of taxa with *s* values above 70% (Fig. 3). The cluster on the left side of Figure 3 includes *C. greenei* with its two subspecies (*greenei* and *filifolius*). Subspecies *filifolius* is separated from *greenei* by its tendency to larger stature and shorter, narrower leaves (Hall and Clements 1923). L. C. Anderson (in his annotation of our specimens) did not recognize subspecific taxa of *C. greenei.* The cluster analysis (Fig. 3, Table 3) shows the *C. greenei* subspecies to be very similar (s = 92%). This similarity along with our observation that many populations containing individual *greenei* and *filifolius* plants as well as intermediate forms leads us to concur with Anderson and recommend that no *C. greenei* subspecies be recognized. *C. greenei* clusters more closely with two *C. viscidiflorus* subspecies (*lanceolatus* and *stenophyllus*) than these subspecies cluster with other *C. viscidiflorus* subspecies (Table 3, Fig. 3). Leading *Chrysothamnus* authorities (Hall and Clements, 1923; Anderson, 1970a, b) maintained *C. greenei* as a separate species, although Hall and Clements (1923) believed *C. greenei* was a close relative of *C. viscidiflorus.* Our data suggest that *C. greenei* should be considered a subspecies of *C. viscidiflorus.* Although there is much synonymy in *Chrysothamnus*, the combination of *C. greenei* as a subspecies of *C. viscidiflorus* apparently has not been made (Hall and Clements 1923; Holmgren and Reveal 1966). The

Table 3. Chromatographic spot percentage similarity values of species and subspecies of *Chrysothamnus*.

	Taxa[1] [2]	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
1	Chgr^{f}																				
2	Chgr^{g}	92																			
3	Chvi^{v}	69	75																		
4	Chvi$^{v\pi 1}$	64	71	86																	
5	Chvi^{12}	71	67	80	79																
6	Chvi^{l}	83	85	71	69	77															
7	Chvi^{s}	77	71	62	60	60	83														
8	Chvi^{p}	60	56	50	47	53	64	71													
9	Chpa^{m}	27	36	31	27	25	21	19	18												
10	Chpa^{a}	27	33	38	47	40	29	25	24	69											
11	Chpa^{n}	33	33	62	50	47	29	26	25	58	58										
12	Chpa^{h}	39	45	69	62	59	41	37	42	50	57	73									
13	Chpa^{a2}	33	40	56	62	57	36	26	29	45	70	62	64								
14	Chli	44	50	56	56	56	47	42	40	38	53	42	53	50							
15	Chde	50	46	38	46	43	55	46	43	40	50	27	47	33	38						
16	Chna^{a}	29	35	39	35	26	31	28	26	38	46	28	39	33	44	50					
17	Chna^{g}	29	35	39	44	33	31	28	26	29	46	28	39	33	44	50	83				
18	Chna^{s}	29	35	39	44	33	31	28	26	38	58	35	47	43	44	40	69	83			
19	Chna^{c}	39	44	47	44	42	41	30	35	31	47	37	47	44	44	50	67	79	67		
20	Chna^{j}	21	26	30	33	25	22	25	19	46	67	41	44	50	43	36	64	76	64	63	
21	Chna^{h}	29	35	32	44	26	31	28	26	38	46	28	39	33	37	50	69	57	62	47	53

[1] Abbreviations for *Chrysothamnus* taxa: Chgr^{f} = *C greenei* ssp. *filifolius;* Chgr^{g} = *C. greenei* ssp. *greenei;* Chvi^{v} = *C. viscidiflorus* ssp. *viscidiflorus;* Chvi^{v-1} = *C. viscidiflorus* spp. *viscidiflorus* introgressed by ssp. *lanceolatus;* Chvi^{12} = *C. viscidiflorus* ssp. *latifolius;* Chvi^{l} = *C. viscidiflorus* ssp. *lanceolatus;* Chvi^{s} = *C. viscidiflorus* ssp. *stenophyllus;* Chvi^{p} = *C. viscidiflorus* ssp. *puberulus;* Chpa^{m} = *C. parryi* ssp. *monocephalus;* Chpa^{a} = *C. parryi* ssp. *asper;* Chpa^{n} = *C. parryi* ssp. *nevadensis;* Chpa^{h} = *C. parryi* ssp. *howardi;* Chpa^{a2} = *C. parryi* ssp. *attenuatus;* Chli = *C. linifolius;* Chde = *C. depressus;* Chna^{a} = *C. nauseosus* ssp. *albicaulis;* Chna^{g} = *C. nauseosus* ssp. *graveolens;* Chna^{s} = *C. nauseosus* ssp. *salicifolius;* Chna^{c} = *C. nauseosus* ssp. *consimilis;* Chna^{j} = *C. nauseosus* spp. *junceus;* Chna^{h} = *C. nauseosus* spp. *hololeucus.*
[2] Data for *C. nauseosus* ssp. taken from Hanks et al., 1975.

principal taxonomic character used to separate *C. greenei* from *C. viscidiflorus* is the attenuate bracts of *C. greenei.* In other respects, the two taxa closely resemble one another and are often misidentified as one for the other. The resemblance is particularly close between *C. greenei* and *C. viscidiflorus* ssp. *stenophyllus.* Both have a low, bushy habit, white-barked stems, and short, narrow leaves. Furthermore, form *axillaris* of *stenophyllus* has attenuate bracts (Anderson 1964).

The second cluster with $s > 0.70$ in the *C.* viscidiflorus complex is composed of *C. viscidiflorus* ssp. *viscidiflorus, C. viscidiflorus* ssp. *latifolius,* and collections intermediate in such morphological characteristics as pubescence and leaf veination between ssp. *viscidiflorus* and *lanceolatus.* Taxa in the second cluster share a pair of prominent spots, 60 and 83 (Fig. 2 and 3). The frequency of spots 60 and 83 is lower (Table 1) in the ssp *viscidiflorus lanceolatus* introgressants than it is in ssp. *viscidiflorus* and *latifolius.* Ssp. *latifolius* may have arisen out of the ssp. *viscidiflorus*-ssp. *lanceolatus* combination. It is a restricted taxon that incorporates leaf and pubescence characteristics of both ssp. *viscidiflorus* and ssp. *lanceolatus.*

The third $s > 0.70$ *vicidiflorus* cluster is composed of the single entity of ssp. *puberulus.* Spots in the lower center and left areas of the chromatogram contribute to the distinctive chromatogram of ssp. *puberulus.* Spots 35 and 36 are characteristic for this subspecies; they are lacking in all others, whereas spot 30 is present in all other subspecies and absent in ssp. *puberulus* (Fig. 2, Tables 1 and 2).

C. linifolius

The position of *C. linifolius* (section *Chrysothamnus*) has been in dispute. Hall and Clements (1923) treated this taxon as a subspecies of *C. viscidiflorus.* Anderson (1964) following Greene (Hall and Clements, 1923) considered it as

Table 4. Chromatographic geographical variation of *Chrysothamnus viscidiflorus* subspecies *viscidiflorus*.

Collection site	Spot number																		
	30	32	33	34	35	36	40	41	50	51	60	70	71	72	80	81	82	83	84
Typical ssp. *viscidiflorus* pattern	x	x		x			x		x	x	x	x	x	x	x	x		x	x
Sigurd, Sevier County, Utah (2)[1]	x			x	x		x	x	x	x	x	x	x	x	x	x		x	x
Eureka, Juab County, Utah (8)	x	x	x	x			x	x	x	x	x	x	x	x	x	x	x	x	x
Summit, Wasatch Pass, Sevier County, Utah (6)	x		x	x			x		x	x	x	x	x	x	x	x	x	x	x
Ivie Creek Drainage east of Wasatch Pass, Sevier County, Utah (2)		x		x			x		x	x	x	x	x	x	x	x		x	x
Salina Creek Drainage, west of Wasatch Pass, Sevier County, Utah (18)	x			x			x		x	x	x		x		x	x		x	x
Panguitch Lake, Garfield County, Utah (2)	x	x		x			x		x	x	x	x	x	x	x	x		x	x
Wells, Elko County, Nevada (2)	x	x	x	x			x			x	x	x	x	x	x	x		x	x
Sparks, Washoe County, Nevada (2)			x	x		x	x		x	x	x	x		x	x	x		x	x

[1] Number of plants.

Table 5. Chromatographic spot percentage similarity values of some other Compositae taxa to each other and to *Chrysothamnus* taxa.

Taxa	No. of samples	No. of spots not found in *Chrysothamnus*	Taxa				
			Petradoria discoidia	*Petradoria pumilia*	*Haplopappus bloomeri*	*Xanthocephalum sarothrae*	*Lepidospartum latisquamum*
Petradoria discoidia	4	0	—				
Petradoria pumilia	3	0	92	—			
Haplopappus bloomeri	2	0	40	38	—		
Xanthocephalum sarothrae	6	2	32	30	40	—	
Lepidospartum latisquamum	2	5	38	36	22	33	—
Chrysothamnus viscidiflorus	296	—	56	52	47	40	41
Chrysothamnus greenei	34	—	60	68	44	46	38
Chrysothamnus nauseosus	192	—	35	35	48	44	23
Chrysothamnus parryi	44	—	44	42	62	35	22
Chrysothamnus linifolius	8	—	44	42	53	45	27
Chrysothamnus depressus	4	—	38	36	55	50	32

a separate species. Our chromatographic evidence supports the independent species status. Chromatograms of *C. linifolius* contain two bright blue spots, 62 and 85, which were not found in those of any other taxa (Fig. 2, Tables 1 and 2). The *s* values between *C. linifolius* and subspecies of *C. viscidiflorus* are low (about 0.49). However, *C. linifolius* clusters more closely with *C. viscidiflorus* than with any other *Chrysothamnus* studied (Fig. 3).

Other *Chrysothamnus*

Chrysothamnus parryi and *C. nauseosus* are both large species complexes, each with several subspecies. Both belong to section *Nauseosi*. Our data (Fig. 3) group these complexes together at a relatively low level (*s* = 0.40). The two together join *C. viscidiflorus* at about *s* = 0.33 [the value *s* = 0.35 of Figure 3 reflects the higher *s* values contributed by *C. linifolius* and *C. depressus* (Table 3)]. Interestingly, *C. parryi* has a higher *s* value (0.38) with *C. viscidiflorus* than does *C. nauseosus* (0.27). This higher *s* value complements morphological characters since *C. parryi* is smaller and has less tomentum than *C. nauseosus*.

Chrysothamnus depressus is the only section *Pulchelli* species we studied. It has relatively low *s* values with all other species included in this study (Table 3). This taxon clustered slightly closer to *C. nauseosus* than any of the other species (Fig. 3).

Some Shrubby Sympatric Compositae

Other shrubby Astereae genera are distributed sympatrically with *Chrysothamnus* species. Some of these are habit-look-alikes and close relatives. At some locations, *Chrysothamnus* species and look-alike relatives grow side by side. Some of these other Astereae taxa have been referred to as *Chrysothamnus* (Hall 1928; Anderson 1963). Others have been suggested as contributing to the parentage of *Chrysothamnus* species (Anderson and Reveal 1966). We compared *s* values of four other Astereae and one Senecioneae species to *Chrysothamnus* species (Table 5).

Petradoria discoidia was formerly classified as *C. gramineus*, section *Chrysothamnus* (Hall and Clements 1923; Anderson 1963). It has a relatively high *s* value with species in this section of *Chrysothamnus* (*C. viscidiflorus*, *C. greenei*, and *C. linifolius*). However, it has an even higher *s* value with *P. pumila*, *s* = 0.92. Our data support Anderson's transfer of *C. gramineus* to *Petradoria*. However, both *Petradoria* species have high *s* values with *Chrysothamnus* species (Table 5). *Petradoria* is a small genus (2 sp.) close to *Haplopappus* and *Chrysothamnus*. Our data support its closeness to *Chrysothamnus*.

Haplopappus bloomeri has relatively high *s* values with *Chrysothamnus* species, especially *C. parryi* (Table 5). *Chrysothamnus* and *Haplopappus* are thought to be phylogenetically close (Hall and Clements 1923; Anderson and Reveal 1966). *H. bloomeri's s* values with other Astereae are lower than its *s* values with *Chrysothamnus*.

Xanthocephalum sarothrae (= *Gutierrezia sarothrae*) (Ruffin 1974a, 1974b) has relatively low *s* values with *Chrysothamnus* and the other Astereae. It has two chromatographic spots not found in *Chrysothamnus*. This species is widespread in the western United States. When its flowers are not available—its heads, unlike *Chrysothamnus*, include ray flowers—it is often confused with *C. viscidiflorus*.

Lepidospartum latisquamum has the lowest *s* values of any taxon listed in Table 5. Its chromatograms produced five spots not detected in *Chrysothamnus* chromatograms. This datum is consistent with *L. latisquamum's* position in the tribe Senecioneae rather than Astereae.

Conclusions

The clustering of taxa generated by the similarity index of chromatograms present in *Chrysothamnus* and a few other Compositae provided useful taxonomic information. This information helps clarify some questions such as the validity of specific rank for *C. linifolius* and the taxonomic proximity of *C. greenei* and *C. viscidiflorus*. It also produced support for the distinctness of the three large species complexes in *Chrysothamnus*—*C. nauseosus, C. parryi*, and *C. viscidiflorus*. Furthermore, it supported the separation from *Chrysothamnus* of tribe Astereae the genera *Petradoria*, *Haplopappus*, *Xanthocephalum*, and the tribe Senecioneae genus, *Lepidospartum*.

Chrysothamnus in general and *C. viscidiflorus* ssp. in particular are important range shrubs. Each taxon has positive values, undesirable qualities, or both. Each taxon should be managed on the basis of its favorable or unfavorable qualities. Chromatography is a useful adjunct to morphological criteria in delineating taxonomic boundaries.

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