

THE *CHRYSOTHAMNUS-ERICAMERIA* CONNECTION (ASTERACEAE)

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ABSTRACT.—The genus *Chrysothamnus* (Asteraceae) contains 16 species. Recently, 4 species were transferred to *Ericameria*, and the remaining 12 were left in *Chrysothamnus*. The remaining species are now transferred to *Ericameria* as *E. albida*, *E. depressa*, *E. eremobia*, *E. graminca*, *E. filifolia* (formerly *C. greenei*), *E. humilis*, *E. linifolia*, *E. molesta*, *E. pulchella*, *E. pulchelloides* (a fossil species), *E. spathulata*, *E. caseyi*, and *E. viscidiflora*. Section alignments are given, and some infraspecific combinations are also made.

Key words: *Chrysothamnus*, *Ericameria*, rabbitbrush, nomenclature transfers.

The Asteraceae are a relatively young group, and yet they have experienced rapid evolution into a great number of species. One result is that many taxa appear more distant morphologically (phenotypically) than they actually are genetically, and, conversely, some taxa may appear more closely related than they are. These situations have created havoc amongst taxonomists in their attempts to circumscribe genera. This is particularly evident in the tribe Astereae. In 1894, E. L. Greene stated:

In North America the Astereae are excessively numerous, and no natural assemblage of plants has seemed to present such difficulties to the systematist; and the widest conceivable diversities of opinion as to the limits of genera have found expression among botanists when undertaking to classify them.

The situation continues a century later.

The genus *Haplopappus* was thought to be an unnatural, polyphyletic assemblage by many (e.g., Shinners 1950, Anderson 1966, Johnston 1970, Turner and Sanderson 1971, Clark 1977, Urbatsch 1978). Nevertheless, because there was no suitable taxonomic reorganization of the group, I continued to describe new taxa in *Haplopappus* (Anderson 1980a, 1983b), even though the species would probably be placed in some other genera at a later date. Recently, additional data have contributed to a clearer understanding of the relationships in this and related groups (Morgan and Simpson 1992), and several genera have been recognized for North American Haplopappi.

In a 1976 presentation at national meetings, I discussed the close affinity of *Chryso-*

thamnus with woody elements of *Haplopappus* and suggested that the *Asiris-Ericameria-Macronema* complex of *Haplopappus* probably should be included in *Chrysothamnus*. But, given the state of knowledge at that time, I deferred. In 1990, Nesom reorganized *Ericameria* as a genus to include *Asiris* and *Macronema*. Recently, based on occurrences of intergeneric hybrids (Anderson and Reveal 1966, Anderson 1970) and DNA data (Morgan and Simpson 1992), Nesom and Baird (1993) transferred four species of *Chrysothamnus* into *Ericameria* (*C. nauseosus* and *C. parryi* of section *Nauseosi* and *C. paniculatus* and *C. teretifolius* of section *Punctati*). They continued to recognize *Chrysothamnus* as a distinct (but smaller) genus and gave arguments for separating the two.

A problem in separating *Ericameria* and *Chrysothamnus* (sensu Nesom and Baird) is the occurrence of hybrids (Anderson 1970, 1973) between *C. nauseosus* (their *Ericameria*) and *C. albidus* (their *Chrysothamnus*). After studying a specimen of only one of the three collections involved, Nesom and Baird (1993) devalued the connection by stating that “the plant in question [is] characteristic of *C. nauseosus*, and we identify it as *C. nauseosus*, finding no strong reason to implicate *C. albidus* in its parentage.” They stated that achenes of *C. albidus* are linear and consistently producing 10 slightly raised nerves, whereas those of *C. nauseosus* are narrowly obovate with 5–7 nerves. Actually, achenes of both species can be characterized as being narrowly cylindrical. The number of vascular bundles (associated with the nerves) in the achenes averages approximately 7 and

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ranges from 5 to 10 (but mostly 6–8 in Ash Meadows) for *C. albidus* (Anderson 1970, 1973), whereas achene bundle number in *C. nauseosus* ranges from 5 to 12 (but is restricted to 5 for those in Ash Meadows).

The interspecific hybrid examined by Nesom and Baird (*Beatley 11894*, KSC) was studied anatomically by Anderson (1973); its hybridity is indicated by low pollen fertility and by morphological intermediacy between the two species in its revolute leaves, in vascular bundle number in the ovary wall, in corolla lobe length, and in anther appendage length. It has secretory canals in the ovary wall and glandular trichomes on the corolla tube (like *C. nauseosus*, unlike *C. albidus*) and ovary wall (unlike *C. nauseosus*, like *C. albidus*). Further, progeny from one of my *C. albidus* garden plants also has low pollen fertility and looks intermediate between its seed parent and *C. nauseosus* (Anderson 1970). Its flowers have secretory canals in the ovary wall and glandular trichomes on the corolla tube but lack glandular trichomes on the ovary wall; those three features are characteristic of *C. nauseosus* but not of *C. albidus* (the seed parent), clearly suggesting hybridity. If existence of interspecific hybrids is used to justify transferring *C. nauseosus* to *Ericameria*, then this feature also argues for bringing the remainder of *Chrysothamnus* into *Ericameria*.

The warranted position of *Chrysothamnus teretifolius* in *Ericameria* is taken by Nesom and Baird (1993: 80) because, like many *Ericameria* species (sensu strictum), that species has the tendency for the “resiniferous ducts that are almost always distinctly associated with the phyllary midvein to expand near the apex of the phyllary.” This characteristic also occurs in many species of *Chrysothamnus* (sensu Nesom and Baird) as illustrated for *C. vaseyi* (Anderson 1963: 660) and cannot be used to distinguish the two groups. I have observed adjacent populations of *C. viscidiflorus* subsp. *puberulus* in which plants of one had prominently enlarged resin ducts at the phyllary tips and plants of the other did not.

With the transferral of four species from *Chrysothamnus* to *Ericameria*, Nesom and Baird (1993) separate the two newly structured genera with six criteria. (1) Leaves 3-nerved for *Chrysothamnus* and 1-nerved for *Ericameria*—but many of their *Ericameria* have prominently 3-nerved leaves. Hall and

Clements (1923) used nerve number to distinguish *C. nauseosus* ssp. *graccolens* from spp. *consimilis* (so the character is variable even within a species). Many of the latter group, such as *C. albidus*, *C. greenei*, and some forms of *C. viscidiflorus*, appear to have 1-nerved leaves. Actually, all species of *Ericameria* and *Chrysothamnus* have trilacunar, 3-trace nodal anatomy (personal observation); thus, the character of 1 versus 3 nerves is a matter of perception, not of fact. (2) Leaf margins ciliate in the former and never in the latter—but *C. albidus*, *C. eremobius*, and *C. viscidiflorus* subsp. *planifolius* of the former have entire leaf margins; also in that group, *C. pulchellus* subsp. *pulchellus* has entire leaf margins, whereas subsp. *baileyi* has ciliate leaf margins, and some populations of *C. gramineus* and *C. vaseyi* have entire leaf margins, but others do not. *Ericameria* (sensu Nesom 1990) has several species that have leaves with ciliate leaf margins, fairly prominent in *E. cooperi* and less so in several other species (e.g., *E. cervina*, *E. nana*, *E. oplitidis*, and *E. zionis*). (3) Corollas more or less abruptly broadened from the tube into the throat with long, recurving or coiling lobes in the former and corollas tubular with short, erect or spreading lobes in the latter—but corollas of *C. spathulatus* (of the latter) have relatively broad tubes that lack noticeably flaring throats, *C. humilis* (of the former) has tubular corollas with short, erect lobes (Anderson 1964: 226), and *C. nauseosus* ssp. *ceruminosus* (of the latter) has corollas that are abruptly broadened from the tube into the throat with long, spreading lobes. (4) Style appendage collecting hairs merely papillate in the former, whereas they are long and sweeping in the latter—but *C. albidus*, *C. molestus*, *C. pulchellus*, and certain populations of *C. viscidiflorus* (all of the former) have style appendages with moderately long, sweeping hairs. Diversity in collecting hairs is greater in *Chrysothamnus* (sensu Anderson 1986) than Nesom and Baird (1993) imply and does not fall into two groups. Collecting hair length may be correlated with other floral features; namely, the corollas, style lengths, and pollen volumes of the former group (Anderson 1966) are generally smaller than those of the latter. (5) Involucral bracts in vertical files in the former (caveat noted) and usually not in vertical files in the latter—but, perhaps the most strongly aligned bracts occur in *C. nauseosus*

ssp. *arenarius* (of the latter). (6) Achenes glandular with nonresinous nerves in the former and eglandular (with duplex hairs) and resinous nerves in the latter—but only five species of the former have glandular achenes (in some they are hidden by duplex hairs) and the other seven do not, having either glabrous achenes or achenes with duplex hairs exclusively (Anderson 1970, 1983a), and many have resin canals associated with the bundles of the achenes, admittedly fewer than in those of the latter but well developed in *C. molestus* of the former. Also, *C. paniculatus* (of the latter grouping) lacks resin canals in its achenes (Anderson 1970). None of these six sets of characteristics can be used to consistently separate the two groups.

Clearly, *Chrysothamnus* (sensu Anderson 1986, not Nesom and Baird 1993) is fairly homogeneous and should not be dismembered. If some are to go into *Ericameria* (and DNA data suggest they should), then all should go into *Ericameria*. Therefore, the remaining 12 species of *Chrysothamnus* are transferred to *Ericameria*, and new combinations are made here.

1. *Ericameria albida* (M. E. Jones ex A. Gray) L. C. Anders., *comb. nov.* Basionym: *Bigelovia albida* M. E. Jones ex A. Gray, Proc. Amer. Acad. Arts 17: 209. 1882. *Chrysothamnus albidus* (M. E. Jones ex A. Gray) E. Greene, Erythea 3: 107. 1895.

2. *Ericameria depressa* (Nutt.) L. C. Anders., *comb. nov.* Basionym: *Chrysothamnus depressus* Nutt., Proc. Acad. Nat. Sci. Philadelphia 4: 19. 1948. *Linowsyris depressa* (Nutt.) Torr., in Stigeaves, Rept. Exped. Zuni & Colorado Rivers 161. 1853. *Bigelovia depressa* (Nutt.) A. Gray, Proc. Amer. Acad. Arts 8: 643. 1873.

3. *Ericameria eremobia* (L. C. Anders.) L. C. Anders., *comb. nov.* Basionym: *Chrysothamnus eremobius* L. C. Anders., Brittonia 35: 23. 1983.

4. *Ericameria graminea* (H. M. Hall) L. C. Anders., *comb. nov.* Basionym: *Chrysothamnus gramineus* H. M. Hall, Muhlenbergia 2: 342. 1916. *Petradoria discoidea* L. C. Anders., Trans. Kansas Acad. Sci. 66: 676. 1964.

5. *Ericameria filifolia* (Rydb.) L. C. Anders., *comb. nov.* Basionym: *Chrysothamnus filifolius* Rydb., Bull. Torrey Bot. Club 28: 503. 1901. *Bigelovia greenii* A. Gray, Proc. Amer. Acad. Arts 11: 75. 1876 [not *Ericameria greenii* (A. Gray) Nesom]. *Chrysothamnus greenii* (A. Gray) E. Greene, Erythea 3: 94. 1895. *Chrysothamnus pumilus* var. *acuminatus* A. Nels., Bot. Gaz. 28: 376. 1899. *Chrysothamnus scoparius* Rydb., Bull. Torrey Bot. Club 28: 504. 1901. *Chrysothamnus laricinus* E. Greene, Pittonia 5: 110. 1903.

6. *Ericameria humilis* (E. Greene) L. C. Anders., *comb. nov.* Basionym: *Chrysothamnus humilis* E. Greene, Pittonia 3: 24. 1896.

7. *Ericameria linifolia* (E. Greene) L. C. Anders., *comb. nov.* Basionym: *Chrysothamnus linifolius* E. Greene, Pittonia 3: 24. 1896.

8. *Ericameria molesta* (Blake) L. C. Anders., *comb. nov.* Basionym: *Chrysothamnus viscidiflorus* var. *molestus* Blake, J. Wash. Acad. Sci. 30: 368. 1940. *Chrysothamnus molestus* (Blake) L. C. Anders., Madroño 17: 222. 1964.

9a. *Ericameria pulchella* (Gray) L. C. Anders., *comb. nov.* Basionym: *Linowsyris pulchella* A. Gray, Pl. Wright. [Smiths. Contr. Knowl.] 3(5): 96. 1856. *Bigelovia pulchella* (A. Gray) A. Gray, Proc. Amer. Acad. Arts 8: 643. 1873. *Chrysothamnus pulchellus* (A. Gray) E. Greene, Erythea 3: 107. 1895.

9b. *Ericameria pulchella* subsp. *baileyi* (Woot. & Standl.) L. C. Anders., *comb. nov.* Basionym: *Chrysothamnus baileyi* Woot. & Standl., Contr. U.S. Natl. Herb. 18: 181. 1913.

9c. *Ericameria pulchella* subsp. *pulchella* var. *elatii* (Standl.) L. C. Anders., *comb. nov.* Basionym: *Chrysothamnus elatii* Standl., Proc. Biol. Soc. Wash. 26: 118. 1913. This variety with uniformly pubescent leaves occurs sporadically in a few populations of the typically glabrous-leaved subspecies *pulchellus* and does not warrant a higher taxonomic status than this quadrinomial affords.

10. *Ericameria spathulata* (L. C. Anders.) L. C. Anders., *comb. nov.* Basionym: *Chrysothamnus spathulatus* L. C. Anders., Madroño 17: 226. 1964. *Chrysothamnus viscidiflorus* var. *ludens* Shinners, Sida 1: 374. 1964.

11. *Ericameria vaseyi* (A. Gray) L. C. Anders., *comb. nov.* Basionym: *Bigelovia vaseyi* A. Gray, Proc. Amer. Acad. Arts 12: 58. 1876. *Chrysothamnus vaseyi* (A. Gray) E. Greene, Erythea 3: 96. 1895. *Chrysothamnus bakeri* E. Greene, Pittonia 4: 152. 1900.

12a. *Ericameria viscidiflora* (Hook.) L. C. Anders., *comb. nov.* Basionym: *Crinitaria viscidiflora* Hook., Fl. Bor. Am. 2: 24. 1834. *Chrysothamnus viscidiflorus* (Hook.) Nutt. Trans. Amer. Philos. Soc. II, 7: 324. 1840. *Bigelovia douglasii* A. Gray, Proc. Amer. Acad. Arts 8: 645. 1873. *Chrysothamnus douglasii* (A. Gray) Clements & Clements, Rocky Mtn. Fls. 226. 1914. *Chrysothamnus pumilus* Nutt., Trans. Amer. Philos. Soc. II, 7: 323. 1840. *Linowsyris serrulata* Torr., Stansbury Rep. 1: 389. 1851. *Chrysothamnus serrulatus* (Torr.) Rydb., Bull. Torrey Bot. Club 33: 152. 1906. *Chrysothamnus tortifolius* E. Greene, Fl. Fran. 368. 1897. *Chrysothamnus leuocladus* E. Greene, Pittonia 5: 59. 1902. *Chrysothamnus stenolepis* Rydb., Bull. Torrey Bot. Club 37: 131. 1910.

12b. *Ericameria viscidiflora* subsp. *viscidiflora* var. *latifolia* (D. C. Eaton) L. C. Anders., *comb. nov.* Basionym: *Linowsyris viscidiflora* var. *latifolia*

D. C. Eaton, Bot. King Expl. 157. 1871. *Chrysothamnus latifolius* (D. C. Eaton) Rydb., Bull. Torrey Bot. Club 33: 152. 1906.

12c. *Ericameria viscidiflora* subsp. *viscidiflora* var. *stenophylla* (A. Gray) L. C. Anders., *comb. nov.* Basionym: *Bigelevia douglasii* var. *stenophylla* A. Gray, Proc. Amer. Acad. Arts 8: 646. 1873. *Chrysothamnus stenophyllus* (A. Gray) E. Greene, Erythea 3: 94. 1895. These quadrinomials (12b) and 12c) identify sporadic but rather distinctive morphotypes that occur in the northern regions of this subspecies (for conceptual distinction between subspecies and variety, see Anderson 1980b)

12d. *Ericameria viscidiflora* subsp. *axillaris* (Keck) L. C. Anders., *comb. nov.* Basionym: *Chrysothamnus axillaris* Keck, Aliso 4: 104. 1958.

12e. *Ericameria viscidiflora* subsp. *lanceolata* (Nutt.) L. C. Anders., *comb. nov.* Basionym: *Chrysothamnus lanceolatus* Nutt., Trans. Amer. Philos. Soc. II, 7: 324. 1840. *Chrysothamnus elegans* E. Greene, Erythea 3: 94. 1895. *Bigelevia douglasii* var. *spathulata* Jones, Proc. Calif. Acad. Sci. II 5: 690. 1895. *Chrysothamnus glaucus* A. Nels., Bull. Torrey Bot. Club 25: 377. 1898. *Chrysothamnus pumilus* var. *latus* A. Nels., Bot. Gaz. 54: 413. 1912.

12f. *Ericameria viscidiflora* subsp. *planifolia* (L. C. Anders.) L. C. Anders., *comb. nov.* Basionym: *Chrysothamnus viscidiflorus* subsp. *planifolius* L. C. Anders., Madroño 17: 223. 1964.

12g. *Ericameria viscidiflora* subsp. *puberula* (D. C. Eaton) L. C. Anders., *comb. nov.* Basionym: *Linosyris viscidiflora* var. *puberula* D. C. Eaton, Bot. King Expl. 158. 1871. *Chrysothamnus puberulus* (D. C. Eaton) E. Greene, Erythea 3: 93. 1895. *Chrysothamnus marianus* Rydb., Bull. Torrey Bot. Club 37: 131. 1910.

The following sections in *Ericameria* are proposed to accommodate these species transfers: *Ericameria* section *Chrysothamnus* (A. Gray) L. C. Anders., *comb. nov.* Basionym: *Bigelevia* section *Chrysothamnus* A. Gray., Proc. Amer. Acad. Arts 8: 641. 1873. This section includes *E. albida*, *E. filifolia*, *E. humilis*, *E. linifolia*, *E. spathulata*, and *E. viscidiflora*. *Ericameria* section *Gramini* (L. C. Anders.) L. C. Anders., *comb. nov.* Basionym: *Chrysothamnus* section *Gramini* L. C. Anders., Proc. Symp. Biology of *Artemisia* and *Chrysothamnus* 29. 1986. This section includes *E. eremobia* and *E. graminea*. *Ericameria* section *Pulchelli* (Hall & Clements) L. C. Anders., *comb. nov.* Basionym: *Chrysothamnus* section *Pulchelli* Hall & Clements, Carnegie Inst. Publ. 326: 175, 193. 1923. This section includes *E. depressa*, *E. molesta*, *E. pulchella*, and *E. vaseyi*.

Additionally, there is a fossil species, *Ericameria pulchelloides* (L. C. Anders.) L. C.

Anders., *comb. nov.* Basionym: *Chrysothamnus pulchelloides* L. C. Anders., Great Basin Naturalist 40: 351. 1980.

Nesom and Baird (1993) suggest the *Chrysothamnus* taxa that I have just transferred to *Ericameria* should be placed in a restructured genus to include elements of *Hesperodoria*, *Petradoria*, and *Vanelevea*. They conclude that chloroplast DNA data (Suh 1989) show *Petradoria* to be integrally related to the *Solidago* lineage and far removed from *Ericameria*. However, they note that neither Suh (1989) nor Morgan and Simpson (1992) sampled any taxa of *Chrysothamnus* sensu Nesom and Baird. These taxa need DNA profiles determined because they certainly do not make a morphologically compatible grouping with *Petradoria* or *Vanelevea*. For example, *Petradoria* (Anderson 1963) has radiate heads with disk flowers that lack stigmatic areas on the style branches and have abortive ovaries, and *Vanelevea* (Anderson and Weberg 1974) has large turbinate heads with many phyllaries, many flowers, and a tardily deciduous pappus of paleaceous awns—none of these conditions are found in *Chrysothamnus* sensu Nesom and Baird. The cohesiveness of *Chrysothamnus* sensu Anderson is further illustrated in that *C. spathulatus* twigs emit odor similar to that of *C. nauseosus* (Anderson 1964: 227).

Two alternate taxonomies are now available: one for *Chrysothamnus* as a genus (Anderson 1986) or as a component of *Ericameria* (Nesom and Baird 1993, and here); both are preferable to merging some elements of *Chrysothamnus* with *Petradoria* or *Vanelevea*.

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