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COMPLETION OF *ERICAMERIA* (ASTERACEAE: ASTEREAE), DIMINUTION OF *CHRYSOTHAMNUS*

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ABSTRACT

Two pairs of species previously treated as *Chrysothamnus* are transferred to *Ericameria*: *C. paniculatus* and *C. teretifolius* to sect. *Ericameria*, and *C. nauseosus* and *C. parryi* to sect. *Macronema*. New combinations are provided for *C. nauseosus* and *C. parryi* as well as numerous infraspecific taxa associated with each of them. Removal of these four species leaves *Chrysothamnus* a monophyletic group (but not holophyletic) inextricably related to the species centered around *Petradoria*.

KEY WORDS: *Ericameria*, *Chrysothamnus*, Astereae, Asteraceae

In the recent consolidation and overview of *Ericameria* Nutt., Nesom (1990) accepted the addition of sect. *Stenotopsis* (Urbatsch & Wussow 1979) to *Ericameria* and formally added two species groups previously treated by most previous taxonomists within *Haplopappus* DC.: sect. *Asiris* and sect. *Macronema* (see Table 1). *Ericameria*, when treated as a separate genus, has most commonly included only the species of sect. *Ericameria*, but Nesom (1990) presented a rationale for circumscribing the genus in an expanded sense. Brown & Keil (1993) have also taken the latter view for the California species.

Chrysothamnus Nutt. has often been noted as closely related to *Ericameria* (or to portions of it, see below). In attempts to clarify the definitions of these and peripheral genera, we have become convinced that *Chrysothamnus* as currently construed (Table 1; *e.g.*, Anderson 1986a, 1993; Welsh 1987) includes four species that should be placed in *Ericameria*. There are three species

TABLE 1. Composition of *Ericameria* and *Chrysothamnus*.

ERICAMERIA Nutt., Trans. Amer. Philos. Soc., ser. 2, 7:318. 1841.

Sect. *Ericameria* (TYPE: *E. ericoides* [Less.] Jepson; 11 others; add *Chrysothamnus* sect. *Punctati*).

Sect. *Stenotopsis* (Rydb.) Urbatsch & Wussow (TYPE: *E. linearifolia* [DC.] Urbatsch & Wussow).

Sect. *Asiris* (H.M. Hall) Nesom (TYPE: *E. nana* Nutt.; 4 others).

Sect. *Macronema* (Nutt.) Nesom (TYPE: *E. suffruticosa* [Nutt.] Nesom; 8 others; add *Chrysothamnus* sect. *Nauseosi*).

CHRYSOTHAMNUS Nutt., Trans. Amer. Philos. Soc., ser. 2, 7:323. 1841.

Sect. *Chrysothamnus* (TYPE: *C. viscidiflorus* [Hook.] Nutt.; 5 others).

Sect. *Pulchelli* H.M. Hall (TYPE: *C. pulchellus* [A. Gray] E. Greene; 3 others).

Sect. *Graminei* L. Anders. (TYPE: *C. gramineus* H.M. Hall; *C. eremobius* L. Anders.).

Sect. *Nauseosi* H.M. Hall (TYPE: *C. nauseosus* [Pallas *ex* Pursh] Britt.; *C. parryi* [A. Gray] E. Greene).

Sect. *Punctati* H.M. Hall (TYPE: *C. paniculatus* [A. Gray] H.M. Hall; *C. teretifolius* [Dur. & Hilg.] Hall & Clements.

groups within *Chrysothamnus* that form the core of the genus and that are closely related among themselves: sect. *Chrysothamnus*, sect. *Pulchelli*, and sect. *Graminei*. The extraneous species of *Chrysothamnus* are *C. paniculatus* (A. Gray) H.M. Hall and *C. teretifolius* (Dur. & Hilg.) Hall & Clements. (sect. *Punctati*) and *C. nauseosus* (Pallas *ex* Pursh) Britt. and *C. parryi* (A. Gray) E. Greene (sect. *Nauseosi*, actually an illegitimate name, preceded by *Bigelovia* sect. *Chrysothamnopsis* A. Gray 1884). The *Punctati* have long been recognized as similar to species of *Ericameria* and have formally designated taxonomic status in the latter genus (see below). Hall & Clements (1923, p. 172) observed that *C. teretifolius* and *C. paniculatus* are "sharply set off from the other members of the genus and do not intergrade into each other." According to Anderson (1966, p. 211), "The generic boundary [between *Chrysothamnus* and *Ericameria*] is further obscured in that *C. paniculatus* and *C. teretifolius* might be better placed in *Haplopappus* sect. *Ericameria*." The *Nauseosi* are abundant, widespread, variable, economically significant, and much-studied (*e.g.*, Weber *et al.* 1985), and they appear to lie at the heart of most informal concepts of *Chrysothamnus*. Gray (1873), Greene (1895), Hall & Clements (1923), Cronquist (1955), and others have observed the similarity between *C. parryi* and *E. discoidea* (Nutt.) Nesom (*Ericameria* sect. *Macronema*), and as noted by Anderson (1966, p. 211), "The closeness of *C. parryi* to [*E. discoidea*] exemplifies the rather arbitrary generic distinction at this point."

The studies of *Chrysothamnus* by Anderson have provided detailed information regarding cytology, anatomy, and morphological variation, and he has provided distinctions among the five sections he accepts for *Chrysothamnus* (1986a). The acknowledged problems of generic delimitation persist, however, and except for a number of new taxa and the recent incorporation (or reincorporation) of *Petradoria discoidea* L. Anders. (= *C. gramineus* H.M. Hall) into *Chrysothamnus* (Anderson 1983, 1986a), Anderson and other taxonomists have essentially followed the generic concept for *Chrysothamnus* early established by E. Greene, A. Nelson, P.A. Rydberg, and solidified by H.M. Hall and Hall & Clements.

The recently described *Chrysothamnus eremobius* L. Anders. (Anderson 1983) was added to *Chrysothamnus* along with *C. gramineus* as sect. *Graminei*, and the discussion of their relationship to the rest of the genus centered on their similarity to species of both sect. *Chrysothamnus* and sect. *Pulchelli*. Anderson has not provided, however, a hypothesis regarding the nature of the relationship of sect. *Punctati* and sect. *Nauseosi* to other *Chrysothamnus*. He has noted that sect. *Nauseosi* appears in some respects to be primitive relative to the rest of the genus (Anderson 1966, 1970a) and has provided listings of species by sections that are in a "phylogenetic sequence (assumed from gross morphology)," placing the *Nauseosi* first and the *Punctati* last (Anderson 1970b). The phylogenetic scheme formulated by Hall & Clements (1923), which is more explicit in its depiction of cladistic relationships and

more detailed in its justification, placed the *Punctati* nearest the divergence point of *Chrysothamnus* from *Haplopappus*.

In the recent consolidation of *Ericameria* (Nesom 1990), its close relationship to *Chrysothamnus* (at that time accepted as a genus sensu Hall and Anderson) was affirmed and parallel trends of variation were noted to occur within the two groups. The present recognition of the biphyletic nature of *Chrysothamnus* clarifies, to a degree, the nature of the observed close relationship between *Ericameria* and *Chrysothamnus* as well as a significant portion of the parallelism between them.

HYBRIDIZATION

There are three cases of interspecific hybridization reported within *Chrysothamnus* sensu Anderson. Two of these, which are well-documented, have been between *C. nauseosus* and *C. parryi* (Anderson 1966, 1984). The only other reported interspecific hybrid was hypothesized to be between *C. nauseosus* and *C. albidus* (Jones *ex* A. Gray) E. Greene (Anderson 1973). This putative hybrid is known from two specimens collected in Ash Meadows, Nye Co., Nevada; the first collection was made by Beatley (*11894*), the second by Anderson & Beatley (*Anderson 9635*) in a search to relocate the plant originally found by Beatley. According to Anderson (1973, p. 176), "The low level of variation in the interspecific hybrid collections (*A 9635* and *B 11894*) would be expected if they represent the same plant collected in different years." This is also suggested by the location of only a single individual of the hybrid in the search by Anderson & Beatley. The distinctly low pollen viability reported by Anderson (1973) for the plants (or plant) represented by these specimens supports the hypothesis that they are hybrids, but the nature of their parentage is not clear. We have examined *Beatley 11894* (KSC).

Anderson's attention was drawn to this plant because (p. 175) it "looked like an 'anemic' *C. nauseosus* near ssp. *hololeucus*. Its foliage and pale yellow flowers suggested it was a hybrid with *C. albidus* parentage." *Chrysothamnus albidus* and *C. nauseosus* both occur in Ash Meadows. In contrast to Anderson, however, we find the leaves, involucral bracts, and corollas of the plant in question to be characteristic of *C. nauseosus* rather than intermediate between it and *C. albidus*, and we identify it as *C. nauseosus*, finding no strong reason to implicate *C. albidus* in its parentage. The stems and leaves produce a "pannose" indument of short, crinkly hairs. The leaves are narrow and flattened, with the midvein clearly visible, and without any distinctly visible glands or punctae. The involucral bracts are hairy, acute at the apices, with a raised and often orange-resinous midvein, this particularly resinous near the bract apex where it often is swollen and gland-like, and the bracts are strongly aligned in vertical files. The corolla walls are thick and blotchy-resinous, with resin ducts

associated with the veins of the lobes, the lobes are relatively short (sinuses cut 1/2-3/8 to the base of the throat) and spreading but not at all reflexing-coiling, and the pale color of the corolla noted by Anderson is not distinctive in the herbarium specimen. None of these features are characteristic of *C. albidus*, but all are characteristic of *C. nauseosus*.

Few aspects of the achene morphology of this putative hybrid were discussed by Anderson, but the achenes, too, suggest that *Chrysothamnus albidus* was not involved in the parentage. The achenes of *C. albidus* are linear, somewhat terete, and consistently produce 10, slightly raised nerves; the achene surface is sparsely strigose near the base but the duplex hairs on the upper third of the achene are absent or reduced in density, replaced by a dense vestiture of glandular hairs. The achenes of the hybrid and of *C. nauseosus* subsp. *mohavensis* (E. Greene) Hall & Clements are narrowly obovate, slightly compressed, and produce 5-7 nerves; they are densely strigose from base to apex and essentially eglandular, although a few glands may be produced among the other hairs near the apex.

According to Anderson (1973), the population of *Chrysothamnus nauseosus* in Ash Meadows is itself of hybrid origin between subsp. *hololeucus* (A. Gray) Hall & Clements and subsp. *mohavensis* (sensu Anderson). The plant discussed here (*Beatley 11894*) is most similar to subsp. *mohavensis*, particularly in its involucral bracts in vertical files. *Chrysothamnus albidus* is a peculiar species within *Chrysothamnus* and similar to some species of *Ericameria* in several striking features, particularly its terete, punctate leaves and its style branches with long, hispid appendages. Nevertheless, it appears to be a member of *Chrysothamnus* rather than *Ericameria* (Baird in prep.). There are no other species of *Chrysothamnus* or *Ericameria* in the same area as the hybrid and its putative parents (Beatley 1971, 1977), but numerous species besides the proposed parental taxa are found in the same general area of southern Nye County (Beatley 1976): eight other species of *Ericameria*, including three other varieties of *E. nauseosus*; and two other species of *Chrysothamnus*, including three varieties of *C. viscidiflorus* (Hook.) Nutt. Ash Meadows itself is a spring-fed lowland area that harbors many endemic species (Beatley 1976).

Notwithstanding our evaluation of *Beatley 11894* from Ash Meadows, Anderson (1970a) has noted the occurrence of another plant hypothesized to be of hybrid origin between *Chrysothamnus nauseosus* and *C. albidus*. It was obtained from achenes produced by the latter and showed characteristics interpreted by Anderson as pointing to parentage by *C. nauseosus*. Even if these specimens should ultimately prove to represent hybrids between *Chrysothamnus albidus* and *C. nauseosus*, it would not change our interpretation of phylogeny or the proposal for associated taxonomic changes. It would suggest, however, that the relationship between the genera *Ericameria* and *Chrysothamnus*, indicated to be distant by cpDNA analysis, should be re-evaluated, or at least the position of *C. albidus* needs to be re-evaluated.

There are also two hybrids reported between *Chrysothamnus nauseosus* and *Ericameria*. One is between *C. nauseosus* subsp. *albicaulis* (Nutt.) Hall & Clements and *Ericameria* (sect. *Macronema*) *discoidea* (Anderson & Reveal 1966). The other is between *C. nauseosus* subsp. *hololeucus* and *Ericameria* (sect. *Ericameria*) *cuneata* (A. Gray) McClatchie (Anderson 1986a, 1993). Thus, the genetic similarity between *C. nauseosus* and *C. parryi* inferred from their compatibility in hybridization is matched by that between *C. nauseosus* and two separate species of *Ericameria*. In the taxonomic interpretation offered in the present paper, these latter crosses are regarded as hybrids between congeneric species (of *Ericameria*), and we now find the only recorded instances of putative interspecific hybridization involving species of *Chrysothamnus* (sensu Baird in prep.) are those with *C. albidus* as one of the parents.

DNA, LATEX, PHENOLICS, AND OTHER COMPOUNDS

While preliminary and restricted in scope, analyses of restriction site variation in chloroplast DNA are in agreement with our apportionment of species between *Ericameria* and *Chrysothamnus* (Suh 1989; Morgan 1990; Morgan & Simpson 1992). In the analysis of Morgan & Simpson, *E. ericoides* (Less.) Jepson, *E. discoidea*, and *C. nauseosus* are strongly indicated (100%) as a monophyletic group (=*Ericameria*, in the present sense), with the latter two taxa also linked (100%) as sister species in a clade coordinate with *E. ericoides* (their Fig. 1). Suh's data show *Petradoria* (represented by *P. pumila* [Nutt.] E. Greene, included in *Chrysothamnus* sensu Baird and the present study) to be integrally related to the *Solidago* lineage, but neither Suh nor Morgan sampled any other of the species we here consider to be among those of typical *Chrysothamnus*. The data of both Morgan & Simpson and Suh place *Ericameria* in a basal and completely peripheral position relative to the *Solidago* lineage as well as other primarily North American groups (see Nesom *et al.* 1990 for a summary).

In a survey of latex production in species of Asteraceae, Hall & Goodspeed (1919) sampled a total of 20 species of *Ericameria* and *Chrysothamnus*. Among these, latex was found in both species of sect. *Punctati* and in *C. nauseosus* but not in *C. parryi*. If these four are considered as species of *Ericameria*, the results of the survey are as follows: latex found in nine species of sect. *Ericameria*, two species of sect. *Asiris*, one species of sect. *Macronema*, one species of sect. *Stenotopsis*, and in one species of *Chrysothamnus*; latex not found in 1 species of sect. *Ericameria*, two species of sect. *Macronema*, and three species of *Chrysothamnus*. In summary, latex was found in thirteen species of *Ericameria*, representing all four sections of the genus. Only one species of *Chrysothamnus* (*C. linifolius* E. Greene) produced latex, and the

trace amounts found there were by far the lowest of any species sampled, except for *E. cooperi* (A. Gray) H.M. Hall, which had about the same amount. More species within *Chrysothamnus* would have to be sampled in order to make a definitive statement, but the information at hand suggests that latex is produced in *Ericameria* but that it is absent or produced only rarely and in minute quantities in *Chrysothamnus.*

In a study of phenolic compounds, McArthur *et al.* (1978) compared taxa of *Chrysothamnus* and species of a few other genera, based on percentage similarity values calculated from the number of spots in common on chromatograms. *Chrysothamnus nauseosus* and *C. parryi* clustered separately from taxa of *Chrysothamnus* in the more restricted sense proposed in the present paper (i.e., *C. greenei* (A. Gray) E. Greene, *C. linifolius*, and *C. viscidiflorus*) with one exception: *C. depressus* Nutt. is weakly associated with the *Nauseosi.* Also as predicted in the present study, *Ericameria bloomeri* (A. Gray) Macbr. of sect. *Macronema* was found to be most similar to *C. parryi.* However, none of the compounds were identified, species of critical importance in the interpretation of the data were not included in the sampling, and the statistical comparisons among the taxa cannot be taken as strong indicators of phylogenetic relationships. There are a few additional chemical studies of species of *Chrysothamnus* and *Ericameria* but none with sufficient comparative data to allow phylogenetic inferences.

Limited support for the relationships hypothesized in the present investigation is found in a study of cyclohexane extractions analyzed by gas chromatography-mass spectrometry (Hegerhorst *et al.* 1987). In that study, *Chrysothamnus nauseosus* (six subspecies) proved to be most similar to *C. teretifolius*, and *C. viscidiflorus* (two subspecies) proved to be most similar to *C. linifolius.*

MORPHOLOGY

Chrysothamnus parryi and *Ericameria discoidea* are similar in their densely pannose stems and heads subtended by foliaceous bracts grading into the outer phyllaries. Some forms of *C. nauseosus* also produce stems with a tendency to become pannose, but the heads lack subtending, foliaceous bracts, and all the phyllaries are somewhat indurated, usually lacking a foliaceous apex. In the latter feature, *Chrysothamnus nauseosus* is more like species of sect. *Asiris* than those of sect. *Macronema*, and the distinction between these two groups may prove to be arbitrary.

The position of *Chrysothamnus teretifolius* within *Ericameria* sect. *Ericameria* is clear. There is a strong tendency within this section for the orange-resiniferous ducts that are almost always distinctly associated with the phyllary midvein to expand near the apex of the phyllary. In some species, this results in the formation of an apical resin pocket identical to that of *C. teretifolius.* Among these species is *E. pachylepis* (H.M. Hall) Urbatsch, which not

only is similar in habit, capitulescence, and phyllary morphology to *C. teretifolius*, but the phyllaries of both of these species have a strong tendency to be arranged in vertical files. In *C. paniculatus*, the resin ducts of the phyllary midvein are not strongly evident and not distally expanded, but in characters of the leaves, flowers, and fruits, it appears to belong in sect. *Ericameria*.

It is remarkable that *Haplopappus* sensu lato, including a large part of *Ericameria*, has been maintained while *Chrysothamnus* has been treated as a separate genus (*e.g.*, Cronquist, Anderson, Welch). The force of recent tradition has provided the primary impetus for this, as observed much earlier by Hall & Clements (1923, p. 159): *Chrysothamnus* and *Haplopappus* are "so close at some points that, if it were not for the almost universal recognition of [*Chrysothamnus*] during the last twenty-five years under one name or another, their complete union into one genus might be seriously considered." Semple *et al.* (1989) also have suggested that any separation of *Ericameria* and *Chrysothamnus* is arbitrary and that the two genera should be combined. *Chrysothamnus* has been held apart primarily because of the importance attributed to vertical alignment of the involucral bracts. According to Hall & Clements (1923, p. 159): "*Chrysothamnus* differs from all species of *Haplopappus* in its consistently narrower heads and, what is of greater importance, a decided tendency of the bracts of the involucre to fall into vertical rows. The difference between this arrangement of the bracts and the regularly imbricate arrangement encountered in the latter genus is perhaps comparable to the difference between opposite and alternate leaves, but the bracts are the modified leaves of a highly specialized structure, the involucre, and hence any variation in their relative positions is of profound significance."

It now appears that vertical alignment of involucral bracts has arisen independently in some species of both *Ericameria* and *Chrysothamnus*. Such an arrangement is uncommon in the Asteraceae, but it occurs in other distantly related genera with narrow, elongated involucres (e.g., *Llerasia* Triana and *Vernoniopsis* Humbert). Further, as noted in floristic keys by numerous authors, the vertical alignment of bracts even within taxa of *Chrysothamnus* itself is often "obscure" or lacking. Bracts that are unequivocally vertically aligned occur primarily in *Chrysothamnus* sect. *Pulchelli*, some but not all varieties of *C. nauseosus*, and the two species of sect. *Punctati*. The case for the common ancestry of the species of sect. *Macronema*, *C. parryi*, and *C. nauseosus* is so strong that the vertical alignment of bracts in the latter must be interpreted as a parallelism with those of *Chrysothamnus* sect. *Pulchelli*. The same is true for the species of sect. *Punctati*.

In a study of the embryology of *Chrysothamnus* and putative relatives (Anderson 1970b), one of the few features in which significant variation was found to occur, the number of antipodals per embryo sac, supported a hypothesis of close relationship between sect. *Punctati* and sect. *Ericameria* and between sect. *Nauseosi* and sect. *Macronema*.

Not only do the *Nauseosi* and *Punctati* show strong similarity to groups of *Ericameria*, but their dissimilarity to *Chrysothamnus* is evident. Features of *Chrysothamnus* that distinguish it from *Ericameria* are the following: (1) leaves with a strong tendency to be 3-nerved, the nerves variable from relatively obscure to distinctly raised, (2) leaf margins ciliate-scabrous with short, stiff hairs different from those elsewhere on the plant, (3) disc corollas more or less abruptly broadened from the tube into the throat, with long, lanceolate lobes that are loosely recurving or coiling, (4) collecting appendages (of disc style branches) with sweeping hairs merely papillate toward the appendage apex or over most of the distal portion of the appendage, (5) involucral bracts in vertical files (with the caveat noted above), and (6) achenes glandular near the apex, otherwise glabrous or invested with relatively short, duplex hairs, and with thin, non-resinous nerves. The features of disc corolla and style appendage morphology in *Chrysothamnus* are also characteristic of the *Solidago* lineage, of which *Chrysothamnus* is hypothesized to be an advanced member (see below). In contrast, in *Ericameria* (1) the leaves are 1-nerved, (2) never with scabrous margins, (3) the disc corollas are tubular with lobes usually short and erect to spreading, (4) the style collecting appendages are usually linear-filiform with long sweeping hairs of nearly equal length from the base of the appendage to the apex, (5) the involucral bracts are imbricated but usually not in vertical files (exceptions noted above), and (6) the achenes are eglandular, usually with long, stiff, duplex hairs, the achenial nerves often prominently resinous.

In summary, we place *Chrysothamnus* sects. *Nauseosi* and *Punctati* within *Ericameria* (see Table 1) based on their dissimilarity to *Chrysothamnus* and their similarity to *Ericameria*, as noted by commentaries in earlier literature and corroborated by our observations, and by comparative embryology, latex production, DNA variation, and various other chemical studies. Together, these suggest that similarities in phyllary arrangement have been unduly weighted in the definition of *Chrysothamnus*. The *Punctati* and *Nauseosi* are absorbed into larger, already established groups of *Ericameria*, where they add considerably less heterogeneity to *Ericameria* than the recent annexation of *E. linearifolia* (DC.) Urbatsch & Wussow (Urbatsch & Wussow 1979), although the inclusion of the latter also appears to be justifiable.

The transfer of these species to *Ericameria* from *Chrysothamnus* significantly reduces the degree of resemblance between the two genera. There remain, however, notable similarities between the two groups in the morphology of the leaves, phyllaries, disc corollas, and style appendages. For example, strongly punctate-glandular leaves similar to those of sect. *Ericameria* are characteristic of *C. albidus*. In *C. albidus* and some forms of *C. pulchellus*, the style appendages become elongated, and in other species, the disc corolla lobes are short and merely spreading, both features approaching the typical morphology of *Ericameria*. Our interpretation of the evolutionary relationship

between the two taxa is influenced by the recent studies of variation in cpDNA restriction sites, which strongly support an hypothesis of relatively distant relationship between them. A survey of phenolic compounds in *Haplopappus* segregates (Clark *et al.* 1980) purported to provide support for considering *Stenotus* a close relative of *Ericameria*, but their conclusions regarding phylogeny were problematic, because the similarities between these groups were hypothesized to be primitive, the survey of taxa was limited, and the study was based on *a priori* hypotheses of relationship. Even if the morphological similarities between *Ericameria* and *Chrysothamnus* were interpreted as evolutionarily parallel rather than convergent, our observations convince us that two phylads are involved and that the groupings recognized here, with corresponding proposals for taxonomic changes, are a necessary step forward in providing a classification concordant with actual evolutionary patterns.

After the transfer of these four species (sects. *Nauseosi* and *Punctati*) to *Ericameria* and the resultant completion of that genus, a holophyletic *Chrysothamnus* is being restructured by Baird (in prep.), who proposes to expand it by including several other species that have been variously placed primarily in the small genera *Hesperodoria* E. Greene, *Petradoria* E. Greene, and *Vanclevea* E. Greene. This accounts for similarities observed by Hall and by Anderson between *Petradoria* and *Chrysothamnus*, which have been verified and extended by studies of Baird, who finds them to be indicative of recent common ancestry. As so defined, *Chrysothamnus* forms a major part of the subtribe Solidagininae (*sensu* Nesom 1993a) in the western United States and is most closely related to the genus *Stenotus* Nutt.

Zhang & Bremer (1993) placed *Ericameria* within their Solidagininae, but genera of that subtribe (*sensu* Nesom 1993a) appear to be unequivocally eliminated as close relatives of *Ericameria* on the basis of molecular studies (Suh 1989; Morgan & Simpson 1992). Nesom (1993b) has hypothesized that *Ericameria* is a member of the Hinterhuberinae, where it is possibly most closely related to the Argentinian-Chilean genus *Chiliophyllum* Phil. Except for *Ericameria* and the recently described Mexican genus *Aztecaster* Nesom, the Hinterhuberinae is distributed exclusively in the Southern Hemisphere, and only *Pteronia* L. of the Solidagininae sensu Zhang & Bremer is included within this subtribe. More detailed comments regarding the definition of the Hinterhuberinae and the placement of *Ericameria* are provided in a separate paper (Nesom 1993b).

TAXONOMY

As concepts of infraspecific taxa within the highly variable species of *Chrysothamnus* were first formulated or at least first codified (Hall 1919), the basic taxonomic elements were treated as varieties. They were later renamed as

subspecies by Hall & Clements (1923) and have been maintained at that rank by Keck (1960) and in all of the studies of Anderson (*e.g.*, 1986a, 1993). In other floristic treatments, they have been treated as varieties (*e.g.*, Cronquist 1955; Welsh 1987), and we follow the latter course, especially since this parallels the treatment provided for *Ericameria* (Nesom 1990). Anderson (1980) has noted that additional variants can be recognized within some of the subspecies of *Chrysothamnus* (including those of *C. nauseosus*) and that he intends to recognize these at the varietal level. In contrast, we employ the category of subspecies to provide larger groupings of varieties, but it seems likely that future studies may arrive at taxonomic assessments of the variation patterns different from any possibilities presently accounted for, especially in view of the complex patterns of infraspecific variation observed by Anderson (1986b). We have provided taxa that are reasonably documented as interspecific hybrids with a specific epithet; their treatment in previous literature has been inconsistent, with names applied at either infraspecific or specific rank.

For each name that follows, the basionym is provided, as well as the species or subspecies name as treated by Anderson under *Chrysothamnus* to allow comparison of the nomenclature.

Ericameria teretifolia (Dur. & Hilg.) Jepson, *Man. Fl. Pl. Calif.* 1024. 1925. BASIONYM: *Linosyris teretifolius* Dur. & Hilg., J. Acad. Philadelphia, ser. 2, 3:41. 1855. *Chrysothamnus teretifolius* (Dur. & Hilg.) H.M. Hall, Univ. Calif. Publ. Bot. 3:57. 1907.

Ericameria paniculata (A. Gray) Rydb., *Fl. Rocky Mts.* 853. 1917. BASIONYM: *Bigelovia paniculata* A. Gray, Proc. Amer. Acad. Arts 8:644. 1873. *Chrysothamnus paniculatus* (A. Gray) H.M. Hall, Univ. Calif. Publ. Bot. 3:58. 1907.

Ericameria nauseosa (Pallas *ex* Pursh) Nesom & Baird, *comb. nov.* BASIONYM: *Chrysocoma nauseosa* Pallas *ex* Pursh, *Fl. Amer. Sept.* 2:517. 1814. *Chrysothamnus nauseosus* (Pallas *ex* Pursh) Britt. *in* Britt. & Brown, *Illustr. Fl.* 3:326. 1898.

We divide the varieties of this species into two subspecies, two groups previously recognized and informally referred to as the "gray forms" and the "green forms" (Hall 1919). Anderson (1986b) has noted that the distinctions are often blurred between these, but his own data suggest that the division may a useful one, at least pragmatically. Various close interrelationships can be recognized among a number of the varieties of *Ericameria nauseosa*, and it seems likely that the taxonomic partitions may be differently applied as a better understanding of the variation patterns is reached.

Ericameria nauseosa (Pallas *ex* Pursh) Nesom & Baird subsp. **nauseosa**. Including the following varieties (the gray forms): *bernardina, bigelovii, glabrata, glareosa, hololeuca, iridis, latisquamea, nana, nauseosa, psilocarpa, salicifolia, speciosa, texensis, washoensis.*

Ericameria nauseosa (Pallas *ex* Pursh) Nesom & Baird subsp. **consimilis** (E. Greene) Nesom & Baird, *comb. nov.* BASIONYM: *Chrysothamnus consimilis* E. Greene, Pittonia 5:60. 1902. *Chrysothamnus nauseosus* (Pallas *ex* Pursh) Britt. subsp. *consimilis* (E. Greene) Hall & Clements, Carnegie Inst. Washington Publ. 326:215. 1923. Including the following varieties (the green forms): *arenaria, arta, ceruminosa, juncea, leiosperma, mohavensis, nitida, turbinata.*

1. **Ericameria nauseosa** (Pallas *ex* Pursh) Nesom & Baird var. **arta** (A. Nels.) Nesom & Baird, *comb. nov.* BASIONYM: *Chrysothamnus oreophilus* A. Nels. var. *artus* A. Nelson, Bot. Gaz. 28:375. 1899.

   Chrysothamnus consimilis E. Greene, Pittonia 5:60. 1902. *Chrysothamnus nauseosus* (Pallas *ex* Pursh) Britt. subsp. *consimilis* (E. Greene) Hall & Clements, Carnegie Inst. Washington Publ. 326:215. 1923.

2. **Ericameria nauseosa** (Pallas *ex* Pursh) Nesom & Baird var. **arenaria** (L. Anders.) Nesom & Baird, *comb. nov.* BASIONYM: *Chrysothamnus nauseosus* (Pallas *ex* Pursh) Britt. subsp. *arenarius* L. Anders., Phytologia 38:311. 1978.

3. **Ericameria nauseosa** (Pallas *ex* Pursh) Nesom & Baird var. **bernardina** (Hall) Nesom & Baird, *comb. nov.* BASIONYM: *Chrysothamnus nauseosus* (Pallas *ex* Pursh) Britt. var. *bernardinus* Hall, Univ. Calif. Publ. Bot. 7:171. 1919. *Chrysothamnus nauseosus* (Pallas *ex* Pursh) Britt. subsp. *bernardinus* (Hall) Hall & Clements, Carnegie Inst. Washington Publ. 326:214. 1923.

4. **Ericameria nauseosa** (Pallas *ex* Pursh) Nesom & Baird var. **bigelovii** (A. Gray) Nesom & Baird, *comb. nov.* BASIONYM: *Linosyris bigelovii* A. Gray, *Pacif. R.R. Rep.* 4(4):98. 1857. *Chrysothamnus nauseosus* (Pallas *ex* Pursh) Britt. subsp. *bigelovii* (A. Gray) Hall & Clements, Carnegie Inst. Washington Publ. 326:217. 1923.

5. **Ericameria nauseosa** (Pallas *ex* Pursh) Nesom & Baird var. **ceruminosa** (Dur. & Hilg.) Nesom & Baird, *comb. nov.* BASIONYM: *Linosyris ceruminosus* Dur. & Hilg., J. Acad. Philadelphia, ser. 2, 3:40. 1855. *Chrysothamnus nauseosus* (Pallas *ex* Pursh) Britt.

subsp. *ceruminosus* (Dur. & Hilg.) Hall & Clements, Carnegie Inst. Washington Publ. 326:216. 1923.

6. **Ericameria nauseosa** (Pallas *ex* Pursh) Nesom & Baird var. **glabrata** (A. Gray) Nesom & Baird, *comb. nov.* BASIONYM: *Bigelovia graveolens* Nutt. var. *glabrata* A. Gray, Proc. Amer. Acad. Arts 8:645. 1873.

   Chrysothamnus nauseosus (Pallas *ex* Pursh) Britt. subsp. *graveolens* (Nutt.) Hall & Clements, Carnegie Inst. Washington Publ. 326:214. 1923.

7. **Ericameria nauseosa** (Pallas *ex* Pursh) Nesom & Baird var. **glareosa** (M.E. Jones) Nesom & Baird, *comb. nov.* BASIONYM: *Bigelovia glareosa* M.E. Jones, Zoe 2:247. 1891. *Chrysothamnus nauseosus* (Pallas *ex* Pursh) Britt. subsp. *glareosa* (M.E. Jones) Hall & Clements, Carnegie Inst. Washington Publ. 326:217. 1923.

8. **Ericameria nauseosa** (Pallas *ex* Pursh) Nesom & Baird var. **hololeuca** (A. Gray) Nesom & Baird, *comb. nov.* BASIONYM: *Bigelovia graveolens* Nutt. var. *hololeuca* A. Gray, Proc. Amer. Acad. Arts 8:645. 1873. *Chrysothamnus nauseosus* (Pallas *ex* Pursh) Britt. subsp. *hololeucus* (A. Gray) Hall & Clements, Carnegie Inst. Washington Publ. 326:211. 1923.

   Chrysothamnus speciosus Nutt. var. *gnaphalodes* E. Greene, Erythea 3:110. 1895.

9. **Ericameria nauseosa** (Pallas *ex* Pursh) Nesom & Baird var. **iridis** (L. Anders.) Nesom & Baird, *comb. nov.* BASIONYM: *Chrysothamnus nauseosus* (Pallas *ex* Pursh) Britt. subsp. *iridis* L. Anders., Great Basin Naturalist 41:311. 1981.

10. **Ericameria nauseosa** (Pallas *ex* Pursh) Nesom & Baird var. **juncea** (E. Greene) Nesom & Baird, *comb. nov.* BASIONYM: *Bigelovia juncea* E. Greene, Bot. Gaz. 6:184. 1881. *Chrysothamnus nauseosus* (Pallas *ex* Pursh) Britt. subsp. *junceus* (E. Greene) Hall & Clements, Carnegie Inst. Washington Publ. 326:216. 1923.

11. **Ericameria nauseosa** (Pallas *ex* Pursh) Nesom & Baird var. **latisquamea** (A. Gray) Nesom & Baird, *comb. nov.* BASIONYM: *Bigelovia graveolens* Nutt. var. *latisquameus* A. Gray, Proc. Amer. Acad. Arts 8:645. 1873. *Chrysothamnus nauseosus* (Pallas *ex* Pursh) Britt. subsp. *latisquameus* (A. Gray) Hall & Clements, Carnegie Inst. Washington Publ. 326:212. 1923.

12. **Ericameria nauseosa** (Pallas *ex* Pursh) Nesom & Baird var. **leiosperma** (A. Gray) Nesom & Baird, *comb. nov.* BASIONYM: *Bigelovia leiosperma* A. Gray, *Syn. Fl. N. Amer.* 1(2):139. 1884.

Chrysothamnus nauseosus (Pallas *ex* Pursh) Britt. subsp. *leiospermus* (A. Gray) Hall & Clements, Carnegie Inst. Washington Publ. 326:221. 1923.

13. **Ericameria nauseosa** (Pallas *ex* Pursh) Nesom & Baird var. **mohavensis** (E. Greene) Nesom & Baird, *comb. nov.* BASIONYM: *Bigelovia mohavensis* E. Greene *in* A. Gray, *Syn. Fl. N. Amer.* 1(2):138. 1884. *Chrysothamnus nauseosus* (Pallas *ex* Pursh) Britt. subsp. *mohavensis* (E. Greene) Hall & Clements, Carnegie Inst. Washington Publ. 326:216. 1923.

14. **Ericameria nauseosa** (Pallas *ex* Pursh) Nesom & Baird var. **nana** (Cronq.) Nesom & Baird, *comb. nov.* BASIONYM: *Chrysothamnus nauseosus* (Pallas *ex* Pursh) Britt. var. *nanus* Cronq., *Vasc. Pl. Pacific Northw.* 5:129. 1955. *Chrysothamnus nauseosus* (Pallas *ex* Pursh) Britt. subsp. *nanus* (Cronq.) Keck, Aliso 4:104. 1958.

15. **Ericameria nauseosa** (Pallas *ex* Pursh) Nesom & Baird var. **nauseosa** BASIONYM: *Chrysothamnus nauseosus* (Pallas *ex* Pursh) Britt. subsp. *nauseosus*

16. **Ericameria nauseosa** (Pallas *ex* Pursh) Nesom & Baird var. **nitida** (L. Anders.) Nesom & Baird, *comb. nov.* BASIONYM: *Chrysothamnus nauseosus* (Pallas *ex* Pursh) Britt. subsp. *nitidus* L. Anders., Phytologia 38:313. 1978.

17. **Ericameria nauseosa** (Pallas *ex* Pursh) Nesom & Baird var. **psilocarpa** (Blake) Nesom & Baird, *comb. nov.* BASIONYM: *Chrysothamnus nauseosus* (Pallas *ex* Pursh) Britt. var. *psilocarpus* Blake, J. Washington Acad. Sci. 27:376. 1937. *Chrysothamnus nauseosus* (Pallas *ex* Pursh) Britt. subsp. *psilocarpus* (Blake) L. Anders., Sida 3:466. 1970.

18. **Ericameria nauseosa** (Pallas *ex* Pursh) Nesom & Baird var. **salicifolia** (Rydb.) Nesom & Baird, *comb. nov.* BASIONYM: *Chrysothamnus salicifolius* Rydb., Bull. Torrey Bot. Club 37:130. 1910. *Chrysothamnus nauseosus* (Pallas *ex* Pursh) Britt. subsp. *salicifolius* (Rydb.) Hall & Clements, Carnegie Inst. Washington Publ. 326:213. 1923.

19. **Ericameria nauseosa** (Pallas *ex* Pursh) Nesom & Baird var. **speciosa** (Nutt.) Nesom & Baird, *comb. nov.* BASIONYM: *Chrysothamnus speciosus* Nutt. [var. *speciosus*], Trans. Amer. Philos. Soc., ser. 2, 7:323. 1840.

    Chrysothamnus speciosus Nutt. var. *albicaulis* Nutt., Trans. Amer. Philos. Soc., ser. 2, 7:324. 1840. *Chrysothamnus nauseosus* (Pallas *ex* Pursh) Britt. subsp. *albicaulis* (Nutt.) Hall & Clements, Carnegie Inst. Washington Publ. 326:212. 1923.

20. **Ericameria nauseosa** (Pallas *ex* Pursh) Nesom & Baird var. **texensis** (L. Anders.) Nesom & Baird, *comb. nov.* BASIONYM: *Chrysothamnus nauseosus* (Pallas *ex* Pursh) Britt. subsp. *texensis* L. Anders., Southw. Naturalist 25:197. 1980.

21. **Ericameria nauseosa** (Pallas *ex* Pursh) Nesom & Baird var. **turbinata** (M.E. Jones) Nesom & Baird, *comb. nov.* BASIONYM: *Bigelovia turbinata* M.E. Jones, Proc. Calif. Acad. Sci., ser. 2, 5:691. 1895. *Chrysothamnus nauseosus* (Pallas *ex* Pursh) Britt. subsp. *turbinatus* (M.E. Jones) Hall & Clements, Carnegie Inst. Washington Publ. 326:217. 1923.

22. **Ericameria nauseosa** (Pallas *ex* Pursh) Nesom & Baird var. **washoensis** (L. Anders.) Nesom & Baird, *comb. nov.* BASIONYM: *Chrysothamnus nauseosus* (Pallas *ex* Pursh) Britt. subsp. *washoensis* L. Anders., Phytologia 38:315. 1978.

Ericameria parryi (A. Gray) Nesom & Baird, *comb. nov.* BASIONYM: *Linosyris parryi* A. Gray, Proc. Acad. Nat. Sci. Philadelphia 1863:66. 1863. *Chrysothamnus parryi* (A. Gray) E. Greene, Erythea 3:113. 1895.

1. **Ericameria parryi** (A. Gray) Nesom & Baird var. **affinis** (A. Nels.) Nesom & Baird, *comb. nov.* BASIONYM: *Chrysothamnus affinis* A. Nels., Bot. Gaz. 28:374. 1899. *Chrysothamnus parryi* (A. Gray) E. Greene subsp. *affinis* (A. Nels.) L. Anders., Sida 3:466. 1970.

2. **Ericameria parryi** (A. Gray) Nesom & Baird var. **aspra** (E. Greene) Nesom & Baird, *comb. nov.* BASIONYM: *Chrysothamnus asper* E. Greene, Leafl. Bot. Observ. 1:80. 1904. *Chrysothamnus parryi* (A. Gray) E. Greene subsp. *asper* (E. Greene) Hall & Clements, Carnegie Inst. Washington Publ. 326:200. 1923.

3. **Ericameria parryi** (A. Gray) Nesom & Baird var. **attenuata** (M.E. Jones) Nesom & Baird, *comb. nov.* BASIONYM: *Bigelovia howardii* (Parry *ex* A. Gray) A. Gray var. *attenuata* M.E. Jones, Proc. Calif. Acad., ser. 2, 5:691. 1895. *Chrysothamnus parryi* (A. Gray) E. Greene subsp. *attenuatus* (M.E. Jones) Hall & Clements, Carnegie Inst. Washington Publ. 326:201. 1923.

4. **Ericameria parryi** (A. Gray) Nesom & Baird var. **howardii** (Parry *ex* A. Gray) Nesom & Baird, *comb. nov.* BASIONYM: *Linosyris howardii* Parry *ex* A. Gray, Proc. Amer. Acad. Arts 6:541. 1865. *Chrysothamnus parryi* (A. Gray) E. Greene subsp. *howardii* (Parry *ex* A. Gray) Hall & Clements, Carnegie Inst. Washington Publ. 326:201. 1923.

5. **Ericameria parryi** (A. Gray) Nesom & Baird var. **imula** (Hall & Clements) Nesom & Baird, *comb. nov.* BASIONYM: *Chrysothamnus parryi* (A. Gray) E. Greene subsp. *imulus* Hall & Clements, Carnegie Inst. Washington Publ. 326:200. 1923.

6. **Ericameria parryi** (A. Gray) Nesom & Baird var. **latior** (Hall & Clements) Nesom & Baird, *comb. nov.* BASIONYM: *Chrysothamnus parryi* (A. Gray) E. Greene subsp. *latior* Hall & Clements, Carnegie Inst. Washington Publ. 326:199. 1923.

7. **Ericameria parryi** (A. Gray) Nesom & Baird var. **monocephala** (A. Nels. & Kennedy) Nesom & Baird, *comb. nov.* BASIONYM: *Chrysothamnus monocephalus* A. Nels. & Kennedy, Proc. Biol. Soc. Washington 19:39. 1906. *Chrysothamnus parryi* (A. Gray) E. Greene subsp. *monocephalus* (A. Nels. & Kennedy) Hall & Clements, Carnegie Inst. Washington Publ. 326:200. 1923.

8. **Ericameria parryi** (A. Gray) Nesom & Baird var. **montana** (L. Anders.) Nesom & Baird, *comb. nov.* BASIONYM: *Chrysothamnus parryi* (A. Gray) E. Greene subsp. *montanus* L. Anders., Phytologia 38:319. 1978.

9. **Ericameria parryi** (A. Gray) Nesom & Baird var. **nevadensis** (A. Gray) Nesom & Baird, *comb. nov.* BASIONYM: *Linosyris howardii* Parry *ex* A. Gray var. *nevadensis* A. Gray, Proc. Amer. Acad. Arts 6:541. 1865. *Chrysothamnus parryi* (A. Gray) E. Greene subsp. *nevadensis* (A. Gray) Hall & Clements, Carnegie Inst. Washington Publ. 326:201. 1923.

10. **Ericameria parryi** (A. Gray) Nesom & Baird var. **parryi** BASIONYM: *Chrysothamnus parryi* (A. Gray) E. Greene subsp. *parryi*

11. **Ericameria parryi** (A. Gray) Nesom & Baird var. **salmonensis** (L. Anders.) Nesom & Baird, *comb. nov.* BASIONYM: *Chrysothamnus parryi* (A. Gray) E. Greene subsp. *salmonensis* L. Anders., Phytologia 38:317. 1978.

12. **Ericameria parryi** (A. Gray) Nesom & Baird var. **vulcanica** (E. Greene) Nesom & Baird, *comb. nov.* BASIONYM: *Chrysothamnus vulcanicus* E. Greene, Leafl. Bot. Observ. 1:80. 1904. *Chrysothamnus parryi* (A. Gray) E. Greene subsp. *vulcanicus* (E. Greene) Hall & Clements, Carnegie Inst. Washington Publ. 326:200. 1923.

Interspecific hybrids:

Ericameria ×**bolanderi** (A. Gray) Nesom & Baird, *comb. nov.* BASIONYM: *Linosyris bolanderi* A. Gray, Proc. Amer. Acad. Arts 7:354. 1868. *Chry-*

sothamnus parryi (A. Gray) E. Greene subsp. *bolanderi* (A. Gray) Hall & Clements, Carnegie Inst. Washington Publ. 326:199. 1923. *Chrysothamnus parryi* (A. Gray) E. Greene var. *bolanderi* (A. Gray) Jepson, *Man. Fl. Pl. California* 1033. 1925. *Chrysothamnus bolanderi* (A. Gray) E. Greene, Erythea 3:114. 1895. *Macronema bolanderi* (A. Gray) E. Greene, Leafl. Bot. Observ. 1:181. 1904. (*Ericameria nauseosa* [Pallas *ex* Pursh] Nesom & Baird var. *speciosa* [Nutt.] Nesom & Baird × *Ericameria discoidea* (Nutt.) Nesom; few plants with strongly reduced pollen fertility; Anderson & Reveal 1966).

Ericameria ×viscosa (Keck) Nesom & Baird, *comb. et stat. nov.* BASIONYM: *Chrysothamnus nauseosus* (Pallas *ex* Pursh) Britt. subsp. *viscosus* Keck, Aliso 4:104. 1958. (*Ericameria nauseosa* [Pallas *ex* Pursh] Nesom & Baird var. *hololeuca* [A. Gray] Nesom & Baird × *Ericameria cuneata* [A. Gray] McClatchie; Anderson 1986a, 1993).

Ericameria ×uintahensis (L. Anders.) Nesom & Baird, *comb. et stat. nov.* BASIONYM: *Chrysothamnus nauseosus* (Pallas *ex* Pursh) Britt. subsp. *uintahensis* L. Anders., Great Basin Naturalist 44:416. 1984. (*Ericameria nauseosa* [Pallas *ex* Pursh] Nesom & Baird var. *hololeuca* [A. Gray] Nesom & Baird × *Ericameria parryi* [A. Gray] Nesom & Baird var. *attenuata* [M.E. Jones] Nesom & Baird; a stabilized hybrid known from one large population; Anderson 1984).

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