

COMMENTS ON "THE *CHRYSOTHAMNUS* - *ERICAMERIA* CONNECTION"

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ABSTRACT

Anderson (1995) has accepted the recent transfer of four species of *Chrysothamnus* into *Ericameria*, but his subsequent transfer of the remaining twelve species of *Chrysothamnus* s. str. into *Ericameria* appears to combine two phyletically disparate elements. In a peripheral concern, two new combinations are proposed to deal with a nomenclatural error and a newly described species of *Haplopappus*: *Ericameria nauseosa* var. *oreophila* (A. Nels.) Nesom & Baird and *Ericameria lignumviridis* (Welsh) Nesom.

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

Anderson (1995) has accepted our recent transfer of four species from *Chrysothamnus* Nutt. to *Ericameria* Nutt. (Nesom & Baird 1993), but he has contended that *Chrysothamnus* (as understood by him) is coherent and that if some of it goes into *Ericameria*, all must. He then supplied the necessary formalities and transferred the remaining twelve extant species and one fossil species, as well as three of the five sectional categories, leaving *Chrysothamnus* a vacant synonym.

Regarding the four species we transferred, however, Anderson did not offer any suggestion or comment regarding their position within *Ericameria*, and we thus assume that he recognizes our placement of them as correct (*i.e.*):

(1) *Ericameria nauseosa* (Pursh) Nesom & Baird and *E. parryi* (A. Gray) Nesom & Baird removed from *Chrysothamnus* and placed among the other nine species of *Ericameria* sect. *Macronema* (Nutt.) Nesom (rather than constituting the ditypic *Chrysothamnus* sect. *Nauseosi* H.M. Hall *sensu* Anderson), and

(2) *Ericameria teretifolia* (Dur. & Hilg.) Jepson and *E. paniculata* (A. Gray) Rydb. removed from *Chrysothamnus* and placed among the other twelve species of *Ericameria* sect. *Ericameria* (rather than constituting the ditypic *Chrysothamnus* sect. *Punctati* H.M. Hall *sensu* Anderson).

Anderson noted that (p. 86) "Clearly, *Chrysothamnus* (*sensu* Anderson 1986, not Nesom & Baird 1993) is fairly homogeneous and should not be dismembered." In fact, however, it appears that he has accepted what we certainly construe to be a dismemberment of *Chrysothamnus* - a removal of four species in two separate elements (sect. *Nauseosi* and sect. *Punctati*) from the other twelve species that we left in the genus. He did not transfer either of these two sectional categories to *Ericameria*, but the twelve remaining species were transferred intact within the three sections that encompassed them in *Chrysothamnus*, with the resultant creation of three additional sections in *Ericameria*.

Our transfer of these four species out of *Chrysothamnus* was based not only on observations from natural hybridization and DNA studies but on a broader range of evidence as well, in contrast to what is acknowledged by Anderson. We transferred the species that were morphologically and chemically out of place in *Chrysothamnus* but easily accommodated within existing groups of *Ericameria*. The placement of *E. teretifolia* (as well as *E. paniculata*) into sect. *Ericameria* is based on its resemblance in a suite of characters, not merely its distinct tendency to produce distally expanded resin ducts in the phyllaries, its only feature to which Anderson gave attention. Similarly, the relationship of *E. parryi* clearly is with sect. *Macronema*; we also placed *E. nauseosa* in sect. *Macronema* but noted that it has similarities to *Ericameria* sect. *Asiris* (H.M. Hall) Nesom that complicate the distinction between the two sections.

With the acceptance of these four species into *Ericameria*, the question becomes "Do the remaining twelve species of *Chrysothamnus* also belong in *Ericameria*?" In a broadened perspective, and as we noted in our earlier paper, the remainder of *Chrysothamnus* (*sensu* Nesom & Baird, including the species of *Hesperodoria* and *Petradoria*) is most similar and apparently most closely related to the genus *Stenotus*, which is a part of the Solidagininae (Nesom 1994). *Ericameria* appears to be one of only two North American genera that belong to the subtribe Hinterhuberinae, which otherwise is restricted to the Southern Hemisphere.

To the six morphological contrasts we used to distinguish *Ericameria* from *Chrysothamnus*, Anderson provided caveats and exceptions and noted that "clearly none of these six sets of characteristics can be used to consistently separate the two groups." We agree with this and clearly did not mean that any *one* of them can be used this way, our own discussion explicitly anticipating some of the same exceptions noted by Anderson. Rather, we viewed these characters as a syndrome which, taken as a whole, are indicative of the relationships suggested. We remain convinced that the two groups can be separated by such broad comparison. It should be remembered that *Chrysothamnus* has been one of the very few genera that even taxonomists maintaining the widest of generic concepts (*e.g.*, H.M. Hall, A. Cronquist, S.L. Welsh, and L.C. Anderson) have long been willing to regard as a genus separate from the *Hap-*

lopappus alliance (including *Ericameria*). In our interpretation, *Ericameria* and *Chrysothamnus* present a case of convergent evolution particularly challenging to systematists. As Anderson noted in his own beginning comments (p. 84), wide morphological differences can falsely imply wide phylogenetic gaps, but in contrast, "some taxa may appear more closely related than they are." Interpretation of the morphology is not unambiguous, however, and a more decisive judgement regarding the divergent opinions on the taxonomy of these species may not be forthcoming until detailed DNA data are available for a range of taxa.

The largest part of Anderson's rationale for joining the rest of *Chrysothamnus* with *Ericameria* rests with the plant from Ash Meadows, Nevada, as well as the progeny from one of his "*C. albidus* garden plants," which he has identified as hybrids between *C. albidus* (A. Gray) E. Greene and *E. nauseosa* var. *mohavensis* (E. Greene) Nesom & Baird. We are still unconvinced that either of these plants is such a hybrid and stand by our earlier comments. But we reiterate: even if these plants should prove to have the parentage suggested by Anderson, the implication is equally or more that *C. albidus* should be considered a phyletically extraneous element within *Chrysothamnus*, as suggested by its peculiar morphology, which makes it difficult to discern the nature of its relationship to the rest of the genus.

We still find it reasonable that *Chrysothamnus*, as the closest relative of *Stenotus* (in our view), should be expanded to include *Petradoria* and *Hesperodoria*. Anderson contends that *Petradoria* is not "morphologically compatible" with *Chrysothamnus* because of its radiate heads and sterile disc ovaries (and concomitant modification of the style branch morphology), yet many Astereae genera encompass this sort of variation (Nesom 1994). *Chrysothamnus spathulatus* L. Anderson is a sporadically radiate species already accepted within the genus. Further, based on an accumulation of morphological evidence from his own studies, Anderson (e.g., Anderson 1963, 1983, 1986; Anderson & Weberg 1974) has recognized a close similarity between *Hesperodoria*, *Petradoria*, and his *Chrysothamnus* sect. *Graminei* L. Anderson, as well as other species of *Chrysothamnus*, especially *C. vaseyi* (A. Gray) E. Greene. Sect. *Graminei* comprises *C. eremobius* L. Anderson and *C. gramineus* H.M. Hall, which has alternatively has been treated as *Petradoria discoidea* L. Anderson. The position of the monotypic *Vanclevea* may lie outside of *Chrysothamnus* s. str., but we believe that the two are closely related, as Anderson's morphological data suggest. The definition of *Chrysothamnus* and its closest relatives is discussed in detail by Baird (in manuscript).

Finally, we observe that Anderson's phrases "morphologically compatible" and "fairly homogeneous" do not provide much guidance for an understanding of *Chrysothamnus*. A "post-Hallian" phyletic overview of the genus has never been provided, and it is perhaps not surprising that Anderson decided to merge it with *Ericameria*, propelling the latter into the same "fairly homogeneous"

state that characterized the earlier *Chrysothamnus* (*sensu* Anderson 1986).

Anderson (p. 87) noted that he has made available two alternate taxonomies, "one for *Chrysothamnus* as a genus (Anderson 1986) or as a component of *Ericameria* (Nesom & Baird 1993, and here)." This appears to be three alternates rather than two, or else Anderson has omitted the solution that we believe is the correct one: of three broad elements of traditional *Chrysothamnus* (sect. *Nauseosi*, sect. *Punctati*, and the rest), the first two have been absorbed within separate components of *Ericameria*, leaving a still recognizable *Chrysothamnus*, which is closely similar to *Ericameria* but only distantly related to it.

TAXONOMIC MODIFICATIONS

We take this opportunity to correct a nomenclatural error in our previous transfers from *Chrysothamnus* to *Ericameria*, resulting from our lack of attention to the implication of the DeMoulin rule.

Ericameria nauseosa (Pallas ex Pursh) Nesom & Baird var. *oreophila* (A. Nelson) Nesom & Baird, *comb. nov.* BASIONYM: *Chrysothamnus oreophilus* A. Nelson, Bot. Gaz. (Crawfordsville) 28:375. 1899. *Chrysothamnus oreophilus* A. Nelson var. *oreophilus* A. Nelson (1912, autonymic, see below). *Chrysothamnus nauseosus* (Pallas ex Pursh) Britt. var. *oreophilus* (A. Nelson) H.M. Hall, Univ. Calif. Pub. Bot. 7:175. 1919.

Chrysothamnus oreophilus A. Nelson var. *artus* A. Nelson, Bot. Gaz. (Crawfordsville) 54:413. 1912. *Chrysothamnus nauseosus* (Pallas ex Pursh) Britt. var. *artus* (A. Nelson) Cronquist, *Vasc. Pl. Pacific Northw.* 5:129. 1955. *Ericameria nauseosa* (Pallas ex Pursh) Nesom & Baird var. *arta* (A. Nelson) Nesom & Baird, *Phytologia* 75:85. 1993. (*comb. illeg.*).

Chrysothamnus consimilis E. Greene, *Pittonia* 5:60. 1902. *Chrysothamnus nauseosus* (Pallas ex Pursh) Britt. var. *consimilis* (E. Greene) H.M. Hall, Univ. Calif. Pub. Bot. 7:176. 1919.

A species recently described (Welsh 1993) from Sevier County, Utah, belongs in *Ericameria* sect. *Macronema*, close to *E. crispa* (L. Anderson) Nesom; the transfer is made here.

Ericameria lignumviridis (Welsh) Nesom, *comb. nov.* BASIONYM: *Haplopappus lignumviridis* Welsh, *Rhodora* 95:398. 1993.

ACKNOWLEDGMENTS

We thank Billie Turner and Mark Mayfield for their comments on the manuscript and Dr. Turner for pointing out the problem in infraspecific nomenclature.

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Nesom, Guy L and Baird, Gary I . 1995. "Comments on "The Chrysothamnus-Ericameria connection"." *Phytologia* 78, 61–65.

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