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TAXONOMIC INFRASTRUCTURE OF *SOLIDAGO* AND *OLIGONEURON*
(ASTERACEAE: ASTEREA) AND OBSERVATIONS ON THEIR
PHYLOGENETIC POSITION

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ABSTRACT

Among *Solidago* and its closest relatives (the subtribe Solidaginiinae, *sensu stricto*), *Solidago* itself is characterized primarily by its non-punctate, often coarsely toothed leaves and thyrsoid or secund capitulescence. Based on morphological features, the genus is formally divided into sections and subsections: sect. *Solidago* (four subsections) and sect. *Unilaterales* (seven subsections). Series are formally designated within some of the subsections. Typification is clarified for formally published names from older literature, and these are either incorporated in the active nomenclature or relegated to synonymy. The monotypic segregate genera *Brintonia* and *Brachychaeta* are treated as synonyms within sect. *Solidago* and sect. *Unilaterales*, respectively. Two genera previously treated within *Solidago* are here regarded as distinct, *Oreo-chrysum* Rydberg (monotypic) and *Oligoneuron* Small (six species). All three of these genera are hypothesized to be phylogenetically basal or near-basal members of the subtribe. In addition to new combinations proposed for the infrageneric taxonomy of *Solidago* and *Oligoneuron*, several others at lower ranks are necessary: *Oligoneuron album*, *O. houghtonii*, *O. rigidum* var. *glabratum*, *O. rigidum* var. *humilis*, as well as others for previously named interspecific hybrids within *Oligoneuron*. "×*Solidaster*" is hypothesized to be an intergeneric hybrid between *Oligoneuron album* and *Euthamia graminifolia*.

KEY WORDS: *Solidago*, *Oligoneuron*, *Oreo-chrysum*, ×*Solidaster*, Asteraceae, Astereae

Solidago L. is a genus of considerable morphological complexity with a long taxonomic history, but there has been no attempt since de Candolle

(1836) and Gray (1882) to present a taxonomic overview of the whole genus, and those bear little resemblance to the one presented here. A number of infrageneric categories at various ranks have been proposed, but all studies of the genus after Asa Gray's synoptical treatments in 1882 and 1884 have been regional or have dealt with only a portion of the taxa. Several segregates of *Solidago*, previously treated at various ranks within the genus, are now generally recognized as distinct genera: *Euthamia* (Nutt.) Nutt., *Chrysoma* Nutt., and *Petradoria* E. Greene (see Nesom 1991c and Nesom *et al.* 1990 for an overview of their phylogenetic placement; all three are within the subtribe Solidagininae). Two other segregates, which have been more generally and recently accepted within *Solidago*, are also excluded in the present treatment: *Oligoneuron* Small and *Oreochrysum* Rydberg. Reasons for their exclusion are given below. The classification of *Solidago* presented here surely will be subject to modification, but it offers a more comprehensive and clearly defined point of reference than has been available for more than a century.

Solidago includes a total of about 80-90 species in North America (including México), with an additional 10-20 of sect. *Solidago* native to Eurasia. Because of taxonomic difficulties among the Old World taxa, they have not been included in the present treatment, but aspects of their taxonomy and variation are discussed below. One other species (*S. microglossa* DC. of sect. *Unilaterales*) is autochthonous in South America (Nesom in prep.) and naturalized in Africa. A number of North American species are naturalized and cultivated in Asia and in Europe, where they are highly regarded as ornamentals. The greatest number of species and the greatest morphological diversity in the genus occur in eastern North America, and its closest generic relatives occur there as well (as hypothesized by Nesom 1991c, the present study, and in prep.).

The base chromosome number of *Solidago* is $x=9$, without exception, as evidenced by hundreds of reports (summary by Semple 1992). Polyploidy is common within and among species. The karyotype appears to be relatively uniform across all groups (*e.g.*, Kapoor & Beaudry 1966; Beaudry 1970b; Kapoor 1975), with a predominance of chromosomes with submedian centromeres.

In the following taxonomic outline, the lists of constituent species sometimes differ from recently proposed taxonomy. Some of the names used may be justifiably applied at a lower rank, but they are included here as species for ease of reference. I have tried to include names in relatively recent use, but the species lists are not an attempt to present a summary of accepted nomenclature; there appears to be little consensus regarding the taxonomy of many subgroups in the genus. Recent references, where available, are provided as guides to definitions of species boundaries, but a large amount of fragmentary literature exists, and there are but few modern, documented, taxonomic summaries of any groups of *Solidago*. Contemporary regional floras provide the best and often only means of identification (those with literature citations

are particularly helpful, e.g., Semple & Ringius 1983, rev. Semple 1992; Taylor & Taylor 1984).

In the application of names published by Torrey & Gray (1842) and by Gray (1884), I have followed the precedent of Holmgren (1979) and Jones (1980). The nomenclature in Gray's synopsis of *Solidago* (1882) is nearly identical to his treatment in the *Synoptical Flora* (1884), and I have considered the earlier work as the first publication for some of the names. Some names of sections and series are adopted from Loudon's *Hortus Britannicus*, following the notice of Sundberg & Jones (1987, 1988). Published names of numerous "species-groups," for which a clearly indicated rank was not provided, can be found in various publications, particularly in Rydberg (1917, 1932) and Mackenzie (1933). I have used some of these as basionyms. All of Rafinesque's generic segregates from *Solidago* are accounted for, except *Aplactis* Rafin. (*Fl. Tellur.* 2:42. 1836 [1837]), which was lectotypified as a synonym of *Chrysoma* by Kapoor & Beaudry (1966). There do not appear to be any taxonomic categories for the Eurasian taxa that would impinge on the nomenclature presented here.

The two main infrageneric groups of *Solidago* are treated as sections, as the use of "subgenus" generally implies a more profound difference than is found within *Solidago* as treated here. Hybridization is relatively common in various parental combinations among species of the subsections as well as between the two sections. The nature of interrelationships among the species groups is not clear, and several of the subsections of sect. *Solidago* might justifiably be treated at a higher rank. Below the rank of section, I have used subsection as the primary taxonomic category, because smaller species groups (series) are recognized within some of the subsections, and other groups evidently exist also, even where they have not been accorded a formal name in this treatment.

Solidago L., *Sp. Pl.* (ed. 1) 878. 1753. LECTOTYPE: *Solidago virgaurea* L. (Britton & Brown, *Illust. Fl. N. U.S.*, ed. 2, 3:380. 1913.)

1. *Solidago* sect. *Solidago*

Solidago subg. *Virgaurea* (DC.) Torr. & Gray, *Fl. N. Amer.* 2:197. 1842. Not Tamamsch. 1959. *Solidago* sect. *Virgaurea* DC., *Prodr.* 5:330. 1836. Torrey & Gray attributed the subgeneric combination to de Candolle, but de Candolle clearly referred to the group as "sect. *Virgaurea*." TYPE: *Solidago virgaurea* L.

Capitulescence branches very short and axillary to longer and ascending, the heads more or less uniformly distributed around the head-bearing branch-

lets, not at all secund, the capitulescence axillary and discontinuous or more nearly terminal and elongate-spicate to somewhat corymboid.

a. *Solidago* subsect. *Solidago*

Solidago sect. *Virgaurea* DC., *Prodr.* 5:330. 1836. TYPE:
Solidago virgaurea L.

Amphirhapis DC., *Prodr.* 5:343. 1836. [pro parte; Hooker & Jackson 1895]. TYPE: not designated

Actipsis Rafin., *Fl. Tellur.* 2:43. 1836. [1837]. LECTOTYPE, designated here: *Solidago glomerata* Michx.

Solidago sect. *Erectae* G. Don in Loudon, *Hort. Brit.* (ed. 1) 348. 1830. *Solidago* [sect. *Virgaurea*] series *Erectae* (G. Don) DC., *Prodr.* 5:335. 1836. TYPE: *Solidago erecta* Pursh.

Solidago [sect. *Erectae*] ser. *Serratae* G. Don in Loudon, *Hort. Brit.* (ed. 1) 348. 1830. LECTOTYPE, designated here: *Solidago virgaurea* L.

Solidago [sect. *Thyrsiflorae*] ser. *Pauciradiatae* Juz., *Fl. URSS* 25:34. 1959. LECTOTYPE, designated here: *Solidago virgaurea* L.

Solidago [sect. *Thyrsiflorae*] ser. *Multiradiatae* Juz., *Fl. URSS* 25:47. 1959. TYPE: *Solidago multiradiata* Ait.

Species included (10): *Solidago calcicola* (Fernald) Fernald, *S. cutleri* Fernald, *S. glomerata* Michx., *S. multiradiata* Ait., *S. nana* A. Gray, *S. plumosa* Small, *S. sciaphila* Steele, *S. simplex* Kunth (incl. *S. bellidifolia* E. Greene, *S. chlorolepis* Fernald, *S. deamii* Fernald, *S. decumbens* E. Greene, *S. gillmanii* [A. Gray] Steele, *S. glutinosa* Nutt., *S. neomexicana* Woot. & Standl., *S. oreophila* Rydb., *S. racemosa* E. Greene, *S. randii* [Porter] Britt., and *S. victorinii* Fernald), *S. spathulata* DC., *S. spithamaea* M.A. Curtis, and some of the autochthonous Old World taxa, including *S. virgaurea* L. – see comments below (Cronquist 1947; Wagenitz 1979; Ringius 1985, 1987; Ringius & Semple 1987, 1991; Nesom 1989b).

Rhizomes short, thick; leaves thick to thin, sometimes glutinous, glabrous to sparsely hairy, shallowly crenate to sharply serrate, net-veined, oblanceolate to obovate, attenuate to a short petiolar region, the basal usually persistent, cauline reduced upward; heads in a cylindrical to ellipsoidal thyrse, distinctly corymboid in *Solidago cutleri*, *S. multiradiata*, and *S. spithamaea*; phyllaries 1-veined; achenes mostly pubescent; pappus bristle apices attenuate.

Solidago glomerata has been hypothesized to be closely related to *S. squarrosa* (Beaudry 1963), but the thick, oblanceolate leaves and thick phyllaries with rounded apices of the former indicate, instead, that it belongs with subsect. *Solidago*. Like *S. spithamaea*, *S. glomerata* appears to be an isolated

relict harbored within the high Appalachians. Several species groups might be recognized within subsect. *Solidago*.

All of the native Old World taxa of *Solidago* are in sect. *Solidago*, but there is a great deal of morphological variability that appears to be poorly understood taxonomically. The greatest range of variation is in eastern Asia, where the capitulescences range from axillary to a broad or narrow thyrse to a relatively compact, terminal cluster. The leaves vary in thickness and in shape from ovate with a winged petiolate to elliptic-lanceolate and epetiolate. Only rarely do the leaves have a strong basal disposition. Many of these forms have been classified within *S. virgaurea*, whereas in North America they would be identified as different species and even placed in different subsections. See further comments below in the "Review of the *S. virgaurea* complex."

b. *Solidago* subsect. *Albigula* (Rafin.) Nesom, *comb. et stat. nov.*

BASIONYM: *Solidago* subg. *Albigula* Rafin., *Fl. Tellur.* 2:42. 1836. [1837]. TYPE: *Solidago bicolor* L.

Solidago subg. *Chrysastrum* Torr. & Gray, *Fl. N. Amer.* 2:195. 1842. *Solidago* sect. *Chrysastrum* (Torr. & Gray) A. Gray, *Proc. Amer. Acad. Arts* 16:80. 1880. LECTOTYPE, designated here: *Solidago squarrosa* Muhl.

Solidago sect. *Squarrosae* A. Gray, *Proc. Amer. Acad. Arts* 17:189. 1882. TYPE: *Solidago squarrosa* Muhl.

Solidago ser. *Integrifoliae* G. Don in Loudon, *Hort. Brit.* (ed. 1) 348. 1830. LECTOTYPE: *Solidago erecta* Pursh.

Anactis Rafin., *Fl. Tellur.* 2:44. 1836. [1837]. Not Cass. 1827. TYPE: *Solidago discoidea* (Ell.) Torr. & Gray.

Brintonia E. Greene, *Erythea* 3:89. 1895. TYPE: *Solidago discoidea* (Ell.) Torr. & Gray.

Species included (9): *Solidago bicolor* L., *S. discoidea* (Ell.) Torr. & Gray, *S. erecta* Pursh, *S. hispida* Muhl., *S. macrophylla* Pursh, *S. porteri* Small, *S. puberula* Nutt., *S. roanensis* Porter, *S. squarrosa* Muhl. (Greene 1895; Monachino 1955; Semple & Ringius 1983).

Rhizomes short; leaves hairy, crenate to serrate or entire, net-veined, oblanceolate to narrowly ovate, attenuate to a relatively long petiole, not clasping, the basal persistent, cauline reduced upward; heads mostly in a terminal, elongated and narrow capitulescence, more or less leafy bracteate toward the base, the lower clusters often becoming elongate and stiffly ascending; phyllaries 1-veined; achenes glabrous or less commonly very sparsely strigose; pappus bristle apices strongly clavate in *Solidago bicolor* and *S. discoidea*, seen only as a slight tendency in the other species.

Solidago bicolor and *S. discoidea*, both of which produce white corollas and strongly clavate pappus bristle apices, have been postulated to be allopatric,

sister species (Nesom 1991c), even though *S. bicolor* hybridizes and perhaps intergrades with *S. hispida* (e.g., Ringius & Semple 1983). The strongly squarrose phyllaries of *S. squarrosa* are distinctive but a similar tendency also exists in *S. erecta* and *S. discoidea*, as well as *S. macrophylla*. These species are among the relatively few in *Solidago* to produce thin phyllaries with narrowly acute apices; the phyllary apices in *S. erecta* tend to be rounded.

The position of *Solidago macrophylla* is problematic. It is tentatively included here in subsect. *Albigula* on the basis of its short rhizomes, leaf morphology and disposition, phyllaries with acute, sometimes squarrose apices, and glabrous achenes. It stands apart from these species, however, and most others in the genus, in its combination of long style appendages, very large heads, carinate phyllaries, and short disc corolla lobes. Dr. L. Brouillet has pointed out to me that *S. macrophylla* is more similar to the plants of subsect. *Glomeruliflorae* in its relatively mesic habitat, and its capitulescence varies from the terminal-virgate characteristic of subsect. *Albigula* to strictly axillary, as in subsect. *Glomeruliflorae*. In yet another possibility, Fernald (1908) observed that *S. macrophylla* was the "nearest American ally" of the Eurasian *S. virgaurea* (subsect. *Solidago*), although he later (1950) changed his mind about this. See further comments below in the "Review of the *S. virgaurea* complex."

- c. **Solidago** subsect. **Glomeruliflorae** (Torr. & Gray) Nesom, *comb. et stat. nov.* BASIONYM: *Solidago* sect. *Glomeruliflorae* Torr. & Gray, *Fl. N. Amer.* 2:197. 1842. LECTOTYPE, designated here: *Solidago caesia* L.

Leioligo subg. *Breviligula* Rafin., *Fl. Tellur.* 2:42. 1836. [1837].
LECTOTYPE, designated here: *Solidago caesia* L.

Solidago subg. *Pleiactila* Rafin., *Fl. Tellur.* 2:42. 1836. [1837].
LECTOTYPE, designated here: *Solidago flexicaulis* L.

Species included (7): *Solidago albopilosa* L. Braun, *S. caesia* L., *S. curtisii* Torr. & Gray, *S. flaccidifolia* Small, *S. flexicaulis* L., *S. lancifolia* (Torr. & Gray) Chpm., *S. ouachitensis* C. & J. Taylor (Andreasen & Eshbaugh 1973; Chmielewski & Semple 1985; Chmielewski *et al.* 1989; Semple *et al.* 1984; Taylor & Taylor 1983, 1986)

Rhizomes usually elongated, creeping; leaves lanceolate to oblanceolate, commonly abruptly narrowed to a winged petiole, net-veined, serrate, the basal not persistent, cauline only gradually reduced upward; lower heads in distantly separated axillary clusters shorter than the subtending leaves, the upper sometimes spicately arranged; phyllaries 1-veined (sometimes 3-5-nerved in *Solidago curtisii*); achenes densely pubescent; pappus bristle apices attenuate. Different from subsect. *Albigula* in its elongate rhizomes, absence of basal leaves, short axillary floral clusters, and hairy achenes.

- d. *Solidago* subsect. *Thyrsoflorae* (A. Gray) Nesom, *comb. et stat. nov.* BASIONYM: *Solidago* sect. *Thyrsoflorae* A. Gray, Proc. Amer. Acad. Arts 17:190. 1882. Not Tamamsch. 1959. *Solidago* ser. *Thyrsoflorae* (A. Gray) Hoffm., Pflanzenf. 4(5):150. 1889. LECTOTYPE, designated here: *Solidago wrightii* A. Gray.

Leioligo Rafin., *Fl. Tellur.* 2:42. 1836. [1837]. LECTOTYPE, designated here: *Solidago petiolaris* Ait.

Leioligo subg. *Doria* Rafin., *Fl. Tellur.* 2:42. 1836. [1837]. LECTOTYPE, designated here: *Solidago petiolaris* Ait.

Leioligo subg. *Liniuque* Rafin., *Fl. Tellur.* 2:42. 1836. [1837]. LECTOTYPE, designated here: *Solidago speciosa* Nutt.

Species included (6): *Solidago buckleyi* Torr. & Gray, *S. hintoniorum* Nesom, *S. orientalis* (Nesom) Nesom, *S. petiolaris* Ait., *S. speciosa* Nutt. (incl. *S. harperi* Mackenzie, *S. jejunifolia* Steele), *S. wrightii* A. Gray (Nesom 1990; Taylor & Taylor 1986).

Rhizomes mostly short, sometimes lengthening; basal leaves not persistent, the cauline gradually reduced upward, broadly to narrowly elliptic to oblanceolate, sessile or with a very short petiole, serrulate to nearly entire, distinctly thickened to coriaceous, net-veined, glabrous to hairy, sometimes glandular (sessile or stipitate); capitulescence elongated, sometimes broad, sometimes somewhat punctuated in the lower portion (in *Solidago buckleyi*), loosely but distinctly corymboid in *S. wrightii*; phyllaries 1(-3)-veined, commonly stipitate-glandular or glutinous; achenes glabrous or with a few hairs; pappus bristles commonly slightly but distinctly dilated toward the apex.

Anderson & Creech (1975) noted a similarity in leaf morphology between *Oligoneuron* and taxa of subsect. *Thyrsoflorae*. This may be reflective of the relatively primitive position of the latter within *Solidago*. Plants of subsect. *Thyrsoflorae* also are the only ones in the genus to produce prominent stipitate glands, another feature suggestive of a primitive position for these species, if the stipitate glands are homologous with the sunken ones (punctae) characteristic of the rest of the subtribe. This is clearly the case in at least some other *Astereae* (e.g., *Isocoma* Nutt., see comments in Nesom 1991d).

2. *Solidago* sect. *Unilaterales* G. Don in Loudon, *Hort. Brit.* (ed. 1) 348. 1830. *Solidago* ser. *Unilaterales* (G. Don) DC., *Prodr.* 5:330. 1836. LECTOTYPE, designated here: *Solidago canadensis* L.

Dr. Semple (pers. comm.) has noted that the identification of specimens listed by Loudon may be problematic, with corresponding problems in typification. The name chosen by Don, however, for

this section (sect. *Unilaterales*) appears to be so appropriate for the secund capitulescence that there could be little doubt what group of species he was referring to. Even if some other species were chosen as the lectotype, the application of the name would not change.

Solidago sect. *Paniculatae* A. Gray, Proc. Amer. Acad. Arts 17:191. 1882. Not Tamamsch. 1959. LECTOTYPE, designated here: *Solidago canadensis* L.

Capitulescence branches ascending-recurved with the heads usually in a distinctly secund arrangement, the capitulescence dense and pyramidal or more open with the branches relatively widely separated.

a. *Solidago* subsect. *Triplinerviae* (Torr. & Gray) A. Gray, Proc. Amer. Acad. Arts 17:195. 1882. *Solidago* sect. *Triplinerviae* Torr. & Gray, *Fl. N. Amer.* 2:222. 1842. LECTOTYPE, designated here: *Solidago canadensis* L.

Solidago ser. *Trinerves* G. Don in Loudon, *Hort. Brit.* (ed. 1) 348. 1830. LECTOTYPE, designated here: *Solidago canadensis* L.

Solidago subg. *Brachyactis* Rafin., *Fl. Tellur.* 2:42. 1836. [1837]. LECTOTYPE, designated here: *Solidago canadensis* L.

Species included (13): *Solidago altiplanites* C. & J. Taylor, *S. altissima* L., *S. canadensis* L., *S. durangensis* Nesom, *S. gigantea* Ait., *S. gypsophila* Nesom, *S. juliae* Nesom, *S. leavenworthii* Torr. & Gray, *S. lepida* DC. (perhaps incl. *S. elongata* Nutt.), *S. microglossa* DC., *S. paniculata* DC., *S. rupestris* Rafin., *S. shortii* Torr. & Gray (Beaudry 1963, 1964, 1970a; Croat 1967, 1972; Melville & Morton 1982; Morton 1984; Taylor & Taylor 1983; Nesom 1989a, 1989d, 1991a; Semple *et al.* 1984, 1990).

Rhizomes elongate, creeping (short in *Solidago shortii*); leaves serrulate, 3-nerved, lanceolate, even-sized and densely arranged along the stem, the basal not persistent; heads densely arranged in a pyramidal panicle; phyllaries 1-veined; achenes pubescent; pappus bristle apices attenuate.

b. *Solidago* subsect. *Nemorales* (Mackenzie) Nesom, *comb. et stat. nov.* BASIONYM: *Solidago* sp.-group *Nemorales* Mackenzie in Small, *Man. Southeast. Fl.* 1348. 1933. TYPE: *Solidago nemoralis* Ait.

Species included (5): *Solidago macvaughii* Nesom, *S. mollis* Bartl., *S. nana* Nutt., *S. nemoralis* Ait. (incl. *S. decemflora* DC.), *S. velutina* DC. (incl. *S.*

arizonica [A. Gray] Woot. & Standl., *S. californica* Nutt., *S. sparsiflora* DC.) (Nesom 1989c; Semple *et al.* 1990, 1992).

Rhizomes short; basal leaves persistent, the cauline strongly reduced upward, oblanceolate, gradually attenuate to a petiolar region, 3-veined (sometimes obscurely so in *Solidago nemoralis*), serrulate, not clasping, usually densely hairy; capitulescence sometimes pyramidal, commonly more loosely arranged; phyllaries 1-veined; achenes hairy; pappus bristle apices attenuate.

- c. *Solidago* subsect. *Venosae* (G. Don) Nesom, *comb. et stat. nov.* BASIONYM: *Solidago* ser. *Venosae* G. Don in Loudon, *Hort. Brit.* (ed. 1) 348. 1830. LECTOTYPE, designated here: *Solidago rugosa* Miller.

Species included (8): *Solidago aestivalis* Bicknell, *S. aspera* Ait. (incl. *S. celtidifolia* Small, *S. drummondii* Torr. & Gray), *S. fistulosa* Mill., *S. latisimifolia* Miller (= *S. elliottii* Torr. & Gray; incl. *S. edisoniana* Mackenzie, *S. mirabilis* Small), *S. microphylla* (A. Gray) Engelm. ex Small (incl. *S. delicatula* Small), *S. radula* Nutt., *S. rugosa* Miller, *S. ulmifolia* Muhl. (Fernald 1936; Beaudry 1960, 1963, 1969; Semple *et al.* 1984; Uttal & Porter 1988).

Rhizomes elongate, creeping (except in *Solidago ulmifolia* and *S. microphylla*); basal leaves not persistent, the cauline relatively little reduced upward until the capitulescence, net-veined, serrulate, sparsely hairy, broadly elliptic, sessile or short-petiolate, sometimes subclasping; capitulescence loose, sometimes loosely pyramidal; phyllaries 1-veined; achenes hairy; pappus bristle apices attenuate.

Different from subsect. *Nemorales* in its creeping rhizomes, net-veined leaves, the basal not persistent, the cauline not reduced upward. *Solidago radula* is placed here because of its creeping rhizomes and primarily cauline leaves, but its leaves sometimes are 3-nerved and the species may be more closely allied to those of subsect. *Nemorales*. Overall, however, subsect. *Venosae* is probably more closely related to subsect. *Argutae*, the primary difference being leaf disposition; the two subsections might justifiably be combined into a single one with three series.

- d. *Solidago* subsect. *Argutae* (Mackenzie) Nesom, *comb. et stat. nov.* BASIONYM: *Solidago* sp.-group *Argutae* Mackenzie in Small, *Man. Southeast. Fl.* 1347. 1933. TYPE: *Solidago arguta* Ait.

Solidago sect. *Secundiflorae* Torr. & Gray, *Fl. N. Amer.* 2:212. 1842. LECTOTYPE, designated here: *Solidago arguta* Ait.

Rhizomes short (slender stolons in *Solidago ludoviciana* and *S. sphacelata*); leaves commonly doubly and coarsely serrate, net-veined, hairy to glabrous,

the basal and lower usually persistent, with a long, winged petiole, the cauline reduced upward and mostly epetiolate; heads in a loose and open capitulescence; phyllaries 1-veined; achenes sparsely hairy to glabrous; pappus bristle apices attenuate.

- * **Solidago ser. Argutae** (Mackenzie) Nesom, *comb. et stat. nov.* BASIONYM: *Solidago* sp.-group *Argutae* Mackenzie in Small, *Man. Southeast. Fl.* 1347. 1933. TYPE: *Solidago arguta* Ait.

Species included (5): *Solidago arguta* Ait. (incl. *S. harrisii* Steele, *S. yadkinensis* [Porter] Small, *S. boottii* Hook.), *S. ludoviciana* (A. Gray) Small (incl. *S. salicina* Ell., *S. strigosa* Small), *S. patula* Muhl., *S. tarda* Mackenzie, *S. verna* Curtis ex Torr. & Gray (Morton 1974).

Basal and lower leaves usually broadly lanceolate, basally attenuate to a winged petiole, the cauline reduced upward; ray flowers relatively numerous; pappus bristles not markedly shortened.

- * **Solidago ser. Brachychaetae** (Torr. & Gray) Nesom, *comb. et stat. nov.* BASIONYM: *Brachychaeta* Torr. & Gray, *Fl. N. Amer.* 2:194. 1842. TYPE: *Solidago sphacelata* Rafin.

Species included (3): *Solidago auriculata* Shuttlew. ex Blake, *S. brachyphylla* Chapman, *S. sphacelata* Rafin.

Basal and lower leaves usually ovate, basally cordate to truncate, with a winged petiole, the cauline strongly reduced upward; ray flowers absent or very few (1-3); pappus bristles markedly shortened.

- e. **Solidago subsect. Odorae** (Mackenzie) Nesom, *comb. et stat. nov.* BASIONYM: *Solidago* sp.-group *Odorae* Mackenzie in Small, *Man. Southeast. Fl.* 1346. 1933. TYPE: *Solidago odora* Ait.

Species included (2): *Solidago chapmanii* Torr. & Gray, *S. odora* Ait. (Cronquist 1977).

Rhizomes short, hairs in lines along the stem, basal leaves not persistent, the cauline numerous, linear to narrowly lanceolate, basally attenuate, sessile, entire, net-veined, glabrous, punctate-glandular; capitulescence loose; phyllaries 1-veined; achenes slightly hairy to glabrate; pappus bristle apices attenuate.

The punctate-glandular leaves of these two species are unique in the genus; no other *Solidago* are punctate-glandular. They are different in anatomy from punctate glands consistently produced in most other species of *Solidagininae* (Anderson & Creech 1975) but perhaps represent the same, ancestral, genetic

potential. *Solidago odora* and *S. chapmanii*, which are sometimes treated as a single species, are similar in habit and perhaps most closely related to the plants of subsect. *Junceae*.

f. ***Solidago* subsect. *Junceae*** (Rydb.) Nesom, *comb. et stat. nov.*

BASIONYM: *Solidago* sp.-group *Junceae* Rydb., *Fl. Prairie & Plains* 792. 1932. TYPE: *Solidago juncea* Ait.

Rhizomes long and stoloniform (shorter in *Solidago pinetorum* and *S. gattingeri* and in ser. *Spectabiles*); basal and lower cauline leaves commonly persistent, linear to narrowly and sharply lanceolate, often somewhat falcate, sessile to obscurely petiolate, 3-nerved (obscurely or sometimes 1-veined in *S. tortifolia* and *S. gattingeri*), entire to remotely serrate, glabrous or slightly hairy, the cauline usually reduced upward (more strongly developed in *S. tortifolia*); capitulescence relatively dense in *S. juncea*, *S. missouriensis*, and *S. tortifolia*, looser in *S. pinetorum* and *S. gattingeri*, flat-topped in *S. ericamerioides*, relatively dense and usually not perceptibly secund in ser. *Spectabiles*; phyllaries 1-veined; achenes glabrous to sparsely hairy; pappus bristle apices attenuate.

* ***Solidago* ser. *Junceae*** (Rydb.) Nesom, *comb. et stat. nov.* BASIONYM: *Solidago* sp.-group *Junceae* Rydb., *Fl. Prairie & Plains* 792. 1932. TYPE: *Solidago juncea* Ait.

Solidago subg. *Triactis* Rafin., *Fl. Tellur.* 2:42. 1836. [1837]. LECTOTYPE, designated here: *Solidago tortifolia* Ell.

Species included (7): *Solidago ericamerioides* Nesom, *S. gattingeri* Chapman, *S. juncea* Ait., *S. missouriensis* Nutt., *S. pinetorum* Small, *S. pringlei* Fernald (incl. *S. muelleri* Standley), *S. tortifolia* Ell. (Nesom 1989a; Semple *et al.* 1992).

Chaffy bracts are produced on the receptacles of *Solidago juncea* (Morton 1968) and *S. missouriensis* (Cronquist 1980) as well as *S. confinis*. These structures are similar to the inner phyllaries, and their occurrence clearly is derived within the genus. *Solidago juncea* and *S. missouriensis* are similar in other features and probably are sister species. *Solidago missouriensis* consistently produces slender stolons, while *S. juncea* does not, but there is a distinct tendency in the latter for the rhizomes to lengthen (Cronquist 1980), and there is some evidence that the two species intergrade. Most of these species (particularly *S. missouriensis* and *S. pinetorum*) have a tendency to produce axillary fascicles of much reduced leaves; *S. pringlei* and *S. ericamerioides* do not. Natural hybrids between *S. juncea* and *S. nemoralis* have been noted by Beaudry (1969).

* *Solidago* ser. *Spectabiles* Nesom, ser. nov. TYPE: *Solidago spectabilis* A. Gray.

Differt a speciebus subsect. *Junceorum* (Rydb.) Nesom foliis parvulis caulinis in fasciculis axillaribus carentibus et capitulescentia relative densa plerumque non perceptibile secunda.

Species included (3): *Solidago confinis* A. Gray, *S. guiradonis* A. Gray, *S. spectabilis* (D.C. Eat.) A. Gray

Semple *et al.* (1992) observed that these three species form the "far western element of the *Solidago missouriensis/juncea* group of goldenrods," with which I agree. Ser. *Spectabiles* is a group well-defined geographically as well as morphologically, the plants particularly tall and with capitulescences that show only a weak tendency, if any, to be secund. Some of the species of ser. *Junceae* also show the same tendency in the capitulescence. The capitulescence of *S. ericamerioides* is flat-topped, but this Mexican gypsophile is highly reduced in stature and probably derived from *S. pringlei* (the latter identified as *S. missouriensis* in an earlier study (Nesom 1989a), which produces only a weakly secund capitulescence. The plants of ser. *Spectabiles* also resemble those of subsect. *Maritimae* (which see for further comments).

g. *Solidago* subsect. *Maritimae* (Torr. & Gray) A. Gray, *Synopt. Fl. N. Amer.* 2(1):149. 1884. *Solidago* sect. *Maritimae* Torr. & Gray, *Fl. N. Amer.* 2:211. 1842. LECTOTYPE, designated here: *Solidago sempervirens* L.

Solidago sect. *Virgatae* Torr. & Gray, *Fl. N. Amer.* 2:201. 1842. TYPE: *Solidago virgata* Michx. (= *S. stricta* Ait.).

Solidago subsect. *Unicostatae* A. Gray, *Synopt. Fl. N. Amer.* 2(1):149. 1884. LECTOTYPE, designated here: *Solidago gracillima* Torr. & Gray.

Lepiactis Rafin., *Fl. Tellur.* 2:43. 1836. [1837]. TYPE: *Solidago virgata* Michx. (= *S. stricta* Ait.).

Solidago subg. *Stenactila* Rafin., *Fl. Tellur.* 2:42. 1836. [1837]. LECTOTYPE, designated here: *Solidago sempervirens* L.

Dasiorima Rafin., *Fl. Tellur.* 2:43. 1836. [1837]. LECTOTYPE, designated here: *Solidago mexicana* L. (= *S. sempervirens* L.).

Species included (5): *Solidago gracillima* Torr. & Gray (incl. *S. austrina* Small, *S. flavovirens* Chapm., *S. perlonga* Fernald, *S. simulans* Fern.), *S. pulchra* Small, *S. sempervirens* L., *S. stricta* Ait., *S. uliginosa* Nutt. (incl. *S. chrysolepis* Fern., *S. neglecta* Torr. & Gray, *S. purshii* Porter, *S. uniligulata*

[DC.] Porter, *S. klughii* Steele) (Goodwin 1937; Beaudry 1963; Chmielewski *et al.* 1985).

Rhizomes short (slender stolons in *Solidago stricta*); leaves thick, mostly glabrous, net-veined, crenate-dentate, the basal and lower oblanceolate, persistent, cauline reduced but slightly upward (strongly reduced in *S. stricta*) and subclasping; heads mostly in a cylindric to narrowly rhomboid panicle but the lower branches commonly secund; phyllaries 1-veined; achenes pubescent to glabrous; pappus bristle apices attenuate.

These are the "marsh and bog goldenrods." There is a distinctive but apparently superficial habitual resemblance between subsect. *Maritimae* and subsect. *Junceae* ser. *Spectabiles*. Plants of both groups are mostly glabrous, entire-leaved, and produce an elongate capitulescence often with little evidence of a secund arrangement of heads. Those of ser. *Spectabiles*, however, differ in their upland habitat, axillary fascicles of small leaves, and lanceolate, non-clasping leaves without parallel lateral veins. Hybrids have been observed between *Solidago stricta* and *S. sempervirens* (Cronquist 1980).

REVIEW OF THE *SOLIDAGO VIRGAUREA* COMPLEX IN NORTH AMERICA AND EURASIA

In De Candolle's (1836) comprehensive treatment of *Solidago*, the brief descriptions of the Old World *S. virgaurea* L. (the generitype) and the New World *S. simplex* Kunth, *S. spathulata* DC., and *S. multiradiata* Ait. were by no means mutually exclusive. Torrey & Gray (1842) treated *S. virgaurea* (including *S. multiradiata* Ait.) as a member of the North American flora, and noted its occurrence from Arctic America and Labrador to the Rocky Mountains and to the White Mountains (New York and New Hampshire). They regarded it as (p. 207) "A very variable species, which in this country is confined to the Northern regions, and the higher mountains of the Northern States. Nearly all the American specimens belong either to the var. β [var. *ericetum*, sensu de Candolle], which very nearly approaches the var. *Cambrica* of Europe, or to the var. γ [var. *alpestris*, sensu de Candolle], which passes insensibly into other forms of this species, to which it should doubtless be united." Later, Gray (1867) restricted this concept somewhat but still recognized two North American varieties of *S. virgaurea*; yet later (1882, 1884), he had narrowed his view of the species in North America to a variable var. *alpina* Bigelow of the northeastern United States and adjacent Canada (this taxon strictly interpreted by Fernald [1908] as *S. cutleri* Fernald, which is very similar and perhaps not different from *S. multiradiata* var. *arctica* [DC.] Fernald). Gray explicitly noted, however, the occurrence of intergrades and problematic distinctions between *S. virgaurea* and related American taxa.

Porter (1893) described additional varieties of *Solidago virgaurea* from the northeastern United States, but he identified high elevation plants from the

White Mountains as the otherwise Old World *S. alpestris* Wald. & Kit. ex Willd. (= *S. virgaurea* var. *alpestris* [Wald. & Kit. ex Willd.] DC. The latter plants were equated by Ringius (1986) with *S. glutinosa* var. *monticola* (Porter) Ringius. Porter noted that (p. 210) "on comparing them with *S. alpestris* from the Swiss and Carpathian Alps of Europe and the Altai Mountains of Asia the differences are so slight that the two must be regarded as identical. And such a conclusion ought to cause no surprise, when we consider the notable company of Old World alpinines which occupy the same mountain-tops. This only adds one more to the number."

Fernald (1899) effected the last nomenclatural connection of North American plants to the Old World species, as he added another variety to *Solidago virgaurea* (var. *calcicola* Fernald). He later decided that this taxon could stand as a separate species (1908) and made the following observation (p. 87): "Recent detailed studies of types and authentic specimens of this group have convinced the writer that we have in eastern North America no plant which can satisfactorily be placed with the Eurasian *S. Virgaurea*. The nearest American ally of that species, as understood by the writer, is *S. macrophylla* Pursh . . ." He added the caveat, however (p. 87), that "*S. calcicola* also simulates forms of *S. Virgaurea*." Over the next 30 years (1915, 1927, 1936), Fernald described a number of new, narrowly endemic species that could be considered similar to *S. virgaurea*, and by 1950 (p. 1392), he had decided, in contrast to his earlier view, that *S. calcicola* rather than *S. macrophylla* is "Our closest approach to Eurasian *S. virgaurea* L.," although he did not specify what segment of this highly polymorphic species he was referring to. These apparently were Fernald's only published comments specifically referring to *S. virgaurea*.

In the early 1900's, with a proliferation of names for North American population systems, regional floristicians (e.g., Rydberg 1917; Wootton & Standley 1915; Friesner 1933) appear to have exclusively adopted the regional nomenclature for these goldenrods. By around mid-century, American floristic studies were, of necessity, strongly concerned with making sense of the accumulated regional names. The complete nomenclatural separation of the American populations from the Eurasian ones appears to have been made implicitly, tacitly (except for a few sentences by Fernald, see above), and primarily on a continental basis, as the American taxa became better known morphologically and geographically, and as they acquired their own complex set of regional nomenclature.

Cronquist (1947) provided a detailed review of a group of American taxa that included many associated historically with *Solidago virgaurea*. He noted the strong tendencies for intergradation among them and gathered them into a single species (*S. glutinosa* Nutt., with five varieties divided among two subspecies), which comprises a group of closely related taxa spread over much of the northern half of North America, and extending southward along the Rocky Mountain cordillera into Colorado and New México, and from there further

south into central México along the Sierra Madre Oriental. Cronquist soon completely revised this nomenclature (Cronquist in Gleason 1952; Cronquist 1955), as he broadened the *S. glutinosa* complex by including the earlier-named *S. spathulata* DC. of the Pacific coast.

Ringius (1986) and Ringius & Semple (1987) recently completed cytological studies and multivariate morphological analyses of the taxa of the *Solidago glutinosa* complex (separate from *S. spathulata*, in their view; also in the view of Keck [1960]). Ringius recognized seven varieties in two subspecies, for the most part adopting Cronquist's basic concepts and taxonomy (of 1947) regarding the complex, but the realization that *S. simplex* is an older name for the same species (Nesom 1989) prompted yet another nomenclatural reorganization of the whole group (Ringius & Semple 1991). The numerical analyses confirmed Cronquist's observation that the taxa of the complex, though identifiable, were separated by differences "only in averages." The added cytological data were significant in showing that members of subsp. *simplex* are diploid ($n=9$), while members of subsp. *randii* (Porter) Ringius are chiefly tetraploid ($n=18$). Old World *S. virgaurea* is known only at the diploid level (Huziwara 1962; Wagenitz 1976).

Solidago multiradiata Ait. is similar to *S. simplex* and the two species apparently hybridize in high elevation habitats of the Rocky Mountains (Ringius 1986). The former has an American distribution nearly as broad as the *S. simplex* complex, occurring from Alaska southward into California, Arizona, and New Mexico, and southeastward into Labrador, Newfoundland, Nova Scotia, and the Gaspé Peninsula of Québec; it lacks a southward extension into México known for *S. simplex*. Tamamschyan (1959) included *S. multiradiata* var. *arctica* (DC.) Fernald as a member of the Siberian flora (as *S. compacta* Turcz.), and Hultén (1968) showed its distribution extending westward from Alaska across the Bering Strait.

Despite the numerous nomenclatural juxtapositions and their implications regarding possible evolutionary relationships between the American and Old World plants of the *Solidago virgaurea* complex, neither Cronquist nor Ringius & Semple have considered (in literature) the nature of their relationship. In recent accounts of the European flora (Wagenitz 1979; Clapham *et al.* 1987) and the Japanese flora (Kitamura 1965), the *S. virgaurea* complex is said to occur in North America. Indeed, close analogs for many eastern American plants of the *S. glutinosa* complex, as well as other taxa, can be found among Eurasian ones. The autochthonous origin and continental endemism of the North American taxa can be accepted as a pragmatic hypothesis until the complex can be studied from a broader perspective, but it seems likely that the relationship between Old and New World taxa may prove closer than currently recognized in American treatments.

I agree with Fernald (see above) that *Solidago macrophylla* and *S. calicicola* both approach the morphology of typical *S. virgaurea*, judging from three

specimens in the Linnaean herbarium (LINN) identified as the latter (LINN-fiche: 998.15-17). I also agree with his eventual elimination of *S. macrophylla* from such consideration, as there are not any Old World taxa with its distinctive floral and capitular features. A fourth Linnaean specimen identified as *S. virgaurea* (998.18) has more or less entire leaves in a basal cluster and is more similar to plants of the *S. simplex* complex. The wide variation (habit, leaf disposition, capitulescence form) in what is currently accepted as *S. virgaurea* suggests that the distinctions I have made among New World subsections of sect. *Solidago* may be artificial. Even the assignment of *S. virgaurea* itself to one of the New World groups is problematic.

The geographic range of *Solidago virgaurea* (sensu lato, as recently considered) extends from the west coast of Europe immediately north into Arctic regions, south as far as North Africa, to the east coast of Asia as far north as the Bering Sea islands. Subsp. *virgaurea* occurs widely throughout Europe, to North Africa and western Asia in the Caucasus and western Siberia (Wagenitz 1979). The geographic distinction of subsp. *virgaurea* from subsp. *minuta* (L.) Arcangeli is not clear, but the latter is said to occur primarily at higher elevations in the mountains of east, central, and northern Europe (McNeil 1976), and as far east as Nepal (Hara *et al.* 1982). Subsp. *leiocarpa* (Benth.) Hultén reportedly occurs from the Himalayas through China to Japan and the Bering Sea Islands (Hara *et al.* 1982); Takasu *et al.* (1980) recorded its occurrence in Japan, the Kuril Islands, Kamchatka, and Sakhalin. Subsp. *gigantea* (Nakai) Kitamura and subsp. *asiatica* Kitamura also occur in eastern Asia. In Japan, five varieties of *S. virgaurea* are recognized along with one closely related endemic species (Kitamura 1965).

Recent European floristic treatments (*e.g.*, McNeil 1976; Wagenitz 1979; Clapham *et al.* 1987) have recognized *Solidago virgaurea* as a single species with many varieties spread among several subspecies. Clapham *et al.* (1987, p. 841) noted that it is "Very polymorphic, with many named varieties differing in stature, pubescence, size, shape and serration of lvs, branching of infl. and size of individual heads." Detailed studies of east Asian plants also show the species to be markedly variable in vegetative and floral characters (Takasu *et al.* 1980). Transplant studies by Turesson (1925, 1930, 1931) showed that the species is highly plastic phenotypically as well as capable of forming locally adapted ecotypes. Experimental manipulation of ambient environmental factors demonstrated similar plasticity (Kawano & Takasu 1972).

Recent treatments of Chinese *Solidago* have recognized only three native species (Ling *et al.* 1985; Hu 1965-72). In contrast, however, to the conservative treatment of a single, highly variable *S. virgaurea*, a number of species are currently segregated from it in Russia, where 10-15 are said to exist (Kemularia-Nathadze 1938; Tamamschyan 1959; Cherpanov 1981). Further, as previously noted in the present paper, the morphological variability within east Asian *Solidago* extends across the boundaries of what are here considered several

subsections of sect. *Solidago*, and the recognition of a number of separate species may be justifiable. The taxonomy of Old World taxa of *Solidago* is badly in need of review and detailed study. With a clearer understanding there, the broader patterns of variation and the problems in inter-continental taxonomy can be addressed.

VARIATION IN *SOLIDAGO* - MORPHOLOGY OF THE CAPITULESCENCE

Cronquist (1980) observed that critical characters for identification of species of *Solidago* are in the nature of the capitulescence, the nature and disposition of the leaves, and the nature of the underground parts. Of these, however, the arrangement of the heads appears to be the most significant in the interpretation of phylogeny. Species of *Solidago* may be divided roughly into four groups, based on their general type of capitulescence: (1) corymboid, distinctly flat-topped, (2) thyrsoïd, a number of relatively elongated flowering branches forming a narrow to broad column, mostly above the well-developed cauline leaves, the lower branches sometimes distinctly elongated and independently thyrsoïd, (3) axillary, the flowering branches distinctly separated along the stem and shorter than subtending, well-developed, cauline leaves, and (4) the heads secund on the flowering branches, these ascending-recurved and forming a loose to relatively dense, pyramidal panicle.

Distinctly flat-topped capitulescences are characteristic of the generic groups hypothesized to be closely related to *Solidago* (Nesom 1991c), as well as of some species groups of the genus *Aster* L. that have features suggestive of a close relationship to *Solidago* (Nesom in prep.). Among the genera of the *Gutierrezia* lineage (Fig. 1), they are produced almost invariably. They are common among genera of the *Chrysothamnus* Nutt. and *Amphipappus* Torr. & Gray groups (Fig. 1), although the variability there in capitulescence form is considerably more pronounced than within the *Gutierrezia* lineage, ranging from dense, strictly flat-topped capitulescences of small heads to solitary and much larger heads. In some species of *Chrysothamnus*, as well as *Gutierrezia*, the capitulescence is opened into a broad panicle; a parallel modification has occurred in some groups of North American *Aster*, e.g., subg. *Symphotrichum* (Nees) A.G. Jones. The capitulescence of *Tonestus* and *Columbiadoria*, while often approaching corymboid, is commonly more open or tends to become racemoid. While this "relaxation" of the corymboid form produces capitulescences somewhat similar to those in *Solidago*, they do not appear to be homologous. This modification of form appears, instead, to be more analogous to that found in the *Heleastrum* group of North American *Aster*: most species produce a strictly corymboid capitulescence, but *A. hemisphericus* Alex. produces a racemose one, immediately derived from the corymboid form found in

its sister species, *A. paludosus* Ait. Corymboid capitulescences are produced in *Oligoneuron* and *Oreochrysum*, which have at times been included within the genus *Solidago*, as well as in a few species of *Solidago* sensu stricto (as recognized here): i.e., species in subsect. *Solidago*, subsect. *Thyrsoiflorae*, and subsect. *Junceae*; see comments above in the taxonomic section).

Because corymbs are the prevalent capitulescence type in every major group of American Solidagininae (except *Solidago*), as well as its potential ancestors, they appear to be the ancestral arrangement for the subtribe, and the few species of *Solidago* with such a capitulescence might be interpreted as relictual species retaining the primitive condition. The flat-topped capitulescences within *Solidago*, however, probably are not strictly homologous with those in the rest of the subtribe, this suggested by the observation that in the few *Solidago* species where they occur, they vary from flat-topped to rounded (capitate) or elongated (short-thyrsoid), thus approaching the more typical thyrsoid arrangement. Further, flat-topped capitulescences occur in three separate groups of *Solidago*, and if they are primitive within the genus, it would be necessary to postulate two independent transitions from a corymboid to thyrsoid capitulescence and one other from corymboid to paniculate-secund. This is possible, but it is simpler to assume that the thyrsoid form is primitive within *Solidago* (but derived within the subtribe from the corymboid form) and as such is an apomorphic feature allowing the recognition of *Solidago* as a monophyletic group. In this interpretation, flat-topped capitulescences in species of *Solidago* (sensu stricto) are secondarily and independently derived from thyrsoid ones characteristic of immediately related species.

Within *Solidago*, it is clear that "thyrsoid" and "axillary" capitulescences are closely related. Axillary clusters may be derived from a thyrsoid arrangement by a strong reduction in length of the flowering branchlets; the lower portion of a narrowly thyrsoid capitulescence sometimes breaks up into axillary clusters, and the distinction between the two types becomes somewhat arbitrary. The thyrsoid form is most similar to the corymboid one and most easily re-formed (apparently) into one that is flat-topped or nearly so.

The manner and evolutionary point of origin of the "secund" capitulescence within *Solidago* are not clear, but it is reasonable to assume that this specialized, asymmetrical form arose from a more symmetrical, thyrsoid ancestor. The secund form is found elsewhere in the Astereae particularly in the *Gutierrezia* lineage, where it has been independently derived in the monotypic genus *Thurovia* Rose and in some seemingly aberrant individuals of *Gutierrezia texana* (DC.) Torr. & Gray. The typical capitulescence in *G. texana* is paniculate, but the ancestral form for both *Gutierrezia* and *Thurovia* is corymboid. A similar capitulescence (secund) also occurs in some species of North American *Aster* (e.g., *A. ericoides* L., *A. lateriflorus* [L.] Britt.), where the immediately ancestral form also is more or less thyrsoid or broadly paniculate. Within *Solidago*, the secund capitulescence is here regarded as a specialization

delimiting a monophyletic group (identified as sect. *Unilaterales*).

In some species of *Solidago* sect. *Unilaterales* (e.g., subsect. *Maritimae*), the secund arrangement of heads may be obvious only in the lowermost branches of the capitulescence. In other species that typically produce a secund capitulescence (in various subsections, e.g., *S. mollis*, *S. lepida*, the *S. spectabilis* group), the heads instead sometimes appear to be borne in a broadened thyrs (but not at all flat-topped). Semple & Ringius (1983) observed that the capitulescence of *S. missouriensis* in Ontario is not secund although it is strongly so elsewhere in its range. The cause of such variability is not clear, but at least it is possible that it reflects an influx of genes from distantly related species within sect. *Solidago*. Hybridization occurs between species of sect. *Solidago* and sect. *Unilaterales* (Fernald 1950), and the hybrids produce capitulescences intermediate in morphology.

PHYLOGENETIC POSITION OF *SOLIDAGO*

A hypothesis regarding the phylogenetic position of *Solidago* and other genera closely related to it is shown in Figure 1. This generalized hypothesis is based on relatively few characters (Table 1) but ones that appear to be useful in indicating directions of phylogeny. The determination of polarities is based on observations above (regarding the capitulescence) and in the following discussion. Additional features of significance in delimiting the generic groups are discussed in the text. Some aspects of the present discussion were introduced earlier (Nesom 1991a, 1991b). The addition of the genus *Sericocarpus* (most recently placed in *Aster*) as a member of this group is discussed in Nesom (1993a). Earlier, I noted that the South American *Chiliotrichum* Cass. group was potentially among the close relatives of *Solidago* (Nesom 1991c), but this is clearly not the case (Nesom 1993b). The broader phylogenetic position of this and other extra-North American genera of Astereae will be considered in separate papers (Nesom in prep.).

The group of genera including *Solidago* in Fig. 1 appears to be holophyletic, and it is strictly equivalent to the Solidagininae, if that subtribe is accepted. This subtribe appears to be derived from ancestors closely related to *Aster* (Nesom in prep.). With two exceptions, the Solidagininae (in the present sense) is entirely North American: *Gutierrezia* has reached South America and radiated there, and *Solidago* has primitive species groups in both the New and Old Worlds as well as an endemic species in South America. This definition of the subtribe contrasts strongly with the corresponding group (in terms of genera and generic groups included) defined in the study by Zhang & Bremer (1993). Of the nine genera (each representing a generic group) included in their Solidagininae (their Figs. 2-4), only three are accepted in the present view: *Solidago*, *Petradoria*, and *Gutierrezia*. Of the other six, three

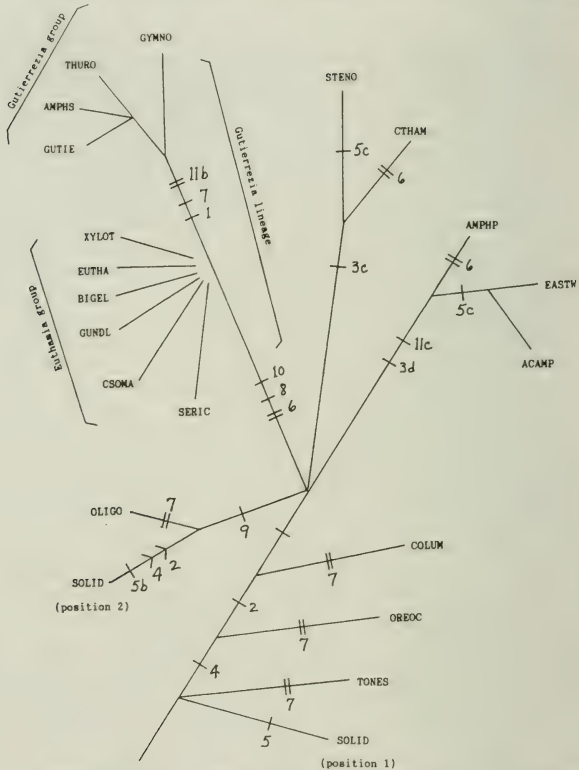


Figure 1. Phylogenetic hypothesis for subtribe Solidagininae (see further comments in text). The genera represented are the following: *Acampopappus* A. Gray (ACAMP), *Amphiachyris* (DC.) Nutt. (AMPHS), *Amphipappus* Torr. & Gray (AMPHP), *Bigelovia* DC. (BIGEL), *Chrysoma* Nutt. (CSOMA), *Chrysothamnus* Nutt. (CTHAM), *Columbiadoria* Nesom (COLUM), *Eastwoodia* Brandeg. (EASTW), *Euthamia* (Nutt.) Nutt. (EUTHA), *Gundlachia* A. Gray (GUNDL), *Gutierrezia* Lag. (GUTIE), *Gymnosperma* Less. (GYMNO), *Oligoneuron* Small (OLIGO), *Oreochrysum* Rydb. (OREOC), *Sericocarpus* Nees (SERIC), *Solidago* L. (SOLID), *Stenotus* Nutt. (STENO), *Thurovia* Rose (THURO), *Tonestus* A. Nels. (TONES), and *Xylothamia* Nesom *et al.* (XYLOT). Single slash = apomorphy; double slash = parallel apomorphy; back arrow = reversal.

Table 1. Characters and character states for subtribe Solidagininae (see further comments in text).

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1. Base chromosome number, (a) $x=9$, (b) $x=5$ and 4
 2. Leaves, (a) stipitate-glandular or non-punctate, (b) resinous, punctate-glandular (except for *Chrysoma*, which is further derived; see Nesom 1991c and Anderson & Creech 1975)
 3. Leaf venation, (a) net-veined, (b) with 1-2 pairs of parallel veins, (c) with 3 strongly raised, parallel veins, (d) with a single, central nerve (midvein)
 4. Leaf margin, (a) toothed, (b) entire
 5. Capitulescence, (a) corymboid, (b) thyrsoid or secund, (c) solitary heads
 6. Heads, (a) mostly pedicellate, (b) mostly sessile, in glomerules
 7. Disc corolla lobes, (a) lanceolate, deeply cut, reflexing-coiling, (b) deltate, shallowly cut, erect
 8. Phyllaries, (a) without a strongly differentiated apical patch, the midvein usually more or less continuous from base to tip, (b) with a viscid apical patch, the midvein weak and visible only in the distal portion
 9. Phyllary veins, (a) without parallel resin ducts, (b) accompanied by orange resin ducts
 10. Achenes, (a) more or less elongated, strigose to glabrous, (b) turbinate, densely strigose-sericeous
 11. Pappus, (a) of bristles, (b) of awns or scales, these mostly strongly reduced, sometimes absent - the *Gutierrezia* group, (c) of awns or scales, these relatively elongated - the *Amphipappus* group
-

belong in the *Machaeranthera* Nees group (*sensu* Morgan & Simpson 1992): *Haplopappus* DC., *Corethrogyne* DC., and *Grindelia* Willd.; *Chrysopsis* (Nutt.) Ell. belongs in the goldenaster group (*sensu* Nesom 1991c); *Engleria* Hoffm. is closely related to the *Felicia* group; and *Pteronia* L. (considered by Zhang & Bremer to be closely related to *Engleria*) and *Ericameria* Nutt. are members of the subtribe Hinterhuberinae (*sensu* Nesom 1993b).

Apart from *Solidago* itself (with respect to capitulescence) and various other specialized taxa, the subtribe Solidagininae is characterized by a combination of the following features, most of which are correlated in their occurrence, and all of which have more specialized conditions within the group: (1) a base chromosome number of $x=9$, (2) leaves punctate, often resinous as well, mostly entire, (3) heads in a distinctly flat-topped (corymboid) capitulescence, (4) a pappus of capillary bristles (5) without a short, outer series, (6) ray flowers yellow, short, and few, or absent, (7) disc corollas abruptly broadened from the tube into the limb, the lobes narrowly lanceolate, deeply cut, and usually reflexing-coiling, (8) the collecting appendages of the disc style branches lanceolate, shorter than the stigmatic portion to nearly as long, with densely arranged sweeping hairs, the proximal hairs sometimes long-spreading but quickly reduced in length toward the style branch apex, where they commonly are no more than small papillae. Sometimes nearly all of the "sweeping hairs" are papilliform. All of these features occur in other Astereae, though not as a correlated group, and all except 2, 5, and 6 are apparently primitive among the Northern Hemisphere genera that are most closely related to the Solidagininae.

Within the Solidagininae, the "*Gutierrezia* lineage" is particularly coherent, comprising plants characterized by the following morphological features: (1) achenes small, turbinate, and densely strigose-sericeous, (2) heads sessile in glomerate clusters, and (3) phyllaries basally indurate, with a punctate or glutinous apical patch, the midvein weakly developed or inconspicuous. Additionally, all genera of the *Gutierrezia* lineage except *Sericocarpus* and *Chrysoma* have disc corollas abruptly expanded from a narrow tube into the limb and throat, the anther filaments inserted at the tube-limb junction. Similar corollas occur in various species of both major groups (sections) of *Solidago* as well as in species of *Chrysothamnus*. Outside of the Solidagininae, within North American Astereae, a similar corolla morphology also occurs in *Xanthocephalum* Willd. and its close relatives, where the corolla lobes are short relative to the limb — this variant has been referred to as "goblet shaped" (Lane 1982). With the lobes variably longer or shorter, abruptly ampliate disc corollas are also found in some species of *Erigeron* L., most genera of the Baccharidinae, most genera of Grangeinae as well as in Old World *Aster* and closely related genera. In fact, this corolla morphology is the most widespread among primitive elements of the Astereae.

The four genera of the "*Gutierrezia* group" form a group delimited by a reduced pappus, short disc corolla lobes, and a base chromosome number reduced from $x=9$ to $x=5$ and $x=4$ (*Gymnosperma* in this problematic interpretation is polyploid; currently under study). The specialized nature of these features is inferred from their correlated transition from states otherwise prevalent in the rest of the subtribe and from the coordinate phylogenetic status of the *Gutierrezia* group with the six genera of the "*Euthamia* group" (Fig. 1). Lane (1982) showed on the basis of morphology that the four genera of the *Gutierrezia* group are most closely related among themselves, and molecular evidence of Suh & Simpson (1991) provides corroboration of this relationship, showing additionally that these genera as a group are most closely related to the *Euthamia* group.

The genus *Solidago* (sensu stricto) can be identified by its thyrsoid (or secund) capitulescence, small, narrowly cylindrical to slightly fusiform achenes that are glabrous to sparsely strigose, and non-punctate leaves commonly with coarsely toothed margins. The leaf morphology and (to some extent) leaf disposition found in some species of *Solidago* are more similar to genera outside of the Solidagininae, such as *Heterotheca* Cass. and some groups of *Aster*, than to any other other genera of the *Gutierrezia* lineage (except for one species of the genus *Sericocarpus*, see Nesom 1993a).

The cladistic position of *Solidago* is somewhat equivocal, but the present study corroborates the previous suggestion that *Solidago* occupies a basal, and even perhaps isolated, position within the subtribe (Nesom 1991c). "Position 1" for it (Fig. 1) is the most parsimonious, given the assumptions that seem reasonable in the present study. In "position 2," two significant reversals must be assumed to have occurred in features otherwise characteristic of the subtribe: (1) the prominently toothed leaves prevalent among species of *Solidago* are secondarily derived from mostly entire ones, and (2) foliar punctations have been lost, then regained in a different form in two of the species. The molecular data of Suh & Morgan indicate that *Solidago* is more closely related to the strictly western North American elements of the subtribe than to the *Gutierrezia* lineage, but I have not been able to corroborate this on a morphological basis. This phylogenetic separation of *Solidago* is further emphasized by its geographic distribution: the primitive species groups are disjunct between Eurasia and eastern North America, and it is the only genus of Solidagininae that shows this pattern of ancient disjunction, one also found in *Aster* (Nesom in prep.).

As observed by Brouillet & Semple (1981), phyllary veins accompanied by conspicuous, parallel resin ducts occur in *Solidago*, *Oligoneuron*, and plants of the *Gutierrezia* lineage (mostly excluding the *Gutierrezia* group itself). The similarity in phyllary morphology is strongest between *Solidago* and *Oligoneuron*, and this is the only trait that might be regarded as a specialization shared by the latter two taxonomic groups. In fact, this feature must be empha-

sized if *Solidago* and *Oligoneuron* are placed as sister taxa. Dilated pappus apices occur in a few species of *Solidago* and one of *Oligoneuron*, but they also occur in *Acamptopappus*, *Amphiachyris*, all species of *Sericocarpus*, some of *Chrysothamnus*, and they are particularly common among primitive groups of *Aster* sensu lato hypothesized to be closely related to *Solidago*.

Amphipappus, *Eastwoodia*, and *Acamptopappus* are whitish-stemmed subshrubs of the southwestern United States that produce uninervate leaves without any other conspicuous nervation and broad (scaly) pappus elements that are probably derived from lateral fusion of bristles (Lane 1988). The first two genera produce large, solitary heads and on this basis are placed here in close relationship, although Lane (1988) has observed that the evolutionary origin of each of these three genera may have occurred with more independence. This trio is closely related to the "*Chrysothamnus* group," which comprises *Chrysothamnus* Nutt., *Stenotus* Nutt., *Petradoria* E. Greene, *Hesperodoria* E. Greene, and *Vancleavea* E. Greene. The basic composition of this latter group was described by Lane (1988), although she also included *Ericameria*; Nesom (1991b) referred to a somewhat more restricted group of these genera as "the *Petradoria* group," but that name is no longer appropriate, since very recent studies of Nesom & Baird (1993) and Baird (in prep.) indicate that all of these genera except *Stenotus* should be incorporated in an expanded concept of *Chrysothamnus* and separated from *Ericameria*, which is part of a different phylad. The molecular data of Suh (1989) and Suh & Simpson (1990) indicate to some extent that the genera of the *Amphipappus* and *Chrysothamnus* groups are closely related among themselves, and their geographic and ecological proximity and tendency toward white-stemmed shrubbiness probably also reflect their closeness of ancestry. These plants possess features diagnostic of the Solidagininae, but there is considerable variability, particularly in capitular and floral morphology (see Nesom [1991a] and Baird [in prep.]), and even in style branch morphology, capitular size, and the number and length of rays, features generally more consistent within the rest of the subtribe.

Tonestus apparently occupies a relatively primitive position within the Solidagininae. It is the only genus beside *Solidago* with net-veined, prominently toothed leaves. The reduced capitulescences and white corollas produced in some species appear to be anomalous, although the latter perhaps are reflective of the ancestry of the subtribe. Although *Tonestus* and *Oreochrysum* differ significantly in many features, both produce phyllaries with foliaceous apices (see further comments below), but there is little else to indicate they might be closely related.

The anatomical data presented by Anderson (1972) and Anderson & Creech (1975) fit the phylogeny and classification of *Solidago* advanced here, including the segregation of *Oligoneuron* and *Oreochrysum*, without essential contradiction, although their sample of taxa was incomplete within the Solidagininae. They found that isolateral mesophyll is mostly restricted to *Solidago* sect. *Uni-*

laterales; it occurs as well in *Oligoneuron*. Secretory cavities are present in the leaves of many species of sect. *Unilaterales* but mostly absent in those of sect. *Solidago* (except subsect. *Solidago*). Secretory cavities also are absent in the leaves of both *Oligoneuron* and *Oreochrysum*.

STATUS OF *OLIGONEURON*

In an earlier study (Nesom 1991c), I regarded the species of *Oligoneuron* (segregated as a genus by Small [1903]) as a group within *Solidago*. A review of the features, however, of *Solidago* and its relatives in surrounding portions of the Astereae now appears to support treatment of *Oligoneuron* as a separate genus rather than a group within *Solidago* itself. *Oligoneuron* appears to be a primitive element within the subtribe (Fig. 1), without any specialization that would clearly ally it with the *Gutierrezia* lineage or with the *Chrysothamnus* or *Amphipappus* groups. Weber & Wittman (1992) noted that they regard *Oligoneuron* "as distinct a genus as *Petradoria*;" although they provided no supporting rationale, their comment almost certainly was intended to point out an analogous position for the two groups rather than one of close relationship.

A critical piece of evidence in the present interpretation of the phylogenetic (and taxonomic) position of *Oligoneuron* has been the observation that its leaves (except apparently for *O. rigidum* [L.] Small) are punctate, although the punctations are sometimes obscure, especially on the upper surface. This feature apparently has not been observed or mentioned in recent literature, even in the morphological and anatomical studies by Kapoor & Beaudry (1966) and Anderson & Creech (1975). The only reference to such that I have found is by Asa Gray (1884), who noted that the leaves of *O. nitidum* (Torr. & Gray) Small are punctate. Torrey & Gray (1842, p. 210) had earlier observed that plants of the same species "exude small quantities of resin when wounded," a phenomenon otherwise unknown in *Solidago* (although a few species are glandular or "glutinous"). Sunken punctations occur almost without exception in plants of the *Gutierrezia* lineage, where there is a minute glandular trichome ("Type C trichome," Nesom 1976) in the center of each one. The punctations of *Oligoneuron* are similar. In *Solidago*, foliar punctations occur only in the leaves of *S. odora* and *S. chapmanii*, where they appear to be derived independently from those of the *Gutierrezia* lineage, apparently lacking the central trichome and subtended by resin cavities different in anatomy (Anderson & Creech 1975). The only species of *Solidago* that produce conspicuous glandular trichomes similar to those of the punctatae are those of subsect. *Thyrsiflorae* (which see for further comments).

Phyllaries in *Oligoneuron* are broadly oblong to oblong-obovate, distinctively broader than any in *Solidago*, and each one usually bears 5-7 (or more) translucent, parallel veins running from the base to the very apex. In *O. album* and sometimes in *O. houghtonii*, only a single vein per phyllary may be

present. A few species of *Solidago* have veins lateral to the midvein, but they are weakly developed and visible usually only near mid-phyllary, not extending fully to the tip and base. Further, although the translucent veins of *Oligoneuron* are similar to those in *Solidago*, they tend to be distinctly paler in color than the strongly golden-yellow ones (colored by associated resin ducts) of the latter genus.

The achenes of all taxa of *Oligoneuron* are large, plump, glabrous, and the thin, whitish to brownish, longitudinal nerves are beneath the achene surface. These contrast with achenes of *Solidago*, which are smaller and more slender and elongated. The achenial nervation in sect. *Solidago* is more similar to that in *Oligoneuron*; achenial nerves in sect. *Unilaterales* are often distinctly raised and associated with orangish resin ducts that are barely or not beneath the fruit surface.

The taxa of *Oligoneuron* are clearly distinguished in morphology (corymboid capitulescence, punctate leaves, broad phyllaries "striate" with parallel veins, and plump and glabrous achenes) from those of *Solidago*. Only two instances of hybridization have been suspected between them, and both are equivocal in interpretation (see comments below regarding \times *Solidaster*). If the phylogenetic position of *Solidago* proves to be similar to "position 2" (Fig. 1), *Oligoneuron* might be retained as a primitive subgroup within *Solidago*, but there it would be removed phenetically as well as genetically (judging from the relative paucity of natural hybridization) from any possibly related species of the genus. Further, the inclusion of *Oligoneuron* within *Solidago* would suggest that two other disparate and apparently primitive species of Solidagininae (the monotypic *Oreochrysum* and *Columbiadoria*) might also be placed in *Solidago*, each in positions analogous to that of *Oligoneuron*. *Oligoneuron* is here regarded as a distinct genus, with taxonomy as follows.

Oligoneuron Small, *Fl. Southeast. U.S.* [ed. 1] 1188. 1903. [22 Jul]. *Solidago* subg. *Oligoneuron* (Small) House, New York State Mus. Bull. 254:693. 1924. LECTOTYPE, designated here: *Solidago rigida* L.

Solidago sect. *Corymbosae* Torr. & Gray, *Fl. N. Amer.* 2:208. 1842.
LECTOTYPE, designated here: *Solidago rigida* L.

A. *Oligoneuron* sect. *Oligoneuron*

Various authors have referred to "sect. *Oligoneuron*" within *Solidago* (e.g., Gleason & Cronquist 1963; Correll & Johnston 1970; Brouillet & Semple 1981), but there is no indication that any such nomenclatural combination has ever been made formally. Semple (1992b) recently noted that the correct name at that rank within *Solidago* is sect. *Corymbosae* Torr. & Gray.

Rhizomes short; leaves net-veined, minutely punctate (distinctly to obscurely, or not so in most forms of *Oligoneuron rigidum*), entire to serrulate, the basal and lower spatulate with a long petiole, the cauline epetiolate, lanceolate or oblanceolate, barely reduced upward; heads in a distinctly flat-topped (corymboid) capitulescence; phyllaries with 3-5 (or more) parallel veins; rays yellow; achenes glabrous, 5-7 (10-20) nerved; pappus bristle apices attenuate.

Species included (Beaudry 1963; Semple & Ringius 1983; Heard & Semple 1988):

1. *Oligoneuron rigidum* (L.) Small, *Fl. Southeast. U.S.* 1188. 1903. BASIONYM: *Solidago rigida* L., *Sp. Pl.* (ed. 1) 880. 1753. (see Heard & Semple [1988] for complete synonymy).
 - a. *Oligoneuron rigidum* (L.) Small var. *rigidum*.
 - b. *Oligoneuron rigidum* (L.) Small var. *humilis* (T.C. Porter) Nesom, *comb. nov.* BASIONYM: *Solidago rigida* L. var. *humilis* T.C. Porter, U.S. Dept. Interior Misc. Publ. 4:63. 1874.
 - c. *Oligoneuron rigidum* (L.) Small var. *glabrata* (E.L. Braun) Nesom, *comb. nov.* BASIONYM: *Solidago rigida* L. var. *glabrata* E.L. Braun, *Rhodora* 44:3. 1942.
2. *Oligoneuron ohioense* (Riddell) G.N. Jones, *Trans. Illinois Acad. Sci.* 35:63. 1942. BASIONYM: *Solidago ohioensis* Riddell, *Syn. Fl. West. States* 57. 1835.

B. *Oligoneuron* sect. *Ptarmicoidei* (House) Nesom, *comb. et stat. nov.* BASIONYM: *Aster* sect. *Ptarmicoidei* House, *New York State Mus. Bull.* 254. 710. 1924. TYPE: *Aster ptarmicoides* Nees.

Unamia E. Greene, *Leaf. Bot. Observ.* 1:6. 1903. [24 Nov]. TYPE: *Oligoneuron album* (Nutt.) Nesom.

Rhizomes short; leaves parallel-veined, minutely punctate (distinctly to very obscurely in *Oligoneuron houghtonii* and *O. album*), entire to serrulate, the basal and lower oblanceolate without a well-defined petiole, the cauline oblanceolate, gradually reduced upward; heads in a distinctly flat-topped (corymboid) capitulescence; phyllaries with 3-5 parallel veins; rays yellow or white; achenes glabrous, 5-7 nerved; pappus bristle apices attenuate or clavate.

- * *Oligoneuron* ser. *Ptarmicoidei* (House) Nesom, *comb. et stat. nov.* BASIONYM: *Aster* sect. *Ptarmicoidei* House, New York State Mus. Bull. 254. 710. 1924. TYPE: *Aster ptarmicoides* Nees.

Ray flowers with white ligules, the pappus bristle apices distinctly clavate, and the phyllaries with a single, distinctly raised, central vein, commonly expanded near the apex into a broad gland-like structure.

3. *Oligoneuron album* (Nutt.) Nesom, *comb. nov.* BASIONYM: *Inula* (*Chrysopsis*) *alba* Nutt., *Gen. N. Amer. Pl.* 2:152. 1818. *Diplopappus albus* (Nutt.) Lindl. *ex Hook.*, *Fl. Bor.-Amer.* 2:21. 1834. *Heleastrum album* (Nutt.) DC., *Prodr.* 5:264. 1836. *Aster albus* (Nutt.) A. Eat. & J. Wright, *N. Amer. Bot.* 147. 1840. Not Willd. *ex Spreng.* 1826. *Eucephalus albus* (Nutt.) Nutt., *Trans. Amer. Philos. Soc.*, ser. 2, 7:299. 1841. *Unamia alba* (Nutt.) Rydb., *Fl. Rocky Mts. & Adj. Plains* 878. 1917. *Doellingeria ptarmicoides* Nees, *Gen. Sp. Aster.* 183. 1832. The epithet of this species in the genus *Doellingeria* Nees was proposed by Nees as a substitute for Nuttall's original, which should have been adopted. *Doellingeria* "*ptarmicoides*" Nees is thus superfluous and illegitimate, and subsequent combinations based on it must also be considered illegitimate. *Aster ptarmicoides* (Nees) Torr. & Gray, *Fl. N. Amer.* 2:160. 1841. *Unamia ptarmicoides* (Nees) E.L. Greene, *Leafl. Bot. Observ.* 1:6. 1903. *Solidago ptarmicoides* (Nees) Boivin, *Phytologia* 23:21. 1972. Not *S. alba* Miller 1768.

- * *Oligoneuron* ser. *Xanthactis* Nesom, *ser. nov.* TYPE: *Oligoneuron riddellii* (Frank) Rydb.

Differt a *O.* ser. *Ptarmicoidei* (House) Nesom praecipue ligulis luteis.

Ray flowers with yellow ligules, the pappus bristle apices slightly clavate (*Oligoneuron houghtonii*) to attenuate, and the phyllaries with several parallel veins (often 1-veined in *O. houghtonii*).

Species included:

4. *Oligoneuron nitidum* (Torr. & Gray) Small, *Fl. Southeast. U.S.* 1188. 1903. BASIONYM: *Solidago nitida* Torr. & Gray, *Fl. N. Amer.* 2:210. 1842.
5. *Oligoneuron riddellii* (Frank) Rydb., *Fl. Prairies & Plains Central N. Amer.* 799. 1932. BASIONYM: *Solidago riddellii* Frank in Riddell, *Syn. Fl. West. States* 57. 1835.

Solidago amplexicaulis Martens, Bull. Acad. Roy. Sci. Bruxelles 8:68. 1841. Not Torr. & Gray *ex Gray* 1884.

6. *Oligoneuron houghtonii* (Torr. & Gray *ex Gray*) Nesom, *comb. nov.* BASIONYM: *Solidago houghtonii* Torr. & Gray *ex Gray*, *Man. Bot. N. U.S.* (ed. 1) 211. 1848.

Oligoneuron album is *Aster*-like in general appearance (leafy stems, long, white rays on relatively large heads), and the species has been treated in *Aster* and as a monotypic genus (see taxonomic summary above). Boivin (1972) transferred it to *Solidago*, noting the high incidence of hybridization between it and other species of *Solidago* (= *Oligoneuron*). In its phyllary morphology, also, it is more similar to *Solidago* but not to any species of *Aster sensu lato* (Brouillet & Semple 1981); each phyllary has a translucent midvein nearly continuous from base to apex and sometimes an additional pair of similar, lateral veins. Anderson & Creech (1975) found a close similarity in leaf anatomy between *O. album* and the species of the *Oligoneuron* group, and Brouillet & Semple (1981) have summarized morphological, chemical, and geographical data in support of the treatment of this species within the *Oligoneuron* group. Jones (1980) excluded the species from *Aster* in her classification of the New World species.

Putative hybrids between *Oligoneuron album* (or any other species of *Oligoneuron*) and species of *Solidago* have been reported only between *O. album* and *S. canadensis*, and the interpretation of these is strongly equivocal (see below). In contrast, *O. album* is known to form natural hybrids with three yellow-rayed species of sect. *Oligoneuron* (Bernard 1969). Morton (1979) hypothesized that the hexaploid genome of *O. houghtonii* may even include that of *O. album*, the former species originating in an ancestral hybridization event between *O. album* and *O. ohioense*. As noted by Brouillet & Semple (1981), however, *O. album* and *O. houghtonii* are more similar to *O. riddellii*, a species not considered by Morton, in their 3-veined and strongly basally disposed leaves, and the latter is more likely to have been involved with *O. album* in the parentage of *O. houghtonii*.

Interspecific hybrids within *Oligoneuron* have been named as *Solidago*. They are formally transferred to *Oligoneuron* with the following combinations:

1. *Oligoneuron* × *lutescens* (Lindl. *ex DC.*) Nesom, *comb. nov.* BASIONYM: *Diplopappus lutescens* Lindl. *ex DC.*, *Prodr.* 5:278. 1836. *Diplopappus albus* [var.] *lutescens* [Lindl. *ex DC.*] Hook. *ex Torr. & Gray*, *Fl. N. Amer.* 2:160. 1841. The indication of varietal status, as implied by Hooker (*Fl. Bor.-Amer.* 2:21. 1834) was not validly published. *Solidago* × *lutescens* (Lindl. *ex DC.*) Boivin, *Phytologia* 23:22. 1972. *Aster*

- lutescens* (Lindl. ex DC.) Torr. & Gray, *Fl. N. Amer.* 2:160. 1841. *Unamia lutescens* (Lindl. ex DC.) Rydb., *Bull. Torrey Bot. Club* 37:147. 1910. (*O. alba* × *O. rigida*).
2. **Oligoneuron** × **krotkovii** (Boivin) Nesom, *comb. nov.* BASIONYM: *Solidago* × *krotkovii* Boivin, *Naturaliste Canad.* 94:647. 1967. (*O. alba* × *O. ohioense*).
 3. **Oligoneuron** × **bernardii** (Boivin) Nesom, *comb. nov.* BASIONYM: *Solidago* × *bernardii* Boivin, *Phytologia* 23:21. 1972. (*O. alba* × *O. riddellii*).
 4. **Oligoneuron** × **maheuxii** (Boivin) Nesom, *comb. nov.* BASIONYM: *Solidago* × *maheuxii* Boivin, *Phytologia* 23:21. 1972. (*O. riddellii* × *O. rigida*).

STATUS OF THE INTERGENERIC HYBRID × *SOLIDASTER*

× *Solidaster* Wehrhahn in Bonstedt, *Pareys Blumeng.* (ed. 1) 2:525. 1932. [described as a hybrid between *Aster* and *Solidago*].

× *Asterago* Everett, *Garden. Chron.*, ser. 3, 101:6, fig. 2. 1937. [*nom. illeg.*].

Solidaster × *luteus* M.L. Green ex Dress, *Baileya* 20:33. 1976. Brouillet & Semple (1981) treated the hybrid as a species of *Solidago* but made the nomenclatural transfer using an invalid name (*Solidaster luteus* "M.L. Green" vs. *Solidaster luteus* "M.L. Green ex Dress"). Articles by Yeo [1971] and Dress [1976, 1979] present the rationale for the belated validation of the name by Dress.

The original hybrid, which was thought to have been produced from an accidental cross between a naturalized *Solidago* and cultivated *Aster*, was discovered around 1910 in a nursery in Lyon, France (Ruys 1931; Bernard 1969). It was fertile and seeds of its progeny were sent to George Arends in Germany, who further propagated it. Arends (1931, p. 190) described the results: "The seedlings showed great diversities in colour and habit of growth. Some plants were nearly true *Aster ptarmicoides*, others being long and slender like a *Solidago*, and showing all shades of color from nearly pure white to golden yellow." It is clear, particularly from these early, first-hand descriptions, as well

as from the morphology of the plants, that "*Aster*" *ptarmicoides* (= *Solidago ptarmicoides* = *Oligoneuron album*) was one of the parents of \times *Solidaster*.

In his investigation of the parentage of \times *Solidaster*, Bernard (1969) reasonably considered other taxa of *Solidago* (sensu lato) besides *Oligoneuron album* that were known to occur as natives or adventives in the area of Lyon, based on a published regional flora cited by him: four native taxa of the *Solidago virgaurea* L. complex (*Solidago* subsect. *Solidago*) and a group of North American species naturalized in the area, including *Solidago caesia* L. and *Solidago flexicaulis* L. (each identified by a synonym, both in *Solidago* subsect. *Glomeruliflorae*), *Solidago canadensis* L., *Solidago gigantea* Ait., and *Solidago arguta* Muhl. (all of sect. *Unilaterales*), *Solidago rigida* (= *Oligoneuron rigidum*), and *Solidago graminifolia* (L.) Salisb. (= *Euthamia graminifolia* [L.] Nutt.). These taxa also are included in broader floristic treatments of the region (e.g., McNeil 1976; Wagenitz 1979), although they have not included *Solidago caesia* or *Solidago flexicaulis*. From among these candidates, Bernard chose *Solidago canadensis* as most likely for the second parent of \times *Solidaster*, but he provided few details regarding the selection process. Bernard did not specify what segment of the variable *S. canadensis* he was referring to, nor is it possible to decide from his characterization of that species. Further, his table of morphological comparisons between the two putative parents and the hybrid dealt with features that are not exclusive to either of his choices of parents. Although he noted that his hypothesis regarding the parentage was "fragile," it has not heretofore been reconsidered. Brouillet & Semple (1981) accepted the hybrid as a cross between *Solidago canadensis* and *Solidago ptarmicoides* (see further comments below).

Although Yeo (1971) did not question hypotheses regarding the parentage of \times *Solidaster*, he published observations on its morphology (pp. 29-32) contrasting with Bernard's approach: it "differs from *Solidago* in its almost perfectly symmetrical inflorescence, long pedicels, absence of clustering of capitula, and the pale ray corollas; from *Aster* it differs in its usually very small capitula and its yellow ray florets." The "capitula [are] not at all clustered, the branches not recurved or secund." Certainly, there is no hint of the distinctive capitulescence of secund branches characteristic of most forms of *Solidago canadensis* (also of *Solidago gigantea* and *Solidago arguta*) to be found in the hybrid, and although the capitulescence of \times *Solidaster* was described as "pyramidal" (Bernard 1969), no one has contradicted Yeo's accurate observation regarding its symmetry and lack of secund branches.

Solidago lepida DC. (perhaps = *Solidago elongata* Nutt.), which is sometimes treated within *Solidago canadensis*, produces small heads that are barely, if at all, secund on the branches of the capitulescence. In habit and disposition of leaves, it is a reasonable candidate for the parentage of \times *Solidaster*, but its leaves are not glutinous, the phyllaries are lanceolate with a single sunken vein and are not at all thickened even toward the base, and the disc corollas are

gradually broadened in width upward. Finally, *Solidago lepida* is not known to occur in Europe and must also be eliminated on this basis.

Of remaining European candidates for the second parent of \times *Solidaster*, *Solidago virgaurea* is improbable because of its relatively thin, non-viscid, basally disposed, distinctively petiolate leaves with serrate margins, virgate (though sometimes broad) capitulescence, relatively large heads, acute phyllary apices, and long ligules. The naturalized *Solidago caesia* and *Solidago flexicaulis* are also unlikely because of their highly distinctive capitulescence as well as other features.

Of all the species considered here as the second parent of \times *Solidaster*, *Euthamia graminifolia* best fits the expected morphology, particularly in its combination of (1) rhizomatous habit, (2) distinctly glutinous, narrow, mostly entire, and predominantly cauline leaves, (3) basally indurate phyllaries, (4) heads borne near the branch tips, not at all secund, and (5) goblet-shaped disc corollas. There are problems in this interpretation of parentage, most significantly the lack of obvious foliar punctations in the hybrid (present in both putative parents), the more conspicuously reticulate foliar venation (inconspicuous in both parents), and the more dense vestiture of longer hairs than usually found on either parent. A comparison of significant features of the hybrid and its putative parents is presented here.

The origin of the hybrid remains problematic and the unequivocal identification of its parents probably will require its experimental reconstruction. This is especially critical if it is not morphologically intermediate but more like one of the parents than the other. Indeed, many features of *Oligoneuron album* appear to be heavily weighted in the hybrid. In view of the hypotheses considered here regarding the generic status of *Oligoneuron* and the parentage of \times *Solidaster*, the plants known as \times *Solidaster* are still regarded as a true intergeneric hybrid, but one in which neither of the probable parents (*Oligoneuron* and *Euthamia*) is represented in its nothogeneric name ("condensed formula").

STATUS OF A PUTATIVE HYBRID INVOLVING *OLIGONEURON* *ALBUM* FROM CANADA

A plant recently collected from eastern Canada (Bruce Co., Ontario: *Semple & Brammall 2775 - WAT!*), has been identified by Semple as a hybrid between *Solidago canadensis* and *Oligoneuron album* (= *S. ptarmicoides*). The label indicates that this plant was the only one of its kind seen in the area but that *O. album*, *S. hispida*, and *S. juncea* were common there. The plant is clearly a *Solidago*, and it might be regarded as a small individual of *S. canadensis* aberrant in vestiture, leaf morphology, capitulescence, and other features. Its only features that could be construed as a contribution from *O. album*, the

HYBRID:

Habit: many stemmed from the base, probably rhizomatous.

Leaves: basal absent, the cauline even in size, not reduced upward, weakly 3-nerved with conspicuous reticulate venation, narrow, entire or with a few, shallow teeth on the distal half, not punctate but strongly glutinous.

Phyllaries: thick and basally indurate, midvein \pm continuous but thickened above, greatly narrowed below.

Receptacle: alveolate.

Heads: numerous, small, short pedicellate, borne near the branch tips in a broad panicle, often approaching corymboid.

Disc corollas: abruptly ampliate above the narrow tube, lobes long.

Style branches (disc flowers): lanceolate and flattened, apices merely papillate.

Achenes: sparsely strigose with very short hairs.

Pappus bristle apices (disc flowers): slightly dilated.

OLIGONEURON ALBUM:

Habit: 1-few stemmed from the base.

Leaves: basal persistent, the cauline strongly reduced upward, strongly to weakly 3-nerved, without conspicuous reticulate venation, narrow, entire or with a few, shallow teeth on the distal half, inconspicuously punctate, sometimes glutinous.

Phyllaries: thick and basally indurate, midvein \pm continuous but thickened above, greatly narrowed below.

Receptacle: alveolate.

Heads: few, large, long-pedicellate, solitary but in broad corymbs.

Disc corollas: gradually widened upward, lobes short.

Style branches (disc flowers): linear and somewhat terete, hispid from base to tip.

Achenes: glabrous.

Pappus bristle apices (disc flowers): dilated.

EUTHAMIA GRAMINIFOLIA:

Habit: many stemmed from the base, rhizomatous.

Leaves: basal absent, the cauline even in size, not reduced upward, strongly 3-nerved, without conspicuous reticulate venation, narrow, entire or with a few, shallow teeth on the distal half, conspicuously punctate, often strongly glutinous.

Phyllaries: thick and basally indurate, midvein only visible distally, not at all raised.

Receptacle: fimbriate.

Heads: numerous, small, sessile, borne in glomerules at the branch tips, in broad corymbs.

Disc corollas: abruptly ampliate above the narrow tube, lobes long.

Style branches (disc flowers): lanceolate and flattened, apices merely papillate.

Achenes: strigose.

Pappus bristle apices (disc flowers): attenuate.

whitish ligules and dilated pappus apices, are also found in *S. bicolor* and *S. hispida*, both of which occur in Ontario, although *Semple & Brammall 2775* shows little morphological affinity to either of those. It is hardly similar to *S. juncea*, nor can it be identified as any species reported from Ontario (Semple & Ringius 1983) or anywhere else. It might be a hybrid in which the synergy of a peculiar combination of genes has masked its parentage, but since one of the parents (*vide* Semple's interpretation) was not in the area of its putative hybrid offspring, there is no compelling reason that the other should have been there. Although neither *S. canadensis* nor *O. album* can be unequivocally eliminated as a parent, there is little evidence to indicate that either, and especially the latter, was involved.

The following description briefly characterizes *Semple & Brammall 2775*: stems 3 from the base, slender and ascending, 28-37 cm tall, unbranched below the capitulescence, glabrate; leaves glabrate, weakly 3-veined but strongly reticulate, narrowly oblanceolate, shallowly serrate, not punctate or resinous, all cauline (the few near the base withered), evenly distributed and becoming shorter upward; capitulescence a small (ca. 17-22 heads), dense, nearly capitate, terminal cluster 2.0-2.5 cm wide and 2-3 cm long; heads 4-5 mm wide, the longest phyllaries 3.0-3.5 mm long, on filiform pedicels 2-4 mm long; phyllary midvein not expanded distally; disc flower style branches with triangular-deltate collecting appendages; ray flowers with creamy ligules ca. 2 mm long; achenes immature but apparently glabrous; pappus bristles slightly clavate at the apex.

STATUS OF THE MONOTYPIC GENUS *OREOCHRYSUM*

Oreochrysum Rydb., Bull. Torrey Bot. Club 33:152. 1906. TYPE and only species: *Solidago parryi* (A. Gray) E. Greene = *Haplopappus parryi* A. Gray = *Oreochrysum parryi* (A. Gray) Rydb.

In recent floristic treatments, this species is variously treated within *Haplopappus* or *Solidago* or as a monotypic genus. In a recent study (Nesom 1991c), I maintained it within *Solidago*, but further observations have convinced me that its treatment as a monotypic genus is the most appropriate. The segregation of *Oligoneuron*, the only other group besides *Oreochrysum* with corymboid capitulescences that has recently been included within *Solidago*, and the conclusion that the thyrsoid capitulescence probably is primitive within *Solidago*, have been significant in formulating the decision regarding *Oreochrysum*. Hybrids between *Oreochrysum* and any other species of *Solidago* or *Oligoneuron* have not been reported.

In his transfer of *Haplopappus parryi* to *Solidago*, Greene (1894) observed that it is "near" *S. multiradiata* (subject. *Solidago* in the present treatment),

but he also noted similarities between it and *S. macrophylla* as well as the taxa of *Oligoneuron*. Rydberg (1906) noted that *Oreochrysum* resembles *Oligoneuron* in habit, but (p. 152) "the character of the involucre and the style appendages, however, distinguish it from *Oligoneuron* as well as from *Solidago* proper." Hall (1938) rejected its placement in either *Solidago* or *Oreochrysum* and maintained it as a monotypic section within *Haplopappus*. In its combination of corymboid capitulescence, disc flowers with narrowly funnellform corollas and short, erect corolla lobes, long style appendages of the disc flowers, and particularly in its barely graduated phyllaries without a continuous midvein (the outer often completely foliaceous), it is significantly removed in morphology from any putatively close relatives in *Solidago*, although reasonably close matches can be found for some of its individual features. On a morphological basis, *Oreochrysum* is set apart from *Solidago* primarily on the basis of its phyllary morphology and arrangement, and its markedly corymboid capitulescence, in combination with a suite of other characters unusual for *Solidago*.

Oreochrysum and *Tonestus* were distinguished as a pair in keys by Rydberg (e.g., 1917) based on their common production of phyllaries with foliaceous apices. The molecular data of Morgan & Simpson (1992) further suggest that *O. parryi* is more closely related to *Tonestus* than to *Solidago* itself. Plants of *Oreochrysum* and *Tonestus*, with a few in subsect. *Thyrsiflorae* (sect. *Solidago*), are the only ones among North American Solidagininae that produce glands on stipes above the leaf surface.

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TAXONOMY OF *SERICOCARPUS* (ASTERACEAE: ASTEREAEE)

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ABSTRACT

Sericocarpus is returned to generic status as a North American endemic hypothesized to be more closely related to relatives of *Solidago* than to *Aster* (or any other white-rayed taxa), where its five species have most recently been included. A technical description of the genus, key to the species, and taxonomic summary of *Sericocarpus* are presented. One new combination is proposed: *Sericocarpus oregonensis* Nutt. var. *californicus* (Durand) Nesom.

KEY WORDS: *Sericocarpus*, *Aster*, *Gutierrezia*, Asteraceae, Astereae, Solidagininae

Sericocarpus Nees has long had a standing and relatively complete nomenclature as a separate genus (see below), surviving even the conglomeritic approaches of Bentham (1873) and Gray (1884) to the concept of *Aster*. It is the element most recently accreted to *Aster* (Cronquist 1947, 1955) as well as one of the most disparate among the American taxa in that genus, as it is now broadly conceived. Gray (1880) regarded *Aster* subg. *Biotia* as "nearly related to *Sericocarpus*," but he never formally merged the latter with *Aster*. Regarding its addition, Cronquist concluded the following (1947, p. 148): "If *Aster* is to be accepted in the extended sense, however, *Sericocarpus* must follow the other segregates to intra-generic rank. The only basis on which the several species of *Sericocarpus* might be distinguished generically is their narrow, relatively few-flowered heads." His comparisons of these features to species of *Aster* (sensu lato) noted similar variation scattered in various other species of the genus, mostly in the *Doellingeria*, *Eucephalus*, and *Biotia* groups, providing him with sufficient evidence to submerge *Sericocarpus*. Most recent treatments of *Sericocarpus* have followed Cronquist by including it within *Aster*. Fernald (1950) and Ferris (1960), however, maintained it as a distinct genus, though without comment. Jones (1980) treated *Sericocarpus* as a subgenus of *Aster*;

Semple & Brouillet (1980a) treated it as a separate section (informally) within subg. *Aster*.

Notwithstanding Cronquist's considerably more lengthy discussion, Torrey & Gray (1841, p. 109) came closest to providing the best rationale for placing *Sericocarpus* within *Aster*. With regard to *A. gracilis* Nutt., they noted that Nuttall [*Gen. N. Amer. Pl.* 2:158. 1818] "correctly remarked the alliance of this plant to *Aster spectabilis* [Ait.] on the one hand (some forms of which it greatly resembles), and to *Sericocarpus conyzoides* (Willd.) Nees [= *S. asteroides* (L.) B.S.P.] on the other: it almost connects the latter genus with *Aster*." Both *A. gracilis* and *A. spectabilis* are unequivocally members of subsect. *Spectabiles* A. Gray, a relatively primitive subgroup within North American *Aster*, and *A. gracilis* and *Sericocarpus* are indeed remarkably similar in their entire, evenly spaced leaves, turbinate-cylindric heads on short pedicels and contracted into a dense corymb, phyllary morphology, white rays, and dilated pappus apices. Critical features of *Sericocarpus*, however, place it with a group of primarily yellow-rayed genera closely related to *Solidago* L., although it certainly is one of the most primitive in the latter group. In my view, the parallel similarity between *A. gracilis* (and other *Spectabiles*) and *Sericocarpus* may reflect their common inheritance of genes from a not-too-distant ancestral matrix out of which the Solidagininae and a portion of North American *Aster* sensu lato arose (Nesom in prep.). The similarity of one of the species of *Sericocarpus* to *Solidago* was alluded to by Michaux in the epithet "solidagineus" (see below). Conversely, the *Aster*-like habit of another of the species was noted in one of the epithets applied to it.

The species of *Sericocarpus* are characterized most significantly by the following features: leaves punctate, sessile but not clasping, heads small, mostly cylindrical, sessile and glomerate or nearly so, borne in a relatively compact, flat-topped capitulescence; phyllaries strongly graduated in length, strongly whitish-indurated and slightly keeled in all but the apex, the apex with a sharply demarcated green patch; ray flowers few, white, and relatively short; disc flowers mostly white with relatively long, recurved-coiling lobes; collecting appendages of the disc style branches merely papillate toward the apex, not spreading hairy from base to apex; achenes densely hairy, mostly turbinate; and pappus bristles distinctly dilated at the apex. In its combination of flat-topped capitulescence, punctate leaves, floral morphology, and morphology of the collecting appendages, it is more closely similar to genera of the subtribe Solidagininae (Nesom 1991b, 1993) than to any species of *Aster* or related, white-rayed genera. Among *Solidago* and its relatives, the sessile-glomerate heads, and the relatively small, sericeous achenes are further specializations shared particularly with the "*Gutierrezia* lineage." Within this group, the relationships of *Sericocarpus* apparently lie most closely with a heterogeneous group of $x=9$ genera centered primarily in the eastern United States, including the white-rayed *Gundlachia* A. Gray and the yellow-rayed *Chrysoma* Nutt.,

Euthamia (Nutt.) Nutt., and *Bigelovia* DC. (Nesom 1993).

If *Sericocarpus* produced yellow rays, its overall resemblance to the subtribe Solidagininae would have been more quickly recognized. White rays are unusual in this predominantly yellow-rayed group, but they are present not only in *Sericocarpus* but also occur in one species of *Solidago* L. as well as other taxa in the subtribe: in the Caribbean genus *Gundlachia*, one species of *Oligoneuron* Small (Nesom 1993), several species of *Gutierrezia* Lag., and one species of the western North American *Tonestus* A. Nels. (Nesom 1991a). The monotypic *Thurovia* Rose of the *Gutierrezia* lineage is rayless but produces distinctly white disc corollas.

The cladistic analysis by Jones & Young (1983) placed *Sericocarpus* within *Aster* subg. *Aster* (sensu Jones 1980 as well as Semple & Brouillet 1980a) as the sister taxon to the *Spectabiles* group; all of these in turn formed the sister group to sect. *Radulini*, sect. *Biotia*, and sect. *Integrifolii*, all also of subg. *Aster*. In their phenetic analysis, and in the "branch-swapping" cladogram based on the initial topology of their published phenogram, the position of *Sericocarpus* changed radically from the "Wagner analysis" cladogram they displayed. A visual inspection of the Jones & Young data (character state changes were not shown on their cladogram) suggests that whatever characters linked *Sericocarpus* to subg. *Aster* must be significantly homoplasious. Further, at least two significant morphological specializations for inferring monophyly in this part of the Astereae were not included in their scoring and analysis: foliar punctations, these sometimes with a sessile-glandular cap, and the nature of the collecting appendages of the disc flower style branches. Among North American taxa that Jones (1980) regarded as *Aster*, punctations are found only in *Sericocarpus* and two other species (*A. nemoralis* Ait. and *A. reticulatus* Pursh); they also occur in two Eurasian species groups sometimes included in *Aster*: *Linosyris* Cass. and *Galatella* DC. Jones & Young did not report any variability in style branch morphology other than the shape and relative length of the disc style appendages.

The placement of *Sericocarpus* within subg. *Aster* (Semple & Brouillet 1980a; Semple *et al.* 1983; Jones & Young 1983) first reflected the implicit assumption that the species indeed belonged in the genus *Aster*. The more specific placement of *Sericocarpus* (by Semple & Brouillet) then relied primarily on chromosome number and similarities in phyllary morphology between *Sericocarpus* and the species of their subsect. *Aster* (the latter mostly equal to the *Spectabiles* group sensu Jones 1980). In a related study emphasizing chromosomal data, however, Semple & Brouillet (1980b) noted that the NOR chromosomes of *Sericocarpus* differed in morphology from those in the rest of the species in their subg. *Aster*, having instead the NOR morphology hypothesized by them to be primitive for *Aster* (sensu lato). While the phyllary morphology of *Sericocarpus* is similar to some species of *Aster* (a distinctly demarcated, green apical patch, indurated below), similar morphology also

occurs in groups outside of *Aster*, including some genera of Solidagininae.

The five species of *Sericocarpus* are split in distribution between the eastern and western United States, but there does not appear to be any correlated morphological division. *Sericocarpus asteroides* stands apart from all the rest of the species in its prominently toothed, basally disposed leaves; *S. tortifolius* (Michx.) Nees is distinctive from the others in the prominent resin globules associated with the punctate glands and also its twisted leaves; *S. linifolius* is distinctive in its lack of vestiture and nearly linear leaves. All are species of open to dry woodlands and margins except *S. rigidus*, which occurs on prairies. *Sericocarpus rigidus* is relatively rare and its reproductive biology has been studied in detail (Clampitt 1987). The chromosome number is uniformly $n=9$ within the genus, with reports for all taxa except *S. rigidus* (Anderson *et al.* 1974; Huziwara 1965; Jones & Smogor 1984; Pinkava & Keil 1977; Semple 1985; Semple & Brouillet 1980b; and Semple *et al.* 1983, 1989). There is no evidence of hybridization among any of the species or between *Sericocarpus* and any other genus.

The species of *Sericocarpus* are well-characterized in many regional treatments, but the last complete treatment of the genus was more than a century ago (Gray 1884). A taxonomic account of *Sericocarpus*, with formal summaries of the species taxonomy, is provided here. The species names as currently found in most literature are marked with an asterisk.

Sericocarpus Nees, *Gen. Sp. Aster.* 148. 1832. LECTOTYPE (Britton & Brown 1913): *Sericocarpus solidagineus* (Michx.) Nees = *Sericocarpus linifolius* (L.) B.S.P. *Aster* subg. *Sericocarpus* (Nees) A.G. Jones, *Brittonia* 32:238. 1980. *Aster* sect. *Sericocarpus* (Nees) Semple, *Phytologia* 58:429. 1985.

Aster sect. *Serratifolii* G. Don, *Hort. Brit.* 347. 1830. LECTOTYPE (Sundberg & Jones 1987): *Aster conyzoides* Willd. = *Sericocarpus asteroides* (L.) B.S.P.

Aster sect. *Leucoma* Nutt., *J. Acad. Nat. Sci. Philadelphia* 7:82. 1834. LECTOTYPE (designated here): *Aster tortifolius* Michx.

Oligactis Rafin., *Fl. Tellur.* 2:44. 1836. Not *Oligactis* (Kunth) Cass. 1825. TYPE: *Sericocarpus asteroides* (L.) B.S.P.

Perennial herbs, with stems erect, mostly unbranched below the capitulescence, with simple or short-branched caudices, arising from a short to long, fibrous-rooted rhizome. Leaves mostly 1(-3)-nerved, entire or toothed, mostly cauline (basally disposed in *Sericocarpus asteroides*), petiolate, not clasping, punctate, the punctae sometimes obscure. Heads small and mostly cylindrical, commonly sessile in glomerules, borne in a relatively compact, flat-topped

capitulescence; phyllaries in numerous series, strongly graduated in length, strongly whitish-indurated (cartilaginous) and slightly keeled in all but the apex, the apex greenish, sometimes squarrose. Ray flowers mostly 3-8, the ligules white, not coiling or only slightly so upon maturity or drying; disc corollas pale yellow to whitish, sometimes becoming purple (mostly in *S. asteroides*), narrowly tubular-funneliform without an abrupt dilation, the lower portion of the tube sometimes becoming indurate at maturity, the lobes relatively long, lanceolate, recurved-coiling; style branches with linear-lanceolate collecting appendages, the collecting hairs long at the base, quickly reduced to papillae on the distal region of the appendages. Achenes obpyramidal (to obconic in *S. oregonensis* Nutt. and *S. tortifolius*), moderately to densely sericeous; pappus of numerous barbellate bristles in 2-3 equal to subequal series (1[-2] series in *S. linifolius*), those of at least the inner florets slightly but distinctly dilated at the apex.

KEY TO THE TAXA OF *SERICOCARPUS*

1. Leaves mostly basally disposed, the lower with prominently toothed margins, the cauline reduced upward, becoming entire, punctations obscure or apparently absent, widespread in the eastern U.S. *S. asteroides*
1. Leaves all cauline, not reduced upward, the margins entire (or sometimes with a distal pair of teeth in *S. tortifolius*), punctations distinct or not. (2)
 2. Leaves linear-oblong to linear-oblancheolate, the lamina glabrous, distinctly punctate; widespread in eastern U.S. *S. linifolius*
 2. Leaves elliptic to elliptic-obovate or oblancheolate, the lamina hairy, foliar punctations distinct to obscurely visible. (3)
3. Leaves densely dotted with minute resin globules associated with the punctate glands; phyllary surface puberulent; southeastern U.S. *S. tortifolius*
3. Leaves punctate mostly on the lower surface, sometimes obscurely so, without resin globules; phyllary surface glabrous; western U.S. (4)
 4. Plants mostly 1-3 dm tall; leaves 2.5-3.5 cm long, lower surface not distinctly reticulate-veined; heads usually in a single cluster; ray flowers (1-)2(-3) per head, ligules 1-3 mm long; Washington and Oregon. *S. rigidus*
 4. Plants mostly 4-12 dm tall; leaves 4-8 cm long, lower surface distinctly reticulate-veined; heads usually in several to many separate

clusters; ray flowers (4-)5(-7) per head, ligules 4-7 mm long; Washington to California. *S. oregonensis* (5)

5. Leaves scabrous-puberulent; northcentral and northwest California to Washington. *S. oregonensis* var. *oregonensis*
5. Leaves densely hirsute or pilose; Sierra Nevada of western California. *S. oregonensis* var. *californicus*

1. *Sericocarpus asteroides* (L.) B.S.P., *Prelimin. Cat. N.Y. Pl.* 26. 1888. Not O. Kuntze 1891. BASIONYM: *Conyza asteroides* L., *Sp. Pl.* 2:861. 1753. *Aster asteroides* (L.) MacMillan, *Metasperm. Minn. Valley* 524. 1892. Not *Aster asteroides* (Colla) Rusby 1893. *Aster marilandicus* Michx. [*nom. nov. illeg.*], *Fl. Bor.-amer.* 2:108. 1803. Based on *Conyza asteroides* L. *Aster conyzoides* Willd. [*nom. nov. illeg.*], *Sp. Pl.* 3:2043. 1803. Based on *Conyza asteroides* L. *Sericocarpus conyzoides* (Willd.) Nees [*nom. illeg.*], *Gen. Sp. Aster.* 150. 1832. **Aster paternus* Cronq. [*nom. nov. illeg.*], *Bull. Torrey Bot. Club* 74:149. 1947. Based on *Conyza asteroides* L.

Sericocarpus asteroides (L.) B.S.P. f. *albopapposus* Farwell, *Pap. Mich. Acad. Sci.* 1:100. 1923.

Sericocarpus asteroides (L.) B.S.P. f. *roseus* Svenson, *Rhodora* 30:136. 1928.

Aster plantaginifolius Nutt. ex Nees, *Gen. Sp. Aster.* 299. 1832.

Aster leucanthemus Rafin., *Med. Repos.* 2, 5:359. 1803.

As observed by Cronquist (1947), the names in *Aster* proposed by Michaux and Willdenow, based on *Conyza asteroides* but with an epithet in replacement of "asteroides," were illegitimate, because that epithet was unoccupied in *Aster* at the time. The much later combination *Aster asteroides* (L.) MacMillan, however, was valid and legitimate, obviating the necessity for another new name for this species. Cronquist (p. 148) noted only that "the name *Aster asteroides* is preoccupied" but provided no details of citation or authority. Unless there is a yet earlier publication of some other "*Aster asteroides*," which I have been unable to find, Cronquist's *Aster paternus* is illegitimate and the correct name in *Aster* for this species is the combination by MacMillan.

2. *Sericocarpus linifolius* (L.) B.S.P., *Prelimin. Cat. N.Y. Pl.* 26. 1888. BASIONYM: *Conyza linifolia* L., *Sp. Pl.* 2:861. 1753. **Aster solidagineus*

Michx., [nom. nov.], *Fl. Bor.-amer.* 2:108. 1803. Based on *Conyza linifolia* L. (see Jones & Lowry 1986); not *Aster linifolius* L. 1753. *Sericocarpus solidagineus* (Michx.) Nees, *Gen. Sp. Aster.* 149. 1832.

Galatella obtusifolia Lehm., *Sem. Hort. Bot. Hamburg* 1837 [fide Torr. & Gray 1841].

3. *Sericocarpus oregonensis* Nutt., *Trans. Amer. Philos. Soc.*, ser. 2, 7:302. 1841.

a. *Sericocarpus oregonensis* Nutt. var. *oregonensis*. **Aster oregonensis* (Nutt.) Cronq., *Vasc. Pl. Pacif. Northw.* 5:91. 1955.

b. *Sericocarpus oregonensis* Nutt. var. *californicus* (Durand) Nesom, *comb. nov.* BASIONYM: *Sericocarpus californicus* Durand, *J. Acad. Nat. Sci. Philadelphia*, ser. 2, 3:90. 1855. *Sericocarpus oregonensis* Nutt. subsp. *californicus* (Durand) Ferris, *Contr. Dudley Herb.* 5:100. 1958. *Sericocarpus rigidus* Lindley in W.J. Hook. var. *californicus* (Durand) Blake, *Proc. Amer. Acad. Arts* 51:515. 1916.

4. *Sericocarpus rigidus* Lindley in W.J. Hook., *Fl. Bor.-amer.* 2:14. 1834. **Aster curtus* Cronq. [nom. nov.], *Vasc. Pl. Pacif. Northw.* 5:80. 1955. Based on *Sericocarpus rigidus* Lindley; not *Aster rigidus* L. 1753.

Sericocarpus rigidus Lindley in W.J. Hook. var. *laevicaulis* Nutt., *Trans. Amer. Philos. Soc.*, ser. 2, 7:302. 1841.

Galatella platylepis Nees ex Torr. & Gray, *Fl. N. Amer.* 2:103. 1841 [in syn.].

5. *Sericocarpus tortifolius* (Michx.) Nees, *Gen. Sp. Aster.* 151. 1832. BASIONYM: **Aster tortifolius* Michx., *Fl. Bor.-amer.* 2:109. 1803.

Conyza bifoliatus sensu Walt., *Fl. Carolin.* 204. 1788. Based on *Conyza bifoliatus* L. 1753. *Sericocarpus bifoliatus* (sensu Walt.) Porter, *Mem. Torrey Bot. Club* 5:322. 1894. *Nom. illeg.* *Aster bifoliatus* (sensu Walt.) Ahles, *J. Elisha Mitch. Sci. Soc.* 80:173. 1964. *Nom. illeg.*

Aster collinsii Nutt., *J. Acad. Nat. Sci. Philadelphia* 7:82. 1834. *Sericocarpus collinsii* (Nutt.) Nutt., *Trans. Amer. Philos. Soc.*, ser. 2, 7:302. 1841. *Sericocarpus tortifolius* (Michx.) Nees var. *collinsii* (Nutt.) Torr. & Gray, *Fl. N. Amer.* 2:103. 1841. *Sericocarpus bifoliatus* (sensu Walt.) Porter var. *collinsii* (Nutt.) Blake, *Proc. Amer. Acad. Arts* 51:515. 1916.

Sericocarpus bifoliatus (sensu Walt.) Porter var. *acutisquamosus* Nash ex Small, *Fl. Southeast. U.S.* 1206. 1903. *Sericocarpus acutisquamosus* (Nash ex Small) Small, *Fl. Southeast. U.S.* 1206. 1903.

As pointed out by Wilbur (1965), it was not Walter's intention to publish a superfluous name but rather to indicate the doubtful identity of the Carolinian plants with the Linnaean species.

Taxa excluded from *Sericocarpus*:

Sericocarpus sipei Henderson = *Aster vialis* (Bradshaw) Blake.

Sericocarpus tomentellus E. Greene = *Aster brickelliioides* E. Greene.

Sericocarpus woodhousei Buckley = *Isocoma pluriflora* (Torr. & Gray) E. Greene.

Jones (1980) included one Asian species, *Aster baccharoides* (Benth.) Steetz, in *Sericocarpus*. This species bears little resemblance to North American *Sericocarpus* but instead apparently is part of the *Aster ageratoides* Turcz. complex in Asia.

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**AZTECASTER (ASTERACEAE: ASTEREA), A NEW DITYPIC GENUS OF
DIOECIOUS SHRUBS FROM MEXICO WITH REDEFINITIONS OF THE
SUBTRIBES HINTERHUBERINAE AND BACCHARIDINAE**

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ABSTRACT

Aztecaster, *gen. nov.*, comprises two species endemic to México: *A. pyramidatus* (B. Robins. & Greenm.) Nesom, of Oaxaca, and *A. matudae* (Rzed.) Nesom, of San Luis Potosí, Zacatecas, Coahuila, and Nuevo León. Both species are glutinous, dioecious shrubs with white-pannose stems, ericoid leaves, heads in an open-spicate capitulescence, and flat achenes. They are the only dioecious species of Astereae not included in the subtribe Baccharidinae, where this sexual condition apparently has been independently derived. Most recently, the two species of *Aztecaster* have been treated as *Baccharis*, but based on features of vegetative, capitular, floral, and fruit morphology, they are more closely related to the North American genus *Ericameria* and a group of genera centered primarily in South America but also reaching Australasia and Africa. This is the subtribe Hinterhuberinae, originally described by Cuatrecasas but amended here to include about 20 genera of the Southern Hemisphere (e.g., *Chiliotrichum*, *Diplostephium*, *Hinterhubera*, *Pteronia*, *Rochonia*, and *Olearia*), in addition to the two North American ones (*Aztecaster* and *Ericameria*). The subtribe Baccharidinae is redefined to include five primarily Afro-Madagascan genera (*Microglossa*, *Psiadia*, *Psiadiella*, *Sarcanthemum*, *Vernoniopsis*) in addition to the three New World genera (*Baccharis*, *Archibaccharis*, *Heterothalamus*) of previous classifications.

KEY WORDS: *Aztecaster*, *Ericameria*, *Baccharis*, Astereae, Hinterhuberinae, Baccharidinae, Asteraceae, dioecy

Recent studies of the genera *Ericameria* Nutt. and *Chrysothamnus* Nutt. (Nesom 1990a; Nesom & Baird 1993; Baird in prep.) focus attention on anomalous species both previously and now included in those groups. One such

species excluded from *Chrysothamnus* has most recently been treated within *Baccharis* L. as *B. pyramidata* (B. Robins. & Greenm.) Rzed. (Rzedowski 1972), but even in the latter genus it has remained a peculiarity. In a taxonomic overview of the North and Central American species of *Baccharis* (Nesom 1990b), *B. pyramidata* was tentatively included in *Baccharis* sect. *Glandulocarpae* Nesom "largely on the basis of its similarity in habit and capitulescence to *B. pteronioides* [DC.], but its stiffly strigose achenes and peculiar ericoid leaf morphology are anomalous among the Mexican species. The species of the South American sect. *Discolores* DC. are similar in leaf morphology but have a different capitulescence as well as details of the phyllaries and achenes" (p. 43).

In addition to transferring *Bigelovia pyramidata* to *Baccharis*, Rzedowski (1972) described a related but geographically separate and morphologically distinct species as *Baccharis matudae* Rzed. In some earlier studies I annotated specimens of the latter as *Baccharis pyramidata* but now recognize that there are indeed two species. In the following discussion, these two are referred to as the "pyramidata pair."

Plants of *Baccharis pyramidatus* were first described as a species of *Bigelovia* DC. by Robinson & Greenman (1896), apparently following Asa Gray's broad concept of that genus (1884), which included shrubby species now apportioned primarily among *Ericameria*, *Chrysothamnus*, and *Isocoma* E. Greene. Its original authors described *Bigelovia pyramidata* as "anomalous in its spicate-paniculate inflorescence but with the other characters of *Bigelovia*" (p. 43), but apart from this observation and the formal description, they provided no other comments regarding its relationship. In their re-segregation and consolidation of *Chrysothamnus*, Hall & Clements (1923) removed from Gray's *Bigelovia* a group of species, including *Bigelovia pyramidata*, that they regarded as constituting *Chrysothamnus*. Their primary criteria for recognizing the latter genus were discoid and cylindrical heads and alignment of phyllaries (involucral bracts) in vertical ranks (see further comments in Nesom & Baird 1993). Hall & Clements described the phyllaries of *C. pyramidatus* (B. Robins. & Greenm.) Hall & Clements, however, as having "ranks obscure" and noted (p. 197) that "The exact position of *C. pyramidatus* in the genus is not certain, but it is placed in the [sect.] *Nauseosi* because of the pannose tomentum of the twigs. The decidedly spicate or subracemose inflorescence is suggestive of a remote relationship with *C. parryi*." They provided no other comments regarding the taxonomy of *C. pyramidatus*, but they placed it basally in sect. *Nauseosi* (their Fig. 25), coordinate in position with the other two species, noting (p. 164) that it "separated from the original stock [of sect. *Nauseosi*] in early times." Blake's subsequent transfer of the species to *Haplopappus* (1926) was not accompanied by any comment, but he returned it to a large, diverse genus, one that included most of Gray's *Bigelovia* and more. In Blake's key, however, the species was identified in the vicinity of species of *Ericameria*.

It was not until 1972 that Rzedowski discovered *Bigelovia* (or *Chrysothamnus*) *pyramidata* to be dioecious and that the previous descriptions and assessments of its taxonomic position had been based on plants bearing heads with only staminate flowers. His ensuing decision to place it in *Baccharis* was reasonable, as dioecious species of Astereae have previously been reported only in this and two other closely related genera of American Baccharidinae (see below). The species has been excluded from *Chrysothamnus* in recent studies (e.g., Anderson 1986) in favor of a position in *Baccharis*. The only other comment that I am aware of regarding this species is from an informal study and specimen annotation by B.L. Turner in 1976 (before he was aware of Rzedowski's publication); Turner noted that it is similar to species of *Haplopappus* that are now treated within the genus *Ericameria* (Nesom 1990a).

As observed by Rzedowski (1972) and Nesom (1990b), the ericoid leaves of *Baccharis pyramidata* are similar to those in some species of South American *Baccharis* sect. *Discolores*. While *Baccharis* is highly diverse in vegetative morphology and the arrangement of heads, resulting in the recognition of about 20-25 formally described sections, the genus is considerably more uniform in features of its phyllaries, flowers, and achenes. In all species of *Baccharis* (with reference to *B. pyramidata*), the phyllaries are more foliaceous, never completely indurated, the apex of the pistillate corollas is represented by a single, small ligule or the tube is apically truncate and merely fimbriate, the sinuses of the staminate corolla lobes are cut nearly to the base of the throat, the staminate style branches are relatively short with abruptly obtuse apices, and the achenes are mostly 0-1.5 mm long, rarely longer, terete or slightly compressed, never flattened, usually glabrous to moderately strigose, uncommonly with glands, and produce 5-11 ribs or nerves. Two other dioecious or polygamo-dioecious genera of American Baccharidinae, *Archibaccharis* Heering and *Heterothalamus* Less., are essentially similar to *Baccharis* in these features, except for the staminate corollas of *Heterothalamus*, which have short lobes.

Baccharis pyramidata and *B. matudae* are anomalous in all of the features noted above as characteristic of Baccharidinae. The heads of these species have strongly indurate phyllaries, actinomorphic pistillate corollas with five apical lobes, staminate corolla lobes with sinuses cut about halfway to the base of the throat, staminate styles with long, strongly tapering branches and appendages, and achenes that are mostly 2.5-3.0 mm long, distinctly flat with two lateral nerves, and moderately to densely strigose. If these two species are to be included in *Baccharis*, they would have to be placed in a subgeneric taxon coordinate in rank with all of the rest of the genus. Alternatively, in their shrubby habit, production of resin, pannose vestiture, narrow ericoid leaves, discoid heads, the morphology of the style branches of the staminate flowers (stigmatic lines absent, concomitant with ovary sterility), and achene morphology, *B. pyramidata* and *B. matudae* have a strong overall similarity to plants of the genus *Ericameria* Nutt. Such a similarity clearly led to the

earlier classification of *B. pyramidata* near species of *Ericameria*, prior to its alignment with *Baccharis*.

The placement of *Bigelovia pyramidata* in *Chrysothamnus* by Hall & Clements (1923) presumably (though unstated by them) was on the basis of their overall similarity and particularly because of their common production of vertically aligned phyllaries. While *Ericameria* and *Chrysothamnus* apparently are phylogenetically distant from each other (see Nesom & Baird 1993), differences between the two are obscured by convergence in many of the morphological features that serve to separate them. The placement of the pyramidata pair in one or the other of these genera would be correspondingly problematic, but the open-spicate capitulescence, long, tapering style branches, and relatively short, flat, few-nerved achenes are features characteristic of *Ericameria* rather than *Chrysothamnus*. Further, this species would be anomalous within *Chrysothamnus* (Baird in prep.). The species of sect. *Nauseosi*, where Hall & Clements originally placed *B. pyramidata*, are now transferred to *Ericameria* (Nesom & Baird 1993).

Baccharis pyramidata and *B. matudae* would also be isolated within *Ericameria*. The geographical range of this pair is completely separate from that of the 31 species of *Ericameria*, which have radiated entirely in the western and southwestern United States and adjacent México. Ericoid leaves are characteristic of sect. *Ericameria* and the pyramidata pair, but in contrast to those of the latter, leaves within sect. *Ericameria* are punctate-glandular. The pyramidata pair are similar to *Ericameria* sect. *Asiris* (H.M. Hall) Nesom in their keeled phyllaries without an orange midvein and their flattened and few-nerved achenes; they are similar to *Ericameria* sect. *Macronema* (H.M. Hall) Nesom in their pannose stem vestiture, heads in a spicate capitulescence immediately subtended by leaves. Their phyllaries lack a distinct apical apiculum or foliar appendage, which is characteristic of the latter two sections, and no approach to the dioecism of the pyramidata pair is found in *Ericameria*.

An examination of the ca. 185 genera of the tribe Astereae shows that the evolutionary relationships of the pyramidata pair can be placed within a broader context. These two species and those of *Ericameria* are part of a significantly larger generic group, here referred to as the subtribe Hinterhuberinae (Table 1). Here also, the geographical isolation, morphological distinctiveness, and the dioecy of the pyramidata pair provide the basis for treating these two species as the new genus *Aztecaster* (see below).

REDEFINITION OF THE SUBTRIBE HINTERHUBERINAE

Cuatrecasas (1969) erected the monotypic Hinterhuberinae to include the species of *Hinterhubera*, which are shrubby plants with sterile disc ovaries and regularly to irregularly lobed pistillate (peripheral) corollas (Cuatrecasas &

Aristeguieta 1956). He later (1986) expanded the group to include the herbaceous genera *Westionella* Cuatr., *Flosmutisia* Cuatr., and *Blakiella* Cuatr., which have similar peripheral corollas and sterile disc ovaries, but these belong in a clade apart from *Hinterhubera* (Nesom in prep.), as do two other herbaceous genera added to the "*Hinterhubera* group" by Zhang & Bremer (1993). The *Hinterhuberinae* as defined by Cuatrecasas was rejected by Zhang & Bremer, but upon the recognition of the wider generic relationships of *Hinterhubera*, it becomes the correct name for the group as a subtribe, here considered its appropriate rank. The generic composition of the subtribe, based on my morphological studies of the *Astereae*, is outlined in the present paper (Table 1), but a more detailed phylogenetic and taxonomic review is in preparation.

The *Hinterhuberinae* as a group is recognized by the following set of features. All except *Oritrophium* are shrubs. Most produce a dense, close, and persistent ("pannose") tomentum on the stems and leaves, and they produce leaves that are evergreen, coriaceous, commonly ericoid in morphology (linear to much broader but almost always with revolute margins and a raised abaxial midrib), and punctate in some of the American genera. Some species of *Ericameria* have thinner leaves. All of the South American genera except *Lepidophyllum*, *Parastrephia*, and *Hinterhubera* have at least some species that produce receptacular bracts (pales). The disc corolla lobes are commonly long but variable in length and the collecting appendages of the disc style branches also are highly variable in length. The ray corollas are primarily yellow but white to pink or blue in some (*Chiliotrichum*, *Diplostephium*, *Oritrophium*, the *Olearia* group, and the "asters" of Madagascar; there is a tendency for loss of ray flowers. The achenes are relatively large, commonly glandular, multi-nerved, and have a strong tendency to be nearly terete in outline, although distinctly flattened achenes also occur. The group has a remarkable geographic distribution: Madagascar, South Africa, South America, North America, and Australasia.

The largest subgroup within the *Hinterhuberinae*, the South American *Chiliotrichum* group, comprises a number of small genera endemic primarily to the southern Andean region, although it extends northward. It has been recognized in various taxonomic stages (Blake 1930; Cabrera 1937, 1944, 1945, 1953, 1954; Zhang & Bremer 1993). I suggested earlier (Nesom 1991) that part of this group might be included within the *Solidagininae* but now view the latter as much more distantly related to the *Hinterhuberinae* (Nesom 1993b). The first seven genera in Table 1 appear to be relatively closely related among themselves. *Aylacophora* and *Paleaepappus* could justifiably be combined with *Nardophyllum*, and there is only weak justification for separating *Parastrephia* from *Lepidophyllum*. In the original description of *Hinterhubera*, Weddell (1855) recognized its resemblance to *Diplostephium*, and Blake (1922) very early observed that *Chiliotrichum* is closely related to *Diplostephium* and *Hinterhubera*. The relationship of *Llerasia* to these genera, however, has not been

previously recognized. *Llerasia* was included by Zhang & Bremer in the *Haplopappus* group, where it has been treated previously as sect. *Diplostephioides* (Hall 1928; Blake 1927), but it is a distinct genus (Cuatrecasas 1969, 1970; Dillon & Sagástegui 1988) with diagnostic features of the *Hinterhuberinae*. Its species are particularly similar to some of *Diplostephium* in their broad leaves and a corymbiform-cymose capitulescence. In recent studies (Nesom 1992, 1993a), I suggested that *Oritrophium* might be most closely related to the North American *Oreostemma* E. Greene, but with further perspective it now appears more likely that *Oritrophium* is a highly derived member of the *Hinterhuberinae* (its only herbaceous member); the possibility of such a relationship was earlier noted by Cuatrecasas (1961).

The North American *Aztecaster* is the only other genus of *Hinterhuberinae* besides *Hinterhubera* with peripheral pistillate flowers apparently modified from disc flowers, both genera also produce flattened achenes and pseudo-hermaphroditic central flowers, and both lack receptacular pales. The relatively close geographic approach of *Hinterhubera* to *Aztecaster* also suggests that they may be closely related. *Hinterhubera*, however, is specialized and different from *Aztecaster* in its very small, closely appressed leaves, vestiture that tends to be glandular, terminal, solitary heads, and 2-3 series of pistillate (peripheral) flowers with long lobes.

Among all the genera of the subtribe, *Ericameria* is the second most variable (in leaf morphology, indument, capitulescence form, achene morphology, presence/absence/reduction of ray flowers) - *Olearia* is even more variable. *Ericameria* has been divided into four sections (Nesom 1990a), but because of significant intergradation among these morphological groups and hybridization in a number of wide parental combinations, the genus has appeared to be monophyletic. Its internal structure and the possibility of polyphyly, however, should be reconsidered in view of its newly hypothesized generic position. The relationship of *Ericameria* within the subtribe is not clear, but there is no particular evidence besides geography that would suggest it is closest to *Aztecaster*, especially in view of the probable close relationship between *Aztecaster* and *Hinterhubera*. *Ericameria* fits the pattern of North American desert shrubs derived from evolutionary antecedents in South America (Johnston 1940; Raven 1963), and it is a reasonable hypothesis that it is derived from plants similar to the yellow-rayed, ericoid-leaved, bristle-pappose *Chilophyllum* of arid, montane regions of Argentina and Chile. These latter species, however, are specialized in several features that suggest *Ericameria* could not have been derived from them (*i.e.*, paleate receptacles, glandular achenes). In fact, the relationship of *Ericameria* to any New World genus appears to be so tenuous that it seems possible its origin in North America was from now-extinct Old World ancestors in the Madro-Tertiary flora (Raven & Axelrod 1978), which arrived via an Afro-Eurasian route (Tiffney 1985; Taylor 1985, 1990). Such also seems to be the case for several other groups of western North

American Astereae of essentially Madrean affinities, e.g., *Rigiopappus* A. Gray and *Tracyina* Blake and *Monoptilon* Torr. & Gray, *Chaetopappa* DC., and *Pentachaeta* Nutt., which appear to be more closely related to *Felicia* Cass. and *Amellus* L. than to any New World species of the tribe (Nesom in prep.). The early Tertiary age associated with their origin is not inconsistent with the potential age of the Hinterhuberinae and other basal groups of Astereae. Further, as noted by Raven & Axelrod (1974, p. 604), "Probably a majority of families and many modern genera of seed plants had come into existence by the Paleocene."

A close relationship between *Nardophyllum* and the South African genus *Pteronia* was observed by Cabrera (1954), and my studies support this view in a general sense. *Pteronia* is a member of the Hinterhuberinae, where it is somewhat isolated; it does not belong with the *Chiliotrichum* group. The analysis by Zhang & Bremer placed *Pteronia* (with *Engleria*) as a basal group in their heterogeneous Solidagininae. Following Engler (1888), they positioned *Engleria* as the sister genus to *Pteronia*, perhaps on the basis of opposite leaves produced by plants of both genera, but the evolutionary affinities of *Engleria* lie with *Felicia* and closely related genera (Nesom in prep.). In addition to the African *Pteronia*, five Madagascan species previously regarded as *Aster* but clearly within the Hinterhuberinae have been recognized as the separate genus *Madagaster* Nesom (Nesom 1993c). The yellow-rayed Madagascan endemic *Rochonia* also belongs in this subtribe; its resemblance to *Madagaster* has been discussed by Nesom (1993c) and earlier by Humbert (1932, 1960), who also noted the strong resemblance of both groups of Madagascan species to *Diplostephium* and *Olearia*.

The composition of the *Olearia* group, which includes the five Australasian genera listed in Table 1, has been discussed in various papers by Drury (1968), Given (e.g., 1969, 1973), and most recently by Nesom (1992, with regard to the relationship between *Celmisia* and *Oritrophium*, and 1993c, with regard to the definition of *Olearia* and its relationship to the Madagascan species). The genus *Remya* Hillebr. ex Benth., considered to be a member of the *Olearia* group (Wagner & Herbst 1987; Zhang & Bremer 1993), is here tentatively excluded from the Hinterhuberinae. Lander (1989) recently segregated a species from *Olearia* as the monotypic genus *Apostates* Lander, which he retained in the Astereae. *Apostates* is similar in habit to some members of Hinterhuberinae, but the combination of its short, apically truncate style appendages, narrowly tapering achene base, and tailed anthers suggest that it is a member of the Inuleae rather than the Astereae. The anther bases of some of the Hinterhuberinae are similar in morphology (see Drury 1968; Given 1973; Zhang & Bremer 1993), but Zhang & Bremer also expressed their reserve regarding the position of *Apostates* by listing it among "isolated genera."

In the recent analysis by Zhang & Bremer, *Chiliotrichum*, *Olearia*, and *Hinterhubera* were positioned together as a subgroup of their subtribe Asteri-

nae (Fig. 3), united by "anther bases cordate or sagittate" and shrubby habit (although only *Hinterhubera* of their *Hinterhubera* group is shrubby). I do not consider the species represented here to be part of the Asterinae, which is a group almost wholly of the Northern Hemisphere (Nesom in prep.), although the two subtribes may be closely related. A more basal position within the tribe for the *Hinterhuberinae* is emphasized by its apparently ancient geographic distribution.

REDEFINITION OF THE SUBTRIBE BACCHARIDINAE

The only other primitively shrubby group of Astereae besides the *Hinterhuberinae* is the *Baccharidinae*, which also has a major disjunction between Africa and South America, but the two subtribes apparently are not particularly closely related. The *Baccharidinae*, whose definition here differs from any previous ones, comprises the American genera *Baccharis* L. (tentatively including *Baccharidastrum* Cabrera, *Baccharidopsis* Barroso, and other segregates), *Archibaccharis* Heering, and *Heterothalamus* Less. and the Afro-Asian *Microglossa* DC., the Afro-Madagascan *Psiadia* Jacq., the Madagascan *Psiadiella* Humbert and *Vernoniopsis* Humbert, and the Mascarene *Sarcanthemum* Cass. Zhang & Bremer's cladistic analysis of the Astereae (1993) placed the American genera as the sister group to the *Psiadia* group (including *Microglossa*, *Psiadia*, and *Psiadiella*, *Sarcanthemum* and two other extraneous genera), and positioned these together in a highly advanced position within their Asterinae. In contrast, I regard the *Baccharidinae* as a primitive group within the tribe (Nesom in prep.). *Psiadia* has sometimes been positioned with *Conyza* L. (e.g., by Hoffmann 1890 in the *Conyzinae*), but plants of *Conyza* and its close relatives are herbs with markedly different vegetative, floral, and fruit morphology. Zhang & Bremer placed *Vernoniopsis* in a group with the endemic Madagascan genus *Apodocephala* Baker, which I regard as an isolated, basal element of the Astereae.

Plants of the *Baccharidinae* are shrubs or small trees with small heads in a corymboid capitulescence, disc corollas with deeply cut, reflexing-coiling lobes, pistillate flowers with reduced corollas (pistillate flowers absent in *Vernoniopsis*) and commonly in several series, small achenes that are multinerved, rarely glandular, and essentially terete (though sometimes flattened, e.g., see Scott 1990), and there is a distinct tendency for the leaves to be punctate-glutinous. The central flowers are functionally staminate in *Psiadia*, *Psiadiella*, *Sarcanthemum*, some species of *Microglossa*, and in almost all of the New World species. Dioecy or a related condition is invariably characteristic of the New World species. Hypotheses regarding various pathways in the development of dioecy in the *Baccharidinae* have been recently discussed (Hellwig 1990; Zanolwiak 1991), but a broader hypothesis of the composition of the subtribe has not been previously put forward.

DEVELOPMENT OF DIOECY IN *AZTECASTE*

Dioecy in the Baccharidinae and in *Aztecaste* appears to have developed along two different pathways. In the ancestral Baccharidinae (the primarily Afro-Madagascan genera), heads are heterogamous with pistillate (peripheral) and staminate (central) flowers, the latter usually pseudo-hermaphroditic with sterile ovaries. The staminate flowers are of typical hermaphroditic morphology, actinomorphic with five apical lobes, but the style branches of these flowers lose the stigmatic lines, sometimes becoming connate for part of their length. The pistillate flowers are fertile and appear to be homologous with those in the rest of the tribe. The Baccharidinae pistillate corolla is unvascularized and commonly produces a short ligule that equals or exceeds the involucre bracts, but it is often merely an apically truncate or fimbriate tube.

The ovarian sterility of the American Baccharidinae is here interpreted as a trait or tendency inherited from an ancestor in common with their Old World relatives. In *Baccharis*, where dioecy and monoecy prevail, a single head produces only pistillate or staminate flowers; in *Archibaccharis*, the segregation of the sexes is incomplete, and the condition is referred to as polygamo-dioecious. The pistillate heads, predominantly with pistillate flowers, almost always bear a few, central flowers of hermaphroditic morphology that may or may not produce fertile ovaries (Jackson 1975). The staminate heads, predominantly with staminate flowers, more rarely produce a few peripheral, pistillate flowers. It seems clear that in the Baccharidinae, the dioecious condition has been preceded by loss of fertility (at least partially) in the ovaries of the central flowers and then has occurred as a result of the loss of either the pistillate or staminate flowers within a single head.

Dioecy appears to be strict in *Aztecaste*, with the heads either completely staminate or completely pistillate. The staminate (pseudo-hermaphroditic) flowers in these plants are morphologically and functionally similar to those of the Baccharidinae, and their ovarian sterility (or tendency for it) probably has been inherited in common with that of its close relatives in the Hinterhuberinae (i.e., *Diplostephium*, *Hinterhubera*). The pistillate flowers of *Aztecaste*, however, appear to be derived from typically hermaphroditic ones by a reduction in size and loss of the stamens. These pistillate corollas are tubular, regular, and with five, distinct, apical lobes, and although the five vascular traces do not reach the lobes, they do extend from the corolla base about halfway up the tube. There is a propensity in the Hinterhuberinae for the loss (in *Ericameria*, the *Chiliotrichum* group, *Llerasia*) or reduction (in *Ericameria*, *Lepidophyllum*, *Parastrephia*, *Hinterhubera*) of ligulate flowers. This makes it a reasonable hypothesis that the species ancestral to *Aztecaste* produced discoid heads bearing only actinomorphic, hermaphroditic flowers (ovaries fertile), without any peripheral, ligulate, pistillate flowers.

Cuatrecasas (1969) observed that aspects of the floral biology of *Diploste-*

phium suggest an approach to dioecy, almost certainly referring to the tendency for ovarian sterility in the central flowers and to earlier observations by Blake (1928). Blake noted that in *D. schultzei* Wedd., the number of pistillate (peripheral) and of pseudohermaphroditic (central) flowers is highly variable, with both tending to be highly reduced, and in some plants, the heads produced only pistillate, ligulate flowers, a condition clearly approximating or approaching dioecy or polygamo-dioecy. Humbert (1960) has observed a similar phenomenon in post-fire regrowth of plants of *Rochonia*.

A hypothesis for the independent derivation of dioecy in the Hinterhuberinae and Baccharidinae receives support from recent studies of restriction site variation in chloroplast DNA. In these studies, *Baccharis* is only distantly related to *Ericameria* within the Astereae (Suh 1989; Morgan 1990; and see Nesom *et al.* 1990 for a summary). Although dioecy, or some close approach to it such as monoecy or polygamo-dioecy, is the rule in American Baccharidinae and appears to be a heritable condition, there are no other dioecious species in the Astereae and it is an uncommon phenomenon in the rest of the family as well (Bentham 1873). Dioecy was not mentioned in any of the various taxonomic or biological discussions in Heywood *et al.* (1977) for any tribe of Asteraceae.

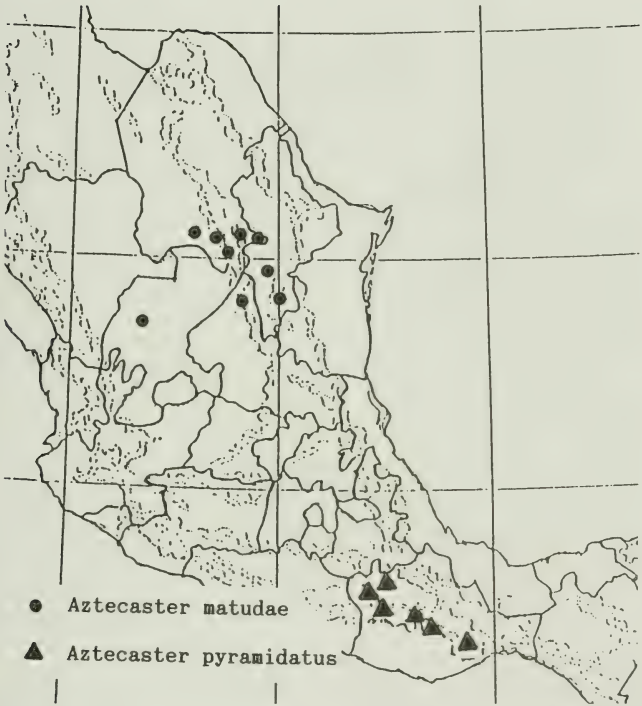
TAXONOMY

Baccharis pyramidata and *B. matudae* are formally segregated here as a new genus, named for the indigenous people of the area where it is endemic and echoing the apparent intent of Robinson & Greenman when they formulated the epithet of the original species. There is nothing obviously "pyramidal" in the morphology of these species. The new genus is compared in the diagnosis to *Ericameria*, its nearest geographic relative.

Aztecaster Nesom, *gen. nov.* TYPE SPECIES: *Aztecaster pyramidatus* (B. Robins. & Greenm.) Nesom.

Speciebus *Ericameriae* Nutt. ut videtur similis sed differt foliis ericoideis, capitulescentia laxe spicata, capitulis foliis proxime subtentis, phyllariis costam aurantiacam ac appendicem apicalem vel apiculum carentibus, achaeniis plerumque 2-nervatis, et praesertim statu sexuali dioecio.

Shrubs 0.5-1.6 m tall, with rigid, straight branches, the young stems densely and closely silvery-white pannose, glabrate with age. Leaves densely arranged along the stems, commonly with axillary fascicles, lightly flocculent, quickly glabrescent, usually glutinous but without visible glands, linear-oblong, 4-20



Map 1. Distribution of *Aztecaster pyramidatus* and *A. matudae*.

Table 1. Composition of the subtribe Hinterhuberinae and the continental distribution of the genera. The numbers in parentheses refer to the number of species in the genus.

HINTERHUBERINAE Cuatr., *Webbia* 24:5. 1969. TYPE GENUS: *Hinterhubera* Sch.-Bip. ex Wedd.

<i>Chiliotrichopsis</i> Cabrera (3).	
<i>Chiliophyllum</i> Phil. (3).	
<i>Aylacophora</i> Cabrera (1).	
<i>Paleaeappus</i> Cabrera (1).	
<i>Nardophyllum</i> Hook. & Arn. (7).	SOUTH AMERICA
<i>Lepidophyllum</i> Cass. (1).	
<i>Parastrephia</i> Nutt. (5).	
<i>Chiliotrichum</i> Cass. (2).	
<i>Diplostephium</i> Kunth (ca. 90, 1 sp. in Costa Rica).	
<i>Oritrophium</i> (Kunth) Cuatr. (ca. 15, 1 sp. in México) (tentatively included in the subtribe).	
<i>Llerasia</i> Triana (14).	
<i>Hinterhubera</i> Sch.-Bip. ex Wedd. (8 or 9).	
<i>Aztecaster</i> Nesom (2).	
<i>Ericameria</i> Nutt. (31).	NORTH AMERICA
<i>Olearia</i> Moench (ca. 100).	
<i>Celmisia</i> Cass. (ca. 60).	
<i>Pleurophyllum</i> J.D. Hooker (2-3).	AUSTRALASIA
<i>Damnomenia</i> Given (1).	
<i>Pachystegia</i> Cheeseman (1).	
<i>Pteronia</i> L. (ca. 80).	SOUTH AFRICA
<i>Rochonia</i> DC. (4).	
<i>Madagaster</i> Nesom (5).	MADAGASCAR

(-26) mm long, 1-2 mm wide, entire, ericoid with strongly revolute margins and the midvein strongly raised on the abaxial surface. Heads sessile in leaf axils, in an open cylindrical-spicate capitulescence, each head immediately subtended by a cluster of leaves; each head either with functionally pistillate flowers or functionally staminate flowers, the pistillate and staminate heads on separate plants and the species dioecious; pistillate involucre 6-8(-10) mm long, 4-6 mm wide, the staminate heads slightly smaller; phyllaries stramineous to greenish-yellow, prominently resinous from biseriate glandular hairs, the inner portion strongly indurated and of similar texture from base to tip, narrowly keeled from base to tip or not, narrowly triangular to narrowly ovate, (0.5-)0.8-1.5(-1.8) mm wide including the narrow to broad scarious margins, in 3-4 imbricate series strongly graduated in length with the outermost ca. 1/3 as long as the inner; receptacle slightly convex, barely alveolate. Staminate (pseudohermaphroditic) flowers with abortive ovaries, 8-9 per head, the corollas actinomorphic, ca. 4-7 mm long, the tube strongly delimited or not, the lobes 0.8-1.2 mm long, triangular, spreading to reflexing, style branches linear-lanceolate, 1.8-2.1 mm long, with short collecting hairs from base to apex, stigmatic lines absent, the vascular trace not at all thickened. Pistillate flowers 5-10 per head, the corollas actinomorphic, narrowly tubular, 4-6 mm long, with 5 lobes 0.5-1.0 mm long, the style branches 1.8-2.0 mm long, with stigmatic margins extending completely around the periphery of each branch; achenes tan, oblong-obovate, flat with a nerve at each margin or sometimes with an additional nerve in the middle of one or both faces, 2.5-3.0 mm long, 0.7-0.9 mm wide, moderately to densely strigose with duplex hairs (Zwillingshaare), eglandular; pappus of ca. 35-50 barbellate bristles with attenuate apices, in essentially a single series. Chromosome numbers unknown but predicted to be $n=9$. Illustrations in Hall & Clements (1923, pl. 30) and Rzedowski (1972, Fig. 1).

KEY TO THE SPECIES

1. Abaxial midvein of leaves strongly raised and distinctly green, with a shallow central groove; central indurated portion of phyllaries ovate to narrowly ovate, 0.6-1.0 mm wide, stramineous but commonly green-tinged in the distal half, the midvein also often distinctly greenish distally, not raised as a keel; pistillate corollas 4.6-5.6 mm long, with lobes 0.6-1.0 mm long; staminate corollas 6.0-6.8 mm long, without a distinctly delimited tubular portion below the throat; the lobes 1.3-1.5 mm long and slightly spreading but not recurving, staminate style branches 2.5-3.0 mm long; Oaxaca. *A. pyramidatus*
1. Abaxial midvein of leaves somewhat raised but not green or strongly conspicuous; central indurated portion of phyllaries linear-lanceolate, 0.3-

0.6 mm wide, completely stramineous, with a narrow, raised keel from base to apex; pistillate corollas 3.8-4.8 mm long, with lobes 0.4-0.6 mm long; staminate corollas 3.5-5.0 mm long, the tube 2.0-2.2 mm long and strongly delimited and abruptly expanded into the throat, the lobes 0.8-1.0 mm long and spreading-recurving, staminate style branches 1.8-2.0 mm long; San Luis Potosí, Zacatecas, Coahuila, and Nuevo León.
 *A. matudae*

Aztecaster pyramidatus (B. Robins. & Greenm.) Nesom, *comb. nov.* BASIONYM: *Bigelovia pyramidata* B. Robins. & Greenm., Proc. Amer. Acad. Arts 32:43. 1896. *Chrysothamnus pyramidatus* (B. Robins. & Greenm.) Hall & Clements, Publ. Carnegie Inst. Washington 326:197. 1923. *Haplopappus pyramidatus* (B. Robins. & Greenm.) Blake, Contr. U.S. Natl. Herb. 23:1491. 1926. *Baccharis pyramidata* (B. Robins. & Greenm.) Rzed., Brittonia 24:398. 1972. TYPE: MEXICO. Oaxaca: hills above Oaxaca, 5500 ft, 16 Nov 1894, C.G. Pringle 6048 (HOLOTYPE: GH!; Isotypes: MO!, UC, US!).

Grassland to matorral, 1600-2350 m; flowering November-March.

Additional specimens examined: MEXICO. Oaxaca: Sierra entre Oaxaca y Tehuantepec, 22 Dec 1968, Boege 1047 (GH); Cañon of the Río Tlahuitoltepec, 19-27 Feb 1937, Camp 2715 (A); Cerro Santo Domingo, 22 Dec 1906, Conzatti 1645 (MEXU); Dist. Centro, El Fortín, 1650 m, 11 Feb 1933, Conzatti 4913 (LL); Monte Alban, 1850 m, 3 Mar 1937, Conzatti & Camp 5239 (MEXU); Dist. Coixtlahuaca, Cerro del Agua, 3.5 km NNW of Concepción Buenavista, 2350 m, 3 Feb 1969, Cruz 2925 (ENCB, TEX); 8 km SW of Tlaxiaco, 1900 m, 7 Feb 1965, McVaugh 22298 (ENCB); Dist. Coixtlahuaca, 2 km NNE of San Mateo Tlapiltepec, 2200 m, 11 Jan 1969, Rzedowski 26676 (ENCB, WIS); Monte Alban, cerca de Oaxaca, 1850 m, 27 Feb 1972, Rzedowski 28827 (ENCB) and 28828 (ENCB, TEX); Portillo San Dionisio, 62 km ESE de Oaxaca, sobre el camino a Tehuantepec, 19 Dec 1972, Rzedowski 30012 (MO) and 30013 (MO); Cañada Sta. María, 8 Dec 1895, Sailor 1477 (GH, MEXU); Monte Alban, 23 Nov 1894, Smith 371 (MO); Monte Alban, ca. 8 km NW of Oaxaca, 28 Dec 1976, Turner P-48 (LL); 1 km por la desviación a Acaquiza-pan, on the Huahuapan de León-Tehuacan highway, 20 Feb 1986, Villaseñor 911 (MEXU, TEX); ca. 24 mi from Mitla on road to Totontepec, 11 Jan 1989, Woodruff 227 (MO, TEX).

Aztecaster matudae (Rzed.) Nesom, *comb. nov.* BASIONYM: *Baccharis matudae* Rzed., Brittonia 24:398. 1972. TYPE: MEXICO. Zacatecas: 5 km al NE de Chalchihuites, 2100 m, orilla de camino, 2 Apr 1957, J. Rzedowski 8758 (HOLOTYPE: ENCB!).

Grassland to matorral and open pinyon pine woodland, ca. 1800-2700 m; flowering February-July.

Additional specimens examined: MEXICO. Coahuila: Sierra Zapaliname, 2480-2600 m, 25 Mar 1990, *Hinton et al. 20225* (TEX) and *20231* (TEX); Carneros, 12 Jul 1934, *Pennell 17302* (GH,US); Sierra de Parras, *Purpus 1326* (UC, as cited by Hall & Clements 1923); E of Saltillo, 6.8 mi E of San Juan de Los Dolores toward La Jacinta, 7600 ft, 17 Dec 1989 (sterile), *Schoenfeld & Fairey 35* (TEX). Nuevo León: Ca. 15 mi SW of Galeana, Cieneguillas to Pablillo by the upper trail, 17 Jun 1934, *Mueller 875* (TEX); 15 mi S of km 168 on Hwy 61, N of Dr. Arroyo, 2140 m, Jul 1982, *Vankat 98* (TEX). San Luis Potosí: Tierras Negras, 12 km S of Mineral de Catorce, 2700 m, roadside, 3 Feb 1956, *Rzedowski 7278* (ENCB).

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COMPLETION OF *ERICAMERIA* (ASTERACEAE: ASTEREAEE),
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 re-incorporation) 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 3635) 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 3635 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, involucre 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 involucre 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 involucre 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. greenii* (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 involucre 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 involucre 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 involucre (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) involucre 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 involucre 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 be 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.

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2. *Ericameria parryi* (A. Gray) Nesom & Baird var. *aspra* (E. Greene) Nesom & Baird, *comb. nov.* BASIONYM: *Chrysothamnus asper* E. Greene, Leaf. 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, Leaf. 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. *atenuata* [M.E. Jones] Nesom & Baird; a stabilized hybrid known from one large population; Anderson 1984).

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**MADAGASTER (ASTERACEAE: ASTEREA), A NEW GENUS OF SUBTRIBE
HINTERHUBERINAE**

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ABSTRACT

The five, white-rayed, Madagascan species previously identified as *Aster* are outside the morphological and phyletic bounds of *Aster*. In contrast, they are closely similar to another endemic genus of Madagascar, the yellow-rayed *Rochonia*, as well as to the white-rayed *Diplostephium* of South America and the Australasian genus *Olearia*. Although the classification is problematic, the white-rayed Madagascan species are here recognized as the new genus *Madagaster* Nesom. *Madagaster* and *Rochonia* are the only Madagascan representatives among the 22 genera that constitute the subtribe Hinterhuberinae, which extends from Madagascar into South Africa, South America, North America, and Australasia.

KEY WORDS: *Madagaster*, *Aster*, *Olearia*, *Diplostephium*, Asteraceae, Asteraceae, Madagascar

Aster L. in Madagascar (Humbert 1960) has been recognized as five species that are shrubs to small trees with large, coriaceous leaves and a persistent, close, tomentose ("pannose") vestiture often produced on the leaves, young branches, and petioles. The heads are relatively large, produced singly or in a corymbiform to paniculate capitulescence, and the receptacles are epaleate. The ray flowers are in a single series and have long, conspicuous, white to bluish ligules. The achenes are strigose but eglandular, narrowly oblanceolate, (4-)5-8-ribbed, and nearly terete to slightly compressed (but not strongly flattened). The pappus is "sub-biseriate," with an inner series of apically dilated, barbellate bristles and an outer group of bristles unequal in length but all somewhat shorter than the inner. The plants apparently are scattered and relatively uncommon, occurring on rocky ridges and summits, often in ericoid vegetation. These species, which have been described and illustrated in detail (Humbert 1960), clearly constitute a monophyletic assemblage.

Humbert (1923) described the second species of this group as *Diplostephium madagascariense* Humbert, emphasizing its similarity to the South American genus *Diplostephium* Kunth, but he also observed its resemblance to the Australasian genus *Olearia* Moench. "La separation de ces trois genres basee en grande partie sur des considerations d'ordre geographique, est difficilement justifiable" (1960, p. 318). He later took an even more conservative approach (1932) in identifying these white-rayed Madagascan species as *Aster* and concurrently transferring the four species of the yellow-rayed, Madagascan endemic *Rochonia* DC. to *Aster*, noting that the only difference between the two species groups was their ray color and emphasizing his observation of the absence of decisive characters to separate *Diplostephium* and *Olearia* from *Aster*. He did specifically note that *Aster* was necessarily considered "sensu lato" in this context, as it is almost completely restricted to the Northern Hemisphere. Humbert reseggregated *Rochonia* in 1960, "ayant observe dans la nature toutes les especes malgaches connues de ce groupe, ... malgre la difficulte de constater en hercier l'homochromie ou l'heterochromie, et tout en maintenant les reserves enoncees [in 1932]" (p. 315). Zhang & Bremer (1993) placed *Rochonia* with *Psiadia* Jacq., *Psiadiella* Humbert, *Microglossa* DC., and others, presumably because of their yellow rays (although *Rochonia* is misplaced there on the basis of several other characters scored by Zhang & Bremer). In my view, *Psiadia* and its closest relatives are part of the Baccharidinae (Nesom 1993). Zhang & Bremer did not consider the white-rayed Madagascan species under discussion apart from *Aster*.

Both white- and yellow-rayed species occur within American Hinterhuberinae (Nesom 1993), but all genera (as currently treated) of the subtribe produce either one color of rays or the other. *Chiliophyllum* Phil. (yellow-rayed) and *Chiliotrichum* Cass. (white-rayed) are relatively similar in overall morphology but differ in features of the achenes and other technical characters that indicate they are separate clades. There is no general reason that yellow- and white-rayed species cannot be accepted within a single genus, and both colors are known within other genera of Astereae, but it is clear that the shrubby, yellow-rayed species of Madagascar constitute a lineage separate from the white-rayed species. Even if these should prove to be sister groups, they are justifiably regarded as separate taxa.

If these white-rayed Madagascan species must be placed in a pre-established genus, *Aster* is the least acceptable of the choices considered by Humbert. In true *Aster*, the plants are herbaceous, without a pannose indument, the leaves are sometimes thickened but never strongly coriaceous, and the achenes are obovate, flat, and 2-ribbed. The only native African species of *Aster* are those centered around *A. bakeranus* C.A. Smith and *A. harveyanus* O. Kuntze of South Africa (Lippert 1973), and the Madagascan species are not related to these (Nesom in prep.). Nor is there any other group of *Aster* in any sense to which the Madagascan species might be closely related.

Rochonia, Madagascan *Aster*, *Diplostegium*, and *Olearia*, are members of the subtribe Hinterhuberinae, which is now redefined to include 22 genera that extend from Madagascar into Africa, South America, North America, and Australasia (Nesom 1993). The identity of both groups of the Madagascan species with this more inclusive subtribe is clear, particularly in their shrubby habit, large, coriaceous leaves, production of a pannose tomentum, and plump, oblanceolate, multinerved achenes. The occurrence of plants of relatively similar, generalized morphology (i.e., in *Olearia*, *Diplostegium*, *Rochonia*, and Madagascan *Aster*) across the whole geographic range of the subtribe suggests that they may be close to the primitive form for the group. The only continental African taxon of the Hinterhuberinae is the South African genus *Pteronia* L. (Hutchinson & Phillips 1917), in which specializations appear to eliminate it from consideration in hypotheses regarding the immediate ancestry and closest relatives of the Madagascan species. The heads in *Pteronia* are discoid (lacking ray flowers), the involucre elongated, the pappus accrescent, and there is a tendency for the production of opposite leaves and beaked achenes.

Diplostegium is primarily northern Andean in distribution, ranging from northern Chile and Bolivia to Colombia and Venezuela, with one species in Costa Rica of Central America. It appears to be monophyletic, and its common ancestry with other South American genera of Hinterhuberinae is indicated by the tendency for production of receptacular pales and disc flowers with sterile ovaries, specialized features not found in the Madagascan species.

Olearia is an Australasian genus (primarily Australia, New Zealand, and New Guinea) of about 100 species highly variable in habit, capitulescence, vestiture, and other technical features. Two separate groups of the genus are closely but independently related to *Celmisia* Cass. and three other, much smaller Australasian genera (e.g., Drury 1968; Given 1969, 1973). All of these are white-rayed and all have unusually high levels of polyploidy (12-ploid or 24-ploid, see comments in Nesom 1992) in addition to their common morphology that indicate that the whole group is monophyletic. Many, if not most, of the other New Zealand species of *Olearia* also have similar levels of ploidy, but many of the Australian species for which reports exist are diploid or tetraploid. The generitype of *Olearia* is an Australian species (*O. tomentosa* [J.C. Wendl.] DC. = *O. dentata* Moench) with alternate leaves and a vestiture of bifurcate, basifixed trichomes; the chromosome numbers of two species of the group that includes *O. tomentosa* have been reported as 10-ploid and 12-ploid (*O. pannosa* Hook. and *O. argophylla* F. Muell., respectively). Species of another group produce stellate trichomes and have diploid chromosome numbers. Species of yet other groups have simple trichomes and diploid numbers. The specialized trichomes are restricted within the subtribe to these Australasian species. Aspects of this variation have been described earlier by botanists who divided the genus into sections based primarily on

trichome morphology (Archer 1861; Bentham 1866; and others mostly following Bentham's modification of Archer's original treatment). Recent studies, however, have unequivocally noted that *Olearia* is polyphyletic (e.g., Drury 1968; Given 1973), and it appears that some of the diploid *Olearia* species with unbranched trichomes may be more closely related to genera outside of the subtribe Hinterhuberinae than to any within it (pers. observ.).

Taxonomy within the *Olearia-Celmisia* complex is highly unsettled, even with regard to the definition and limits of *Olearia* itself. The taxonomic position of the white-rayed Madagascan species relative to *Olearia* sensu lato is equally obscure, but there is no group of *Olearia* to which they might have an unequivocally close relationship. There are no published chromosome counts for the Madagascan species of *Aster* or *Rochonia*; all reports for *Pteronia* as well as the South American species of Hinterhuberinae, however, are diploid ($n=9$).

The white-rayed "asters" of Madagascar can no longer be formally treated as *Aster*. Instead, they are members of the Hinterhuberinae, where they should be placed either within *Rochonia*, within *Olearia*, or as a genus distinct from both. A position for these species apart from *Rochonia* is consistent with current views of variation and associated taxonomy within the subtribe, as noted above. With regard to *Olearia*, the only native Australasian genus of Astereae that also occurs outside of that region is *Lagenifera* Cass. The latter has additional species and its closest relatives in South America, and the relationships of many other Australasian Astereae also lie in that direction. The Australian species of *Erigeron* L. do not belong in that genus; Given (1973) has already made this observation for *E. pappochroma* Labill. Baccharidinae of Africa and Madagascar have their closest relatives in South America (Nesom 1993), and African grangeoid herbs with relatives in Australasia have even more closely related intermediaries in South America (Nesom in prep.). In view of these and the considerations in the preceding paragraph, I believe there is no justification for treating Australasian *Olearia* as congeneric with the Madagascan "asters." A decision to recognize the latter as a separate genus certainly reflects the conclusion that such a treatment has the greatest probability of remaining stable.

Madagaster Nesom, *gen. nov.* TYPE SPECIES: *Madagaster mandrarensis* (H. Humb.) Nesom

Speciebus *Rochoniae* DC., *Diplostephii* Kunth, *Oleariae* Moench, ac generibus ceteris subtribus Hinterhuberinae habitu fruticoso, capitulis amplis, foliis amplis coriaceis, et tomento persistenti similis. Differt a *Rochonia* ligulis albis, setis pappi dilatatis ad apices, et acheniis majoribus. Differt a *Astro* L. habitu, vestimento, et morphologia foliorum ac acheniorum.

1. **Madagaster madagascariensis** (H. Humb.) Nesom, *comb. nov.* BASIONYM: *Diplostephium madagascariense* H. Humb., Mem. Soc. Linn. Norm. 25:53. 1923. *Aster madagascariensis* (H. Humb.) H. Humb., *Fl. Madag.*, Composeés 1:318. 1960.
2. **Madagaster mandrarenensis** (H. Humb.) Nesom, *comb. nov.* BASIONYM: *Aster mandrarenensis* H. Humb., Bull. Mus. Paris, ser. 2, 4(8):1017. 1932.
3. **Madagaster saboureaui** (H. Humb.) Nesom, *comb. nov.* BASIONYM: *Aster saboureaui* H. Humb., *Fl. Madag.*, Composeés 1:320. 1960.
4. **Madagaster senecionoides** (Baker) Nesom, *comb. nov.* BASIONYM: *Rochonia senecionoides* Baker, J. Linn. Soc. 25:326. 1890. *Aster baronii* H. Humb., Bull. Mus. Paris, ser. 2, 4(8):1018. 1932. Not *Aster senecionoides* Franch. 1896.
5. **Madagaster andohahelensis** (H. Humb.) Nesom, *comb. nov.* BASIONYM: *Aster andohahelensis* H. Humb., Bull. Mus. Paris, ser. 2, 4(8):1016. 1932.

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STUDIES ON THE GENUS *BIDENS* L. (COMPOSITAE) FROM THE
EASTERN HEMISPHERE. 6. A NEW SPECIES FROM SIERRA LEONE

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ABSTRACT

A new species, *Bidens gledhillii* T.G.J. Rayner, is described and illustrated. It is endemic to the submontane and montane savanna of the Loma Mountains of north-eastern Sierra Leone, occurring chiefly in the vicinity of Bintumane Peak. It is considered to lack close relatives in Africa but has, nevertheless, frequently been confused with *B. camporum* (Hutch.) Mesfin and *B. borianiana* (Sch. Bip. ex Schweinf.) Cufod., two species of great disparity with which it is compared

KEY WORDS: *Bidens*, Compositae, taxonomy, Sierra Leone

Continuing revisional studies of Eastern Hemisphere *Bidens* L. have revealed the following new species from Sierra Leone.

Bidens gledhillii T.G.J. Rayner, *sp. nov.* TYPE: SIERRA LEONE. Loma Mountains, below summit, alt. 1710 m, 27 Mar. 1964, *J.K. Morton & D. Gledhill SL.1095* (HOLOTYPE: WAG; Isotypes: FHI,GC,K).

Coreopsis camporum auct. non Hutch.: C.D. Adams in Hutch. & Dalziel, *Fl. W. Trop. Afr.*, ed. 2, 2:232. 1963, quoad *Deighton 5095 & Jaeger 516*.

Species nova *Bidenti borianianae* (Sch. Bip. ex Schweinf.) Cufod. affinis sed ab ea differt plantis perennibus, foliis principalibus profunde 1 vel 2 pinnatipartitis usque ad 7.5 centimetra longis margine segmentorum integro, capitulis 2.6-4.7 centimetris diametro sub anthesi, pedunculis ad (5-)13-38 centimetra longis,

phyllariis exterioribus 7-8(-9) anguste ovatis vel anguste ovato-ellipticis e medio versus apicem plerumque attenuatis 4.6-8.1 millimetris longis 1.5-2.4 millimetris latis sub anthesi (1-)3-6 nervatis, phyllariis interioribus usque ad 10.4 millimetra longis 4.5 millimetra latis, flosculis radii 1.2-1.9 centrimetris longis 5.5-8.2 millimetris latis, tubis flosculorum radii 1.6-2.7 millimetris longis glabris, paleis pallido- vel atrobadiis, corollis flosculorum disci 3.8-6.3 millimetris longis, antheris 2.0-3.1 millimetris longis, filis staminum 0.5-1.3 (-1.6) millimetris longis, collis florum 0.20-0.25 millimetri longis, ramis stigmatum 1.1-1.6 millimetris longis, cypselis pallido- vel atrofuscis (3.8-)5.0-9.2 millimetris longis 1.9-3.9 millimetris latis (alis inclusis), alis 0.15-1.30 millimetris latis generaliter latissimis ad medium vel parum infra medium plerumque sensim supra medium attenuatis, saepe infra apicem terminatis, aristis cypselarum trigonis; differt a *Bidente camporum* (Hutch.) Mesfin foliis principalibus ovatis vel late ovatis vel ovato-trullatis vel late ovato-rhombicis in ambitu (0.8-)1.4-7.5 centrimetris longis margine segmentorum integro, petiolis ad 1.3-11.4(-14.6) millimetra longis, capitulis 8-12 millimetris altis sub anthesi solitariis ad apices caulium et ramorum, pedunculis ad (5-)13-38 centrimetra longis glabris vel pilis sejunctis, phyllariis exterioribus 7-8(-9) anguste ovatis vel anguste ovato-ellipticis e medio versus apicem plerumque attenuatis 4.6-8.1 millimetris longis 1.5-2.4 millimetris latis (1-)3-6 nervatis dorsis glabris, phyllariis interioribus uniseriatis (7-)8(-9) non connatis 2.6-4.5 millimetris latis, flosculis radii (7-)8 neutris ovario 1.3-3.2 millimetris longo 0.9-1.4 millimetris lato stylo nullo, paleis anguste ovato-oblongis vel anguste oblongo-ellipticis 4.6-8.8 millimetris longis sub anthesi, in statu fructifero usque ad 10.2 millimetra longis, appendicibus basibus antherarum collum fli basem non attingentibus, filis staminum 0.5-1.3(-1.6) millimetris longis, collis florum 0.20-0.25 millimetri longis, stylis 4.3-7.0 millimetris longis, cypselis alatis 1.9-3.9 millimetris latis (alis inclusis) pallido- vel atrofuscis non profunde 8-10 sulcatis venteribus planis vel valde concavis, aristis cypselarum 0.10-0.15 millimetri latis basi.

Perennial clump forming herbs, to 0.4-1.3 m tall; stems several, arising from a branched, woody rootstock, branched at base and also usually above; stems and branches erect or ascending, terete to terete-tetragonal or obtuse angled-tetragonal especially above, 1.9-8.2 mm diam. at base, 1.6-4.3 mm diam. beneath peduncles, more or less smooth or shallow to deeply sulcate, striate, often dark brown especially below or pale brown and green-brown above, glabrous, woody chiefly toward base of stems and lower branches. Leaves decussate or sometimes uppermost alternate especially on flowering branches, sessile

to petiolate, rarely sessile; lamina deeply 1-2-pinnatipartite, with 3-5(-7) segments, rarely undivided; divided leaves ovate to broadly ovate or ovate-trullate to broadly ovate-rhombic in outline, (0.8-)1.4-7.5 cm long \times (0.5-)0.7-7.2 cm wide; primary leaf segments opposite or subopposite, undivided or deeply and often irregularly few-lobed, to (0.3-)1.2-5.4 cm long; lobes and undivided segments opposite to alternate, antrorsely inserted at 25-80° to rachis, narrowly linear-elliptic or narrowly linear-ovate to linear, usually gradually attenuated from middle toward apex and base, acute to rarely obtuse and sometimes shortly apiculate at the callose indurated apex, entire at the rounded and indurated margin, 0.2-4.7 cm long \times 0.4-3.1(-4.3) mm wide, straight or frequently somewhat incurved, flat or often broadly V-shaped in section, rarely almost conduplicate especially when young, papyraceous to subcoriaceous, pale green to green, more rarely yellow-green, glabrous or sparsely to subdensely hispid on margin, with minute (0.05-0.15 mm long), antrorse, suberect to more or less adpressed, few-cellular, sharply pointed hairs; petioles to 1.3-11.4(-14.6) mm long \times (0.4-)1.1-2.7 mm wide, usually canaliculate, narrowly to broadly winged, with wings to (0.1-)0.3-1.1 mm wide, not or slightly dilated above and below, barely clasping stem at the connate bases, glabrous or with more or less isolated, 0.1-0.3 mm long, erect, thick, basally 2 to few-cellular, uniseriate hairs toward base of margin; rachis narrowly obtriangular-oblong to narrowly obtriangular, 0.6-4.9 mm wide, flat to slightly involute at margin; uppermost alternate leaves tripartite to pinnatipartite or rarely undivided, 0.6-2.1 cm long. Capitula radiate, heterogamous, erect, 2.6-4.7 cm diam. \times 0.8-1.2 cm high at anthesis, to 1.5 cm high in fruit, solitary at stem and branch apices; receptacles flat to slightly convex; peduncles to (5-)13-38 cm long, 0.9-3.1 mm diam. at anthesis, unchanged in fruit, terete to terete-tetragonal or tetragonal, shallow to deeply sulcate, glabrous or with isolated, minute (to 0.1-0.2 mm long), erect, few-cellular, often basally swollen, uniseriate, rarely dark brown hairs; ebracteate or with 1-3(-6), alternate, divided or undivided bracts resembling the primary leaf segments, divided bracts 0.5-1.8 cm long \times 0.3-1.6 cm wide, undivided bracts and lobes 0.4-1.1 mm wide. Involucre depressed-hemispheric, glabrous or sparsely hispid-pubescent at base; outer phyllaries subbiseriate to biseriate, 7-8(-9), narrowly ovate to narrowly ovate-elliptic and usually attenuated from middle to apex, acute to obtuse and usually shortly apiculate at the slightly callose indurated apex, entire at margin, 4.6-8.1 mm long \times 1.5-2.4 mm wide at anthesis, unchanged in fruit, erect to spreading, subcoriaceous, green, often slightly darker in apical half, with (1-)3-6, usually branched, frequently paired, red-brown nerves, glabrous or ventral surface sparsely to subdensely pubescent chiefly in basal half, with minute (0.05-0.15 mm long), thin, uniseriate, unibasal, few-cellular, often pale brown, flexuous hairs; inner phyllaries uniseriate, not fused, (7-)8(-9), narrowly ovate to ovate or rarely triangular-ovate, subacute to obtuse or rounded at apex, entire at margin, 6.1-10.4 mm long \times 2.6-4.5 mm wide at anthesis, unchanged in fruit,

erect, papyraceous above, becoming callose thickened and coriaceous below, pale to dark brown, often black-brown at apex, stramineous at the 0.2-0.7 mm wide, membranous margin, with numerous, longitudinal, percurrent nerves, dorsal surface sparsely hairy, with minute (ca. 0.1 mm long \times ca. 0.1 mm wide), spherical to subspherical or conical, sessile, few-cellular, brown to black-brown, glandular hairs, ventral surface glabrous, apex and often apical half of margin puberulous, with 0.10-0.15(-0.20) mm long, uniseriate, few-cellular, thin, erect, apically rounded, straight, often brown or brown-black hairs. Ray florets (7-)8, neuter; ovary oblong to obovate-oblong, 1.3-3.2 mm long \times 0.9-1.4 mm wide, apex and apical 1/2-2/3 of margin with minute (0.05-0.15 mm long), erect, few-cellular hairs, style absent; corolla tube 1.6-2.7 mm long, glabrous; ray yellow, ovate-elliptic to oblong-elliptic, 1.2-1.9 cm long \times 5.5-8.2 mm wide, with (10-)12-18, darker nerves, glabrous; apex rounded, entire or usually irregularly 2-3(-4)-denticulate, with teeth 0.2-1.3 mm long \times 0.1-1.6 mm wide. Paleae narrowly ovate-oblong to narrowly oblong-elliptic, acute to obtuse or rounded and sometimes shallow erose at apex, entire at margin, 4.6-8.8 mm long \times 1.0-3.1 mm wide at anthesis, to 10.2 mm long in fruit, thin and membranous, glabrous, pale stramineous, with 5-21, mostly paired, light to dark red-brown, percurrent, longitudinal nerves. Disc florets (28-)36-47; corolla yellow, glabrous; limb campanulate-cylindric to campanulate, 2.5-3.8 mm long \times 0.9-1.2 mm diam., usually slightly annularly thickened at base, apex 5-lobed; lobes triangular, acute at apex, 0.4-0.7 mm long \times 0.3-0.5 mm wide; limb abruptly or subabruptly attenuated below into a narrow, 1.3-2.5 mm long \times 0.5-0.6 mm wide, terete tube; anthers 2.0-3.1 mm long \times 0.7-0.9 mm diam., dark brown to black; endothelial tissue with polarized thickening; apical appendages ovate to broadly ovate or broadly ovate-triangular, acute to obtuse at apex, 0.30-0.35 mm long \times 0.25-0.30 mm wide, with a pale, longitudinal median nerve, margins slightly reflexed; basal appendages sagittate, not reaching base of the filament collar; collar 0.20-0.25 mm long \times 0.10-0.15 mm wide; filament 0.5-1.3(-1.6) mm long, flat to convex and involute; style 4.3-7.0 mm long, cylindric to slightly or decidedly bulbous at base, with caudate, 1.1-1.6 mm long branches; stylopodium cupuliform. Cypselas laterally bialate; wings shiny, stramineous, flat or slightly to decidedly incurved and partially concealing ventral face of cypselas, occasionally somewhat recurved, 0.15-1.30 mm wide, generally broadest at or slightly below middle, usually gradually attenuated above and often terminating below apex, margin densely setose, with to 0.4 mm long, suberect, antrorse, pale stramineous, pointed setae; body narrowly elliptic to elliptic or rarely narrowly ovate-elliptic, (3.8-)5.0-9.2 mm long \times 1.9-3.9 mm wide incl. wings, light to dark brown, strongly compressed; dorsal face slightly to strongly convex; ventral face flat to strongly concave, usually with a raised, longitudinal, median rib; both faces shallow 8-10-sulcate, glabrous or with minute (to 0.1-0.2 mm long), more or less adpressed, antrorse setae chiefly in apical half and along ventral median rib; apex shortly erect-

setose, laterally biaristate or rarely exaristate; aristae erect to slightly divergent, rigid, trigonous, pale brown, to 0.4-4.8(-5.3) mm long \times 0.10-0.15 mm wide at base, antrorsely barbed only on angles, with barbs to 0.1 mm long and gradually diminishing above; base of cypselas with a short (to 0.1-0.3 mm long), ventrally dilated, dorsally produced, cartilaginous carpopodium. Figure 1.

FLOWERING. Throughout the year. **HABITAT.** Submontane savanna, grassland. Alt. 1300-2000 m.

PARATYPES: SIERRA LEONE. Northern Province - Kabala, Mt. Loma, Bintumane [09° 13' N 11° 07' W], 21 Nov. 1965, *J.-G. Adam 22105* (MO); Bintumane Mt. [09° 13' N 11° 07' W], alt. 1670-2000 m, 18 Jul. 1960, *T.S. Bakshi 240* (K); Bintumane Peak [09° 13' N 11° 07' W], alt. 1830 m, 2 May 1949, *F.C. Deighton 5095* (K); Loma Mts., National Park on plateau [09° 11' N 11° 08' W-09° 14' N 11° 11' W], 18 Feb. 1966, *D. Gledhill 958* (FHI,GC,K,WAG); Mt. Loma [09° 18' N 10° 55' W-09° 05' N 11° 12' W], Nov. 1944, *P. Jaeger 516* (P); Mt. Loma [09° 18' N 10° 55' W-09° 05' N 11° 12' W], alt. 1900 m, 26 Sep. 1945, *P. Jaeger 1140* (P); Mt. Loma [09° 18' N 10° 55' W-09° 05' N 11° 12' W], alt. 1600 m, 29 Jul. 1964, *P. Jaeger 6945* (G[2 sheets],P); Mt. Loma [09° 18' N 10° 55' W-09° 05' N 11° 12' W], alt. 1600 m, 3 Dec. 1965, *P. Jaeger 8368* (P); Mt. Loma [09° 18' N 10° 55' W-09° 05' N 11° 12' W], alt. 1600 m, 31 Jan. 1966, *P. Jaeger 9172* (P); Mt. Loma [09° 18' N 10° 55' W-09° 05' N 11° 12' W], alt. 1550 m, 24 Feb. 1966, *P. Jaeger 9390* (K,M,P); Mt. Loma [09° 18' N 10° 55' W-09° 05' N 11° 12' W], alt. 1300 m, 15 Mar. 1966, *P. Jaeger 9523* (P).

Bidens gledhillii is restricted to the Loma Mountains of north-eastern Sierra Leone, occurring chiefly on Bintumane Peak and the surrounding plateaux. The Loma Mountains form part of the Guinea Dorsale which extends from the Fouta Djallon Plateau in western Senegal, across north-eastern Sierra Leone to the Simandou Massif, the Nimba Mountains in north-eastern Liberia and southern Guinea, to the Man in western central Ivory Coast. The greater part of the Loma is a north-south running plateau of about 750 m on which rests the 1300 m plateau at the north containing the truncated pyramid of Bintumane Peak (Cole 1968) which at 2130 m is the highest point in Sierra Leone. The major parent rock is granite interspersed with acid gneisses (Anderson 1966) which produces as the result of climatic and vegetational weathering a zonal lateritic soil. The predominant vegetation type on the plateau is forest-savanna mosaic, with montane vegetation occurring with increasing altitude on Bintumane Peak. At the lower reaches of its occurrence *B. gledhillii* is found in submontane shrub savanna (ca. 910-1700 m). Much of this area of Loma is ravaged annually by fire at the end of the wet season in December and January, producing a composition of shrubby plants scattered at 6-30 m from each other among low grasses and herbs (Cole 1968). The commonest shrubs include *Dissotis fruticosa* (Brenan) Brenan & Keay, *Kotschyia ochreatea* (Taub.)



Figure 1. *Bidens gledhillii* T.G.J. Rayner. A. Habit. B & C. Principal leaves. D. Outer phyllary. E. Inner phyllary. F. Ray floret. G. Ovary of ray floret. H. Palea. I. Disc floret. J. Stamens. K. Style. L. Cypsela. Scale bar: A = 2.0 cm. B & C = 1.4 cm. D, E, & H = 2.0 mm. F = 3.6 mm. G = 1.0 mm. I = 1.6 mm. J = 1.2 mm. K = 1.4 mm. L = 2.6 mm. All drawn from *Morton & Gledhill SL.1095* (WAG).

Dewit. & P.A. DuVign. and *Syzygium guineense* (Willd.) DC. In the grass-herb synusia the dominant plants are *Ctenium newtonii* Hack., *Hyparrhenia chrysargyrea* (Stapf) Stapf, *Loudetia kagerensis* (K. Schum.) C.E. Hubb., *Panicum congoense* Franch., *Rhytachne rotthoellioides* Desv., and *Tristachya fulva* C.E. Hubb. Above 1700 m submontane shrub savanna gradually gives way to montane grass savanna, a low grass community interspersed with low shrubs and herbs. Here the most widely distributed species is *Hyparrhenia diplandra* (Hack.) Stapf. Montane grassland has an abundance of cryptophytes and hemicyptophytes including *Cyanotis longiflora* Benth., *Gladiolus psittacinus* Hook., *Leocus lyratus* A. Chev., and *Solenstemnon monostachyus* (P. Beauv.) Briq., a number of succulents with thickened leaf bases including *Euphorbia depauperata* Hochst. ex A. Rich., *Sopubia mannii* Skan, *Thesium tenuissimum* Hook. f. and *Vernonia jaegeri* C.D. Adams, and several caespitose grasses and sedges (Cole 1968).

Bidens gledhillii is one of a large number of African species of *Bidens* with restricted distribution which occur in montane or subalpine vegetation on solitary or closely grouped and isolated elevated plateaux or mountains. It appears to lack close relatives, being perhaps allied to *Bidens camporum* (Hutch.) Mesfin from north-eastern to western central Africa, a taxon with which it has been confused by many workers including Adams (1963) and Mesfin who has recently determined the specimen of *Morton & Gledhill SL.1095* at WAG with this name. These two species are often of similar habit, with many populations of *B. camporum*, especially those occurring at altitude in Ethiopia, possessing the tufted stems characteristic of *B. gledhillii*. In addition, the deeply pinnatifid leaves with narrow segments and lobes of *B. gledhillii* are found on many specimens of *B. camporum*, although on complete herbarium specimens some leaves with broad segments are usually also present. The two species also possess a number of other similarities, including the frequently alternate leaves on the upper part of the stem, the diameter of the flowering capitula, the subbiseriate or biseriate outer phyllaries with sparse to subdense pubescence on the ventral surfaces, the callose thickening at the bases of the inner phyllaries in fruiting capitula, the number of nerves and shape of the ray florets, and the shape and size of the apical appendages of the anthers. *Bidens gledhillii* is most easily distinguished from *B. camporum*, however, by the following characters: capitula solitary at the apices of the stems and branches (few to several in lax, sometimes corymbose, cymes in *B. camporum*), peduncles usually 13-38 cm long and glabrous or with isolated hairs (not usually 6-17 cm long and more or less densely pilose especially beneath the capitula) and cypselas winged (not unwinged). In addition a large number of other differences between the two taxa are apparent (see Table 1) which strongly suggest that the similarities exhibited by the two taxa are the result of parallelism.

Another taxon with which *Bidens gledhillii* has been confused is *B. borianiana* (Sch. Bip. ex Schweinf.) Cufod., a species which occurs in a broad band

TABLE 1. Morphological differences between *Bidens gledhillii* and *B. camporum*.

	<i>B. gledhillii</i>	<i>B. camporum</i>
<i>Principal leaves</i>		
shape in outline	ovate to broadly ovate or ovate-trullate to broadly ovate-rhombic	ovate-triangular to broadly ovate-triangular or triangular
length	(3.7-)4.3-7.5 cm	5.5-19.0(-27.3) cm
margin of segments	entire	coarsely lobed or serrate
petiole length	3.6-11.4(-14.6) mm	19.8-63.1 mm
<i>Capitula</i>		
height at anthesis	8-12 mm	5-8 mm
no. and arrangement	solitary at stem and branch apices	few to several in lax, sometimes corymbose, cymes
<i>Peduncles</i>		
indumentum	glabrous or with isolated hairs	more or less densely pilose especially beneath capitula
length	to (5-)13-38 cm	to 6-17 cm
<i>Outer phyllaries</i>		
shape	broadest below middle; narrowly ovate to narrowly ovate-elliptic	broadest at middle or above; linear to narrowly oblong or narrowly elliptic-oblong to narrowly obovate-oblong
no.	7-8(-9)	8-21(-30)
no. of nerves	(1-)3-6	1-3(-4)
size	4.6-8.1 × 1.5-2.4 mm	2.9-18.0(-32.9) × 0.5-1.7 mm
dorsal surface indumentum	glabrous	pilose
<i>Inner phyllaries</i>		
no. of series	uniseriate	subbiseriate or biseriate
no.	(7-)8(-9)	(10-)12-16(-21)
width	2.6-4.5 mm	0.9-2.7 mm
connation	not fused	fused for 1/6-1/2 of length

TABLE 1. Continued.

<i>Ray florets</i>		
no.	(7-)8	(7-)8-15(-18)
ovary	neuter, style absent, 1.3-3.2 × 0.9-1.4 mm	fertile, cypsela 2.0- 6.2 × 0.9-1.8 mm
<i>Paleae</i>		
shape	broadest at or below middle; narrowly ovate- oblong to narrowly oblong-elliptic	broadest above middle; narrowly oblong-obovate to narrowly elliptic- obovate
length at anthesis	4.6-8.8 mm	2.3-5.0 mm
length in fruit	to 10.2 mm	to 8.1 mm
<i>Anthers</i>		
basal appendages	not reaching base of filament collar exceeding base of	usually reaching or filament collar, occasionally not reaching
collar length	0.20-0.25 mm	0.35-0.40 mm
filament length	0.5-1.3(-1.6) mm	1.7-2.7 mm
style length	4.3-7.0 mm	2.8-4.6 mm
<i>Disc cypselas</i>		
wings	present	absent
width	1.9-3.9 mm incl. wings	0.5-1.7(-2.2) mm
body colour	light to dark brown	black
ornamentation	shallow 8-10-sulcate	4-8-sulcate
ventral face shape	flat to strongly concave	convex
aristae width at base	0.10-0.15 mm	0.05-0.08 mm

TABLE 2. Morphological differences between *Bidens gledhillii* and *B. borianiana*.

	<i>B. gledhillii</i>	<i>B. borianiana</i>
<i>Life period</i>	perennial	annual
<i>Leaves</i>		
lamina dissection	deeply 1-2-pinnatipartite with 3-5(-7) segments, rarely undivided	tripartite, sometimes undivided
length	(0.8-)1.4-7.5 cm	(3.7-)4.3-23.5 cm
shape of undivided segments and lobes	narrowly linear-elliptic or narrowly linear-ovate to linear	narrowly ovate to narrowly elliptic
margin	entire	distantly serrate
<i>Capitula</i>		
diam. at anthesis	2.6-4.7 cm	(4.3-)5.8-9.6 cm
<i>Peduncles</i>		
length	to (5-)13-38 cm	to (3-)5-21 cm
<i>Outer phyllaries</i>		
no.	7-8(-9)	(7-)8-18(-26)
shape	broadest below middle; narrowly ovate to narrowly ovate-elliptic	broadest at middle; narrowly oblong or narrowly oblong-elliptic to linear
size at anthesis	4.6-8.1 × 1.5-2.4 mm	6.3-15.6 × 0.5-1.7 mm
length in fruit	unchanged	to 2.8 cm
no. of nerves	(1-)3-6	1-3
<i>Inner phyllaries</i>		
size in fruit	to 10.4 × 4.5 mm	to 16.1(-19.3) × 7.7 mm
<i>Ray florets</i>		
ray size	1.2-1.9 cm × 5.5-8.2 mm	(1.8-)2.7-5.3 cm × 8.0-19.2 mm
corolla tube length	1.6-2.7 mm	2.6-3.9 mm
corolla tube indumentum	glabrous	sparsely to subdensely pubescent

TABLE 2. Continued.

<i>Paleae</i>		
no. of nerves	5-21	2-8
colour of nerves	light to dark red-brown	light orange to orange-brown
<i>Disc florets</i>		
corolla length	3.8-6.3 mm	6.6-9.8(-10.1) mm
anther length	2.0-3.1 mm	2.8-4.0 mm
collar length	0.20-0.25 mm	0.30-0.35 mm
filament length	0.5-1.3(-1.6) mm	2.7-4.1(-4.8) mm
style branch length	1.1-1.6 mm	1.5-2.3 mm
<i>Cypselas</i>		
colour	light to dark brown	black
size	(3.8-)5.0-9.2 × 1.9-3.9 mm incl. wings	9.4-21.0 × 3.6-9.1 mm incl. wings
wing width and shape	0.15-1.30 mm, broadest at or slightly below middle, usually attenuated above	0.35-3.85 mm, broadest at or slightly below apex, attenuated below
aristae shape	trigonus	subulate

across Africa, chiefly in the Sudanian and Guineo-Congolian/Sudanian transition phytochoria (*sensu* White 1983). The primary cause of this failure to distinguish between these two taxa has been due to attempts to identify fragmentary herbarium specimens of *B. gledhillii* consisting only of the apical part of a stem or branch with immature or fruiting capitula. In such specimens only the atypical, often tripartite, apical leaves are present. These may be easily confused with those of *B. borianiana*, in which species they are characteristic. Secondly, the laterally bialate cypselas of *B. gledhillii* were previously only known for *B. borianiana* for those species of *Bidens* recorded for westernmost Africa. The latter species, however, occurs at lower altitude (210-1330 m) than *B. gledhillii*, and has only once been collected in Sierra Leone; from near Falaba, close to the border with Guinea. In addition, the two species may be distinguished by numerous morphological characters (see Table 2). *Bidens borianiana* is an annual with only a short, unbranched taproot. Its leaves are typically tripartite with distantly serrate margins, and its flowering capitula are frequently about twice as large (usually 5.8-9.6 cm diam.) and, as a consequence, their constituent parts frequently more numerous or larger than those of *B. gledhillii*. Further, the cypselial wings of *B. borianiana* are mostly much wider and characteristically broadest at or slightly below the apex, whereas in *B. gledhillii* they are broadest near the middle.

This species is named in honour of Dr. David Gledhill, joint collector of the type specimen and my early mentor in taxonomy. As an undergraduate I will always remember his kindness towards me and his enthusiasm for plants, especially those of Sierra Leone, which instilled in me a desire to study the African flora. It has been my good fortune to have encountered such a man in my informative years.

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