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REVIEW OF THE TAXONOMY OF *ASTER* SENSU LATO (ASTERACEAE: ASTEREAE), EMPHASIZING THE NEW WORLD SPECIES

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ABSTRACT

The genus *Aster* (as typified by *A. amellus* L.) and its closest relatives comprise the subtribe Asterinae *s. str.* These ca. 306 species in thirteen genera are primarily restricted to the Old World; *Aster* is the largest of these (with ca. 180 species) and is restricted to the Northern Hemisphere of the Old World, except for the seventeen species of *Aster* sect. *Calimeridei* (the *A. harveyanus* Kuntze group), which occurs in southeastern Africa, and *A. alpinus* L., which occurs in Asia and North America. The status of problematic, potentially generic-level Asian groups presently maintained within *Aster* s. str. is discussed. *Boltonia* is the only American genus hypothesized to be in the Asterinae. The New World species previously classified primarily within *Aster* are here apportioned among eleven previously described genera and two new ones, including the following (with number of species indicated): *Almutaster* (1), **Ampelaster** *gen. nov.* (1), *Chloracantha* (1), **Canadanthus** *gen. nov.* (1), *Doellingeria* (11 – three from North America, eight from Asia), *Eucephalus* (11), *Eurybia* (28), *Ionactis* (5), *Oclemena* (3), *Oreostemma* (3), *Psilactis* (6), *Sericocarpus* (5), and *Symphyotrichum*, including *Virgulus* (97). The status of *Tonestus* (eight species) within the Asterinae is considered, but it probably is best placed within the Solidagininae. A taxonomic account is provided for infrageneric categories and all 181 species of these fourteen American genera (including *Tonestus*), with new combinations necessary to establish a complete nomenclature; morphological summaries are provided for all. The validity and typification of the name *Eurybia* (Cass.) S.F. Gray is discussed in detail. Asian Asterinae are generally characterized by obovate, flattened, 2-nerved achenes commonly with glandular faces and are hypothesized to comprise a monophyletic group. American species (the Symphyotrichinae) are generally characterized by their cylindric to fusiform, terete, multinerved, and eglandular achenes, but transitions to flattened and few-nerved achenes apparently have occurred in parallel with Asian taxa.

Similarities between the two groups and the apparent basal position of the American taxa suggest that all should be included within a single subtribe, the Asterinae. Phylogenetic hypotheses are presented for relationships among the American genera. A discussion of chromosome evolution within the tribe Astereae is provided, with reference to the definition of Asterinaean genera.

KEY WORDS: *Aster*, Asterinae, Astereae, Asteraceae, Old World, New World

INTRODUCTION

Most systematists dealing with the genus *Aster* have recognized it as taxonomically difficult with regard to the delimitation of species as well as the recognition of natural groupings of species. There have been numerous published studies in the last fifteen years at both levels of the taxonomy of *Aster*. Two such studies, concentrating on the North American taxa, have provided independent and divergent overviews of the taxonomic structure of the genus (Jones 1980a; Semple & Brouillet 1980a). These botanists, and others, have also provided a great deal of new and critical data on chromosome numbers (see summary by Semple 1992) and morphology within the *Aster* alliance, clarifying the boundaries of species and species groups. The present study reviews recent developments in the taxonomy of *Aster* s. lat. and provides a significantly different perspective on the taxonomy of the group, based primarily on a morphological survey. The taxonomic status of New World and Old World groups is considered; alternative treatments are proposed for a number of the New World species and suggestions are made for alternative treatments of Old World species and species groups.

The comments of Cronquist (1947, p. 147-148) can serve as a starting point in the present review:

> "Until the publication of the first part of the second volume of the *Genera Plantarum* [Bentham and Hooker 1873], it was customary at least in America to regard the various *Aster*-segregates as valid genera. Asa Gray rather reluctantly followed Bentham's sweeping reduction of most of the segregates, and further pointed out that if these were to be reduced, *Brachyactis* would have to follow."
>
> "While the extended definition of *Aster* has certainly not been uniformly accepted, it has been followed by the majority of American taxonomists since Gray's adoption of it, more especially so since the swing away from the splitting vogue of the first quarter

of this century. The Benthamian definition, with Gray's addition of *Brachyactis*, was also adopted by Hoffmann [1890] in his treatment of Compositae for the *Natürlichen Pflanzenfamilien*."

"Although I do not wish to become involved at this time in a discussion of the propriety of the extended definition of *Aster*, I must support it, with some misgivings, at least until a thorough study of the old-world as well as the American species provides a reasonable basis on which all species can be referred either to *Aster* proper or to a morphologically definable segregate."

The direction of the present review is based on two broad observations, derived in part from a study of the entire tribe Astereae (Nesom 1994e). First, typical *Aster* and its closest relatives (the subtribe Asterinae *s. str.*, comprising fourteen genera) appear to be restricted to the Old World (except for the New World *Boltonia*). And second, more than half of the species that have been included within New World *Aster* appear to constitute a diverse but coherent group (the genus *Symphyotrichum*, as interpreted here), and a smaller number of North American species groups represent separate phylads. Most of the latter have previously been segregated as independent genera, their morphological and phyletic distinctions equivalent to those among other genera in the rest of the tribe.

In an earlier study (Nesom 1993c) I placed *Sericocarpus* as a basal member of the subtribe Solidagininae. In contrast, it is placed here among the North American groups of asters, with the acknowledgment that Cronquist (1947b) was correct in adding this group of species to those that constitute *Aster* in the broadest sense and that Semple & Brouillet (1980a) and Jones & Young (1983) correctly placed it near most of its closest relatives in their classification. *Sericocarpus* is hypothesized here to be most closely related to the North American genus *Eurybia*, although its plesiomorphic similarities to the Solidagininae may reflect a closeness of common ancestry. Similarly, *Ionactis* was recently hypothesized to be the most primitive member of the Chrysopsidinae (Nesom & Leary 1992), but that subtribe is a well-defined group without *Ionactis*, which is hypothesized here to be relatively isolated but perhaps most closely related to the genus *Eucephalus* among North American asters.

In the present view, relatively few species of only one other genus, *Psilactis*, need to be added to the other New World species before the entire assemblage could be considered a single, heterogeneous genus. Species of *Psilactis* have been included in *Aster*, most recently by McVaugh (1984), and Morgan's molecular data (1990, 1993) suggest that species of *Psilactis* are closely related to others treated here within *Symphyotrichum*.

One species of the genus *Tonestus* has been included in *Aster* (*T. kingii* [D.C. Eaton] Nesom, see Nesom 1991b). The genus was included among the North American asters in my subtribal classification (Nesom 1994e), and it is

tentatively maintained there in the present review. It is anomalous there, however, in its mix of discoid and yellow- and white-rayed species and the papillate collecting appendages of the disc flowers. The other species of *Tonestus* were mostly treated previously within *Haplopappus*, which has now been completely dismantled in North America (Nesom & Morgan 1990) and distributed among a number of phylogenetically disparate genera. The molecular data of Morgan (1990) suggest that *Tonestus* is closer to the Solidagininae.

In a recent overview and taxonomic summary of the tribe Astereae (Nesom 1994e), I suggested that North American *Aster* should be divided into a number of genera. That course is discussed in detail below and the necessary taxonomy formalized, with two significant updates. I have since realized that the earliest, legitimate, available generic name for the species I divided between *Heleastrum* and *Herrickia* is *Eurybia* (Cass.) S.F. Gray (see detailed discussion below). And with additional perspective, I find that the distinction between the subtribes Asterinae and Symphyotrichinae cannot be maintained, and the latter (newly proposed by me) becomes a synonym of the former.

Maintenance of a "conservative" treatment, or a "traditional" treatment, of *Aster* has sometimes been stressed as a valuable objective or at least implied to be such. Use of these terms, however, to describe the most current classifications of *Aster* is only partly appropriate, as nomenclature is already in place for long-recognized segregates. Further, the current view of *Aster* was engendered by a fundamental, abrupt (vs. conservative) broadening wrought primarily by Bentham and Gray and extended nearly to its limit by Cronquist. Some of such North American segregates have been included in *Aster* for a shorter time than they were treated as independent genera, and a truly traditional approach, with no other considerations, would be to treat them separately. The current, broad concept of *Aster* may be conservative in the sense of inclusiveness, but significant elements of what is conserved have been accreted in recent years. Further, until now the taxonomy of the genus has not been critically examined within the context of other genera of Astereae or, for the most part, even among a broad representation of species and genera from outside of North America that might be closely related to *Aster* s. lat. The treatment presented here could be considered conservative in that it maintains, in large part, a large and morphologically diverse group of species within a single genus (*Symphyotrichum*).

I. Review of recent *Aster* classifications

Both of the recent taxonomic overviews of *Aster* (Jones 1980a; Semple & Brouillet 1980a) included within the genus all of its previously proposed North American generic segregates, as well as several Old World ones, both studies beginning with the assumption that such a broadly conceived *Aster* is indeed

a monophyletic group. Both studies sharpened the definitions of subgroups within North American *Aster*, but neither provided a circumscription of the genus that would enable the exclusion of any group. In fact, it is difficult to find any more specific definition of *Aster* (as currently treated) than as erect, leafy-stemmed, mostly rhizomatous herbs with white or blue rays, involucral bracts herbaceous or with an indurate base and herbaceous tip, style branches of disc flowers with lanceolate collecting appendages, and a pappus of capillary bristles. Even among the features in this most general of characterizations, there are significant exceptions and qualifications to every character except the basic nature of the pappus.

The taxonomic system by Jones is essentially phenetic, recognizing many formally designated subgenera (further divided into sections and subsections) grouped informally by similarity in chromosome number. Semple & Brouillet weighted the significance of the morphology of the satellite (NOR) chromosomes and the morphology of the phyllaries, and they also were guided by their stated assumption that groups of Astereae with base chromosome numbers of x=5 are for the most part cladistically far-removed from x=9 and x=8 taxa. The taxonomic categories of Semple & Brouillet were informally designated. The two classifications are similar in some essential features: the x=9 groups in both include typical *Aster* as well as other diverse groups; both recognized the x=8 species as constituting a monophyletic group; both recognized the "grass-leaved species" (subg. *Heleastrum*) as a natural subgroup but differed in regard to its placement within the genus (additional comments below); and both recognized the "virguloid" x=5 species as monophyletic. In contrast, Jones included both x=5 and x=9 species in her subg. *Oxytripolium*, while Semple & Brouillet suggested that the x=5 members of *Oxytripolium* should be separated from *Aster* as a distinct genus. Semple & Brouillet (1980a) formally elevated the virguloid species to generic status (as the genus *Lasallea* E. Greene, re- formalized as *Virgulus* Rafin. by Reveal & King 1981), observing that the species of their new genus "do not show any more relationship to the species of *Aster* than to other genera of the tribe" (additional discussion below).

The phylogenetic analysis by Jones & Young (1983), which was the first to provide such a perspective for *Aster*, hypothesized that groups traditionally recognized as subgenera and sections are cladistically intermixed, given the initial assumptions and data of the study. Their analysis alternatively positioned *Heleastrum* as a subgroup within *Virgulus* or as its sister group; *Oxytripolium* was positioned either as the sister group to the x=8 species (including *Brachyactis* = subg. *Conyzopsis*) or close to it, the combined element in both cases nested within *Aster* proper. This phylogenetic hypothesis was then used as part of an argument for retaining a broadly conceived *Aster*, including the species of *Virgulus*, *Oxytripolium*, and *Brachyactis*.

The analysis by Jones & Young (1983), however, was inherently unable

to demonstrate that *Aster*, as they viewed it, was a natural group. They chose *Erigeron* as the single outgroup to establish the evolutionary polarity of character state changes within *Aster*. The assumption that *Erigeron* is the closest relative of *Aster* apparently was based in large part on statements by Cronquist (*e.g.*, 1947), who seems to have developed this view based primarily on similarities in habit, although he never provided details of justification. The species of *Erigeron* sect. *Fruticosi* G. Don, which were utilized by Jones & Young (1983) as the sister group of *Aster*, produce rhizomes and tall, leafy stems and are superficially similar to some species of *Aster*, but in details of vestiture, capitula, flowers, and fruits, they are similar to the rest of *Erigeron* but not to any group of *Aster* s. lat. A species interpreted as an intergeneric hybrid between *Aster* and *Erigeron* (*Asterigeron watsonii* [A. Gray] Rydb. = *Aster watsonii* A. Gray) clearly has its closest relatives within *Erigeron* (Nesom 1989a) and is placed there as *E. watsonii* (A. Gray) Cronq. Some monocephalous species of *Aster* (e.g., *A. alpinus* L.) resemble some species of *Erigeron*, and vice versa (*e.g.*, the Asian *E. thunbergii* A. Gray has been treated as *Aster*), but *Erigeron* and *Aster* can be separated by reference to a set of various features (*e.g.*, Cronquist 1947; Tamamschyan 1959; Grierson 1964), the resemblance between the two genera a result of convergent evolution. The closest relatives of *Erigeron* are hypothesized to be the primarily South American *Conyza* and four other genera entirely restricted to South America, these six genera constituting the subtribe Conyzinae (Nesom 1994e).

In the review and appraisal of their own analysis, Jones & Young (1983, p. 80) noted that the delimitation of major groups ("principal clusters") could be made with confidence but that "considerable instability was evident in the lower branches, and we have little confidence in the putative relationships among the clusters, as defined by the lowermost nodes." In their summary diagram of the phylogeny of *Aster* (Figure 5, "Putative relationships within *Aster*"), seven major groups arise independently from a hypothetical common ancestor, these groups corresponding to those delimited in their "branch-swapping" cladogram (Figure 4), which were derived from the input of a phenetic analysis rather than their "Wagner" analysis (Figure 2). *Aster* s. str. was placed in the summary diagram in a group with *Sericocarpus* and several groups of American *Aster*, but *Aster* s. str. was positioned in their "Wagner" cladogram as the sister group to a much larger clade including their *Symphyotrichum* and *Tripolium* s.l. They did not indicate why they chose the results of one analysis rather than the other.

As Jones & Young noted (1983, p. 83), a better answer to the question of whether or not *Aster* is monophyletic "probably can be found only in a comparison of potential segregate genera with other genera in the Astereae." Such necessity for a broader approach in the assessment of evolutionary affinities has been emphasized by recent DNA studies including a broad range of genera of North American Astereae by Suh (1989) and Morgan (1990), who have shown

that the species of *Aster* in their samples form a group more closely related to genera of Astereae other than *Erigeron* (see Nesom *et al.* 1990 for a summary of broadly defined phyletic lines in North American Astereae), particularly those of the subtribes Machaerantherinae (Morgan & Simpson 1992), Chrysopsidinae (Nesom 1991b), and Solidagininae (Nesom 1991c, 1991d, 1993c). Ten North American species sampled by Morgan (1990) form a monophyletic group in part corresponding to what has traditionally been recognized as *Aster*: *A. ericoides* L. (subg. *Virgulus*) is closely related to *A. drummondii* Lindl. and *A. carnerosanus* S. Wats. (both of subg. *Symphyotrichum*, as treated here) and these three in turn are phyletically close to a group that includes the *Oxytripolium* group of *Aster* (*sensu* Sundberg 1986), *Aster pauciflorus* Nutt., and the species of *Psilactis* (*sensu* Morgan 1993). Although these studies are significant, species of *Aster* s. lat. occupying critical positions (mostly those phylogenetically more basal) in hypotheses formulated in the present paper have not yet been included in molecular analyses, and the taxonomic placement of Morgan's species is equivocal in a larger context.

My ideas regarding the phylogeny of North American asters and corresponding taxonomic arrangement may not be exactly aligned with What Nature Has Wrought but they are based on detailed observation and broadly based consideration. The species groupings of the present treatment are similar in many ways to those of earlier studies, but the taxonomic system here is a notable departure from other relatively recent summaries (*i.e.*, Jones; Jones & Young; Semple & Brouillet). Molecular studies (chloroplast DNA) now underway in the laboratory of Dr. John Semple will soon provide an independent evaluation of these morphologically based treatments.

II. Recent additions to New World *Aster*

In the last twelve years, many nomenclatural changes have been proposed within *Aster*, primarily among North American taxa, particularly with regard to delimitation and redefinition of species and varieties. The majority of such studies have been by A.G. Jones, J.C. Semple, K.L. Chambers, or associated research groups. Many of these are cited in other contexts in the present paper; other representative studies are cited here (Semple 1984; Semple & Chmielewski 1987; Lamboy *et al.* 1991). Several new species have been described (Sundberg & Jones 1986; Lamboy 1988; Campbell & Medley 1989; Nesom 1989b; Cronquist 1994). *Chrysopsis breweri* A. Gray, a rayless species from California and adjacent Nevada, was recently transferred by Semple (1988) into *Aster* subg. *Eucephalus*, a group that clearly includes its closest relatives. Most of the new taxa at or near specific rank have had little direct bearing on problems regarding generic definitions or subgeneric classification.

III. Recent segregates from New World *Aster*

Since the 1980 classificatory papers and the phylogenetic study in 1983, a number of species or species groups have been transferred, segregated, or resegregated from *Aster* to other genera:

(1) *Aster lepidopodus* B. Rob. & Fern. to *Erigeron* L. (Nesom 1981);

(2) *Aster riparius* Kunth to *Machaeranthera* sect. *Arida* Hartman (Stucky 1978; Jones 1983a);

(3) two new genera recently segregated from *Aster* (*Almutaster* and *Weberaster*) and several nomenclatural transfers made from *Aster* to the established genus *Symphyotrichum* Nees (Löve & Löve 1982); no comments past the nomenclatural necessities were provided in justification of their proposed taxonomy, but these taxa are discussed in detail in the present paper;

(4) *Aster intricatus* (A. Gray) S.F. Blake to *Machaeranthera* sect. *Arida* Hartman (Nesom 1989d);

(5) *Aster blepharophyllus* A. Gray to *Machaeranthera* sect. *Arida* Hartman (Nesom, Vorobik, & Hartman 1990);

(6) *Aster spinosus* Benth. to *Chloracantha* Nesom *et al.* (Nesom *et al.* 1991a; Sundberg 1991), completing the dismantlement of *Aster* [subg. *Oxytripolium*] sect. *Spinosi* (Alex.) A.G. Jones (the only other species included was *Aster intricatus* - see number 4 above);

(7) *Aster kingii* D.C. Eaton to *Tonestus* A. Nelson (Nesom 1991b);

(8) the three species of *Aster* subg. *Ianthe* (Torr. & Gray) A. Gray to the genus *Ionactis* E. Greene (Nesom & Leary 1992 for a summary and new species; Nesom 1992b for the incorporation of a fifth species);

(9) the three species of *Aster* subg. *Oreostemma* (E. Greene) Peck to the genus *Oreostemma* E. Greene (Nesom 1993a; also see Nesom 1992a);

(10) the five species of *Aster* subg. *Sericocarpus* (Nees) A.G. Jones to the genus *Sericocarpus* Nees (Nesom 1993b);

(11) *Aster ptarmicoides* (Nees) Torr. & Gray to *Solidago* L. (Boivin 1972; Brouillet & Semple 1981) but more recently placed in the genus *Oligoneuron* Small (Nesom 1993c);

(12) five species of *Aster* from Madagascar segregated as the new genus *Madagaster* Nesom of subtribe Hinterhuberinae (Nesom 1993d);

(13) *Aster grisebachii* Britton from Cuba confirmed as a species of the "pinifolia group" of *Hysterionica* (Nesom 1993e), this group subsequently resegregated as the genus *Neja* DC. (Nesom 1994d);

(14) eleven species of *Aster* [subg. *Doellingeria*] sect. *Triplopappus* (Torr. & Gray) A.G. Jones consolidated from among American and Asian species and treated as the separate genus *Doellingeria* Nees (Nesom 1993f);

(15) *Aster warmingii* Baker and *A. tuberosus* Less. *ex* Baker segregated as the primarily Brazilian genus *Apopyros* Nesom (Nesom 1994a), which is a member of the *Leptostelma* D. Don group of the Conyzinae;

(16) *Aster camporum* Gardner transferred to the South American genus *Inulopsis* O. Hoffm. (Nesom 1994b);

(17) *Aster* subg. *Conyzopsis* (Torr. & Gray) A. Gray resegregated as the genus *Brachyactis* Ledeb. (Jones 1984, 1985), but a conflicting view has been held by Houle & Brouillet (1985) and the group is maintained in the present treatment as congeneric with a broader group of North American species treated as *Symphyotrichum* (detailed comments below).

A number of other genera have been segregated from *Aster* prior to 1980 and are now generally accepted as distinct; many of these have been assigned to scattered phylogenetic positions (*e.g.*, Grau 1977; Zhang & Bremer 1993; Nesom 1994e). Among them are (for example) the New World genera *Diplostephium* and *Oritrophium* (Hinterhuberinae), *Machaeranthera* and *Xylorhiza* (Machaerantherinae), and *Noticastrum* (Chrysopsidinae), as well as Old World groups such as *Felicia* (Feliciinae), *Olearia* (Hinterhuberinae), *Heteropappus* and *Kalimeris* (Asterinae), and others noted in the following discussion.

In the following and preceding comments, if a species or other infrageneric taxon is not provided with an authority, the full, formal name can be found in the taxonomic summaries (Appendices I and II). Authorities for genera of Astereae can be found in Nesom (1994e).

ASTER S. STR. AND ITS ASIAN RELATIVES

I. Overview of *Aster* in Europe and Asia

There are about 180 species of *Aster* s. str. in the Old World (including the seventeen of the African *A. harveyanus* group, see below). The Northern Hemisphere species are natively concentrated mostly from the Himalayan region of Tibet (Sikang Province, China) and Nepal eastward in China through

Yunnan Province and Sichuan Province to Guangdong and Taiwan; considerably fewer species occur in east-central and northeastern China. Relatively few species of *Aster*, including the generitype, are centered in Europe or extend across northern Asia into western Europe. Most of these that have been identified as *Aster* s. lat. are in the groups regarded here as the genera *Crinitaria* (= *Linosyris*) and *Galatella*.

Only a single species of Old World *Aster*, *A. alpinus*, reaches the New World. *Symphyotrichum* (*Aster*, *Brachyactis*) *ciliatum* (Lindl.) Nesom and *Eurybia* (*Aster*) *sibirica* (L.) Nesom also have ranges that include both Asia and North America, but the phyletic origins of these two species lie in the New World and their extension across the north Pacific into Asia apparently is relatively recent.

Primary, broad sources of systematic and floristic information on Eurasian *Aster* include the following: Japan (Kitamura 1937; Ohwi 1965); Korea (Lee 1979); China (Hu 1965; Ling, Chen, & Shih 1985); Himalayan area (Grierson 1964); USSR (Tamamschyan 1959); Europe (Merxmüller *et al.* 1976; Wagenitz 1979). Other references are found throughout the discussions here.

The segregation of *Galatella*, *Crinitaria*, *Asterothamnus*, *Krylovia*, and other generic-level taxa previously included within a heterogeneous Old World *Aster* (Table 1) is apparently only recently reaching acceptance. The treatment of Chinese Astereae by Ling *et al.* (1985) appears to approach the presentation of monophyletic taxa, but anomalous elements with Asian *Aster* remain to be evaluated more closely. Some of the *Aster* "series" described by Ling (in Ling *et al.* 1985) are more distinctive than others and their taxonomic rank needs to be evaluated in a broad context. But after the exclusion of a few, small, disparate elements from *Aster* s. str. (see suggestions below), the genus appears to be more internally homogeneous. Even then, however, there is no firm evidence or explicit hypothesis that Old World *Aster* is monophyletic.

Grierson (1964) apportioned the Himalayan species of *Aster* among three sections: *Aster*, *Orthomeris*, and *Alpigeni*, the latter with four subsections. Ling *et al.* (1985) treated all of the ca. 135 Chinese species in the same three sections as Grierson, creating a number of infra-sectional categories (as "series") to accommodate the range of variation in each section. A provisional summary of the proposed, broad taxonomic structure of *Aster* s. str. is outlined in Appendix I. Some of the most conspicuous problematic species and species groups are discussed in the sections that follow below.

II. *Aster* sect. *Aster* and close relatives

The type of *Aster* is *A. amellus* L. (as lectotypified by Britton *in* Britton & Brown 1913; see Hitchcock & Green 1935), a species of southern Europe into west-central Asia. There are relatively few species clearly closely similar

to *A. amellus* (see sect. *Aster*, Appendix I), including *A. amelloides* Bess., *A. catalaunicus* Willk. & Costa, *A. ibericus* M. Bieb., *A. indamellus* Grierson, *A. peduncularis* Wall. *ex* Nees, and a few others, these mostly from Europe to the Himalayas. *Aster amellus* and the Himalayan *A. thomsonii* C.B. Clarke are the parents of a well-known horticultural hybrid of Europe (Grierson 1964). Ling *et al.* (1985) have considerably broadened the concept of sect. *Aster* with the addition of other species groups whose relationship to *A. amellus* is less clear. *Aster amellus* and its closest relatives are characterized especially by the following features: stems leafy, bearing a few heads in a loose corymb, sometimes reduced to monocephaly; phyllaries broad, graduated in ca. 3 series, somewhat indurated below, herbaceous above but mostly without a strongly demarcated, green apical patch; disc corollas tubular, the tube ca. half the corolla length, abruptly ampliate, with spreading-reflexing lobes; style appendages short, nearly deltate, closely papillate; achenes obovate, strongly flattened, with two, thickened, lateral ribs, the faces commonly with sessile glands near the apex; pappus bristles in 2-3 series, those of the inner series sometimes apically dilated, the outer series of short setae or bristles reduced in length.

The achenial morphology of *Aster amellus* is significant, as this feature is emphasized in the present investigation of subtribal boundaries and the definition of monophyletic lineages. As observed by Grierson (1964, p. 77), the achenial morphology of *Aster* s. str. is notably conservative: "Apart from size, the achenes show little variation throughout the genus. They are all of the bilaterally compressed type with two marginal ribs or with an additional rib on one or both sides as in *A. trinervius* D. Don, and sometimes with six ribs in *A. albescens*." The taxonomic position of the latter species is discussed below, where it is suggested that it is phyletically separate from most of Old World *Aster*.

Aster amellus was placed by Semple & Brouillet (1980a) in *Aster* subsect. *Aster* with the North American species treated here as *Eurybia* sect. *Calliastrum*, emphasizing their production of a corymboid capitulescence and broad phyllaries with a basally truncate apical patch. The present treatment, however, concludes that these similarities are convergent or widely parallel. The same conclusion holds for the NOR chromosome morphology of these species, which is implied to be similar according the taxonomy of Semple & Brouillet (1980a) (but see discussion below of NOR chromosomes for other references regarding *A. amellus*). Jones (1980a) also noted that the North American species most closely resembling *A. amellus* are among those of sect. *Calliastrum*, but this putative proximity was ambiguous in the analysis by Jones & Young (1983).

Aster sect. *Macrocephali*

Aster maackii Regel has been segregated as *Aster* sect. *Macrocephali* (Appendix I) by Jones (1980a). This species, which occurs in Japan, Korea, and Manchuria, is distinctive in its relatively tall stature (4-9 dm tall), sessile, serrate cauline leaves, long rays, and its elliptic-obovate, distally foliaceous phyllaries with purple scarious margins and a pair of large, lateral gland-like swellings near the apex. In floral and fruit morphology, however, as well as aspects of phyllary morphology, *A. maackii* resembles *A. amellus* and some of its close relatives (sect. *Aster*) as much or more than any other species. It is here maintained within sect. *Aster*, where Ling *et al.* (1985) have recently positioned it.

Jones (1980a) and Ling *et al.* (1985), following Kitamura (1937), placed *Aster tataricus* L. *f.* with *A. maackii* in sect. *Macrocephali.* Plants of these two species, however, have lanceolate, slightly keeled phyllaries without a foliaceous apex, subterete, 6-7-nerved achenes with a multiseriate pappus of even length bristles, and they are regarded here as only distantly related to *A. maackii* (see discussion below, "The *Aster tataricus* group"). *Aster sibiricus* also has been placed with these species, but it is here included within *Eurybia.*

Aster sect. *Alpigeni*

Aster alpinus L. (the type of sect. *Alpigeni*, see Appendix I) is similar to *A. amellus* in the morphology and glandular vestiture of its achenes and its externally differentiated pappus. Putative hybrids have been reported between these two species (*e.g.*, see Tamamschyan 1959, p. 111-112). Plants of *Aster alpinus* are strictly monocephalous, and the phyllaries differ from those of *A. amellus* in being oblong-lanceolate, completely herbaceous, and arranged in 2(-3) series of nearly equal length, and the lobes of the disc corollas are relatively short and erect. The pappus of *A. alpinus* commonly has a shorter, outer series, but the degree of differentiation is variable.

Aster alpinus ranges from northern Europe eastward across Asia and apparently is the only species accepted here as *Aster* s. str. that reaches North America, where (as *A. alpinus* var. *vierhapperi* [Onno] Cronq.) it occurs sporadically from Alaska to Colorado (Cronquist 1955; Hultén 1968; Weber & Wittman 1992). *Aster culminis* A. Nelson (the type from Colorado) is a synonym of *A. alpinus* var. *vierhapperi* (Weber & Wittman 1992). The wide variability in *A. alpinus* and its correspondingly complex taxonomy was discussed in detail by Onno (1932) and more recently summarized by Tamamschyan (1959), who recognized some of the more distinct subspecific taxa at specific rank. *Aster pyrenaeus* (Desf.) *ex* DC. of central Europe closely resembles *A. alpinus.* Grierson (1964) observed that *A. alpinus* does not reach the Himalayan region, but sect. *Alpigeni* is represented there by *A. tricephalus* C.B.

Clarke and its allies (nine species in the Himalayas), which Grierson divided between subsect. *Homochaeta* and subsect. *Heterochaeta.* Most of the species included by Onno (1932) in his delineation of *Aster* sect. *Alpigeni* were Old World *Aster*, but also included were American species of *Eurybia*, *Symphyotrichum*, *Xylorhiza*, and *Erigeron.* Ling *et al.* (1985) have suggested further broadening of sect. *Alpigeni* within *Aster* s. str.

Subdivisions of sect. *Alpigeni* based on variation in pappus morphology apparently are largely artificial; the subsections recognized by Grierson have been combined by Ling *et al.* (1985) as subsect. *Alpigeni* and placed in coordinate position with a group with the suggested name (but unvalidated) "subsect. *Senecioides*" (see Appendix I).

Regarding *Aster alpinus*, Cronquist (1955, p. 76) observed that, "Although it is necessarily included in *Aster*, this species approaches *Erigeron* in habit, achenes, and early flowering." The broadly obovate shape of the achenes and the presence of achenial glands, as well as the disc corolla shape, however, are anomalous within *Erigeron.* The similarity between *A. alpinus* and *Erigeron* has resulted from evolutionary convergence (see detailed comments above).

Aster sect. *Ageratoides*

The group of Old World species previously treated within *Aster* sect. *Orthomeris* is here regarded as *Aster* sect. *Ageratoides*, typified by *A. ageratoides* Turcz. (see Appendix I). Sect. *Orthomeris* s. str. becomes a synonym of the North American genus *Oclemena* (see discussion below).

Plants of sect. *Ageratoides* are characterized by flexuose stems, particularly in the capitulescence, toothed, often 3-veined leaves, the surfaces commonly sessile-glandular, heads in a corymboid capitulescence, lanceolate, thin-indurate (hardly herbaceous) phyllaries often with orange veins, and abruptly ampliate disc corollas. They are remarkably similar to *Oclemena*, but the disc achenes of the Asian species are flat and 2-nerved, although the ray achenes may be 3-4 nerved. Other differences are found in the morphology of the phyllaries, disc corollas, and pappus (see discussion of *Oclemena*, below). Nevertheless, the resemblance between sect. *Ageratoides*, *Oclemena*, and *Eucephalus* suggests that Old World *Aster* should be investigated for the possibility that it is polyphyletic.

Ling *et al.* (1985) have added a number of small, peripheral groups to sect. *Ageratoides*, but it is considerably more homogeneous with the suggested removal of *A. albescens* (DC.) Hand.-Mazz. and its close relatives (see below, "The status of *Aster albescens*), which have been included by both Grierson and Ling within sect. *Ageratoides. Aster molliusculus* (DC.) C.B. Clarke, which was treated by Ling *et al.* as the monotypic ser. *Molliusculi* within sect. *Ageratoides*, resembles the African species placed here in *Aster* sect. *Calimeridei.*

III. *Aster* in Africa

Many species of southeastern Africa were originally described as *Aster*, but most of these have now been transferred to the Astereaean genera *Felicia* (Grau 1971, 1973), *Polyarrhena* (Grau 1970), and a few others. A group of five Madagascan species described as *Aster* has been segregated as the genus *Madagaster* (Nesom 1993a). Only one group of seventeen native African species is still currently accepted as *Aster*, the "*A. harveyanus* group" (or the "*A. bakeranus* Burtt Davy *ex* C.A. Smith group"), these treated in detail by Lippert (1971, 1973). One species is recently added (Hilliard & Burtt 1985) and one transferred to the genus *Macowania* Oliv. of the Inuleae (Burtt & Grau 1972; Hilliard & Burtt 1976).

In Grau's study of *Felicia* (1973), his graphic depiction of its close relatives (p. 251) placed the *Aster harveyanus* group (as the genus *Aster*) in a close relationship with other South African genera. He was unwilling to formally segregate this group without a broader survey of *Aster*, but he noted (1971, p. 279) that "there is still lacking a valid generic name for the herbaceous 'Diplopappi'." The generic name *Diplopappus* Cass., which has been applied to the South African species of *Aster* sensu Lippert (*e.g.*, de Candolle 1836; Harvey 1865), must be typified by a North American species (Nesom 1993g). In any case, however, the species of the *A. harveyanus* group do not appear to be closely related to other African genera of Astereae (Nesom 1994e).

De Candolle (1836) treated *Diplopappus asper* Less. (= *Aster bakeranus*) within his *Diplopappus* sect. *Calimeridei*; the other species of this section (*sensu* DC.) are Himalayan taxa accepted by Grierson (1964) as true *Aster*, including *A. molliusculus* and *A. trinervius* (both placed by Grierson in sect. *Orthomeris*) and *A. peduncularis* (placed by Grierson in sect. *Aster*). The one remaining species of de Candolle's sect. *Calimeridei* is now treated as a species of the genus *Kemulariella* (*K. caucasica* [Willd.] Tamamsch.) (Tamamschyan 1959).

I have not been able to find any morphological character that would unequivocally eliminate the *Aster harveyanus* group from *Aster* s. str., particularly in view of its close similarity to the Asian species *A. molliusculus*, which appears to be closely related. *Aster harveyanus* and close relatives produce flat, 2-nerved, obovate achenes with glands scattered over the surfaces, a biseriate pappus (inner series of persistent, barbellate bristles, the outer series short and scaly), and thick, mostly herbaceous phyllaries. They constitute a distinctive phylad characterized by thick, 3-nerved, entire, mostly cauline leaves with a subclasping base, solitary heads on long peduncles, disc corollas with short and sharply reflexing lobes, and thickened, nearly tuberous, fibrous roots. The group is endemic to grasslands at moderate elevations in the Afromontane floristic region, an elongate series of isolated highland areas in southeastern Africa (see summary by Goldblatt 1978; Killick 1978).

Outside of the *Aster harveyanus* group, no other species of typical *Aster* occurs in Africa as part of its native distribution. In the present interpretation, from an origin in Himalayan Asia, the "harveyanus" ancestral complex probably migrated southward along the mountains of the eastern margin of Africa, where it remains extant only in the southernmost region, reaching as far as the Drakensberg Mountains. This distinctive group is provided here with the formal designation of *Aster* sect. *Calimeridei*, validated in Appendix I.

IV. Problematic species in *Aster*

Some species of Old World *Aster* that have been treated as generic segregates or else suggested to be potentially distinct are tentatively maintained here within *Aster* (see Appendix I, *Aster* Incertae Sedis). These and other problematic species are discussed in the following subtopics.

The status of *Bellidiastrum*, *Bellis*, and *Bellium*

Aster bellidiastrum (L.) Scop. , a species sometimes segregated from *Aster* as the monotypic genus *Bellidiastrum* (as *B. michelii* Cass.) is similar to typical *Aster* in its achene and pappus morphology and to some species of *Aster* in its monocephalous habit, phyllaries of nearly equal length, and short disc corolla lobes. The distinctiveness of *A. bellidiastrum* was early perceived, as it received at least three other names (besides *Bellidiastrum*) at generic rank. It occurs in south-central and southeastern Europe, where it is distinguished from other Old World species particularly by its combination of a scapose, monocephalous habit, spatulate, eglandular leaves in a basal rosette, conical receptacles, and achenes fully pappose with barbellate bristles.

De Jong (1965, p. 487) observed that *Aster bellidiastrum* (as the genus *Bellidiastrum*) is most closely related to *Bellis* L. and *Bellium* L. "on the basis of the scapose habit, spathulate toothed or entire radical leaves, herbaceous, biseriate phyllaries, and ribbed achenes which the three genera have in common." In addition, they also are similar in their phyllaries of completely herbaceous texture, short and erect disc corolla lobes, short and papillate collecting appendages atop markedly short style branches, and a biseriate pappus. Plants of *A. bellidiastrum*, *Bellis*, and some species of *Bellium* are scapose (caulescent in some species of *Bellium*), and all species of these three genera are monocephalous. *Aster bellidiastrum*, however, produces a well-developed pappus of barbellate bristles, often with a short, outer series of setae, in contrast to the scales and bristles in *Bellium* and relatively reduced pappus in *Bellis*, and the treatment of *Bellidiastrum* and *Aster* as congeneric apparently has emphasized their similarity in this plesiomorphic feature. If *A. bellidiastrum* is accepted

as a species of typical *Aster*, it must be with the hypothesis that it is specialized in its reduced habit and involucre. But its seemingly isolated position within *Aster* and its remarkable resemblance to *Bellis*, including the conical receptacles, suggests that its relationships and taxonomic position should be investigated in more detail. It may prove best regarded as a monotypic genus or even included within *Bellis*.

Bellis has been treated as the monotypic subtribe Bellidinae (Nesom 1994e), emphasizing its rosulate leaves, scapose, monocephalous stems, conical receptacles, herbaceous, pauciseriate phyllaries, and flat, essentially epappose achenes. Bentham (1873) noted possible points of phylogenetic connection between *Bellis* and other genera such as *Grangea*, *Lagenifera*, and *Brachycome*, each recently considered (Nesom 1994e) to be a member of a separate subtribe (*i.e.*, Grangeinae, Lageniferinae, and Brachycominae). The current treatment of *Bellis* recognizes its apparently intimate position among these groups and maintains it at a coordinate rank.

Bellium produces a flat to low-hemispheric receptacle, concave phyllaries with scarious margins, an outer pappus of scales. It is similar in these respects to genera of the subtribe Feliciinae, where it has been recently placed (Nesom 1994e), and is apparently only distantly related to *Bellis* and *Aster*.

The status of *Aster fastigiatus* (= *Turczaninowia*)

Aster fastigiatus Fisch. was segregated as the monotypic genus *Turczaninowia* by de Candolle in 1836. It has generally been treated within *Aster*, but Tamamschyan (1959), Ling *et al.* (1985), and Bremer (1994) have accepted it as a separate genus. This species, which occurs in eastern Asia (Japan and Korea to Mongolia, Manchuria, and eastern Siberia), is briefly characterized as follows: perennial or biennial herbs, the stems few-branched until the capitulescence; leaves linear to narrowly lanceolate, entire, evenly arranged along the stems; stems and undersurface of leaves densely and minutely strigillose with thick hairs, the vestiture often completely obscuring the surface, the leaves also minutely granular-glandular; heads small (5-8 mm wide) in dense terminal corymboid clusters; phyllaries in 2-3 graduated series, not keeled; ray flowers fertile, white, usually fewer than 10 in number, barely extending past the involucre; disc corollas with a narrow tube abruptly ampliate into the limb, the lobes long and coiling-reflexing, style branches with short, papillate collecting appendages, the inner flowers sometimes functionally staminate; achenes 1.0-1.2 mm long, obovate-oblong, 2-nerved but plump, the surfaces glandular and slightly strigose; pappus of (1-)2 series of equal-length bristles, with attenuate apices; chromosome number, n=9.

Among the most remarkable features of plants of *Aster fastigiatus* are their dense vestiture and small heads (with flowers and fruits reduced correspond-

ingly) in a compact capitulescence, but these are qualitative differences compared to other Asian species of *Aster*. In most floral and fruit characters, there is nothing to exclude *A. fastigiatus* from sect. *Ageratoides*. The ovarian sterility of the inner disc flowers may be a specialization connected with the reduction and compression of the flowers within a small head. Similar tendencies for reduction of heads, flowers, and fruits (except for the sterility) occur in other species of *Aster* (e.g., *A. sampsonii* (Hance) Hemsl. of southern China), and it is difficult to segregate *A. fastigiatus* on this basis. Following the suggestion of Tamamschyan (1959), however, the possibility of a close relationship between *A. fastigiatus* and *Galatella* needs to be investigated.

The status of *Aster bipinnatisectus*

Aster bipinnatisectus Ludlow *in* Grierson is endemic to rock faces in southeastern Tibet at 3200 meters elevation and was placed in the monotypic sect. *Bipinnatisecti* by Grierson (1964) in connection with the original description of the species. Most recently, however, Ling *et al.* (1985) have reduced sect. *Bipinnatisecti* in rank and treated it within sect. *Aster* as ser. *Bipinnatisecti*. The species is briefly characterized as follows: dwarf, caespitose, perennial herbs from stout taproot and short woody caudex branches, leaves bipinnatisect, in a basal rosette, densely white-sericeous, the hairs forming "dense cottony balls at the top of the rootstock" (the leaf bases), heads solitary, ray and disc flowers fertile, the rays light purple, and densely sericeous achenes with an inner pappus of slender setae and outer pappus of stout subpaleaceous setae. It resembles *Machaeranthera* in habit and leaf morphology, as noted by Grierson, but its pappus and phyllary morphology place it closer to the Asterinae than any New World groups. *Aster bipinnatisectus* appears to be morphologically isolated within *Aster*, but its habit is more common in other genera of the subtribe, e.g., *Krylovia*, *Psychrogeton*. The peculiarities in vestiture of *A. bipinnatisectus*, however, suggest that a close relationship to the Hinterhuberinae should be investigated, although such a relationship seems unlikely on a geographical basis.

The status of *Aster lanuginosus* (*Wardaster*) and *Aster prainii* (*Chlamydites*)

The monotypic genus *Wardaster* (Small 1926) was originally collected from south-central China near the Szechuan-Yunnan border on "high cliffs and boulder screes of slate" at 15,000 feet elevation. It is briefly characterized as follows (as described and illustrated by Small 1926): dwarf, densely lanate, rhizomatous perennials with spatulate, entire basal leaves and short-scapose monocephalous stems prominently thickened just below the heads; heads with phyllaries in 3 series nearly equal in length; receptacles alveolate; ray flowers

with lilac-violet ligules ca. 15 mm long; style branches of the disc flowers with papillate, deltate collecting appendages; bases of the anther thecae with short tails; achenes obovate-oblanceolate, flattened, 2-nerved, and 2.5-3.0 mm long.

Wardaster (*Aster lanuginosus* [J. Small] Y.L. Chen) is similar to *A. alpinus* and other species of typical *Aster* in habit (monocephalous, leaves mostly basal), but it is anomalous in vestiture. Further, the anther morphology suggests that the possibility of a relationship with the Hinterhuberinae should be investigated. In Grierson's examination of *Wardaster*, however, he observed (p. 75) that the anther bases "seem to be only slightly longer and more pointed than those of *A. flaccidus* subsp. *tsarungensis* or *A. fuscescens* which have anthers of comparable size."

Another monotypic genus remarkably similar in habit and vestiture to *Wardaster* was described earlier by J.R. Drummond (1907) from southeastern Tibet: *Chlamydites*. These plants were described as having phyllaries connate toward the base, rays apparently yellow, anther thecae without tails, and linear, "subcompressed," particularly large achenes (6-8 mm long). The "true affinity" of the species was hypothesized in the original description to be with the Chinese-Nepalese genus *Cremanthodium* Benth. (Senecioneae - Tussilagininae). Recently, however, *Chlamydites prainii* J.R. Drumm. has been transferred to *Aster* and placed with *Aster lanuginosus* as *Aster* [sect. *Alpigeni*] ser. *Prainiana* by Ling *et al.* (1985), who used the tailed anthers as one of the characters separating these from other species groups. Further, they described the ray color of *A. prainii* (J.R. Drumm.) Y.L. Chen as deep blue and the achenes to be 3 mm long, in contrast to the original description. The taxonomic position of both of these species needs further study.

The status of *Aster albescens* and *Aster* ser. *Albescentes*

Aster albescens is a widespread species that occurs in northwest India, Kashmir, Nepal, and Tibet, and then to Burma and Assam. It is briefly characterized as follows: commonly woody-stemmed subshrubs or shrubs 0.3-2.0 meters or more in height; leaves narrowly elliptic-lanceolate, sessile to distinctly short-petiolate, entire to serrate, closely pinnate-veined with relatively straight laterals, the margins often revolute; stems and lower leaf surfaces often closely and densely white-tomentose, punctate-glandular beneath the tomentum with sessile, resinous glands, (or) tomentum absent and the surfaces only glandular, (or) the surfaces eglandular; heads relatively small, 5-7(-9) mm wide and borne in tight corymbs; phyllaries broadly lanceolate, keeled, strongly graduate in length, stramineous, relatively even-textured, the margins sometimes purplish; rays white to bluish, not coiling; disc corollas lobes long and recurving-coiling, sometimes shorter and somewhat erect; disc style branches with closely papillate collecting appendages; achenes fusiform to narrowly obovoid, terete, (4-)6-nerved, 1.5-2.0 mm long, glabrate to short-strigose,

sometimes minutely glandular, the glands caducous but visible at least before fruit maturity; pappus of 1-2 equal length series of apically dilated bristles, commonly with a few short setae in an additional outer series.

Many varieties have been recognized within *Aster albescens* (see Grierson 1964, p. 109): "Leaf shape, size and indumentum are variable in this species as is also the size and shape of the capitulum, phyllaries and ligules. Coloration of the ligules and phyllaries is likewise often a distinctive but variable feature of these plants. There is little apparent correlation between these characters ..."

Grierson (1964) described a Tibetan species closely resembling *Aster albescens*. According to him (1964, p. 111), *A. fulgidulus* Grierson "is obviously related to *A. albescens* from which it differs in its larger ovate leaves with their glistening areas of epidermis over and between the minor veins on the lower surface." *Aster fulgidulus* is more restricted in distribution (known only from southeast Tibet) and is apparently much more uniform in morphology than *A. albescens*. Both *A. albescens* and *A. fulgidulus* are illustrated in Grierson's treatment. More recently, Ling *et al.* (1985) segregated these two species with yet four others as *Aster* [sect. *Orthomeris*] ser. *Albescentes* (see Appendix I).

Ser. *Albescentes* appears to be isolated among Old World *Aster*. Its keeled phyllaries, terete and multinerved achenes, and pappus bristles with a tendency for dilated apices suggest that it is more closely related to the North American groups, where it would be positioned near *Doellingeria* (Figure 1). As noted below (see "The Northern Hemisphere Subtribes"), this group of genera and species may constitute a basal "grade" only slightly removed from ancestral stock here hypothesized to resemble Hinterhuberinae. Ser. *Albescentes* resembles *Eucephalus* in its closely tomentose vestiture and keeled phyllaries; it resembles *Doellingeria* in achene morphology, *Oclemena* in its tendency for glandular achenes (but this also common in *Aster* s. str.), and *Oclemena* and *Sericocarpus* in sessile-glandular leaves (this feature also in *Aster* s. str.). Plants of ser. *Albescentes* are habitally distinct (as woody-based shrubs) and have other characters in a combination not found in other North American taxa.

Clarke (1876) placed *Aster albescens* within the genus *Microglossa* (Baccharidinae *sensu* Nesom 1994e), presumably influenced by the resemblance of these plants in shrubby habit, large, distinctly petiolate, and prominently pinnately veined leaves, relatively small heads in close corymbs, and relatively small, cylindrical, multinerved achenes. Previous ambiguity in the generic placement of *A. albescens* reinforces the suggestion that it (with ser. *Albescentes*) is isolated among Asian Astereae. In the tentative view here, the segregation of ser. *Albescentes* at generic rank apparently would be justifiable.

The *Aster tataricus* group

Aster tataricus and *A. faureri* Levl. & Van. (*sensu* Kitamura 1937) are considered here as the "*A. tataricus* group" (see Appendix I). The two are closely similar and have been considered varieties of a single species (see Kitamura 1936, 12:534.). *Aster tataricus* occurs in northeast Asia and is widely naturalized in the eastern United States, where it has escaped from cultivation. *Aster faureri* is endemic to the Manchurian region. These plants are briefly characterized as follows: perennials mostly 0.8-2.0 m tall, stems herbaceous, with numerous, prominent, raised ribs; leaves eglandular, thick, the basal persistent, elliptic, with a broadly winged petiole, the cauline subpetiolate, not clasping, the lower coarsely and evenly serrate, becoming entire upward; heads numerous in a loose, broadly paniculate to corymboid capitulescence, the terminal branchlets with heads in corymboid clusters; receptacles prominently alveolate; phyllaries lanceolate with acute apices, in 5-6 series slightly to strongly graduate in length, herbaceous, 1-nerved, with a green band along the midvein from base to tip, often purple-margined, often distinctly low-keeled; rays bluish, not coiling; disc corollas abruptly ampliate, with long, reflexing-coiling lobes; disc style branches with papillate, deltate-triangular collecting appendages; achenes fusiform to broadly ellipsoid or obovoid, 1.5-2.0 mm long, terete, (4-) 5-7 nerved, glabrous to sparsely short-strigose, eglandular, the fruit wall often becoming purplish; pappus of 2 series of apically attenuate bristles of equal length; base chromosome number, x=9.

Plants of the *Aster tataricus* group generally have been placed with *A. maackii* within ser. (or sect.) *Macrocephali* (e.g., Kitamura 1936, 1937; Jones 1980a; Ling *et al.* 1985), but *A. maackii* has phyllaries with broad, foliaceous apices and flattened, obovate, 2-nerved achenes and is closely similar to species of sect. *Aster* (see comments above). The *A. tataricus* group might be retained within *Aster* s. str. as an isolated element, but the keeled phyllaries and terete achenes suggest that the closest relatives of the group are among North American species. The phyllaries and achenes are particularly suggestive of *Doellingeria*.

V. Delimitation of the Asterinae s. str.

The species of the Asian genera placed here in the Asterinae (Table 1) have almost all been formerly treated as congeneric within *Aster* (as have the American species). The monotypic *Arctogeron* was originally described by Linnaeus as *Erigeron* and much later transferred by Komarov to *Aster*; *Psychrogeton* has been treated within *Erigeron* (see below). *Psilactis* has been treated within *Machaeranthera*. The Asterinae is briefly characterized as follows: perennial herbs, sometimes with a woody base; capitulescence corymboid, often reduced

Table 1. Composition of subtribe Asterinae. The date of publication and an estimate of the number of constituent species are indicated in parenthesis for each accepted genus. Additional synonyms for accepted genera can be found in Appendices I and II.

1. *Aster* group

    Aster L. 1753 (ca. 180)

2. *Kalimeris* group

    Kalimeris (Cass.) Cass. 1822 (8)

        SYN= *Asteromoea* (Blume) Makino 1898

    Callistephus Cass. 1825 (1)

    Heteropappus Less. 1832 (20)

    Miyamayomena Kitam. 1982 (6)

        SYN= *Gymnaster* Kitam. 1937, *non* Schutt 1891

    Boltonia L'Herit. 1789 (5)

3. *Galatella* group

    Galatella Cass. 1825 (30)

    Crinitaria Cass. 1825 (13)

        SYN= *Linosyris* Cass. 1825, *non* Ludw. 1757

        SYN= *Pseudolinosyris* Novopokr. 1918

    Tripolium Nees 1832 (1)

4. *Asterothamnus* group

    Asterothamnus Novopokr. 1950 (7)

    Kemulariella Tamamsch. 1959 (6)

    Krylovia Schischk. 1949 (4)

    Psychrogeton Boiss. 1875 (20)

    Arctogeron DC. 1836 (1)

Table 1 continued.

5. *Eurybia* group

Eurybia (Cass.) S.F. Gray 1821 (28)
Sericocarpus Nees 1832 (5)
Oreostemma E. Greene 1900 (3)
Ampelaster Nesom 1994 (1)
Psilactis A. Gray 1849 (6)
Almutaster Löve & Löve 1982 (1)
Canadanthus Nesom 1994 (1)
Symphyotrichum Nees 1832 (95)

6. *Doellingeria* group

Doellingeria Nees 1832 (11)
Oclemena E. Greene 1903 (3)
Eucephalus Nutt. 1841 (11)

7. *Ionactis* group

Ionactis E. Greene 1897 (5)

8. Incertae sedis

Chloracantha Nesom, Suh, Morgan, Sundberg, & Simpson 1991 (1)
Tonestus A. Nelson 1904 (8)

to monocephaly or sometimes modified as an open panicle; rays white, yellow in some taxa of *Psychrogeton*; achenes obovate, flattened, 2-nerved, often with glandular faces; pappus multiseriate, the outer series commonly shortened; base chromosome number, $x=9$, without exception. All groups except two are primarily restricted to Asia: *Boltonia* is North American and *Aster* sect. *Calimeridei* is African. Fourteen genera are formally recognized here, but six distinctive generic-level groups (see Appendix I), each potentially given generic status, are recognized and discussed. Two of these, which produce terete achenes, may be more closely related to species placed here in New World genera.

A. The status of *Boltonia* and *Kalimeris*

Boltonia s. str. is an eastern North American genus of five species (Anderson 1987). Bentham (1861, 1873), however, viewed these New World species as so close to those of the Asian genus *Kalimeris* that he considered them all congeneric. In contrast, Gray (1884) limited *Boltonia* to only the American species, and botanists since then have merged or separated the two genera in various combinations or else treated *Kalimeris* within *Aster* while keeping *Boltonia* separate. Recently, for example, Grierson (1964) considered *Boltonia* and *Kalimeris* congeneric, while Grau (1977) regarded them as separate. A revisional study of *Kalimeris* (Gu 1987, in press) has defensibly maintained the two as separate genera, based on the winged achenes and slightly different pappus morphology of the New World plants, but they are otherwise so similar in morphology that a hypothesis of close relationship between them is reasonable.

Boltonia is morphologically isolated in the New World, although it has been placed by Zhang & Bremer (1993) as closely related to genera treated by Nesom (1994e) within the subtribe Brachycominae. The closest relatives of *Kalimeris*, in contrast, apparently are more easily discerned and include a group of small Asian genera that have been segregated as satellites of *Aster*, including *Heteropappus*, *Miyamayomena*, and *Callistephus* (Table 1). Chung & Kim (1991) included *Boltonia* as part of this group and noted that the receptacles of *Boltonia*, *Kalimeris*, and *Gymnaster* are conical or steeply hemispheric. Natural hybrids are known between species of *Kalimeris* and *Heteropappus* (Tara 1973) as well as between *Kalimeris* and Asian species of *Aster* (particularly *A. ageratoides*, e.g., Inoue 1970; Tara 1972; Gu 1987). The genera of the *Kalimeris* group appear to be closely related among themselves and to typical *Aster*, both on genetic and morphological grounds. From this perspective, the cladistic relationship of *Boltonia* is here hypothesized to be as close or closer to *Aster* s. str. than to any of the North American taxa segregated from *Aster* in the present study.

Notwithstanding the hypothesis here of its close relationship to Asterinae, *Boltonia* produces short-tubed disc corollas with orange veins more like Southern Hemisphere groups, including Brachycominae, and the relatively small, scarious-winged achenes also are more consistently placed in the latter subtribe. *Boltonia* is further anomalous in the Asterinae in its pappus elements, which are of two lengths but not clearly in more than a single series; the phyllary midrib tends to be orangish, thick, and distinctly raised, and the habit also is reminiscent of the North American *Chloracantha* and *Eurybia* (*Aster*) *chapmanii* (Torr. & Gray) Nesom. A karyotype of *Boltonia* might produce valuable evidence of relationship, as the NOR chromosomes would be predicted to be of the Asterinae type (see discussion below) and distinctly different from those of American asters.

The *Kalimeris* group

Callistephus and *Miyamayomena* tend to produce broadly obovate leaves with coarsely and widely dentate margins, short-tubed disc corollas with short lobes and short, papillate collecting appendages of the style branches, and they have a tendency for reduction of the pappus. *Callistephus* has caducous bristles; *Miyamayomena* is essentially epappose; the capitulescence is reduced in both. The similarity in habit and general appearance, as well as the similar tendency for pappus reduction, between these genera and some species of *Myriactis* (Lageniferinae) is remarkable. In general, plants of these genera produce a loosely organized capitulescence (like the American *Symphyotrichum*) rather than a corymboid cyme.

Heteropappus is more similar to *Boltonia* and *Kalimeris* in its habit and loosely paniculate capitulescence, and the achenes commonly produce a distinctly biseriate pappus, the outer series of scales. In all species of *Heteropappus* except *H. altaicus* (Willd.) Novopokr., the ray achenes are epappose or have a reduced pappus. Species of *Kalimeris* form natural intergeneric hybrids with *Heteropappus* (Huziwara 1950; Tara 1973) and *Aster* (Inoue 1970; Tara 1972, 1979).

B. The status of *Galatella* and *Crinitaria*

The Eurasian groups *Aster* sect. *Galatella* (Cass.) Reichenb. (= *Galatella*) and *Aster* sect. *Linosyris* (Cass.) O. Hoffm. (= *Crinitaria*) have been treated as within *Aster* by Merxmüller *et al.* (1976) and Wagenitz (1979) but as separate genera in other studies (*e.g.*, Grierson 1975; Grierson & Rechinger 1982; Tamamschyan 1959; and a recent checklist of Asteraceae of the USSR [Cherpanov 1981]). *Galatella* includes, for example (by their names in *Aster*), *A. albanicus* Degen, *A. aragonensis* Asso, *A. sedifolius* L., *A. punctatus* Waldst. &

Kit., and *A. canus* Waldst. & Kit.; *Crinitaria* includes *A. linosyris* (L.) Bernh. and *A. oleifolius* (Lam.) Wagenitz. These two generic-level taxa were positioned by Jones & Young (1983) among the initial, primitive branches of *Aster* most closely related to sect. *Ianthe* and sect. *Eucephalus* but within a group that included *Doellingeria* as well. Similarly, Semple & Brouillet (1980a) suggested that *Galatella* and *Crinitaria* should be placed in "subgenus *Ionactis*," which in their view included both *Ionactis* and *Eucephalus*.

Both *Galatella* and *Crinitaria* have features (or at least tendencies) that indicate their close relationship to typical *Aster*: sessile-glandular leaves, disc style branches with relatively short (triangular-deltate) densely papillate collecting appendages, and flat, obovate, 2-(4-)ribbed achenes with the faces often glandular at least near the apex. Particularly in their glandular-punctate leaves and flat-topped capitulescences of relatively small heads, these taxa have a superficial resemblance to genera of North American Solidagininae, and I suggested (Nesom 1991d) that *Galatella* and *Crinitaria* might belong within the Solidagininae. With additional perspective, however, it appears that such similarities have developed in parallel and that *Galatella* and *Crinitaria* are more closely related to typical *Aster*.

Galatella and *Crinitaria* are distinct in morphology and set apart from other groups of *Aster*. Plants of both genera have a strong tendency to produce glandular herbage, strongly single-veined leaves, and broad, parallel-nerved phyllaries. Those of *Galatella* have sterile ray flowers usually with white to blue, non-coiling ligules, relatively shallow disc corolla lobes, and an essentially uniseriate pappus. Those of *Crinitaria* usually completely lack ray flowers, produce disc corollas with long, somewhat coiling-reflexing lobes, and a multiseriate pappus. As noted by Tamamschyan (1959), there are a number of relatively discrete morphological groups in both genera and the interrelationships among them are not clearly understood, suggesting that generic boundaries may yet be redefined. *Pseudolinosyris* of central Asia is one of these subgroups, separated from *Crinitaria* by narrowly lanceolate stylar collecting appendages and narrower, multinerved achenes; it is here tentatively included within *Crinitaria*.

C. The status of *Aster tripolium* (= *Tripolium*)

Another species of Eurasian *Aster* that has with some justification been treated as a monotypic genus is *A. tripolium* L. (= *Tripolium vulgare* Nees = *Tripolium pannonicum* [Jacq.] Dobrocz.). This species is most commonly found in saline habitats of sea coasts and coastal marshes and around inland salt lakes. It occurs from northern Europe southward to Italy and North Africa, from there to Turkey, northern Iran, and the Caucasus region, and then apparently scattered eastward across Asia to the Pacific coast from central

China, Japan, and Korea northward to Manchuria and Siberia. The range of this species is sometimes attributed to North America; the only records I know of from this region apparently were collected as waifs on "ballast" in Philadelphia, Pennsylvania (23 Sep 1877, *Parker s.n.* [US!]; Aug 1878, *Martindale s.n.* [US!]). *Tripolium* is remarkably specialized in its habitat, annual duration, glabrous, somewhat succulent leaves, and strongly accrescent pappus. It has a superficial resemblance to some species of the New World *Symphyotrichum* sect. *Oxytripolium* in habitat and vegetative morphology (glabrous, taprooted annual with thick, entire, and narrowly lanceolate leaves), but the strongly corymboid capitulescence, broad, thin-herbaceous and parallel-veined phyllaries in few (1-3) series, and the flat, obovate, 2-ribbed achenes, commonly with a mixture of eglandular and glandular trichomes of *Tripolium* indicate that it is related to the species and species groups of Old World Asterinae. Sundberg (1986) noted most of the peculiar morphological features of *Tripolium* and emphasized its base chromosome number of $x=9$ in its elimination from sect. *Oxytripolium*, the latter interpreted by him as strictly an $x=5$ group.

Aster tripolium has mostly been treated within *Aster* (*e.g.*, Merxmüller *et al.* 1976; Wagenitz 1979; Ohwi 1975), where it has been recognized at various ranks, from sect. *Tripolium* (Nees) Benth. to a possible member of *Aster* "subg. *Ionactis* sect. *Eucephalus*" (Semple & Brouillet 1980a). Tamamschyan (1959) accepted it as a monotypic genus, as did Zhang & Bremer (1993). Its distinctly corymboid capitulescence, herbaceous, broadly rounded, multinervate phyllaries, and tendency for raylessness (*e.g.*, Sterk & Wijnands 1970) are similar to *Crinitaria* and *Galatella* and suggest that these taxa may be closely related. Such a combination of features apparently does not occur elsewhere in *Aster* or its close relatives, and in this interpretation, *Tripolium* is reasonably treated as a monotypic genus. Within *Aster*, it is isolated.

D. The *Asterothamnus* group

As recognized here, the *Asterothamnus* group (Table 1) includes a number of relatively small genera characterized as perennials from a woody base, commonly caespitose in habit, the stems and leaves often sessile-glandular and often tomentose, with few or solitary heads and strongly coiling rays. These are segregates of *Aster*, similar to the latter in the following set of features: glandular vestiture (*Krylovia*, *Psychrogeton*, Asian "*Brachyactis*"); white to bluish rays in a single series; short and papillate collecting appendages of the disc style branches; phyllaries variable in morphology but without an apical patch; disc corollas abruptly ampliate, long-lobed in *Asterothamnus* and *Krylovia*; achenes obovate and flattened (sometimes 3-angled), the faces commonly glandular at least near the apex; and pappus multiseriate, the outer series often strongly shortened, the inner bristles sometimes apically dilated

(in *Asterothamnus*, *Krylovia*, and *Kemulariella*). The group occurs primarily in central Asia: *Asterothamnus* and *Arctogeron* in the steppes of central Asia (Siberia, Mongolia, and China) in open, stony habitats; *Krylovia* in rock crevices and talus of montane central Asia; *Kemulariella* in montane Caucasus; *Psychrogeton* and Asian "*Brachyactis*" in the Himalayas, central Asia, and montane Asia Minor.

Grierson (1964, p. 116) observed that *Asterothamnus* is segregated from *Aster* on habital and vegetative characters "but is not distinguished by characters involving the involucre, flowers, achenes or pappus." While all of the *Aster* segregates of the *Asterothamnus* group certainly are in need of more detailed investigation, the distinctly keeled phyllaries of *Asterothamnus* and *Krylovia* set them apart from most other Old World *Aster*. There is reason to consider the group monophyletic, and the well-defined and well-accepted genus *Psychrogeton* appears to be a member of it. Continued recognition of *Psychrogeton* suggests that the others should be accorded coordinate taxonomic status.

Asterothamnus is a remarkably distinctive genus. The plants are strongly branching subshrubs with revolute-margined, linear or narrowly elliptic leaves, the stems and leaves closely and thinly tomentose and gray-green, and the heads radiate or eradiate and solitary or few in a loose corymb. Plants of *Krylovia* are caespitose perennials from a taproot and thick caudex branches, producing a persistent basal rosette of broad, toothed, sessile-glandular leaves, and the heads are few or solitary on scapose stems. *Krylovia* is similar in habit and vestiture to many species of *Psychrogeton*. *Asterothamnus* and *Krylovia* apparently are closely related though markedly different in habit. They are similar in their *Eucephalus*-like phyllaries, evenly yellow-green or sometimes purple-margined, and with a low but distinct central keel, disc corollas with long, coiling-reflexing lobes, flat, obovate, 2-nerved achenes with glandular surfaces, and a 1-3-seriate pappus, sometimes with a short outer series, the bristles apically attenuate or dilated.

Arctogeron has a caespitose habit like *Krylovia* but is immediately distinct in its stiffly linear-filiform leaves. The single species, *A. gramineum* (L.) DC., was originally described by Linnaeus as *Erigeron*, but its resemblance to the latter genus is interpreted here as convergent. *Arctogeron* differs from *Erigeron* in its 3-veined phyllaries, differently shaped achenes, and there are no prominent resin ducts accompanying the veins of herbage and achenes. There is a strong habital resemblance between *Arctogeron* and some species of *Ionactis*, but *Arctogeron* differs from these in its scapose stems, relatively short and papillate collecting appendages, 3-nerved, unkeeled phyllaries in 3-4 series of nearly equal length, and its consistently flat and 2-nerved achenes.

Kemulariella, as defined and treated by Tamamschyan (1959), is a genus endemic to the Caucasus region. It was described as different from *Aster* in its double pappus (the outer series distinctly shortened and often scaly),

but a differentiated, multiseriate pappus is also characteristic of many species of *Aster*, including the type (see previous discussion). *Kemulariella caucasica* (Willd.) Tamamsch., the generitype, is very different from the other five species in its tall, herbaceous, solitary stems with large cauline leaves and was placed by Tamamschyan as a monotypic section. The other species of *Kemulariella* resemble *Krylovia* in their caespitose habit with woody rhizome and caudex branches and relatively more numerous stems from the base. The definition of *Kemulariella* and its internal consistency need to be reexamined.

Psychrogeton

Plants of *Psychrogeton* are mostly perennial (few annual or biennial), usually with a thick, woody taproot or at least short, woody caudex branches. They are similar to *Krylovia* in their caespitose habit, and the leaves and stems commonly are sessile-glandular as well as lanate or tomentose; the leaves are petiolate and obovate to rotund with coarsely toothed margins. The phyllaries often are distinctly foliaceous and even in length, similar to those of Asian "*Brachyactis*" (see below). The ray corollas are strongly reduced in size, barely exceeding the involucre in most species, and sometimes apically lobed. The ligules are mostly white, but they are yellow in some species, clearly a derived condition. *Psychrogeton* is particularly distinctive in its disc flowers with short-lobed corollas and sterile ovaries (functionally staminate). The genus has been treated as *Erigeron* subg. *Conyzastrum* (Boiss.) M. Pop. (see Botschantsev 1959), but the flowers and fruits are those of Asterinae. *Psychrogeton* has received a detailed treatment at generic rank by Grierson (1967).

Asian "*Brachyactis*"

The ca. five endemic Asian species (Appendix I) that have been identified as *Brachyactis* are not congeneric with the typical, primarily American species of *Brachyactis* (= *Symphyotrichum* sect. *Conyzopsis*), as noted in the discussion that follows below. Both groups are characterized by multiseriate, nearly eligulate pistillate flowers and foliaceous phyllaries, these features developed convergently. Gray (1880) and Grierson (1967, 1982) have noted that the southwest Asian and Himalayan species of *Brachyactis* are similar to *Conyza*, which is similar in its numerous, highly reduced pistillate flowers. The latter is broadly interpreted in the Old World, but Asian "*Brachyactis*" differs from *Conyza* in features of phyllary, achene, and pappus morphology, and I am unaware of any species of *Conyza*, from the Old or New World, that could be considered congeneric with Asian "*Brachyactis*."

In contrast, there is a resemblance suggestive of close relationship between Asian "*Brachyactis*" and *Psychrogeton* in their habit, glandular vestiture, tendency for foliaceous phyllaries, and flattened, obovate, glandular achenes. Geographically as well, these two groups are similar. Asian "*Brachyactis*" differs, however, in its fertile central flowers and tendency for heads on axillary peduncles. The species of the latter have not been consistently aligned with any other genus, and I agree with Grierson (1982), who has noted that two undescribed genera may be represented among this small number of species.

THE NORTHERN HEMISPHERE SUBTRIBES

In a study and classification of the tribe Astereae (Nesom 1994d), the five primarily Northern Hemisphere subtribes are hypothesized to be monophyletic and distinct as a group from those of the Southern Hemisphere. The Asterinae and Solidagininae appear to be the least specialized among the essentially North American subtribes, and some species in each group are very similar to Hinterhuberinae. The Asterinae are mostly herbaceous (vs. woody), but a number of genera of Solidagininae are similar to Hinterhuberinae in their shrubby habit; both subtribes produce mostly eglandular achenes (vs. commonly glandular in the Hinterhuberinae). Many Solidagininae produce punctate-resinous leaves, a feature commonly found in the Hinterhuberinae. Keeled phyllaries are characteristic of some basal Asterinae as well as the Chrysopsidinae and some Machaerantherinae, but not of the Solidagininae. Some genera of Hinterhuberinae produce keeled phyllaries. Primitive features in at least the apparently basal genera of Asterinae and Solidagininae (assuming that the primitive states are found in the Hinterhuberinae) include the following: a corymboid capitulescence; disc corollas with relatively long, coiling-reflexing lobes; papillate (vs. hairy) collecting appendages of the disc style branches; terete, multinerved achenes; and multiseriate pappus of equal-length bristles, these sometimes with dilated apices.

The four autochthonous New World subtribes (Asterinae, Solidagininae, Machaerantherinae, and Chrysopsidinae) are characterized by essentially terete, cylindric or fusiform, multinerved, mostly eglandular achenes, while plants of the Old World groups of Asterinae consistently produce flat, obovate, mostly 2-nerved achenes commonly with glandular faces. Outside of the Northern Hemisphere, species of the Hinterhuberinae are most similar to those of the northern groups and it is likely that this subtribe is the closest representative of the ancestral stock from which they arose. Members of the Hinterhuberinae produce mostly terete, multinerved achenes, as do those of the tribes that have been hypothesized to be ancestral or near-ancestral to the Astereae (*i.e.*, Anthemideae, Gnaphalieae, and Senecioneae).

The primitive ray color for the Northern Hemisphere subtribes is not clear, although there is reason to suspect that the primarily yellow-rayed Chrysop-

sidinae and Machaerantherinae both may have been derived from white-rayed ancestors (see below). Genera of the Hinterhuberinae are divided in ray color (some with white, others with yellow rays). Basal Solidagininae (particularly *Solidago* and *Oligoneuron*) differ from the Asterinae primarily in their yellow rays, although white-rayed species occur in both of these genera as well as others of the subtribe. *Tonestus*, in which ray color varies between white and yellow, is questionably included in the Asterinae; the genus would be the only one in the Asterinae with yellow-rayed species.

The Solidagininae is less rigidly fixed in its ray color, as white-flowered species and genera occur sporadically throughout the tribe (Nesom 1993c). In some phylogenetically basal Solidagininae (*Solidago* and *Oligoneuron*), the white-rayed species also produce pappus bristles with dilated apices. The correspondence of these features is so striking and so similar to basal elements of the Asterinae that it seems plausible their appearance results from the expression (perhaps derepression) of a barely ancestral set of linked genes. White-rayed taxa (but without apically dilated pappus bristles) also occupy basal or near-basal positions in the Chrysopsidinae (i.e., *Noticastrum*; Nesom 1991b) and in the Machaerantherinae (*Xylorhiza*; Morgan & Simpson 1992).

The Solidagininae appears to be a relatively loose association of several genera and distinct generic groups (Nesom 1993c, 1994e). I previously suggested that *Doellingeria* and *Sericocarpus* are members of the Solidagininae (Nesom 1993c), but they are placed here in the Asterinae; the placement of *Tonestus* is still equivocal. The seemingly small differences that suggest placement of these genera in one group rather than the other emphasize the putatively close relationship between these subtribes.

The subtribes Machaerantherinae and Chrysopsidinae are similar to basal Asterinae in their primitively corymboid capitulescence, carinate phyllaries, terete, multinerved achenes, and multiseriate pappus; they are similar between themselves in their yellow ray flowers and specialized tendency for the production of large, straight-sided crystals in the disc corollas. The Machaerantherinae have a base chromosome number of $x=6$, taprooted habit, often glandular vestiture, strongly graduated phyllaries commonly with a distinctly delimited, green apical patch, and a multiseriate pappus of stiff bristles markedly uneven in length; the collecting appendages of the disc style branches of primitive groups are papillate and relatively short. The Chrysopsidinae have a base chromosome number of $x=9$, phyllaries more evenly pigmented and strongly carinate, and a multiseriate pappus with the outer series usually distinctly shorter than the inner; the disc collecting appendages are long and hairy even in the primitive groups. These two subtribes apparently are restricted to the New World (Nesom 1994e), with several possible exceptions (see previous discussion of Asterinae). Further evidence for their apparent common ancestry with the Solidagininae and Asterinae is provided by molecular data (Suh 1989; Morgan 1990; Suh & Simpson 1991; Morgan & Simpson 1993). With their mix

of primitive and specialized features, however, the segregation of neither the Machaerantherinae nor the Chrysopsidinae appears to create paraphyly within any other group of Astereae.

Eucephalus and *Ionactis*, as discussed below, show morphological similarities to both the Chrysopsidinae and Asterinae, which may provide a focal point in the investigation of relationships among these subtribes (Figure 2). Similarly, some species of *Symphyotrichum* show apparently parallel morphological resemblance to some Machaerantherinae, and artificial hybrids have been constructed between taxa of *Symphyotrichum* and *Machaeranthera* (see Nesom 1994f).

THE AMERICAN GENERA

Recognition that the ca. 181 primarily New World species of Asterinae are distinct as a group from *Aster* and the thirteen other primarily Old World genera that are its closest relatives also suggests that the New World species should be accorded corresponding nomenclatural status. There appear to be two broad options for meeting this requirement.

(1) All New World species previously treated as *Aster* could be maintained within a single genus, for which the oldest available generic name is *Eurybia* (Cass.) S.F. Gray (from 1821, see comments below). The next oldest names, *Doellingeria*, *Sericocarpus*, and *Symphyotrichum*, were all published by Nees in 1832. The first two of these have a long tradition as separate genera and have recently been accepted as such (Nesom 1993b, 1993f, and the present treatment); the third, *Symphyotrichum* (*Aster novi-belgii* L., the type), is applicable in the strict sense to a group of about eleven species placed by Jones (1980a) within *Aster* subg. *Symphyotrichum* sect. *Salicifolii*, although these species clearly are congeneric with a broader group that totals ca. 77 species (see Appendix II, *Symphyotrichum* subg. *Symphyotrichum*, as treated here). As noted in the introduction of the present paper, the congeneric treatment of the even larger, diverse group of 180 species of American Asterinae apparently would require the addition of *Psilactis*, and perhaps *Tonestus*, to complete an otherwise paraphyletic group.

(2) The New World species could be partitioned into smaller genera that appear to correspond with patterns of phylogeny and morphological variation. Some of these groups of Asterinae have been established as separate genera, at least in their basic concept, for a long period. And notwithstanding recent heterogeneous concepts, even a botanist as deeply immersed in the study of North American *Aster* as Lloyd Shinners suggested that *A. linariifolius* L., *A. acuminatus* Michx., and *A. umbellatus* Mill., among West Virginian species (1945), would be better treated within segregate genera. The segregates *Ionactis*, *Heleastrum*, and *Doellingeria* were recognized relatively recently in the treatment of Texas Asteraceae (Correll & Johnston 1970).

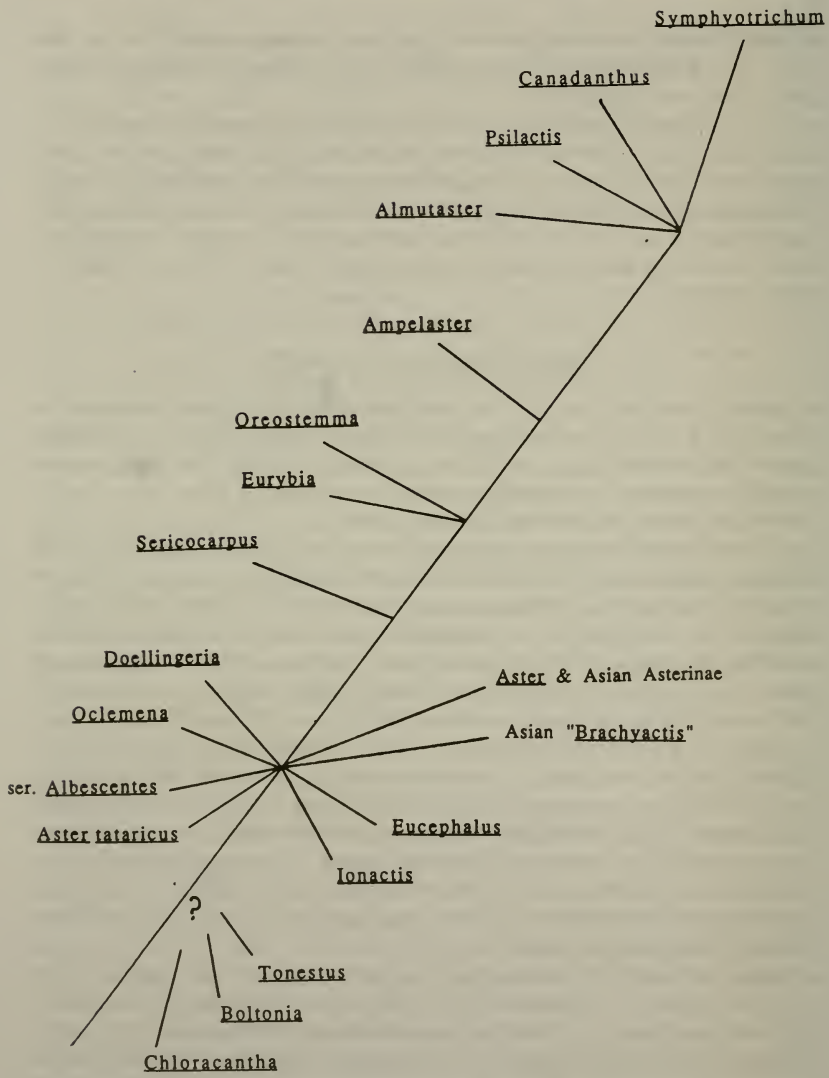

Figure 1. Phyletic arrangement of the genera of the "Eurybian lineage" in relation to other genera and generic level groups of Asterinae. See discussion in text.

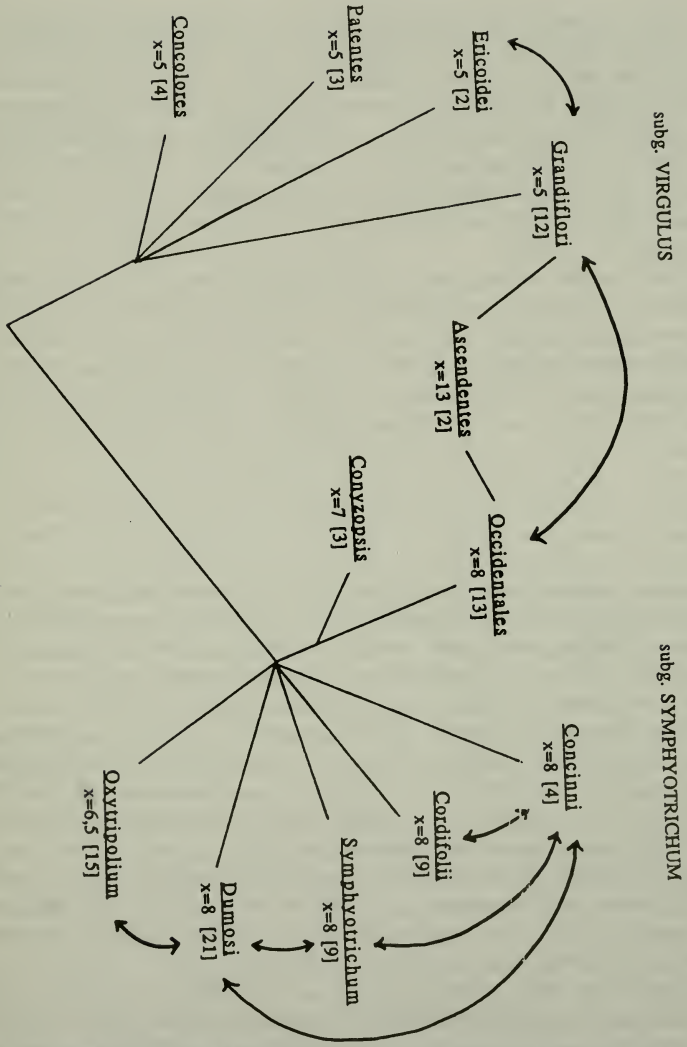

Figure 2. Diagramatic representation of the two subgenera and twelve sections of the genus *Symphyotrichum*. The base chromosome number and the number of species (in square brackets) are shown for each section. Natural hybrids occur between the sections connected by double-pointed arrows. See discussion in text.

I have followed the second option, accommodating the New World species of *Aster* s. lat. within twelve pre-existing genera, adding two newly described, monotypic ones to account for the pattern of variation. The genera accepted in the present treatment appear to be monophyletic, with the few caveats provided in the following discussions of individual groups, and for the most part each is sharply bounded and easy to recognize. More than half of the American species are placed in *Symphyotrichum*; this genus comprises two relatively distinct subgenera (in the present treatment), incorporating the group recently segregated as *Virgulus*.

Phylogenetic hypotheses for the American genera of Asterinae (Figure 1, although relatively unresolved) and for the subgenera and sections within *Symphyotrichum* (Figure 2) are provided in the present study, but details of the cladistic relationships among the taxa are equivocal. Additional comments are provided below under "The Eurybian lineage." The major features and infrastructure of these genera and considerations in their delimitation are discussed below.

I. *Doellingeria*

Eleven species have recently been consolidated as the genus *Doellingeria* (Nesom 1993f) and placed in two sections, primarily based on differences in leaf morphology: sect. *Doellingeria* has lanceolate, epetiolate, and mostly entire leaves, while sect. *Cordifolium* has cordate, petiolate, and serrate leaves. The three species of eastern North America are sect. *Doellingeria*; two of the eastern Asian species are sect. *Doellingeria*, the others sect. *Cordifolium*. The genus is briefly characterized as follows: perennial herbs, eglandular, glabrous to sparsely strigose; heads in a corymboid capitulescence; phyllaries in 2-4 graduate series, broad, apically rounded, with a raised midvein (but not keeled) and often several lateral veins, without a herbaceous apical patch; rays white, few, not coiling; disc corollas abruptly ampliate, with deeply cut, reflexing-coiling lobes; achenes eglandular, terete with 5-9 raised, often resinous veins, elongating to 3-4 mm long at maturity; pappus 2-3 seriate, the bristles with dilated apices; base chromosome number, $x=9$.

Doellingeria was earlier placed within the Solidagininae (Nesom 1993f), emphasizing its similarities to *Solidago* and *Oligoneuron*. Its phyletic position is somewhat equivocal, but it is here positioned within the Asterinae, emphasizing the white rays and distinctly 3-seriate pappus (with a shorter outer series) that it shares with *Oclemena*, *Eucephalus*, and *Ionactis*.

II. *Oclemena*

Oclemena is a North American group first recognized as a discrete phylad and segregated at generic rank by Greene (1903), who included *O.* (*Aster*) *acuminata* (Michx.) E. Greene and *O.* (*Aster*) *nemoralis* (Aiton) E. Greene in the genus. Nuttall (1840) also early recognized the distinctiveness of *O. nemoralis* by placing it as the type and only species of his *Galatella* sect. *Calianthus*. One additional species, *O.* (*Aster*) *reticulata* (Pursh) Nesom, is added to the group in the present treatment.

Plants of *Oclemena* are briefly characterized as follows: cauline leaves diminished in size toward the stem base, the lowermost reduced to scale-like bracts; leaf surfaces sessile-glandular, each gland producing a clear, orange-resinous head; stems densely invested with long, loose hairs with colored cross-walls; capitulescence corymboid, the heads on long, naked peduncles; phyllaries in 3-4 series graduated in length, narrowly oblong-lanceolate to linear-lanceolate with acute apices, evenly thin-herbaceous or scarious (without an indurated basal portion), essentially flat but the midvein often raised and then the phyllaries slightly but distinctly keeled; disc corollas pink or reddish at anthesis, with deltate, erect lobes; collecting appendages of the disc style branches narrowly lanceolate and papillate at least on the distal half; achenes fusiform to narrowly oblong in outline, plump though often evidently flattened, with 5-8 evenly spaced, longitudinal nerves, the entire surface moderately to densely invested with resinous glands, and the achene base markedly stipitate; and pappus multiseriate, with 2-3 inner series of long, barbellate bristles, with an outer series of much shorter setae in *O. acuminata* and *O. reticulata*. The chromosome number of all species is $n=9$ (*e.g.*, Hill & Rogers 1970), and the morphology of the NOR chromosome is the primitive type (*sensu* Semple *et al.* 1983).

Greene's recognition of *Oclemena* (1903) was prompted by his field observation that the heads (in bud) of *O. acuminata* are nodding. The same behavior has been confirmed for *O. nemoralis* (L. Brouillet pers. comm.) and Burgess (1903, p. 1227) also observed it in *O. acuminata*: "Remarkable for its soft-pubescent limp subviscid leaves and its decurved buds becoming erect and fragrant in flower." Greene (p. 4) also noted that *O. acuminata* "propagates by tubers rather than by stolons. At the end of each long slender subterraneous branch a small organ is formed which, exactly resembles a small potato, and from each of these springs a plant for the next year." The other taxa also produce swollen rhizome tips (not so abruptly swollen as a "small potato"), a feature more easily preserved and observed from herbarium specimens than the orientation of buds.

The three species of *Oclemena* can be identified by the following contrasts:

1. Leaves broadly obovate, relatively thin, lower surfaces sessile-glandular or apparently eglandular, the margins coarsely serrate, not revolute; cool

forests, Appalachian Mts. from Georgia and North Carolina northward to the eastern Great Lakes area, Ontario, Québec, Nova Scotia, and Newfoundland. ..... *O. acuminata*

1. Leaves narrowly to broadly elliptic, coriaceous, lower surfaces prominently sessile-glandular, the margins entire or slightly serrate distally, distinctly revolute. ..... (2)

   2. Peduncles eglandular, hairs with colored crosswalls absent or rare; achenes glandular, without other hairs; rays 10-17; pappus 2-seriate; boggy habitats, from New Jersey northward and westward to Ontario, Québec, Nova Scotia, and Newfoundland. .... *O. nemoralis*

   2. Peduncles glandular, heavily invested with hairs with colored crosswalls; achenes glandular and conspicuously hairy; rays (5-)7-11 (-14); pappus 3-seriate, the inner of 2 series of bristles of equal length, the outer shorter; dry, woodland habitats in Florida and South Carolina. ..... *O. reticulata*

Oclemena reticulata and *O. nemoralis* are similar in overall appearance, but *O. reticulata* and *O. acuminata* are similar in their biseriate inner pappus and dense vestiture of long hairs with colored crosswalls. *Oclemena acuminata* and *O. nemoralis* have a more northern distribution and occur in montane and moist habitats (see Brouillet & Simon 1981). *Oclemena reticulata* is similar to *Doellingeria* in its relatively few rays, long disc corolla lobes, 3-seriate pappus, and pappus bristles with clavate apices, but such features apparently are primitive in the lineage from which *Oclemena* and *Doellingeria* have arisen.

The observation that *Oclemena* × *blakei* (Porter) Nesom originates as a fertile, recurrent hybrid between *O. acuminata* and *O. nemoralis* has been made by numerous botanists (see Pike 1970), and this has subsequently been corroborated in detail (Pike 1970; Hill & Rogers 1970, 1973; Hill 1976). Detailed information regarding the distribution and biology of the parental species is provided by Brouillet & Simon (1981).

Oclemena reticulata (as *Aster*) was treated within sect. *Triplopappus* of *Aster* subg. *Doellingeria* by Jones (1980), Semple & Brouillet (1980), and Semple *et al.* (1991) rather than with its closer relatives (as placed here), but Semple *et al.* (1991) recognized that *O. reticulata* was set apart from the three species of *Doellingeria* treated by them. The tradition for the separate classification of *O. reticulata* was established by Torrey & Gray (1841), who included the species (as one of its synonyms, *Diplopappus obovatus* [Nutt.] Torr. & Gray) in *Diplopappus* subg. *Triplopappus* along with other species now identified within the genus *Doellingeria* (Nesom 1993f). Torrey & Gray included *A. reticulatus* Pursh among species of *Aster* hardly known to them and even speculated that it might belong to some other genus than *Aster*. In

their *Aster* subg. *Orthomeris*, Torrey & Gray included two species of *Oclemena* (as *A. acuminatus* and *A. nemoralis* Aiton) as well as one species presently treated in the genus *Xylorhiza*, two in *Eucephalus*, and *Aster ptarmicoides* (Nees) Torr. & Gray (= *Oligoneuron album* [Nutt.] Nesom). Their discussion of the relationships of subg. *Orthomeris* is the most reasonable if subg. *Orthomeris* is lectotypified by *A. acuminatus* (see Appendix II), and *Aster* subg. *Orthomeris* sensu stricto becomes equivalent to *Oclemena*.

Various Old World taxonomists have used "sect. *Orthomeris*" in a broad sense for certain Asian species of *Aster*. Kitamura (1936) placed *A. glehnii* Fr. Schmidt and *A. dimorphophyllus* Franch. & Sav. within ser. *Orthomeris* and formally described several other series within a broader [sect.] *Orthomeris*. *Aster glehnii* does closely resemble *Oclemena* (comments below), but *A. dimorphophyllus* has most recently been treated as a species of *Doellingeria* (Nesom 1993f). Kitamura separated [sect.] *Orthomeris* from typical *Aster* (sect. *Aster*) in 1936 but the next year (1937, p. 328) noted that "In Eastern Asia, *Euaster* and *Orthomeris* are not so distinct as in North America" and included [ser.] *Orthomeris* in a much larger, heterogeneous group.

Aster "sect. *Orthomeris*" was also used by Grierson (1964) to circumscribe a group of Asian species, including *A. albescens*, *A. trinervius*, *A. ageratoides*, and others. Of these, *A. glehnii*, *A. trinervius*, and *A. ageratoides*, in particular, resemble *Oclemena* in their flexuose stems, loosely corymboid capitulescence, resinous-glandular leaves with toothed margins, and glandular achenes. In these species, however, the achenes are non-stipitate, obovate, and distinctly flat with two lateral nerves (or the ray achenes sometimes with an extra nerve on one or both faces), the pappus is generally 1-seriate, the disc corollas are abruptly ampliate above the tube, with lanceolate, deeply cut, reflexing-coiling lobes, the style branches have shorter, closely papillate collecting appendages, and the phyllaries are somewhat variable in morphology but unkeeled. In a broader view, this latter set of features, especially the achene and style branch morphology, are characteristic of most of true (typical) *Aster*, and sessile-glandular leaves also occur in many species. A sample of other relatively well-known Asian species that appear to be closely related to *A. glehnii*, *A. trinervius*, and *A. ageratoides* are *A. baccharoides* Steetz, *A. lasiocladus* Hayata, *A. philippinensis* Moore, and *A. vestitus* Franch. (and others, see Appendix I, *Aster* sect. *Ageratoides*).

A combination of other features of *Oclemena*, in contrast, suggest that it is more closely related to North American taxa, especially to *Doellingeria*, than to Old World species of *Aster*. The most significant of these features (vs. typical *Aster*) are its subterete, narrowly oblong-fusiform, multinerved achenes (vs. flat, obovate achenes with two, distinctly marginal nerves, sometimes 1-2 others on the faces), pappus bristles (in *O. reticulata*) with dilated apices (vs. attenuate bristle apices), and disc corollas often pinkish or purplish at anthesis (vs. remaining yellowish). Phyllaries strongly graduated in

length and a multiseriate pappus occur both in *Doellingeria* and in typical *Aster*. The NOR chromosome morphology of *Oclemena* is similar to that of *Doellingeria*, *Eucephalus*, and *Sericocarpus* (Semple *et al.* 1983), but the Old World species of *Aster* (primarily sect. *Ageratoides*) to which *Oclemena* is most similar morphologically have different NOR morphology (see discussion below, under "Chromosome evolution in the Astereae").

Oclemena differs from *Doellingeria* in a number of features, eight of which were noted and scored by Jones & Young (1982); two of the most significant features of *Oclemena*, however, glandular leaves and achenes, were not included in their scoring. Differences between the two genera are summarized in the following couplet.

Key to *Oclemena* and *Doellingeria*

A. Buds and young heads nodding; phyllaries linear-lanceolate with acute apices, 1-nerved, usually with a low keel, the outer not basally indurated; disc corolla lobes deltate, mostly erect; mature achenes fusiform to narrowly oblong in outline, usually somewhat compressed at maturity, apically attenuate, with 5-8, slightly raised, non-resinous nerves, the achenes surface with a vestiture of sessile glands; achenes not lengthening to the full height of the involucre; pappus bristles sometimes slightly dilated in *O. reticulata* but apically attenuate in the other taxa. ..... *Oclemena*

A. Buds and heads erect; phyllaries with rounded apices, usually with distinct lateral nerves, not keeled, the outer somewhat basally indurated; disc corolla lobes lanceolate, spreading-reflexing; mature achenes somewhat obovate in outline, mostly terete at maturity, apically shouldered, with 4-8 longitudinal, strongly raised, orange-resinous nerves, glabrous to strigose, eglandular; achenes elongating to the full height of the involucre; pappus bristles prominently apically dilated. ..... *Doellingeria*

In summary, there is evidence to consider *Oclemena* a monophyletic, North American endemic more closely related to *Doellingeria* and other North American groups as to species of Old World *Aster*. Of the North American groups hypothesized to be closely related to elements of Old World *Aster* (particularly sect. *Ageratoides*), however, *Oclemena* appears to be among the most similar to them, and the parallel development of *Oclemena* (as hypothesized here) probably is indicative of common ancestry not far removed. The nomenclature within *Oclemena* is already available for two species, and a third species is added here, along with the commonly recognized and formally named interspecific hybrid *O.* × *blakei*.

III. *Eucephalus*

Eucephalus has long been recognized as a separate genus and most of the required nomenclature for its segregation already exists. The species are distributed primarily in California and nearby areas of northwestern United States and adjacent Canada. It is a remarkably coherent group in morphology, recognized particularly by its scale-like lower cauline leaves, corymboid capitulescence, broad, strongly keeled phyllaries without a sharply delimited apical patch, flattened, obovate, eglandular achenes, and multiseriate pappus of apically dilated bristles.

Eucephalus is briefly characterized as follows: perennials usually from creeping rhizome, sometimes tap-rooted in *E. paucicapitatus* (B. Rob.) E. Greene; glabrous or sparsely pilose with thin-based hairs to closely tomentose, granular-glandular or minutely sessile-glandular in *E. gormanii* Piper, *E. paucicapitatus*, and *E. glabratus* (E. Greene) E. Greene (under the heads); stems mostly simple or few-branched until the capitulescence, arising directly from the rhizome without an evident caudex; leaves all cauline, scale-like on the basal portions of the stems, large and relatively even-sized and evenly arranged above, sessile, not clasping (or slightly subclasping), entire, sometimes 3-nerved, the secondary venation reticulate; heads sometimes reduced to one but mostly 6-20 and corymboid (loosely so or paniculate in *E. breweri* [A. Gray] Nesom); phyllaries in 4-6 series strongly graduated in length, ovate, often convex, distinctly keeled from base to tip, stramineous-indurate, relatively even textured, the margins (inner series) thin-hyaline, often purplish distally, without a distinctly delimited apical patch but the apical area sometimes green; disc corollas yellow, usually remaining yellow, tubular, the tube ca. 1/3 the corolla length, the lobes deltate and erect to triangular and reflexing; disc corolla style branches with collecting appendages lanceolate to linear, mostly papillate above the base (hairy in some species); rays white to bluish, slightly coiling; achenes obovate, not basally stipitate, strongly flattened with a pair of lateral nerves, 2-nerved (e.g., *E. ledophyllus* [A. Gray] E. Greene and *E. engelmannii* [D.C. Eat.)] E. Greene), in other species commonly with 1-2 additional nerves on each face, eglandular; carpopodium symmetrical, orthogonal; pappus of terete bristles usually dilated at the apex, in 2-3 series, all of equal length or the outer sometimes markedly shorter; base chromosome number, x=9, the NOR chromosome morphology of the primitive type (*fide* Semple *et al.* 1983).

The rayless Californian species *Eucephalus breweri* was transferred from *Heterotheca* and correctly placed by Semple (1988) among the species of *Eucephalus* (as a subgenus of *Aster*). The discoid condition also occurs in *E. vialis* Bradshaw, *E. brickellioides* (E. Greene) Nesom, and *E. glabratus*, although the latter two species may sometimes produce 1-5 ray flowers. The earlier treatment of *E. breweri* within both *Chrysopsis* and *Heterotheca* and its long taxonomic persistence there reflects its remarkable resemblance to

plants of the Chrysopsidinae, much as Nesom & Leary (1992) earlier observed a strong similarity between *Ionactis* and the Chrysopsidinae.

If the flattening and apparent reduction in venation in *Eucephalus* achenes is homologous with that of Asian Asterinae, it suggests that the former may occupy an ancestral position with respect to the latter. This is especially plausible in view of other similarities between them. The achenes of *Canadanthus* (*C. modestus* [Lindl.] Nesom) are distinctly flattened and oblanceolate, but they are multinervate and the flattening appears to be a more evident specialization within its lineage, where its closest relatives have mostly cylindric achenes. The flattened, few-nerved achenes of *Symphyotrichum* also are clearly specialized. *Ionactis* produces somewhat flattened achenes with reduced venation, but the nature of its relationship to other genera is more obscure.

The species of *Eucephalus* resemble some species of Old World *Aster*, particularly those of sect. *Ageratoides*, in their relatively tall stature, leafy habit, and flattened, obovate achenes. *Eucephalus* differs from Old World *Aster*, however, in a combination of features: keeled phyllaries, disc corollas not abruptly ampliate, greatly elongated collecting appendages of the disc style branches, eglandular achenes, "triseriate" pappus (with a shorter outer series) of apically dilated pappus bristles, and chromosome morphology. Instead, *Eucephalus* appears to be closer to other North American groups in this same set of characters, although some of them appear to be plesiomorphic similarities.

IV. *Ionactis*

Ionactis is primarily a genus of the western United States (with four species in that region), but the most widespread species (*I. linariifolia* [L.] E. Greene) is restricted the eastern North America (Nesom & Leary 1992; Nesom 1992b). The group has long been recognized as a natural one.

Plants of *Ionactis* are briefly characterized as follows: low perennials from a taproot or thick, woody caudex branches; stems and leaves glandular in *I. caelestis* Leary & Nesom, the other species eglandular; leaves stiff, congested on the stems (internodes short); heads usually solitary, sometimes 2-3 and loosely corymboid; phyllaries strongly graduated in length, strongly keeled, relatively even textured, without an apical patch; disc corollas narrowly tubular; disc style branches with collecting appendages lanceolate, hairy from base to tip; rays bluish, coiling; achenes narrowly obovate in outline, those of the disc 2(-4)-nerved, of the ray (2-)3-nerved, flattened, not stipitate, glandular in *I. stenomeres* (A. Gray) E. Greene and *I. elegans* (Soreng & Spellenb.) Nesom, the disc achenes sterile in *I. caelestis*; carpopodium oblique; pappus of apically attenuate bristles in 1-2 series of equal length, with a much shorter outer series of bristles or scales; base chromosome number, x=9.

The species of *Ionactis* are particularly similar to *Eucephalus* and they have been hypothesized to be closely related (Semple & Brouillet 1980a; Jones &

Young 1983). These two genera are similar in their evenly distributed and even-sized (mostly) cauline leaves, strongly graduate, keeled phyllaries without an apical patch, few-nerved, relatively flattened achenes, and multiseriate pappus with a short outer series. *Eucephalus* differs from *Ionactis* in a number of features: taller stature, rhizomatous base, leaves not congested, stems and leaves without stiff, thick-based hairs, heads usually more numerous and often distinctly corymboid, disc style branches commonly with papillate collecting appendages, achenes more distinctly flattened and more broadly obovate, carpopodia symmetrical, and pappus bristles apically dilated. In most of these features, *Ionactis* is the more specialized.

The hypothesized phyletic alliance of *Ionactis* with the Chrysopsidinae (Nesom & Leary 1992, Nesom 1991b) emphasized their common production of carinate phyllaries without an apical patch, linear-lanceolate and hairy collecting appendages, oblique carpopodia, strongly shortened outer pappus series, and (in one species) glandular cauline vestiture. Plants of *Ionactis*, however, lack the large, straight-sided crystals in the disc corollas that are characteristic of the Chrysopsidinae, the rays are bluish to white rather than yellow, and the achenes have fewer nerves than in the goldenasters, except for *Heterotheca*, where the reduction in nervation is interpreted as a specialization within the subtribe. Similar features of pappus, phyllaries, and vestiture can also be found among species of *Eucephalus*, as noted above, but *Ionactis* is very different from *Eucephalus* in its habit and small, rigid, congested leaves with stiffly ciliate margins. *Ionactis* is regarded here as a relatively isolated genus, perhaps close to *Eucephalus* or perhaps more distantly separated from the Asterinaean lineage.

Plants of *Ionactis* are similar in habit and overall appearance to those of the Asian genus *Arctogeron*, but the latter produce papillate collecting appendages and broadly obovate achenes and can be considered securely placed among Asian Asterinae.

THE EURYBIAN LINEAGE

The Eurybian lineage includes nine genera (Figure 1), from *Sericocarpus* to *Symphyotrichum*. The major groups of the lineage are generally characterized by phyllaries in 3-5 series strongly graduated in length and with a green, distinctly demarcated apical patch. Mostly herbaceous, equal-length phyllaries are characteristic of *Oreostemma*, *Psilactis*, *Almutaster*, *Canadanthus*, and a similar tendency also occurs in some species within *Eurybia*, subg. *Virgulus*, and subg. *Symphyotrichum*, but this is interpreted here as specialization within the lineage. Species of *Aster* sect. *Aster* produce a sharply delimited apical patch similar to that in *Sericocarpus* and *Eurybia*; some taxa of the Machaerantherinae and Solidagininae also produce an apical patch, and the

similar morphology in these taxa appears to have developed in parallel to that of the Eurybian lineage.

Sericocarpus is the most primitive genus of the Eurybian lineage, retaining a set of unspecialized features: sessile-glandular vestiture (vs. stipitate-glandular), the capitulescence generally a corymboid cyme (the tendency to produce glomerated heads is specialized), disc corollas distinctly widened in the throat and limb, with long, reflexing-coiling lobes and remaining white or creamy at maturity, disc style branches with short, papillate collecting appendages, ligules essentially non-coiling, and pappus 2-3 seriate, the bristles with dilated apices.

The remaining, more specialized genera of the Eurybian lineage are characterized as follows: disc corollas narrowly tubular with short, erect lobes (abruptly ampliate distally in some of the primitive species of *Eurybia* and subg. *Symphyotrichum*), at least the apex usually becoming distinctly reddish or purplish at maturity; disc style branches with linear-triangular collecting appendages spreading-hairy from base to tip (rarely papillate in some species of *Eurybia*); and ray flowers with coiling, blue or purple ligules (less commonly white, not strongly coiling in some *Eurybia*).

The five most specialized genera, the *Symphyotrichum* subgroup (Figure 1), have consistently shortened achenes compared to the longer, narrowly cylindric ones of *Eurybia*, *Oreostemma*, and *Ampelaster*, although the position of the latter is somewhat equivocal on the basis of other characters. The *Symphyotrichum* subgroup, including *Ampelaster*, have a 1-seriate pappus of bristles consistently attenuate at the apex and an open, variably paniculate capitulescence (compared to the distinctly corymboid cymes of *Eurybia* and *Sericocarpus* and most of the other putatively primitive genera of the subtribe; the homology of the highly reduced capitulescence of *Oreostemma* is not evident). Further, all of the Asterinaean species with chromosome numbers reduced from $x=9$ are members of the *Symphyotrichum* subgroup, and all of this subgroup except *Almutaster* have cauline leaves with clasping bases, at least in the putatively primitive species.

The unity of the Eurybian lineage is further emphasized by morphological similarities (homologous and parallel) among the genera. This is reflected in Cronquist's observation (1955, p. 71) that the "characters of the various groups [of North American *Aster*] interlock most confusingly." Although parallelisms suggest that these groups are closely interrelated, natural groups among the American asters can be seen as much more discrete as a result of relatively recent studies, including the present one. Distinctive and genetically isolated groups of the Eurybian lineage have already been treated as separate genera (*Psilactis*, *Oreostemma*, *Almutaster*, *Virgulus*). If the whole Eurybian lineage were considered a single genus, such a group would be unparalleled in the tribe (Nesom 1994e) in its composition of highly distinctive, discrete, and genetically isolated subgroups. Other North American generic segregates

from *Aster* recognized in the present treatment (e.g., *Doellingeria*, *Oclemena*, *Ionactis*, *Eucephalus*) are simple to recognize and correspondingly distinct in phylogeny (outside of the Eurybian lineage).

V. *Sericocarpus*

Sericocarpus comprises five species, three in the eastern United States and two in the western U.S. A taxonomic summary and discussion of its main features and relationships was recently presented (Nesom 1993b). It is briefly characterized as follows: perennial herbs from woody roots, sometimes short-rhizomatous; leaves sessile- or punctate-glandular; heads sessile or subsessile in glomerate clusters; phyllaries keeled, with a sharply delimited, basally truncate, green apical patch, strongly indurate-thickened and convex below; disc corollas white, not purplish at maturity, funnelform, hardly abruptly ampliate; style branch appendages papillate; rays white, not coiling; achenes narrowly obconic to nearly cylindric, not basally stipitate, multinerved, strigose-sericeous; pappus in 2-3 series of equal length, the bristles apically dilated; base chromosome number, x=9. The morphology of the NOR chromosome is the primitive type (*sensu* Semple *et al.* 1983).

Sericocarpus has long been recognized as a distinct genus, and it was the most recent addition to North American *Aster* (Cronquist 1947b). As noted in the Introduction to this paper, and in contrast to my earlier view (1993b), I acknowledge that Cronquist as well as Semple & Brouillet were correct in placing *Sericocarpus* close to other species of North American asters. In the present treatment, *Sericocarpus* is regarded as closely related to *Eurybia*, although the similarities between them apparently are mostly plesiomorphic. The similarities between *Sericocarpus* and the Solidagininae, which I emphasized earlier, are here interpreted as parallel rather than homologous. In this view, however, this remarkable set of parallelisms indicates a recency of common ancestry, and the apparent phyletic proximity of the Asterinae and Solidagininae is noted elsewhere in the present discussion.

The resemblance between the Solidagininae and *Sericocarpus* and the corresponding distinction of the latter from *Eurybia* support the recognition of *Sericocarpus* at generic rank. Details of the morphological distinction between *Sericocarpus* and *Eurybia* are provided under the latter (in the following discussion).

VI. *Eurybia*

This genus has been consolidated primarily from a number of groups previously recognized by a variety of names: *Biotia*, *Heleastrum*, *Herrickia*, *Weberaster*, *Aster* sect. *Radulini*, and *Aster* sects. *Calliastrum* and *Spectabiles*.

The 28 species are divided into nine sections (in two subgenera) and recognized by a generic name that has not generally been applied to North American species.

A. Usage of the name *Eurybia*

The oldest generic name potentially applicable to any North American segregate from *Aster* s. lat. is *Eurybia* (Cass.) S.F. Gray (see below), based on *Aster* subg. *Eurybia* Cass., a combination at generic rank that has previously been attributed to Cassini. The name *Eurybia* has been applied in a limited sense to species of the North American *Aster* subg. *Biotia* DC. *ex* Torr. & Gray (*sensu* Jones 1980a; also see Lamboy & Jones 1987b). The name *Biotia* DC. (1836) at generic rank for this group is a heterotypic, later homonym of *Biotia* Cass. (1825) and use of de Candolle's name is illegitimate in reference to a genus. *Eurybia* has generally been regarded as a synonym of *Olearia* (e.g., Bentham 1866), a genus of Australia and New Zealand, but there apparently has been no pointed discussion regarding the typification and definition of *Eurybia*. *Index Nominum Genericorum* (Farr *et al.* 1979) and *Australian Plant Names Index* (Chapman 1991) both noted that a type for it has not been designated. Two problems are considered in the following discussion. When and by whom was the legitimate combination at generic rank made for *Eurybia*? And how is the name to be typified and interpreted, in view of considerable ambiguity in its early application?

a. Cassini's establishment of *Eurybia*

In the original description of *Eurybia* (as *Aster* subg. *Eurybia* Cass., Bull. Sci. Soc. Philom. Paris 1818:166. 1818.), Cassini placed three species within this taxon, without specifying any one of them as the type: *A. chrysocomoides* (Desf.) Desf., *A. tripolium* L., and *A. corymbosus* Sol. *ex* Aiton. Only the third of these is a North American species; it is a member of the *Biotia* group.

Cassini provided no specific comment regarding the derivation of the name *Eurybia*, but the Greek adjective "eurys" connotes "broad, wide, or widespread," while "baios" connotes "little, scanty, or few." It seems reasonable to speculate that *Eurybia* refers to the species treated here within sect. *Eurybia*, which produce relatively few ray flowers with little-coiling (thus wide-spreading) ligules.

In 1820, Cassini provided a review of the main features of his three "sous-genres" of *Aster* (*Dict. Sci. Nat.* 16:46. 1820.), which had received a more cursory treatment in 1818, but he did not include any of the three, originally cited species of subg. *Eurybia* in the discussion. Instead, he included only four Australian species now placed within *Olearia*, although it is not clear that he intended to limit the genus to those four. Further, Cassini began

the first sentence of the 1820 discussion with "This new genus of plants," but following that, he repeatedly referred to the group as a subgenus. Because of this ambiguity, it cannot be clearly established that *Eurybia* was validated at generic rank in 1820.

In his 1820 discussion, Cassini apparently began setting up new nomenclature for *Eurybia* as a genus, drawing in four, previously named Australian species (*Dict.* 16:47-48). For two of these names, he took the original epithet into *Eurybia*; for the other two, he substituted a new epithet that may have seemed more appropriate to him than the original for the plants involved (the substituted epithets match his chosen colloquial names). But because of the ambiguity of rank for *Eurybia* in 1820 and the corresponding interpretation regarding its validity as a genus, all four of Cassini's new combinations or new names in *Eurybia* must be regarded as invalid under any circumstance. Either (1) they were offered only as provisional names, anticipating the formal change to generic rank for his subg. *Eurybia*, (2) they were intended only as statements of taxonomic position of the species within *Aster* subg. *Eurybia*, or (3) they were proposed as a system of alternative nomenclature equivalent to the existing names in *Aster*.

Cassini was more definite regarding the status of *Eurybia* as a genus in yet another taxonomic summary of the group a short time later (*Dict. Sci. Nat.* 37:486-488. 1825.). In that discussion, he included nine species, including biotian species as well as *Olearia*, and made a number of new combinations in *Eurybia* (including *Eurybia corymbosa* [Aiton] Cass.). *Aster tripolium* and *A. chrysocomoides* were not among these nine, the latter species treated by Cassini in 1825 as the monotypic genus *Nolletia* Cass. (see below).

The 1820 article by Cassini has been considered the date of valid publication for *Eurybia* as a genus, apparently by Cassini himself (*Dict. Sci. Nat.* 37:462. 1825.) and by others, *e.g.*, de Candolle (1836), Hooker & Jackson (1895), Farr *et al.* (1979), and Chapman (1991). Notwithstanding Cassini's unambiguous treatment in 1825, the elevation in rank of *Eurybia* must be attributed to the British naturalist S.F. Gray.

b. S.F. Gray's treatment of *Eurybia*

The name *Eurybia* was used in 1821 by S.F. Gray (*Nat. Arrang. Brit. Pl.* 2:464-465. 1821.), apparently to provide a name for a circumscription at generic rank; the name was in a coordinate position with others clearly at that rank. As the heading of his entry 232, Gray cited "EURYBIA. Cassine" and the identity of the taxon in reference is unequivocal. Although Gray did not cite a potential basionym or its place of publication by Cassini (or any other publication by Cassini), his reference to "EURYBIA. Cassine" is no more or no less indirect than Cassini's own treatment of the name and implied new combination in 1825.

Because Gray did not specifically associate his own name with *Eurybia* at generic rank, it is not clear that it was his intention to validate the name by making a new combination. It is clear, however, that Gray intended to use the name *Eurybia* at generic rank, whether or not he considered the name already available (see comments above regarding Cassini's problematic 1820 discussion) and that he intended to provide a name for one of Cassini's original three species included within *Eurybia*. Thus, regardless of his intentions, the name *Eurybia* at generic rank can be legitimately attributed to S.F. Gray in 1821 as "(Cass.) S.F. Gray."

Gray applied the name *Eurybia* to only a single species, *Aster tripolium* L. (and cited the name among the synonyms), but he coined for it the new name "*Eurybia maritima*," apparently drawing from one of the polynomials he cited in synonymy: "Aster maritimus coeruleus Tripolium dictus, *Raii Syn.* 175, 2." Lamarck validly published *Aster maritimus* Lam. (a synonym of *A. tripolium*) in 1789, but Lamarck's name was not cited by Gray. Thus "*Eurybia maritima* S.F. Gray" apparently should be taken as superfluous (as seems to be the interpretation in *Index Kewensis*), not a legitimate combination at specific rank.

In Gray's comments, it was not "clearly indicated by direct citation including the term 'type' or an equivalent" (as required the *ICBN*, Article 8.3) that *Eurybia maritima* (= *Aster tripolium*) was to be considered the lectotype of *Eurybia*. Nor did Gray cite or specifically exclude the other two species (potential types) originally included by Cassini in *Aster* subg. *Eurybia*. Thus, while *Eurybia* (Cass.) S.F. Gray can be accepted as a valid name, the basis for typification of *Eurybia* was not established by Gray, and the possibility was left open that other species might also be included within *Eurybia* as a genus.

c. Nees's treatment of *Eurybia*

Nees (1832) included in the genus "*Eurybia* Cass." five taxa of North American biotians as well as three Australian taxa (all three of the latter now regarded as *Olearia*). In introductory comments to his treatment of *Aster* (p. 21), he noted that *Eurybia* in the strict sense should include only the American species, and in the taxonomic section he separated the biotian species as subgroup "Genuinae." He did not formally recognize a lectotype for *Eurybia*, but he concurrently transferred *Aster tripolium* into a separate genus (see below) and was aware that Cassini (1825), who he followed (see below), similarly segregated *A. chrysocomoides*, leaving only *Aster corymbosus* within *Eurybia* (of its three original species). W.J. Hooker (*Fl. Bor.-Amer.* 2:14. 1840.) followed Nees in identifying the biotian species as *Eurybia*, although Hooker noted that there appeared to be insufficient basis to warrant their separation from *Aster*.

d. *Eurybia* of de Candolle and others

De Candolle (*Prodr.* 5:264-271. 1836.) distinguished the biotian species and the associated Australian species as two genera (*Biotia* DC. and *Eurybia*, respectively), without commenting on the difference between his nomenclatural interpretation and that of Nees. He listed "*Eurybia* Cass. genuina" and "*Eurybiae* genuinae Nees" as synonyms of his *Biotia*, while crediting Cassini with the authorship of *Eurybia* ("*Eurybia* Cass. bull. philom. 188. p. 166. *dict.* 16. p. 486" – the last "486" apparently a misprint for the page "46" of Cassini's 1820 article). De Candolle accepted *Aster chrysocomoides* as the monotypic genus *Nolletia* (sensu Cassini & Lessing), and he treated *Aster tripolium* as a monotypic section within the genus *Tripolium* Nees. Roughly since the time of de Candolle's influential treatment, *Eurybia* has generally been associated with Australian species, accumulating many species in the 1850's primarily from the work of J.D. Hooker and F. Mueller, although it was subsequently subsumed as a synonym of *Olearia*. Burgess (1906, p. 61) noted specifically that "Cassini's *Eurybia* was originally meant for the Tasmanian group of shrubby species which de Candolle retained in it."

e. Lectotypification of *Eurybia*

Notwithstanding Cassini's apparent inconsistency in the definition of *Eurybia* past its original circumscription, some ambiguity regarding the date and place of publication of *Eurybia* as a genus, and the current taxonomic equilibrium regarding its position as a synonym of *Olearia*, the correct application of the name must be directed by a lectotypification drawn from the three species originally included within *Aster* subg. *Eurybia*. Cassini's brief description of this taxon (1818, *loc. cit.*, p. 166, quoted here in full) does not allow an unequivocal selection of a type: "Ce sous-genre de l'*Aster* comprend les especes de ce genre qui ont la couronne feminiflore comme les vrais *Aster* et le pericline de squames appliquees comme les *Galatea*; tels sont les *A. chrysocomoides*, *tripolium*, *corymbosus*, etc. Le sous-genre comprenant les vrais *Aster* se distingue des deux autres par la couronne feminiflore, et le pericline de squames inappliquees, appendiciformes; tels sont les *A. novi-belgii*, *longifolius*, *amplexicaulis*, etc."

There are three choices for the type of *Eurybia*.

1. *Aster* (*Conyza*) *chrysocomoides* (Desf.) Desf. This species is the type of *Nolletia* Cass. (*Dict. Sci. Nat.* 37:461, 479. 1825.) and is currently treated as *Nolletia chrysocomoides* [Desf.] Cass. (1825, *loc. cit.*). Depending on the interpretation of the legitimacy

of Cassini's combination, the species also has been treated as *Nolletia chrysocomoides* (Desf.) Cass. *ex* Less. (*Syn. Gen. Comp.* 187. 1832.). Desfontaines originally described the species as *Conyza* (*Fl. Atlant.* 2:269, t.232. 1799.) but transferred it to *Aster* (Tabl. ecole bot. [ed. 2] 121. 1815.) after observing in cultivated plants of the species that the peripheral, pistillate flowers (normally only tubular) sometimes produced evident ligules. Cassini did not believe these to be conspecific, but in any case, he explicitly indicated that he based his generic description of *Nolletia* on the type specimen of *Conyza chrysocomoides* Desf., which was confirmed as *Nolletia* by Jones & Lamboy (1987). If *Eurybia* were typified with this species, *Eurybia* would replace *Nolletia* as the earliest name for this well-established, Old World genus of ca. ten species.

2. *Aster tripolium* L. This species is now sometimes treated as the monotypic genus *Tripolium* Nees (*Gen. Sp. Aster.* 10, 152. 1832.) and is accepted as such in the present overview of *Aster* and related genera. *Eurybia* would replace *Tripolium* as the earliest generic name for this species, were it to be treated as a separate genus.

3. *Aster corymbosus* Aiton (= *Eurybia corymbosa* [Aiton] Cass. = *Aster divaricatus* L.). This species is a member of *Aster* subg. *Biotia* sensu Jones (1980a; also see Lamboy *et al.* 1991), part of a large North American segregate genus. If lectotypified by *A. corymbosus*, *Eurybia* becomes the legitimate name at generic rank for this group, which is recognized here for the first time as a distinct genus. Nees's early treatment (1832) was unambiguous regarding the composition of typical *Eurybia*, with the direct implication that *Aster corymbosus* should serve as the lectotype, but the formal designation of that species is made here, apparently for the first time (see Appendix II).

Tripolium and *Nolletia* have long been treated as separate genera; the names are clearly typified and well-established. Nees interpreted *Eurybia* as applicable to the North American biotian species, and early combinations by Nees and Cassini in *Eurybia* are available for some of those species. Cassini himself, however, was inconsistent in his enumeration of the constituent species of *Eurybia*, and as a result (at least partly), de Candolle's association of the name with species of *Olearia* has persisted up to the present. Nevertheless, the long association of *Eurybia* with *Olearia* is unjustified; application of *Eurybia* to the North American species appears to be legitimate as well as pragmatically satisfactory.

B. Definition of the genus *Eurybia*

The species of *Eurybia* are briefly characterized as follows: leaves and stems mostly glabrate, stipitate-glandular in a few species (*E. spectabilis* [Aiton] Nesom, *E. pulchra* [S.F. Blake] Nesom, *E. conspicua* [Lindl.] Nesom); leaves linear to obovate or cordate, venation parallel to pinnate but usually with 3-5 veins entering in parallel from the petiole base, with margins entire to serrate or spinulose, sessile, not clasping or slightly so in *E. compacta* Nesom; capitulescence loosely corymboid, reduced to 1 or a few heads in *E. sibirica*; receptacles commonly distinctly foveolate, sometimes fimbriate as well; phyllaries in 5-7 series strongly graduated in length, often thickened, usually distinctly low-carinate, basally indurate with a sharply demarcated green apical patch (or "striate" in some species, see below), the inner often 3-veined, the margins minutely ciliate-fringed in most species groups ; disc flowers with style appendages ca. 1/5-1/2 the length of the branches, the appendages linear-triangular and mostly hairy (vs. papillate) from base to tip, but papillate in *E. radulina* (A. Gray) Nesom and with a similar tendency in some other western species; achenes narrowly oblong in outline, cylindric or subcylindric, (2-)3-5(-7) mm long, with 8-12(-18) ribs, more or less stipitate basally, eglandular; pappus (1-)2-seriate, of flattened, often stiff bristles, these usually with dilated apices but slightly or not at all in a few species; and base chromosome number x=9 (NOR chromosome morphology of euaster type, but primitive type in *E. glauca* (Nutt.) Nesom and *E. sibirica*, fide Semple *et al.* 1983). Many of the species have a tendency to produce thickened leaves, and there is considerable variation in other foliar features. The disc corollas vary from narrowly tubular to long-tubed and abruptly ampliate in the distal third. Rays are mostly blue and coiling, but they are white and often little coiling in sect. *Eurybia*.

The close connection between subg. *Eurybia* and subg. *Heleastrum* has long been recognized. Torrey & Gray's original *Aster* subg. *Calliastrum* corresponds to sect. *Calliastrum* and subg. *Heleastrum* together; only later (1880, 1884) did Gray segregate *Heleastrum* s. str. into a separate subgenus. Gray (1880) made the further observation that subg. *Heleastrum*, sect. *Biotia* (= sect. *Eurybia*), and *Sericocarpus* (the latter treated as a separate genus by Gray) are closely related among themselves. Bentham's concepts (1873) were similar: he included species of subg. *Heleastrum* within his sect. *Calliastrum* and placed the biotian species as a separate section. Bentham also held *Sericocarpus* as a distinct genus.

Jones (1980a) placed sect. *Eurybia* (as sect. *Biotia*) with other sections in her subg. *Aster*; among the others were sect. *Radulini* and sect. *Aster* (including subsect. *Calliastrum*). In the analysis by Jones & Young (1983), sect. *Eurybia* was most closely related to *Sericocarpus* and to two other groups within subg. *Aster* (sensu Jones 1980a), sect. *Calliastrum* and sect. *Radulini*. Lamboy *et al.* (1991) followed Jones & Young in observing that a close relationship

exists between sect. *Eurybia*, sect. *Calliastrum*, and sect. *Radulini*, but they added *Doellingeria* as a close relative to these instead of *Sericocarpus*. They made no distinctions regarding the relative proximity of relationship among these four groups, nor did they provide specific comments regarding the bases for their hypotheses of relationship. The treatment by Semple & Brouillet (1980a) also was similar, as they placed sect. *Eurybia* closest to sect. *Calliastrum* and part of sect. *Radulini* (these two groups consolidated within subsect. *Aster*). Burgess noted (1906, p. 60) that "I have not recognized this Biotian group [sect. *Eurybia*] as a genus, for it grades too imperceptibly into *Aster* species of the *spectabilis* group, especially in involucre, the chief character by which it had been separated." The close relation between sect. *Eurybia* and sect. *Calliastrum* is emphasized by the occurrence of an intersectional hybrid (see comments below under sect. *Eurybia*).

As hypothesized here, the closest relative of *Eurybia* is the genus *Sericocarpus* (see additional comments above and in the Introduction). Plants of these two genera are strikingly similar in phyllary morphology and at least some species of both retain a number of putatively primitive features (especially multiseriate pappus of bristles with dilated apices and disc corollas abruptly ampliate distally). The resemblance in habit and leaf morphology of *E. compacta* (sect. *Calliastrum*) to *Sericocarpus* is particularly remarkable; it is interpreted here as parallel but indicative of close common ancestry. Similarly, Semple *et al.* (1983) correctly noted a resemblance in rhizome morphology between *Sericocarpus* and some species of subg. *Heleastrum*. *Eurybia* and *Sericocarpus* are distinguished by the following contrasts:

1. Leaves stipitate-glandular in a few species, otherwise eglandular; heads distinct, pedicellate, somewhat congested in *E. compacta*; disc corollas yellowish, becoming reddish or purplish at maturity, narrowly tubular, in some species abruptly expanded into the throat; style branch appendages mostly spreading hairy from base to tip; rays blue and strongly coiling, or mostly white and non-coiling in sect. *Eurybia*; achenes usually with a short stipe, glabrous to moderately strigose; NOR chromosomes of euaster type. ..... *Eurybia*

1. Leaves sessile- or punctate-glandular; heads sessile or subsessile, in glomerate clusters; disc corollas white, remaining so at maturity, broadly funnelform; style branch appendages papillate; rays white, not coiling; achenes not stipitate, sparsely densely strigose-sericeous; NOR chromosomes of primitive type. ..... *Sericocarpus*

Subgenus *Heleastrum*

Subg. *Heleastrum* comprises six species in three distinct subgroups endemic to the southeastern United States. It has been regarded as a separate genus by Greene (1896), Shinners (1949, 1969), and Correll and Johnston (1970), but the only recent treatment of all its species has been by Cronquist (1980), who retained it within a broadly conceived *Aster*. These are sometimes referred to as the "grass-leaved asters," characterized by linear to narrowly oblanceolate, sessile (not clasping), often crowded, mostly basally disposed, thickened and stiff, glabrous to glabrate leaves, a corymboid capitulescence (spicate in *Eurybia hemispherica* (Alexander) Nesom and *E. spinulosa* (Chapm.) Nesom, loosely paniculate in *E. chapmanii*), blue, coiling rays, and narrowly tubular disc corollas with short, erect lobes.

Jones (1980b) noted similarities between subg. *Heleastrum*, sect. *Oxytripolium*, and subg. *Virgulus* (the latter two groups of the genus *Symphyotrichum*) in achene morphology, phyllary morphology, and the production of cormoid rhizomes (particularly in *Eurybia hemispherica*), and these similarities have also been part of the basis for other comments by Jones and by Sundberg (noted below) regarding hypotheses of close relationship between subg. *Heleastrum* and sect. *Oxytripolium*. This also apparently reflected Jones' early conclusion that the base chromosome number of both groups was x=5. There also are similar tendencies in subg. *Heleastrum* and species of sect. *Oxytripolium* as well as others of subg. *Symphyotrichum* in the production of glabrous, narrowly lanceolate leaves, the upper grading into the phyllaries. Subg. *Heleastrum* was positioned as a specialized group within subg. *Virgulus* in the analysis of Jones & Young (1983), but morphological similarities between these two groups were attributed by Semple (1982) to evolutionary parallelism. Semple & Brouillet (1980a) placed subg. *Heleastrum* as an informal section within subg. *Aster* (sensu Semple & Brouillet 1980a), which also included other groups of *Symphyotrichum* (as "sect. *Dumosi*"), among others. Comments provided by Semple regarding potential close relatives of subg. *Heleastrum* are the following (1982, p. 60): "Many morphological similarities exist between the less specialized species of [subg.] *Heleastrum* and many species of sects. *Aster* and *Sericocarpus* of subgenus *Aster*" and (p. 67) *Heleastrum* is a "specialized offshoot of the typical asters with *A. paludosus* Aiton being most like species in other sections."

The similarity perceived by Jones between subg. *Virgulus* and subg. *Heleastrum* underlay her hypothesis (1985) that x=9 in the latter is derived by aneuploid loss of one chromosome from an ancestral, presumably *Virgulus*-like tetraploid based on x=5 ($2x$ = 10-1 = 9). The chromosome morphology of subg. *Heleastrum* does not support this idea, as the chromosomes are similar to those of the rest of *Eurybia* as well as subg. *Symphyotrichum* (euaster NOR type) but not to the highly specialized ones of subg. *Virgulus*.

Eurybia chapmanii is exceptional in its base chromosome number of $x=7$ (Semple 1982). Jones & Young (1983) hypothesized that this species originated as a hybrid between $x=9$ species of subg. *Heleastrum* and $x=5$ species of *Symphyotrichum* sect. *Oxytripolium*. *Eurybia chapmanii* also differs from others of subg. *Heleastrum* in its phyllaries, which are elliptic with a raised central nerve from base to tip and lack a distinctly delimited, green apical patch. It differs further in several features that are similar to those in plants of *Symphyotrichum*: relatively small heads in an open, somewhat paniculate-corymboid capitulescence and slender, terete pappus bristles without apical dilation. These features, along with its glabrous surfaces, give *E. chapmanii* the appearance of sect. *Oxytripolium*. The immediate ancestry of *E. chapmanii*, however, appears to lie with other species of subg. *Heleastrum* on the basis of their similar habit, and leaf, capitular, and achenial morphology; the chromosome number of *E. chapmanii* is interpreted here as a reduction from $x=9$, in agreement with Semple (1982). Further, *E. chapmanii* produces a compacted rhizome and persistent cluster of linear basal leaves similar to those of *E. eryngiifolia* (Torr. & Gray) Nesom and *E. spinulosa*.

Eurybia eryngiifolia and *E. spinulosa* are distinctive within subg. *Heleastrum* in their spinulose leaves, persistent basal leaves, and their phyllaries without a strongly indurate basal portion but with anastamosing longitudinal strands that produce a distinctive, green-striate appearance. The phyllaries are notably similar to those of *E. radula* (Aiton) Nesom (sect. *Radulini*). If *Heleastrum* were treated as a separate genus, there would be little to recommend against its further fragmention by the segregation of *E. spinulosa* and *E. eryngiifolia*, as well as *E. chapmanii*.

C. Subgenus *Eurybia*
Sections *Radulini*, *Calliastrum*, and *Integrifoliae*

Eurybia radula and *E. saxicastellii* (Campbell & Medley) Nesom of the eastern United States are similar to western species, particularly *E. radulina* and *E. conspicua*, in their broadly obovate leaves with toothed margins and disc corollas with a long, narrow tube abruptly ampliate into a broad limb in the distal third. In their disc corolla morphology, they are similar to species of sect. *Eurybia*. Torrey & Gray (1841) noted that *E. radula* approaches the species of sect. *Eurybia*, and the similarity of *E. radula* in phyllary morphology to *E. eryngiifolia* and *E. spinulosa* of subg. *Heleastrum* has been noted above.

Eurybia sibirica is remarkable within sect. *Radulini* in its low habit, few, loosely corymboid heads or reduction of the capitulescence to a solitary head, and herbaceous phyllaries of relatively even length, usually without a strongly developed, basally indurate portion or green apical patch. The connection of this species to others of sect. *Radulini* (particularly *E. radulina*) is seen in its

closest relatives, *E. merita* (A. Nelson) Nesom and *E. pygmaea* (Lindl.) Nesom, which also tend to be reduced in habit but which have phyllary morphology more characteristic of others in subg. *Eurybia*. As interpreted here, the loose, foliaceous phyllaries of *E. sibirica* (and sometimes *E. merita* and *E. pygmaea*) are specialized.

Three eurybian species of the eastern United States with entire leaves, a tendency to maintain the basal leaves, and narrowly tubular disc corollas are treated here as sect. *Calliastrum*. Similarities between these species and those of subg. *Heleastrum* are conspicuous. Torrey & Gray (1841) included *Aster paludosus* (sect. *Heleastrum*) as a member of their subg. *Calliastrum*. Cronquist (1980, p. 156) noted that *Eurybia compacta* "approaches *A. surculosus* Michx., on one hand, and *A. paludosus* and *A. avitus*, on the other." *Eurybia surculosa* (Michx.) Nesom is particularly similar in habit and leaf morphology to plants of sect. *Heleastrum*.

Eurybia integrifolia (Nutt.) Nesom is seemingly isolated within the genus and is treated here as a monotypic section. It is distributed in montane habitats of the northwestern United States and characterized by large, entire, persistent basal leaves, a densely long-stipitate glandular vestiture, and relatively large heads in an elongate to nearly spicate capitulescence.

Section *Herrickia*

A distinctive species from northern New Mexico and adjacent southern Colorado was originally recognized by Wooton & Standley (1913) as the monotypic genus *Herrickia* (*H. horrida* Wooton & Standl.). Blake (1937) subsequently transferred the species to *Aster*, noting that its closest relative appeared to be *Eurybia* [*Aster*] *wasatchensis* (M.E. Jones) Nesom. *Herrickia horrida* was not included in the taxonomic surveys of *Aster* by Jones (1980a) or by Semple & Brouillet (1980a), its position as a monotypic genus perhaps accepted by these botanists. It was recently included within *Aster* in a recent treatment of the New Mexico flora (Martin & Hutchins 1981) but treated as monotypic *Herrickia* in recent checklists (Kartesz & Kartesz 1980; Weber & Wittman 1992; Kartesz 1994).

Eurybia horrida (Wooton & Standley) Nesom is immediately recognized by its subshrubby habit often with numerous stems arising from near the base, its evenly arranged, epetiolate, subclasping, stiff and regularly crenate-spinulose leaves, stipitate-glandular vestiture, and loose phyllaries in 3-4 series of nearly equal length. But the corymboid capitulescence, bluish and coiling rays, narrowly tubular, reddening disc corollas with linear-lanceolate collecting appendages hairy from base to tip, narrowly cylindric, glabrous achenes, and the base chromosome number of x=9 of *E. horrida* are similar to those commonly produced by other species of *Eurybia*. Although the phyllaries are

specialized, they tend to produce a distinct, basally truncate apical patch like other species of *Eurybia*; the inner phyllaries are keeled and usually have an indurate-chartaceous base. Thick, nearly coriaceous leaves, with margins ranging from entire to distinctly spinulose-toothed, also occur in subg. *Heleastrum* and a glandular vestiture and subclasping, thick, coarsely serrate leaves are characteristic of species of sect. *Radulini*.

Eurybia wasatchensis is treated here in the same section as *E. horrida*, in agreement with the early observation by Blake of their similarity, particularly in their habit, sessile, subclasping leaves, subequal phyllaries, and tendency to produce foliaceous bracts immediately subtending the involucre. The former species differs from *E. horrida* primarily in its somewhat thinner, entire leaves and lightly strigose achenes.

Eurybia glauca (= *Aster glaucodes* S.F. Blake) of the western United States, is similar in habit to *E. horrida* and *E. wasatchensis* and produces short thick, entire, subclasping leaves with a similar gray-green color. The phyllaries of *E. glauca*, however, are strongly graduated in length and foliaceous bracts are absent. The achenes produce an unusually large number of nerves (14-18), but in other features this species seems to fit well within *Eurybia*, notwithstanding its previous association with *Eucephalus* and *Symphyotrichum turbinellum* (Lindl.) Nesom (Jones 1980a; Semple & Brouillet 1980a; Jones & Young 1983).

Eurybia pulchra, previously recognized as a variety of *Aster glaucodes*, is treated here at species rank and included within sect. *Herrickia*; it differs from *E. glauca* in its smaller leaves, apically acute phyllaries, and well-developed glandularity, which is relatively uncommon in the genus but which does occur in similar form in *E. spectabilis* and *E. horrida*. *Eurybia pulchra* has a restricted geographic range, and in the specimens I have examined, there appears to be no intermediacy between it and *E. glauca*. Cronquist (1994) placed *E. pulchra* as a synonym of *E. wasatchensis*; his comment regarding a degree of intermediacy between the latter and *E. glauca* almost certainly stems from the generally unrecognized existence of *E. pulchra*.

Section *Eurybia*

Sect. *Eurybia* comprises seven species endemic primarily to montane and temperate forest habitats in the eastern United States. These have recently been studied in detail by Lamboy and colleagues (see Literature Cited). Within *Eurybia*, the plants are characterized primarily by the following features: basal and lower cauline leaves with cordate blades on long, non-clasping petioles, disc corollas with a long, narrow tube abruptly ampliate in the distal 1/3-1/4 to a much broader limb, the lobes deeply cut and erect to slightly loose or reflexing, and the ligules white to light lavender and only weakly coiling if at all. The ovate-cordate, long-petiolate basal leaves are similar to those of

some species of *Symphyotrichum* sects. *Concinni* and *Cordifolii*, *Doellingeria*, as well as some *Solidago*, but this foliar morphology apparently has developed in parallel in each of these groups. Without basal leaves, however, plants of sect. *Eurybia* are strikingly similar in overall aspect to some of *Eurybia* sect. *Radulini*. In sect. *Eurybia*, the white, little coiling ligules and abruptly ampliate disc corollas with long lobes are similar to *Doellingeria* and genera of Solidagininae hypothesized to be primitive within the subtribe. Similar disc corollas also occur in sect. *Radulini*.

Eurybia × *herveyi* (A. Gray) Nesom is a natural, recurring, intersectional hybrid between *E. macrophylla* (L.) Cass. (sect. *Eurybia*) × *E. spectabilis* (sect. *Calliastrum*) that forms clonally persistent colonies of at least partially fertile plants. The hybrid nature of these has been confirmed by experimental crosses (Uttal 1962). The F_1's are usually more similar to the biotian parent than the other, but introgressant populations occur. Both parents are reported to have a hexaploid chromosome number, a fact almost certainly connected with the observation of a high degree of variability among the F_1 progeny of these species. According to Lamboy *et al.* (1991), the origin of *E. macrophylla* itself probably is complex; they speculated that its parentage might involve some species outside the group of its immediate relatives (sect. *Eurybia*), but no other species were included in their analyses.

VII. *Oreostemma*

Oreostemma is a sharply delimited group of three species of western North America (Cronquist 1948; Nesom 1993a). One of the species, *O. elatum* (E. Greene) E. Greene, was regarded as a synonym of *O. alpigenum* (Torr. & Gray) E. Greene in a recent summary of Californian *Aster* by Allen (1993). The plants are herbaceous, taprooted (sometimes thick-rhizomatous) perennials with monocephalous, essentially scapose stems arising from a basal rosette of linear to narrowly oblanceolate, entire, 3-nerved leaves. One remarkable individual of *O. alpigenum* var. *haydenii* (T.C. Porter) Nesom from Utah (*Recker 4255* [US]) has spinulose leaf margins. *Oreostemma peirsonii* (C.W. Sharsmith) Nesom has a glandular vestiture, otherwise the plants are eglandular; the upper stems and phyllaries commonly are finely and loosely tomentose. The phyllaries are in 3-4 series of about equal length, nearly completely foliaceous (basal margins of at least the inner are indurate in *O. elatum* and some individuals of *O. alpigenum*), sometimes with evident stomates, and often with a low but evident keel. Disc corollas are tubular with short, erect lobes and remain yellowish at maturity; the style branch appendages are extremely long, commonly reaching 2 mm. Achenes are narrowly cylindric, 4-5 mm long, with 5-10 raised nerves, glabrous or sparsely short-strigose; the pappus is mostly 1-seriate but sometimes has a few short bristles or setae in a second series.

The base chromosome number of *Oreostemma* is $x=9$. My characterization (Nesom 1993a) of its NOR chromosome morphology as the primitive type was was inferred from the placement by Semple & Brouillet (1980a) of *Oreostemma* as a subgenus separate from subg. *Aster*, the latter including all the species with the euaster type NOR morphology (except *Sericocarpus*). But apparently the only published illustration and description of the karyotype of *Oreostemma* has been by Huziwara (1958 - *O. alpigenum*), who did not observe the NOR morphology.

I hypothesized earlier that the relationships of *Oreostemma* might lie with the South American genus *Oritrophium*, but the latter is now included as a member of the subtribe Hinterhuberinae (Nesom 1994e), and *Oreostemma* is distantly related to that group.

VIII. *Ampelaster*

Ampelaster carolinianus (Walt.) Nesom, which has been recognized as the sole species of *Aster* sect. *Sagittiferi*, is endemic to the Atlantic coastal plain from Florida to North Carolina. It is treated here as a monotypic genus and is briefly characterized as follows: perennial, eglandular herbs from a woody base, vines or at least with a distinctly scandent tendency; stems densely hirsutulous or pilosulous; leaves oblanceolate to oblong-oblanceolate, 1-nerved, auriculate-clasping at the base; heads relatively large, blue-rayed, solitary or 2-8 in short-pedicellate, loose, terminal clusters; phyllaries thick, linear-oblong, subequal in length, low-keeled, with a pronounced, nearly truncate (but sometimes basally attenuate), foliaceous apical patch, usually apically reflexed; disc style branches with collecting appendages relatively short (ca. 1/3 the branch length); pappus 1-seriate, the bristles apically attenuate; achenes narrowly cylindric or slightly fusiform, 2.5-3.0 mm long, glabrous, with 9-12 whitish, slightly raised ribs, sometimes with purplish pigmentation (at maturity); and chromosome number of $n=9$.

Ampelaster carolinianus was included within *Virgulus* by Semple & Brouillet (1980a) and maintained there by Reveal & Keener (1981) as *Virgulus* sect. *Sagittiferi*. The chromosome number of this species, however, has proven to be $x=9$ (Jones 1985; S. Sundberg unpublished) rather than $x=5$ invariably characteristic of subg. *Virgulus*, and its morphological features are equivocal in suggesting a generic placement. It is similar to some species of *Symphyotrichum* sect. *Symphyotrichum* as well as to *S. novae-angliae* (L.) Nesom and others of subg. *Virgulus* in its sessile-auriculate leaves and narrow, subequal phyllaries, and 1-seriate pappus, but its chromosome number of $x=9$, eglandular vestiture, long, narrowly cylindric achenes, and the tendency for aggregation of heads suggests that it is not far removed from the primitive species of *Eurybia*. The species might be accreted to *Symphyotrichum*, especially in view

of the taxonomic conjunction maintained here between subg. *Symphyotrichum* and subg. *Virgulus*, but it appears to occupy an isolated, seemingly intermediate phyletic position between *Eurybia* and *Symphyotrichum*, and other taxa (*Psilactis*, *Canadanthus*, *Almutaster*) appear to be more closely related to *Symphyotrichum* than is *Ampelaster*. *Ampelaster* differs from all other species of Asterinae in its scandent to subscandent habit and will hardly be mistaken for any other species.

IX. *Almutaster*

The monotypic *Almutaster* (= *Aster* sect. *Pauciflori* = *Aster pauciflorus*) was recently segregated by Löve & Löve (1982). The species is distributed from south-central Canada through the western United States into south-central México. Plants of *Almutaster* are characterized as follows: rhizomatous, perennial herbs with stipitate-glandular vestiture and well-developed, linear-lanceolate, non-clasping, 3-nervate, entire, cauline leaves margined by a narrow, white, smooth rim (the few persistent basal leaves sometimes oblanceolate to oblong-spatulate); capitulescence loosely corymboid or sometimes reduced to a single head; heads small with white rays; phyllaries pauciseriate and only weakly graduated in length, without a distinctly developed apical patch and with stomates often evident on the distal portion; disc corollas remaining yellowish at maturity; narrowly subcylindric achenes 1.7-2.5(-3.5) mm long, with 8-12 nerves and 1-seriate pappus; base chromosome number, x=9.

A number of botanists have noted the morphological similarity between *Almutaster* and the species of *Psilactis*, particularly in their densely glandular indument with few or no eglandular hairs and their relatively small, fusiform achenes with numerous, pronounced ribs (*e.g.*, Shinners 1949; Sundberg 1986; Hartman 1990; Morgan & Simpson 1992; Morgan 1993). Semple *et al.* (1989) noted the similarity between *Almutaster* and *Symphyotrichum* sect. *Oxytripolium* (presumably in their hydrophilic tendency, linear-acute leaves, and small, white-rayed heads in a loose corymboid inflorescence) and suggested that *Almutaster pauciflorus* (Nutt.) Löve & Löve (with base chromosome number of x=9) may be an allopolyploid combining the x=4 genome of a *Psilactis* species and the x=5 genome of one of sect. *Oxytripolium*, apparently relinquishing an earlier hypothesis (Semple *et al.* 1983) suggesting that *A. pauciflorus* is most closely related to *Eurybia integrifolia* and *Aster modestus* Lindl. (the latter treated here as *Canadanthus*). Jones & Young (1983) suggested that *A. pauciflorus* should be interpreted as a hybrid derivative between *Machaeranthera* (probably referring to *Psilactis*) and sect. *Oxytripolium*. Sundberg (1986) considered the possibility that *A. pauciflorus* may be an alloploid derivative of a cross between a species of *Symphyotrichum* subg. *Virgulus* and *Psilactis*.

The hypothesis that *Almutaster pauciflorus* is an alloploid has arisen from morphological observations, but it has not been supported by other lines of ev-

idence. Gottlieb (1981) found that *A. pauciflorus* (as well as *Psilactis brevilingulata* Sch.-Bip. *ex* Hemsl. , also with n=9) produced about the same number of isozyme loci as three other *Psilactis* species, each with x=4, rather than the doubled number expected for a species of allopolyploid origin. Further, the karyotype of *A. pauciflorus* is markedly symmetrical (Stucky & Jackson 1975), showing no chromosomal evidence of disparate parentage. The molecular (cpDNA and nuclear rDNA) data of Morgan (1993) place the x=9 species of *Psilactis* (including *A. pauciflorus*) in a primitive or at least coordinate phyletic position relative to the species with lower numbers. *Almutaster pauciflorus* does not have an amount of nuclear DNA double that of its putatively close relatives with n=4, which might be expected if its origin had been through alloploidy (Stucky & Jackson 1975), although these data and their interpretation are problematic (see Jackson *et al.* 1993 for comments and references; also Michaelson *et al.* 1991).

There are no documented hybrids between *Almutaster pauciflorus* and species of *Psilactis*. Sundberg (1986) made unsuccessful attempts to produce these experimentally. In his study, all attempts to produce hybrids among x=4 species of *Psilactis*, x=9 *A. pauciflorus*, x=5 species of sect. *Oxytripolium*, and x=9 *Aster tripolium* were completely unsuccessful. In contrast, Stucky (1978) reported that he produced artificial hybrids between *Psilactis tenuis* S. Wats. and *P. asteroides* A. Gray (both x=4) as well as intergeneric hybrids between *A. pauciflorus* and each of two x=5 species of *Machaeranthera* (*M. arida* [Kunth] A.G. Jones and *M. parviflora* A. Gray). In summary, evidence from DNA studies suggests that *Psilactis* is close to *Symphyotrichum* although genomic similarities suggest that the phyletic distance between *Psilactis*, *Almutaster*, and even *Machaeranthera* also may be relatively small (see Nesom 1994f for comments on hybridization).

X. *Psilactis*

Psilactis includes six species (*sensu* Morgan 1993) distributed from the southwestern United States into south-central México, with one species essentially continuing into northwest South America. They are similar among themselves in their tendency to inhabit moist or wet habitats, stipitate-glandular vestiture, clasping to subclasping leaves, small heads with white to bluish rays and other details of floral and fruit morphology, particularly their epappose ray achenes. *Psilactis odysseus* (Nesom) Morgan is rhizomatous and perennial, with monocephalous stems; the others are taprooted and annual or short-lived perennial in duration, with a loosely paniculate capitulescence. The phyllaries are only weakly graduated in length and tend to be mostly herbaceous although they may be indurated along the basal margins. Achenes are short-elliptic to broadly obovate, 1-3(-4) mm long, somewhat compressed, 5-14(-18)

nerved and produce a 1-seriate pappus of apically attenuate bristles. The two most divergent and apparently most specialized species (*P. odysseus* and *P. brevilingulata*) have a base chromosome number of x=9, while the other four have x=4 or x=3. The group has received detailed study (Turner & Horne 1964; Stucky 1974; Nesom 1978; Arnold & Jackson 1979; Hartman & Lane 1987; Morgan 1993).

Psilactis has been regarded as a subgroup within the genus *Machaeranthera* in recent treatments (Turner & Horne 1964; Stucky 1974; Hartman 1990). Cuatrecasas (1969) treated it separately, however, and Morgan (1993) returned the whole group to generic rank with a revisionary study and several new combinations. Until relatively recently, all of *Machaeranthera* commonly was submerged within *Aster* (Cronquist & Keck 1957), but the particular basis for the association of *Psilactis* with *Machaeranthera* (as part of sect. *Arida* R.L. Hartman) has proven to be a convergent similarity both in vegetative and achenial features. *Psilactis* was not included in the analysis by Jones & Young (1983), but two species of the group were included within *Aster* by McVaugh (1984). Shinners (1949, p. 54) noted in his description of a new species of *Psilactis* (as a genus) that "It has remarkable superficial resemblance to *Aster pauciflorus* Nutt. and its Mexican allies" (the latter evidently referring to taxa of sect. *Oxytripolium*). Turner & Horne (1964) referred to *Psilactis* s. str. as "*Aster*-like" in habit; they commented on the vegetative similarity between sect. *Oxytripolium* and *Psilactis*, although they regarded it as superficial because of other similarities between *Psilactis* and *Machaeranthera* that were more significant, in their view. Based on chloroplast DNA restriction site variation (Morgan 1993), species of *Psilactis* are cladistically intermixed with species of *Oxytripolium*, and *Psilactis* is paraphyletic without sect. *Oxytripolium*. Morgan's data from nuclear ribosomal DNA, however, support the treatment of *Psilactis* as a separate group and place sect. *Oxytripolium* closer to subg. *Symphyotrichum* and subg. *Virgulus*.

Despite the often invoked association between *Psilactis* and *Almutaster pauciflorus*, the two are different in significant features: in *A. pauciflorus* the leaves are stiffly linear and slightly sheathing at base (vs. looser in texture, broader, and distinctly subclasping, sometimes auriculate), the capitulescence tends to be corymboid (vs. loosely paniculate), the phyllaries usually not differentiated into an indurate base and green apical region (vs. indurate basal region sometimes evident), and the ray achenes are pappose (vs. epappose).

Morgan's reinstatement of *Psilactis* as a genus was based on the following reasoning. Based on DNA data, it is clearly separate from *Machaeranthera* and close to North American species generally treated within *Aster*, although his molecular data were not conclusive regarding the nature of their interrelationship. Morgan declined to combine *Psilactis* with *Aster*, because (p. 296) "the result would only increase the morphological and cytological diversity in a genus that is already diverse and poorly understood." Further, he ob-

served a suggestion of genetic influence from *Machaeranthera*, as seen in the apparently "*Machaeranthera*-like" morphological features of *Psilactis* (*i.e.*, low chromosome number, tap-rooted habit, leaves with spinulose lobes, lack of ray pappus).

Psilactis stands as a relatively isolated group, but similar *Machaeranthera*-like features (except epappose achenes) also occur in various other species and groups within New World asters, and *Psilactis* has particularly notable similarities with other taxa placed here in *Almutaster* and subg. *Virgulus*.

XI. *Canadanthus*

The species identified as *Aster modestus* Lindl. is here segregated as a monotypic genus, *Canadanthus*, and characterized as follows: perennial, thin-rhizomatous herbs, the stems simple and arising singly from the base, 3-8 dm tall; vestiture of long-stipitate glands (stems and phyllaries), without other hairs; leaves all cauline, eglandular, glabrate to thinly short-strigose above, loosely and thinly pilosulous beneath, epetiolate, subclasping, lanceolate to elliptic-lanceolate with an acuminate apex, entire to serrate, 5-12 cm long, 15-25(-40) mm wide, the lowermost strongly reduced in size; capitulescence loosely corymboid, mostly 3-20 flowered, less commonly 1, sometimes many more, and the capitulescence thyrsoid, heads on leafy peduncles, mostly 2-4(-6) cm long, usually with 1-3 reduced leaves or bracts; phyllaries linear-lanceolate, flat, in 2-3 series of nearly equal length, thin-foliaceous, without a green apical patch or indurated basal region, the inner often with a slightly raised keel and usually strongly purplish; disc corollas narrowly tubular, 5-7 mm long, with short, erect lobes; disc style branches 1.0-1.4 mm long, the collecting appendages triangular, hairy, more than half the length of the branches; ray corollas 25-40 with purple, coiling ligules; achenes oblanceolate with a narrowly acute, stipitate base, 2.5-4.0 mm long, strongly flattened, 4-8 nerved, and eglandular; pappus 1(-2)-seriate; and chromosome number of n=9. It occurs from Alaska southward to Washington and Oregon, and eastward through Alberta to eastern Ontario and Minnesota.

The singly produced, unbranched stems of plants of *Canadanthus modestus* produce a habit similar to those of some species of *Eurybia* (particularly sect. *Eurybia*) and *Oclemena*. In his description of *Aster sayianus* Nutt. (a synonym of *A. modestus*), Nuttall (1841, p. 294) noted that "This species has much the habit of a *Galatella*," probably referring to *Oclemena* (*Aster*) *nemoralis*, for which he accepted Nees's early referral to *Galatella* (see Appendix II). Jones (1980a) and Jones & Young (1983) placed *Aster modestus* with *Eurybia radulina*. Semple & Brouillet (1980a) informally separated *Aster modestus* and *Eurybia sibirica* and set them together distantly apart from most other x=9 and x=8 taxa as *Aster* "subg. *Modesti*;" Semple *et al.* (1983) viewed

Almutaster (*Aster*) *pauciflorus* as closely related to *Canadanthus*, citing similarities in habit, phyllaries, and achenes, but they did not reevaluate their earlier positioning of *A. modestus*.

Nuttall also noted that his *Aster sayianus* is "Nearly allied to *A. modestus*, and proximately to *A. novae-angliae*." The similarity of these latter two species is immediately evident and often has been referred to directly, as in Nuttall's observation, or indirectly, particularly as the two species tend to fall out together in identification keys. They are similar in their stipitate-glandularity, clasping cauline leaves, heads on leafy peduncles, purple rays, linear, purple phyllaries of nearly even length, and oblanceolate achenes with a tendency for reduced pappus. The capitulescence of *A. modestus* tends to be corymbiform and the heads are borne on leafy peduncles and are loosely associated, more like capitulescences found in *Symphyotrichum* (particularly *S. novae-angliae*) than in *Eurybia*, *Oclemena*, or other putatively primitive genera with a corymboid arrangement of heads, usually on peduncles with few or no bracts.

A combination of morphological and chromosomal features, however, suggests that *Canadanthus* is phyletically separated from *Symphyotrichum* subg. *Virgulus*: leaves are relatively broad, thin, and with toothed margins (vs. narrow, thick, and entire); phyllaries are completely without an apical patch; stems arise singly from the base; achenes are strongly flattened; and the pappus sometimes is formed of two distinct series of equal-length bristles. Similar comparisons were made by Jones (1980b). The habit, vestiture, phyllaries, achenes, and pappus of *Canadanthus* remove it from subg. *Symphyotrichum*. Its chromosome number of $n=9$ (with "primitive" NOR morphology, *fide* Semple *et al.* 1983) also places *Canadanthus* in a more basal position than any species of *Symphyotrichum*. In summary, *C. modestus* is here considered to be closely related to *Symphyotrichum*, but it appears to occupy an isolated position at least as distinct from the latter as *Almutaster*, *Psilactis*, and *Ampelaster*. Although some practical problems in identification may be associated with the recognition of this monotypic genus, its amalgamation with *Symphyotrichum* would require for consistency that these other distinct and isolated taxonomic elements also be added.

XII. *Symphyotrichum*

The greatest number of species identified here as *Symphyotrichum* have recently been classified as *Aster* subg. *Symphyotrichum* (Jones 1980a). These are the species with base chromosome numbers of $x=8$ and $x=7$. To these is added a closely similar group of species previously recognized as sect. *Oxytripolium*, which have base chromosome numbers of $x=6$ and $x=5$; the accepted number of species in this section is considerably enlarged (past that of Sundberg

1986) in the present discussion. *Symphyotrichum* is further broadened by the incorporation of the $x=5$ species previously segregated as the genus *Virgulus*. *Symphyotrichum* is divided into two subgenera, subg. *Symphyotrichum* (8 sections, 76 species) and subg. *Virgulus* (4 sections, 21 species).

Naturally formed, relatively fertile hybrids occur between species of *Symphyotrichum* of disparate morphology, of different chromosome numbers, and of different sections and subgenera (Figure 2). Such wide crosses are known to occur between (2) various combinations of species in different sections of subg. *Symphyotrichum*, including sect. *Dumosi* and sect. *Oxytripolium*, and (2) sect. *Occidentales* (subg. *Symphyotrichum*) and sect. *Oblongifolii* (subg. *Virgulus*).

Symphyotrichum subg. *Symphyotrichum* appears to be monophyletic, based on a remarkable consistency in the achene morphology, lack of glands, production of stem hairs in lines, and in phyllary morphology. The group is more specialized in these respects than is *Virgulus*, which retains a number of relatively unspecialized features and which could not have been derived from subg. *Symphyotrichum*. Correspondingly, reduction of the base chromosome number from $x=9$ to $x=8$ and $x=5$ in these two groups appears to have occurred independently. Despite strong evidence for the discrete nature of these two groups, hybrid species and introgressants produced across different levels of ploidy (see discussion below) indicate that the genetic divergence between *Virgulus* and species of subg. *Symphyotrichum* is relatively slight (see Nesom 1994f), in spite of differences in morphology, chromosome number, and karyotype. These two groups are treated here as congeneric to avoid intractable problems in practical taxonomy (*i.e.*, how to deal with the intersubgeneric hybrids and backcrosses). As noted by Allen (1985, p. 276), the apparent close homology between these $x=5$ and $x=8$ genomes offers "a counter to recent suggestions for removing the $x=5$ elements of *Aster* into a separate genus."

The other generic level groups that are most closely related to *Virgulus* and *Symphyotrichum* (i.e., *Psilactis*, *Almutaster*, *Canadanthus*) might also be included as subgenera within *Symphyotrichum*, especially in view of their base chromosome number of $x=9$ and the evident paraphyly of *Symphyotrichum* and *Virgulus* without the inclusion of $x=9$ species, from which the $x=8$'s and $x=5$'s clearly have been derived. Each of the apparently basal groups, however, is morphologically and genetically discrete, and the nature of their relationship to *Symphyotrichum* s. lat. is not clearly evident.

Typification of *Symphyotrichum*

The genus *Symphyotrichum* was established by Nees, the single species, *S. unctuosum* Nees, based on a horticultural specimen transmitted to Germany from Glasgow. Nees described the pappus of this plant as coherent in a basal ring (whence the generic name), but this tendency must be rare since it is not

characteristic of any species of *Symphyotrichum*; thus, while the application of Nees's name to this large group of species is legally required, it is peculiar. De Candolle (1836, or "Lindley *ex* de Candolle") and Torrey & Gray (1841) early recognized and reported the identity of *S. unctuosum* with *Aster tardiflorus* L. Gray (1884) later placed *S. unctuosum* as a synonym of *Aster novi-belgii* var. *litoreus* A. Gray, and Jones (1980a) noted simply that *S. unctuosum* was synonymous with *A. novi-belgii*. As observed by Jones & Hiepko (1981), *A. novi-belgii* and *A. tardiflorus* are very similar and often intergrade, and they are considered to be conspecific in the present treatment (as *Symphyotrichum novi-belgii*). The larger species group of which *S. novi-belgii* is a member has recently been identified as *Aster* subg. *Symphyotrichum* (Jones 1980a).

A. Subgenus *Symphyotrichum*

Eight sections within subg. *Symphyotrichum* are recognized here, these corresponding to previously recognized and closely associated species groups, except for the addition of sect. *Oxytripolium*. The species of the subgenus are characterized by their reduced vestiture except for the tendency to produce hairs in lines on the stems, lack of glands, unkeeled (or only slightly keeled) phyllaries usually with a sharply defined, basally attenuate apical patch (often with stomates visible), achenes somewhat foreshortened to a narrowly obovate shape, (1.0-)1.5-3.5(-4.0) mm long, distinctly flattened to varying degrees, and with (2-)3-5(-6) nerves, and base chromosome number of $x=8$, independently reduced to $x=7$ and to $x=6$ or $x=5$ in specialized sections. The capitulescence is generally paniculate, with the heads scattered in a relatively loose organization. It may sometimes appear broadly pyramidal or columnar, or the peduncles may be very short and arrangement of heads racemoid or nearly spicate. If the capitulescence appears corymboid, the peduncles usually bear a number of reduced leaves or bracts, unlike the mostly naked peduncles in the corymboid cymes of *Eurybia*. The species vary in habit, duration, leaf morphology (shape, insertion, and distribution), head size, phyllary morphology, and ray color.

Through reinterpretations of previous chromosome counts and the addition of many new ones for species of subg. *Symphyotrichum*, Jones (1977) established that the base number for the group is $x=8$. Remaining meiotic counts of $n=9$ pairs within the group have further been suggested to be based on supernumerary chromosomes (Semple *et al.* 1983). Further, it is clear that some aneuploidal instability in chromosome number may exist among these species, particularly in polyploids (*e.g.*, Allen 1985; Legault & Brouillet 1989).

There are many hybrids and intergrading forms among the species of subg. *Symphyotrichum*, mostly between those within a section, but the relatively common occurrence of intersectional hybrids emphasizes the coherence of this

large group. Polyploidy is common and presumably contributes to the ease with which fertile hybrids are formed. Jones (1980b, p. 241) has observed that many of these species "have extensive geographic ranges and are extremely heteromorphic" and might be viewed as "ecological species" (*sensu* Van Valen 1976). They may be "influenced more by populations of other species with which they are sympatric than by geographically distant populations of the same species." Semple & Brammall (1982), in contrast, noted that much of the taxonomically confusing variation among these species may be more attributable to phenotypic plasticity than to hybridization. Judging, however, from the formal taxonomic complexity admitted for some of the species complexes (*e.g.*, Semple & Chmielewski 1987), more than phenotypic plasticity must be held responsible for the general form of some of the variation patterns.

Features of foliar morphology in some species of subg. *Symphyotrichum* are shared with those of subg. *Virgulus* and *Psilactis*, as well as some species of *Eurybia*, especially the epetiolate, more or less oblong, clasping to subclasping cauline leaves. This set of features is interpreted as the unspecialized condition. In sect. *Symphyotrichum* and sect. *Occidentales*, where this morphology is pronounced, there also is a distinct tendency for corymboid or subcorymboid capitulescence, also an unspecialized condition in the Eurybian lineage. The sessile, non-clasping cauline leaves and the diffuse capitulescence characteristic of most species of sect. *Dumosi* and sect. *Oxytripolium* is specialized.

Sects. *Oxytripolium* and *Conyzopsis* are particularly distinct groups, each with a derived chromosome number and specialized morphology, both regarded as separate subgenera in earlier treatments (*e.g.*, Jones 1980a) or even as separate genera (see below). Sect. *Conyzopsis* (x=7) is similar in significant respects to sect. *Occidentales* (see below); the distribution of these two groups is primarily in the western United States, in contrast to many other *Eurybia*, and they appear to be genetically isolated as well, judging from the lack of natural hybrids with the rest of the genus (Figure 2). There are many similarities between sect. *Oxytripolium* (x=6,5) and sect. *Dumosi* (x=8) and natural interploidal hybrids apparently are formed between the two sections (see below).

The position of *Aster carnerosanus*

Symphyotrichum (*Aster*) *carnerosanum* (S. Wats.) Nesom was placed (with a question) by Jones (1980a) among the species of her subsect. *Spectabiles*, which have a base chromosome number of x=9. She later acknowledged its morphological alliance with subg. *Symphyotrichum* (Jones 1984), and it is similarly placed in the present treatment as a member of sect. *Dumosi* (subsect. *Divergentes*). Morgan (1993) assigned a chromosome number of n=9 to this

species, but a documented chromosome count for *S. carnerosanum* apparently has not yet been published. Based on the present classification, the species is predicted to have a number of x=8.

The position of *Aster turbinellus*

The taxonomic position of *Symphyotrichum* [*Aster*] *turbinellum* has been the subject of considerably different interpretation. Semple & Brouillet (1980a) regarded it as belonging among the species of *Eucephalus*. Jones (1980a) treated *S. turbinellum* within *Aster* sect. *Eucephalus* subsect. *Turbinelli*, which included only one other species, *Aster glaucodes* (placed here within subg. *Eurybia* sect. *Calliastrum*), hypothesizing shortly thereafter (Jones & Young 1983) that it might be of hybrid origin. Still later (1989), she has treated it as a monotypic section of subg. *Symphyotrichum*. Although *S. turbinellum* is an unusual species, a combination of features suggests that it belongs with subg. *Symphyotrichum*: stem hairs in lines, an open-paniculate capitulescence, phyllaries with a sharply delimited, basally attenuate apical patch, slender pappus bristles of even length and with acute apices, and a base chromosome number (apparently) of x=8. The chromosome number of *S. turbinellum* was first reported as n=50 (Avers 1957; Jones 1980b), but recent reinterpretations and recounts (Semple & Brouillet 1980a; Semple *et al.* 1983) show the number is apparently n=48 (or 2n=96), here interpreted as dodecaploid based on x=8. Other features suggest that within *Symphyotrichum* it is closest to the species of sect. *Concinni* (this proximity much earlier observed by Asa Gray 1884): petiolate, often truncate or subcordate basal leaves, thick, stiff cauline leaves, slightly keeled phyllaries, and turbinate heads in a very open panicle, borne on long, bracteate peduncles, with the uppermost peduncular bracts grading into involucral bracts. The achenes of *S. turbinellum* are typical of those within subg. *Symphyotrichum*; they are 4-5 nerved, obovate-oblong, and slightly compressed; the pappus is 1-seriate.

The position of *Aster retroflexus*

Symphyotrichum retroflexum (DC.) Nesom (*Aster retroflexus* Lindl. *ex* DC. = *A. curtisii* Torr. & Gray) was placed in sect. *Calliastrum* by Torrey & Gray (1841), although they noted that it might belong instead with sect. *Grandiflori* (subg. *Virgulus*); the species was maintained within the *Calliastrum* group by Gray (1884). Jones (1980a) viewed it essentially as did Gray, placing it in sect. *Spectabiles*. With a chromosome number of x=8 recently confirmed for the species (Jones 1983b), however, she transferred it to a position among other x=8 taxa in subg. *Symphyotrichum*, noting morphological similarities to *S. laeve* (L.) Löve & Löve and *S. oolentangiense* (Riddell) Nesom (sect. *Concinni*

in the present treatment). Semple *et al.* (1983) suggested that it belongs with *S. novi-belgii* and *S. puniceum* (L.) Löve & Löve of subg. *Symphyotrichum* (sect. *Symphyotrichum*).

Symphyotrichum retroflexum is characterized by nearly glabrous stems, leaves, and phyllaries (or stem hairs barely evident and in lines), petiolate, basal leaves with truncate or subcordate blades, sessile and non-clasping cauline leaves, few and relatively large heads usually racemoid to nearly spicate but sometimes more loosely arranged, with keeled, squarrose phyllaries with a sharply demarcated, basally truncate apical patch and convex, white-indurated base, and glabrous, slightly flattened, oblong-oblanceolate, 4-5 nerved achenes with a 1-seriate pappus of apically attenuate bristles. The disc corollas are abruptly ampliate into the throat with deeply cut lobes; this primitive morphology occurs in some species of *Eurybia* as well as *Symphyotrichum* sect. *Cordifolii*. Particularly in its large heads and their arrangement, phyllary morphology, and corolla morphology, the species does have a remarkable resemblance to some in *Eurybia* sect. *Calliastrum*, but its combination of cauline vestiture, leaf shape, achene and pappus morphology, and chromosome number provide evidence for placing it in subg. *Symphyotrichum*.

The status of *Brachyactis* s. str.

There are three species of *Brachyactis* s. str. (= *Symphyotrichum* sect. *Conyzopsis*, as treated here): two are endemic to North America and the third (*S. ciliatum*, the generitype, = *Aster brachyactis* S.F. Blake) is widespread in North America and across the North Pacific to northcentral and northeastern Asia (the type collected in Siberia). The latter species is unusual among species of *Aster* s. lat. in its bicontinental, nearly circumpolar, distribution. A nomenclatural summary for the group is available (Jones 1984), amended by the observation that *Symphyotrichum laurentianum* (Fernald) Nesom is a distinctive species rather than a part of *S. ciliatum* (Gleason & Cronquist 1963, 1991; Houle & Brouillet 1985; Houle & Haber 1990).

The species of sect. *Conyzopsis* were treated as *Aster* subg. *Conyzopsis* by Jones (1980), informally as "sect. *Brachyactis*" of subg. *Aster* by Semple & Brouillet (1980a), as *Aster* sect. *Conyzopsis* by Houle & Brouillet (1985), and as *Aster* "subg. *Brachyactis*" by Nesom (1994e). They were first incorporated into *Aster* by Torrey & Gray (1841), as a subgroup of subg. *Oxytripolium*. Bentham & Hooker (1873) maintained them as the genus *Brachyactis*, positioning it next to *Erigeron*, acknowledging the similarity in floral morphology of these species to *Erigeron* subg. *Trimorpha*. Explicitly influenced by Bentham's view, Gray (1873) extracted the species from *Aster*, though with a caveat regarding the composition of the group (see below). A few years later, however, Gray (1880, 1884) returned them to *Aster* as subg. *Conyzopsis*, noting

that the reduced ligules, few disc flowers, and accrescent pappus of *Symphyotrichum* (*Aster*) *subulatum* (Michx). Nesom "must be held to invalidate the genus *Brachyactis*," and aptly observing (see comments below) that within *Aster* it is "the analogue of the section *Trimorphaea* in *Erigeron*" (1880, p. 99). Prior to 1980, other North American botanists who have dealt with the nomenclature or taxonomy of sect. *Conyzopsis* (e.g., Blake, Wooton & Standley, Ferris, Cronquist) have not provided any comment that would serve as a rationale for treating the group at one rank or another or for placing it in any phylogenetic position.

The analysis of Jones & Young (1983) placed sect. *Conyzopsis* as the sister taxon of subg. *Symphyotrichum* (see below). But in spite of Jones's explicitly inclusive view of the composition of *Aster*, she changed her mind about the rank of sect. *Conyzopsis* (1984, 1985) and has treated it since then as the distinct genus *Brachyactis* (e.g., 1992). In justification of this, she provided only the suggestion that these species may have a strong Old World connection.

Sect. *Conyzopsis* (= *Brachyactis* s. str.) is briefly characterized as follows: (1) annuals usually from a taproot; (2) leaves non-clasping; (3) capitulescence narrowly paniculate, sometimes nearly columnar; (4) phyllaries evenly foliaceous and of subequal length; (5) disc corollas narrowly tubular and short-lobed; (6) pistillate flowers in ca. 2-4 series in a broad outer zone, more numerous than the disc flowers; (7) ligules absent or rudimentary to filiform and short; (8) achenes eglandular, narrowly oblong, flattened, and 2(-4)-nerved; and (9) pappus bristles in 2 series of equal length, conspicuously lengthening (accrescent) with achene maturation. All chromosome numbers reported for these three species have been x=7 (Houle & Brouillet 1985).

Semple & Brouillet made two observations regarding their positioning of "sect. *Brachyactis*" (1980b, p. 1037): "Karyotypically it could easily be derived from some member of sect. *Dumosi*" (= subg. *Symphyotrichum* in the present account, all x=8); and (1980a, p. 1019) "The phyllaries of *Aster brachyactis* are like those of sect. *Dumosi*, subsect. *Foliacei*" (= sect. *Occidentales* in the present account). Dr. Brouillet has pointed out (pers. comm.) that he regards similarities in habitat, leaf morphology, and involucral morphology between sect. *Conyzopsis* and *Symphyotrichum spathulatum* (Lindl.) Nesom (= *A. occidentalis* [Nutt.)] Torr. & Gray) (and other x=8 species closely related to the latter) to be indicative of their immediate common ancestry, especially in view of the similar NOR chromosome morphology (euaster type). My observations are in agreement. Additionally, *S. spathulatum* most commonly produces a short, fibrous-rooted rhizome, but there is a distinct tendency in this species for condensation of the rhizome and the corresponding production of a taproot, bringing this aspect of its habit very close to that of sect. *Conyzopsis*. In this interpretation of relationship, which is accepted here, the distinctive morphology of sect. *Conyzopsis* reflects a suite of specialized features (the highly reduced floral morphology probably connected with autogamy) derived from

ancestral states in x=8 ancestors similar to species of sect. *Occidentales*. The distinction of sect. *Conyzopsis* as a highly autapomorphic and strongly genetically isolated group within subg. *Symphyotrichum* is unique, and on a phenetic basis the group might justifiably be treated as a separate genus, but not for the reason that Jones (1984, 1985) has recently suggested.

In the analysis by Jones & Young (1983), the phyletic connection between sect. *Conyzopsis* and subg. *Symphyotrichum* is provided by four characters: stem pubescence in lines; capitulescence typically ample, much-branched, and more or less diffuse; phyllary apex with a scarious rim; and base chromosome number x=8 or x=7. The assumption that the two chromosome numbers are homologous is supported by the observation that both have NOR chromosomes of the same morphology. Despite their assertion (p. 82) that subg. *Symphyotrichum* and sect. *Conyzopsis* are "separated on the cladogram by only one homoplasious synapomorphy" (leaf nervation, character 8), the latter is the only taxon in their analysis besides *Erigeron* (the outgroup) scored as having ray flowers in several series (character 25). Further, sect. *Conyzopsis* (and not subg. *Symphyotrichum*) is one of the few taxa in their analysis (as scored by them) to share with the outgroup "phyllaries with a chlorophyllous areole forming a band of more or less uniform width that extends from base to apex" (character 14).

In my observations, the 2-seriate pappus of sect. *Conyzopsis* appears to be distinct within *Symphyotrichum* – the pappus of all other species of the genus, as well as its closest generic relatives (*Psilactis*, *Almutaster*, *Canadanthus*), is 1-seriate or nearly so. A multiseriate pappus is primitive within the Asterinae, but in the phyletic interpretation here, the 2-seriate pappus of sect. *Conyzopsis* apparently has been re-elaborated from the 1-seriate condition of its closest relatives.

The suite of floral features that makes sect. *Conyzopsis* immediately distinctive is shared with other Asterean genera only distantly related to *Symphyotrichum* or the Asterinae. Trimorphic flowers have been developed in Asian genus *Nannoglottis*, which has been positioned in the Solidagininae (Nesom 1994e; Ling & Chen 1965). Annual duration, numerous pistillate flowers in a broad outer zone of ca. 2-4 series, ligules reduced or absent, an accrescent pappus, and flattened, 2-nerved achenes are found in *Psychrogeton* - Asterinae (Grierson 1967, 1982), *Laennecia* - Podocominae (Nesom 1990a), some species of *Conyza* (Nesom 1990b) and *Erigeron* subg. *Trimorpha* - Conyzinae (Nesom 1989c, 1994e). All of these have been treated in the past as close associates, relatives, or subgroups of *Erigeron*, but the similarities in floral and capitular morphology among these genera, as they are placed in different subtribes, are evolutionarily convergent.

The species of the Himalayas and central Asia that have been identified as *Brachyactis* remain taxonomically problematic. Asa Gray (1873) noted that *Brachyactis* as a genus (*sensu* Bentham 1873) probably is biphyletic. The

Asian plants produce "broader and flat achenia with prominent marginal ribs, and a pappus of two distinct sorts of bristles, those of the outer set not longer than the width of the achenium" (Gray 1873, p. 648). Further, achenes of the Asian species commonly are glandular on the faces near the apex, their herbage is sessile-glandular, and their base chromosome number is x=9 (Podlech & Dieterle 1969; Mehra & Remanandan 1969, 1974). In this set of features, as well as their geographical distribution, they fit comfortably among the Old World genera of subtribe Asterinae, and it is clear that they are phyletically distant from *Symphyotrichum* sect. *Conyzopsis* (see preceding comments on Asian "*Brachyactis*" in the present treatment).

Section *Oxytripolium*

Sect. *Oxytripolium* has been known as *Aster* subg. *Oxytripolium* (DC.) Torr. & Gray, but Nuttall's name at the subgeneric rank (subg. *Astropolium*) preceded that of Torrey & Gray (see Appendix II). Sect. *Oxytripolium* has been recently reviewed by Sundberg (1986), who restricted it to three American species: *Aster subulatus* Michx. (with five varieties, each of these treated here at species rank), *A. potosinus* A. Gray, and *A. tenuifolius* L. (with two varieties). These have a base chromosome number of x=5 and commonly grow in damp or marshy habitats. Reports of a chromosome number of n=9 for *A. subulatus* from eastern Asia (Lee 1970; Huziwara 1958; Peng & Hsu 1977, 1978) need to be reviewed.

The *Oxytripolium* species were taxonomically formalized as a group first by de Candolle (1836), who divided the genus *Tripolium* into two groups, a monotypic sect. *Tripolium* (*T. pannonicum* = *Aster tripolium*, see comments above) and sect. *Oxytripolium* (*T. subulatum* (L.) Nees, the type). In the cladistic analysis of *Aster* by Jones & Young (1983), *Aster tripolium* (x=9) and sect. *Oxytripolium* were placed within a monophyletic group that also included the distantly related *Aster spinosus* (= *Chloracantha spinosa* (Benth.) Nesom, x=9). As discussed above, however, the monotypic, Old World genus *Tripolium* is more closely related to typical *Aster* and some of its Old World relatives and is without an intimate relationship to any North American species. *Almutaster* (*Aster*) *pauciflorus* was treated by Jones (1980a) within subg. *Oxytripolium*, but it was excluded from the subsequent phyletic analysis by Jones & Young because they hypothesized it to be an allopolyploid.

Sundberg (1986) excluded South American species from his concept of *Aster* subg. *Oxytripolium*, but Jones & Lowry (1986) examined the type of *Aster regnellii* Baker *in* Mart. and noted that it is related to *A. subulatus*. I agree that *A. regnellii* belongs with sect. *Oxytripolium* and further note that this group comprises at least eleven species, most of these endemic to eastern and southeastern South America in habitats of relatively low to moderate

elevations. In fact, many of the autochthonous South American species that have persisted within the genus *Aster* in recent taxonomic treatments belong to sect. *Oxytripolium*; the nomenclature remains unsettled and a few species of this group perhaps are yet undescribed. Some of the better known indigenous species of South American sect. *Oxytripolium* (treated here within *Symphyotrichum*) are *S. patagonicum* (Cabrera) Nesom, *S. peteroanum* (Phil.) Nesom, and *S. vahlii* (Gaud.) Nesom. The species of sect. *Oxytripolium* from Central America and southern North America represent the northernmost elements of this group. *Symphyotrichum subulatum* (or segregates) and *S. squamatum* (Spreng.) Nesom are cosmopolitan weeds.

As in the North American species of sect. *Oxytripolium*, the South American ones include taprooted annuals as well as rhizomatous perennials; all are glabrous or with greatly reduced vestiture, the leaves are more or less thickened, linear to oblanceolate, parallel-veined, and commonly with scabrous margins, the phyllaries usually with a distinctly delimited, basally attenuate apical patch, the disc corollas are narrowly tubular with deltate, erect lobes, and the ligules are sometimes reduced in length but usually strongly coiling. The achenes are 3-5(-6)-nerved and commonly are flattened; the pappus is 1-seriate and in some species (*Symphyotrichum vahlii*, *S. regnellii* (Baker) Nesom, *S. squamatum*) tends to be noticeably accrescent. Similar features also occur in *Symphyotrichum* sect. *Dumosi*, where there is a strong tendency for glabrous leaves and stems, non-clasping, narrowly lanceolate leaves, the upper cauline becoming merely bracteate and grading into phyllaries, a loosely paniculate capitulescence, phyllaries with a basally attenuate apical patch, and achenes of similarly reduced size and nervation. In the view here, sect. *Oxytripolium* is included with *Symphyotrichum* as a specialized member, perhaps derived from ancestors that would be placed in sect. *Dumosi*. Morphological similarities that have been observed between sect. *Oxytripolium* and *Eurybia* sect. *Heleastrum* are considered to be evolutionarily parallel.

Cuatrecasas (1969) transferred the South American *Aster vahlii* (Gaud.) Hook. & Arn. to the genus *Oritrophium*, although he acknowledged that the record of this species in Colombia was based on scanty material needing further investigation. This species figured in the delimitation of the geographic range of *Oritrophium* (Nesom 1992a), but in my recent examination of *A. vahlii* from over its range, it is clear that it belongs within *Symphyotrichum* sect. *Oxytripolium* rather than *Oritrophium*. Most conspicuously, the plants are essentially glabrous and the disc flowers produce fertile ovaries, both features anomalous in *Oritrophium*. Further, the only report of a chromosome number for any of the indigenous South American *Symphyotrichum* species other than *S. squamatum* has been for *S. vahlii* as n=12 (Moore 1981). This number almost certainly is based on x=6 and is more likely to be homologous with the x=5 previously reported for sect. *Oxytripolium* than the x=9 known for *Oritrophium* (Nesom 1992a). With the exclusion of *S. vahlii*, *Oritrophium*

becomes better defined in geographic range and ecology as essentially a northern Andean phylad of high-elevation habitats. Cuatrecasas (pers. comm. 1993) has acknowledged that what he identified as *S. vahlii* in Colombia is instead a long-stemmed form of *O. limnophilum* (Sch.-Bip.) Cuatr.

a. Relationships of sect. *Oxytripolium*

Sundberg (1986) noted that South American plants identified as *Aster regnellii* and *A. squamatus* (Spreng.) Hieron. *in* Sod. var. *graminifolius* (Spreng.) Hieron. *in* Sod. appear to be intermediate between [*Symphyotrichum*] sect. *Oxytripolium* and [*Eurybia*] sect. *Heleastrum*. Jones (1982) and Jones & Young (1983a) suggested that *Eurybia chapmanii* (x=7, subg. *Heleastrum*) may have originated in a cross involving an x=9 plant of subg. *Heleastrum* and an x=5 one of sect. *Oxytripolium*. An hypothesis of immediate common ancestry for subg. *Heleastrum* and [*Symphyotrichum*] subg. *Virgulus* was based on observations of apparently specialized similarities between these two taxa (Jones & Young 1983) and Jones's early conclusion that the base chromosome number of both groups was x=5.

Another indication of the evolutionary affinities of sect. *Oxytripolium* was discovered by Sundberg (1986) in a population of asters from northern Oaxaca, México. These plants are closest in morphology to *Symphyotrichum potosinum* (A. Gray) Nesom (x=5, sect. *Oxytripolium*), but they have a chromosome number of n=13 and morphological features that suggest they originated in a hybrid cross between *S. potosinum* and *S. bullatum* (Klatt) Nesom (x=8, subg. *Symphyotrichum* sect. *Dumosi*), which occurs in the same region, although the two putative parental taxa are now completely allopatric. In an experimental cross between these n=13 plants and *S. potosinum* from Arizona, Sundberg produced fertile progeny nearly identical to the n=13 plants but with a chromosome number of n=18. The alloploid origin of these x=13 plants is biologically and taxonomically analogous to that of *S. ascendens* (Lindl.) Nesom (discussed above) and provides evidence of a close relationship between sect. *Oxytripolium* and other groups of *Symphyotrichum*.

Symphyotrichum bullatum is one of the two southernmost species of subg. *Symphyotrichum* in geographic distribution (the other is *S. schaffneri* [S.D. Sundb. & A.G. Jones] Nesom) and thus relatively close to the geographic center of diversity for sect. *Oxytripolium*. *Symphyotrichum bullatum* is similar to plants of sect. *Oxytripolium* in overall appearance, especially in its narrowly lanceolate, nearly glabrous leaves, but its stem hairs in lines, chromosome number of n=8 (Anderson *et al.* 1974; Strother 1983), and other features indicate that its placement in sect. *Dumosi* is reasonable (Jones 1980; Jones & Young 1983). Sundberg (1986) also noted the possible occurrence of hybridization between *S. bullatum* and *S. schaffneri*, which is also a member of

sect. *Dumosi*. On the stems of *S. potosinum* itself, the hairs are produced in vertical lines, especially just above the nodes, a feature probably indicative of common ancestry of *S. potosinum* and sect. *Dumosi*. Both *S. potosinum* and *S. bullatum* produce a loosely corymboid capitulescence. It is remarkable that Cronquist (1980) hypothesized that *S. simmondsii* (Small) Nesom may be a hybrid between *S. bracei* (Britton *ex* Small) Nesom (sect. *Oxytripolium*) and *S. dumosum* (L.) Nesom (sect. *Dumosi*), a situation analogous to the relationship postulated by Sundberg between *S. potosinum* and *S. bullatum*. Whatever the evolutionary situation may be, it is clear that the morphological difference between sect. *Oxytripolium* and sect. *Dumosi* is slight.

Semple & Brouillet (1980a) postulated that a close relationship exists between *Symphyotrichum* sects. *Oxytripolium* (the x=5 members) and subg. *Virgulus*, a view apparently dominated by consideration of their similarity in chromosome number (the NOR chromosome morphology is different). They observed the logical necessity (in their system) of recognizing sect. *Oxytripolium* at generic rank, coordinate with *Virgulus* (a separate genus, in their interpretation), but they have deferred from excluding these species from *Aster* s. lat. "for nomenclatural reasons" (Semple *et al.* 1989). Such reluctance, however, almost certainly reflects a perception of the biological complexity of the situation as well as possible problems associated with the nomenclature. In fact, species of sect. *Oxytripolium* have already been treated at generic rank, first by Rafinesque (1837, as *Mesoligus*) and much later by Tamamschyan (1959, as *Conyzanthus*).

b. The status of *Aster subulatus* s. lat.

Sundberg (1986, yet formally unpublished) treated *Symphyotrichum subulatum* as a polymorphic species of *Aster* with five varieties (their names as accepted here in parenthesis): var. *subulatus* (= *S. subulatum*), var. *elongatus* Bosserd. (= *S. bahamense* [Britton] Nesom), var. *ligulatus* Shinners (= *S. divaricatum* [Nutt.] Nesom), var. *parviflorus* Nees (= *S. expansum* [Poepp. *ex* Spreng.] Nesom), and var. *sandwicensis* (A. Gray) A.G. Jones (= *S. squamatum*). Sundberg's taxonomy emphasized the obvious close similarity and relationship among these taxa (as compared to the other two species of sect. *Oxytripolium* that he recognized), a hypothesis of hybrid origin for two of them, and the occurrence of intermediates in three instances (see below) among the taxa involved. In contrast, each of these five is treated here as a species, a morphologically distinct and reproductively isolated entity with a distinct geographic range. The present discussion relies in significant part on information from Sundberg's dissertation.

In their native (New World) ranges, the geographic distribution of each of these five taxa is discrete, each almost completely allopatric with the others

(Sundberg 1986). In those with partially contiguous ranges, their close approach to each other with relatively few intermediates in relatively small areas is as notable as the observation that intermediates do occur. While acknowledging that the morphological differences among them are relatively small, the taxa are discrete and readily distinguishable. Further, *Symphyotrichum subulatum* and *S. expansum* are self-compatible (and presumably autogamous) with correspondingly reduced floral morphology; the other taxa are outcrossers. *Symphyotrichum squamatum* and *S. bahamense* are tetraploids (n=10), while the other taxa are diploids.

Naturally occurring intermediates have been noted by Sundberg to occur between (1) *Symphyotrichum bahamense* and *S. subulatum*, (2) *S. bahamense* and *S. expansum*, and (3) *S. divaricatum* and *S. expansum*. The hybrids resulting from crosses between tetraploid *S. bahamense* and the two diploids *S. subulatum* and *S. expansum* are triploid and almost completely sterile. Sundberg also has noted (p. 63) that "Artificial hybrids produced in the greenhouse among these [five] varieties [in all combinations] are highly sterile."

The geographic ranges of *Symphyotrichum divaricatum* and *S. expansum* are intermittently contiguous roughly along the Texas-México border and into New Mexico. Although Sundberg noted that plants intermediate in ligule length occur in trans-Pecos Texas, New Mexico, and northeastern Chihuahua, these apparently are uncommon, and the two recently have been collected at the same locality in southwest Texas without evidence of intermediacy (Presidio Co., *Worthington 22636* and *22637* [TEX,UTEP]). These two taxa differ in capitular and floral morphology and are distinctly different in habit as well. The ranges of *S. divaricatum* and *S. subulatum* approach each other in Louisiana, but the latter species is restricted to coastal marshes, and there is no indication that it occurs together or intergrades at all with *S. divaricatum*. On the northern margin of its range, *S. bahamense* appears to form intermediates with *S. subulatum*, and it forms intermediates with *S. expansum* on its southern margin. Such intermediates do not appear to be common, and the F_1's are triploid.

A similar view with respect to the taxonomy of *Symphyotrichum tenuifolium* (L.) Nesom and *S. bracei* is followed here. These taxa were maintained as varieties of a single species by Sundberg but have been kept as separate species by others (*e.g.*, Cronquist 1980; Wunderlin 1982), with the acknowledgment that some apparent intermediates occur even though the two taxa are otherwise generally distinct over most of their ranges. Whether a broader or narrower species concept is adopted, a new generic nomenclature must be applied to these Oxytripolioid taxa. The narrower interpretation followed here is the most reasonable, I believe, but which will ultimately prove more reflective of the biological situation remains to be decided by further study.

B. Subgenus *Virgulus*

Subg. *Virgulus* comprises a variable but evidently monophyletic group of species, as recognized by both Jones (1980a) and Semple & Brouillet (1980a), although there have been varying interpretations regarding patterns of similarity (and implied relationships) among its constituent species (Jones 1980a; Semple & Brouillet 1980a; Nesom 1989b). It is variable in vegetative and capitular morphology but the species have a specialized base chromosome number of x=5 and a distinctive NOR chromosome morphology. The group is briefly characterized as follows: leaves mostly oblong, epetiolate, and clasping or subclasping, and except for one group of four species (sect. *Concolores*), the stems, leaves, and phyllaries are stipitate-glandular; capitulescence open-paniculate to terminal and corymbiform (mostly in *Symphyotrichum novae-angliae*); phyllaries usually with a distinctly delimited, green apical patch, varying from basally truncate to attenuate; disc corollas narrowly tubular; achenes subterete. short-cylindric to obovate, (1.2-)2.5-3.5(-4.0) mm long, with (5-)6-10(-11) longitudinal nerves, producing a 1-seriate pappus. The achenes usually are densely strigose to sericeous but some species (e.g., *S. concolor* [L.] Nesom) produce glabrous achenes. Subg. *Virgulus* differs from subg. *Symphyotrichum* in a combination of characters: glandular vestiture, non-glandular stem hairs generally distributed (not in lines), subterete, multinerved achenes, phyllaries with a tendency for basally truncate apical patches, and its chromosome number and karyotype.

The rationale for the treatment of *Virgulus* at generic rank was primarily based on its distinction as a natural group (including the distinctive morphology of the NOR chromosomes), the lack of an unequivocal hypothesis of relationship between it and any other species within the rest of *Aster*, and the assumption by Semple & Brouillet (1980b) that within the Astereae the x=5 groups are distantly related to the x=9/8 groups. For example (p. 1011): "Our primary reasons [for segregating subg. *Virgulus* as a genus] were based on morphology, but our interpretation of phylogeny in the Tribe Astereae was also critical." And "On the basis of the cytological evidence alone (Semple & Brouillet, 1980b), we would be reluctant to assign the x=5 species of [subg. *Virgulus*] to the x=9 genus *Aster*." The claim by Semple & Brouillet (1980a) that subg. *Virgulus* is more closely related to Astereae outside of *Aster* was accompanied only by the following statement (p. 1010): "Its affinities are with such x=5 genera as *Machaeranthera*, *Psilactis*, *Astranthium* and more distantly with *Chrysopsis* sensu Semple, *Xanthisma*, *Bradburia* and the x=6 genera *Xylorhiza*, *Prionopsis*, *Grindelia* and *Pyrrocoma*." There has been no morphological evidence adduced that might ally subg. *Virgulus* with any other genus outside of the traditional *Aster* alliance. In contrast, preliminary molecular studies by Suh (1989), Morgan (1990), and Morgan & Simpson (1992), as well as other morphological and genetic evidence (see below), suggest that subg.

Virgulus is closely related to New World groups generally treated as *Aster* and that subg. *Virgulus* is not closely related to any of the genera in the *Machaeranthera* lineage (x=6/5) or any of the others listed by Semple & Brouillet. This is confirmed in a morphologically based survey and classification of the entire tribe (Nesom 1994e).

Almost all of the taxa placed in subg. *Virgulus* by Semple & Brouillet have a chromosome number based on x=5 (or reduced to x=4; but two "virguloid" species have been reported as x=9. *Aster carolinianus* Walt. does not belong with subg. *Virgulus* (see comments above under *Ampelaster*), although its status has not been reevaluated by Semple. Nor has the chromosome number and mode of origin of *A. gypsophilus* B.L. Turner (Turner 1974) been accounted for. *Symphyotrichum* (*Aster*) *gypsophilum* (B.L. Turner) Nesom is similar in habit, vegetative morphology, and floral and fruit morphology to a group of primarily Mexican species with a known chromosome number of x=5, including *S. moranense* (Kunth) Nesom and *S. trilineatum* (Sch.-Bip. *ex* Klatt) Nesom. *Symphyotrichum oblongifolium* (Nutt.) Nesom (x=5) appears to be closely related to these (Nesom 1989b and included references) and its NOR chromosome morphology has been determined to be virguloid. The predicted base chromosome number of *S. gypsophilum* would be x=5 (with n=10 as tetraploid) rather than x=9; an intensive effort in 1993 to relocate plants of this rare species for a chromosomal study was unsuccessful.

A hypothesis for the complete separation of *Virgulus* from x=9/8 phylads is contradicted by its morphological similarity to plants of *Symphyotrichum* s. str. and by the existence of natural hybrids between plants of *Symphyotrichum* subg. *Symphyotrichum* (x=8) and subg. *Virgulus* (x=5). *Symphyotrichum ascendens*, a distinctive and common species of the western United States, has diploid, tetraploid, and octoploid populations based on x=13, an amphiploid condition resulting from a hybrid cross between *S. spathulatum* (x=8, subg. *Symphyotrichum*) and *S. falcatum* (Lindl.) Nesom (x=5, subg. *Virgulus*) (Jones 1977; Allen *et.al.* 1983; Dean & Chambers 1983; Allen 1985). *Symphyotrichum ascendens* backcrosses with *S. spathulatum* and forms natural, highly fertile hybrids with at least three other x=8 species of the *S. spathulatum* complex (Allen 1985). *Symphyotrichum defoliatum* (Parish) Nesom (= *Aster bernardinus* Hall; n=18), another species closely similar to *S. spathulatum*, is a stabilized amphiploid formed as a backcross between *S. ascendens* and *S. falcatum* (Allen 1986). The two hybrid species are more or less intermediate in habit and capitulescence between the diploid parental species; they are more similar to the virguloid line in their vestiture of generally distributed trichomes and multinerved, subterete achenes, but they do not produce the glandular trichomes characteristic of the virguloid parents.

In an alternative resolution to the taxonomic problem associated with *Symphyotrichum ascendens*, *S. defoliatum*, and their backcrosses to other species, Semple (1985) placed these two species into the separate genus *Virgulaster*,

in parallel with the maintenance of *Virgulus* as a genus separate from *Aster*. He simultaneously proposed a new category for them within *Aster* ("subg. *Ascendentes*"). In the present system, these two species are treated within *Symphyotrichum* sect. *Ascendentes* (see Appendix II), near other species with which they have usually been placed on the basis of morphology, and with the recognition that their genomes include divergent elements. The introgressants are variously identified, according to their morphologically closest parent.

XIII. Incertae sedis - *Chloracantha*

The variable and widespread North American species *Aster spinosus* received a name as *Erigeron* (*E. ortegae* S.F. Blake) but it was recently segregated as the monotypic genus *Chloracantha* (Nesom *et al.* 1991; Sundberg 1991). The plants are remarkably similar in habit to *Boltonia* (Asterinae), but their relatively small (1.5-3.5 mm long), terete achenes with 5(-6) nerves are more like those of specialized taxa of *Symphyotrichum* and some Solidagininae than any species closely related to *Aster* s. str. Several features of *Chloracantha*, however, appear to eliminate it from inclusion among the groups of the Eurybian lineage (phyllaries 3-5 nerved with rounded apices, unkeeled, and herbaceous without an apical patch, deltate and papillate style branch appendages, disc corollas with orange resin ducts accompanying the veins, remaining yellow at maturity, and pappus of 1-2 series of equal length bristles, sometimes with a few short, outer setae). Other distinctive features of *Chloracantha* are summarized as follows: rhizomatous, completely glabrous perennials, usually restricted to wet habitats, the stems spiny and chlorophyllous but becoming internally woody and producing true axillary resting buds with bud scales, the leaves early deciduous, leaving only the stems at flowering, and heads small, terminal and solitary, scattered in a diffuse panicle.

The remarkable morphological specializations of *Chloracantha* do not provide evidence of a close relationship with any other species. In a preliminary interpretation of data from chloroplast DNA studies, however, Nesom *et al.* (1991) ventured that *Chloracantha* (as well as *Boltonia*) are closely related to each other and that their phylogenetic position lies near the base of the Chrysopsidinae. This is a problematic interpretation, however, because the samples for molecular study by Morgan & Suh did not include species apparently among the primitive stock of the group recognized here as the Asterinae, and the possibility seems strong that *Chloracantha* early diverged from stock close to the base of all of the Northern Hemisphere subtribes (see further comments above).

XIV. Incertae sedis - *Tonestus*

Tonestus is briefly characterized as follows: perennial herbs arising from thick, woody caudex branches (*T. kingii* apparently taprooted; *T. lyallii* (A. Gray) A. Nelson with a system of slender rhizomes); basal leaves commonly persistent, but the stems leafy, the cauline leaves grading into phyllaries; leaves 3-veined from the base, obovate, subclasping but not auriculate, the margins often toothed-spinulose; stems, leaves, and phyllaries distinctly and densely pilose-glandular with long, vitreous, biseriate, gland-tipped hairs (Type C trichomes); heads sometimes few and loosely corymboid but most commonly reduced to one; phyllaries in 3-4 series mostly of equal length, at least the outer foliaceous; rays yellow, white, or absent; disc corollas narrowly tubular, the tube ca. 30% of the corolla length, opening into a slightly broader limb; achenes narrowly oblong in outline, terete to somewhat compressed, 5-nerved, 5-8 nerved, or 8-12 nerved (see below), glabrous to strigose; pappus mostly 2-seriate (*T. kingii* 1-seriate; *T. pygmaeus* (Torr. & Gray) A. Nelson often with a short outer series), the bristles apically attenuate; base chromosome number, x=9.

Tonestus as constituted here is variable in most of the features that might be used in its definition: habit, vestiture, leaf margins, degree of cauline leaf development, the nature of the capitulescence, phyllary morphology, style appendage morphology, ray color, and achene and pappus morphology. Like *Eurybia* (below), however, the relatively few species of *Tonestus* appear to be "interlocking" in their overlapping pattern of variability, and it is difficult to pry the group apart, although the possibility remains that the genus, as considered here, is polyphyletic. *Tonestus kingii*, *T. aberrans* (A. Nelson) Nesom & Morgan, and *T. graniticus* (Tiehm & Schulz) Nesom & Morgan appear to form a distinctive subgroup on the basis of the following features: (1) keeled phyllaries that tend to be graduated in length (especially in *T. graniticus*); (2) hairy disc style appendages (in *T. kingii* and *T. aberrans*, as well as *T. eximius* (H.M. Hall) A. Nelson & Macbr., but not *T. graniticus*) vs. appendages closely papillate in the other species; and (3) 5-nerved achenes (5-8-nerved in *T. graniticus*) vs. 8-12-nerved in the other species. *Tonestus kingii* produces white rays, while *T. aberrans* and *T. graniticus* are rayless; the other species are yellow-rayed (or rayless in *T. alpinus* [Anderson & Goodrich] Nesom & Morgan). *Tonestus lyallii* (the generitype), with entire leaves and a system of relatively slender rhizomes, stands alone in habit among the other species, but its dense vestiture of long-stipitate glands is modal in the genus. *Tonestus pygmaeus* also produces entire leaves but is distinctive in its lack of glands.

Haplopappus microcephalus Cronq. was treated within *Tonestus* by Nesom & Morgan (1990) but is better placed in the vicinity of the genus *Petradoria* of the Solidagininae. The species will be formally treated by Gary Baird,

who includes it along with *Petradoria* within *Chrysothamnus* in a forthcoming review of the latter genus.

Tonestus has been placed close to *Solidago* and its relatives in analyses based on DNA data (Morgan & Simpson 1993; *T. pygmaeus* the sampled species), and I have treated *Tonestus* within the Solidagininae (Nesom 1993c), noting that it occupies an isolated position there but that it has similarities (particularly in vestiture and foliaceous phyllaries) to *Oreochrysum* and *Nannoglottis*, the latter two genera hypothesized to be closely related between themselves and placed near the phylogenetic base of the Solidagininae. DNA sampling of Astereae, however, has been highly incomplete with respect to putatively basal taxa of the Solidagininae and Asterinae, and in a broader morphological context, *Tonestus* also appears to be similar to genera placed here in the Asterinae although it would be the only genus there with yellow-rayed species. It clearly lies outside the Machaerantherinae and Chrysopsidinae. Most features of *Tonestus* are ambiguous in regard to its possible placement in the Asterinae or Solidagininae (*e.g.*, ray color, style branch morphology, achene and pappus morphology), but the glandular vestiture, subclasping, spinulose leaves, and foliaceous, equal-length phyllaries are more common in the Asterinae, particularly among the taxa of *Eurybia* subg. *Oreostemma*, as treated here. The position of *Tonestus* is uncertain, but it may have originated from stock very similar to the ancestors of both the Solidagininae and Asterinae.

BIOGEOGRAPHY OF *ASTER* SENSU LATO

Genera, species groups, and species disjunct between eastern North America and southeastern Asia have long been well-known (*e.g.*, Gray 1859; Li 1952; Graham 1972; Zhengyi 1983; Tiffney 1985b). Other taxa are disjunct between Asia and western North America, yet others have a tricentric pattern with populations in Asia and both areas of North America, and there are various other permutations of these patterns (Ying 1983). A few of these taxa, especially those with representation in eastern North America, have an additional series of disjunct populations in México or Central America. Asteraceae have seldom been mentioned or included in such accounts, and Zhengyi's inclusion of *Brachyactis* in a summary of this nature (1983) is problematic from several standpoints (see discussion above of *Symphyotrichum* sect. *Conyzopsis*). In contrast, Tiffney (1985a) noted that nineteen genera of Asteraceae are represented both in Asia and eastern North America, although only a few of these have disjunct species, species pairs, or species groups. *Doellingeria* (Nesom 1993f), *Solidago* (Nesom 1993c), *Eupatorium* (King & Robinson 1970), *Cacalia*, and *Prenanthes* are examples that belong with the latter group.

The evolutionary radiation and geographic dispersion of *Doellingeria* and *Solidago* probably were roughly contemporaneous, as the phyletic position of both genera is hypothesized to lie near the divergence of the Solidagininae (*sensu* Nesom 1993c) and Asterinae. The more primitive species of *Solidago* (sect. *Solidago*) occur primarily in eastern North America and southeastern Asia, with the advanced groups (sect. *Unilaterales* D. Don) restricted to the New World. The species of *Doellingeria* sect. *Doellingeria* are divided between eastern North America and southeastern Asia. If the relationship between the American *Boltonia* (Asterinae) and the genera of the Asian *Kalimeris* group is as close as postulated in the present study, this provides an analogous example of such a relictual pattern of disjunction within the Astereae. Further, as noted above, the pattern of relationship of *Eucephalus* and *Oclemena* to Old World *Aster* is not clear, and these may yet prove to be closely but independently related. Finally, several Old World groups presently maintained within *Aster* (see discussion of "Problematic species") may prove to be more closely related to genera of American Asterinae than to Asian ones.

An early Cenozoic "boreotropical flora" included many temperate deciduous forest species with patterns of distribution similar to *Doellingeria*, *Solidago*, and the *Kalimeris* group (including *Boltonia*), and these Asteraceae can reasonably be regarded as members of the same flora, which apparently extended from southeast Asia westward along the Tethys Seaway into Europe, Greenland, and eastern North America (Taylor 1990). The Asian-eastern American connection apparently was made across a North Atlantic route that, while often loosely connected, was available for overland dispersal in the early Cenozoic (Paleocene into the Eocene and perhaps up to early Miocene: *e.g.*, Hamilton 1983; McKenna 1983; Tiffney 1985b; Taylor 1990). The boreotropical flora reached its maximum extent by early Eocene (Tiffney 1985b), and Hsu (1983, p. 506) observed that paleobotanical evidence shows that "after the Eocene Chinese vegetation was rapidly modernized by the loss of the American elements." A north-Pacific (Beringian) land bridge also was open during the Eocene (particularly middle and late Eocene) and apparently facilitated the migration of deciduous forest species between western North America and Asia (Wolfe 1985; Tiffney 1985b). According to Wolfe (1987, p. 789) "The microthermal vegetation and flora [of the Rocky Mountains] of the Late Cretaceous and the Paleocene have few similarities to Eocene and later vegetation and flora," but (p. 792) "the great majority of extant genera of woody microthermal angiosperms had evolved by the end of the Eocene." The broader nature of the connection of the western North American boreotropical flora to the Eurasian elements, whether solely across the north Pacific or also across the north Atlantic (and thus subsequently across mid-continental North America) is not clear. In summary, although palynological evidence has placed the primary diversification of the Compositae in the Miocene (Muller 1981) and Raven & Axelrod (1974) have allowed an origin for the family no earlier than

Oligocene, biogeographic evidence suggests that taxa of at least two or three Astereaean groups (basal Solidagininae and Asterinae and the *Kalimeris* group of Asterinae) were already differentiated by the Eocene and dispersed in the Northern Hemisphere of the Old and New Worlds.

Among other taxa of strictly New World Asterinae, *Oclemena* is restricted to eastern North America. *Sericocarpus* is divided between eastern and western North America. The closely related *Eurybia* is relatively widespread; the putatively basal taxa are primarily eastern North American, but other species and species groups are primarily western North American. The species of *Symphyotrichum* subg. *Symphyotrichum* appear to follow a similar pattern of distribution. *Tonestus* and *Eucephalus*, in contrast, are restricted to western North America. *Ionactis* is a western genus except for *I. linariifolia* (L.) E. Greene, which occurs only in eastern North America.

A few North American asters (e.g., *Eurybia sibirica* and *Symphyotrichum* [*Brachyactis*] *ciliatum*) have distributions from the Rocky Mountains into Alaska and across a Beringian route into Asia. *Aster alpinus*, which has its closest relatives in Asia, crosses into North America by the same route. It is likely that the dispersion of such species between these two continents was relatively recent, as noted by Mizushima (1972) and Kruckeberg (1983) for other taxa.

According to Jones (1977, p. 342), "There is general agreement that the center of origin of *Aster proper* lies in North America (Huziwara 1958; Raven *et al.* 1960). The largest number of species and also the highest degree of diversity are found in this continent. .... The Old World species belong partly in sections unique to that vast area; in a large part, however, they are derivatives of New World asters." Semple & Brouillet (1980a, p. 1016) were of essentially the same view: "The genus presumably originated in North America and therefore all the non-North American groups are derived directly or indirectly from North American groups." Grierson (1964) deferred from speculating on the area of origin of the Old World species. In the phylogenetic hypothesis presented in the present study, phyletically basal elements of the Asterinae are divided between Eurasia and North America, but a greater concentration of primitive species and species groups remain in North America.

Some genera and generic groups from the Asterinae and other subtribes with their center of diversity and apparent center of origin in North America have disjunct but relatively closely related representatives in South America. The southward extensions of *Symphyotrichum* sect. *Oxytripolium* and *Psilactis* into South America, *Gutierrezia* (Solidagininae) and *Grindelia* (Machaerantherinae) into the southern Andes, and *Solidago* (Solidagininae) into southeastern South America probably are relatively recent in origin compared to the Asian-American disjunctions of Astereae. The South American *Haplopappus* (Machaerantherinae), an Andean endemic, is closely related to and perhaps conspecific with *Hazardia*, which is primarily centered in Baja California. *Noticastrum* (Chrysopsidinae), however, is an endemic genus primarily

of southeast-central South America with its closest relatives all North American genera. The mode and geological time of dispersal of this array of taxa probably is diverse.

CHROMOSOME EVOLUTION IN THE ASTEREAE

The systematic treatment of American Asterinae focuses attention on two long-standing cytological problems in the Astereae: the base chromosome number of the tribe, and the apparent close relationships of species with a chromosome number of $x=9$ to those with a number of $x=5$ or $x=4$. Resolution of these problems may prove to be part of a more general insight that accounts for the difference between genera of Astereae with a highly conservative base chromosome number of $x=9$ (e.g., *Erigeron*, *Olearia*, *Townsendia*, *Solidago*, *Heterotheca*, *Ericameria*, *Baccharis* and all other Baccharidinae, with $x=9$) and other clearly or hypothetically monophyletic groups where an array of chromosome numbers occurs, particularly those with $x=9/8$ lowered to $x=5$ or near it.

The hypothesis that $x=9$ is the primitive state for the Astereae is supported by a significant number of monophyletic groups known with both $x=9$ and an array of decreasing numbers, together with the preponderance of strictly $x=9$ groups found in genera of all subtribes of Astereae except the Machaerantherinae. Phylogenies produced from molecular evidence, at all taxonomic levels within the tribe, also consistently place $x=9$ taxa in phylogenetically basal positions. The hypothesis of primitive $x=9$ in the Astereae has been advanced at least since 1959 (see Jones 1985 for a review). Finally, outside of the New World, across all subtribes of Astereae, genera with base chromosome numbers other than $x=9$ are rare. In those Old World groups where lower numbers do occur, in almost every case they are clearly derived from an ancestral $x=9$ (see examples below).

Evidence cited against the primitive status of $x=9$ in the Astereae has been based primarily on a lack of expected intermediate steps in the derivation of $x=5$ from $x=9$ (mostly $x=7$ level, but $x=6$ and $x=8$ also are relatively uncommon) (Brown 1972; Turner *et al.* 1961). This argument is countered, however, by an analogous observation: if $x=9$ is derived as an amphiploid between $x=5$ and $x=4$ plants, or between $x=5$ and $x=5$ with a subsequent aneuploid decrease of one pair, then such an occurrence has been extremely frequent, and base numbers of $x=10$ and $x=8$ (as amphiploids of two $x=5$'s or two $x=4$'s) should also be expected and at a much higher frequency than is found. In fact, there are no genera or generic groups of Astereae with a base number of $x=10$ (with the possible exception of *Centipeda*) and few with $x=8$ (see examples below). This also suggests that if $x=9$ in the Astereae has been derived by a reduction in number from an ancestral $x=10$ genome, such an event must have occurred

prior to the inception and evolutionary radiation of the tribe. Further, a large number of the x=9 species of *Aster* and *Solidago* have chromosomes that are even-sized and mostly submetacentric, a condition that has been interpreted as primitive in many groups of vascular plants (*e.g.*, Stebbins 1971).

Evidence for a base chromosome of x=9 (or x=8), with subsequent aneuploid decrease, can be seen in the following Astereaean genera and generic groups with wide variability in base number:

Calotis (x=8, to 7,5,4, with evidence for descending aneuploidy: Stace 1978);

Brachycome (one section conservative with only x=9; the other section with x=9, to 8,7,6,5,4,3,2, as well as n=10,11,12,13,14,15,16, the latter numbers variously constituted primarily by amphiploidal crosses between lower numbers: Smith-White *et al.* 1970; Carter 1978; Watanabe & Short 1992);

Felicia (x=9, to 8,6,5: see Grau 1973);

Amellus (x=9, to 8,6: see Rommel 1977; Podlech & Dieterle 1969);

Symphyotrichum subg. *Symphyotrichum* (8,7,6: the present summary);

Symphyotrichum subg. *Virgulus* (5,4: the present summary);

Psilactis (x=9, to 4,3, although it is not clearly established that the lower numbers are primitive);

among the genera of the *Townsendia* group (x=9, to 5,4,3: Nesom in prep.), including *Townsendia*, *Geissolepis*, *Astranthium*, *Dichaetophora*, and *Aphanostephus*;

among the genera of the *Gutierrezia* lineage (x=9, to 5,4, perhaps including x=8: see Nesom 1991c, 1993c);

among the genera of the Chrysopsidinae (x=9, to 7,6,5,4: see Nesom 1991b).

among genera of the Grangeinae; the genus *Centipeda* has a chromosome number of n=10; the other genera of the subtribe (see Nesom 1994e) are reported as x=9, there are no other species or genera of Astereae known with a base number of x=10, and it seems most likely that these *Centipeda* species are tetraploid based on x=5, although an aneuploid increase to x=10 is possible;

disparate counts based on x=5 and x=9 are reported within the South American genus *Hysterionica*, but these need to be reinvestigated (see Nesom 1994d for a summary).

There is at least strong circumstantial evidence in the examples above (except the last two) for descending aneuploidy as the primary process of evolutionary change in chromosome number. This reduction in chromosome number appears primarily to involve the redistribution of chromatic material onto fewer chromosomes, with a corresponding loss of centromeres but without a genetic loss (Gottlieb 1981; this process referred to as "meroaneuploidy" by Jackson 1971; Stucky & Jackson 1975). Astereaean genomes of x=5, in particular, have chromosomes with a great amount of resultant structural reorganization, compared to those of x=9. Ascending aneuploidy apparently is rare in the Astereae, but it has been documented within a single species (Watanabe & Smith-White 1987; Jackson 1992; Jackson *et al.* 1993) and suggested to occur within the genus *Astranthium* (De Jong 1965). In these cases, the ascent has been from a number less than n=9. Evidence indicates that aneuploid increase also has occurred in polyploid hybrids involving the Old World *Aster ageratoides* (Tara 1973) and the American *Symphyotrichum* (*Aster*) *foliaceum* (DC.) Nesom (Allen 1984, 1985).

The concentration in North America of genera with low base chromosome numbers might be taken as an indication these numbers reflect a pattern of common ancestry, but this is contradicted both by morphological and molecular evidence (Nesom 1994e). In almost every case, American genera with base chromosome numbers lower than x=9 are known to be closely related to others with x=9. The greatest number of these low-numbered taxa are among the fifteen genera of the Machaerantherinae (x=6 for the subtribe, reduced to x=5,4,3,2; Morgan & Simpson 1992) and within American Asterinae, where reductions directly from x=9 apparently have occurred independently at least four times: (1) the origin of *Symphyotrichum* subg. *Virgulus* (x=5); (2) the origin of *Symphyotrichum* subg. *Symphyotrichum* (x=8); (3) the derivation of *Eurybia chapmanii* (x=7); and (4) the derivation of x=4 species within *Psilactis*.

The only other genera of Astereae with a lowered base chromosome number are the four of the *Gutierrezia* group of the Solidagininae (probably x=8, reduced to x=5,4; Nesom 1991d, 1993); three within North American Brachycominae (x=5, reduced to x=4,3; Nesom in prep.); two of the *Monoptilon* group within subtribe Feliciinae, i.e., *Monoptilon* and *Chaetopappa* (x=8; Nesom 1992b); and three of the Chrysopsidinae (x=7 and x=5, with reductions to x=6,5,4; Nesom 1991b).

The derivation of x=5 and x=4 genomes from x=9 ones might occur by the dissociation of ancestral components of x=5 and x=4, as in polyhaploidy (*cf.* deWet 1971), but there is little evidence to suggest that x=9 in the Astereae is of amphiploid origin. Semple & Chinnappa (1980a, 1980b) showed that x=9 in *Chrysopsis* is constituted by alloploidy from an immediate ancestry of x=4 and x=5 parents, which could be interpreted as the reassociation of such putative components. Although the ancestor of *Chrysopsis* clearly had

a base chromosome number of $x=5$, the genus is a member of the subtribe Chrysopsidinae, a phylad hypothesized to have a base of $x=9$ (Nesom 1991b). The species of *Psilactis* (see Morgan 1993) constitute the only other group within the Astereae with an array of base chromosome numbers based on 9 and lower numbers completely "disjunct" at $x=4$ or $x=3$. Further, the loss of entire sets of chromosomes does not appear possible through "meroaneuploidy" (Jackson 1975), although this process theoretically might be responsible for the rapid occurrence of such a large gap (*i.e.*, the 9/5 gap) in a succession of contiguous steps. Jackson (1973) has documented a chromosome number reduction by two in the Astereae, and a wide discontinuity ($x=10$ and $x=4$) has been reported between two closely related, Central American species within the genus *Fleischmannia* Sch.-Bip. (Eupatorieae), where $x=10$ is the base number (see King & Robinson 1987 for comments and references). In view of the probable $x=9$ ancestry for the Astereae (see above), it seems likely that the correct explanation for the paucity of $x=7$ (and 8 and 6) has not yet been clearly discerned. It may prove to be related to a relative adaptive advantage accompanying the lower numbers (for comments and references, see Jackson 1971, Stucky & Jackson 1975) or to some other phenomenon, but it seems clear that this "gap" is not merely an artifact of interpretation.

NOR chromosome morphology

Studies by Semple and colleagues (Semple & Brouillet 1980b; Semple *et al.* 1983) have provided valuable information regarding the morphology of "satellite" or NOR chromosomes (chromosomes bearing the nucleolar organizer region). They have classified the NOR chromosomes of primarily North American species of *Aster* s. lat. into several different types, depending on the relative lengths of the satellite and proximal portion of the short arm: "primitive" type, with the satellite and proximal portion of about the same length; "euaster" type, with the satellite markedly longer than the remainder of the arm; and "virguloid" type, with a minute satellite and correspondingly long arm. The primitive type is characteristic of *Doellingeria* (including both American and Asian species), *Oclemena*, *Eucephalus*, *Ionactis*, and *Sericocarpus*. A karyotypic description apparently has not been published for the species of *Chloracantha* and *Tonestus*. The euaster NOR type might be better termed the "eurybia" type or the "symphyotrichum" type, as it is characteristic of most of the species of those two groups (see caveats below), but Semple *et al.* (1983) also reported that the generitype of *Aster*, *A. amellus*, has primitive type NOR chromosomes. In view of the variability of the chromosomes of the latter species and conflicting reports regarding its karyotype, a more detailed study is in order.

The NOR chromosomes of *Symphyotrichum* sect. *Oxytripolium* have acrocentric NOR chromosomes, both the satellite and arm highly reduced in length;

these also are unique within the Asterinae and are here termed the "oxytripolioid" type. In published photographs of somatic chromosomes of *Psilactis* (Stucky 1978; Hartman & Lane 1987), the identity and morphology of the NOR chromosome is not immediately apparent, although one of the longest chromosomes of *P. asteroides* seems to have a small satellite at the end of a much longer arm, approaching the virguloid type (see Stucky 1978, Figures 5 and 7). The NOR morphology of the n=9 species of *Psilactis* has not been observed. *Almutaster pauciflorus*, *Eurybia sibirica*, *Eurybia glauca*, and *Canadanthus modestus* have been reported to have primitive type NOR chromosomes (Semple & Brouillet 1980b; Semple *et al.* 1983), those of *Symphyotrichum turbinellum* to be of "varying morphology." In view of the phylogeny hypothesized here (Figure 2), it appears that the euaster ("eurybia") type has been independently evolved at least two times within the genus. Alternatively, it would be necessary to postulate "reversions" to the primitive type in the taxa noted above.

The NOR chromosomes of *Symphyotrichum* subg. *Virgulus* appear to be markedly different in morphology from all others within the Asterinae, and it is clear that the virguloid NOR morphology is specialized. As noted by Semple & Brouillet (1980b, p. 1035), however, "satellite or NOR chromosomes with morphology like those of [subg. *Virgulus*] may have evolved independently several times in the tribe," and the same possibility must also be admitted for the other NOR types. Karyotypic repatterning is known to occur within numerous monophyletic groups of Astereae, *e.g.*, the genus *Astranthium* (De Jong 1965) and even within single species, e.g., *Aster amellus* (Chatterji 1962), *Machaeranthera riparia* (Kunth) A.G. Jones (Stucky 1978), and *Aster ageratoides* (Irifune 1990). Differences in NOR chromosome morphology clearly are useful in indicating the limits of monophyletic groups, but without an unambiguous interpretation of homologies, karyotypic differences by themselves provide no justification for the determination of taxonomic rank or phylogenetic position of the groups concerned.

Huziwara (1967) observed that the chromosomes of Asian and European species of *Aster* differ from those of American species, the latter generally smaller in size as well as distinct in morphology, but the Asian species have not been included in the recent classification of NOR types. Remarkably, the Old World species consistently produce an NOR morphology (here termed the "Asterinae" type) that differs from all of the New World species: the satellite is much shorter than the remainder of the arm but not reduced to the minute size of the of the virguloid satellite. The Asterinae type has been documented for a range of Old World species among various taxa (see primarily numerous references by Huziwara; also Chatterji 1962), including the following: *A. amellus*, *A. amelloides*, *A. ibericus*, and *A. maackii* (sect. *Aster*), *A. alpinus* (sect. *Alpigeni*), *A. ageratoides* (sect. *Ageratoides*); *A. tataricus* and *A. fastigiatus* (both placed tentatively within *Aster* and in an uncertain position, see discus-

sion). The Asterinae NOR type also is found in species that are treated here within genera outside of *Aster* s. str.: *Heteropappus*, *Kalimeris*, and *Tripolium*.

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APPENDIX I.

Abbreviated taxonomy of the main groups within *Aster* s. str. The list of species included in each group is not complete, but it provides at least a general, illustrative sketch of the composition of the group and the existing nomenclature.

ASTER L., *Sp. Pl.* 2:872. 1753.

Lectotype (Britton & Brown 1913; Hitchcock & Green 1935): *Aster amellus* L.

A. *Aster* sect. *Aster*

Aster sect. *Amelli* Nees, *Gen. Sp. Aster.* 39. 1832. *Aster* [sect. *Aster*] ser. *Amelli* (Nees) Kitamura, J. Jap. Bot. 12:535. 1936.

Type: *Aster amellus* L.

Kalimeres Rafin., *Fl. Tellur.* 2:46. 1836 [1837].

Type: *Aster amellus* L.

Aster [sect. *Aster*] ser. *Macrocephali* Kitam., J. Jap. Bot. 12:533. 1936. *Aster* sect. *Macrocephali* (Kitamura) A.G. Jones, Brittonia 32:237. 1980.

Type: *Aster maackii* Regel.

INCL: *Aster aitchisonii* Boiss., *A. amellus* L., *A. amelloides* Bess., *A. catalaunicus* Willk. & Costa, *A. ibericus* M. Bieb., *A. indamellus* Grierson, *A. laka* C.B. Clarke, *A. maackii* Regel, *A. poliothamnus* Diels, *A. thomsonii* C.B. Clarke.

B. *Aster* sect. *Alpigeni* Nees, *Gen. Sp. Aster.* 24. 1832.

Lectotype (Jones 1980a): *Aster alpinus* L.

Diplactis Rafin., *Fl. Tellur.* 2:45. 1836 [1837].

Lectotype (designated here): *Aster alpinus* L.

Aster sect. *Alpinaster* Tamamsch. [nom. illeg.], *Fl. URSS* 25:104. 1959. [superfluous; no Latin diagnosis]

Lectotype: *Aster alpinus* L.

a. *Aster* subsect. *Homochaeta* Onno, Bibliot. Bot. 106:7. 1932.

Lectotype (designated here): *A. alpinus* L. To stabilize the usage of this name, the choice of a lectotype follows the precedent by Grierson (1964), who included within subsect. *Homochaeta* a group of Himalayan species closely related to *A. alpinus.*

Aster [sect. *Alpigeni* subsect. *Homochaeta*] subser. *Alpini* (Rydb.) Onno, Bibliot. Bot. 106:7. 1932. *Aster* sp.-group *Alpini* Rydb., *Fl. Rocky Mts.* 880. 1922.

Type: *Aster alpinus* L.

Aster sect. *Alpigeni* ser. *Salwinenses* Ling [*nom. illeg.*], *Fl. Reip. Pop. Sin.* 217. 1985. [no Latin diagnosis].

Type: *Aster salwinensis* Onno.

INCL: *Aster alpinus* L., *A. barbellatus* Grierson, *A. bietii* Franch., *A. heliopsis* Grierson, *A. himalaicus* C.B. Clarke, *A. ionoglossus* Ling, *A. korshinskyi* Tamamsch., *A. neo-elegans* Grierson, *A. oreophilus* Franch., *A. pyrenaeus* Desf. *ex* DC., *A. retusus* Ludlow, *A. salwinensis* Onno, *A. serpentimontanus* Tamamsch., *A. spathulifolius* Maxim., *A. stracheyi* J.D. Hook., *A. tolmatschevii* Tamamsch., *A. tricephalus* C.B. Clarke.

Aster [sect. *Alpigeni* subsect. *Homochaeta*] ser. *Macrochaeti* Onno, Bibliot. Bot. 106:7. 1932.

Lectotype (designated here), *Aster glabriusculus* (Nutt.) Onno = *Xylorhiza glabriuscula* Nutt. (the group becoming a synonym of the North American genus *Xylorhiza*).

b. *Aster* subsect. *Heterochaeta* (DC.) Benth. *in* Benth. & Hook., *Gen. Pl.* 2:272. 1873. *Heterochaeta* DC., *Prodr.* 5:282. 1836.

Lectotype (designated here): *Aster asteroides* (DC.) O. Ktze.

Aster sect. *Alpigeni* ser. *Latibracteati* Ling [*nom. illeg.*], *Fl. Reip. Pop. Sin.* 224. 1985. [no Latin diagnosis].

Aster sect. *Alpigeni* subsect. *Brachychaeti* (Onno) Grierson [*nom. illeg.*], Notes Roy. Bot. Gard. Edinb. 26:83. 1964 [basionym not cited by Grierson]. *Aster* [sect. *Alpigeni*] ser. *Brachychaeti* Onno, Bibl. Bot. 106:7. 1932.

Lectotype (designated here): *Aster tongolensis* Franch.

Aster sect. *Alpigeni* ser. *Tongolenses* Ling [*nom. illeg.*], *Fl. Reip. Pop. Sin.* 213. 1985. [no Latin diagnosis].

Type: *Aster tongolensis* Franch.

Aster sect. *Alpigeni* ser. *Asteroides* Ling [*nom. illeg.*], *Fl. Reip. Pop. Sin.* 234. 1985. [no Latin diagnosis].

Type: *Aster asteroides* (DC.) O. Ktze.

INCL: *Aster asteroides* (DC.) O. Ktze., *A. brevis* Hand.-Mazz., *A. diplostephioides* (DC.) C.B. Clarke, *A. falconeri* (C.B. Clarke) Hutch., *A. farreri* W.W. Smith, *A. flaccidus* Bunge, *A. giraldii* Diels, *A. hololachnus* Ling, *A. jeffreyanus* Diels, *A. latibracteatus* Franch., *A. likiangensis* Franch., *A. lipskyi* Komar., *A. megalanthus* Ling, *A. setchuenensis* Franch., *A. souliei* Franch., *A. tongolensis* Franch., *A. yunnanensis* Franch.

c. *Aster* subsect. *Senecioides* Ling [*nom. nud. illeg.*], *Fl. Reip. Pop. Sin.* 201. 1985. [no type or Latin diagnosis].

Aster sect. *Alpigeni* ser. *Senecioides* Ling, [*nom. illeg.*], *Fl. Reip. Pop. Sin.* 249. 1985. [no type or Latin diagnosis].

Aster sect. *Alpigeni* ser. *Batangenses* Ling, [*nom. illeg.*], *Fl. Reip. Pop. Sin.* 252. 1985. [no type or Latin diagnosis].

INCL: *Aster batangensis* Bur. & Franch., *A. rockianus* Hand.-Mazz., *A. senecioides* Franch., *A. staticifolius* Franch.

C. **Aster** sect. **Ageratoides** (Kitam.) Nesom, *comb. et stat. nov.* BASIONYM: *Aster* sect. *Orthomeris* ser. *Ageratoides* Kitamura, J. Jap. Bot. 12:535. 1936.

Type: *Aster ageratoides* Turcz.

Aster sect. *Ageraton* Tamamsch. (*nom. illeg.*), *Fl. URSS* 25:101. 1959. [no type or Latin diagnosis].

Aster [sect. *Aster*] ser. *Turczaninowia* (DC.) Kitam., J. Jap. Bot. 12:535. 1936. *Turczaninowia* DC., *Prodr.* 5:238. 1836.

Type: *Aster fastigiatus* Fisch. (= *Turczaninowia fastigiata* [Fisch.] DC.).

INCL (e.g.): *Aster alatipes* Hemsl., *A. ageratoides* Turcz., *A. baccharoides* Steetz, *A. falcifolius* Hand.-Mazz., *A. fastigiatus* Fisch., *A. formosanus* Hayata, *A. glehnii* Fr. Schmidt, *A. helenae* Merr., *A. homochlamydeus* Hand.-Mazz., *A. hunanensis* Hand.-Mazz., *A. lasiocladus* Hayata, *A. luxurifolius* Tamamsch., *A. morrisonensis* Hayata, *A. nigromontanus* Dunn, *A. ovalifolius* Kitamura, *A. philippinensis* Moore, *A. pycnophyllus* W.W. Smith, *A. sampsonii* (Hance) Hemsl., *A. sikkimensis* Hook., *A. taiwanensis* Kitam., *A. trinervius* D. Don, *A. turbinatus* S. Moore, *A. vestitus* Franch.

D. **Aster** sect. **Calimeridei** (DC.) Nesom, *comb. nov.* BASIONYM: *Diplopappus* sect. *Calimeridei* DC., *Prodr.* 5:276. 1836 (excluding all species but the type, see comments in discussion).

Lectotype (designated here): *Diplopappus asper* Less. (= *Calendula hispida* Thunb. = *Aster bakeranus* Burtt Davy *ex* C.A. Smith.

Diplopappus Cass. sect. *Herbaceae* Harvey *in* Harvey & Sond., *Fl. Cap.* 3:84. 1865.

Lectotype (designated here): *Diplopappus asper* Less.

INCL: Seventeen species of southeast Africa (see Lippert 1973 and discussion above); the Asian *Aster molliusculus* (DC.) C.B. Clarke and *A. brachytrichus* Franch. may also belong here (see comments in text).

Aster Incertae Sedis

1. *Aster* sect. *Bellidiastrum* (Micheli *ex* Scopoli) Hayek, *Fl. Steierm.* 2:493. 1913. *Bellidiastrum* Micheli *ex* Scopoli, *Fl. Carn.* 376. 1760 (not Cass. 1816; not Less. 1832).

Type: *Aster bellidiastrum* (L.) Scop. (= *Bellidiastrum michelii* Cass. (*Dict. Sci. Nat.* 4, Suppl. 7. 1817.).

Bellidiaster Dumort., *Fl. Belg.* 66. 1827.

Margarita Gaud., *Fl. Helv.* 5:335. 1829.

Brachyaster Ambrosi, *Fl. Tirol. Austr.* 2:379. 1857.

INCL: *Aster bellidiastrum* (L.) Scop.

2. *Aster* [sect. *Alpigeni*] ser. *Prainiani* Ling, *Fl. Reip. Pop. Sin.* 360. 1985.

Type: *Aster prainii* (J.R. Drumm.) Y.L. Chen.

Wardaster J. Small, Trans. Bot. Soc. Edinb. 29:230. 1926.

Type: *Wardaster lanuginosus* J. Small.

Chlamydites J.R. Drumm., Kew Bull. Misc. Inform. 90. 1907.

Type: *Chlamydites prainii* J.R. Drumm.

INCL: *Aster lanuginosus* (J. Small) Y.L. Chen, *A. prainii* (J.R. Drumm.) Y.L. Chen.

3. *Aster* sect. *Bipinnatisecti* Grierson, Notes Royal Bot. Gard. Edinb. 26:83. 1964. *Aster* sect. *Aster* ser. *Bipinnatisecti* (Grierson) Ling, *Fl. Reip. Pop. Sin.* 249. 1985.

Type: *Aster bipinnatisectus* Ludlow *in* Grierson.

INCL: *Aster bipinnatisectus* Ludlow *in* Grierson.

4. *Aster* [sect. *Orthomeris*] ser. *Albescentes* Ling, *Fl. Reip. Pop. Sin.* 357. 1985.

Type: *Aster albescens* (DC.) Hand.-Mazz.

INCL: *Aster albescens* (DC.) Hand.-Mazz., *A. argyropholis* Hand.-Mazz., *A. fulgidulus* Grierson, *A. hypoleucus* Hand.-Mazz., *A. lavandulifolius* Hand.-Mazz., *A. polius* Schneid.

5. The *Aster tataricus* group (see discussion in text).

INCL: *Aster faureri* Levl. & Van., *A. tataricus* L.*f.*

6. The Asian species of "*Brachyactis*" (see discussion in text).

INCL: *Brachyactis chinensis* Bur. & Franch., *B. menthodora* Benth., *B. obovata* Benth., *B. pubescens* (DC.) Aitch. & Clarke, *B. roylei* (DC.) Wendelbo.

APPENDIX II.
Taxonomy of American Asterinae (s. lat.)

The genera are treated below in alphabetical sequence. Details of additional synonyms, subcategories, and typification are found primarily in the following: Jones 1980a; Jones & Hiepko 1981; Jones & Lowry 1986; Lamboy & Jones 1987a; and Sundberg 1986.

Asa Gray was equivocal in the designation of rank for infrageneric categories; for consistency in the interpretation of such categories established by Asa Gray for *Aster* (1842, 1880, 1884) as well as for *Solidago* (see Nesom 1993c), I have followed the interpretation and precedent set by Brizicky (1969), Holmgren (1979), and Jones (1980a). Following original indications by Gray, these later authors have regarded as SUBGENERA the substantive infrageneric names in larger print (and all capitals) and marked with the symbol "§" (e.g., *ASTER*, *BIOTIA*, *IANTHE*, *ORITROPHIUM*, *ORTHOMERIS*; Gray's use of these taxa was consistent in all three publications, and in the latter two (1880, 1884) he clearly referred to them as subgenera of *Aster*. Adjectival subcategories of the subgenera in smaller print (upper and lower case in 1842, all upper in 1880) are treated as sections. A set of subsectional categories for *Aster* was added by Gray in 1884, these in small print (upper and lower case) and italics.

Species were listed by Jackson (in *Index Kewensis*) for genera created by Rafinesque. Rafinesque, however, merely listed such species without making valid combinations for them, and Merrill (1949) has attributed the combinations to Jackson (as Rafin. *ex* B.D. Jackson in *Index Kewensis* 1895).

I. *ALMUTASTER* A. Löve & D. Löve, Taxon 31:356. 1982.

Type: *Almutaster* (*Aster*) *pauciflorus* (Nutt.) Löve & Löve.

Aster sp.-group *Pauciflori* Rydb., *Fl. Rocky Mts.* 789. 1917. *Aster* sect. *Pauciflori* (Rydb.) A.G. Jones [*nom. superfl.*], Brittonia 32:233. 1980. (not *Aster* sect. *Pauciflori* Loudon 1830.).

Type: *Aster pauciflorus* Nutt.

1. *Almutaster pauciflorus* (Nutt.) Löve & Löve, Taxon 31:356. 1982. BASIONYM: *Aster pauciflorus* Nutt., *Gen. N. Amer. Pl.* 2:154. 1818.

II. AMPELASTER Nesom, *gen. nov.*

Type: *Ampelaster* (*Aster*) *carolinianus* (Walt.) Nesom.

Herbae perennes eglandulosae scandentes ad basim lignosae; caules dense hirsutulosi vel pilosi; folia oblanceolata vel oblongi-oblanceolata, ad basim auriculati-amplectentia; capitula solitaria vel 2-8 brevipedicellata in fasciculos laxis terminalibus; phyllaria crassa lineari-oblonga in longitudine subaequalia parum carinata, area apicali viridi ad basim truncata, plerumque reflexa ad apices; corollae disci anguste tubulosae; achenia glabra anguste cylindrica vel parum fusiformia, 2.5-3.0 mm longa, nervis 9-12 parum elevatis; pappus 1-seriatus, setis ad apices attenuatis; chromosomatum numerus n=9.

Aster sect. *Sagittiferi* A. Gray, *Synopt. Fl.* 1(2):179. 1884. *Virgulus* sect. *Sagittiferi* (A. Gray) Reveal & Keener, Taxon 30:650. 1981.

Type: *Aster carolinianus* Walt.

Aster sp.-group *Caroliniana* Small, *Man. Southeast. Fl.* 1367. 1933. *Lasallea* [sect. *Grandiflorae*] subsect. *Carolinianae* (Small) Semple & Brouillet, Amer. J. Bot. 67:1023. 1980.

Type: *Aster carolinianus* Walt.

1. **Ampelaster carolinianus** (Walt.) Nesom, *comb. nov.* BASIONYM: *Aster carolinianus* Walt., *Fl. Carol.* 208. 1788. *Lasallea caroliniana* (Walt.) Semple & Brouillet, Amer. J. Bot. 67:1023. 1980. *Virgulus carolinianus* (Walt.) Reveal & Keener, Taxon 30:650. 1981.

III. CANADANTHUS Nesom, *gen. nov.*

Type: *Canadanthus* (*Aster*) *modestus* (Lindl.) Nesom.

Herbae perennes tenui-rhizomatosae, caulibus 3-8 dm elatis simplicibus ex basi singulatim exorientibus, vestimento (caulorum ac phyllariorum) glanduloso longi-stipitato; folia caulina eglandulosa epetiolata subamplectentia 5-12 cm longa lanceolata vel elliptici-lanceolata apice acuminato marginibus integris vel serratis; capitulescentia laxe corymboidea, capitulis in pedunculis foliaceis; phyllaria lineari-lanceolata tenui-foliacea complanata in seriebus 2-3 in longitudine parum aequalibus, aream viridem apicalem carentia, haec seriei interioris saepe carinata plerumque purpurascentia; corollae disci anguste tubulosae; corollae radii 25-40 ligulis purpuratis circinatis; achenia eglandulosa oblanceolata vel anguste obovata 2.5-4.0 mm longa, 4-8 nervata, valde complanata, ad basim stipitata anguste acuta; pappus 1(-2)-seriatus, setis ad apices attenuatis; chromosomatum numerus n=9.

1. **Canadanthus modestus** (Lindl.) Nesom, *comb. nov.* BASIONYM: *Aster modestus* Lindl. *in* Hook., *Fl. Bor.-Amer.* 2:8. 1834. *Weberaster modestus* (Lindl.) Löve & Löve, Taxon 31:359. 1982.

   Aster unalaschkensis Less. var. *major* Hook., *Fl. Bor.-Amer.* 2:7. 1834. *Aster major* (Hook.) Porter, Mem. Torrey Bot. Club 5:325. 1894. *Aster modestus* Lindl. *in* Hook. var. *major* (Hook.) Muenscher, *Fl. Whatcom Co., Wash. (Vasc. Pl.)* 128. 1941.

   Aster sayianus Nutt., Trans. Amer. Philos. Soc., ser. 2, 7:294. 1840.

IV. *CHLORACANTHA* Nesom, Suh, Morgan, & Simpson, Phytologia 70:378. 1991.

Type: *Chloracantha spinosa* (Benth.) Nesom.

1. *Chloracantha spinosa* (Benth.) Nesom, Phytologia 70:378. 1991. BASIONYM: *Aster spinosus* Benth., *Pl. Hartweg.* 20. 1839.

   a. *Chloracantha spinosa* (Benth.) Nesom var. *jaliscensis* (McVaugh) S.D. Sundb., Phytologia 70:388. 1991. BASIONYM: *Aster spinosus* Benth. var. *jaliscensis* McVaugh, Contr. Univ. Mich. Herb. 9:363. 1972.

      Erigeron ortegae S.F. Blake, Proc. Biol. Soc. Washington 37:55. 1924.

   b. *Chloracantha spinosa* (Benth.) Nesom var. *spinosa*

c. *Chloracantha spinosa* (Benth.) Nesom var. *spinosissima* (Brandeg.) S.D. Sundb., Phytologia 70:386. 1991. BASIONYM: *Aster spinosus* Benth. var. *spinosissimus* Brandeg., Univ. Calif. Publ. Bot. 6:375. 1917.

d. *Chloracantha spinosa* (Benth.) Nesom var. *strictospinosa* S.D. Sundb., Phytologia 70:389. 1991.

IV. *DOELLINGERIA* Nees, *Gen. Sp. Aster.* 177. 1832 [1833].

Type: *Doellingeria umbellata* (Mill.) Nees.

A. *Doellingeria* sect. *Doellingeria*

Aster subg. *Doellingeria* (Nees) A. Gray, *Synopt. Fl.* 1(2):196. 1884. *Aster* sect. *Doellingeria* (Nees) Kitam., J. Jap. Bot. 12:721. 1936.

Diplopappus sect. *Triplopappus* Torr. & Gray, *Fl. N. Amer.* 2:182. 1841. *Aster* subg. *Doellingeria* sect. *Triplopappus* (Torr. & Gray) A.G. Jones, Brittonia 32:237. 1980.

Type: *Aster umbellatus* Mill.

Aster ser. *Sohayakienses* Kitamura, J. Jap. Bot. 12:722. 1936.

Type: *Aster sohayakiensis* Koidzumi.

a. *Doellingeria* ser. *Doellingeria*

1. *Doellingeria infirma* (Michx.) E. Greene, Pittonia 3:52. 1896. BASIONYM: *Aster infirmus* Michx., *Fl. Bor.-Amer.* 2:109. 1803.

2. *Doellingeria sericocarpoides* Small, Bull. Torrey Bot. Club 25:620. 1898. *Aster sericocarpoides* (Small) K. Schum., Just. Bot. Jahresb. 26(1):375. 1900.

3. *Doellingeria umbellata* (Miller) Nees, *Gen. Sp. Aster.* 178. 1832. BASIONYM: *Aster umbellatus* Miller, *Gard. Dict.*, ed. 8, no. 22. 1768.

a. *Doellingeria umbellata* (Miller) Nees var. *umbellata*

b. *Doellingeria umbellata* (Miller) Nees var. *pubens* (A. Gray) Britton, *Britton & Br. Illus. Fl.* 3:392. 1898. BASIONYM: *Aster umbellatus* Miller var. *pubens* A. Gray, *Synopt. Fl.* 1(2):197. 1884.

4. *Doellingeria sohayakiensis* (Koidzumi) Nesom, Phytologia 75:456. 1993. BASIONYM: *Aster sohayakiensis* Koidzumi, Tokyo Bot. Mag. 37:56. 1923.

5. *Doellingeria rugulosa* (Maxim.) Nesom, Phytologia 75:456. 1993. BASIONYM: *Aster rugulosus* Maxim., *Mel. Biol.* 7:333. 1870.

B. *Doellingeria* sect. *Cordifolium* (Kitamura) Nesom, Phytologia 75:456. 1993. BASIONYM: *Kalimeris* sect. *Cordifolium* Kitam., Mem. Coll. Sci. Kyoto Univ., ser. B. 8:312. 1937.

Lectotype: *Biotia japonica* Miq.

Aster sect. *Teretiachaenium* Kitamura, Mem. Coll. Sci. Kyoto Univ., ser. B. 8:357. 1937.

Lectotype: *Aster scaber* Thunb.

b. *Doellingeria* ser. *Cordifolium* (Kitamura) Nesom, Phytologia 75:456. 1993. BASIONYM: *Kalimeris* sect. *Cordifolium* Kitam., Mem. Coll. Sci. Kyoto Univ., ser. B. 8:312. 1937.

Lectotype: *Doellingeria japonica* (Miq.) Nesom.

6. *Doellingeria japonica* (Miq.) Nesom, Phytologia 75:456. 1993. BASIONYM: *Biotia japonica* Miq., Ann. Mus. Bot. Lugduno-Batavum 2:170. 1866. *Aster japonicus* (Miq.) Franch. & Sav., *Enum. Pl. Japon.* 2:398. 1876. (not *Aster japonicus* Less. *ex* Nees 1832.). *Aster miquelianus* Hara [*nom. nov.*], J. Jap. Bot. 12:338. 1936.

7. *Doellingeria marchandii* (Levl.) Ling, *Icon. Cormorph. Sin.* 4:423. 1975. BASIONYM: *Aster marchandii* Levl., Fedde Repert. Sp. Nov. 11:306. 1912.

8. *Doellingeria longipetiolata* (Chang) Nesom, Phytologia 75:457. 1993. BASIONYM: *Aster longipetiolatus* Chang, Sunyatsenia 6:22. 1941.

c. *Doellingeria* ser. *Papposae* Nesom, Phytologia 75:457. 1993.

Type: *Doellingeria scabra* (Thunb.) Nees.

9. *Doellingeria scabra* (Thunb.) Nees, *Gen. Sp. Aster.* 183. 1832. BASIONYM: *Aster scaber* Thunb., *Fl. Jap.* 316. 1784.

10. *Doellingeria komonoensis* (Makino) Nesom, Phytologia 75:457. 1993. BASIONYM: *Aster komonoensis* Makino, Tokyo Bot. Mag. 12:65. 1898.

11. *Doellingeria dimorphophylla* (Franch. & Sav.) Nesom, Phytologia 75:457. 1993. BASIONYM: *Aster dimorphophyllus* Franch. & Sav., *Enum. Pl. Japon.* 1:224. 1875.

Excluded taxa:

Doellingeria obovata (Nutt.) Nees = *Oclemena reticulata* (Pursh) Nesom.

Doellingeria reticulata (Pursh) E. Greene = *Oclemena reticulata* (Pursh) Nesom.

V. *EUCEPHALUS* Nutt., Trans. Amer. Philos. Soc., ser. 2, 8:298. 1841. *Aster* [sect. *Orthomeris*] subsect. *Eucephalus* (Nutt.) Benth. *in* Benth. & Hook., *Gen. Pl.* 2:273. 1873. *Aster* sect. *Eucephalus* (Nutt.) Munz & Keck *ex* A.G. Jones, Brittonia 32:236. 1980.

Lectotype (Jones 1980a): *Eucephalus elegans* Nutt.

1. **Eucephalus breweri** (A. Gray) Nesom, *comb. nov.* BASIONYM: *Chrysopsis breweri* A. Gray, Proc. Amer. Acad. Arts 6:542. 1866. *Heterotheca breweri* (A. Gray) Shinners, Field & Lab. 29:71. 1951. *Aster breweri* (A. Gray) Semple, Syst. Bot. 13:545. 1988.

Chrysopsis wrightii A. Gray, *Synopt. Fl.* 1(2):445. 1884.

2. **Eucephalus brickellioides** (E. Greene) Nesom, *comb. nov.* BASIONYM: *Aster brickellioides* E. Greene, Pittonia 2:16. 1889.

3. *Eucephalus elegans* Nutt., Trans. Amer. Phil. Soc. 2, 7:298. 1840. *Aster elegans* (Nutt.) Torr. & Gray [*comb. illeg.*], *Fl. N. Amer.* 2:159. 1841. (not *Aster elegans* Willd. 1803.). *Aster perelegans* Nelson & Macbr. [*nom. nov.*], Bot. Gaz. (Crawfordsville) 56:477. 1913. *Eucephalus perelegans* (Nelson & Macbr.) Weber, Phytologia 51:374. 1982.

Eucephalus frigidus Gandoger, Bull. Soc. Bot. France 65:40. 1918.

Eucephalus scaber Gandoger, Bull. Soc. Bot. France 65:40. 1918.

4. *Eucephalus engelmannii* (D.C. Eat.) E. Greene, Pittonia 3:54. 1896. BASIONYM: *Aster elegans* (Nutt.) Torr. & Gray var. *engelmannii* D.C. Eat., *Bot. King Expl.* 144. 1871. *Aster engelmannii* (D.C. Eat.) A. Gray, *Synopt. Fl.* 1(2):199. 1884.

5. *Eucephalus glabratus* (E. Greene) E. Greene, Pittonia 3:56. 1896. *Aster glabratus* (E. Greene) S.F. Blake *ex* Peck, *Man. Higher Pl. Oregon* 726. 1941. BASIONYM: *Aster brickellioides* E. Greene var. *glabratus* E. Greene, Pittonia 2:17. 1889.

Aster siskiyouensis Nelson & Macbr., Bot. Gaz. (Crawfordsville) 56:477. 1913.

Eucephalus glandulosus Eastw., Proc. Calif. Acad. Sci., ser. 4, 20:157. 1931.

6. *Eucephalus glaucescens* (A. Gray) E. Greene, Pittonia 3:56. 1896. BASIONYM: *Aster engelmannii* (D.C. Eat.) A. Gray var. *glaucescens* A. Gray, *Synopt. Fl.* 1(2):200. 1884. *Aster glaucescens* (A. Gray) S.F. Blake, Rhodora 30:278. 1928.

Eucephalus glaucophyllus Piper, Contr. U.S. Natl. Herb. 11:570. 1906. *Aster glaucophyllus* (Piper) Frye & Rigg, *Northw. Fl.* 385. 1912.

Eucephalus serrulatus E. Greene, Pittonia 3:55. 1896. *Aster serrulatus* (E. Greene) Frye & Rigg, *Northw. Fl.* 385. 1912.

?*Eucephalus macounii* E. Greene, Pittonia 4:70. 1899.

7. *Eucephalus gormanii* Piper, Proc. Biol. Soc. Washington 29:101. 1916. *Aster gormanii* (Piper) S.F. Blake, Rhodora 30:278. 1928.

8. *Eucephalus ledophyllus* (A. Gray) E. Greene, Pittonia 3:55. 1896. BASIONYM: *Aster engelmannii* (D.C. Eat.) A. Gray var. *ledophyllus* A. Gray, Proc. Amer. Acad. Arts 8:388. 1872. *Aster ledophyllus* (A. Gray) A. Gray, Proc. Amer. Acad. Arts 16:98. 1880.

a. *Eucephalus ledophyllus* (A. Gray) E. Greene var. *ledophyllus*

b. **Eucephalus ledophyllus** (A. Gray) E. Greene var. **covillei** (E. Greene) Nesom, *comb. nov.* BASIONYM: *Eucephalus covillei* E. Greene, Pittonia 3:162. 1897. *Aster covillei* (E. Greene) S.F. Blake *ex* Peck, *Man. Higher Pl. Oregon* 725. 1941. *Aster ledophyllus* (A. Gray) A. Gray var. *covillei* (E. Greene) Cronq., *Vasc. Pl. Pacif. Northw.* 5:89. 1955.

9. *Eucephalus paucicapitatus* (B. Rob.) E. Greene, Pittonia 3:56. 1896. BASIONYM: *Aster engelmannii* (D.C. Eat.) A. Gray var. *paucicapitatus* B. Rob., Proc. Amer. Acad. Arts 26:176. 1891. *Aster paucicapitatus* (B. Rob.) B. Rob., Proc. Amer. Acad. Arts 29:329. 1894.

10. *Eucephalus tomentellus* (E. Greene) E. Greene, Pittonia 3:55. 1896. BASIONYM: *Sericocarpus tomentellus* E. Greene, Pittonia 1:283. 1889. *Aster tomentellus* (E. Greene) Frye & Rigg, *Northw. Fl.* 385. 1912. (not *Aster tomentellus* Hook. & Arn. 1833.).

Eucephalus bicolor Eastw., Proc. Calif. Acad. Sci., Ser. 4, 20:157. 1931.

11. *Eucephalus vialis* Bradshaw, Torreya 20:122. 1921. *Aster vialis* (Bradshaw) S.F. Blake, Rhodora 30:228. 1928.

Sericocarpus sipei Henderson, Madroño 2:105. 1933.

Excluded taxa:

Eucephalus ericoides (L.) Nutt. = *Symphyotrichum ericoides* (L.) Nesom.

Eucephalus nemoralis (Aiton) E. Greene = *Oclemena nemoralis* (Aiton) E. Greene.

Eucephalus wasatchensis (M.E. Jones) Rydb. = *Eurybia wasatchensis* (M.E. Jones) Nesom.

Eucephalus glaucus Nutt. = *Eurybia glauca* (Nutt.) Nesom.

Eucephalus formosus E. Greene = *Eurybia glauca* (Nutt.) Nesom.

VI. *EURYBIA* (Cass.) S.F. Gray, *Nat. Arrang. Brit. Pl.* 2:464. 1821. BASIONYM: *Aster* subg. *Eurybia* Cass., Bull. Sci. Soc. Philom. Paris 1818:166. 1818.

Lectotype (designated here, see discussion in text): *Aster corymbosus* Aiton (= *Aster divaricatus* L. = *Eurybia divaricata* [L.] Nesom).

1. *Eurybia* subg. *Eurybia*

A. *Eurybia* sect. *Eurybia*

Aster subg. *Biotia* DC. *ex* Torr. & Gray, *Fl. N. Amer.* 2:104. 1841. *Aster* sect. *Biotia* DC. *ex* Hoffmann *in* Engler & Prantl, *Natürl. Pflanzenf.* 4(5):162. 1890. *Aster* [subg. *Aster* sect. *Aster*] subsect. *Biotia* (DC. *ex* Torr. & Gray) Semple, Phytologia 58:429. 1984. Cited as *Aster* "sect. *Biotia*" by Jones 1980a, although she indicated in the same paper that this taxon (as published by Torrey & Gray) should be treated at the rank of subgenus (see comments at the beginning of Appendix II).

Biotia DC. [*nom. illeg.*], *Prodr.* 5:264. 1836. (not *Biotia* Cass. 1825; see Lamboy & Jones 1987b.).

Lectotype (Jones 1980a): *Aster schreberi* Nees.

INCL: *Eurybia chlorolepis* (Burgess) Nesom, *E. divaricata*, *E. furcata* (Burgess) Nesom, *E. jonesiae* (Lamboy) Nesom, *E. macrophylla* (L.) Cass., *E. mirabilis* (Torr. & Gray) Nesom, *E. schreberi* (Nees) Nees.

B. **Eurybia** sect. **Radulini** (Rydb.) Nesom, *comb. nov.* BASIONYM: *Aster* sp.-group *Radulini* Rydb., *Fl. Rocky Mts.* 879. 1917. *Aster* sect. *Radulini* (Rydb.) A.G. Jones, Brittonia 32:237. 1980.

Type: *Aster radulinus* A. Gray.

a. **Eurybia** subsect. **Radulini** (Rydb.) Nesom, *comb. nov.* BASIONYM: *Aster* sp.-group *Radulini* Rydb., *Fl. Rocky Mts.* 879. 1917.

Type: *Aster radulinus* A. Gray.

Weberaster Löve & Löve, Taxon 31:359. 1982.

Type: *Weberaster* (*Aster*) *radulinus* (A. Gray) Löve & Löve.

INCL: *Eurybia conspicua* (Lindl.) Nesom, *E. radula* (Aiton) Nesom, *E. radulina* (A. Gray) Nesom, *E. saxicastellii* (Campbell & Medley) Nesom.

b. **Eurybia** subsect. **Sibiricae** Nesom, *subsect. nov.*

Type: *Eurybia sibirica* (L.) Nesom.

Phyllariis herbaceis, capitulis in numero deminutis distinctae.

INCL: *Eurybia merita* (A. Nelson) Nesom, *E. pygmaea* (Lindl.) Nesom, *E. sibirica.*

C. **Eurybia** sect. **Integrifoliae** Nesom, *sect. nov.*

Type: *Eurybia integrifolia* (Nutt.) Nesom.

Foliis basalibus persistentibus oblanceolatis integribusque, capitulis in capitulescentia spicata plerumque dispositis distinctae.

INCL: *Eurybia integrifolia.*

D. **Eurybia** sect. **Calliastrum** (Torr. & Gray) Nesom, *comb. nov.* BASIONYM: *Aster* subg. *Calliastrum* Torr. & Gray, *Fl. N. Amer.* 2:106. 1841. *Aster* sect. *Calliastrum* (Torr. & Gray) Benth. *in* Benth. & Hook., *Gen. Pl.* 2:271. 1873.

Lectotype designated here: *Aster spectabilis* Aiton.

Aster sect. *Spectabiles* A. Gray, *Synopt. Fl.* 1(2):175. 1884.

Type: *Aster spectabilis* Aiton.

The group described by Gray in 1884 as sect. *Spectabiles* was essentially the same as he described as subg. *Calliastrum* in 1841, as noted by Gray himself. From sect. *Spectabiles*, he transferred *Aster paludosus* to subg. *Heleastrum*; to it, he added *A. radulinus* and *A. herveyi* A. Gray. To reflect the essential identity of these two groups, I have lectotypified sect. *Calliastrum* with the same species that stands as the type of sect. *Spectabiles*.

INCL: *Eurybia compacta* Nesom, *E. spectabilis* (Aiton) Nesom, *E. surculosa* (Michx.) Nesom.

E. **Eurybia** sect. **Herrickia** (Torr. & Gray) Nesom, *comb. et stat. nov.* BASIONYM: *Herrickia* Wooton & Standl., Contr. U.S. Natl. Herb. 16:186. 1913.

Type: *Herrickia horrida* Wooton & Standl. (= *Eurybia horrida* [Wooton & Standl.] Nesom).

INCL: *Eurybia glauca* (Nutt.) Nesom, *E. horrida*, *E. pulchra* (S.F. Blake) Nesom, *E. wasatchensis* (M.E. Jones) Nesom.

2. **Eurybia** subg. **Heleastrum** (DC.) Nesom, *comb. nov.* BASIONYM: *Heleastrum* DC., *Prodr.* 5:263. 1836. *Aster* subg. *Heleastrum* (DC.) A. Gray, Proc. Amer. Acad. Arts 16:97. 1880. [*Synopt. Fl.* 1(2):173. 1884.]. *Aster* [sect. *Calliastrum*] subsect. *Heleastrum* (DC.) Benth *in* Benth. & Hook., *Gen. Pl.* 2:271. 1873.

Lectotype (Jones 1980a): *Aster paludosus* Aiton.

F. **Eurybia** sect. **Heleastrum** (DC.) Nesom, *comb. et stat. nov.* BASIONYM: *Heleastrum* DC., *Prodr.* 5:263. 1836.

Lectotype (Jones 1980a): *Aster paludosus* Aiton.

Leiachenis Rafin., *Fl. Tellur.* 2:45. 1836 [1837].

Lectotype (designated here): *Aster paludosus* Aiton.

INCL: *Eurybia avita* (Alexander) Nesom, *E. hemispherica* (Alexander) Nesom, *E. paludosa* (Aiton) Nesom.

G. **Eurybia** sect. **Eryngiifolii** (Alexander) Nesom, *comb. nov.* BASIONYM: *Aster* sp.-group *Eryngiifolii* Alexander *in* Small, *Man. Southeast. Fl.* 1365. 1933. *Aster* [sect. *Heleastrum*] subsect. *Eryngiifolii* (Alexander) Semple, Phytologia 58:429. 1985.

Type: *Aster eryngiifolius* Torr. & Gray.

INCL: *Eurybia eryngiifolia* (Torr. & Gray) Nesom, *E. spinulosa* (Chapm.) Nesom.

H. **Eurybia** subg. **Heleastrum** sect. **Chapmaniani** (Semple) Nesom, *comb. nov.* BASIONYM: *Aster* [sect. *Heleastrum*] subsect. *Chapmaniani* Semple, Phytologia 58:429. 1985.

Type: *Aster chapmanii* Torr. & Gray.

INCL: *Eurybia chapmanii* (Torr. & Gray) Nesom.

Species of *Eurybia*:

1. **Eurybia avita** (Alexander) Nesom, *comb. nov.* BASIONYM: *Aster avitus* Alexander, Castanea 4:60: 1939.

2. **Eurybia chapmanii** (Torr. & Gray) Nesom, *nom. nov.* BASIONYM: *Aster chapmanii* Torr. & Gray, *Fl. N. Amer.* 2:161. 1841. *Heleastrum chapmanii* (Torr. & Gray) Shinners [*nom. illeg.*], Sida 3:348. 1969 (not *Heleastrum chapmanii* [Torr. & Gray] E. Greene 1896.).

3. **Eurybia chlorolepis** (Burgess) Nesom, *comb. nov.* BASIONYM: *Aster chlorolepis* Burgess *in* Small, *Fl. Southeast. U.S.* 1211, 1339. 1903.

4. **Eurybia compacta** Nesom, *nom. nov.* Based on: *Aster gracilis* Nutt., *Gen. N. Amer. Pl.* 2:158. 1818 (not *Eurybia gracilis* Benth. 1837.).

5. **Eurybia conspicua** (Lindl.) Nesom, *comb. nov.* BASIONYM: *Aster conspicuus* Lindl. *in* Hook., *Fl. Bor. Amer.* 2:7. 1834.

6. **Eurybia divaricata** (L.) Nesom, *comb. nov.* BASIONYM: *Aster divaricatus* L., *Sp. Pl.* 873. 1753.

   Aster corymbosus Sol. *ex* Aiton, *Hort. Kew.* 3:207. 1789. *Eurybia corymbosa* (Aiton) Cass., *Dict. Sci. Nat.* 37:487. 1825.

7. **Eurybia eryngiifolia** (Torr. & Gray) Nesom, *comb. nov.* BASIONYM: *Aster eryngiifolius* Torr. & Gray, *Fl. N. Amer.* 2:502. 1843.

   Prionopsis chapmanii Torr. & Gray, *Fl. N. Amer.* 2:245. 1842. *Heleastrum chapmanii* (Torr. & Gray) E. Greene, Pittonia 3:49. 1896.

8. **Eurybia furcata** (Burgess) Nesom, *comb. nov.* BASIONYM: *Aster furcatus* Burgess *in* Britton & Brown, *Illus. Fl.* 3:358. 1898.

9. **Eurybia glauca** (Nutt.) Nesom, *comb. nov.* BASIONYM: *Eucephalus glaucus* Nutt., Trans. Amer. Philos. Soc., ser. 2, 7:299. 1841. *Aster glaucus* (Nutt.) Torr. & Gray [*nom. illeg.*], *Fl. N. Amer.* 2:159. 1841. (not Nees 1818.). *Aster glaucodes* S.F. Blake [*nom. nov.*], Proc. Biol. Soc. Washington 35:174. 1922.

   Eucephalus formosus E. Greene, Pittonia 4:156. 1900. *Aster glaucodes* S.F. Blake var. *formosus* (E. Greene) Kittell *in* Tidestrom & Kittell, *Fl. Ariz. & New Mexico* 404. 1941.

10. **Eurybia hemispherica** (Alexander) Nesom, *comb. nov.* BASIONYM: *Aster hemisphericus* Alexander *in* Small, *Man. Southeast. Fl.* 1391, 1509. 1933. *Heleastrum hemisphericum* (Alexander) Shinners, Field & Lab. 17:170. 1949. *Aster paludosus* Sol. *ex* Aiton subsp. *hemisphericus* (Alexander) Cronq., Bull. Torrey Bot. Club 74:145. 1947. *Aster paludosus* Sol. *ex* Aiton var. *hemisphericus* (Alexander) Waterf., Rhodora 62:320. 1960.

   Aster pedionomus Alexander *in* Small, *Man. Southeast. Fl.* 1391, 1509. 1933.

   Aster gattingeri Alexander *in* Small, *Man. Southeast. Fl.* 1391, 1509. 1933.

   Aster verutifolius Alexander *in* Small, *Man. Southeast. Fl.* 1392, 1509. 1933.

11. **Eurybia horrida** (Wooton & Standl.) Nesom, *comb. nov.* BASIONYM: *Herrickia horrida* Wooton & Standl., Contr. U.S. Natl. Herb. 16:186. 1913. *Aster horridus* (Wooton & Standl.) S.F. Blake, J. Washington Acad. Sci. 27:379. 1937.

12. **Eurybia integrifolia** (Nutt.) Nesom, *comb. nov.* BASIONYM: *Aster integrifolius* Nutt., Proc. Amer. Philos. Soc., ser. 2, 7:291. 1840.

13. **Eurybia jonesiae** (Lamboy) Nesom, *comb. nov.* BASIONYM: *Aster jonesiae* Lamboy, Syst. Bot. 13:192. 1988.

14. *Eurybia macrophylla* (L.) Cass., *Dict. Sci. Nat.* 37:487. 1825. BASIONYM: *Aster macrophyllus* L., *Sp. Pl.*, (ed. 2) 2:1232. 1763.

   Eurybia jussiei Cass., *Dict. Sci. Nat.* 37:487. 1825. (see Lamboy & Jones 1987a.).

15. **Eurybia merita** (A. Nelson) Nesom, *comb. nov.* BASIONYM: *Aster meritus* A. Nelson, Bot. Gaz. (Crawfordsville) 37:268. 1904. *Aster richardsonii* Spreng. var. *meritus* (A. Nelson) Raup, Contr. Arnold Arb.

6:204. 1934. *Aster sibiricus* L. var. *meritus* (A. Nelson) Raup, Sargentia 6:240. 1947.

16. **Eurybia mirabilis** (Torr. & Gray) Nesom, *comb. nov.* BASIONYM: *Aster mirabilis* Torr. & Gray, *Fl. N. Amer.* 2:165. 1841.

17. **Eurybia paludosa** (Aiton) Nesom, *comb. nov.* BASIONYM: *Aster paludosus* Sol. *ex* Aiton, *Hort. Kew.* 3:201. 1789. *Heleastrum paludosum* (Aiton) DC., *Prodr.* 5:264. 1836.

18. **Eurybia pulchra** (S.F. Blake) Nesom, *comb. et stat. nov.* BASIONYM: *Aster glaucodes* S.F. Blake subsp. *pulcher* S.F. Blake, Proc. Biol. Soc. Washington 35:174. 1922.

19. **Eurybia pygmaea** (Lindl.) Nesom, *comb. nov.* BASIONYM: *Aster pygmaeus* Lindl. *in* Hook., *Fl. Bor.-Amer.* 2:6. 1834. *Aster sibiricus* L. var. *pygmaeus* (Lindl.) Cody, Canad. Field-Nat. 68:117. 1954. *Aster sibiricus* L. subsp. *pygmaeus* (Lindl.) Löve & Löve, Bot. Notiser 128:521. 1975.

20. **Eurybia radula** (Aiton) Nesom, *comb. nov.* BASIONYM: *Aster radula* Sol. *ex* Aiton, *Hort. Kew.* 3:210. 1789.

21. **Eurybia radulina** (A. Gray) Nesom, *comb. nov.* BASIONYM: *Aster radulinus* A. Gray, Proc. Amer. Acad. Arts 8:388. 1872. *Weberaster radulinus* (A. Gray) Löve & Löve, Taxon 31:359. 1982.

22. **Eurybia saxicastellii** (Campbell & Medley) Nesom, *comb. nov.* BASIONYM: *Aster saxicastellii* Campbell & Medley, Sida 13:277. 1989.

23. *Eurybia schreberi* (Nees) Nees, *Gen. Sp. Aster.* 137. 1832. BASIONYM: *Aster schreberi* Nees, *Synops. Ast. Herb.* 16. 1818.

    Aster glomeratus Bernh. *in* Nees [*pro syn.*], *Gen. Sp. Aster.* 139. 1832. *Eurybia glomerata* (Bernh.) Nees, *Gen. Sp. Aster.* 139. 1832.

24. **Eurybia sibirica** (L.) Nesom, *comb. nov.* BASIONYM: *Aster sibiricus* L., *Sp. Pl.*, (ed. 2) 872. 1753.

    a. *Eurybia sibirica* (L.) Nesom var. *sibirica*

    b. **Eurybia sibirica** (L.) Nesom var. **gigantea** (Spreng.) Nesom, *comb. nov.* BASIONYM: *Aster richardsonii* Spreng. var. *giganteus* Hook., *Fl. Bor.-Amer.* 2:7. 1834. *Aster sibiricus* L. var. *giganteus* (Hook.) A. Gray, *Synopt. Fl.* 1(2):177. 1884.

Aster richardsonii Spreng., *Syst. Veg.* 3:258. 1826. *Aster sibiricus* L. subsp. *richardsonii* (Spreng.) Löve & Löve, Bot. Notiser 128:521. 1975.

Aster behringensis Gandoger, Bull. Soc. Bot. France 65:38. 1918.

c. **Eurybia sibirica** (L.) Nesom var. **subintegerrima** (Trautv.) Nesom, *comb. nov.* BASIONYM: *Aster subintegerrimus* Trautv. *in* Middendorf, *Reise* 1:161. 1847. *Aster sibiricus* L. subsp. *subintegerrimus* (Trautv.) Löve & Löve, Bot. Notiser 128:521. 1975.

25. **Eurybia spectabilis** (Aiton) Nesom, *comb. nov.* BASIONYM: *Aster spectabilis* Sol. *ex* Aiton, *Hort. Kew.* 3:209. 1789.

Eurybia commixta Nees, *Gen. Sp. Aster.* 142. 1832 [1833]. *Aster commixtus* (Nees) O. Kuntze, *Rev. Gen. Pl.* 2:315. 1891.

26. **Eurybia spinulosa** (Chapm.) Nesom, *comb. nov.* BASIONYM: *Aster spinulosus* Chapm., *Fl. Southern U.S.* 199. 1860. *Heleastrum spinulosum* (Chapm.) E. Greene, Pittonia 3:50. 1896.

27. **Eurybia surculosa** (Michx.) Nesom, *comb. nov.* BASIONYM: *Aster surculosus* Michx., *Fl. Bor.-Amer.* 2:112. 1803.

28. **Eurybia wasatchensis** (M.E. Jones) Nesom, *comb. nov.* BASIONYM: *Aster glaucus* (Nutt.) Torr. & Gray var. *wasatchensis* M.E. Jones, Proc. Calif. Acad. Sci., ser. 2, 5:694. 1895. *Eucephalus wasatchensis* (M.E. Jones) Rydb., *Fl. Rocky Mts.* 878, 1067. 1917. *Aster wasatchensis* (M.E. Jones) S.F. Blake, Contr. U.S. Natl. Herb. 25:557. 1925.

Hybrid:

Eurybia × herveyi (A. Gray) Nesom, *comb. nov.* BASIONYM: *Aster herveyi* A. Gray [*pro sp.*], *Manual*, (ed. 5) 229. 1867. [*E. macrophylla* × *E. spectabilis*; Uttal 1962.].

Excluded taxa:

Biotia spp. from Asia (= *Aster* s. str. and *Doellingeria*).

Heleastrum album (Nutt.) DC. = *Oligoneuron album* (Nutt.) Nesom.

VII. *IONACTIS* E. Greene, Pittonia 3:245. 1897.

Type: *Ionactis linariifolia* (L.) E. Greene.

Diplopappus Cass. subg. *Ianthe* Torr. & Gray, *Fl. N. Amer.* 2:181. 1841. *Aster* subg. *Ianthe* (Torr. & Gray) A. Gray, *Synopt. Fl.* 1(2):197. 1884.

Type: *Ionactis linariifolia* (L.) E. Greene.

1. *Ionactis alpina* (Nutt.) E. Greene, Pittonia 3:245. 1897. BASIONYM: *Chrysopsis alpina* Nutt., J. Acad. Philad. 7:34. 1834. *Aster scopulorum* A. Gray [*nom. nov.*], Proc. Amer. Acad. Arts 16:98. 1880. (not *Aster alpinus* L. 1753.).

2. *Ionactis elegans* (Soreng & Spellenb.) Nesom, Phytologia 73:420. 1992. BASIONYM: *Chaetopappa elegans* Soreng & Spellenb., Syst. Bot. 9:1. 1984.

3. *Ionactis caelestis* Leary & Nesom, Brittonia 44:247. 1992.

4. *Ionactis linariifolia* (L.) E. Greene, Pittonia 3:245. 1897. BASIONYM: *Aster linariifolius* L., *Sp. Pl.*, (ed. 2) 874. 1753.

   Aster linariifolius L. var. *victorinii* Fernald, Rhodora 16:194. 1914.

5. *Ionactis stenomeres* (A. Gray) E. Greene, Pittonia 3:246. 1897. BASIONYM: *Aster stenomeres* A. Gray, Proc. Amer. Acad. Arts 17:209. 1882.

VIII. *OCLEMENA* E. Greene, Leafl. Bot. Observ. Crit. 1:4. 1903.

Type: *Aster acuminatus* Michx.

Aster subg. *Orthomeris* Torr. & Gray, *Fl. N. Amer.* 2:156. 1841. (*pro parte*). *Aster* sect. *Orthomeris* (Torr. & Gray) Benth. *in* Benth. & Hook., *Gen. Pl.* 2:273. 1873. *Aster* ser. *Orthomeris* (Torr. & Gray) Kitam., J. Jap. Bot. 12:533. 1936.

Lectotype (designated here): *Aster acuminatus* Michx. (see explanatory comments in text).

Galatella sect. *Calianthus* Nutt., Trans. Amer. Philos. Soc., ser. 2, 7:303. 1840.

Type: *Aster nemoralis* Aiton.

Aster [subg. *Orthomeris*] sect. *Nemorali* House, New York State Mus. Bull. 254:710. 1924.

Type: *Aster nemoralis* Aiton.

Aster [subg. *Doellingeria*] sect. *Acuminati* (Alexander) A.G. Jones, Brittonia 32:237. 1980. *Aster* sp.-group *Acuminati* Alexander *in* Small, *Man. Southeast. Fl.* 1365. 1933.

Type: *Aster acuminatus* Michx.

1. *Oclemena acuminata* (Michx.) E. Greene, Leafl. Bot. Observ. Crit. 1:4. 1903. BASIONYM: *Aster acuminatus* Michx., *Fl. Bor.-Amer.* 2:109. 1803.

   Aster acuminatus Michx. var. *magdalenensis* Fernald, Rhodora 51:101. 1949.

2. *Oclemena nemoralis* (Aiton) E. Greene, Leafl. Bot. Observ. Crit. 1:5. 1903. BASIONYM: *Aster nemoralis* Sol. *ex* Aiton, *Hort. Kew.* 3:198. 1789. *Galatella nemoralis* (Aiton) Nees, *Gen. Sp. Ast.* 173. 1832. *Eucephalus nemoralis* (Aiton) E. Greene, Pittonia 3:57. 1896.

   Aster nemoralis Sol. *ex* Aiton forma *albiflora* Fernald, Rhodora 51:99. 1949.

3. **Oclemena reticulata** (Pursh) Nesom, *comb. nov.* BASIONYM: *Aster reticulatus* Pursh, *Fl. Amer. Sept.* 2:458. 1814. *Doellingeria reticulata* (Pursh) E. Greene, Pittonia 3:50. 1896.

   Inula obovata Nutt., *Gen. N. Amer.* 2:152. 1818. *Doellingeria obovata* (Nutt.) Nees, *Gen. Sp. Aster.* 182. 1832. *Diplopappus obovatus* (Nutt.) Torr. & Gray, *Fl. N. Amer.* 2:184. 1841.

   Aster dichotomus Ell., *Sketch* 2:366. 1824.

Hybrid:

Oclemena × blakei (Porter) Nesom, *comb. nov.* BASIONYM: *Aster nemoralis* Sol. *ex* Aiton var. *blakei* Porter, Bull. Torrey Bot. Club 21:311. 1894. *Aster blakei* (Porter) House [*pro sp.*], N.Y. State Museum Bull. 219-220:244. 1920. [*Oclemena nemoralis* × *O. acuminata*].

Aster nemoralis Sol. *ex* Aiton var. *major* Peck, N.Y. State Museum Rep. 47:115. 1894.

IX. *OREOSTEMMA* E. Greene [*nom. nov.*], Pittonia 4:224. 1900. Based on *Oreastrum* E. Greene, Pittonia 3:146. 1896 (not *Oriastrum* Poeppig 1843). *Aster* subg. *Oreostemma* (E. Greene) Peck, *Man. Higher Pl. Oregon* 719. 1941.

Type: *Oreostemma alpigenum* (Torr. & Gray) E. Greene.

1. *Oreostemma alpigenum* (Torr. & Gray) E. Greene, Pittonia 4:224. 1900. BASIONYM: *Haplopappus alpigenus* Torr. & Gray, *Fl. N. Amer.* 2:241. 1842. *Aster alpigenus* (Torr. & Gray) A. Gray, Proc. Amer. Acad. Arts 8:389. 1872. *Oreastrum alpigenum* (Torr. & Gray) E. Greene, Pittonia 3:147. 1896.

   a. *Oreostemma alpigenum* (Torr. & Gray) E. Greene var. *alpigenum*

   b. *Oreostemma alpigenum* (Torr. & Gray) E. Greene var. *andersonii* (A. Gray) Nesom, Phytologia 74:312. 1993. BASIONYM: *Erigeron andersonii* A. Gray, Proc. Amer. Acad. Arts 6:540. 1865. *Aster andersonii* (A. Gray) A. Gray, Proc. Amer. Acad. Arts 7:352. 1868. *Oreastrum andersonii* (A. Gray) E. Greene, Pittonia 3:147. 1896. *Oreostemma andersonii* (A. Gray) E. Greene, Pittonia 4:224. 1900. *Aster alpigenus* (Torr. & Gray) A. Gray subsp. *andersonii* (A. Gray) Onno, Bibl. Bot. 26 (Heft 106):15. 1932. *Aster alpigenus* (Torr. & Gray) A. Gray var. *andersonii* (A. Gray) Peck, *Man. Higher Pl. Oregon* 721. 1941.

   c. *Oreostemma alpigenum* (Torr. & Gray) E. Greene var. *haydenii* (T.C. Porter) Nesom, Phytologia 74:313. 1993. BASIONYM: *Aster haydenii* T.C. Porter, *Cat. Pl.* 485 *in* Hayden, *Prelim. Rep. U.S. Geol. Surv. Montana.* 1872. *Oreastrum haydenii* (T.C. Porter) Rydb., Mem. New York Bot. Gard. 1:398. 1900. *Oreostemma haydenii* (T.C. Porter) E. Greene, Pittonia 4:224. 1900. *Aster alpigenus* (Torr. & Gray) A. Gray subsp. *haydenii* (T.C. Porter) Cronq., Leafl. West Bot. 5:77. 1948. *Aster alpigenus* (Torr. & Gray) A. Gray var. *haydenii* (T.C. Porter) Cronq., *Vasc. Pl. Pacific Northw.* 5:76. 1955.

2. *Oreostemma elatum* (E. Greene) E. Greene, Pittonia 4:224. 1900. BASIONYM: *Oreastrum elatum* E. Greene, Pittonia 3:147. 1896. *Aster elatus* (E. Greene) Cronq., Leafl. West. Bot. 5:80. 1948.

3. *Oreostemma peirsonii* (C.W. Sharsmith) Nesom, Phytologia 74:314. 1993. BASIONYM: *Aster peirsonii* C.W. Sharsmith, Leafl. West. Bot. 5:50. 1947.

X. *PSILACTIS* A. Gray, Mem. Amer. Acad. Arts, ser. 2, 4:71. 1849. *Machaeranthera* sect. *Psilactis* (A. Gray) Turner & Horne, Brittonia 16:321. 1964.

Type: *Psilactis asteroides* A. Gray.

1. *Psilactis asteroides* A. Gray, Mem. Amer. Acad. Arts, ser. 2, 4:72. 1849. (not *Aster asteroides* [DC.] Kuntze 1891.; not *Aster asteroides* [Colla] Rusby 1893.). *Aster boltoniae* E. Greene, Pittonia 3:248. 1897. *Machaeranthera boltoniae* (E. Greene) Turner & Horne, Brittonia 16:330. 1964. (not *Machaeranthera asteroides* [Torr.] E. Greene 1892.).

2. *Psilactis brevilingulata* Sch.-Bip. *ex* Hemsley, *Diagn. Pl. Nov. Mexic.* 2:34. 1879. *Machaeranthera brevilingulata* (Sch.-Bip. *ex* Hemsley) Turner & Horne, Brittonia 16:324. 1964. *Aster brevilingulatus* (Sch.-Bip. *ex* Hemsley) McVaugh, Contr. Univ. Michigan Herb. 9:362. 1972.

3. *Psilactis gentryi* (Standley) Morgan, Syst. Bot. 18:302. 1993. BASIONYM: *Aster gentryi* Standley, Field Mus. Natl. Hist., Bot. Ser. 22:60. 1940. *Machaeranthera gentryi* (Standley) R.C. Jackson *ex* B.L. Turner, Phytologia 25:57. 1972.

   Machaeranthera mexicana Turner & Horne, Brittonia 16:329. 1964.

4. *Psilactis heterocarpa* (Hartman & Lane) Morgan, Syst. Bot. 18:301. 1993. BASIONYM: *Machaeranthera heterocarpa* Hartman & Lane, Brittonia 39:253. 1987.

5. *Psilactis odysseus* (Nesom) Morgan, Syst. Bot. 18:298. 1993. BASIONYM: *Machaeranthera odysseus* Nesom, Syst. Bot. 218. 1978.

6. *Psilactis tenuis* S. Wats., Proc. Amer. Acad. Arts 26:139. 1891. *Machaeranthera tenuis* (S. Wats.) Turner & Horne, Brittonia 16:330. 1964.

XI. *SERICOCARPUS* Nees, *Gen. Sp. Aster.* 148. 1832 [1833]. *Aster* subg. *Sericocarpus* (Nees) A.G. Jones, Brittonia 32:238. 1980. *Aster* sect. *Sericocarpus* (Nees) Semple, Phytologia 58:429. 1985.

Type: *Sericocarpus solidagineus* (Michx.) Nees = *Sericocarpus linifolius* (L.) B.S.P.

1. *Sericocarpus asteroides* (L.) B.S.P., *Prelim. Cat. N.Y. Pl.* 26. 1888. BASIONYM: *Conyza asteroides* L., *Sp. Pl.* 2:861. 1753. *Aster paternus* Cronq. [*nom. nov.*], Bull. Torrey Bot. Club 74:149. 1947. *Aster asteroides* MacMillan [*nom. nov. illeg.*] 1892. (not *Aster asteroides* [DC.] Kuntze 1891.; not *Aster asteroides* [Colla] Rusby 1893.). Cronquist's new name (*Aster paternus*) is the correct one if this species is treated within *Aster*, in contrast to an earlier suggestion of mine (Nesom 1993b.).

2. *Sericocarpus linifolius* (L.) B.S.P., *Prelim. 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. (not *Aster linifolius* L. 1753.). *Sericocarpus solidagineus* (Michx.) Nees, *Gen. Sp. Aster.* 149. 1832.

3. *Sericocarpus oregonensis* Nutt., Trans. Amer. Philos. Soc., ser. 2, 7:302. 1841. *Aster oregonensis* (Nutt.) Cronq., *Vasc. Pl. Pacif. Northw.* 5:80. 1955.

   a. *Sericocarpus oregonensis* Nutt. var. *oregonensis*

   b. *Sericocarpus oregonensis* Nutt. var. *californicus* (Durand) Nesom, Phytologia 75:51. 1993. BASIONYM: *Sericocarpus californicus* Durand, J. Acad. Nat. Sci. Philad., ser. 2, 3:90. 1855. *Sericocarpus oregonensis* Nutt. var. *californicus* (Durand) Ferris, Contr. Dudley Herb. 5:100. 1958.

4. *Sericocarpus rigidus* Lindl. *in* Hook., *Fl. Bor.-Amer.* 2:14. 1834. *Aster curtus* Cronq. [*nom. nov.*], *Vasc. Pl. Pacif. Northw.* 5:80. 1955. (not *Aster rigidus* L. 1753.).

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

Excluded taxa:

Sericocarpus sipei Henderson = *Eucephalus vialis* Bradshaw.

Sericocarpus tomentellus E. Greene = *Eucephalus tomentellus* (E. Greene) E. Greene.

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

XII. *SYMPHYOTRICHUM* Nees, *Gen. Sp. Aster.* 135. 1832 [1833]. *Aster* subg. *Symphyotrichum* (Nees) A.G. Jones, Brittonia 32:234. 1980.

Type: *Symphyotrichum unctuosum* Nees (= *Aster novi-belgii* L.).

1. *Symphyotrichum* subg. *Symphyotrichum*

A. *Symphyotrichum* sect. *Symphyotrichum*

Aster sect. *Salicifolii* Torr. & Gray, *Fl. N. Amer.* 2:134. 1841.

Type: *Aster salicifolius* Lam. (= *Aster puniceus* L.).

Aster [sect. *Homophylli*] subsect. *Vulgares* A. Gray, *Synopt. Fl.* 1(2):187. 1884.

Lectotype (designated here): *Aster novi-belgii* L.

INCL: *Symphyotrichum anticostense* (Fernald) Nesom, *S. crenifolium* (Fernald) Nesom, *S. elliottii* (Torr. & Gray) Nesom, *S. firmum* (Nees) Nesom, *S. longifolium* (Lam.) Nesom, *S. novi-belgii* (L.) Nesom, *S. prenanthoides* (Muhl. *ex* Willd.) Nesom, *S. puniceum* (L.) Löve & Löve, *S. subgeminatum* (Fernald) Nesom.

B. **Symphyotrichum** sect. **Cordifolii** (G. Don) Nesom, *comb. nov.* BASIONYM: *Aster* sect. *Cordifolii* G. Don *in* Loudon, *Hort. Brit.* 347. 1830.

Type: *Aster cordifolius* L. (= *Aster heterophyllus* Willd.).

Aster [sect. *Genuini* Nees] B *Heterophylli* Nees, *Gen. Sp. Aster.* 52. 1832. *Aster* sect. *Heterophylli* (Nees) A. Gray, *Synopt. Fl.* 1(2):181. 1884. *Aster* [subg. *Aster* sect. *Dumosi*] subsect. *Heterophylli* (Nees) Semple, Phytologia 58:429. 1985.

Type: *Aster cordifolius* L. (= *Aster heterophyllus* Willd.).

INCL: *Symphyotrichum anomalum* (Engelm.) Nesom, *S. ciliolatum* (Lindl.) Löve & Löve, *S. cordifolium* (L.) Nesom, *S. drummondii* (Lindl.) Nesom, *S. lowrieanum* (Porter) Nesom, *S. sagittifolium* (Wedem. *ex* Willd.) Nesom, *S. shortii* (Lindl.) Nesom, *S. undulatum* (L.) Nesom, *S. urophyllum* (DC.) Nesom.

C. **Symphyotrichum** sect. **Concinni** (Nees) Nesom, *comb. nov.* BASIONYM: *Aster* [sect. *Genuini* B *Homophylli*] sp.-group *Concinni* Nees, *Gen. Sp. Aster.* 118. 1832. *Aster* sect. *Concinni* (Nees) Torr. & Gray, *Fl. N. Amer.* 2:115. 1841.

Type: *Aster concinnus* Willd. (= *Aster laevis* L.).

a. **Symphyotrichum** subsect. **Laeves** (A. Gray) Nesom, *comb. nov.* BASIONYM: *Aster* [sect. *Homophylli*] subsect. *Laeves* A. Gray, *Synopt. Fl.* 1(2):183. 1884.

Type: *Aster laevis* L.

Aster [sect. *Genuini* B *Homophylli*] sp.-group *Concinni* Nees, *Gen. Sp. Aster.* 118. 1832.

Type: *Aster concinnus* Willd. (= *Aster laevis* L.).

INCL: *Symphyotrichum laeve* (L.) Löve & Löve, *S. oolentangiense* (Riddell) Nesom, *S. retroflexum* (DC.) Nesom.

b. **Symphyotrichum** subsect. **Turbinelli** (Rydb.) Nesom, *comb. nov.* BASIONYM: *Aster* sp.-group *Turbinelli* Rydb., *Fl. Prairies & Plains* 803. 1932. *Aster* [sect. *Eucephalus*] subsect. *Turbinelli* (Rydb.) A.G. Jones, Brittonia 32:237. 1980. *Aster* subg. *Symphyotrichum* sect. *Turbinelli* (Rydb.) A.G. Jones, Illinois Nat. Hist. Survey Bull. 34:144. 1989.

Type: *Aster turbinellus* Lindl.

INCL: *Symphyotrichum turbinellum* (Lindl.) Nesom.

D. **Symphyotrichum** sect. **Dumosi** (Torr. & Gray) Nesom, *comb. nov.* BASIONYM: *Aster* sect. *Dumosi* Torr. & Gray, *Fl. N. Amer.* 2:127. 1841.

Type: *Aster dumosus* L.

a. **Symphyotrichum** subsect. **Dumosi** (Torr. & Gray) Nesom, *comb. nov.* BASIONYM: *Aster* sect. *Dumosi* Torr. & Gray, *Fl. N. Amer.* 2:127. 1841.

Type: *Aster dumosus* L.

INCL: *Symphyotrichum dumosum* (L.) Nesom, *S. simmondsii* (Small) Nesom.

b. **Symphyotrichum** subsect. **Divergentes** (A. Gray) Nesom, *comb. nov.* BASIONYM: *Aster* [sect. *Homophylli*] subsect. *Divergentes* A. Gray, *Synopt. Fl.* 1(2):185. 1884.

Type: *Aster lateriflorus* (L.) Britton (= *Aster divergens* Aiton).

Aster [sect. *Genuini*] B *Homophylli* Nees, *Gen. Sp. Aster.* 52. 1832. *Aster* sect. *Homophylli* (Nees) A. Gray, *Synopt. Fl.* 1(2):183. 1884.

Lectotype (designated here): *Aster diffusus* Aiton (= *Aster divergens* Aiton = *Aster lateriflorus* [L.] Britton).

Nees's "Homophylli" group comprised 64 species that are dispersed through a number of sections in the current treatment. The selection of a lectotype is arbitrary, intended to be taxonomically non-intrusive.

Aster subsect. *Leucanthi* (Nees) A.G. Jones, Brittonia 32:235. 1980.

Lectotype (Jones 1980a.): *Aster simplex* Willd. (= *Aster lanceolatus* Willd.).

INCL: *Symphyotrichum boreale* (Torr. & Gray) Löve & Löve, *S. bullatum* (Klatt) Nesom, *S. burgessii*(Britton) Nesom, *S. carnerosanum* (S. Wats.) Nesom, *S. eulae* (Shinners) Nesom, *S. fontinale* (Alexander) Nesom, *S. lanceolatum* (Willd.) Nesom, *S. lateriflorum* (L.) Löve & Löve, *S. leone* (Britton) Nesom, *S. ontarione* (Wieg.) Nesom, *S. praealtum* (Poir.) Nesom, *S. racemosum* (Elliott) Nesom, *S. schaffneri* (S.D. Sundb. & A.G Jones) Nesom, *S. tradescantii* (L.) Nesom.

c. **Symphyotrichum** subsect. **Porteriani** (Rydb.) Nesom, *comb. nov.* BASIONYM: *Aster* sp.-group *Porteriani* Rydb., *Fl. Colorado* 352. 1906. *Aster* sect. *Porteriani* (Rydb.) A.G. Jones, Brittonia 32:235. 1980. *Aster* [subg. *Aster* sect. *Dumosi*] subsect. *Porteriani* (Rydb.) Semple, Phytologia 58:429. 1985.

Type: *Aster porteri* A. Gray.

INCL: *Symphyotrichum depauperatum* (Fernald) Nesom, *S. parviceps* (Burgess) Nesom, *S. pilosum* (Willd.) Nesom, *S. porteri* (A. Gray) Nesom, *S. priceae* (Britton) Nesom.

E. **Symphyotrichum** sect. **Oxytripolium** (DC.) Nesom, *comb. nov.* BASIONYM: *Tripolium* sect. *Oxytripolium* DC., *Prodr.* 5:253. 1836 (*pro parte*). *Aster* subg. *Oxytripolium* (DC.) Torr. & Gray, *Fl. N. Amer.* 2:161. 1841.

Lectotype (Jones 1980a): *Aster tenuifolius* L.

Gray (1880, 1884) referred the perennial species of sect. *Oxytripolium* (*Aster tenuifolius* L., specifically) to subg. *Orthomeris*; in the same treatment, however, he formally maintained subg. *Oxytripolium* to include the annual species (i.e., *A. subulatus*).

Tripolium subg. *Astropolium* Nutt., Trans. Amer. Philos. Soc., ser. 2, 7:295. 1840.

Lectotype (following Sundberg 1986): *Aster tenuifolius* L.

Aster sect. *Heterastrum* Benth. *in* Benth. & Hook., *Gen. Pl.* 2:273. 1873.

Lectotype (designated here): *Aster vahlii* Gaud.

Fimbristima Rafin., *Fl. Tellur.* 2:46. 1836. [1837.].

Lectotype (designated here): *Fimbristima squamata* (Spreng.) Rafin. (= *Aster squamatus* [Spreng.] Hieron.).

Mesoligus Rafin., *Fl. Tellur.* 2:44. 1836. [1837.].

Type: *Mesoligus subulatus* (Michx.) Rafin. (= *Aster subulatus* Michx.).

Conyzanthus Tamamsch., *Fl. U.R.S.S.* 24:583. 1959.

Type: *Conyzanthus squamatus* (Spreng.) Tamamsch. (= *Aster squamatus* [Spreng.] Hieron.).

INCL: *Symphyotrichum bahamense* (Britton) Nesom, *S. bracei* (Britton *ex* Small) Nesom, *S. divaricatum* (Nutt.) Nesom, *S. expansum* (Poepp. *ex* Spreng.) Nesom, *S. glabrifolium* (DC.) Nesom, *S. graminifolium* (Spreng.) Nesom, *S. martii* (Cabrera) Nesom, *S. patagonicum* (Cabrera) Nesom, *S. peteroanum* (Phil.) Nesom, *S. potosinum* (A. Gray) Nesom, *S. regnellii* (Baker) Nesom, *S. squamatum* (Spreng.) Nesom, *S. subulatum* (Michx.) Nesom, *S. tenuifolium* (L.) Nesom, *S. vahlii* (Gaud.) Nesom.

F. **Symphyotrichum** sect. **Conyzopsis** (Torr. & Gray) Nesom, *comb. nov.* BASIONYM: *Aster* [subg. *Oxytripolium*] sect. *Conyzopsis* Torr. & Gray, *Fl. N. Amer.* 2:162. 1841. *Aster* subg. *Conyzopsis* (Torr. & Gray) A. Gray, Proc. Amer. Acad. Arts 16:99. 1880.

Lectotype species (Jones 1980a): *Aster brachyactis* S.F. Blake (= *Symphyotrichum ciliatum* [Ledeb.] Nesom).

Brachyactis Ledeb., *Fl. Ross.* 2:495. 1845.

Type: *Brachyactis ciliata* (Ledeb.) Ledeb.

INCL: *Symphyotrichum ciliatum* (Ledeb.) Nesom, *S. frondosum* (Nutt.) Nesom, *S. laurentianum* (Fernald) Nesom.

G. **Symphyotrichum** sect. **Occidentales** (Rydb.) Nesom, *comb. nov.* BASIONYM: *Aster* sp.-group *Occidentales* Rydb., *Fl. Colorado* 352. 1906. *Aster* sect. *Occidentales* (Rydb.) A.G. Jones, Brittonia 32:235. 1980. *Aster* subsect. *Occidentales* (Rydb.) A.G. Jones, Phytologia 55:381. 1984.

Type: *Aster occidentalis* (Nutt.) Torr. & Gray (= *A. spathulatus* Lindl.).

Aster sp.-group *Foliacei* Rydb., *Fl. Colorado* 352. 1906. *Aster* subsect. *Foliacei* (Rydb.) A.G. Jones, Brittonia 32:235. 1980.

Type: *Aster foliaceus* Lindl. *ex* DC.

Aster sp.-group *Foliosi* Rydb., *Fl. Rocky Mts.* 882. 1922. *Aster* [sect. *Alpigeni* subsect. *Homochaeta* ser. *Macrochaeti*] subser. *Foliosi* (Rydb.) Onno, Bibliot. Bot. 106:7. 1932.

Type: *Aster foliaceus* Lindl. *ex* DC.

INCL: *Symphyotrichum bracteolatum* (Nutt.) Nesom, *S. chilense* (Nees) Nesom, *S. cusickii* (A. Gray) Nesom, *S. foliaceum* (DC.) Nesom, *S. greatae* (Parish) Nesom, *S. hallii* (A. Gray) Nesom, *S. hendersonii* (Fernald) Nesom, *S. jessicae* (Piper) Nesom, *S. lentum* (E. Greene) Nesom, *S. molle* (Rydb.) Nesom, *S. spathulatum* (Lindl.) Nesom, *S. subspicatum* (Nees) Nesom, *S. welshii* (Cronq.) Nesom.

H. **Symphyotrichum** sect. **Ascendentes** (Rydb.) Nesom, *comb. et stat. nov.* BASIONYM: *Aster* sp.-group *Ascendentes* Rydb., *Fl. Colorado* 352, 354. 1906. *Aster* subg. *Ascendentes* (Rydb.) Semple [*nom. illeg.*, see Lamboy 1986], Phytologia 58:430. 1985.

Type: *Aster ascendens* Lindl.

Virgulaster Semple [*nom. illeg.*, see Lamboy 1986], Phytologia 58:430. 1985.

Type: *Aster ascendens* Lindl.

INCL: *Symphyotrichum ascendens* (Lindl). Nesom, *S. defoliatum* (Parish) Nesom (= *Aster bernardinus* Hall).

2. **Symphyotrichum** subg. **Virgulus** (Rafin.) Nesom, *comb. nov.* BASIONYM: *Virgulus* Rafin., *Fl. Tellur.* 2:46. 1836 [1837]. *Aster* subg. *Virgulus* (Rafin.) A.G. Jones, Brittonia 32:233. 1980.

Type: *Virgulus concolor* (L.) Rafin. (= *Aster concolor* L.).

Virgaria Rafin. *ex* DC. [*pro syn.*], *Prodr.* 5:243. 1836.

Type: *Virgaria concolor* (L.) Rafin. *ex* DC. (= *Aster concolor* L.).

Lasallea E. Greene [*nom. superfl. illeg.*], Leafl. Bot. Observ. Crit. 1:5. 1903. (not *Lasallia* Merat 1821.).

Type: *Lasallea sericea* (Vent.) E. Greene (= *Aster sericeus* Vent.)

A. **Symphyotrichum** sect. **Grandiflori** (Torr. & Gray) Nesom, *comb. nov.* BASIONYM: *Aster* sect. *Grandiflori* Torr. & Gray, *Fl. N. Amer.* 2:142. 1841. *Lasallea* sect. *Grandiflorae* (Torr. & Gray) Semple & Brouillet, Amer. J. Bot. 67:1022. 1980. *Virgulus* sect. *Grandiflorae* (Torr. & Gray) Reveal & Keener, Taxon 30:649. 1981.

Type: *Aster grandiflorus* L.

Aster sect. *Glandulosi* A. Gray, *Synopt. Fl.* 1(2):177. 1884.

Lectotype (designated here): *Aster grandiflorus* L.

Gray broadened his sect. *Grandiflori* of 1841 and gave it a different name (sect. *Glandulosi*), but six of the eight species included in the latter are virguloid species.

a. **Symphyotrichum** subsect. **Grandiflori** (Torr. & Gray) Nesom, *comb. et stat. nov.* BASIONYM: *Aster* sect. *Grandiflori* Torr. & Gray, *Fl. N. Amer.* 2:142. 1841.

Type: *Aster grandiflorus* L.

INCL: *Symphyotrichum grandiflorum* (L.) Nesom.

b. **Symphyotrichum** subsect. **Polyligulae** (Semple & Brouillet) Nesom, *comb. nov.* BASIONYM: *Lasallea* [sect. *Grandiflorae*] subsect. *Polyligulae* Semple & Brouillet, Amer. J. Bot. 67:1023. 1980.

Type: *Aster novae-angliae* L.

Aster sp.-group *Oblongifolii* Rydb., *Fl. Colorado* 351. 1906. *Aster* sect. *Oblongifolii* (Rydb.) A.G. Jones, Brittonia 32:233. 1980. *Virgulus* sect. *Oblongifoli* (Rydb.) Reveal & Keener, Taxon 30:649. 1981.

Type: *Aster oblongifolius* Nutt.

INCL: *Symphyotrichum campestre* (Nutt.) Nesom, *S. fendleri* (A. Gray) Nesom, *S. novae-angliae* (L.) Nesom, *S. oblongifolium* (Nutt.) Nesom, *S. yukonense* (Cronq). Nesom.

c. **Symphyotrichum** subsect. **Mexicanae** Nesom, *subsect. nov.*

Type: *Symphyotrichum moranense* (Kunth) Nesom.

Foliis parvis sessilibus trinervatis, capitulis solitariis, flosculis radii plerumque albis, et distributione in Mexici distinctus.

INCL: *Symphyotrichum gypsophilum* (B.L. Turner) Nesom, *S. hintonii* (Nesom) Nesom, *S. moranense*, *S. trilineatum* (Sch.-Bip. *ex* Klatt) Nesom.

d. **Symphyotrichum** subsect. **Brachyphylli** (Torr. & Gray) Nesom, *comb. nov.* BASIONYM: *Aster* sect. *Brachyphylli* Torr. & Gray, *Fl. N. Amer.* 2:114. 1841. *Lasallea* [sect. *Grandiflorae*] subsect. *Brachyphyllae* (Torr. & Gray) Semple & Brouillet, Amer. J. Bot. 67:1023. 1980.

Type: *Aster walteri* Alexander.

INCL: *Symphyotrichum adnatum* (Nutt.) Nesom, *S. walteri* (Alexander) Nesom.

B. **Symphyotrichum** sect. **Ericoidei** (Torr. & Gray) Nesom, *comb. nov.* BASIONYM: *Aster* sect. *Ericoidei* Torr. & Gray, *Fl. N. Amer.* 2:123. 1841. *Aster* [sect. *Homophylli*] subsect. *Ericoidei* A. Gray, *Synopt. Fl.* 1(2):184. 1884. *Virgulus* sect. *Ericoidei* (Torr. & Gray) Reveal & Keener, Taxon 30:649. 1981. [See comments in Jones 1982, 1983d.].

Type: *Aster ericoides* L.

Aster [sect. *Homophylli*] subsect. *Multiflori* A. Gray, *Synopt. Fl.* 1(2):185. 1884. *Aster* sect. *Multiflori* (A. Gray) R.A. Nelson, Rhodora 35:323. 1933. *Lasallea* sect. *Multiflori* (A. Gray) Semple & Brouillet, Amer. J. Bot. 67:1022. 1980.

Type: *Aster ericoides* L.

Aglotoma Rafin., *Fl. Tellur.* 2:44. 1836. [1837.].

Type: *Aster ericoides* L.

Rafinesque cited as the type "*Aster multiflorus* M. alia sp." What he meant by the authority citation is not clear, but the *A. multiflorus* in general use at the time seems to have been that with the name proposed by Solander, which is a synonym of *Aster ericoides*.

INCL: *Symphyotrichum ericoides* (L.) Nesom, *S. falcatum* (Lindl.) Nesom.

C. **Symphyotrichum** sect. **Patentes** (Torr. & Gray) Nesom, *comb. nov.* BASIONYM: *Aster* sect. *Patentes* Torr. & Gray, *Fl. N. Amer.* 2:114. 1841. *Virgulus* sect. *Patentes* (Torr. & Gray) Reveal & Keener, Taxon 30:650. 1981.

Type: *Aster patens* Aiton.

INCL: *Symphyotrichum georgianum* (Alexander) Nesom, *S. patens* (Aiton) Nesom, *S. phlogifolium* (Muhl. *ex* Willd.) Nesom (see R. Jones 1983, 1992).

D. **Symphyotrichum** sect. **Concolores** (Torr. & Gray) Nesom, *comb. nov.* BASIONYM: *Aster* sect. *Concolores* Torr. & Gray, *Fl. N. Amer.* 2:113. 1841. *Lasallea* [sect. *Lasallea*] subsect. *Concolores* (Torr. & Gray) Semple & Brouillet, Amer. J. Bot. 67:1022. 1980.

Type: *Aster concolor* L.

Virgulus [sect. *Virgulus*] subsect. *Lasallea* (E. Greene) Semple [*comb. illeg.*], Phytologia 58:431. 1985. *Lasallea* E. Greene [*nom. superfl. illeg.*], Leafl. Bot. Observ. Crit. 1:5. 1903. (not *Lasallia* Merat 1821.).

Type: *Lasallea sericea* (Vent.) E. Greene (= *Aster sericeus* Vent.).

Aster sect. *Sericeo-concolores* A. Gray, *Synopt. Fl.* 1(2):179. 1884. Lectotype (designated here): *Aster concolor* L.

INCL: *Symphyotrichum concolor* (L.) Nesom, *S. lucayanum* (Britton) Nesom, *S. pratense* (Rafin.) Nesom, *S. sericeum* (Vent.) Nesom.

Species of *Symphyotrichum*:

1. **Symphyotrichum adnatum** (Nutt.) Nesom, *comb. nov.* BASIONYM: *Aster adnatus* Nutt., J. Acad. Nat. Sci. Philad. 7:82. 1834. *Lasallea adnata* (Nutt.) Semple & Brouillet, Amer. J. Bot. 67:1023. 1980. *Virgulus adnatus* (Nutt.) Reveal & Keener, Taxon 30:650. 1981.

2. **Symphyotrichum anomalum** (Engelm.) Nesom, *comb. nov.* BASIONYM: *Aster anomalus* Engelm. *in* Torr. & Gray, *Fl. N. Amer.* 2:503. 1843.

3. **Symphyotrichum anticostense** (Fernald) Nesom, *comb. nov.* BASIONYM: *Aster anticostensis* Fernald, Rhodora 17:16. 1915.

Aster gaspensis Victorin, Contr. Lab. Bot. Univ. Montreal 20:3. 1932.

Aster longifolius Lam. var. *villicaulis* A. Gray, *Synopt. Fl.* 1(2):189. 1884. *Aster novi-belgii* L. var. *villicaulis* (A. Gray) Boivin, Naturaliste Canad. 94:645. 1967.

Aster johannensis Fernald, Rhodora 17:12. 1915. *Aster novi-belgii* L. subsp. *johannensis* (Fernald) A.G. Jones, Phytologia 55:384. 1984. *Aster novi-belgii* L. var. *johannensis* (Fernald) A.G. Jones, Phytologia 63:132. 1987.

4. **Symphyotrichum ascendens** (Lindl.) Nesom, *comb. nov.* BASIONYM: *Aster ascendens* Lindl. *in* Hook., *Fl. Bor.-Amer.* 2:8. 1834. *Virgulaster ascendens* (Lindl.) Semple [*nom. illeg.*], Phytologia 58:431. 1985.

5. **Symphyotrichum bahamense** (Britton) Nesom, *comb. nov.* BASIONYM: *Aster bahamensis* Britton, Bull. Torrey Bot. Club 41:14. 1914.

   Aster subulatus Michx. var. *elongatus* Bosserd., Taxon 19:250. 1970.

6. *Symphyotrichum boreale* (Torr. & Gray) Löve & Löve, Taxon 31:358. 1982. BASIONYM: *Aster laxiflorus* Lindl. var. *borealis* Torr. & Gray, *Fl. N. Amer.* 2:138. 1841. *Aster borealis* (Torr. & Gray) Provanch., *Fl. Canad.* 1:308. 1862.

   Aster junciformis Rydb., Bull. Torrey Bot. Club 37:142. 1910.

7. **Symphyotrichum bracei** (Britton *ex* Small) Nesom, *comb. nov.* BASIONYM: *Aster bracei* Britton *ex* Small, *Fl. Miami* 190, 200. 1913.

   Aster tenuifolius L. var. *aphyllus* R. Long, Rhodora 72:40. 1970.

8. **Symphyotrichum bracteolatum** (Nutt.) Nesom, *comb. nov.* BASIONYM: *Aster bracteolatus* Nutt., Trans. Amer. Philos. Soc., ser. 2, 7:293. 1841.

   Aster eatonii (A. Gray) T.J. Howell, *Fl. N.W. Amer.* 310. 1900. BASIONYM: *Aster foliaceus* Lindl. *ex* DC. var. *eatonii* A. Gray, *Synopt. Fl.* 2(1):194. 1884.

9. **Symphyotrichum bullatum** (Klatt) Nesom, *comb. nov.* BASIONYM: *Aster bullatus* Klatt, Ann. Naturhist. Mus. Vienna 9:359. 1894.

   Aster jalapensis Fernald, Proc. Amer. Acad. Arts 35:572. 1900.

10. **Symphyotrichum burgessii** (Britton) Nesom, *comb. nov.* BASIONYM: *Aster burgessii* Britton, Bull. Torrey Bot. Club 41:14. 1914.

11. **Symphyotrichum campestre** (Nutt.) Nesom, *comb. nov.* BASIONYM: *Aster campestris* Nutt., Trans. Amer. Philos. Soc., ser. 2, 7:293. 1841.

    Virgulus campestris (Nutt.) Reveal & Keener, Taxon 30:649. 1981.

    a. **Symphyotrichum campestre** (Nutt.) Nesom var. **bloomeri** (A. Gray) Nesom, *comb. nov.* BASIONYM: *Aster bloomeri* A. Gray, Proc. Amer. Acad. Arts 6:539. 1865. *Aster campestris* Nutt. var. *bloomeri* (A. Gray) A. Gray, *Synopt. Fl.* 1(2):178. 1884. *Virgulus campestris*(Nutt.) Reveal & Keener var. *bloomeri* (A. Gray) Reveal & Keener, Taxon 30:649. 1981.

b. *Symphyotrichum campestre* (Nutt.) Nesom var. *campestre*

12. **Symphyotrichum carnerosanum** (S. Wats.) Nesom, *comb. nov.* BASIONYM: *Aster carnerosanus* S. Wats., Proc. Amer. Acad. Arts 26:139. 1891.

13. **Symphyotrichum chilense** (Nees) Nesom, *comb. nov.* BASIONYM: *Aster chilensis* Nees, *Gen. Sp. Aster.* 123. 1832.

    a. *Symphyotrichum chilense* (Nees) Nesom var. *chilense*

    b. **Symphyotrichum chilense** (Nees) Nesom var. **invenustum** (E. Greene) Nesom, *comb. nov.* BASIONYM: *Aster invenustus* E. Greene, *Man. Bay Reg.* 179. 1894. *Aster chilensis* Nees var. *invenustus* (E. Greene) Jepson, *Man. Fl. Pl. Calif.* 1047. 1925.

    c. **Symphyotrichum chilense** (Nees) Nesom var. **medium** (Jepson) Nesom, *comb. nov.* BASIONYM: *Aster chilensis* Nees var. *medius* Jepson, *Man. Fl. Pl. Calif.* 1047. 1925.

14. **Symphyotrichum ciliatum** (Ledeb.) Nesom, *comb. nov.* BASIONYM: *Erigeron ciliatus* Ledeb., *Ic. Pl.* 24. 1829. *Brachyactis ciliata* (Ledeb.) Ledeb., *Fl. Ross.* 2:495. 1846. *Aster brachyactis* S.F. Blake [*nom. nov.*], Contr. U.S. Natl. Herb. 25:564. 1925. (not *Aster ciliatus* Walter 1788.; not *Eurybia ciliata* Benth. 1837.).

    Tripolium angustatum Lindl. *in* Hook., *Fl. Bor.-Amer.* 2:15. 1834. *Aster angustatus* (Lindl.) Torr. & Gray, *Fl. N. Amer.* 2:162. 1841. *Brachyactis ciliata* (Ledeb.) Ledeb. subsp. *angustata* (Lindl.) A.G. Jones, Phytologia 55:376. 1984.

15. *Symphyotrichum ciliolatum* (Lindl.) Löve & Löve, Taxon 31:359. 1982. BASIONYM: *Aster ciliolatus* Lindl. *in* Hook., *Fl. Bor.-Amer.* 2:9. 1834.

    a. *Symphyotrichum ciliolatum* (Lindl.) Löve & Löve var. *ciliolatum*

    b. **Symphyotrichum ciliolatum** (Lindl.) Löve & Löve var. **comatum** (Fernald) Nesom, *comb. nov.* BASIONYM: *Aster lindleyanus* Torr. & Gray var. *comatus* Fernald, Rhodora 6:142. 1904. *Aster ciliolatus* Lindl. *in* Hook. var. *comatus* (Fernald) A.G. Jones, Phytologia 55:379. 1984.

    c. **Symphyotrichum ciliolatum** (Lindl.) Löve & Löve var. **maccallae** (Rydb.) Nesom, *comb. nov.* BASIONYM: *Aster maccallae* Rydb., Bull. Torrey Bot. Club 37:138. 1910. *Aster ciliolatus* Lindl. *in* Hook. var. *maccallae* (Rydb.) A.G. Jones, Phytologia 55:380. 1984.

d. **Symphyotrichum ciliolatum** (Lindl.) Löve & Löve var. **wilsonii** (Rydb.) Nesom, *comb. nov.* BASIONYM: *Aster wilsonii* Rydb., Bull. Torrey Bot. Club 37:138. 1910. *Aster ciliolatus* Lindl. *in* Hook. var. *wilsonii* (Rydb.) A.G. Jones, Phytologia 55:379. 1984.

16. **Symphyotrichum concolor** (L.) Nesom, *comb. nov.* BASIONYM: *Aster concolor* L., *Sp. Pl.*, (ed. 2) 2:874. 1763. *Lasallea concolor* (L.) Semple & Brouillet, Amer. J. Bot. 67:1022. 1980. *Virgulus concolor* (L.) Reveal & Keener, Taxon 30:649. 1981.

17. **Symphyotrichum cordifolium** (L.) Nesom, *comb. nov.* BASIONYM: *Aster cordifolius* L., *Sp. Pl.* 2:875. 1753.

a. *Symphyotrichum cordifolium* (L.) Nesom var. *cordifolium*

b. **Symphyotrichum cordifolium** (L.) Nesom var. **furbishiae** (Fernald) Nesom, *comb. nov.* BASIONYM: *Aster cordifolius* L. var. *furbishiae* Fernald, Proc. Portland Soc. Nat. Hist. 2:129. 1897.

c. **Symphyotrichum cordifolium** (L.) Nesom var. **lanceolatum** (Porter) Nesom, *comb. nov.* BASIONYM: *Aster cordifolius* L. var. *lanceolatus* Porter, Bull. Torrey Bot. Club 16:68. 1889. *Aster lowrieanus* Porter var. *lanceolatus* (Porter) Porter, Bull. Torrey Bot. Club 21:121. 1894.

Aster cordifolius L. var. *incisus* Britton, Bull. Torrey Bot. Club 19:224. 1892. *Aster lowrieanus* Porter var. *incisus* (Britton) Porter, Bull. Torrey Bot. Club 21:121. 1894.

d. **Symphyotrichum cordifolium** (L.) Nesom var. **moratum** (Shinners) Nesom, *comb. nov.* BASIONYM: *Aster finkii* Rydb. var. *moratus* Shinners, Amer. Midl. Nat. 26:407. 1941. *Aster cordifolius* L. var. *moratus* (Shinners) Shinners, Castanea 10:65. 1945.

e. **Symphyotrichum cordifolium** (L.) Nesom var. **polycephalum** (Porter) Nesom, *comb. nov.* BASIONYM: *Aster cordifolius* L. var. *polycephalus* Porter, Bull. Torrey Bot. Club 21:120. 1894.

f. **Symphyotrichum cordifolium** (L.) Nesom var. **racemiflorum** (Fernald) Nesom, *comb. nov.* BASIONYM: *Aster cordifolius* L. var. *racemiflorus* Fernald, Rhodora 19:155. 1917.

18. **Symphyotrichum crenifolium** (Fernald) Nesom, *comb. nov.* BASIONYM: *Aster crenifolius* (Fernald) Cronq., Bull. Torrey Bot. Club 74:143. 1947. *Aster foliaceus* Lindl. *ex* DC. var. *crenifolius* Fernald, Rhodora 17:15. 1915.

19. **Symphyotrichum cusickii** (A. Gray) Nesom, *comb. nov.* BASIONYM: *Aster cusickii* A. Gray, Proc. Amer. Acad. Arts 16:99. 1880. *Aster*

foliaceus var. *cusickii* (A. Gray) Cronq., Amer. Midl. Natur. 29:443. 1943.

20. **Symphyotrichum defoliatum** (Parish) Nesom, *comb. nov.* BASIONYM: *Aster defoliatus* Parish, Bot. Gaz. (Crawfordsville) 38:461. 1904.

    Aster bernardinus Hall, Univ. Calif. Pub. Bot. 3:79. 1907. *Virgulaster bernardinus* (Hall) Semple [*nom. illeg.*], Phytologia 58:431. 1985.

21. **Symphyotrichum depauperatum** (Fernald) Nesom, *comb. nov.* BASIONYM: *Aster depauperatus* Fernald [*nom. nov.*], Rhodora 10:94. 1908. (not *Aster pusillus* Hornem.). *Aster ericoides* L. var. *depauperatus* Porter [*nom. illeg.*, a substitution for Gray's var. *pusillus*, see Jones 1984], Mem. Torrey Bot. Club 5:323. 1894.

    Aster ericoides L. var. *pusillus* A. Gray, *Synopt. Fl.* 1(2):184. 1882. *Aster pilosus* Willd. var. *pusillus* (A. Gray) A.G. Jones, Phytologia 55:382. 1984.

22. **Symphyotrichum divaricatum** (Nutt.) Nesom, *comb. nov.* BASIONYM: *Tripolium divaricatum* Nutt., Trans. Amer. Philos. Soc. 7:296. 1841. *Aster divaricatus* (Nutt.) Torr. & Gray [*nom. illeg.*], *Fl. N. Amer.* 2:163. 1841. (not *Aster divaricatus* L. 1753.).

    Aster neomexicanus Wooton & Standl., Contr. U.S. Natl. Herb. 16:187. 1913.

    Aster subulatus Michx. var. *ligulatus* Shinners, Field & Lab. 21:159. 1953.

23. **Symphyotrichum drummondii** (Lindl.) Nesom, *comb. nov.* BASIONYM: *Aster drummondii* Lindl. *in* Hook., Comp. Bot. Mag. 1:97. 1835.

    a. *Symphyotrichum drummondii* (Lindl.) Nesom var. *drummondii*

    b. **Symphyotrichum drummondii** (Lindl.) Nesom var. **parviceps** (Shinners) Nesom, *comb. nov.* BASIONYM: *Aster texanus* Burgess var. *parviceps* Shinners, Field & Lab. 21:156. 1953. *Aster drummondii* Lindl. *in* Hook. subsp. *parviceps* (Shinners) A.G. Jones, Phytologia 55:381. 1984. *Aster drummondii* Lindl. *in* Hook. var. *parviceps* (Shinners) A.G. Jones, Phytologia 63:131. 1987.

    c. **Symphyotrichum drummondii** (Lindl.) Nesom var. **texanum** (Burgess) Nesom, *comb. nov.* BASIONYM: *Aster texanus* Burgess *in* Small, *Fl. Southeast. U.S.* 1214, 1339. 1903. *Aster drummondii* Lindl. *in* Hook. subsp. *texanus* (Burgess) A.G. Jones, Phytologia

55:380. 1984. *Aster drummondii* Lindl. *in* Hook. var. *texanus* (Burgess) A.G. Jones, Phytologia 63:131. 1987.

24. **Symphyotrichum dumosum** (L.) Nesom, *comb. nov.* BASIONYM: *Aster dumosus* L., *Sp. Pl.* 2:873. 1753.

    a. **Symphyotrichum dumosum** (L.) Nesom var. **dodgei** (Fernald) Nesom, *comb. nov.* BASIONYM: *Aster dumosus* L. var. *dodgei* Fernald, Rhodora 11:31. 1909.

    b. *Symphyotrichum dumosum* (L.) Nesom var. *dumosum*

    Aster coridifolius Michx., *Fl. Bor.-Amer.* 2:112. 1803. *Aster dumosus* L. var. *coridifolius* (Michx.) Torr. & Gray, *Fl. N. Amer.* 2:128. 1841.

    c. **Symphyotrichum dumosum** (L.) Nesom var. **gracilipes** (Wieg.) Nesom, *comb. nov.* BASIONYM: *Aster dumosus* L. var. *gracilipes* Wieg., Rhodora 30:166. 1928.

    d. **Symphyotrichum dumosum** (L.) Nesom var. **pergracile** (Wieg.) Nesom, *comb. nov.* BASIONYM: *Aster dumosus* L. var. *pergracilis* Wieg., Rhodora 30:166. 1928.

    e. **Symphyotrichum dumosum** (L.) Nesom var. **strictior** (Torr. & Gray) Nesom, *comb. nov.* BASIONYM: *Aster dumosus* L. var. *strictior* Torr. & Gray, *Fl. N. Amer.* 2:128. 1841.

    f. **Symphyotrichum dumosum** (L.) Nesom var. **subulifolium** (Torr. & Gray) Nesom, *comb. nov.* BASIONYM: *Aster dumosus* L. var. *subulifolius* Torr. & Gray, *Fl. N. Amer.* 2:128. 1841.

25. **Symphyotrichum elliottii** (Torr. & Gray) Nesom, *comb. nov.* BASIONYM: *Aster elliottii* Torr. & Gray, *Fl. N. Amer.* 2:140. 1841. *Aster puniceus* L. subsp. *elliottii* (Torr. & Gray) A.G. Jones, Phytologia 55:384. 1984. *Aster puniceus* L. var. *elliottii* (Torr. & Gray) A.G. Jones, Phytologia 63:132. 1987.

26. **Symphyotrichum ericoides** (L.) Nesom, *comb. nov.* BASIONYM: *Aster ericoides* L., *Sp. Pl.* 2:875. 1753. *Lasallea ericoides* (L.) Semple & Brouillet, Amer. J. Bot. 67:1023. 1980. *Virgulus ericoides* (L.) Reveal & Keener, Taxon 30:649. 1981.

    a. *Symphyotrichum ericoides* (L.) Nesom var. *ericoides*

    Aster multiflorus Sol. *ex* Aiton, *Hort. Kew.* 3:203. 1789.

    b. **Symphyotrichum ericoides** (L.) Nesom var. **pansum** (S.F. Blake) Nesom, *comb. nov.* BASIONYM: *Aster multiflorus* Sol. *ex* Aiton var. *pansus* S.F. Blake, Rhodora 30:227. 1928. *Aster pansus* (S.F.

Blake) Cronq., Leafl. W. Bot. 6:45. 1950. *Aster ericoides* L. var. *pansus* (S.F. Blake) Boivin, Naturaliste Canad. 89:70. 1962. *Virgulus ericoides* (L.) Reveal & Keener var. *pansus* (S.F. Blake) Reveal & Keener, Taxon 30:649. 1981.

c. **Symphyotrichum ericoides** (L.) Nesom var. **prostratum** (Kuntze) Nesom, *comb. nov.* BASIONYM: *Aster multiflorus* Sol. *ex* Aiton var. *prostratus* Kuntze, *Rev. Gen.* 1:313. 1891. *Aster ericoides* L. var. *prostratus* (Kuntze) S.F. Blake, Rhodora 32:138. 1930.

d. **Symphyotrichum ericoides** (L.) Nesom var. **stricticaule** (Torr. & Gray) Nesom, *comb. nov.* BASIONYM: *Aster multiflorus* Sol. *ex* Aiton var. *stricticaulis* Torr. & Gray, *Fl. N. Amer.* 2:125. 1841. *Aster ericoides* L. var. *stricticaulis* (Torr. & Gray) F.C. Gates, Trans. Kansas Acad. Sci. 42:138. 1940.

27. **Symphyotrichum eulae** (Shinners) Nesom, *comb. nov.* BASIONYM: *Aster eulae* Shinners, Field & Lab. 18:35. 1950.

28. **Symphyotrichum expansum** (Poepp. *ex* Spreng.) Nesom, *comb. nov.* BASIONYM: *Erigeron expansus* Poepp. *ex* Spreng., *Syst. Veg.* 3:518. 1826.

Aster inconspicuus Less. *in* Schlecht. & Cham., Linnaea 5:143. 1830.

Aster madrensis M.E. Jones, Contr. West. Bot. 12:43. 1908.

Tripolium subulatum (L.) Nees var. *parviflorum* Nees, *Gen. Sp. Aster.* 157. 1832.

Tripolium subulatum (L.) Nees var. *cubensis* DC., *Prodr.* 5:254. 1836. *Aster subulatus* Michx. var. *cubensis* (DC.) Shinners, Field & Lab. 21:161. 1953.

29. **Symphyotrichum falcatum** (Lindl.) Nesom, *comb. nov.* BASIONYM: *Aster falcatus* Lindl. *in* Hook., *Fl. Bor.-Amer.* 2:12. 1834. *Lasallea falcata* (Lindl.) Semple & Brouillet, Amer. J. Bot. 67:1023. 1980. *Virgulus falcatus* (Lindl.) Reveal & Keener, Taxon 30:649. 1981.

a. *Symphyotrichum falcatum* (Lindl.) Nesom var. *falcatum*

b. **Symphyotrichum falcatum** (Lindl.) Nesom var. **commutatum** (Torr. & Gray) Nesom, *comb. nov.* BASIONYM: *Aster multiflorus* Sol. *ex* Aiton var. *commutatus* Torr. & Gray, *Fl. N. Amer.* 2:125. 1841. *Aster falcatus* Lindl. var. *commutatus* (Torr. & Gray) A.G. Jones, Phytologia 63:131. 1987.

Aster nahanniensis W.J. Cody, Naturaliste Canad. 101:888. 1974.

c. **Symphyotrichum falcatum** (Lindl.) Nesom var. **crassulum** (Rydb.) Nesom, *comb. nov.* BASIONYM: *Aster crassulus* Rydb., Bull. Torrey Bot. Club 28:504. 1901. *Aster falcatus* Lindl. var. *crassulus* (Rydb.) Cronq., Bull. Torrey Bot. Club 74:144. 1947.

30. **Symphyotrichum fendleri** (A. Gray) Nesom, *comb. nov.* BASIONYM: *Aster fendleri* A. Gray, Mem. Amer. Acad. Arts II, 4:66. 1849. *Virgulus fendleri* (A. Gray) Reveal & Keener, Taxon 30:649. 1981.

31. **Symphyotrichum firmum** (Nees) Nesom, *comb. nov.* BASIONYM: *Aster firmus* Nees, *Synops. Ast. Herb.* 25. 1818. *Aster puniceus* L. subsp. *firmus* (Nees) A.G. Jones, Phytologia 55:384. 1984.

Aster lucidulus (A. Gray) Wieg., Rhodora 26:4. 1924.

32. **Symphyotrichum foliaceum** (DC.) Nesom, *comb. nov.* BASIONYM: *Aster foliaceus* Lindl. *ex* DC., *Prodr.* 5:228. 1836.

a. **Symphyotrichum foliaceum** (DC.) Nesom var. **apricum** (A. Gray) Nesom, *comb. nov.* BASIONYM: *Aster foliaceus* Lindl. *ex* DC. var. *apricus* A. Gray, *Synopt. Fl.* 1(2):193. 1884.

b. **Symphyotrichum foliaceum** (DC.) Nesom var. **canbyi** (A. Gray) Nesom, *comb. nov.* BASIONYM: *Aster foliaceus* Lindl. *ex* DC. var. *canbyi* A. Gray, *Synopt. Fl.* 1(2):193. 1884.

c. *Symphyotrichum foliaceum* (DC.) Nesom var. *foliaceum*

d. **Symphyotrichum foliaceum** (DC.) Nesom var. **parryi** (D.C. Eat.) Nesom, *comb. nov.* BASIONYM: *Aster ascendens* Lindl. *in* Hook. var. *parryi* D.C. Eat., *Bot. King Exp.* 139. 1871. *Aster foliaceus* Lindl. *ex* DC. var. *parryi* (D.C. Eat.) A. Gray, *Synopt. Fl.* 1(2):193. 1884.

33. **Symphyotrichum fontinale** (Alexander) Nesom, *comb. nov.* BASIONYM: *Aster fontinalis* Alexander *in* Small, *Man. Southeast. Fl.* 1382, 1509. 1933.

34. **Symphyotrichum frondosum** (Nutt.) Nesom, *comb. nov.* BASIONYM: *Tripolium frondosum* Nutt., Trans. Amer. Philos. Soc., ser. 2, 7:296. 1840. *Aster frondosus* (Nutt.) Torr. & Gray, *Fl. N. Amer.* 2:165. 1841. *Brachyactis frondosa* (Nutt.) A. Gray, Proc. Amer. Acad. Arts 8:647. 1873.

35. **Symphyotrichum georgianum** (Alexander) Nesom, *comb. nov.* BASIONYM: *Aster georgianus* Alexander *in* Small, *Man. Southeast. Fl.* 1381, 1509. 1933. *Virgulus patens* (Aiton) Reveal & Keener var. *georgianus* (Alexander *in* Small) Reveal & Keener, Taxon 30:649. 1981.

36. **Symphyotrichum glabrifolium** (DC.) Nesom, *comb. nov.* BASIONYM: *Erigeron glabrifolius* DC., *Prodr.* 5:287. 1836. *Aster glabrifolius* (DC.) Reiche, Anales Univ. Chile 109:337. 1901.

37. **Symphyotrichum graminifolium** (Spreng.) Nesom, *comb. nov.* BASIONYM: *Conyza graminifolia* Spreng., *Syst. Veg.*, (ed. 16) 3:515. 1826. *Aster squamatus* (Spreng.) Hieron. *in* Sod. var. *graminifolius* (Spreng.) Hieron. *in* Sod., Bot. Jahrb. Syst. 29:19. 1900. *Conyzanthus graminifolius* (Spreng.) Tamamsch., *Fl. U.R.S.S.* 25:186. 1959.

38. **Symphyotrichum grandiflorum** (L.) Nesom, *comb. nov.* BASIONYM: *Aster grandiflorus* L., *Sp. Pl.* 2:887. 1753. *Lasallea grandiflora* (L.) Semple & Brouillet, Amer. J. Bot. 67:1022. 1980. *Virgulus grandiflorus* (L.) Reveal & Keener, Taxon 30:649. 1981.

39. **Symphyotrichum greatae** (Parish) Nesom, *comb. nov.* BASIONYM: *Aster greatae* Parish, Bull. S. Calif. Acad. 1:15. 1902.

40. **Symphyotrichum gypsophilum** (B.L. Turner) Nesom, *comb. nov.* BASIONYM: *Aster gypsophilus* B.L. Turner, Southw. Nat. 19:123. 1974.

41. **Symphyotrichum hallii** (A. Gray) Nesom, *comb. nov.* BASIONYM: *Aster hallii* A. Gray, *Synopt. Fl.* 1(2):191. 1884. *Aster chilensis* Nees subsp. *hallii* (A. Gray) Cronq., Amer. Midl. Natural. 29:462. 1948.

42. **Symphyotrichum hendersonii** (Fernald) Nesom, *comb. nov.* BASIONYM: *Aster hendersonii* Fernald, Bull. Torrey Bot. Club 22:273. 1895.

    Aster cusickii A. Gray var. *lyallii* A. Gray, *Synopt. Fl.* 1(2):195. 1884.

    Aster foliaceus Lindl. *ex* DC. var. *lyallii* (A. Gray) Cronq., Amer. Midl. Nat. 29:443. 1943.

43. **Symphyotrichum hintonii** (Nesom) Nesom, *comb. nov.* BASIONYM: *Aster hintonii* Nesom, Phytologia 67:342. 1989.

44. **Symphyotrichum jessicae** (Piper) Nesom, *comb. nov.* BASIONYM: *Aster jessicae* Piper, Erythea 6:30. 1878.

45. *Symphyotrichum laeve* (L.) Löve & Löve, Taxon 31:359. 1982. BASIONYM: *Aster laevis* L., *Sp. Pl.* 2:876. 1753.

    a. **Symphyotrichum laeve** (L.) Löve & Löve var. **concinnum** (Willd.) Nesom, *comb. nov.* BASIONYM: *Aster concinnus* Willd., *Enum. Hort. Berol.* 2:884. 1809. *Aster laevis* L. var. *concinnus* (Willd.) House, Bull. N.Y. State Mus. 243-244:15. 1923.

b. **Symphyotrichum laeve** (L.) Löve & Löve var. **geyeri** (A. Gray) Nesom, *comb. nov.* BASIONYM: *Aster laevis* L. var. *geyeri* A. Gray, *Synopt. Fl.* 1(2):183. 1884. *Aster geyeri* (A. Gray) Howell, *Fl. N.W. Amer.* 1:308. 1900.

Aster laevis L. var. *guadalupensis* A.G. Jones, Sida 9:173. 1981.

c. *Symphyotrichum laeve* (L.) Löve & Löve var. *laeve*

d. **Symphyotrichum laeve** (L.) Löve & Löve var. **purpuratum** (Nees) Nesom, *comb. nov.* BASIONYM: *Aster purpuratus* Nees, *Gen. Sp. Aster.* 118. 1832. *Aster laevis* L. var. *purpuratus* (Nees) A.G. Jones, Phytologia 55:377. 1984.

46. **Symphyotrichum lanceolatum** (Willd.) Nesom, *comb. nov.* BASIONYM: *Aster lanceolatus* Willd., *Sp. Pl.* 3:2050. 1803.

A. **Symphyotrichum lanceolatum** (Willd.) Nesom subsp. **hesperium** (A. Gray) Nesom, *comb. nov.* BASIONYM: *Aster lanceolatus* Willd. subsp. *hesperius* (A. Gray) Semple & Chmielewski, Canad. J. Bot. 65:1060. 1987.

a. **Symphyotrichum lanceolatum** (Willd.) Nesom var. **hesperium** (A. Gray) Nesom, *comb. nov.* BASIONYM: *Aster hesperius* A. Gray, *Synopt. Fl.* 1(2):192. 1884. *Aster foliaceus* Lindl. *ex* DC. var. *hesperius* (A. Gray) Jepson, *Man. Fl. Pl. Calif.* 1047. 1925. *Symphyotrichum hesperium* (A. Gray) Löve & Löve, Taxon 31:359. 1982.

Aster hesperius A. Gray var. *wootonii* E. Greene, Bull. Torrey Bot. Club 25:119. 1898. *Aster wootonii* (E. Greene) E. Greene, Leafl. Bot. Observ. Crit. 1:146. 1905.

B. *Symphyotrichum lanceolatum* (Willd.) Nesom subsp. *lanceolatum*

Aster lanceolatus Willd. subsp. *simplex* (Willd.) A.G. Jones, Phytologia 55:383. 1984. *Aster simplex* Willd., *Enum. Hort. Berol.* 2:887. 1809. *Symphyotrichum simplex* (Willd.) Löve & Löve, Taxon 31:359. 1982. *Aster lanceolatus* Willd. var. *simplex* (Willd.) A.G. Jones, Phytologia 63:132. 1987.

b. **Symphyotrichum lanceolatum** (Willd.) Nesom var. **hirsuticaule** (Semple & Chmielewski) Nesom, *comb. nov.* BASIONYM: *Aster lanceolatus* Willd. var. *hirsuticaulis* Semple & Chmielewski, Canad. J. Bot. 65:1058. 1987.

c. **Symphyotrichum lanceolatum** (Willd.) Nesom var. **interior** (Wieg.) Nesom, *comb. nov.* BASIONYM: *Aster interior* Wieg., Rhodora 33:35. 1933. *Aster lanceolatus* Willd. var. *interior* (Wieg.)

Semple & Chmielewski, Canad. J. Bot. 65:1058. 1987.; A.G. Jones, Phytologia 63:132. 1987. *Aster lanceolatus* Willd. subsp. *interior* (Wieg.) A.G. Jones, Phytologia 55:383. 1984.

d. *Symphyotrichum lanceolatum* (Willd.) Nesom var. *lanceolatum*

e. **Symphyotrichum lanceolatum** (Willd.) Nesom var. **latifolium** (Semple & Chmielewski) Nesom, *comb. nov.* BASIONYM: *Aster lanceolatus* Willd. var. *latifolius* Semple & Chmielewski, Canad. J. Bot. 65:1060. 1987.

47. *Symphyotrichum lateriflorum* (L.) Löve & Löve, Taxon 31:359. 1982. BASIONYM: *Solidago lateriflorus* L., *Sp. Pl.* 2:879. 1753. *Aster lateriflorus* (L.) Britton, Trans. New York Acad. Sci. 9:11. 1884.

a. **Symphyotrichum lateriflorum** (L.) Löve & Löve var. **angustifolium** (Wieg.) Nesom, *comb. nov.* BASIONYM: *Aster lateriflorus* (L.) Britton var. *angustifolius* Wieg., Rhodora 30:174. 1928.

b. **Symphyotrichum lateriflorum** (L.) Löve & Löve var. **flagellare** (Shinners) Nesom, *comb. nov.* BASIONYM: *Aster lateriflorus* (L.) Britton var. *flagellaris* Shinners, Field & Lab. 21:157. 1953.

Aster lateriflorus (L.) Britton var. *indutus* Shinners, Field & Lab. 21:158. 1953.

c. **Symphyotrichum lateriflorum** (L.) Löve & Löve var. **hirsuticaule** (DC.) Nesom, *comb. nov.* BASIONYM: *Aster hirsuticaulis* Lindl. *ex* DC., *Prodr.* 5:242. 1836. *Aster lateriflorus* (L.) Britton var. *hirsuticaulis* (DC.) Porter, Mem. Torrey Bot. Club 5:324. 1894.

d. **Symphyotrichum lateriflorum** (L.) Löve & Löve var. **horizontale** (Desf.) Nesom, *comb. nov.* BASIONYM: *Aster horizontalis* Desf., *Cat. Pl. Hort. Reg. Paris.* (ed. 3) 402. 1829. *Aster lateriflorus* (L.) Britton var. *horizontalis* (Desf.) Farw., Asa Gray Bull. 3:21. 1895.

e. *Symphyotrichum lateriflorum* (L.) Löve & Löve var. *lateriflorum*

Aster vimineus Lam., *Encycl.* 1:306. 1783.

f. **Symphyotrichum lateriflorum** (L.) Löve & Löve var. **spatelliforme** (Burgess) Nesom, *comb. nov.* BASIONYM: *Aster spatelliformis* Burgess *in* Small, *Fl. Southeast. U.S.* 1225, 1340. 1903. *Aster lateriflorus* (L.) Britton var. *spatelliformis* (Burgess) A.G. Jones, Phytologia 55:379. 1984.

g. **Symphyotrichum lateriflorum** (L.) Löve & Löve var. **tenuipes** (Wieg.) Nesom, *comb. nov.* BASIONYM: *Aster lateriflorus* (L.) Britton var. *tenuipes* Wieg., Rhodora 30:174. 1928.

Aster acadiensis Shinners, Rhodora 46:31. 1944.

48. **Symphyotrichum laurentianum** (Fernald) Nesom, *comb. nov.* BASIONYM: *Aster laurentianus* Fernald, Rhodora 16:59. 1914. *Brachyactis laurentianus* (Fernald) Botsch., Not. Syst. Herb. Inst. Bot. Acad. Sci. URSS 16:384. 1954.

Aster laurentianus Fernald var. *magdalenensis* Fernald, Rhodora 16:59. 1914.

49. **Symphyotrichum lentum** (E. Greene) Nesom, *comb. nov.* BASIONYM: *Aster lentus* E. Greene, *Man. Bay Reg.* 180. 1894. *Aster chilensis* Nees var. *lentus* (E. Greene) Jepson, *Man. Fl. Pl. Calif.* 1047. 1925.

Aster sonomensis E. Greene, *Man. Bay Reg.* 179. 1894. *Aster chilensis* Nees var. *sonomensis* (E. Greene) Jepson, *Man. Fl. Pl. Calif.* 1047. 1925.

50. **Symphyotrichum leone** (Britton) Nesom, *comb. nov.* BASIONYM: *Aster leonis* Britton, Mem. Torrey Bot. Club 16:114. 1920.

51. **Symphyotrichum longifolium** (Lam.) Nesom, *comb. nov.* BASIONYM: *Aster longifolius* Lam., *Encycl.* 1:306. 1783.

52. **Symphyotrichum lowrieanum** (Porter) Nesom, *comb. nov.* BASIONYM: *Aster lowrieanus* Porter, Bull. Torrey Bot. Club 21:121. 1894.

Aster cordifolius L. var. *laevigatus* Porter, Bull. Torrey Bot. Club 16:67. 1889.

53. **Symphyotrichum lucayanum** (Britton) Nesom, *comb. nov.* BASIONYM: *Aster lucayanus* Britton, Bull. N.Y. Bot. Gard. 4:143 1906. *Virgulus lucayanus* (Britton) Reveal & Keener, Taxon 30:649. 1981.

54. **Symphyotrichum martii** (Cabrera) Nesom, *comb. nov.* BASIONYM: *Aster martii* Baker *in* Mart., *Fl. Bras.* 6(3):23. 1882.

55. **Symphyotrichum molle** (Rydb.) Nesom, *comb. nov.* BASIONYM: *Aster mollis* Rydb., Bull. Torrey Bot. Club 28:22. 1901.

56. **Symphyotrichum moranense** (Kunth) Nesom, *comb. nov.* BASIONYM: *Aster moranensis* Kunth, *Nov. Gen. & Sp.* 4 [folio]:73. 1818. *Virgulus moranensis* (Kunth) Reveal & Keener, Taxon 30:650. 1981.

a. *Symphyotrichum moranense* (Kunth) Nesom var. *moranense*

Aster lima Lindl. *ex* DC., *Prodr.* 5:230. 1836. *Virgulus lima* (DC.) Reveal & Keener, Taxon 30:650. 1981.

b. **Symphyotrichum moranense** (Kunth) Nesom var. **turneri** (S.D. Sundb. & A.G. Jones) Nesom, *comb. nov.* BASIONYM: *Aster moranensis* Kunth var. *turneri* S.D. Sundb. & A.G. Jones, Bull. Torrey Bot. Club 113:176. 1986.

57. **Symphyotrichum novae-angliae** (L.) Nesom, *comb. nov.* BASIONYM: *Aster novae-angliae* L., *Sp. Pl.* 2:875. 1753. *Lasallea novae-angliae* (L.) Semple & Brouillet, Amer. J. Bot. 67:1022. 1980. *Virgulus novae-angliae* (L.) Reveal & Keener, Taxon 30:649. 1981.

58. **Symphyotrichum novi-belgii** (L.) Nesom, *comb. nov.* BASIONYM: *Aster novi-belgii* L., *Sp. Pl.* 2:877. 1753.

a. **Symphyotrichum novi-belgii** (L.) Nesom var. **elodes** (Torr. & Gray) Nesom, *comb. nov.* BASIONYM: *Aster elodes* Torr. & Gray, *Fl. N. Amer.* 2:136. 1841. *Aster novi-belgii* L. var. *elodes* (Torr. & Gray) A. Gray, *Synopt. Fl.* 1(2):190. 1884.

b. **Symphyotrichum novi-belgii** (L.) Nesom var. **litoreum** (A. Gray) Nesom, *comb. nov.* BASIONYM: *Aster novi-belgii* L. var. *litoreus* A. Gray, *Synopt. Fl.* 1(2):189. 1884.

c. *Symphyotrichum novi-belgii* (L.) Nesom var. *novi-belgii*

d. **Symphyotrichum novi-belgii** (L.) Nesom var. **tardiflorum** (L.) Nesom, *comb. nov.* BASIONYM: *Aster tardiflorus* L., *Sp. Pl.*, (ed. 2). 2:1231. 1763. *Aster novi-belgii* L. subsp. *tardiflorus* (L.) A.G. Jones, Phytologia 55:385. 1984. *Aster novi-belgii* L. var. *tardiflorus* (L.) A.G. Jones, Phytologia 63:132. 1987.

59. **Symphyotrichum oblongifolium** (Nutt.) Nesom, *comb. nov.* BASIONYM: *Aster oblongifolius* Nutt., *Gen. N. Amer. Pl.* 2:156. 1818. *Lasallea oblongifolia* (Nutt.) Semple & Brouillet, Amer. J. Bot. 67:1022. 1980. *Virgulus oblongifolius* (Nutt.) Reveal & Keener, Taxon 30:650. 1981.

Aster oblongifolius Nutt. var. *angustatus* Shinners, Amer. Midl. Nat. 26:418. 1941. *Virgulus oblongifolius* (Nutt.) Reveal & Keener var. *angustatus* (Shinners) Reveal & Keener, Taxon 30:650. 1981.

Aster oblongifolius Nutt. var. *rigidulum* A. Gray, *Synopt. Fl.* 1(2):179. 1884.

60. **Symphyotrichum ontarione** (Wieg.) Nesom, *comb. nov.* BASIONYM: *Aster ontarionis* Wieg., Rhodora 30:179. 1928. (See Semple & Brammall 1982.).

61. **Symphyotrichum oolentangiense** (Riddell) Nesom, *comb. nov.* BASIONYM: *Aster oolentangiensis* Riddell, Synopsis Fl. W. States, West. J. Med. & Phys. Sci. 8:495. 1835.

a. *Symphyotrichum oolentangiense* (Riddell) Nesom var. *oolentangiense*

Aster oolentangiensis Riddell var. *laevicaulis* (Fernald) A.G. Jones, Bull. Torrey Bot. Club 110:41. 1983.

Aster azureus Lindl. *in* Hook., Comp. Bot. Mag. 1:98. 1835.

b. **Symphyotrichum oolentangiense** (Riddell) Nesom var. **poaceum** (Burgess) Nesom, *comb. nov.* BASIONYM: *Aster poaceus* Burgess *in* Small, *Fl. Southeast. U.S.* 1215, 1339. 1903. *Aster oolentangiensis* Riddell var. *poaceus* (Burgess) A.G. Jones, Bull. Torrey Bot. Club 110:41. 1983.

Aster vernalis Engelm. *ex* Burgess *in* Small, *Fl. Southeast. U.S.* 1215, 1339. 1903.

62. **Symphyotrichum parviceps** (Burgess) Nesom, *comb. nov.* BASIONYM: *Aster ericoides* L. var. *parviceps* Burgess *in* Britton & Brown, *Illus. Fl.* 3:379. 1898. *Aster parviceps* (Burgess) Mack. & Bush, *Man. Fl. Jackson Co. Missouri* 196. 1902. *Aster pilosus* Willd. subsp. *parviceps* (Burgess) A.G. Jones, Phytologia 55:381. 1984.

63. **Symphyotrichum patens** (Aiton) Nesom, *comb. nov.* BASIONYM: *Aster patens* Sol. *ex* Aiton, *Hort. Kew.* 2:201. 1789. *Lasallea patens* (Aiton) Semple & Brouillet, Amer. J. Bot. 67:1023. 1980. *Virgulus patens* (Aiton) Reveal & Keener, Taxon 30:650. 1981.

a. **Symphyotrichum patens** (Aiton) Nesom var. **gracile** (Hook.) Nesom, *comb. nov.* BASIONYM: *Aster patens* Sol. *ex* Aiton var. *gracilis* Hook., Comp. Bot. Mag. 1:97. 1835. *Virgulus patens* (Aiton) Reveal & Keener var. *gracilis* (Hook.) Reveal & Keener, Taxon 30:650. 1981.

b. *Symphyotrichum patens* (Aiton) Nesom var. *patens*

c. **Symphyotrichum patens** (Aiton) Nesom var. **patentissimum** (DC.) Nesom, *comb. nov.* BASIONYM: *Aster patentissimus* Lindl. *ex* DC., *Prodr.* 5:232. 1836. *Aster patens* Sol. *ex* Aiton var. *patentissimus* (DC.) Torr. & Gray, *N. Amer. Fl.* 2:115. 1841. *Virgulus patens* (Aiton) Reveal & Keener var. *patentissimus* (DC.) Reveal & Keener, Taxon 30:650. 1981.

64. **Symphyotrichum patagonicum** (Cabrera) Nesom, *comb. nov.* BASIONYM: *Aster patagonicus* Cabrera, *Fl. Patag.* 7:74. 1971.

65. **Symphyotrichum peteroanum** (Phil.) Nesom, *comb. nov.* BASIONYM: *Aster peteroanus* Phil., Anales Univ. Chile 87:406. 1894.

66. **Symphyotrichum phlogifolium** (Muhl. *ex* Willd.) Nesom, *comb. nov.* BASIONYM: *Aster phlogifolius* Muhl. *ex* Willd., *Sp. Pl.* 3:2034. 1803. *Virgulus patens* (Aiton) Reveal & Keener var. *phlogifolius* (Muhl. *ex* Willd.) Reveal & Keener, Taxon 30:650. 1981.

67. **Symphyotrichum pilosum** (Willd.) Nesom, *comb. nov.* BASIONYM: *Aster pilosus* Willd., *Sp. Pl.* 3:2025. 1803.

    a. *Symphyotrichum pilosum* (Willd.) Nesom var. *pilosum*

    b. **Symphyotrichum pilosum** (Willd.) Nesom var. **pringlei** (A. Gray) Nesom, *comb. nov.* BASIONYM: *Aster ericoides* L. var. *pringlei* A. Gray, *Synopt. Fl.* 1(2):184. 1884. *Aster pringlei* (A. Gray) Britton *in* Britton & Brown, *Illus. Fl.* 3:379. 1898. *Aster pilosus* Willd. var. *pringlei* (A. Gray) S.F. Blake, Rhodora 32:140. 1930.

        Aster pilosus Willd. var. *demotus* S.F. Blake, Rhodora 32:139. 1930.

68. **Symphyotrichum porteri** (A. Gray) Nesom, *comb. nov.* BASIONYM: *Aster porteri* A. Gray, Proc. Amer. Acad. Arts 16:99. 1881.

    Aster ericoides L. var. *strictus* Porter *in* Porter & Coulter, U.S. Dept. Interior Misc. Pub. 4:56. 1874.

69. **Symphyotrichum potosinum** (A. Gray) Nesom, *comb. nov.* BASIONYM: *Aster potosinus* A. Gray, Proc. Amer. Acad. Arts 15:32. 1880.

70. **Symphyotrichum praealtum** (Poir.) Nesom, *comb. nov.* BASIONYM: *Aster praealtus* Poir., *Encycl., Suppl.* 1(2):493. 1811.

    a. **Symphyotrichum praealtum** (Poir.) Nesom var. **angustior** (Wieg.) Nesom, *comb. nov.* BASIONYM: *Aster praealtus* Poir. var. *angustior* Wieg., Rhodora 35:24. 1933.

    b. *Symphyotrichum praealtum* (Poir.) Nesom var. *praealtum*

        Aster coerulescens DC., *Prodr.* 5:235. 1836. *Aster praealtus* Poir. var. *coerulescens* (DC.) A.G. Jones, Phytologia 55:383. 1984.

        Aster praealtus Poir. var. *imbricatior* Wieg., Rhodora 35:26. 1933.

        Aster nebraskensis Britton *in* Britton & Brown, *Illus. Fl.* 3:375. 1898. *Aster praealtus* Poir. var. *nebraskensis* (Britton) Wieg., Rhodora 35:25. 1933.

c. **Symphyotrichum praealtum** (Poir.) Nesom var. **subasperum** (Lindl.) Nesom, *comb. nov.* BASIONYM: *Aster subasper* Lindl. *in* Hook., Comp. Bot. Mag. 1:97. 1835. *Aster praealtus* Poir. var. *subasper* (Lindl.) Wieg., Rhodora 35:24. 1933.

d. **Symphyotrichum praealtum** (Poir.) Nesom var. **texicola** (Wieg.) Nesom, *comb. nov.* BASIONYM: *Aster praealtus* Poir. var. *texicola* Wieg., Rhodora 35:25. 1933.

71. **Symphyotrichum pratense** (Rafin.) Nesom, *comb. nov.* BASIONYM: *Aster pratensis* Rafin., *Fl. Ludov.* 67. 1817. *Lasaliea sericea* (Vent.) E. Greene var. *pratensis* (Rafin.) Semple & Brouillet, Amer. J. Bot. 67:1022. 1980. *Virgulus pratensis* (Rafin.) Reveal & Keener, Taxon 30:649. 1981.

Aster phyllolepis Torr. & Gray, *Fl. N. Amer.* 2:113. 1841.

Aster sericeus Vent. var. *microphyllus* DC., *Prodr.* 5:233. 1836.

72. **Symphyotrichum prenanthoides** (Muhl. *ex* Willd.) Nesom, *comb. nov.* BASIONYM: *Aster prenanthoides* Muhl. *ex* Willd., *Sp. Pl.* 3:2046. 1803.

73. **Symphyotrichum priceae** (Britton) Nesom, *comb. nov.* BASIONYM: *Aster priceae* Britton, *Man.* 960. 1901. *Aster pilosus* Willd. var. *priceae* (Britton) Cronq., Rhodora 50:28. 1948.

74. *Symphyotrichum puniceum* (L.) Löve & Löve, Taxon 31:359. 1983. BASIONYM: *Aster puniceus* L., *Sp. Pl.* 2:875. 1753.

a. **Symphyotrichum puniceum** (L.) Löve & Löve var. **calderi** (Boivin) Nesom, *comb. nov.* BASIONYM: *Aster calderi* Boivin, Canad. Field-Nat. 65:14. 1951. *Aster puniceus* L. var. *calderi* (Boivin) Lepage, Naturaliste Canad. 79:181. 1952.

b. *Symphyotrichum puniceum* (L.) Löve & Löve var. *puniceum*

Aster salicifolius Lam., *Encycl.* 306. 1783.

c. **Symphyotrichum puniceum** (L.) Löve & Löve var. **scabricaule** (Shinners) Nesom, *comb. nov.* BASIONYM: *Aster scabricaulis* Shinners, Field & Lab. 21:156. 1953. *Aster puniceus* L. var. *scabricaulis* (Shinners) A.G. Jones, Phytologia 55:384. 1984.

75. **Symphyotrichum racemosum** (Elliott) Nesom, *comb. nov.* BASIONYM: *Aster racemosus* Elliott, *Sketch* 2:348. 1823.

Aster fragilis Willd., *Sp. Pl.* 3:2051. 1803. (misapplied, see Gleason & Cronquist 1991.).

a. *Symphyotrichum racemosum* (Elliott) Nesom var. *racemosum*

Aster brachypholis Small, *Man. Southeast. Fl.* 1389, 1509. 1933. *Aster fragilis* Willd. var. *brachypholis* (Small) A.G. Jones, Phytologia 55:377. 1984.

b. **Symphyotrichum racemosum** (Elliott) Nesom var. **subdumosum** (Wieg.) Nesom, *comb. nov.* BASIONYM: *Aster vimineus* Lam. var. *subdumosus* Wieg., Rhodora 30:171. 1928. *Aster fragilis* Willd. var. *subdumosus* (Wieg.) A.G. Jones, Phytologia 55:378. 1984.

76. **Symphyotrichum regnellii** (Baker) Nesom, *comb. nov.* BASIONYM: *Aster regnellii* Baker *in* Mart., *Fl. Brasil.* 6(3):21. 1882. (not *Erigeron regnellii* Sch.-Bip., Linnaea 22:571. 1849. [*nom. nud.*]).

77. **Symphyotrichum retroflexum** (DC.) Nesom, *comb. nov.* BASIONYM: *Aster retroflexus* Lindl. *ex* DC., *Prodr.* 5:244. 1836.

Aster curtisii Torr. & Gray, *Fl. N. Amer.* 2:110. 1841.

78. **Symphyotrichum sagittifolium** (Wedem. *ex* Willd.) Nesom, *comb. nov.* BASIONYM: *Aster sagittifolius* Wedem. *ex* Willd., *Sp. Pl.* 3:2035. 1803. *Aster cordifolius* L. subsp. *sagittifolius* (Wedem. *ex* Willd.) A.G. Jones, Brittonia 32:249. 1980. *Aster cordifolius* L. var. *sagittifolius* (Wedem. *ex* Willd.) A.G. Jones, Phytologia 63:131. 1987.

79. **Symphyotrichum schaffneri** (S.D. Sundb. & A.G. Jones) Nesom, *comb. nov.* BASIONYM: *Aster schaffneri* Sch.-Bip. *ex* S.D. Sundb. & A.G. Jones, Bull. Torrey Bot. Club 113:173. 1986.

80. **Symphyotrichum sericeum** (Vent.) Nesom, *comb. nov.* BASIONYM: *Aster sericeus* Vent., *Hort. Cels.* t. 33. 1800. *Lasallea sericea* (Vent.) E. Greene, Leafl. Bot. Observ. Crit. 1:5. 1903. *Virgulus sericeus* (Vent.) Reveal & Keener, Taxon 30:649. 1981.

81. **Symphyotrichum shortii** (Lindl.) Nesom, *comb. nov.* BASIONYM: *Aster shortii* Lindl. *in* Hook., *Fl. Bor.-Amer.* 2:9. 1834.

82. **Symphyotrichum simmondsii** (Small) Nesom, *comb. nov.* BASIONYM: *Aster simmondsii* Small, *Fl. Miami* 190, 200. 1913.

83. **Symphyotrichum spathulatum** (Lindl.) Nesom, *comb. nov.* BASIONYM: *Aster spathulatus* Lindl. *in* Hook., *Fl. Bor-Amer.* 2:8. 1834. *Aster subspathulatus* Rydb. [*nom. nov.*], Mem. New York Bot. Gard. 1:395. 1900. See comments by Cronquist 1994.

a. **Symphyotrichum spathulatum** (Lindl.) Nesom var. **fremontii** (Torr. & Gray) Nesom, *comb. nov.* BASIONYM: *Aster ascendens* Lindl. *in* Hook. var. *fremontii* Torr. & Gray, *Fl. N. Amer.* 2:503. 1841. *Aster fremontii* (Torr. & Gray) A. Gray, *Synopt. Fl.* 1(2):191. 1884. *Aster occidentalis* (Nutt.) Torr. & Gray var. *fremontii* (Torr. & Gray) A.G. Jones, Phytologia 63:132. 1987.

b. **Symphyotrichum spathulatum** (Lindl.) Nesom var. **intermedium** (A. Gray) Nesom, *comb. nov.* BASIONYM: *Aster occidentalis* (Nutt.) Torr. & Gray var. *intermedius* A. Gray, *Synopt. Fl.* 1(2):192. 1884. *Aster spathulatus* Lindl. *in* Hook. var. *intermedius* (A. Gray) Cronq., *Intermountain Fl.* 5:294. 1994.

c. *Symphyotrichum spathulatum* (Lindl.) Nesom var. *spathulatum*

Aster delectabilis Hall, Univ. Calif. Pub. Bot. 3:82. 1907. *Aster occidentalis* (Nutt.) Torr. & Gray var. *delectabilis* (Hall) Ferris, Madroño 15:128. 1959.

Aster fremontii (Torr. & Gray) A. Gray var. *parishii* A. Gray, *Synopt. Fl.* 1(2):192. 1884. *Aster occidentalis* (Nutt.) Torr. & Gray var. *parishii* (A. Gray) Ferris, Madroño 15:128. 1959.

Tripolium occidentale Nutt., Trans. Amer. Philos. Soc., ser. 2, 7:296. 1840. *Aster occidentalis* (Nutt.) Torr. & Gray, *Fl. N. Amer.* 2:164. 1841.

d. **Symphyotrichum spathulatum** (Lindl.) Nesom var. **yosemitanum** (A. Gray) Nesom, *comb. nov.* BASIONYM: *Aster ascendens* Lindl. *in* Hook. var. *yosemitanus* A. Gray, *Synopt. Fl.* 1(2):191. 1884. *Aster occidentalis* (Nutt.) Torr. & Gray var. *yosemitanus* (A. Gray) Cronq., Amer. Midl. Nat. 29:467. 1943.

Aster paludicola Piper, Contr. U.S. Natl. Herb. 16:210. 1913.

84. **Symphyotrichum squamatum** (Spreng.) Nesom, *comb. nov.* BASIONYM: *Conyza squamata* Spreng., *Syst. Veg.*, (ed. 16) 3:515. 1826. *Aster squamatus* (Spreng.) Hieron. *in* Sod., Bot. Jahrb. Syst. 29:19. 1900. *Conyzanthus squamatus* (Spreng.) Tamamsch., *Fl. U.R.S.S.* 25:186. 1959.

Aster subtropicos Morong, Ann. N.Y. Acad. Sci. 7:139. 1893.

Aster subulatus Michx. var. *sandwicensis* (A. Gray) A.G. Jones, Brittonia 36:465. 1984. *Aster divaricatus* var. *sandwicensis* A. Gray, Proc. Amer. Acad. Arts 7:173. 1867.

Tripolium conspicuum Lindley *ex* DC., *Prodr.* 5:254. 1836.

Baccharis asteroides Colla, Mem. Reale Accad. Sci. Torino 38:14. 1835. *Aster asteroides* (Colla) Rusby, Mem. Torrey Bot. Club 4:213. 1893.

85. **Symphyotrichum subgeminatum** (Fernald) Nesom, *comb. nov.* BASIONYM: *Aster foliaceus* Lindl. *ex* DC. var. *subgeminatus* Fernald, Rhodora 17:16. 1915. *Aster subgeminatus* (Fernald) Boivin, Naturaliste Canad. 75:211. 1948. [*E. ciliolata* × *E. tardiflora*?].

86. **Symphyotrichum subspicatum** (Nees) Nesom, *comb. nov.* BASIONYM: *Aster subspicatus* Nees, *Gen. Sp. Aster.* 74. 1832.

Aster douglasii Lindl. *in* Hook., *Fl. Bor.-Amer.* 2:11. 1834.

a. *Symphyotrichum subspicatum* (Nees) Nesom var. *subspicatum*

b. **Symphyotrichum subspicatum** (Nees) Nesom var. **grayi** (Suksd.) Nesom, *comb. nov.* BASIONYM: *Aster grayi* Suksd., Werwenda 1:41. 1927. *Aster subspicatus* Nees var. *grayi* (Suksd.) Cronq., *Vasc. Pl. Pac. Northw.* 5:97. 1955.

87. **Symphyotrichum subulatum** (Michx.) Nesom, *comb. nov.* BASIONYM: *Aster subulatus* Michx., *Fl. Bor.-Amer.* 2:111. 1803. *Mesoligus subulatus* (Michx.) Rafin., *Fl. Tellur.* 2:44. 1836 [1837].

88. **Symphyotrichum tenuifolium** (L.) Nesom, *comb. nov.* BASIONYM: *Aster tenuifolius* L., *Sp. Pl.* 2:873. 1753.

89. **Symphyotrichum tradescantii** (L.) Nesom, *comb. nov.* BASIONYM: *Aster tradescantii* L., *Sp. Pl.* 2:876. 1753.

Aster vimineus Lam. var. *saxatilis* Fernald, Rhodora 1:188. 1899. *Aster saxatilis* (Fernald) Blanch. [*comb. illeg.*], Amer. J. Bot. 7:27. 1904. (not *Aster saxatilis* [Remy] O. Kuntze 1891.).

90. **Symphyotrichum trilineatum** (Sch.-Bip. *ex* Klatt) Nesom, *comb. nov.* *Aster trilineatus* Sch.-Bip. *ex* Klatt, Leopoldina 20:91. 1844.

Aster bimater Standl. & Steyerm., Field Mus. Publ., Bot. 23:141. 1944. *Virgulus bimater* (Standl. & Steyerm.) Reveal & Keener, Taxon 30:650. 1981.

91. **Symphyotrichum turbinellum** (Lindl.) Nesom, *comb. nov.* BASIONYM: *Aster turbinellus* Lindl *in* Hook., Comp. Bot. Mag. 1:98. 1835.

92. **Symphyotrichum undulatum** (L.) Nesom, *comb. nov.* BASIONYM: *Aster undulatus* L., *Sp. Pl.* 2:875. 1753.

Aster undulatus L. var. *asperulus* Wood, *Amer. Bot. Fl.* 162. 1870.

Aster undulatus L. var. *loriformis* Burgess *in* Britton & Brown, *Illus. Fl.* 3:365. 1898.

93. **Symphyotrichum urophyllum** (DC.) Nesom, *comb. nov.* BASIONYM: *Aster urophyllus* Lindl. *ex* DC., *Prodr.* 5:233. 1836. *Aster sagittifolius* Wedem. *ex* Willd. var. *urophyllus* (DC.) Burgess *in* Britton & Brown, *Illus. Fl.* 3:365. 1898.

94. **Symphyotrichum vahlii** (Gaud.) Nesom, *comb. nov.* BASIONYM: *Erigeron vahlii* Gaud., Ann. Sci. Nat. (Paris) 5:104. 1825. *Aster vahlii* (Gaud.) Hook. & Arn., Companion Bot. Mag. 2:49. 1836.

    a. *Symphyotrichum vahlii* (Gaud.) Nesom var. *vahlii*

    b. **Symphyotrichum vahlii** (Gaud.) Nesom var. **tenuifolium** (Phil.) Nesom, *comb. nov.* BASIONYM: *Tripolium tenuifolium* Phil., Anales Univ. Chile 87:404. 1894. *Aster vahlii* (Gaud.) Hook. & Arn. var. *tenuifolius* (Phil.) Cabrera, Revista Chil. Hist. Nat. 40:227. 1936.

95. **Symphyotrichum walteri** (Alexander) Nesom, *comb. nov.* BASIONYM: *Aster walteri* Alexander *in* Small, *Man. Southeast. Fl.* 1382, 1509. 1933. *Lasallea walteri* (Alexander) Semple & Brouillet, Amer. J. Bot. 67:1023. 1980. *Virgulus walteri* (Alexander) Reveal & Keener, Taxon 30:650. 1981.

96. **Symphyotrichum welshii** (Cronq.) Nesom, *comb. nov.* BASIONYM: *Aster welshii* Cronq., *Intermountain Fl.* 5:291. 1994.

97. **Symphyotrichum yukonense** (Cronq.) Nesom, *comb. nov.* BASIONYM: *Aster yukonensis* Cronq., Madroño 8:98. 1945. *Virgulus yukonensis* (Cronq.) Reveal & Keener, Taxon 30:650. 1981.

Hybrids in *Symphyotrichum*:

1. **Symphyotrichum × amethystinum** (Nutt.) Nesom, *comb. nov.* BASIONYM: *Aster amethystinus* Nutt. [*pro sp.*], Trans. Amer. Philos. Soc., ser. 2, 7:294. 1841. *Lasallea × amethystana* (Nutt.) Semple & Brouillet, Amer. J. Bot. 67:1022. 1980. *Virgulus × amethystanus* (Nutt.) Reveal & Keener, Taxon 30:649. 1981. [*S. ericoides × S. novae-angliae*].

2. **Symphyotrichum × batesii** (Rydb.) Nesom, *comb. nov.* BASIONYM: *Aster batesii* Rydb. [*pro sp.*], Brittonia 1:102. 1931. [*S. ericoides × S. oblongifolium*].

3. **Symphyotrichum × columbianum** (Piper) Nesom, *comb. nov.* BASIONYM: *Aster columbianus* Piper [*pro sp.*], Contr. U.S. Natl. Herb.

16:210. 1913. *Aster multiflorus* Sol. *ex* Aiton var. *columbianus* (Piper) S.F. Blake, Rhodora 30:227. 1928. *Virgulus* × *columbianus* (Piper) Reveal & Keener, Taxon 30:649. 1981. [*S. campestre* × *S. ericoides* var. *pansum*].

4. **Symphyotrichum × finkii** (Rydb.) Nesom, *comb. nov.* BASIONYM: *Aster finkii* Rydb. [*pro sp.*], Brittonia 1:102. 1931. [*S. cordifolium* × *S. shortii*].

5. **Symphyotrichum × gravesii** (Burgess) Nesom, *comb. nov.* BASIONYM: *Aster gravesii* Burgess *in* Britton [*pro sp.*], *Man.* 961. 1901. [*S. dumosum* × *S. laeve*].

6. **Symphyotrichum × longulum** (Sheldon) Nesom, *comb. nov.* BASIONYM: *Aster longulus* Sheldon [*pro sp.*], Minnesota Bot. Stud. 1:18. 1894. [*S. boreale* × *S. puniceum*].

7. **Symphyotrichum × salignum** (Willd.) Nesom, *comb. nov.* BASIONYM: *Aster salignus* Willd. [*pro sp.*], *Sp. Pl.* 3:2040. 1803. [*S. lanceolatum* × *S. novi-belgii*].

8. **Symphyotrichum × schistosum** (Steele) Nesom, *comb. nov.* BASIONYM: *Aster schistosus* Steele [*pro sp.*], Contr. U.S. Natl. Herb. 13:373. 1911. [*S. cordifolium* × *S. laeve*].

9. **Symphyotrichum × versicolor** (Willd.) Nesom, *comb. nov.* BASIONYM: *Aster versicolor* Willd. [*pro sp.*], *Sp. Pl.* 3:2045. 1803. [*S. laeve* × *S. novi-belgii*].

10. **Symphyotrichum × woldenii** (Rydb.) Nesom, *comb. nov.* BASIONYM: *Aster woldenii* Rydb. [*pro sp.*], Brittonia 1:103. 1931. [*S. praealtum* × *S. laeve*].

Unknown and excluded taxa:

Aster exilis Elliott, *Sketch Bot. S. Carolina* 344. 1823.

This taxon has been associated with *Symphyotrichum* (*Aster*) *subulatum*, but as noted by Shinners (1953) and Sundberg (1986), the type specimen apparently is not extant. Further, it was collected in western Georgia, outside of the range of *A. subulatus*, and it is likely that it represents some species outside of sect. *Oxytripolium*.

Aster sp.-group *Exiles* Rydb., *Fl. Prairies & Plains* 803. 1932. *Aster* sect. *Exiles* (Rydb.) A.G. Jones, Brittonia 32:233. 1980.

Type: *Aster exilis* Elliott.

Venatris Rafin., *Fl. Tellur.* 2:47. 1836. [1837].

Lectotype (designated here): *Venatris falcata* Rafin., *Fl. Tellur.* 2:47. 1836. [1837].

Rafinesque cited various species as "types" of this *Aster* segregate, but *Venatris falcata* was noted by him as the "best type of the G." The latter is based on a collection with the following citation: "East Kentucky, falls of Cumberland, pedal." The plant was described as glabrous, with erect, sessile, falcate, linear-lanceolate, 1-nerved, and subentire leaves, bearing 3-5 heads with purple rays, and it appears likely to be a species of *Symphyotrichum*. *Venatris falcata* is regarded here as a new species first described by Rafinesque, as there is no indication that the name was based on *Aster falcatus* Lindl., nor does this species occur in eastern Kentucky. The identity of *Venatris falcata* has not been established.

XIII. *TONESTUS* A. Nelson, Bot. Gaz. (Crawfordsville) 37:262. 1904.

Type: *Tonestus lyallii* (A. Gray) A. Nelson.

1. *Tonestus aberrans* (A. Nelson) Nesom & Morgan, Phytologia 68:178. 1990. BASIONYM: *Macronema aberrans* A. Nelson, Bot. Gaz. (Crawfordsville) 53:226. 1912. *Haplopappus aberrans* (A. Nelson) H.M. Hall, Carnegie Inst. Washington Publ. 389:185. 1928.

2. *Tonestus alpinus* (Anderson & Goodrich) Nesom & Morgan, Phytologia 68:178. 1990. BASIONYM: *Haplopappus alpinus* Anderson & Goodrich, Great Basin Nat. 40:73. 1980.

3. *Tonestus eximius* (H.M. Hall) Nelson & Macbr., Bot. Gaz. (Crawfordsville) 65:70. 1918. BASIONYM: *Haplopappus eximius* H.M. Hall, Univ. Calif. Pub. Bot. 6:170. 1915.

4. *Tonestus graniticus* (Tiehm & Schulz) Nesom & Morgan, Phytologia 68:178. 1990. BASIONYM: *Haplopappus graniticus* Tiehm & Schulz, Brittonia 37:165. 1985.

5. *Tonestus kingii* (D.C. Eaton) Nesom, Phytologia 71:125. 1991. BASIONYM: *Aster kingii* D.C. Eaton, *Bot. Fortieth Parallel* 5:141. 1871. *Machaeranthera kingii* (D.C. Eaton) Cronq. & Keck, Brittonia 9:239. 1957.

a. *Tonestus kingii* (D.C. Eaton) Nesom var. *barnebyana* (Welsh & Goodrich) Nesom, Phytologia 71:125. 1991. BASIONYM: *Machaeranthera kingii* (D.C. Eaton) Cronq. & Keck var. *barnebyana* Welsh & Goodrich, Brittonia 33:299. 1981. *Aster kingii* D.C. Eaton var. *barnebyana* (Welsh & Goodrich) Welsh, Great Basin Nat. 43:221. 1983.

b. *Tonestus kingii* (D.C. Eaton) Nesom var. *kingii*

6. *Tonestus lyallii* (A. Gray) A. Nelson, Bot. Gaz. (Crawfordsville) 37:262. 1904. BASIONYM: *Haplopappus lyallii* A. Gray, Proc. Acad. Nat. Sci. Philad. 1863:64. 1864. *Stenotus lyallii* (A. Gray) J.T. Howell, *Fl. N.W. Amer.* 300. 1900.

7. *Tonestus peirsonii* (Keck) Nesom & Morgan, Phytologia 68:178. 1990. BASIONYM: *Haplopappus eximius* H.M. Hall subsp. *peirsonii* Keck, Madroño 5:169. 1940.

8. *Tonestus pygmaeus* (Torr. & Gray) A. Nelson, Bot. Gaz. (Crawfordsville) 37:262. 1904. BASIONYM: *Stenotus pygmaeus* Torr. & Gray, *Fl. N. Amer.* 2:237. 1842. *Haplopappus pygmaeus* (Torr. & Gray) A. Gray, Amer. J. Sci., ser. 2, 33:238. 1862.

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HYBRIDIZATION IN THE TRIBE ASTEREAE (ASTERACEAE)

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ABSTRACT

Interspecific hybrids occur naturally in the Astereae within a number of genera, but hybrids also occur between species of distinct and generally accepted but closely related genera. Intergeneric hybrids also have been artificially synthesized between species of more distantly related genera (of different but closely related subtribes).

KEY WORDS: hybrids, Astereae, Asteraceae

In the course of a survey and classification of the tribe Astereae (Nesom 1994b), I have assembled observations regarding hybridization that have a general bearing on the interpretation of taxonomic patterns within the tribe. This paper summarizes the findings.

INTERSPECIFIC HYBRIDS WITHIN A GENUS

Spontaneous, infrageneric hybrids are reported to occur between species within numerous genera of Astereae; they appear to be commonly formed in several large, homobasic genera where species have overlapping geographic ranges, suggesting that isolating mechanisms may be external (primarily geographic) rather than internal. This is emphasized by studies of genera where natural hybrids are relatively rare or unknown but where artificial interspecific hybrids are readily synthesized (e.g., *Tetramolopium*, Lowrey 1986). The effect of internal isolating mechanisms is more evident in genera where chromosome numbers are reduced (less than x=8) and different among the species (e.g., in *Machaeranthera* sensu lato – Jackson 1993; Jackson *et al.* 1993; *Astranthium* – DeJong 1965), this attributable at least in part to structural incompatibility of the chromosomes. Fertile hybrids between widely heterobasic species within the North American *Symphyotrichum* (a segregate from *Aster*; Nesom 1994c), however, make such a generalization difficult (see below).

Natural hybrids are particularly well-known in *Townsendia* (Beaman 1957) and in *Solidago* and *Symphyotrichum* (*e.g.*, see comments on both genera in Gleason & Cronquist ed. 1, 1963 and ed. 2, 1991; representation of intersectional and intersubgeneric hybridization in Nesom 1994c; *Symphyotrichum* formerly considered a large group of North American *Aster*). Semple & Brammall (1982), however, noted that the extent of interspecific hybridization in *Symphyotrichum* is perhaps not as wide as generally supposed, much of the confusing variation within species instead attributable to phenotypic plasticity. Intersectional hybrids occur in *Solidago* (see Nesom 1993) as well as in *Symphyotrichum* (see below). Hybrids in various combinations of species also are known within *Oligoneuron*, which has sometimes been treated within *Solidago*, but the only putative hybrid between *Solidago* and *Oligoneuron* is the taxon ×*Solidaster* (see Nesom 1993 and comments below), formed and evidently perpetuated from the results of a single, spontaneous crossing event.

Fertile, naturally occurring hybrids occur within *Symphyotrichum* between homobasic parents (diploid and polyploid) as well as between species of different base chromosome number and highly modified karyotypes. Sundberg (1986) discovered a population system of fertile plants from Oaxaca, México with a chromosome number of n=13, apparently the result of a cross between an x=5 parent (sect. *Oxytripolium*) and an x=8 parent (sect. *Dumosi*). In a series of papers, Jones (1977), Dean & Chambers (1983), Allen *et al.* (1983), and Allen (1984, 1985, 1986) have documented the hybrid origin of a fertile, well-known species *S.* (*Aster*) *ascendens* (Lindl.) Nesom, n=13 and polyploid levels) between heterobasic parents of different subgenera (x=8 – subg. *Symphyotrichum* and x=5 – subg. *Virgulus* and the reticulate nature of phyletic relationships in this species complex. Another accepted species (*S. defoliatum* (Parish) Nesom = *Aster bernardinus* Hall; n=18) originated as a backcross between *S. ascendens* (n=13) and *S.* [*Aster*] *falcatum* (Lindl.) Nesom (n=5), one of the parents of *S. ascendens*. Both of these alloploid species backcross in various combinations to both parents as well as other taxa (extra-parental, in both subgenera) of this species complex. Semple (1985) has divided the plants of this complex among three genera: the virguloid and symphyotrichoid parents each representing a different genus and those with a genetic amalgam (F_1's and backcrosses) representing a third. Such a taxonomic approach is unique in the Astereae and, in my opinion, overemphasizes the degree of evolutionary divergence of the parents.

One artificially produced hybrid within *Symphyotrichum* (reported as *Aster*, Avers 1957) that was originally regarded as "wide" has been reinterpreted as a cross between two related species with the same base chromosome number (x=8): *S. cordifolium* (L.) Nesom (n=8) and *S. turbinellum* (Lindl.) Nesom (n=48). Within both *Symphyotrichum* subg. *Symphyotrichum* (sect. *Dumosi*) and the genus *Eurybia* (= *Aster* subg. *Biotia*), some species apparently are of hybrid origin (Semple & Brammall 1982; Lamboy *et al.* 1991) and the inter-

pretation of species relationships is correspondingly complex. The occurrence of an intersectional hybrid between sect. *Eurybia* and sect *Calliastrum* (Uttal 1962; Nesom 1994b), the parental species strongly divergent in morphology, is perhaps facilitated by the high ploidy level of both parents.

Another remarkable and well-documented area of natural hybridization in the Astereae is in the genus *Chrysopsis* (Semple & Chinnappa 1980a, 1980b; Semple 1981), which has a base chromosome number of x=5. One of the species, *C. gossypina* Ell., is an alloploid (n=9) originating as a hybrid between parents with n=5 and n=4. Naturally occurring n=7 hybrids exist between *C. gossypina* and two of the n=5 species (one of the hybrids a backcross), and an artificial $2n$=13 hybrid has been constructed between *C. gossypina* and one of the x=4 species. The x=9 alloploids also have been artificially synthesized.

In the large genus *Erigeron*, there are relatively few putative natural hybrids, perhaps because of the restricted (non-overlapping) geographic distributions of many of the species, and there are no known hybrids between species of different sections. Within *Erigeron* sect. *Olygotrichium*, however, agamic polyploid complexes involving hybrids between *E. divergens* Torr. & Gray and its close relatives are common. Widespread interspecific hybridization in *Baccharis* (Hellwig 1990), apparently strictly infra-sectional, is responsible for at least a part of the taxonomically confusing variation found in that genus. A sample of other Astereaean genera where interspecific hybrids are reported between relatively closely related species are *Celmisia* (Allan 1961), *Felicia* (Grau 1973), *Oclemena* (Pike 1970; see summary in Nesom 1994c), *Boltonia* (Anderson 1987), *Xylorhiza* (T. Watson pers. comm.), and *Machaeranthera*.

A naturally formed hybrid has been reported between homobasic species (x=9) of the Australian genera *Pleurophyllum* and *Damnamenia*, but the species involved are closely related and probably are best considered congeneric (Drury 1968; Given 1973). Natural hybrids occur between *Galatella angustissima* (Tausch.) Novopokr. and *Crinitaria villosa* (L.) Grossh. (Tamamschyan 1959), but the inter-relationships of the subgroups within these two closely related genera are poorly understood, as noted by Tamamschyan. Similarly, an artificial "intergeneric" hybrid between *Haplopappus* and *Machaeranthera* (Jackson 1993) is reinterpreted as a cross between two species of *Machaeranthera*. Natural hybrids reported between taxa of *Chrysothamnus* and *Ericameria* have been reinterpreted as crosses within the latter genus (Nesom & Baird 1993). A recurrent hybrid combination between two species of *Ericameria* strongly divergent in habit and capitulescence has been documented by Urbatsch & Wussow (1979), who placed them in the same section of the genus.

INTERGENERIC HYBRIDS

Among genera of Astereae reasonably accepted as distinct (Nesom 1994b),

there are reports (documented in varying degrees) of naturally occurring hybrids between the following:

Aster ageratoides Turcz. ($2n$=36) × *Kalimeris incisa* (Fisch.) DC. ($2n$=72); homobasic, x=9, the hybrids fertile (Inoue 1970; Tara 1972, 1979; Gu 1987 and in press);

Heteropappus hispidus (Thunb.) Less. (2n=36) × *Kalimeris incisa* ($2n$=72); homobasic, x=9, the hybrids fertile (Huziwara 1950; Inoue 1955; Tara 1973);

Polyarrhena reflexa (L.) Cass. × *Zyrphelis taxifolia* (L.) Cass.; homobasic, x=9, the hybrids of unknown fertility (see Nesom 1994a) and needing confirmation of their status;

Isocoma veneta (Kunth) E. Greene × *Xanthocephalum humile* Benth.; homobasic, x=6, the hybrids vegetatively robust but largely sterile (Lane & Hartman 1991);

Erigeron [subg. *Trimorpha*] *acris* L. × *Conyza canadensis* (L.) Cronq.; homobasic, x=9, the hybrids recurring but rare and apparently weak and sterile (Stace 1975).

Four instances of putative natural hybridization have been reported between species of *Olearia* and *Celmisia* (summarized by Clarkson 1988). Among these, at least three of the *Olearia* parents have been plants of the shrubby species *O. arborescens* (Forst. f.) Ckn. & Laing; the *Celmisia* parents are species representing at least three subgenera (*sensu* Given 1969) and range from woody subshrubs to herbs. The hybrids studied in detail by Clarkson (*O. arborescens* × *C. gracilenta* J.D. Hook.) are relatively rare and almost completely sterile.

I recently suggested that the parents of the spontaneously formed and fertile (but apparently only once-formed) intergeneric hybrid ×*Solidaster* might be *Oligoneuron album* (Nutt.) Nesom and a species of *Euthamia* (Nesom 1993). The hybrid is maintained in the florist trade (generally by cuttings and divisions), and after being able to observe living material, where the shape of the capitulescence in at least some plants may be more asymmetrical than in the herbarium material I have studied, it appears that *Solidago canadensis* L. (rather than *Euthamia*) may be a reasonable parental candidate, as suggested previously by other botanists (see summary in Nesom 1993). In either case, each parent of *Solidaster* has a base chromosome number of x=9, and they are relatively closely related within the Solidagininae. At least the original plant of *Solidaster* produced fertile achenes; the "F_2" progeny also were fertile, although whether they were backcrosses or true F_2's is not clear.

Intergeneric hybrids have been artificially synthesized between the following species of different but closely related Astereaean genera (within a subtribe):

Grindelia papposa Nesom & Suh (= *Prionopsis ciliata* [Nutt.] Nutt.) × *Haplopappus annuus* Rydb.; homobasic, x=6 (Jackson 1966) (Machaerantherinae); *H. annuus* is a member of the "phyllocephalus group," accepted as a generic-level group of the Machaerantherinae (Nesom 1994b); both *Grindelia* and the "phyllocephalus group" are members of the "*Xanthocephalum* Willd. group."

Isocoma veneta (Kunth) E. Greene × *Haplopappus aureus* A. Gray; homobasic, x=6 (Jackson 1966) (Machaerantherinae); *H. aureus* is a member of the "phyllocephalus group"; *Isocoma* and the "phyllocephalus group" are members of the "*Xanthocephalum* group."

Tracyina rostrata S.F. Blake × *Rigiopappus leptocladus* A. Gray; homobasic, x=9 (Ornduff & Bohm 1975) (Feliciinae).

Intergeneric hybrids have been artificially synthesized between species of North American Astereae apparently more widely separated in relationship:

Almutaster (*Aster*) *pauciflorus* (x=9) × *Machaeranthera arida* (Kunth) A.G. Jones (x=5) (Stucky 1978) (Asterinae × Machaerantherinae);

Almutaster (*Aster*) *pauciflorus* (x=9) × *Machaeranthera parviflora* A. Gray (x=5) (Stucky 1978) (Asterinae × Machaerantherinae);

Symphyotrichum (*Aster*) *tenuifolium* (x=5) × *Machaeranthera riparia* (Kunth) A.G. Jones (x=5) (Jackson 1992a) (Asterinae × Machaerantherinae);

Haplopappus ("phyllocephalus group") *aureus* A. Gray (x=6) × *Machaeranthera arenaria* (Benth.) Shinners (x=4) (Jackson 1985) (Machaerantherinae);

Haplopappus ("phyllocephalus group") *annuus* (x=6) × *Machaeranthera havardii* (Waterf.) Shinners (x=4) (Jackson 1966) (Machaerantherinae).

The eight crosses above, with the resultant hybrids weak and infertile, appear to be the widest such documented in the tribe. They represent, however, only a fraction of the wide, artificial crosses that might prove successful but which have not been attempted. The hybrids appear to confirm initial hypotheses (which led to the experiments) that evolutionary divergence among the species involved has not completely effaced their genomic similarities.

In contrast to these artificial crosses, natural intergeneric hybrids in the Astereae have been reported only between species of genera that are clearly

closely related. In Powell's view (1985, p. 56), "any natural 'intergeneric' hybridization, where at least partial fertility of the hybrids can be established, should be strongly considered as evidence that the taxa involved are congeneric." Some natural hybrids in the Astereae are sterile (following the general pattern described by Powell), but those produced in crosses involving *Aster*, *Kalimeris*, and *Heteropappus* show varying degrees of fertility, and at least the immediate descendants of the original *Solidaster* produced fertile achenes. In the instances of natural intergeneric hybridization summarized here, the parental species may have been considered congeneric in earlier taxonomic concepts, but there is a consensus in more modern treatments for their recognition as members of distinct genera. There is no strong indication that Astereaean intergeneric hybrids, with caveats above regarding *Pleurophyllum* × *Damnamenia* and *Galatella* × *Crinitaria*, should be interpreted as evidence for a broadening (or re-broadening) of generic concepts to include both parents.

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