WOODLOT ALTERNATIVES, INC.
ENVIRONMENTAL CONSULTANTS

B o t a n i c a l N o t e s

A newsletter dedicated to dispersing taxonomic and ecological information useful for plant identification and conservation in Maine

Available online at http://www.woodlotalt.com/publications/publications.htm

Number 7. 10 December 2001 122 Main Street, Number 3, Topsham, ME 04086

CLARIFYING THE GENERIC CONCEPTS OF *ASTER SENSU LATO* IN NEW ENLGAND

Aster sensu lato (*i.e.*, in the broad sense) is a large genus (*ca*. 306 species) that is distributed in the northern hemisphere of both Eurasia and North America (Nesom 1994). Recent evidence suggests that New World species are distinct at the generic level from Old World species and that a major revision is needed to rectify the "artificialness" of *Aster*. This note briefly discusses some of the key evidence for splitting *Aster s.l.* into smaller, more homogenous genera and provides morphological methods for discriminating the genera in New England.

In the nineteenth century, North American botanists regarded *Aster* segregates as valid genera. For example, flat-topped white aster (formerly *A. umbellatus* Mill.) was first recognized to belong to the distinct genus *Doellingeria* as early as 1832. Bentham and Hooker (1873) formally unified asters under a large and variable *Aster* with the publication of the second volume of *Genera Planetarum.* Asa Gray reluctantly followed this approach (Cronquist 1947). Since that time, North American floristicians have treated asters as a single heterogenous genus. Nesom (1994) used morphology to show that North American asters were part of a natural group (*i.e.*, monophyletic) with a single origin from South American/Old World composite species. Xiang (1994) and Xiang and Semple (1996), summarized in Semple *et al.* (1996), used chloroplast DNA (cpDNA) to reconstruct the phylogeny (*i.e.*, evolutionary history) of North American asters. Their results confirmed some of the assertions of Nesom. They showed that two genera of yellow-rayed composites (*e.g.*, *Solidago*, *Heterotheca*) were derived from within North American asters. Recognition of a broad and variable *Aster* that did not include within its generic bounds these two genera, would be defined on arbitrary grounds (in this case, white rays). Most recently, Brouillet *et al.* (2001a and 2001b) used DNA sequences of over 80 composite species to confirm that New World asters are separate from Old World and South American species (Figure 1).

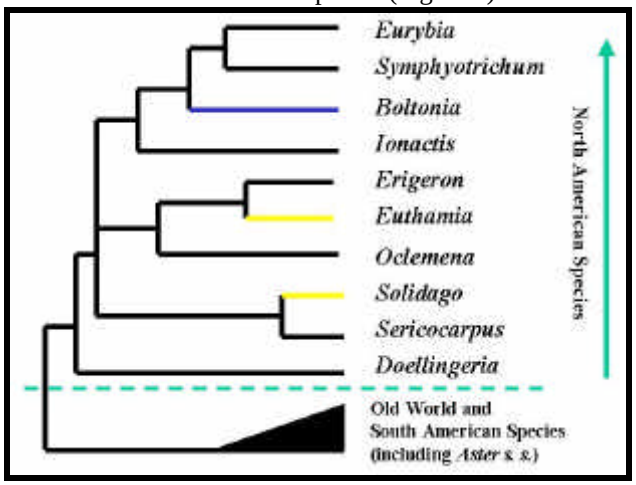

Figure 1. Simplified phylogeny of *Aster sensu lato* based on ITS nrDNA (Brouillet *et al.* 2001a and 2001b). The yellow branches indicate genera with yellow ray flowers. The black branches above the green line indicate genera that are typically included in *Aster* in modern day manuals.

Interestingly, both Semple *et al.* (1996) and Brouillet *et al.* (2001a and 2001b) showed that some asters are more closely related to fleabanes (*Erigeron*) than they are to North American "asters". Noyes and Rieseberg (1999) were first to use Internal Transcribed Spacers of nuclear ribosomal DNA (ITS nrDNA) to examine the phylogeny of western hemisphere Asteraceae, focusing on asters. Their work, later strengthened by adding additional taxa (Brouillet *et al.* 2001a and 2001b) supported the results of Nesom (1994) that the genus *Aster* is actually restricted to Eurasia. This implies that North American asters are endemic to the continent and should be recognized as distinct genera.

In summary, eight different researchers using multiple data sets (including morphology, chromosome number, cpDNA, and ITS nrDNA) have arrived at a relatively similar conclusion—North American asters must be subdivided into segregate genera in order for the nomenclature to accurately reflect the true evolutionary history of the group. If this is not done, the following genera (which is only a partial list) would have to be subsumed in *Aster* to create a natural and monophyletic taxon: *Boltonia*, *Chrysothamnus*, *Erigeron*, *Euthamia*, *Grindelia*, *Gutierrezia*, *Heterotheca*, *Machaeranthera*, *Oreostemma*, and *Solidago*. If that were done, the genus *Aster* would be so large as to lose its value as a generic rank.

1. NATIVE NEW ENGLAND GENERA

Key to *Aster* segregates of New England

1a. Surface of ovary with minute glands; capitula nodding in bud; leaves reduced in size toward the base, the lowest scale-like ..... ***Oclemena***
1b. Surface of ovary without glands; capitula erect in bud; leaves larger toward the stem base.
  2a. Capitula frequently in glomerules, with 3–8 ray flowers; foliage leaves with sessile glands ..... ***Sericocarpus***
  2b. Capitula usually borne singly at the ends of peduncles, with 8–100 ray flowers; foliage leaves without glands (bracteal leaves sometimes with stipitate-glands).
    3a. Pappus bristles of two distinctly uneven lengths—a very short outer series and 1 or 2 series of elongate bristles of nearly even length; phyllaries neither foliaceous nor with a distinct, green apical zone
      4a. Longer series of pappus bristles thickened at the apex; phyllaries with a raised midvein, but not keeled; rays not coiling; disk flowers abruptly expanded apically; ovaries terete .. ***Doellingeria***
      4b. Longer series of pappus bristles slender at the apex; phyllaries somewhat keeled; rays coiling; disk flowers tubular; ovaries compressed ***Ionactis***
    3b. Pappus bristles all elongate, in 2 or 3 series of nearly even length; phyllaries with a distinct green apical zone or entirely foliaceous in a few species
      5a. Phyllaries less than 2.5 times as long as wide, rounded to obtuse at the apex, with a basally truncate green zone at the tip; capitulescence corymb-like; pappus bristles sometimes thickened at the apex; ovary terete ..... ***Eurybia***
      5b. Phyllaries more than 3.0 times as long as wide, obtuse to acuminate at the apex, with a rhombic or basally tapered green zone at the tip; capitulescence commonly panicle-like when well-formed; pappus bristles slender at the apex; ovary compressed in most species ... ***Symphyotrichum***

The following discussion of *Aster* segregate genera is restricted to New England species.

Doellingeria Nees

In New England, *Doellingeria* is an easily identified genus of white-rayed composites with flat-topped capitulescences and entire leaves (Figure 2). The phyllaries are generally light green to yellow-green throughout (similar to *Erigeron*) and lack the distinct green apical zone present in the genus *Symphyotrichum* (Figure 3; compare with Figure 15). The pappus is dimorphic—a short outer series of bristles and a long inner one or two series of bristles that are thickened at the apex (Figure 4). The ovaries are terete in cross-section.

Figure 2. Habit of *Doellingeria umbellata*.

Figure 3. Involucre of *Doellingeria umbellata*. Note the absence of a distinct green apical zone on the phyllaries.

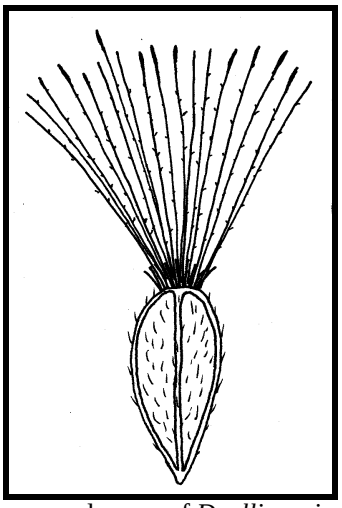

Figure 4. Pappus and ovary of *Doellingeria umbellata*. Note the short outer series of pappus bristles and the apically-thickened longer series.

Eurybia (Cass.) S.F. Gray

The genus *Eurybia* is characterized by a flat-topped capitulescence, broad and apically rounded phyllaries, and terete ovaries (Figures 5 and 6). The phyllaries typically are ciliate on the margin and have a basally truncate green zone at the tip (*i.e.*, shaped like a thumb nail; Figure 6). The pappus bristles are sometimes thickened near the apex, similar to *Doellingeria* (Figure 4), but are of nearly uniform length. In some species, the leaves are both cordate and borne on a petiole, whereas in others they are sessile and taper to the base. *Biota*, *Heleastrum*, and *Weberaster* are some of the additional generic names that have been applied to members of this group.

Figure 5. Capitulescence of *Eurybia divaricata*. Note the relatively flat-topped, corymb-like aspect.

Figure 6. Involucre of *Eurybia radula*. Note the relatively broad phyllaries with a rounded apex and basally truncate green zone.

Ionactis Greene

Ionactis is represented by a single species in New England—*Ionactis linariifolius* (L.) Greene (Figure 7). It is distinct in several micromorphological features, including dimorphic pappus bristles (*i.e.*, a short outer series and longer inner series) that taper to the apex, tubular disk flowers, and keeled phyllaries lacking a distinct green apical zone (Figure 8; compare with Figure 15). Its clustered, wiry stems; numerous, narrow, stiff leaves; and reduced capitulescence serve to quickly distinguish this species by habit alone.

Figure 7. Habit of *Ionactis linariifolius.*

Figure 8. Involucre of *Ionactis linariifolius.* Note the thin keel along the midvein of the phyllaries.

Oclemena Greene

Oclemena is a small genus of asters with flat-topped capitulescences, scarious-margined phyllaries, disk flowers apruptly expanded apically, and stipitate-glandular ovaries that are generally compressed (Figures 9, 10, and 11). It has many morphological features that serve to distinguish it as separate from the remaining asters in New England. These include capitula that nod in bud, leaves reduced in size toward the base of the stem, sessile resin glands on the leaves, and stem hairs with colored crosswalls (except *O. nemoralis*). In contrast to the phyllaries of *Symphyotrichum*, which have a distinct green apical zone, the green pigment (chlorophyll) in *Oclemena* is aligned in two thin zones on either side of the phyllary midrib.

Figure 9. Habit of *Oclemena acuminata*.

Figure 10. Involucre of *Oclemena acuminata*. Note the absence of a distinct green apical zone and scarious margin of the individual phyllaries.

Figure 11. Ovary of *Oclemena acuminata*. Note the glands on the surface of the ovary that appear as minute, cylindrical projections.

Sericocarpus Nees

Sericocarpus shares several features with *Eurybia*. These include broad, apically rounded phyllaries with a basally truncate green zone, pappus bristles that are thickened at the apex, terete ovaries, and flat-topped capitulescences (Figures 12 and 13). *Sericocarpus* differs in that it has glomerulate and few-rayed capitula (3–8 rays), densely sericeous ovaries, white disk flowers, and sessile resin glands on the foliage. *Eurybia*, in contrast, has pedunculate and many-rayed capitula, sparsely sericeous ovaries, yellow disk flowers that become red to purple in age, and lacks sessile resin glands on the foliage (though sometimes with stipitate glands in the capitulescence).

Figure 12. Capitulescence of *Sericocarpus asteroides*. Note the corymb-like aspect and few rayed capitula.

Figure 13. Involucre of *Sericocarpus asteroides*.

Symphyotrichum Nees

Symphyotrichum is the largest and most variable segregate genus in the northeast. Leaf morphology and general plant habit is too diverse to generalize, however, most New England species have a tall, panicle-like capitulescence (Figure 14). Micromorphological characters, on the other hand, are relatively consistent These are monomorphic pappus bristles that taper to the apex; narrow, more or less pointed phyllaries; disk flowers abruptly expanded apically; and compressed ovaries (subterete ovaries in subgenus *Virgulus*). Further, most species have a characteristic phyllary morphology—a pale chartaceous base with a distinct green apical zone [Figure 15]). The distinct green apical zone is also found in *Eurybia* and *Sericocarpus*, but in *Symphyotrichum* the green zone is rhombic or basally tapered (compare Figures 5, 13, and 15). Some species (*e.g.*, *S. frondosum*, *S. novi-belgii*, *S. puniceum*), however, have phyllaries that are green nearly or entirely throughout (Figure 16). Species with a single series of green phyllaries, formerly separated as *Brachyactis*, are now realized to belong to this genus (Nesom 1994). *Lasallea* and *Virgulus* are additional generic names that have been applied to members within this group.

Figure 14. Capitulescence of *Symphyotrichum cordifolium.* Note the relatively tall, panicle-like aspect.

Figure 15. Involucre of *Symphyotrichum cordifolium.* Note the distinct green apical zone on the individual phyllaries.

Figure 15. Capitulum of *Symphyotrichum puniceum.* Note the rather foliaceous individual phyllaries that are green nearly throughout their length.

2. *ASTER SENSU STRICTO*

Aster sensu stricto occurs primarily in the Old World. One species of *Aster* does occur in New England as a rare escape from gardens—*A. tataricus* L. f. Micromorphological features for this plant include herbaceous phyllaries with a low keel and often a purple margin, disk flowers expanded apically, pappus bristles in 2 equal series that taper to the apex, and terete ovaries. This species is further characterized by basally disposed leaves in which the lowest are very large (up to 40 × 15 cm), flat-topped capitulescence, and capitula with 15–20 purple or blue rays (Figure 17).

Figure 17. *Aster tataricus*, scale bar=5 cm. Left—capitulescence. Right—Involucre.

3. CHECKLIST OF ASTERS OF NEW ENGLAND

The following checklist includes species and named hybrids. Critical synonyms are provided.

Aster tataricus L. f.

Doellingeria umbellata (P. Mill.) Nees
Doellingeria infirma (Michx.) Greene

Eurybia divaricata (L.) Nesom
Eurybia ×*herveyi* (Gray) Nesom
(= *E. macrophylla* × *E. spectabilis*)
Eurybia macrophylla (L.) Cass.
Eurybia radula (Ait.) Nesom
Eurybia schreberi (Nees) Nees
Aster glomeratus (Bernh. ex Nees) Burgess
Eurybia spectabilis (Ait.) Nesom

Ionactis linariifolius (L.) Greene

Oclemena acuminata (Michx.) Greene
Oclemena ×*blakei* (Porter) Nesom
Oclemena nemoralis (Ait.) Greene

Sericocarpus asteroides (L.) B.S.P.
Aster paternus Cronq.
Sericocarpus linifolius (L.) B.S.P.
Aster solidagineous Michx.

Symphyotrichum ×*amethystinum* (Nutt.) Nesom
(= *S. ericoides* × *S. novae-angliae*)
Symphyotrichum anticostense (Fern.) Nesom
Symphyotrichum boreale (Torr. & Gray) Löve & Löve
Symphyotrichum ciliolatum (Lindl.) A. & D. Love
Symphyotrichum concolor (L.) Nesom
Symphyotrichum cordifolium (L.) Nesom
Symphyotrichum dumosum (L.) Nesom
var. *dumosum*
var. *strictior* (Torr. & Gray) Nesom
var. *subulifolium* (Torr. & Gray) Nesom
Symphyotrichum ericoides (L.) Nesom
Symphyotrichum falcatum (Lindl.) Nesom var. *commutatum* (Torr. & Gray) Nesom
Symphyotrichum frondosum (Nutt.) Nesom
Brachyactis frondosa (Nutt.) Gray
Symphyotrichum laeve (L.) A. & D. Love
Symphyotrichum lanceolatum (Willd.) Nesom
Aster simplex Willd.
Symphyotrichum lateriflorum (L.) A. & D. Love
var. *angustifolium* (Wieg.) Nesom
var. *hirsuticaule* (DC.) Nesom
var. *lateriflorum*
Symphyotrichum lowrieanum (Porter) Nesom
Symphyotrichum novae-angliae (L.) Nesom
Symphyotrichum novi-belgii (L.) Nesom
var. *elodes* (Torr. & Gray) Nesom
var. *novi-belgii*
Aster foliaceus
var. *villicaule* (Gray) J. Labrecque & L. Brouillet
Aster johannensis Fernald
Symphyotrichum patens (Ait.) Nesom
Symphyotrichum pilosum (Willd.) Nesom
var. *pilosum*
var. *pringlei* (Gray) Nesom
Symphyotrichum phlogifolium (Muhl. *ex* Willd.) Nesom
Aster patens Ait. var. *phlogifolius* (Muh. *ex* Willd.) Nees
Symphyotrichum praealtum (Poir.) Nesom
var. *angustior* (Wieg.) Nesom
var. *praealtum*
Symphyotrichum prenanthoides (Muhl. *ex* Willd.) Nesom
Symphyotrichum puniceum (L.) A. & D. Love
Symphyotrichum racemosum (Ell.) Nesom
Aster vimineus sensu Fernald
Symphyotrichum subulatum (Michx.) Nesom
Symphyotrichum tenuifolium (L.) Nesom
Symphyotrichum tradescantii (L.) Nesom
Symphyotrichum undulatum (L.) Nesom
Symphyotrichum urophyllum (Lindl.) Nesom
Aster sagittifolium sensu Cronquist

Acknowledgments

John Semple is thanked for his contributions to this note.

Literature Cited

Bentham, G., and J.D. Hooker. 1873. *Genera Planetarum.*

Brouillet, L., G. Allen, J.C. Semple, and M. Ito. 2001a. ITS Phylogeny of North American asters (Asteraceae: Astereae): basal grade to North American American lineages and distinct from Eurasian ones. Abstract, CBA/ABC Annual Meetings, Okanagan University College, Kelowna, British Columbia, Canada.

Brouillet, L., G. Allen, J.C. Semple, and M. Ito. 2001b. ITS Phylogeny of North American asters (Asteraceae: Astereae. Botany 2001 [ASPT/BSA/IOPB joint meeting] Albuquerque, New Mexico, USA.

Cronquist, A.C. 1947. Notes on the Compositae of the northeastern United States–V. Astereae. Bulletin of the Torrey Botanical Club 74: 142–150.

Nesom, G.L. 1994. Review of the taxonomy of *Aster sensu lato* (Asteraceae: Astereae), emphasizing the New World Species. Phytologia 77(3): 141–297.

Noyes, R.D., and L.H. Rieseberg. 1999. ITS sequence data support a single origin for North American Astereae (Asteraceae) and reflect deep geographic division in Aster s.l. American Journal of Botany 86: 398–412.

Semple, J.C., S.B. Heard, and ChunSheng Xiang. 1996. The Asters of Ontario (Compositae: Astereae): *Diplactis* Raf., *Oclemena* E.L. Greene, *Doellingeria* Nees, and *Aster* L. (including *Canadanthus* Nesom, *Symphyotrichum* Nees, and *Virgulus* Raf.). University of Waterloo Biology Series Number 38.

Xiang, ChunSheng. 1994. Molecular systematics study of *Aster sensu lato* and related genera (Asteraceae: Astereae) based on chloroplast DNA restriction site analysis. Ph.D. Dissertation, Unversity of Waterloo, Waterloo, Ontario.

Xiang, ChunSheng, and J.C. Semple. 1996. Molecular systematic study of *Aster sensu lato* and related genera (Asteraceae: Astereae) based on chloroplast DNA restriction site analyses and mainly North American taxa. Pp. 393–423 *in* D.J.N. Hinds and H. Beetge, editors. Proceedings of the International Compositae Conference, Kew, 1994, volume 1, Systematics.

Text, illustrations, and images contributed by Arthur Haines except for images of *Aster tataricus* and ovary of *Oclemena acuminata*, which were contributed by John C. Semple.