

**TAXONOMIC DECISIONS AT GENERIC RANK
IN TRIBE ASTEREAE (ASTERACEAE)
FOR THE GLOBAL COMPOSITAE DATABASE**

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ABSTRACT

The account of Astereae for the Global Compositae Database (GCD) includes 208 genera. Most of the decisions regarding which to recognize are straightforward but some are relatively subjective and will not meet with unanimous agreement. Five genera of Conyzinae are recognized that are nested within the phylogenetic branches of *Erigeron*. *Oligoneuron* apparently is sister to *Solidago* sensu stricto and is treated as a distinct genus (***Oligoneuron vossii*** (Pringle & Laureto) Nesom, **comb. nov.**, completes the nomenclature) but as sisters they might be regarded as congeneric. Most of the generic segregates of Old World *Aster* are retained in the GCD account although most of them are within the cladistic bounds of *Aster* sensu stricto as recently proposed — *Aster* as so proposed, however, is highly diverse and it seems probable that narrower concepts of genera will eventually be accepted. Taxonomic decisions regarding several other examples of North American genera also are discussed, particularly where morphology and geography do not accord with taxonomy based on molecular phylogeny.

The Global Compositae Database (GCD; Compositae Working Group 2020) aims toward providing an account of the genera and species of the entire family and their taxonomic arrangement. The Astereae contribution so far has been limited to modifications and additions of currently recognized genera of Astereae, leaving the editing and arrangement of species (especially in larger genera) as a second step — both steps involve consideration of morphological, molecular, and geographic evidence. The current (10 April 2019) GCD account recognizes 208 genera of Astereae.

Most of the decisions are relatively straightforward but some do not find complete agreement among taxonomists. Those controversial perhaps to a greater degree are illustrated here by examples in *Erigeron*, Old World *Aster*, and a few other genera. For *Erigeron* and *Aster*, molecular data have accumulated toward an understanding of species relationships. In *Erigeron* (about 400 species, with a North American center of diversity), a relatively complete overview is at hand. A relatively consistent view of the overall phylogenetic structure of Old World *Aster* (200+ species) also is emerging.

In *Erigeron*, decisions regarding generic rank rest on whether or not to recognize morphologically distinct taxa whose evolutionary origin is within the branches of the genus and whose separation leaves the genus non-monophyletic. For many, consistent objectivity and the goal of recognizing only monophyletic genera simplify such decisions. Toward a pragmatic taxonomy (with distinctive genera of consistent morphology), however, a few of these taxa are recognized at generic rank in the GCD, with the acknowledgment that their evolutionary position is clear and understood.

Taxonomic decisions in the Old World *Aster* "complex" are in part related to the lack of a detailed morphological overview of the entire group and commitments to a formally revised taxonomy. Numerous genera remain to be described. Examples are provided from other North American groups where molecular data underlie decisions that appear to be contradicted by morphological and geographic evidence.

The primary problems involved here are not new, nor are the taxonomic alternatives. The aim of this brief commentary is to put the basis of these GCD decisions in Astereae on record, pointing out

common kinds of problems that may exist unnoticed within what might seem to be a uncomplicated account.

Erigeron

Species identified as *Conyza* have arisen independently within *Erigeron* at least two times, and the diagnostic feature of *Conyza*, short-ligulate ray flowers, appears elsewhere sporadically throughout *Erigeron*. The type, *Conyza chilensis* (= *Erigeron primulifolia*), is in the same clade as the cosmopolitan *Erigeron* [*Conyza*] *bonariensis* and various *Erigeron* species of Mexico and South America. The majority of the ca. 60-100 South American *Conyza* species also appear to share this relationship but have not been analyzed molecularly. The world-wide weed *Erigeron* [*Conyza*] *canadensis* is in a different clade with *Erigeron* [*Conyza*] *apurensis*, *E. leptorhizon*, the Revillagigedo Islands endemics *E. crenatus* and *E. socorroensis*, and *E. divaricatus* (= *Conyza ramosissima*). *Conyzas* were treated within *Erigeron* until the 1940's and names as *Erigeron* for most species are in place — all of these species are treated as *Erigeron* in the GCD.

Aphanostephus, including 4 species (plus varietal taxa) of the south-central USA and northern Mexico (Nesom 2006, 2008), had never been suspected of a close relationship with *Erigeron* until molecular data (Noyes 2000; Andrus et al. 2008) indicated that it shares immediate ancestry with a group of Caribbean *Erigeron*, a group of Mexican species, and *Darwiniothamnus*. In its involucre morphology and achene morphology (wall structure, surface vestiture, and pappus) there is nothing comparable in *Erigeron*, and its chromosome number of $x=5$ contrasts with the otherwise invariable $x=9$ within the cladistic branches of *Erigeron* sensu lato (subtr. Conyzinae). Even with the understanding that *Erigeron* thus is non-monophyletic, *Aphanostephus* was included at generic rank in the Flora of North America (Nesom 2006) and it also is treated as such in the GCD.

Darwiniothamnus sensu stricto (*Erigeron tenuifolius* and *E. lancifolius* of the Galapagos Islands) was segregated from *Erigeron* in 1962 on the basis of its shrubby, "rosette" habit, leaves in terminal whorls with short internodes, heads in a condensed corymbiform capitulescence, and slightly dimorphic ray and disc achenes. Molecular data (Andrus et al. 2008) indicate that these sister species are most closely related to Mexican and Caribbean species of *Erigeron*, and the distinctive growth form of *Darwiniothamnus* developed in parallel with other Asteraceae species of oceanic islands. In the GCD, *Darwiniothamnus* is placed within *Erigeron*, although there is justification for its separation as a genus.

Evolutionary divergence within the branches of *Erigeron* sensu lato among species with an "austral-brasilien" distribution has been pronounced. Four distinctive species groups from this region, comprising a single clade, are treated in the GCD at generic rank — this clade is closely related to *Erigeron primulifolia*, *Erigeron bonariensis* and probably most of the South American conyzas, South American species traditionally identified as *Erigeron*, and two primarily Mexican species groups. Species of the sisters *Neja* (6 species) and *Hysterionica* (7 species) are consistently yellow-rayed (yellow otherwise rare in *Erigeron*) and the numerous, raised, resinous-glandular achenial ribs of *Neja* are unique within *Erigeron* sensu lato. Prior to their segregation at generic rank, the two species of *Apopyros* were identified as *Aster* — they are characterized by shiny-indurate, parallel-veined, strictly cauline leaves, disciform heads with eligulate ray flowers, and subterete, 5-nerved achenes. The plants are fire-adapted, the tall, erect stems arising quickly after a burn from a thick, woody rhizome or tuber. *Leptostelma* (6 species), with prominent white or yellow rays and compressed achenes, is the most *Erigeron*-like of these four genera. Bentham (*Genera Plantarum*, 1873) and Baker (*Flora Brasiliensis*, 1882) treated the two original species as *Erigeron* sect. *Leptostelma* and Cabrera described four of the species in 1957 and 1959, placing them in *Erigeron*. Teles et al. (2008) completed the nomenclature in *Leptostelma*. *Leptostelma* is disjunct from the range of typical South American *Erigeron*, which is centered in the Andean region, but sympatric with species of conyzoid species. For consistency within this remarkable clade, it is recognized at generic rank.

Old World Aster complex

The overall evolutionary structure of Old World aster is becoming relatively clear in molecular analyses (Li et al. 2012; Jafari et al. 2015; Korolyuk et al. 2015). The main groups and many critical species have been included, although perhaps less than half of the species have been sampled. No formal, matching taxonomic framework exists but an excellent informal overview is provided by Li et al. (2012). Main features of the recent molecular-phylogenetic arrangements are noted below.

* *Galatella*, *Tripolium*, and *Crinitina* (the *Galatella* clade) are sister to the Bellidinae. Li et al. (2012) have suggested that all three may be appropriately treated as a single genus; Jafari et al. (2015) suggest that *Tripolium* and *Galatella* are distinct. Based on morphology, Karanović et al. (2015) also found that each of the two is distinct.

* *Chamaegeron* and *Lachnophyllum* together are sister to the *Galatella*-Bellidinae clade.

* *Sheareria* is placed as sister to the *Kalimeris* clade by the analyses of Li et al. (2012) and Korolyuk et al. (2015) but by Li et al. (2017) as sister to the *Aster amellus* clade.

* The *Kalimeris* clade (the *Aster ageratoides* group) includes species of *Kalimeris*, *Heteropappus*, *Aster ageratoides*, *A. orephilus*, *A. souliei*, and others. *Kalimeris* and *Heteropappus* are not each other's closest relative within the larger clade.

* The morphologically diverse *Aster amellus* clade (*Aster sensu stricto*) includes *Rhinactinidia*, *Rhynchospermum*, *Miyamayomena*, *Turczaninowia*, *Aster tataricus*, *Aster baccharoides*, *Aster maackii*, *Aster alpinus*, and others. *Miyamayomena angustifolia* (= *Aster sinoangustifolius*) is sister to the *Kalimeris*-*Aster amellus* clade pair.

* The "doellingerioid" species (*Aster scaber* et al.) are sister to the *Asterothamnus* clade, which includes *Asterothamnus*, *Arctogeron*, *Aster sikuensis*, *A. falcifolius*, and others. Species of *Kemulariella* (see Firat 2016) have not been sampled, but it seems likely from their Caucasus geography that they belong in the *Asterothamnus* clade.

* *Aster hersileoides* and *A. nitidus* as a pair are basal to the large *Aster sensu stricto* of Li et al. (2012), which includes the *Kalimeris*, *Aster amellus*, and *Asterothamnus* clades.

* *Psychrogeton* (excluding *P. obovatus*) and *Neobrachyactis* also are basal to the large *Aster sensu stricto* of Li et al.

* *Callistephus*, the morphologically isolated *Aster longipetiolatus*, *Myriactis Neobrachyactis*, and *Psychrogeton* are in a clade along with several apparently natural groups of *Aster* (e.g., *A. diplostephioides*, *A. asteroides*, *A. flaccidus*, *A. panduratus*, *A. fuscescens*, and others). The *Callistephus* group is either sister to all other Old World aster species or in an unresolved position related to the Australasian lineage.

Li et al. (2012) have suggested that *Aster sensu stricto* follow the boundaries of the molecular analysis to include the *Kalimeris*, *Asterothamnus*, and *Aster amellus* clades, with recognition of distinctive inner groups at the rank of section and series (e.g., *Arctogeron*, *Asterothamnus*, *Kemulariella*, *Psychrogeton*, *Rhinactinidia*, *Rhynchospermum*, and *Sheareria*, plus other previously unnamed species groups). They point out 18 species in 8 groups that should be removed from *Aster* and treated at generic rank.

Li et al. (2012) noted that their recircumscribed *Aster sensu stricto* remains morphologically complex — it seems probable that future taxonomy will argue for morphologically more homogeneous genera, with recognition of some smaller groups and isolated species within *Aster* (*sensu* Li et al.) at generic rank. For the GCD, pending a generally accepted taxonomy that accounts for new insights (via DNA and morphology) into phylogenetic structure and provides accompanying morphological definitions, all of these formally named segregates are recognized at generic rank with an implicit understanding of their phylogenetic position.

Symphyotrichum

The mostly North American *Symphyotrichum* (ca. 100 species) includes distinctive and mostly non-intergrading species groups. Among them, sect. *Conyzopsis* (3 species; the genus *Brachyactis*) is arguably the most distinctive — the plants are taprooted annuals with a unique chromosome number of $x=7$, biseriate and accrescent pappus, and ray florets in an outer zone of 2-4 series, with ligules absent or greatly reduced. While molecular data clearly indicate that *Brachyactis* arose from within $x=8$ *Symphyotrichum* (e.g., Vaezi & Brouillet 2009), this small group is morphologically and cytologically isolated from the rest of the genus and the rationale for not treating it at generic rank rests on a requirement for strictly monophyletic genera. Since the recent realignment of genera within American asters (in 1994), it has generally been included and accepted within *Symphyotrichum*.

Doellingeria-Eucephalus

Doellingeria (3 species, eastern North America) and *Eucephalus* (10 species, northwestern North America) are evolutionarily sister genera (e.g., Brouillet et al. 2009). They are morphologically distinct, particularly in involucre, fruits, ray color, and habit (*Eucephalus* is rhizomatous, *Doellingeria* fibrous-rooted), and there has never been a question about their delimitation. Based on plastid and ITS/ETS DNA data, however, Allen et al. (2019) have shown that *E. elegans* is sister to the *Doellingeria* species rather than to the rest of *Eucephalus*. They hypothesize that genetic interchange occurred in a hybridization event during early radiation of the *Doellingeria-Eucephalus* clade. In order to make the molecular-phylogenetic topology and the nomenclature congruent, they have enlarged *Doellingeria* to 13 species by formally transferring the *Eucephalus* species into it.

A genetic influence of *Doellingeria* on *Eucephalus elegans* is evident neither in morphology nor geography — the species of *Eucephalus* differ among themselves in relatively small ways and *E. elegans* is in no way out of place. *Doellingeria* and *Eucephalus* are discontinuously distinct and are maintained as such in the GCD. The paleo-historic and vestigial effect of hybridization can be pointed out by reference to a cladogram derived from molecular data.

Solidago and Oligoneuron

Oligoneuron (7 species) is treated by Semple and Cook (2006) as congeneric with typical *Solidago* (ca. 120 species) but the two are morphologically discontinuous and easily distinguished. Species nomenclature for *Oligoneuron* is completed below with a new combination. The horticultural entity \times *Solidaster* was formed spontaneously in Europe as a garden hybrid between *Oligoneuron album* (*Aster ptarmicoides* = *Solidago asteroides*) and *Solidago canadensis* (Schilling et al. 2008) but natural hybrids are not known (comments in Nesom 1993). Although it clearly is closely related to *Solidago*, molecular data have not resolved the phyletic position of *Oligoneuron* (e.g., Semple et al. 1999; Brouillet et al. 2009) — an intuitive diagram shown by Semple (2016) indicates a sister relationship with *Solidago*. *Oligoneuron* is placed as a separate genus in the GCD.

Oligoneuron vossii (Pringle & Laureto) Nesom, **comb. nov.** *Solidago vossii* Pringle & Laureto, Michigan Bot. 49: 108. 2010.

An octoploid, apparently with ancestry involving *Oligoneuron houghtonii* and *O. album*, known only from Crawford and Kalkaska counties, Michigan (Laureto & Pringle 2010; Michigan Flora Online 2020).

Toiyabea

Based on morphological and geographic evidence, the genus *Toiyabea* has been expanded from one species to include three other species previously placed in *Tonestus* and *Lorandersonia* (both of the latter genera are still recognized) (Nesom 2020). Distribution of the four *Toiyabea* species in the previous taxonomy suggests that interpretations were over-reliant on ambiguous molecular data and/or that ancestral hybridization influences the structure of phylogenetic trees but has little or no influence on extant morphology and current geography.

Mexican species in the Gundlachia-Gutierrezia group

The genus *Aquilula* was established (Nesom 2018) to accommodate a highland Mexican species that, along with three other species of desert habitats of Mexico, was placed by Urbatsch and Roberts (2004) in the Caribbean genus *Gundlachia*. The Mexican species are morphologically and geographically disparate when joined to the Caribbean clade and molecular data do not contradict keeping them separate (as *Gundlachia* with 7 species, monotypic *Aquilula*, and *Xylothamia* sensu stricto with 3 species).

Medranoa (1 species), *Chihuahuana* (1 species), *Xylovirgata* (1 species), and *Neonesomia* (2 species) were described as new genera of the Chihuahuan Desert by Urbatsch and Roberts (2004), segregated from a clearly polyphyletic *Xylothamia*. Despite strong morphological distinctions among the species, molecular data indicate that they are closely related and the data do not provide unambiguous support for recognition of four closely related new genera among five species. Close geographic proximity and the production of zygomorphic disc corollas by each support their recognition as a single lineage. All five species have been united within *Medranoa* (Nesom 2007), with *Chihuahuana*, *Neonesomia*, and *Xylovirgata* treated as synonyms.

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