

HYBRIDIZATION IN THE TRIBE ASTEREAЕ (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 *Symphotrichum* (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 *Symphotrichum* (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; *Symphotrichum* formerly considered a large group of North American *Aster*). Semple & Brammall (1982), however, noted that the extent of interspecific hybridization in *Symphotrichum* 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 *Symphotrichum* (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 \times *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 *Symphotrichum* 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. *Symphotrichum* 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 allopolyploid 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 *Symphotrichum* (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 *Symphotrichum* subg. *Symphotrichum* (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 allopolyploid ($n=9$) 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 $x=9$ allopolyploids 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 Astereae 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 *Damnania*, 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 *Eri-cameria* have been reinterpreted as crosses within the latter genus (Nesom & Baird 1993). A recurrent hybrid combination between two species of *Eri-cameria* 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. ($2n=36$) \times *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. ($2n=36$) \times *Kalimeris incisa* ($2n=72$); homobasic, $x=9$, the hybrids fertile (Huziwaru 1950; Inoue 1955; Tara 1973);

Polyarrhena reflexa (L.) Cass. \times *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 \times *Xanthocephalum humile* Benth.; homobasic, $x=6$, the hybrids vegetatively robust but largely sterile (Lane & Hartman 1991);

Erigeron [subg. *Trimorpha*] *acris* L. \times *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* \times *C. gracilentia* 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 \times *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 "F₂" progeny also were fertile, although whether they were backcrosses or true F₂'s is not clear.

Intergeneric hybrids have been artificially synthesized between the following species of different but closely related Astereae genera (within a subtribe):

Grindelia papposa Nesom & Suh (= *Prionopsis ciliata* [Nutt.] Nutt.) \times *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 \times *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 \times *Rigiopappus leptocladus* A. Gray; homobasic, $x=9$ (Ornduff & Bohm 1975) (Feliciniinae).

Intergeneric hybrids have been artificially synthesized between species of North American Astereae apparently more widely separated in relationship:

Almutaster (*Aster*) *pauciflorus* ($x=9$) \times *Machaeranthera arida* (Kunth) A.G. Jones ($x=5$) (Stucky 1978) (Asterinae \times Machaerantherinae);

Almutaster (*Aster*) *pauciflorus* ($x=9$) \times *Machaeranthera parviflora* A. Gray ($x=5$) (Stucky 1978) (Asterinae \times Machaerantherinae);

Symphytotrichum (*Aster*) *tenuifolium* ($x=5$) \times *Machaeranthera riparia* (Kunth) A.G. Jones ($x=5$) (Jackson 1992a) (Asterinae \times Machaerantherinae);

Haplopappus ("phyllocephalus group") *aureus* A. Gray ($x=6$) \times *Machaeranthera arenaria* (Benth.) Shinners ($x=4$) (Jackson 1985) (Machaerantherinae);

Haplopappus ("phyllocephalus group") *annuus* ($x=6$) \times *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 Astereae intergeneric hybrids, with caveats above regarding *Pleurophyllum* × *Damnania* 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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