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A review of chromosome numbers in Asteraceae with hypotheses on chromosomal base number evolution

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INTRODUCTION

In spite of the great variability in the chromosome numbers ... a pattern can be seen when the evidence is fully reviewed. — Robinson et al. 1981, p. 8

Asteraceae are the largest family of flowering plants and have long been of cytological interest. The first chromosome counts for members of the family were published more than a century ago (Juel 1900; Land 1900; Merrell 1900). The total number of chromosome number reports has increased dramatically with major efforts to determine chromosome numbers of large numbers of composites being conducted in the 1960–1980 period (e.g., Raven et al. 1960; Anderson et al. 1974). Prior to DNA sequence-based phylogenetic analyses, hypotheses on chromosomal base numbers in Asteraceae were hampered by a lack of understanding of which genera were basal within tribes and which tribes were basal within the family. For example, Cronquist (1981) reported that Asteraceae had a range of base numbers from $x = 2$ to $x = 19+$ and suggested that perhaps $x = 9$ was ancestral. Earlier, Solbrig (1977) had also concluded $x = 9$ was the ancestral base number of the family based on an analysis of habit and frequency of chromosome numbers. Bremer (1994) merely noted that chromosome number data were conveniently summarized in Solbrig (1977) and subsequent indices. In

more recent years following the introduction of molecular techniques for analyzing phylogenies through DNA restriction fragment length polymorphisms and base pair sequence analyses, authors have compared molecular results with chromosomal basal number data in order to reach conclusions on ancestral base numbers within groups of genera and among tribes (e.g., Baldwin et al. 2002; Ito et al. 2000; Chapter 37). Accessing data in all of the tens of thousands of publications reporting chromosome numbers in Asteraceae has not been convenient until very recently, when much of the information was put online in Watanabe's (2008) *Index to Chromosome Numbers in Asteraceae* (<http://www.lib.kobe-u.ac.jp/products/asteraceae/index.html>). This paper presents analyses of chromosome numbers in the online database in light of recent understanding of the phylogeny of Asteraceae (e.g., Funk et al. 2005). The first objective of the study was to compile a summary database of every genus in the family. The second objective was to determine the chromosomal base number for every genus in the family for which data were available. The third objective was to plot chromosome counts and basal chromosome numbers of every taxon onto the supertree (=metatree) phylogeny (Funk et al. 2005). The fourth object was to formulate hypotheses on patterns of chromosomal base number evolution in the family having “fully reviewed” the evidence.

MATERIALS AND METHODS

Two datasets were used as primary sources of information on chromosome numbers. The most critical of these were the data available online at <http://www.lib.kobe-u.ac.jp/products/asteraceae/index.html>, Watanabe's *Index to Chromosome Numbers of Asteraceae* (2008). The database has been updated multiples times as data from additional publications are added to the matrix. Our analysis is based on entries in the database as of March 2007. This included records on more than 38,000 chromosome number reports at the time of our analysis listed by author and taxon; and 41,000 as of September 2007. Each search of counts in a genus included a summary of the number of reports, but not a calculated total of the actual numbers of counts included in the records. When a publication reported multiple counts for a single taxon, these were not listed separately. However, the information could be tallied from data presented in the search results. Also, searches for some genera include the names of taxa for which no chromosome counts have been reported in the literature. Thus, the number of "records" listed at the top of a search report needed to be recalculated to yield the actual number of individual chromosome number reports for a genus included in the summary data matrix created for this paper. The Watanabe dataset included data extracted from 4521 publications at the time of our analysis, and 4800 as of September 2007. Details on these can be accessed from the search reports generated by the web site and are not listed here. Searches of the database for this chapter were facilitated by working off-line directly from the Microsoft Excel™ data file (*.xls) created by Watanabe. Generic nomenclature in the Watanabe database follows Bremer (1994) with post March 2007 changes to reflect treatments of taxa in *Flora of North America* (Flora of North America Editorial Committee 2006).

The second data source for chromosome counts was the first author's research database files on chromosome number reports for asters, goldenrods and miscellaneous other genera of Astereae (primarily taxa of the subtribe Chrysopsidinae Nesom and miscellaneous other North American Astereae). The Semple datasets collectively included information on 10,835 individual counts at the time of our analysis and are based on individual voucher data. These were compiled for research on cyto-geographic and taxonomic studies. Nomenclature in the Semple databases follows that of generic treatments of the Asteraceae in *Flora of North America* (vols. 19–21) with a data field indicating the name under which the count was originally published. These datasets are not available online. Each of the data files (*.ask) was created in askSam™ v.5.1.2.367 (Seaside Software Inc. dba askSam Systems, Perry, Florida).

A database summarizing information by genus on chromosome number data was constructed using askSam working from the Watanabe and Semple datasets plus information in generic treatments in *Flora of North America* (vols. 19–21). Eighteen data fields were included for each genus document. These are listed in Table 4.1 and included data on nomenclature and numbers of species, number of chromosome number reports (actual or estimated total number of counts), a list of chromosome numbers reported in the literature, ancestral and derived base numbers determined in this study, other cytological data (ploidy levels, aneuploidy, dysploidy and supernumerary chromosomes), geographic distribution information, and a field for miscellaneous observations, e.g., alternative sources of data, etc.

The completed generic summary database was searched to generate reports on a number of different cytological and taxonomic questions. Lists of genera with cytological data were generated for each tribe, subtribe or clade. Separate lists of all genera sorted alphabetically, by chromosomal base number, and by numbers of reports were also generated. Reports were saved as *.ask files, which can be exported as *.txt, *.rtf, *.html and several other file formats.

RESULTS AND DISCUSSION

Data on 1587 genera of Asteraceae and 15 genera of Calyceraceae and Goodeniaceae were included in the generic summary database. The results of analyses of numbers of counts and reports by genus are summarized by tribe/clade in Table 4.2 listed in the order of branching of clades on the supertree phylogeny of Funk et al. (2005). Included in Table 4.2 by tribe/clade are the numbers of genera included in this study compared with the number of genera reported for each tribe/clade in Bremer (1994), the percent of genera with at least one chromosome number report, an estimate of the number of species, and an estimate of the number of count reports.

An estimated 58,320 chromosome number reports were summarized; 58,124 of these reports were for Asteraceae. The actual number of chromosome number count determinations made on individuals is not known because this information was not always included in a publication. In some cases, a report was based on a chromosome count from a single individual of a taxon. In other cases, several hundred to more than a thousand counts were reported for a single taxon in one publication (e.g., Semple 1989). Papers reporting very large numbers of counts (>100) for a taxon were usually cyto-geographic studies. At least one chromosome count has been reported for a taxon in 978 genera of Asteraceae (61.6%); no data were available for 611 genera in the family. Thirteen genera were found

to have more than 1000 chromosome number reports in total (Table 4.3). The majority of genera have ten or fewer chromosome number reports (598 genera; 37.7%); 203 genera (12.8%) have been sampled only once.

The number of species of composites is estimated to be 22,472 (= total of all estimated numbers of species by genus) in 1587 genera. Cronquist (1981) estimated there to be about 1000 genera and 20,000 species in Asteraceae. Bremer (1994) recognized 1535 genera and raised the number of species to around 23,000. Bremer (1994) was the primary database on most genera included in our analysis, and thus it is not surprising that our numbers of genera and species are similar to those in Bremer (1994). The larger number of genera of Astereae reported here is the direct result of numerous DNA sequence studies published in recent years and incorporated into the generic limits followed in *Flora of North America*.

Some other errors were also undoubtedly introduced into the summary of genera in the database due to nomenclatural problems and data entry errors. The *International Plant Names Index* (<http://www.ipni.org/index.html>) was frequently consulted in the creation of the summary data matrix in order to reduce the number of errors due to nomenclature. Checking synonymy sometimes revealed a case of double counting of a species and including its cytological data under two genera. The case with asters is informative and indicative of possible sources of error

at the time our analysis was first completed and involves the two authors of this paper. In the Watanabe database in March 2007, counts for asters were generally listed in the genus *Aster* L. under which the majority of the counts were originally reported. The online index contained 1753 records for *Aster* s.l. and one record for the North America aster genus *Symphotrichum* Nees. The Semple database had 4578 reports for *Symphotrichum* and only about 100 reports for the Eurasian genus *Aster* s.str. (clearly reflecting a geographic bias in data entry to date). However, when the numbers of reports were tallied for the Eurasian species included in the Watanabe database, it contained 2128 reports for 27 Eurasia species of *Aster* s.str. The number of reports for North American species of *Symphotrichum* was larger in the Semple database than the Watanabe database because the former included more than 600 unpublished counts to be reported in unfinished cytogeographic studies. The conclusion to draw from the asters case is simple: anyone searching a database on chromosome numbers must pay attention to the generic concepts followed in entering the data. Many of these kinds of potential errors were sorted out using the synonymy in generic treatments in *Flora of North America*. We are pleased to note that changes to the nomenclature of asters in the Watanabe database post March 2007 were made so that reports of counts for North American species of asters are listed when searching *Doellingeria*, *Eurybia*,

Table 4.1. Data fields included in the summary database on genera.

PHYL[Number for phylogenetic ordering of clades/tribes in reports 0–37
TRIBE[
CLADE[Any major but informal subtribal groupings
SUBTRIBE[
GENUS[
AUTH[Authority(-ies) of generic name
SPP[Number of species
REPS[Number of published reports in on-line Index Chromo Asteraceae
X=[Base number (not always obvious)
X2=[Derived base numbers (not always obvious)
2n=[All sporophytic numbers, meiotic and mitotic
POLY[Yes/no polyploidy present
PLEVELS[2x, 4x, 6x, etc.
DYSP[Yes/no dysploidy present; base number shift up or down
ANEU[Aneuploid numbers reported (interpretation of Index data)
SUPERS[Yes/no supernumeraries (fragments, B's, etc.)
LOC[General information on distribution; continent, country; state or province for North American taxa
OBS[Notes on cytology, classification, problems to check; some synonyms

Table 4.2. Summary of numbers of genera with and without chromosome data by tribe/clade.

No.	Tribe	Included in this study	No. of genera in Bremer (1994)	% of total genera included ^a	Genera with counts	Genera without counts	% genera included with counts	Estimated number of species	Estimated number of count reports
Basal Grade									
1	Barnadesieae	9	9	100%	6	3	67%	92	28
2	<i>Stiffitia</i> clade	3	2	150%	1	2	33%	18	1
3	Mutisieae	55	58	95%	27	28	49%	685	238
4	Gochnatieae	3	3	100%	2	1	67%	77	2
5	<i>Hecastocleis</i> clade	1	1	100%	1	1	100%	1	1
Carduoideae									
6	Dicomeae	7	7	100%	3	4	43%	103	5
7	Oldenburgieae	1	1	100%	1	0	100%	4	3
8	Tarchonantheae	2	2	100%	2	0	100%	17	3
9	Cardueae	83	83	100%	53	30	64%	2,557	4,093
10	Pertyeae	4	4	100%	2	2	50%	69	58
11	Gymnarrheneae	1	1	100%	1	1	100%	1	2
Cichorioideae									
12	Gundelieae	2	2	100%	2	0	100%	3	9
13	Cichorieae	100	98	102%	80	20	80%	1,850	11,635
14	Arctotideae	17	17	100%	8	9	47%	209	66
15	Liabeae	14	14	100%	12	2	86%	159	88
16	Vernonieae ^b	105	98	107%	42	63	40%	897	1001
17	unassigned	3	3	100%	1	2	33%	30	3
Asteroideae									
18	Senecioneae	120	120	100%	65	55	54%	3,196	2,784
19	Calenduleae	8	8	100%	6	2	75%	112	194
20	Gnaphalieae	181	162	112%	95	86	52%	2,014	1,419
21	Astereae	215	170	126%	140	75	65%	2,638	20,052
22	Anthemideae	110	109	101%	69	41	63%	1,732	4,598
23	Inuleae	67	67	100%	35	32	52%	716	729
24	Athroismeae	3	3	100%	2	1	67%	27	2
Helenieae–Helianthoid clade									
25	Helenieae	13	13	100%	12	1	92%	117	441
26	Coreopsideae	24	20	120%	16	8	67%	420	980
27	Neurolaeneae	1	2	50%	1	0	100%	13	11
28	Tageteae	33	32	103%	23	10	70%	265	598
29	Chaenactideae	3	3	100%	3	0	100%	20	101
30	Bahieae	18	18	100%	17	1	94%	73	240
31	Polymnieae	2	2	100%	2	0	100%	9	67
32	Heliantheae	132	108	122%	95	37	72%	1,350	3,010

Table 4.2. Continued.

No.	Tribe	Included in this study	No. of genera in Bremer (1994)	% of total genera included ^a	Genera with counts	Genera without counts	% genera included with counts	Estimated number of species	Estimated number of count reports
33	Millerieae	34	38	89%	25	9	74%	358	737
34	Madieae	36	36	100%	36	0	100%	200	1,445
35	Perityleae	5	5	100%	4	1	80%	76	177
36	Eupatorieae	168	170	99%	89	79	53%	2,350	3,316
Incertae sedis									
	<i>Galeana</i>	1	1	100%	0	1	0%	3	0
	Villanova clade	2	2	100%	1	1	50%	10	2
	<i>Welwitschiella</i>	1	1	100%	0	1	0%	1	0
	Totals	1,587	1,493		978	611	61.6%	22,472	58,136

^a The total number of genera is based on Bremer (1994) or the tribal description in *Flora of North America* (2006).

^b Number of genera counted and percentages based on data provided by Dr. Harold Robinson to update Watanabe database.

Symphotrichum etc., rather than collectively under *Aster* s.l. The asters case demonstrates the advantage of on-line databases that can be updated and modified often, which is not the situation with printed databases or static online databases. The effort needed to keep a database such as Watanabe's *Index* up-to-date is large and time-consuming. For genera in other parts of the world, we have less confidence in decisions made while creating the summary of genera database. For nomenclature-related

problems in genera within the same branch of the super-tree of Funk et al. (2005), errors in assigning species and their chromosome counts to the correct genus have little or no significance to the tribal and family level conclusions presented below.

In Table 4.2, a wide range in the percent of genera for which at least one chromosome count has been reported among tribes/clades is presented. At least one chromosome number has been reported for all 36 primary clades in the family. All genera have been sampled in a number of the smaller tribes, e.g., Gundelieae and Polymnieae. For tribes with more than ten genera, the range of those sampled was 40%–100%. For the seven tribes with more than 100 genera, the average number of genera sampled was 60.75%. Vernoniaceae were the least well sampled with chromosome counts reported for only 40% of the genera using data in the Watanabe *Index* that was updated late in this study with the assistance of Dr. Harold Robinson. However, prior to assigning counts originally published under the generic name *Vernonia* to the many genera that have been segregated from it, only 23% of the genera in Vernoniaceae had at least one chromosome number reported. The average number of genera sampled for the six other large tribes was 64.2%, which is slightly more than for the entire family; the six tribes Senecioneae, Gnaphalieae, Astereae, Anthemideae, Heliantheae and Eupatorieae include about 57% of the genera in the family.

A very large range in chromosome numbers and chromosomal base numbers occurs in Asteraceae. More than 180 different mitotic counts have been reported: $2n = 4, 4+1-3, 5, 6, 6+1-2Bs, 7, 8, 8+1-6Bs, 9, 10, 10+1-2B, 11, 12, 12+1, 12+1-4Bs, 13, 14, 14+1-2, 15, 16, 17, 18, 18+1,$

Table 4.3. Thirteen genera with more than 1000 chromosome count reports.

No. of reports	Genus	Tribe
4578	<i>Symphotrichum</i>	Astereae
4549	<i>Solidago</i>	Astereae
4017	<i>Taraxacum</i>	Cichorieae
2129	<i>Aster</i>	Astereae
2128	<i>Crepis</i>	Cichorieae
1905	<i>Eupatorium</i>	Eupatorieae
1884	<i>Brachyscome</i>	Astereae
1709	<i>Hieracium</i>	Cichorieae
1605	<i>Senecio</i>	Senecioneae
1600	<i>Xanthisma</i>	Astereae
1489	<i>Centaurea</i>	Cardueae
1400	<i>Artemisia</i>	Anthemideae
1158	<i>Erigeron</i>	Astereae

18+1-4B, 18+2, 19, 20, 20+1-5, 20+1-6B, 21, 22, 22+1-3, 24, 24+1, 24+1B, 24+5-9, 25, 26, 27, 28, 29, 30, 30+2, 30+2B, 31, 32, 33, 34, 34+1frag, 35, 36, 36+1, 36+1-2, 37, 38, 39, 40, 40-45, 40-47, 40+2Bs, 42, 42-44, 44, 45, 45-50, 46, 47+3, 48, 48+1, 48+3Bs, 50, 50-52, 51, 51-52, 52, 53, 54, 54+1-5supers, 55, 56, 56-58, 57, 58, 58-59, 60, 61, 62, 63, 64, 65, 66, 67, 68, 69-72, 70, 72, 72-74, 76, 78, 80, 81, 84, 85, 86, 87, 88, 90, 92, 95, 96, 98, 100, 108, 110, 112, 114, 120, 122, 130, 138, 140, 146, 154, 160, 160+, 171, 176, 180, 184, 198, ca. 228, ca. 288, ca. 324, ca. 432. The most frequent number in the database was $2n = 18$ because it is the most frequent number reported in Astereae, which has the largest number of counts reported, and in several other larger tribes. Two species in the tribe Astereae have the very low sporophytic number of $2n = 4$, *Brachyscome dichromosomatica* C.R. Carter and *Xanthisma gracile* (Nutt.) D.R. Morgan & R.L. Hartman. The highest number reported is $2n =$ ca. 432 ($48x$; $x = 9$) for *Olearia albida* Hook. f. (Beuzenberg and Hair 1984), also in the tribe Astereae.

More than 170 different meiotic counts have been reported: $2n = 2_{II}$, 3_{II} , $3_{II}+1-8B$, 4_{II} , $4_{II}+2sup$, $4_{II}+1-3_1Bs$, $4_{II}+1-2_{II}Bs$, 5_{II} , $5_{II}+1$, $5_{II}+1-4Bs$, $5_{II}+10_1$, 6_{II} , $6_{II}+1-2Bs$, $7_{II}+2_1$, 8_{II} , $8_{II}+1$, $8_{II}+1-2B$, 9_{II} , $9_{II}+1-2_1$, $9_{II}+2Bs$, $9_{II}-12_{II}$, 10_{II} , $10_{II}+1$, $10_{II}+1-2Bs$, $10_{II}+10_1$, 11_{II} , $11_{II}+1_1$, $11_{II}+8_1$, 12_{II} , $12_{II}+3Bs$, 13_{II} , $13-14_{II}$, $13_{II}+1_1$, $9_{II}+9_1$, 14_{II} , 15_{II} , $15_{II}-16_{II}$, $15_{II}-17_{II}$, $15_{II}+1B$, $15_{II}+1frag$, 16_{II} , $16_{II}+1_1$, $16_{II}+1_1$, $16_{II}-18_{II}$, 17_{II} , $17_{II}-24_{II}$, $17_{II}+1-4frags$, $17_{II}+1_1$, $17_{II}+1_1$, $17_{II}+5_1$, $17_{II}+6B$, 18_{II} , $18_{II}-20_{II}$, $18_{II}-27_{II}$, $18_{II}-20_{II}$, $18_{II}+1frag$, $18_{II}+1_1$, 19_{II} , $19_{II}+1frag$, $19_{II}+1_1$, $19_{II}+2-3Bs$, $19_{II}+2-3frag$, $19_{II}+4-7B$, 20_{II} , $20_{II}+1_1$, $20_{II}+1frag$, 21_{II} , $21_{II}+1_1$, 22_{II} , 23_{II} , 24_{II} , $24_{II}-27_{II}$, $24_{II}-30_{II}+8-20_1$, 25_{II} , $25_{II}+1-6frag$, $25_{II}+Bs$, 26_{II} , $26_{II}+1-3Bs$, 27_{II} , $27_{II}+6_1$, $27-28_{II}$, $27_{II}-30_{II}$, 28_{II} , $28_{II}+2_1$, $28_{II}-29_{II}$, 29_{II} , $29_{II}+1_1$, 30_{II} , $30_{II}+2_1$, $32_{II}+1_{II}$, $32_{II}-34_{II}$, 33_{II} , $33_{II}-34_{II}$, 34_{II} , $34_{II}-36_{II}$, $34_{II}+2_1$, 36_{II} , $36_{II}-38_{II}$, 38_{II} , 39_{II} , 40_{II} , 41_{II} , $42_{II}-44_{II}$, 43_{II} , 44_{II} , $44-45_{II}$, 45_{II} , 46_{II} , $47-48_{II}$, $47_{II}+3_1$, 48_{II} , 50_{II} , $50_{II}+1-8supers$, 51_{II} , 52_{II} , 54_{II} , 59_{II} , $59-60_{II}$, 60_{II} , 64_{II} , 68_{II} , $68_{II}-69_{II}$, 70_{II} , 72_{II} , 80_{II} , 86_{II} , $89-96_{II}$, 100_{II} , $102_{II}-108_{II}$, ca. 108_{II}, ca. 110_{II}, ca. 131_{II}. The range in meiotic counts is the same as for mitotic counts with the exception of only reaching about $30x$ to $32x$. Meiotic irregularities and precocious divisions of some bivalents account for many of the reported numbers. These make determining with certainty the chromosome number of polyploid individuals more difficult. In our experience, interpreting meiosis is generally more difficult than counting mitotic chromosomes, and this is particularly true because such a large number of composites are of polyploid origin. However, growing live plants for root tip squashes to obtain mitotic counts is often not possible.

Two categories of chromosomal base numbers occur in Asteraceae. First, x numbers include the ancestral base numbers (plesiomorphies) and the base numbers derived

from these via dysploidy. Dysploidy is the change in the chromosomal base number through a rearrangement of chromatin and loss or gain of a centromere without necessarily changing the amount of chromatin in the karyotype. In Asteraceae, dysploidy decreases are common to very common in some clades, while increases appear to be rare or very rare depending upon how the higher x numbers are interpreted. Base numbers of $x = 2, 3, 4, 5, 6, 7, 8, 9, 10$, and 11 occur in the family. Some of these numbers may be the result of a dysploid increase, others are undoubtedly the result of a series of dysploid decreases. There are many, many cases of dysploid series from higher to lower base numbers in Asteraceae, and these are found in nearly all of the 36 main branches of the phylogeny. Dysploidy is unknown in a few of the branches due to a lack of data (no counts or very few counts). Even some of the smaller branches with few taxa have some dysploidy. Dysploidy occurs in 102 genera with x base numbers and in 112 genera with derived x_2 base numbers. In total, dysploidy occurs in 214 genera, 21.9% of the 978 genera with counts reported.

Numerous secondarily derived base numbers (x_2) are also common in the family. These evolved in several different ways. Derived base numbers can result from allopolyploid combinations of x numbers. For example, the $x_2 = 9$ base number in *Chrysopsis* (Astereae) is derived from hybridizing $x = 4$ and $x = 5$ parental taxa and subsequent chromosome number doubling and diploidization (Semple and Chinnappa 1980). Alternatively, derived base numbers can result from autopolyploidy and subsequent diploidization of the karyotype resulting in a x_2 that is a multiple of the ancestral x number of the clade. Nearly the entire *Olearia* II clade in Astereae appears to be based on a diploidized $12x$ ploidy level (Cross et al. 2002; Chapter 37). Dysploid decreases also occur in clades with derived x_2 . The following derived base numbers occur in the family: $x_2 = 19, 18, 17, 16, 15, 14, 13, 12, 11, 10, 9, 8, 7, 6, 5, 4$, and 3. Dysploidy has also occurred in polyploids of these derived numbers resulting in much larger x_2 numbers and dysploid numbers derived from them.

Polyploidy is common in Asteraceae and occurs in most major clades. In total, polyploidy occurs in 570 genera, 58.3% of the 978 genera with counts reported; this includes all genera of the major Hellenioid-Helianthoid clade. Polyploidy occurs in 247 genera without x_2 base numbers, 25.3% of the 978 genera with counts reported. Polyploidy is common in the most basal branch of Asteraceae, subfam. Barnadesioideae, in which only *Schlechtendalia* is known to occur at a presumed diploid level with a dysploid derived base number. The following ploidy levels occur in Asteraceae: $2x, 3x, 4x, 5x, 6x, 7x, 8x, 9x, 10x, 12x, 14x, 15x, 16x, 18x, 20x, 22x, 24x, 32x, 36x$, and $48x$. Frequencies of ploidy levels are summarized in Table 4.4. Diploids are most frequent and

Table 4.4. Frequencies of ploidy levels in Compositae.

Ploidy level	Number of genera		% of 978 genera with counts		Genus	Tribe
	Only level	With other levels	Only level	With other levels		
Base numbers (x)						
2x	270	440	27.6%	45.0%		
3x	0	34	0.0%	3.5%		
4x	25	193	2.6%	19.7%		
5x	0	16	0.0%	1.6%		
6x	20	93	2.0%	9.3%		
7x	0	6	0.0%	0.6%		
8x	1	41	0.1%	4.2%	<i>Paragynoxys</i>	Senecioneae
9x	0	5	0.0%	0.5%		
10x	3	25	0.3%	2.6%		
12x	1	24	0.1%	2.5%	<i>Pachystegia</i>	Astereae
14x	0	5	0.0%	0.5%		
12x + 14x	1	4	0.1%	0.4%	<i>Soliva</i>	Anthemideae
15x	0	1	0.0%	0.1%	<i>Werneria</i>	Senecioneae
16x	0	3	0.0%	0.3%	<i>Antennaria</i>	Gnaphalieae
					<i>Raoulia</i>	Gnaphalieae
					<i>Werneria</i>	Senecioneae
18x	0	2	0.0%	0.2%	<i>Tetradymia</i>	Senecioneae
					<i>Antennaria</i>	Gnaphalieae
20x	0	2	0.0%	0.2%	<i>Antennaria</i>	Gnaphalieae
					<i>Werneria</i>	Senecioneae
22x	0	1	0.0%	0.1%	<i>Olearia</i> II	Astereae
32x	0	1	0.0%	0.1%	<i>Olearia</i> II	Astereae
36x	0	1	0.0%	0.1%	<i>Olearia</i> II	Astereae
48x	0	1	0.0%	0.1%	<i>Olearia</i> II	Astereae
Derived base numbers (x ₂)						
2x	289	300	29.6%	30.7%		
3x	0	27	0.0%	2.8%	<i>Amauriopsis</i>	Bahieae (apomict)
4x	8	129	0.8%	13.2%		
5x	0	10	0.0%	1.0%		
6x	1	41	0.1%	4.2%	<i>Erechtites</i>	Senecioneae
7x	0	2	0.0%	0.2%		
8x	0	21	0.0%	2.1%		
9x	0	0	0.0%	0.0%		
10x	0	7	0.1%	0.7%		
12x	0	9	0.0%	0.9%		
16x	0	2	0.0%	0.1%	<i>Chromolaena</i>	Eupatorieae
					<i>Leptinella</i>	Anthemideae
20x	0	1	0.0%	0.1%	<i>Leptinella</i>	Anthemideae
24x	0	1	0.0%	0.1%	<i>Leptinella</i>	Anthemideae

were the only ploidy level occurring in 270 genera with x base numbers and in 289 genera with diploidized x_2 base numbers, 27.6% and 29.6% of the 978 genera with counts reported, respectively. Higher ploidy levels occur with decreasing frequency as the ploidy level increases; 7.4% (x) and 2.9% (x_2) of the 978 genera with counts reported include ploidy levels of $8x$ to $10x$; 3.9% (x), and 1.3% (x_2) of the 978 genera with counts reported include ploidy levels of $12x$ and higher levels.

Supernumerary chromosomes of various kinds have been reported in 143 genera of Asteraceae. Of these, 45 genera have been reported to have B chromosomes. It was not determined by us whether or not these reports were for true B chromosomes (Jones and Rees 1982) such as found and well studied in *Xanthisma gracile* and *X. texanum* DC. or were merely supernumerary chromosomes mislabeled as B chromosomes. Some reports may even have been errors in reporting the distal portion of the satellite chromosome as a supernumerary when the satellite was well separated from the proximal portion of the chromosome. For example, the large distal portion of the satellite chromosomes in *Eurybia* and *Symphotrichum* (both Astereae) could easily be mistaken for separate small supernumerary chromosomes (J.C. Semple, pers. obs.) or separate autosomal chromosomes (Watanabe et al. 2007).

The frequency of aneuploidy was also analyzed. True aneuploidy is the gain or loss of single chromosomes without changing the base chromosome number. Due to the large number of ambiguous chromosome counts published as “circa” reports or as errors in reports based on sectioning techniques, it was unclear if ranges in numbers about a base number or multiple of the base number in polyploids were indications of aneuploidy occurring in a taxon or if these ranges were counting errors. Therefore, no reliable frequency of aneuploidy can be reported here.

Chromosomal base number evolution in Asteraceae

Speculating on base chromosome numbers offers, perhaps, the finest of all vehicles for intellectual auto-stimulation. — e-mail from J.L. Strother to J.C. Semple, 16 June 2006

Ancestral base numbers for each of the 36 main branches of the supertree phylogeny (Funk et al. 2005) were determined, as were the base numbers for Goodeniaceae and Calyceraceae. The latter two families have a base number of $x = 9$ with lower base numbers of $x = 8$ and $x = 7$ derived by downward dysploidy. In the *rbcL* DNA phylogeny of Asterales (Gustaffson et al. 1996), the basal grade in Goodeniaceae included *Anthotium* R. Br., *Dampiera* R. Br., *Lechenaultia* R. Br. and *Brunonia* Smith. All four genera have base numbers of $x = 9$ (Peacock 1963). In

Goodeniaceae, *Goodenia* and *Cooperookia* with $x = 8$ or 7 were in a derived position in the family (Gustaffson et al. 1996). A phylogeny of Asteraceae with ancestral chromosomal base numbers superimposed is shown in Fig. 4.1. An ancestral base number of $x = 9$ is hypothesized for Barnadesieae with $x = 8$ being derived by downward dysploidy. The genera *Arnaldoa*, *Chuquiraga* and *Dasyphyllum* have polyploid chromosome numbers with $x_2 = 27$ based on counts in Watanabe’s online index and Watanabe et al. (2007). *Doniophyton* has reported numbers of $2n = 24_{II}$, 48, and 25_{II} suggesting base numbers of $x_2 = 25$ and $x_2 = 24$ derived from an ancestral $x_2 = 27$ via downward dysploidy. The hexaploid ploidy level would have reduced the rate of evolution allowing these genera to retain plesiomorphic traits for the family. Chromosome numbers reported for *Barnadesia* ($2n = 12_{II}$, 14_{II} , 25_{II} , 50–52, 52, 54, 62, ca. 50_{II}) suggest more karyotype evolution has taken place in the genus than other related genera or some of the counts are inaccurate. *Schlechtendalia* has a base number of $x = 8$, which is likely derived by dysploid decrease. However, it is difficult to infer dysploid reduction from $2n = 54$ to $2n = 18$ or 16 at a bound. Thus it is possible that the $x = 8$ base number for *Schlechtendalia* has been derived from the ancestral $x = 9$ by dysploid reduction and $2n = 54$ for *Barnadesia* and *Dasyphyllum* is a hexaploid state based on the original base chromosome number, $x = 9$. Stuessy et al. (1996) considered *Schlechtendalia* to be primitive within Barnadesioideae, but this is not supported by the derived position of the genus on the supertree (Funk et al. 2005); the phylogram in Stuessy et al. (1996) shows little similarity to the generic arrangement in the supertree. A basal position for *Schlechtendalia* based on new molecular sequence data, however, is an alternative that still cannot be refuted (see Chapter 13).

The chromosome number/habit situation in Barnadesieae looks similar to primitive angiosperm families with the high base chromosome numbers and with the woody habits in the woodland or forests (= the closed plant community). These high chromosome numbers, the woody habits (tree, shrub or liana) and their habitats in the closed plant communities are linked very closely. In contrast, the herbaceous members, *Acicarpha spathulata* (Calyceraceae), *Schlechtendalia luzulaefolia* and *Hecastocleis shockleyi* (Asteraceae) have the lower chromosome number of $2n = 16$ and their habitats are open plant communities such as the maritime coastal sand-dune (*Acicarpha spathulata*) and arid semi-desert (*Hecastocleis shockleyi*). They have very specialized morphology such as succulent (*Acicarpha spathulata*) or spiny (*Hecastocleis shockleyi*) leaves, and seeds embedded within the receptacle (*Acicarpha spathulata*). In sister families of Asteraceae, members of Goodeniaceae and Calyceraceae are herbs and have the low chromosome base number $x = 9$ and occur in open plant communities. In more basal Asteraceae, the $n = 8$

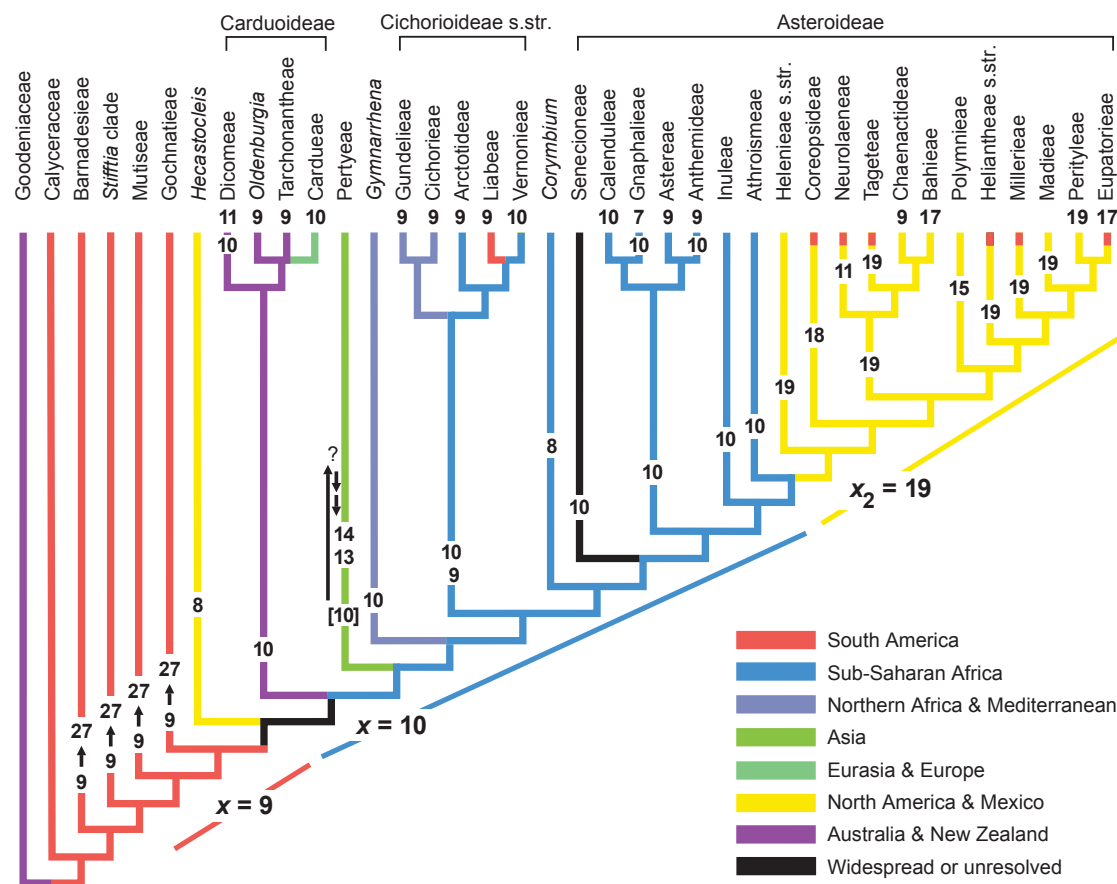


Fig. 4.1. Chromosomal base number evolution in Asteraceae. Hypothesized base numbers are superimposed on the summary tree of the supertree (=metatree) phylogeny presented by Funk et al. (2005).

for *Schlechtendalia luzulaefolia* and *Hecastocleis shockleyi* is a derived number. These specialized habitat taxa have a more restricted recombination system and more immediate fitness instead of genetic flexibility. Such a genetic system appeared to be causally connected with the dependence on ample seed production as the only means of propagation in short lived plants and with rapid population establishment in labile and briefly available habitats (Grant 1958; Stebbins 1958; Ehrendorfer 1970).

An $x=9$ ancestral base number is hypothesized for the next three branches on the supertree (Fig. 4.1). The chromosome counts reported for the *Stiffia* clade are $2n=54$ (Gibbs and Ingram 1982; Watanabe et al. 2007). This also is hypothesized to be a paleopolyploid with $x_2=27$ derived from an $x=9$ ancestor. Additional counts for this clade are needed. Genera in Mutisieae include chromosome counts indicating that both polyploidy and dysploidy have occurred multiple times. Base numbers of x or $x_2=8, 9, 10, 11, 12, 14, 15, 22, 23, 24, 25, 26, 27, 36$ are indicated by the many counts for the tribe. We hypothesize that multiple downward dysploid events from polyploids based on $x=9$ account for all,

or nearly all, of the base numbers listed. These are the result of long dysploid series from polyploids of $x_2=27$. There was a reduction in chromosome number from $x_2=27$ (e.g., *Acourtia*) to $x_2=14$ and 11 (*Chaetanthera*) with a change in growth form from shrub to herb habit within Mutisieae. In Gochnatieae, four counts have been reported; $2n=54$ for *Cyclolepis* and $2n=54, 2n=ca. 23_{II}$ and $2n=44$ for *Gochmatia*. A paleopolyploid base of $x_2=27$ is hypothesized, again being derived from an $x=9$ ancestor. Therefore, the basal grade of tribes native to South America all are hypothesized to have an ancestral chromosomal base number of $x=9$. Alternatively, the *Stiffia* clade, Mutisieae and Gochnatieae could have an ancestral base number of $x_2=27$, with all other numbers in the three clades derived from this presumably diploidized hexaploid number. Such a possibility would then necessitate a long, and undocumented, dysploidy series from $x_2=27$ to $x_2=11, 10, 9$ and 8 in the next series of tribes/clades on the supertree. We remind the reader of Strother's comment on base numbers at this point in the discussion. If Barnadesieae were also hypothesized to be $x_2=27$ and this is assumed to be basal for Asteraceae,

then all chromosome numbers in the family would be x_2 numbers. This does not seem likely at this time.

The next branch on the supertree includes just *Hecastocleis* with one report of $2n = 16$. A base number of $x = 8$ is indicated for this North American genus. We hypothesize that it is derived by downward dysploidy from $x = 9$. Additional chromosome counts are needed to test this hypothesis.

Funk et al. (2005) noted that next nine major branches on the supertree were likely African in origin. The red lines of the South American grade were replaced by blue, lavender and green lines on their phylogeny. Shifts from $x = 9$ to $x = 10$ and 11 are hypothesized to have occurred accompanying the shift in geography. Ancestral base numbers of $x = 10$ or 11 (Dicomeae), $x = 10$ (Cardueae, *Gymnarrhena*, Vernoniaeae, Senecioneae, Calenduleae, Gnaphalieae, Anthemideae, Inuleae [including Plucheae] and Athroismeae) and $x = 9$ (*Oldenburgia*, Tarchonanthaeae, Gundelieae, Cichorieae, Arctotideae, Liabeae, and Astereae) are hypothesized based on the known chromosome numbers of basal members of these clades. Therefore, the base number of Carduoideae is $x = 10$. The base number of Cichorioideae could be either $x = 10$ or $x = 9$. We hypothesize that it was ancestrally $x = 10$.

The four core Asteroideae tribes also are likely to have been ancestrally $x = 10$. In Calenduleae, Nordenstam (1994) concluded a base number of $x = 10$ appeared likely, and we agree that this is most parsimonious with $x = 8$ and $x = 7$ derived by downward dysploidy. In Anthemideae and Gnaphalieae, decreases from $x = 10$ early in their histories to $x = 9$ and 7, respectively, are hypothesized. Watanabe et al. (1999) noted the difficulty in determining the ancestral base number in Gnaphalieae due to a lack of chromosome counts for African taxa. The few counts available for members of the subtribe Relhaniinae suggest base numbers of $x = 9$, 8, and 7, but the majority of genera have not yet been sampled cytologically even once. Counts with $x = 10$ have been reported in a few genera of Anthemideae. Only Astereae shifted to $x = 9$ via downward dysploidy before diversifying. However, the two most basal genera in Astereae, *Denekia* and *Printzia*, are unknown cytologically. Should either of these be found to have $x = 10$ as a base number, then Astereae also would be ancestrally $x = 10$.

Based on the preponderance of clearly downward dysploidy events in Asteraceae, it seems likely that upward dysploidy events are much more difficult to successfully complete. An increase in base number could result from trisomic aneuploidy of a single chromosome homologue that does not produce a lethal increase in gene product from the three copies of each gene. Aneuploidy would readily provide the new centromere needed for the increase in base number, and chromosome rearrangements and loss or suppression of critical genes could result in

a stabilized new higher base number. Such an evolutionary process involves more difficult steps than simply rearranging existing chromatin on fewer centromeres to achieve a dysploid decrease. This difference in likelihood would account for the rarity of dysploid increases in the family and the relative commonness of dysploid decreases. Therefore, we have hypothesized very few ancestral dysploid increases in favor of many long dysploid series with gaps in base numbers from high to low due to extinctions or lack of discovery.

The two other tribes in this middle portion of the supertree are hypothesized to have derived base numbers. Pertyeae have chromosome numbers indicating possibly derived base numbers of $x_2 = 14$, and 13. We hypothesize that these are not derived by serial upward dysploidy from base number of $x = 10$ or 9 or 8, but rather they are derived by a series of downward dysploid events from a polyploid ancestor with $n = 20$, 18 or 16. The same series of events is a documented pattern in the Helenioid–Helianthoid clade and also appears to have occurred in Vernoniaeae with $x_2 = 17$ being derived from $x = 10$, 9 and 7 ancestors. This appears to be the “easier” evolutionary process than multiple dysploid increases to reach $x = 14$. *Corymbium* forms the other mid tree clade with a derived base number, but in this case $x = 8$ is indicated by the single count of $2n = 16$. Two downward dysploid events from an $x = 10$ ancestor are hypothesized in this branch of the supertree.

Numerous and sometimes well documented downward dysploid series have occurred in Cichorieae, Astereae and Gnaphalieae. Some of these cases are classical studies in cytotaxonomy and need not be discussed further here, e.g., *Crepis* and *Brachyscome*. Polyploidy is also frequent in these tribes resulting in them being some of the more intensively studied tribes cytologically over many years.

Funk et al. (2005) noted a second major geographic shift in the location of composite evolution indicated on their supertree diagram by a shift from blue, lavender and green lines to yellow lines for North American origins. This is the large terminal Helenioid–Helianthoid clade of the phylogeny. Baldwin et al. (2002) discussed this portion of the tree in detail noting the high derived ancestral base numbers for all the tribes in the clade; they hypothesized that $x_2 = 18$ was ancestral with multiple upward dysploidy events to yield $x_2 = 19$. Decades earlier, Smith (1975) and later Robinson et al. (1981) hypothesized $x = 17$ –19 as basal for Heliantheae s.l., with Robinson et al. presenting arguments suggesting $x = 19$ being derived via aneuploidy from $2n = 4x = 20$. During this same pre-DNA sequence time period, base numbers of $x = 8$ or 9 (Stuessy 1977) and $x = 8$ –12 (Solbrig et al. 1972) were suggested for Heliantheae s.l. We hypothesize that $x_2 = 19$ is ancestral for the entire clade (Fig. 4.1) because we believe multiple dysploid increases are much less likely than

numerous dysploid decreases. In our database, $x_2 = 19$ taxa occur in Helenieae, Tageteae, Bahieae, Heliantheae, Millerieae, Madieae, and Perityleae. Dysploid derived numbers of $x_2 = 18, 17, 15,$ and 11 appear to be ancestral in Coreopsideae, Eupatorieae, Polymnieae, and Neurolaeneae, respectively. The ancestral base number in Chaenactideae may be $x_2 = 9$, with $x_2 = 17$ being secondarily derived, but this is not certain (Mooring 1965; Baldwin et al. 2002).

There are several ways that $x_2 = 19$ could have evolved, and we do not favor one possibility over another due to a lack of conclusive evidence. In each scenario, downward dysploidy would have been involved, but the timing differs. Athroismeae are sister to the entire clade, and this has a base number of $x = 10$. The $x_2 = 19$ base number could be an allopolyploid derived from $x = 10$ and $x = 9$ parental taxa. The dysploid event would have occurred before the polyploid event. Alternatively, a tetraploid taxon with $n = 20$ and $x = 10$ could have undergone subsequent downward dysploidy and diploidization to yield $x_2 = 19$. There is evidence that both scenarios have occurred in other tribes, although the base numbers involved are different. Robinson et al. (1981) noted a tendency for higher base numbers to stabilize at numbers less than double the original lower base number. This observation lends support to $x_2 = 19$ evolving with polyploidy first ($2n = 4x = 20$) and subsequent dysploidy and karyotype diploidization.

Within the Helenioid–Helianthoid clade, short to long downward dysploid series occur in many different genera. In most of these, gaps occur in the series, either due to a lack of data or extinction of intermediate base number taxa. Many taxa remain to be sampled cytologically and some of the gaps may be filled in with new data. Other series will likely remain incomplete.

The evolution of base numbers in Eupatorieae is striking because $x_2 = 17$ is likely both ancestral and derived (Ito et al. 2000; this study did not include any $x = 18$ taxa). Like most other tribes in the Helenioid–Helianthoid clade, a derived high ancestral base number is plesiomorphic, in this case $x_2 = 19–18$. Many subtribes within the tribe have a base number of $x_2 = 10$ derived by downward dysploid series. In some subtribes, secondarily derived base numbers of $x_2 = 20, 19, 18, 17, 16$ and 14 occur as a result of polyploidy on $x_2 = 10$ and subsequent downward dysploidy for a second time in the history of those phylads. Of note is the unusual $x = 25$ base number in one of two groups of *Neomirandea* (Watanabe et al. 1995). We choose not to speculate on the origin of this remote, high chromosome number pending further data. Without DNA sequence phylogenies, it is unlikely that such redundant patterns of karyotype evolution would have been fully resolved. The combination of morphological, cytological and molecular studies together reveal the details in the history of Eupatorieae and the family as a whole.

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