

CYTOLOGY IN THE SYSTEMATICS, PHYLOGENY AND EVOLUTION IN PLANTS V. ASTERACEAE

P. M. MATHEW^{1*} AND CINTHYA CHRISTOPHER^{2**}

¹Perakathuseril, Muttada P.O., Thiruvananthapuram 695 025

²Department of Botany, All Saints' College, Chackai, Thiruvananthapuram 695 007

** For correspondence. Email: cinthya_wilfred@yahoo.com

(Received 25 July 2018, revised accepted 23 October 2018)

SUMMARY

A brief review of the major findings emerged from the cytological study of the Asteraceae carried out by the senior author in collaboration with doctoral students in the 1980s is provided. The cytological evolution of the family has been viewed *vis-a-vis* the implication of cytology in the systematics and evolution of the group. Most of the cytologically known genera possess the basic number of 10 along with derived constitutions ($x = 9, 8$ and 12 etc.) from $x = 10$, which is held by most workers as the earlier evolved basic constitution in the family derived from an ancestral $n = 5$ state. The higher basic constitutions like $16, 17$ and 18 could be polyploid derivatives from $x = 8$ and 9 . Polyploidy and aneuploidy on $x = 9$ and 10 are incident in many genera at different ploidy levels, which have greatly contributed to evolution and speciation in the family. Great deal of discord prevails concerning the composition, phylogeny and affinities of the family. The systematic relationships of different tribes and affinity of the family are viewed in the light of cytological data. The suggested affinities are with, (a) Complanulales, (b) Gentianales, (c) Rubiaceae and (d) Calyceraceae. The chromosome data of Asteraceae is so complex that it can yield no reliable cytological clues favouring any of the suggested affinities. It has been pointed out that the resemblances of Asteraceae with other families are more superficial than fundamental, and hence, cannot be regarded as descended from or closely related to any other modern family.

Keywords: Asteraceae, cytology, systematics, evolution.

INTRODUCTION

The daisy family, Asteraceae are the largest among the flowering plants, comprising about 2000 genera and over 25,000 species (Mabberley 2017), distributed the world over. Despite the immensely large size, wide global distribution and ecological singularities of the group, its geographic origin and patterns and processes of distribution remain poorly understood. Based on both fossil and phylogenetic evidences, it has been held that the family is of South African origin, from where believed to have experienced a major subsequent diversification followed by an African explosion (Barreda et al. 2010). The African radiation was followed by the movement of various lineages into other parts of the globe;

* Formerly Professor and Head of the Department of Botany, University of Kerala, Thiruvananthapuram.

and much remains unclear about how quickly it colonized globally and became so incredibly diverse (Katinas et al. 2016). It is pointed out that understanding of the spatiotemporal processes that shaped the global distribution of the group still remains an enigmatic issue in biogeography (Nie et al. 2016). The family includes quite a large number of useful plants, of which many are ornamentals, some medicinally important, and a few valued as sources of edible oil and human food. Great bulk of the species is annual or perennial herbs, and some shrubs and rarely trees.

The first comprehensive systematic treatment of the family is the one by Bentham (1873), and this was followed by a line of classificatory treatments which include Cronquist (1955), Hutchinson (1969), Takhtajan (1969), Turner (1977), Wagenitz 1976, and the most modern APG III (2009), APG IV (2016) and Mabberley (2017). Although there is remarkable similarity among the various systems of classifications, considerable controversy exists concerning the composition, phyletic interrelationships and affinities. Although it is well recognized that chromosome data, including karyomorphology of a large number of taxa from a single geographical region are helpful for tackling taxonomic tangles and elucidation of disputed systematic relationships and phylogenetic issues, such detailed information on the Asteraceae is sparse except for the contributions of Turner (1977) and associates, mostly on North American taxa, and by Mehra's (1977) school of cytology in the North Indian group. An extensive chromosome study, including karyomorphology was initiated by the senior author in the University of Kerala on a large assemblage of South Indian taxa in the 1980s, and the results published in a series of papers, notable of which are, Jose & Mathew (1989), Mathew & Mathew (1975, 1976, 1978, 1982 a, b, 1987), Mathew & Mathew (1975a, b, 1980, 1983), Mathew & Thomson (1984), Thomson & Mathew (1989) and Usha et al. (2009, 2013). The chromosome study of the South Indian group covered over 160 species in 62 genera and 11 tribes. This paper aims at providing a review highlighting the major findings emerged from the above study, considered in relation to the systematics, phylogeny and evolution of the group.

Cytological evolution

For meaningful discussion of the cytological evolution, it is important to make use of valid data of parameters such as (a) behaviour of chromosomes at meiosis, (b) the number and morphology of somatic chromosomes, (c) the basic chromosome constitution and (d) the factors which bring about numerical and structural changes in chromosomes at different taxonomic levels. The factor of basic chromosome number at the level of genera, tribes and families has played a significant role in ascertaining the direction of chromosome evolution, and for formulating phylogenetic speculations (Jones 1970). Polyploidy has greatly influenced the evolution of basic numbers, mostly of the higher order often producing new and unrelated basic numbers. The chromosome data known on the Asteraceae show a wide spectrum of basic numbers ($x = 2-19$). Perusal of tribewise distribution presented by Turner (1970) reveals that 214 genera (33%) have the putative basic number of $x = 9$, while 195 genera (30%) have $x = 10$, the former predominating in the tribes Anthemideae, Astereae and Cichorieae, and the latter in the Eupatorieae, Senecioneae and Inuleae. Generawise data of chromosome numbers and basic numbers of the tribes represented in the South Indian study is furnished in Table 1, and tribewise evolution is presented.

TABLE 1: Generawise chromosome data of the South Indian Asteraceae and tribewise basic numbers and ploidy of cytologically known taxa of the family.

Tribe	Genus	Chromosome number		Basic number	Ploidy
		n	2n		
Vernonieae				8, 9, 10, 11	2x, 4x
	<i>Struchium</i> P. Browne	16	32	8	
	<i>Centrantherum</i> Cass.	9	18	9	
	<i>Vernonia</i> Schreb.	9, 10, 11	18, 20, 40	9,10	
	<i>Elephantopus</i> Vaill. ex L.	11	22	11	
	<i>Phyllocephallum</i> Blume.	16	32	8	
Eupatorieae				9, 10	2x, 3x, 4x
	<i>Adenostemma</i> Forst & G. Forst	10, 20	20,40	10	
	<i>Eupatorium</i> Tourn. ex L.	16, 20	40, 56, 60	8,10	
	<i>Mikania</i> Willd.	18	36	9	
	<i>Ageratum</i> L.	10,18	-	9, 10	
Astereae				9, 11	
	<i>Aster</i> Tourn. ex L.	10	20	10	
	<i>Solidago</i> L.	-	44	11	
	<i>Dichrocephala</i> L'Her. ex DC.	9	18	9	
	<i>Mirciactis</i> DC.	18	-	9	
	<i>Erigeron</i> L.	36, 54	-	9	
	<i>Conyza</i> Less.	9	18	9	
Inuleae				7, 8, 9, 10	2x, 4x
	<i>Blumea</i> DC.	8, 9,18	16, 36	8,9	
	<i>Laggera</i> Sch. Bip. ex Benth.	10	-	10	
	<i>Sphaeranthus</i> Vaill. ex L.	10	20	10	
	<i>Gnaphalium</i> Vaill. ex L.	7, 14	-	7	
	<i>Helichrysum</i> Mill.	14	-	7	
	<i>Vicoa</i> Cass.	9	18	9	
Heliantheae				6, 7, 8, 9, 10, 11, 12, 16, 17	2x, 3x, 4x, 6x
	<i>Lagascae</i> Cav.	17	-	17	
	<i>Acanthospermum</i> Sohrank.	-	22	11	
	<i>Parthenium</i> L.	18	36	9	
	<i>Xanthium</i> Tourn. ex L.	18	36	9	
	<i>Zinnia</i> L.	11	22	11	
	<i>Sigesbeckia</i> L.	15, 30	-	15	
	<i>Melampodium</i> L.	12	24	12	
	<i>Eclipta</i> L.	11	22	11	
	<i>Blainvillia</i> Cass.	17	-	17	
	<i>Wedelia</i> Jacq.	20, 50	-	10	
	<i>Tithonia</i> Desf.ex.Juss.	17	34	17	
	<i>Spilanthes</i> Jacq.	20	40	10	
	<i>Helianthus</i> L.	17	34	17	
	<i>Synedrella</i> Gaertn.	20	40	10	
	<i>Coreopsis</i> L.	14	-	7	
	<i>Dahlia</i> Cav.	16	32	8	
	<i>Cosmos</i> Cav.	12	24	12	
	<i>Bidens</i> Tourn. ex L.	36	72	9	
	<i>Galinosoga</i> Ruiz & Pavon.	8,16	-	8	
	<i>Tridax</i> L.	18	-	9	

(Continued)

TABLE 1: (Concluded)

Helenieae			12, 17	2x
	<i>Tagetes</i> L.	12	-	6
	<i>Gaillardia</i> Foug.	17	-	17
Anthemedeae			9, 10	2x, 4x, 6x
	<i>Colula</i> Hook. f	18	-	9
	<i>Chrysanthemum</i> Tourn. ex L.	10	20	10
	<i>Achillea</i> Vaill. ex L.	9	-	9
	<i>Artemisia</i> Tourn. ex L.	10	20	10
Senecioneae			5, 10	2x, 4x, 6x
	<i>Gynura</i> Cass.	20	40	10
	<i>Crassocephallum</i> Moench	20	40	10
	<i>Emilia</i> (Cass.) Cass.	5	10	5
	<i>Notonia</i> DC.	10	20	10
	<i>Senecio</i> Tourn. ex L.	10,20	20, 40	10
Calenduleae			8, 9, 10	2x, 4x, 6x
	<i>Calendula</i> L.	16	-	8
Cynareae			9, 10, 17	2x, 4x, 6x
	<i>Carduus</i> Vaill. ex L.	20	-	10
	<i>Cnicus</i> Tourn. ex L.	17	-	17
Cichorieae			4, 5, 8, 9	2x, 4x
	<i>Picris</i> L.	5	10	5
	<i>Crepis</i> L.	8	-	8
	<i>Hypochaeris</i> Vaill. ex L.	5	10	5
	<i>Taraxacum</i> Weber ex Wigg.	4	-	4
	<i>Lactuca</i> Tourn. ex L.	8	-	8
	<i>Sonchus</i> Tourn. ex L.	9	-	9
	<i>Launaea</i> Cass	9	18	9

Vernonieae

Available chromosome data show that the existing basic numbers in this tribe, worldwide are, $x = 7, 8, 9, 10, 11, 15, 16$ and 17 , of which $x = 8, 9, 10$ and 11 are found in the South Indian taxa. In the entire tribe, the $x = 9$ and 10 are most predominant, of which $x = 10$ considered the likely earlier evolved constitution, from which the $x = 9$ and 8 arose by descending aneuploidy (Mathew & Mathew 1987, Mehra & Ramanandan 1975). This possibility gains support from the karyomorphological data in which the $x = 10$ group of species have relatively more symmetrical and unspecialized karyotypes than those of the $x = 9$ ones (Mathew & Mathew 1987). The $x = 11$ occurring in the species of *Elephantopus* may be the product of ascending aneuploidy from $x = 10$. The higher numbers ($x = 16$ and 17) reported in the alien species of *Vernonia* could be of secondary evolution by polyploidy from $x = 9$ followed by aneuploid reduction at the tetraploid level.

Eupatorieae

Only four genera were studied from South India, and they are all $x = 9$ and 10 basic (Mathew & Mathew 1987, Usha et al. 2013). But a very long line of basic numbers exists in the tribe globally ($x = 4, 5, 9, 10, 11, 12, 15, 17$ and 18) of which $x = 10$ and 17 are most frequent. Turner et al. (1967) have contended that the $x = 10$ and 17 groups of the tribe are parallel ancestral lines evolved from a prototype with $x = 5$. Grant (1953) however, has held that ancestral $x = 5$ and 4 may have given rise to those with higher constitutions ($x = 9, 10$ and 17) through successive allopolyploidy. Mehra & Ramanandan (1975) have held that the Eupatorieae are a primitive group with many representatives still retaining the features of the Heliantheoid group, and that it may have originated directly from an ancestral $x = 5$ which is present in the tribe as in the genus *Adenostemma*, a view also held by Turner & Irwin (1960). Moreover, multiples of this number ($n = 15$) is present in the genus *Trichocoronis* (Turner et al. 1967), and also a regular series ($n = 10, 15, 20$ and 25) in *Eupatorium* (Turner & King 1964). Mehra & Ramanandan (1975) have held that the secondary basic numbers ($x = 10, 17$ and 18) which constitute the major group of the tribe may have originated and got established in the later course of evolution. The lowest number of $x = 4$ present in herbaceous species of *Eupatorium* may have arisen by aneuploid reduction from $x = 5$.

Astereae

This is a large tribe with 133 genera of which seven species in six genera were represented in the South Indian study such as *Aster*, *Solidago*, *Dicrocephala*, *Myriactis*, *Erigeron* and *Conyza*, and most are $x = 9$ basic. Based on the overwhelming preponderance of species based on $x = 9$ globally, Solbrig et al. (1972) have held $x = 9$ as the ancestral constitution of the tribe from which the other ones have arisen by aneuploidy. But Turner et al. (1967) have held the view that genera of the tribe could have evolved at a very early period at the basic level of $x = 5$, and further speciation proceeded from diploid, polyploid and secondary polyploid lines. According to them, such a possibility can account for the rarity of taxa with $n = 7$ and $n = 6$ in such natural and widespread taxa like *Aster chrysopsis*. Arando (1965), Mehra & Ramanandan (1975) and Mathew & Mathew (1987) also favoured the view that $x = 9$ in the tribe to be an aneuploid derivation from $x = 10$, which in turn a polyploid product of the ancestral $x = 5$.

Inuleae

A number of species belonging to six genera of the tribe (*Blumea*, *Laggera*, *Sphaeranthus*, *Gnaphalium*, *Helichrysum* and *Vicoa*) were studied from South India, and the basic numbers in them are, $x = 7, 8, 9$ and 10 , while a long line known in the tribe globally ($x = 3-14$) of which $x = 7$ predominating followed by $x = 8, 9$ and 10 , mostly occurring in genera like *Blumea*, *Laggera* and *Inula*. Based on the data of the Australian taxa in which lower numbers predominate, Turner (1970) held the view that $x = 4$ and 5 could be the ancestral lines in the tribe, and also suggested that taxa with $x = 7$ and 13 in the tribe could have evolved through forms with $x = 9, 10$ and 11 arisen by polyploidy on $x = 5$ through $x = 10$, followed by descending and ascending aneuploidy leading to $x = 9$ and 11 respectively. Mehra & Ramanandan (1975) and Mathew & Mathew (1987) also held the same view, of which the former contended that there could be two groups in the tribe, one with $x = 10$, possibly direct derivation from the ancestral $x = 5$, and the other group with $x = 7$ representing a more evolved section than those of $x = 10$.

Concerning the origin of $x = 13$, their view is that it could be a derivation from the $n = 14$ line. The $x = 5$ basic species are frequent in the primitive genera like *Odontospermum*, *Buphthalmum*, *Tessaria* etc. The secondary $x = 10$, the supposed derivation from $x = 5$ along with its ascending $x = 11$ and descending $x = 9$ and 8 lines predominate in the South Indian genera like *Blumea* and *Laggera*. Since these genera occupy an intermediate position, and those with $x = 7$ the more advanced, the possibility of $x = 7$ being of derivative from $x = 8$ by descending aneuploidy is held as a possibility (Mathew & Mathew 1987). This assumption gains support from the coexistence of taxa with $x = 7, 8$ and 9 in genera like *Helichrysum* and *Helipterum*.

Heliantheae

This is one of the large and diverse tribes of the Asteraceae. Characteristics which are considered primitive are retained in many of its members. Of more than 210 genera, chromosome data are known for about 75% of the species. The South Indian study covers 40 species in 20 genera including a few exotics (Jose & Mathew 1989, Mathew & Mathew 1987, Thomson & Mathew 1989). The basic numbers of the tribe known globally constitute a long line ($x = 8-19$). Chromosome numerical variation is striking in genera with less than $x = 10$, and considerable stability is apparent in these with $x = 17-19$. As in many angiosperms, the chromosome numbers in the tribe show a correlation with habit of the plant, the annual herbaceous species possessing lower numbers than that of perennials and woody. Taxa with higher basic numbers ($x = 11, 12, 15, 17, 18$ and 19) show a higher incidence of which those with $x = 17$ predominating. Opinions differ concerning the original basic state of the tribe. Smith (1975) suggested $x = 17-19$ to be the earlier evolved condition, from which the entire lower ones derived by progressive aneuploid reduction, while Stuessy (1977) held the view that the different basic constitutions of the tribe constitute three lines emerged from the $x = 8$ or 9 ancestral complex such as (1) the Verbisineae line ($x = 15, 16$ and 17), (2) the Galinsogineae line ($x = 8$ and 9) and (3) the Coreopsidineae line ($x = 12, 15$ and 16). He considers $x = 8$ or 9 as the possible ancestral state, and the still lower ones, $x = 7, 6$ and 5 and even 4 to be derivatives from $x = 8$; and he also assumed the relatively higher $x = 16, 17$ and 18 as polyploid derivatives from $x = 8$ and 9 . Solbrig et al. (1972) have held that the original constitution of the tribe may be lying between $x = 8$ and 12 , with $x = 9$ as the most probable one. Mathew & Mathew (1987) and Robinson & King (1977) have favoured the view of $x = 10$ as the likely original state, having evolved from an ancestral $x = 5$, from which arisen the $x = 9, 8$ etc. by descending aneuploidy. However, the question of the original basic structure of the tribe is still enigmatic, especially as the original basic condition may have become obscured by polyploidy followed by aneuploidy and that the ancestral numbers may have even got altered in both directions in the course of evolution. Notwithstanding this, the chromosome states in certain primitive taxa such as *Tridax* with $x = 10$ appear to yield some clues as to the possible ancestral basic state swinging in favour of 10 , which in turn a polyploid derivative of $x = 5$. The karyomorphological data of species from South Indian study assumes importance here. The karyotypes of the $x = 9$ taxa were more specialized and evolved than those of the $x = 10$, implying that the $x = 9$ constitution could be the derived state. Moreover, the occurrence of taxa with $n = 5$ along with those with higher haploid numbers including $x = 9$ and 10 in the subtribe, Medineae of the tribe Heliantheae provides credence to the possibility of $x = 10$ being evolved from $x = 5$. Other relatively lower constitutions like $x = 9, 8, 7$ and 6 may be products of descending aneuploidy from $x = 10$, and the

$x = 18$ occurring more frequently in the subtribe may be a derivation from $x = 9$ by polyploidy from which the $x = 17$ arisen by descending aneuploidy and/or by secondary hybrid polyploidy involving $x = 9$ and 8 taxa. The occurrence of three cytotypes in *Parthenium hysterophorus* with $n = 9, 17$ and 18 is important in this connection. The other relatively higher basic numbers in the tribe such as $x = 16$ and 15 may be the products of progressive reduction from $x = 17$. The remaining intermediate conditions like $x = 14, 13$ and 12 could be the derivations from lower states of $x = 7$ and 6 by polyploidy followed by aneuploidy. The $x = 11$ could be an ascending derivations from $x = 10$. Occurrence of two cytotypic forms of *Eclipta prostrata* of the tribe lends support to this possibility (Thomson & Mathew 1989).

Helenieae

This is a small tribe of about 70 genera, considered to be of polyphyletic origin (Turner & Powell 1977). Over 60 genera are cytologically known, the data showing a wide array of basic numbers ($x = 4 - 19$), of which basic numbers below $x = 10$ are very few, and the most commonly occurring one being $x = 18$ followed by $x = 12$. The South Indian study reported mostly $x = 17$ and 12, with lower $x = 8, 7$ and 6 in a few species which could be descending aneuploid derivations from $x = 9$ which in turn a descending derivative from $x = 10$. The occurrence of taxa with $n = 5$ favours the possibility of origin of $x = 10$ by polyploidy from $n = 5$. The more frequent $x = 16, 17, 18$ and 19 may be polyploid derivations of $x = 8$ and 9 or tertiary condition through aneuploidy from polyploids. The $x = 11, 12$ and 13 may be ascending aneuploid derivations from $x = 10$.

Anthemideae

This is fairly a large tribe of about 102 genera, of which about 50% are cytologically known; and the data show basic numbers $x = 8, 9, 10, 13$ and 17, of which $x = 9$ overwhelmingly predominant, which is the established basic constitution in the tribe. A series of polyploids occur on this up to 12-ploid. Occurrence of both $x = 9$ and 10 in a few genera such as *Cotula* and *Artemesia* is suggestive of $x = 9$ to be derivation from $x = 10$ (Mathew & Mathew 1987), a view held by Turner (1970) as well. The $x = 3$ as in *Artemesia* could be a descending derivation from $x = 5$.

Senecioneae

Five genera of the tribe (*Gynura, Crassocephalum, Emilia, Notonia, Senecio*) were represented in the South Indian study, and the basic numbers in them reported globally are $x = 5, 9, 10, 12$ and 19, of which $x = 10$ is predominating (Ornduff et al. 1963). There are two views concerning the ancestral basic number, some holding $x = 10$ (Ornduff et al. 1963) and others $x = 5$ (Mathew & Mathew 1987, Mehra & Ramanandan 1975, Turner & Lewis 1965). The possibility of $x = 5$ derived from $x = 10$ by stepwise reduction is less probable, especially as the intermediate forms ($x = 6$ and 7) are absent in any genera of the tribe, like *Emilia* and *Senecio*, both of which possess $n = 5$ and 10.

Cynareae

Species of only two genera were studied from South India (*Carduus, Cnicus*). The worldwide data show a long line of basic numbers from $x = 8-19$, with $x = 10$ predominating. Arando (1965)

considered the $x = 17$ as the ancestral state from which derived the lower ones. His contention is that $x = 17$ could have arisen as aneuploid reduction from a tetraploid of $x = 9$, which in turn possibly originated from $x = 10$. Both Mathew & Mathew (1987) and Mehra & Ramanandan (1975) have favoured the possibility of origin of this from an ancestral stock with $x = 10$ which in turn from a primary $x = 5$.

Cichorieae

Cytologically this is the most widely known tribe. Seven genera were studied from South India, in which the basic numbers ranged from $x = 4-9$. Stebbins et al. (1953) have considered $x = 9$ as the original state from which arose taxa with lower constitutions, originated by progressive aneuploid reduction. They have substantiated this with karyotype data of taxa of $x = 9$ being symmetrical as against more specialized in those with lower basic numbers. Arando (1965) who also favoured $x = 9$ as the original state, but holding that this originated from $x = 5$. Mathew & Mathew (1987) and Mehra & Ramanandan (1975) have both considered the $x = 9$ as the derived condition from an ancestral $x = 5$ through tetraploid followed by reduction.

Ancestral basic number

An array of basic numbers exists in the Asteraceae, ranging from $x = 2-19$ which can be arbitrarily classified into three groups, (1) very low ($x = 2-5$); (2) intermediate ($x = 6-10$) and high ($x = 11-19$). The very low category is frequent in the tribe Cichorieae. Among the South Indian groups, the lower numbers exist only in a few genera, viz., $x = 5$ in *Emilia* (Senecioneae) and *Hypochaeris* (Cichorieae), and $x = 4$ in *Taraxacum* (Cichorieae). Basic numbers of the intermediate category constitute the bulk, of which $x = 9$ predominating followed by $x = 10$ conspicuously in the Heliantheae, Cynareae & Mutisieae. Regarding the ancestral basic constitution, there are two major postulates, (1) the $x = 9$ constitution held by Solbrig et al. (1972), whose contention is that taxa with lower constitutions are ancient derivations by phylogenetic reduction from $x = 9$ and (2) $x = 5$ as the ancestral assumed by Turner (1977), and also by Mehra and Ramanandan (1975) and Mathew & Mathew (1987). According to this view, the $x = 5$ has given rise to $x = 10$ by polyploidy, from which the other lower ones arisen by stepwise descending aneuploidy. The karyotype data emerged from the South Indian study in genera like *Blumea* and *Vernonia* support this, in which the species with $x = 10$ have symmetrical and unspecialized karyotypes (1A/2A) than those with $x = 9$. Four different basic numbers exist in *Blumea* ($x = 8, 9, 10$ and 11). Based on this, Mathew & Mathew (1987) suggested $x = 10$ constitution as the earlier evolved one from which evolved the lower ones by descending aneuploidy. The occurrence of accessory chromosomes in some of the species of *Blumea* with $x = 9$ prompted them to assume that aneuploid reduction from $x = 10$ could have been through formation of B-chromosomes followed by their elimination.

Polyploidy

Polyploidy is the most widespread cytogenetic process that has contributed to speciation and evolution in plants. This is mainly due to the ability of polyploids to increase the chance of fertilization

by breaking down reproductive barriers and also to their invasive potential and tolerance to adverse environmental conditions (Stebbins 1971). In the Asteraceae, around 50 % of the cytologically known species are polyploids, which are more frequent in tribes Eupatorieae, Heliantheae, Anthemideae, Senecioneae, Calenduleae and Cynarieae (Table 1). The frequency of polyploids, basic chromosome numberwise are maximum on $x = 10$ and 9 at different levels ($3x$, $4x$, $5x$, $6x$, $8x$). Most of the polyploids showed normal meiotic behavior characterized by regular bivalent formation, suggestive of allopolyploidy. In certain cases, the possibility of autopolyploidy/segmental allopolyploidy was also apparent. There were cases in which notable meiotic abnormalities evident as in the tetraploid species of *Blumea* and *Erigeron*, in the former complete asynapsis, suggestive of hybridity, and in the latter varying frequencies of quadrivalents, trivalents, bivalents and univalents suggestive of autopolyploidy. There was evidence of triploid hybridity also, as in *Eupatorium glandulosum*, and of autoallopolyploidy in *E. odoratum*.

Intraspecific polyploidy has been reported in a large number of species globally, however, this was sparsely noticed among the South Indian group, barring only in a few taxa. However, in the case of a few others, previous workers have reported different cytotypes as occurring in other geographical regions. Striking examples of this are, *Artemisia nilagirica* in which five cytotypes are known ($2x$, $3x$, $4x$, $5x$ and $6x$) of which the $6x$ in South India, and others from North India.

Aneuploidy

In angiosperms, aneuploidy occurs most often at the diploid level (Stebbins 1971). The chromosome data on the Asteraceae show that aneuploid alternations have been widespread in the family which is evident from the large number of genera being multibasic at the diploid level. Aneuploid reduction is most evident in the genus *Crepis* in which $x = 6$ is the earlier evolved state, from which derived a line of descending series ($x = 5, 4, 3$). Aneuploid reduction at the diploid level was evident in many South Indian genera, especially in *Vernonia*, *Artemisia* etc. Aneuploid increase, however, was rare in this region. But previous reports have shown this in many cases eg. *Wedelia*, *Gynura* etc. The $x = 11$ and 12 in these genera could be ascending aneuploid derivations from $x = 10$. Four basic numbers exist in the genus *Blumea* ($x = 8, 9, 10$ and 11) of which the first two occur in South India and the other two in the North. In *Blumea*, aneuploidy has occurred in either direction from $x = 10$ ($8 \leftarrow 9 \leftarrow 10 \rightarrow 11$). Similar situation is seen in *Eupatorium* in which $x = 8$ and 12 are descending/ascending products from $x = 10$. Apart from aneuploidy at the diploid level, this has occurred at polyploid levels as well as in *Vernonia*, *Artemisia* etc, in the former, numbers such as $n = 17, 16, 15$ and 14 reported in alien taxa, which could be products of aneuploid reduction from $n = 18$ which in turn a tetraploid of $x = 9$. Intraspecific aneuploidy is frequent in a number of genera globally, while rarely noticed in the South Indian group, noticed in just one species (*Coreopsis grandiflora*).

Systematic considerations

The recognition and identification of members of the Asteraceae have long been centered on the basic type of inflorescence (capitulum), the connate introse anthers, the pappus (modified calyx) perched on the achene and the bifid style, of which the morphology and evolution of the capitulum has

received substantial attention because of its crucial reproductive function (Katinas et al. 2016, Pozner et al. 2012). A number of classificatory treatments of the family are known, both classical and modern, of which most comprehensive is the one by Bentham (1873), who recognized 13 tribes under two subfamilies, the Tubiflorae and the Liguliflorae. Although Bentham's classical system remained widely accepted, the modified systems, which appeared subsequently, especially the recent ones, are different from the classical one in many respects, including composition and interrelationships. The latest APG IV (2016) system differs markedly, in which the Asteraceae (considered under the clade Asterales) is subdivided into 13 subfamilies of which Asteroideae is one, and in this treatment, there is no tribal categorization. It is understandable that in the case of such a very large and ancient family with wide distribution, any attempt to discretely define the composition, systematic relationships and affinities cannot be conclusive (Turner 1977). There are mainly three views regarding the origin of different tribes such as (a) monophyletic origin (Cronquist 1955) and supported by Turner (1977), (b) biphyletic (Carlquist 1966) and (c) polyphyletic, which postulates none of the tribes to be exclusively primitive or advanced (Mathew & Mathew 1987). But, majority of the systematists consider the Heliantheae as the most primitive of the tribes. Cytological data show a wide range of basic numbers in the family, of which no number is common to any of the tribes. A few of the notable suggestions of intertribal relationships are as follows :

- (1) Some favoured separate tribal status for the Helenieae (Carlquist 1959, 1966) but Cronquist (1955) does not favour a separate tribal status for this, and he prefers transfer of various genera of this into the Heliantheae. According to Powell & Turner (1974), the Helenieae is an unnatural assemblage which should be abandoned.
- (2) Members of the tribes Eupatorieae, Vernonieae, Cynareae and Mutisieae possess mostly homogeneous capitula with tubular corolla. The tribes Eupatorieae and Vernonieae show similarity in that they possess the same predominant basic number, $x = 10$, while the Cynareae and Mutisieae possess a wide range such as $x = 6, 8-18$, and $x = 6, 8-15$ and 17 respectively.
- (3) The tribes Senecioneae and Inuleae are suggested to have relationship with Heliantheae and Helenieae (Wagenitz 1976). The Senecioneae constitute a cytologically stable group with $x = 10$, (Ornduff et al. 1963) a situation not existing in any of the other tribes. But it is more closer cytologically with Vernonieae through $x = 10$.
- (4) Tribe Astereae and Anthemideae are closer through common basic numbers $x = 9$.
- (5) Most systematists consider Cichorieae as a separate group standing out from the rest of the tribes. According to Mehra (1977), this is an advanced tribe with little difference between and among its genera. Cytologically this is closer to Astereae/Anthemideae through the basic number $x = 9$, with remarkable reduction series ($x = 9-3$).
- (6) The tribes Astereae and Anthemideae form a homogeneous group cytologically with overwhelming predominance of $x = 9$. These two tribes are considered related to Heliantheae on morphological consideration (Hutchinson 1969). But, cytologically they are far apart.

Solbrig et al. (1972) finds no relationship between Astereae and Heliantheae, because members of the Astereae, possessing Helianthoid features, have totally unrelated and very low chromosome numbers ($n = 2, 4, 5, 6, 8$ and 9) in contrast to very high basic numbers in the Heliantheae.

Phylogeny and affinities

The question of the sister groups of Asteraceae has been discussed for a long time, and several different families were suggested as possible ally candidates such as (a) Complanulales, as ancestor to Asteraceae (Hutchinson 1969), (b) Takhtajan (1969) considered the Asterales having been derived from Gentianales, (c) Cronquist (1955) holds Rubiaceae as ancestral to Asteraceae, which is largely based on similarities in certain floral characters and (d) Turner (1977) based on chromosomal evidence, strongly supported affinity with Calyceraceae. In the recent treatment (APG IV 2016) affinity has been suggested with Calyceraceae, Complanulaceae, Menyanthaceae etc. along with a few other families. Among the different families suggested as having affinity with Asteraceae, most of the evidences indicate (Lundberg & Bremer 2003, Funk et al. 2009) that the Australian-centered Goodeniaceae is the sister group of the Calyceraceae which in turn is morphologically closest to Asteraceae. Some possible synapomorphies for Goodeniaceae-Calyceraceae-Asteraceae clade are the presence of secondary pollen presentation, a dry papillate stigma and persistent calyx. The Calyceraceae-Asteraceae clade is supported by many synapomorphies such as capitula inflorescence, pollen morphology and unilocular ovary with a single ovule (Lundberg 2009). From an evolutionary perspective, Hanson (1992) postulated that the morphology-based phylogeny among the internal branches of Asteraceae could change if some features are repolarized, such as the shape of the style apex and the style's sweeping hairs. Even though current classifications within the Asteraceae and its phylogenetic relationships with other families are mostly based on molecular data, the major taxonomic groups such as tribes and subfamilies are defined and supported by morphological characters (Katinas et al. 2016).

The chromosome data of Asteraceae is so complex that it can yield no reliable clues regarding its interfamilial relationship (Turner 1977). Although the family exhibits a very large array of basic numbers ranging from $x = 2-19$, the $x = 9, 10, 8$ and 7 are the most frequently occurring basic numbers in most tribes. Of the different families to which affinity proposed, the Rubiaceae possess the much unrelated basic number of $x = 11$, a constitution almost nonexistent in the Asteraceae. However, the $x = 9$ and/or $10, 8, 7$ which occur frequently in the Asteraceae are also incident in many of the other families to which affinity suggested so much so it is difficult to pin-point any of them to be most related to Asteraceae. Stebbins (1977), based on a comparative study of the Asteraceae with the other related families has contended that resemblance of the Asteraceae with the other families are more superficial than fundamental, and he suggested parallel and convergent evolution. His strong view is that Asteraceae cannot be regarded as descended from or closely related to any other modern family.

ACKNOWLEDGEMENT

Valuable suggestions and comments offered by anonymous referees are gratefully acknowledged.

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