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CHROMOSOMES OF THE BROMELIACEAE

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ABSTRACT. Recent results from Bromeliaceae chromosome research support Marchant's proposed $x = 25$ as the extant base number for the family. Mitotic chromosome numbers are variable and some discrepancies exist between mitotic and meiotic counts of the same species. These may be explicable in terms of the association with the epiphytic habit. It is hypothesized that chromosomal alterations are more likely to be retained within the cells of holdfasts that have lost most of their physiological functions as organs of absorption than are such alterations in roots whose functions are more complex. If this hypothesis is true we would expect to find greater stability in somatic counts of roots of terrestrial taxa and less stability in holdfasts of epiphytic taxa. Our observations are in concordance with this hypothesis. Polyploidy appears to have been important in the evolution of the family, and a polyploid trend in *Tillandsia* subgenus *Diaphoranthema* has recently been discovered.

Chromosomal evolution within Bromeliaceae is poorly understood. Just over seven percent of the 2,100 species have any chromosomal information on record. McWilliams (1974) was the last to summarize the literature concerning chromosome numbers and evolution for the family. Three subfamilies are recognized: Bromelioideae (27 genera, 536 species), Pitcairnioideae (13 genera, 750 species), and Tillandsioideae (six genera, 810 species) (Smith & Downs, 1974, 1977, 1979). The Tillandsioideae and Pitcairnioideae are poorly known with chromosome number reports for only four percent of the species. In the Bromelioideae 15 percent of the species are known by at least one chromosome number report.

Research in cytotaxonomy of the Bromeliaceae has been hindered by limited accessibility to the plants. We have tried to solve this problem in part through the development of a network of collaborating field participants and resident botanists in Latin America (Gilmartin & Brown, 1986). Until recently (e.g., Brown et al., 1984; Varadarajan & Brown, 1985; Brown & Gilmartin, unpubl.) most chromosomal studies within Bromeliaceae had been conducted by workers utilizing plant material from botanical garden collections (e.g., Lindschau, 1933; Gauthe, 1965; Weiss, 1965; Marchant, 1967; Sharma & Ghosh, 1971). Reliance upon botanical garden material has often proved unreliable because usually no accurate collection data exists (e.g., native source, field collected, trade from another garden, purchase from dealer, gift).

Another problem concerns the fact that most botanical garden collections exist because they have some sort of horticultural value. Most of the chromosome number reports have been from these showy species, which accounts for the recurring chromosome number reports by different authors for the same taxon. In addition numerous taxa are difficult to grow or are rare in botanical gardens because of their size (e.g., many pitcairnioids). Other species are not horticulturally attractive and therefore also have been neglected. The high rates of misidentification of bromeliad holdings in most botanical gardens (H. Luther, pers. comm.) injects doubt as to the taxonomic identity of numerous chromosome number reports. The problem of accurate identification is compounded further when herbarium vouchers are not prepared.

Cytological and developmental aspects of bromeliad flowers contribute to difficulties in research with meiotic (microsporocytic) material. The small, poorly staining chromosomes probably have been the greatest hindrance in chromosome studies within the family. In addition, thick, rigid, rib-like secondary wall thickenings of the anther endothecium (Gilmartin & Brown, 1985) necessitate removal of microsporangiate masses from the anther to ensure proper squashing. In many species, additional mechanical resistance to squash preparations is encountered in the thick callose layer that encloses the microsporocyte. Usually, this callose layer has to be broken to release the cytoplasm for suitable specimen preparations.

Despite the paucity of chromosome number data for Bromeliaceae, there has been considerable speculation and disagreement concerning

TABLE 1. Meiotic (n=) and mitotic (2n=) chromosome number reports for the Bromeliaceae.

	Chromosome numbers		
Taxa	n=	2n=	Habit*
Pitcairnioideae			
Dyckia brevifolia Baker in Saunders	25	50	Terrestrial
D. encholirioides (Gandichaud) Mez	25	50	Terrestrial
Fosterella penduliflora (C. H. Wright) L. B. Smith	25, 75	100	Terrestrial
Pitcairnia andreana Linden	25	50	Terrestrial
P. flammea Lindley	25	50	Terrestrial
P. heterophylla (Lindley) Beer	25	50	Terrestrial/epiphyte
P. pulverulenta Ruiz & Pavon	25	50	Terrestrial
P. xanthocalyx Martius	25	50	Terrestrial
Puya chilensis Molina	24	50	Terrestrial
P. spathacea (Grisebach) Mez	25	50	Terrestrial
Bromelioideae			
Aechmea coelestis (K. Koch) E. Morren	25	50	Terrestrial/epiphyte
Ananas comosus (L.) Merril	25	50, 75	Terrestrial
Billbergia chlorosticta Saunders Hortus	25	54	Unknown
B. nutans H. Wendland ex Regel	25	54	Epiphyte
B. pyramidalis (Sims) Lindley	25	50, 54	Terrestrial
Cryptanthus acaulis (Lindley) Beer	17	34	Terrestrial
C. zonatus (Visiani) Beer	17	34, 36	Terrestrial
Neoregelia concentrica (Vellozo) L. B. Smith	25	54	Epiphyte
N. spectabilis (Moore) L. B. Smith	25	46	Epiphyte
Tillandsioideae			
Tillandsia anceps	25	56	Epiphyte
T. capillaris Ruiz & Pavon	50	87, 88, 89, 92, 96	Epiphyte
T. fasciculata Swartz	25	64	Epiphyte
T. imperialis E. Morren ex Mez	25	64	Epiphyte/terrestrial (saxicolous)
T. tricolor Schlechtendal & Chamisso	25	64	Epiphyte
Guzmania monostachia (L.) Rusby ex Mez	25	48	Epiphyte
G. musaica (Linden & Andre) Mez	25	48	Epiphyte
Vriesea splendens (Brongniart) Lemaire	25	48	Epiphyte

* Data from Smith and Downs (1974, 1977, 1979).

aspects of chromosomal evolution within the family. Suggested base numbers for Bromeliaceae include $x = 9$ (Lindschau, 1933), $x = 8$, with several levels of polyploidy for Tillandsioideae (Weiss, 1965), and $x = 25$ (Marchant, 1967). Marchant considered the Bromeliaceae, with minor exceptions (e.g., *Cryptanthus*, n = 17), to have a homogeneous base number, which evolved from primitive stock with $x = 25$. Sharma and Ghosh (1971) recognized base numbers of $x = 9$ or 25 for Bromelioideae, $x = 25$ for Pitcairnioideae, and $x = 8$ or 16 for Tillandsioideae. McWilliams (1974) presented a scheme for chromosome evolution in Bromeliaceae that is derived from $x = 8$. Raven (1975) places the familial base number at $x = 17$ or 25. Cronquist (1981) lists the generic base numbers as $x = 8$ to 28, but most often 25. Goldblatt (1980) sees little reason to doubt $x = 25$ as basic for the family.

We are in agreement with Marchant (1967) and Goldblatt (1980) that the extant base number for the Bromeliaceae is $x = 25$. The ancestral base number for the family appears to be $x = 8$ (Brown & Gilmartin, unpubl.).

Nonconcordance Between Mitotic and Meiotic Chromosome Numbers

Detailed analysis of existing Bromeliaceae chromosome literature in combination with new chromosome number data (Brown & Gilmartin, unpubl.) suggest one explanation for the conflicting chromosome base number hypotheses thus far proposed for the family. Nonconcordance between mitotic and meiotic chromosome numbers is frequent in some genera. Three examples, one from each subfamily, demonstrate both concordance and nonconcordance between mitotic and meiotic chromosome numbers.

Of the three subfamilies, Pitcairnioideae dis-

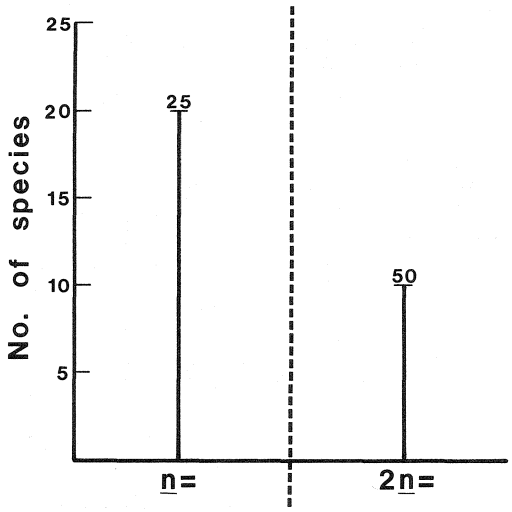

FIGURE 1. Frequency of reported meiotic (n=) and mitotic (2n=) chromosome numbers in *Pitcairnia* (Pitcairnioideae).

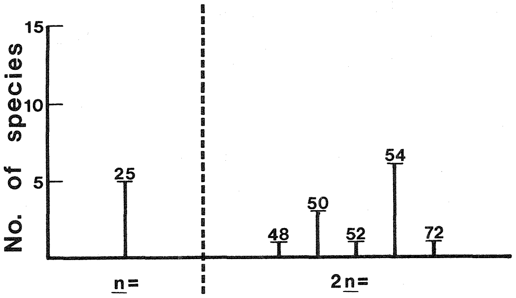

FIGURE 2. Frequency of reported meiotic (n=) and mitotic (2n=) chromosome numbers in *Billbergia* (Bromelioideae).

plays the most homogeneity in chromosome numbers. At both generic and specific ranks, chromosome numbers, whether based upon mitotic or meiotic material have been in consistent agreement. This concordance is illustrated in *Pitcairnia* (TABLE 1; FIGURE 1), which has a high degree of morphological and anatomical variability (Varadarajan, 1985), is the largest genus in the Pitcairnioideae, and has more chromosome number information than any other genus in the subfamily.

There is less stability of meiotic and mitotic chromosome numbers for taxa in Bromelioideae and Tillandsioideae (TABLE 1). As an example from Bromelioideae, the genus *Billbergia* is characterized by the gametic (meiotic) number of n = 25 (FIGURE 2). In contrast, a range of somatic (mitotic) reports other than the expected 2n = 50 are known with 2n = 54 being the most frequent. An examination of all Bromelioideae taxa known to have both meiotic and mitotic chromosome number reports (TABLE 1) illustrates that certain of these taxa (e.g., *Billbergia nutans, Neoregelia concentrica,* and *N. spectabilis*) do not exhibit the expected concordance in meiotic/mitotic chromosome number.

Members of Tillandsioideae, the largest subfamily, display a lower incidence of meiotic/mitotic chromosome number concordance (TABLE 1). For *Tillandsia* (ca. 410 species), reported meiotic chromosome numbers are at n = 25 except for four species (FIGURE 3). In contrast, most mitotic number reports are values that do not equate to an expected meiotic counterpart of n = 25 (i.e., 2n = 50). There are five species of *Tillandsia* with both meiotic and mitotic chromosome number reports (TABLE 1). In each, as well as all other Tillandsioideae taxa where gametic and somatic chromosome numbers are reported, there is obvious nonconcordance between the reported values (TABLE 1).

The meiotic chromosome number reports for *Tillandsia* other than n = 25 (FIGURE 3) merit further discussion. Billings (1904) reported n = 16 for *T. usneoides* (L.) L., a count we view as questionable. Billings utilized microtome sections to determine the chromosome number (both gametic and somatic) for *T. usneoides.* In light of the preparation technique and small size and tendency for poor staining of bromeliad chromosomes, it seems possible that Billings may have overlooked several chromosomes. Till (1984) reports *T. usneoides* to be a diploid with 2n = 50. Thus the Billings report continues to remain unconfirmed. *Tillandsia usneoides* has the widest distribution of any taxon in the family (Smith, 1934), and the possibility of chromosomal races cannot be ruled out at this time.

Brown and Gilmartin (1983) reported n = 18 (determined from microsporocytes at metaphase I) for *Tillandsia umbellata* Andre (FIGURE 3). The systematic significance of this distinctive chromosome number, if any, is not yet known.

Tillandsia complanata (FIGURE 3) accounts for the reported numbers of n = 20 (Brown et al., 1984) and n = 22 (Brown & Gilmartin, unpubl.). Presumably descending aneuploidy from an ancestral n = 25 is responsible for the reduction in chromosomes. The significance and mechanism(s) remain unknown.

The tetraploid meiotic count of n = 50 (FIGURE 3) is for *Tillandsia capillaris* (Brown & Gilmartin, unpubl.). Mitotic chromosome number reports for *T. juncea* (Ruiz & Pavon) Poiret (2n = 96, Lindschau, 1933; 2n = 96, Gauthe, 1965) and *T. butzii* Mez (2n = 96, Weiss, 1965) approach the tetraploid level, however, no mitotic

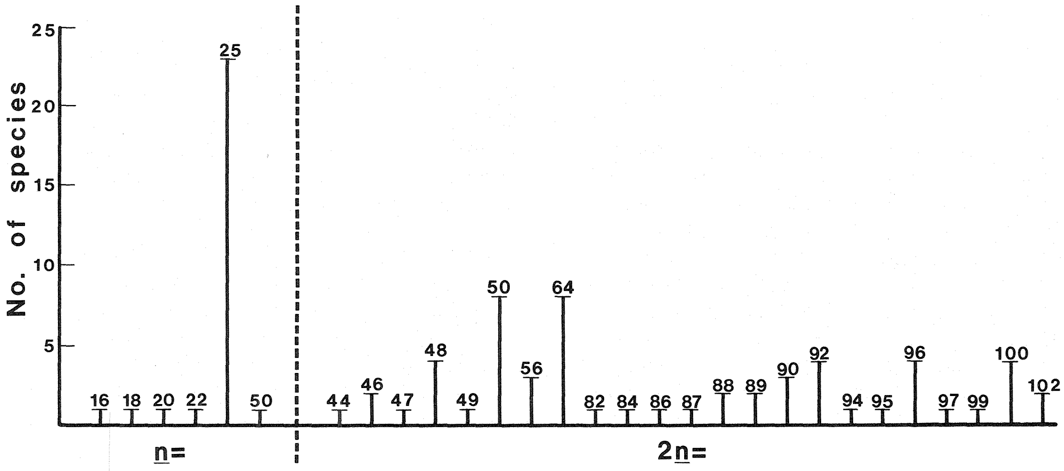

FIGURE 3. Frequency of reported meiotic (n=) and mitotic (2n=) chromosome numbers in *Tillandsia* (Tillandsioideae).

numbers with the exact gametic equivalent of a tetraploid had been known in *Tillandsia* until Till's (1984) work (see below).

In addition to nonconcordance between meiotic and mitotic chromosome numbers in certain taxa of Bromeliaceae, chromosome number reports from root tip material appear to be highly unreliable in some cases. Observations by Sharma and Ghosh (1971) are particularly instructive in this regard. In their analysis of root tip mitosis they report chromosome number variability ranging from 2n = 88 to 2n = 94 between cells from the same root tip squash preparation. Till (1984) makes similar comments concerning the inability to precisely discern chromosome numbers from mitotic tissues in species of *Tillandsia* subgenus *Diaphoranthema.* He attributes the problem to a combination of chromosome stickiness and small size, yet does stress that it is possible to assign ploidy level despite this problem of exact number accuracy. In light of the variability and unreliability of mitotic chromosome counts, hypotheses concerning chromosome evolution within Bromeliaceae (especially Bromelioideae and Tillandsioideae) that are based on mitotic counts (e.g., Lindschau, 1933; Gauthe, 1965; Weiss, 1965) must be suspect.

Some of the apparent chromosome number variation may not be real. Till (1984) suggested that difficulty of preparation and observation of bromeliad chromosomes may be responsible for disparate number reports. Smaller chromosomes might contribute to counting errors and thus the apparent lack of stability. Yet Pitcairnioideae, which has the smallest chromosomes and the shortest genome lengths for the family (Brown, unpubl.), exhibits the greatest mitotic number stability among the three subfamilies. Small chromosome size and counting errors cannot alone account for the reported mitotic chromosome number variability.

An association between nonconcordance of meiotic and mitotic chromosome number within the Bromeliaceae and the epiphytic mode of growth may exist. The available data indicate (TABLE 1) that terrestrial taxa are concordant in meiotic and mitotic counts, while those taxa that are epiphytic or saxicolous show low meiotic/mitotic concordance. In order to properly test this association more research is needed, especially in comparing meiotic and mitotic (i.e., root tip) chromosome numbers from the same individual for both epiphytic and terrestrial taxa.

Roots of epiphytic bromeliads, if present at all, act as holdfasts and do not function as organs of absorption, which is accomplished by the leaves (Benzing & Ott, 1981). We suggest that bromeliad roots that function only as holdfasts have less physiological significance than do roots of terrestrial species that are engaged in uptake of water and nutrients. Thus, somatic chromosome number alterations in the holdfasts of epiphytes might be less deleterious than they would be in roots with more complex functions. Consequently, the retention of considerable variation in chromosome number in cells of holdfast roots of epiphytic bromeliads might be expected. In an extreme case, e.g., *Tillandsia usneoides,* the holdfast function of roots is also lacking (Billings, 1904). Perhaps a loss in control of normal mitotic processes (i.e., replication or faulty operation of the spindle-fiber apparatus, or induced fragmentation of chromosomes) can be tolerated in root tips of epiphytic species in which roots serve no apparent physiological function and where, according to Benzing and Ott (1981), the presence of well-developed, normally functioning roots would be a disadvantage (i.e., a wasteful carbon sink).

The occurrence of aberrant and variable mitotic chromosome numbers in epiphytic bromeliads (and thus, nonconcordance with meiotic chromosome numbers) mandates further research to test the hypothetical connection between loss of root function by roots and loss of regular mitotic control in vestigial holdfast roots. This will require an accumulation of meiotic counts from many individuals of one species and mitotic counts from roots and non-root parts of the same individual to determine if mitosis is actually irregular in vestigial roots.

POLYPLOIDY

Based on the criterion established by Grant (1963, 1981) for identifying polyploids, i.e., chromosome number of n = 13 or higher, polyploidy has played a major role in the evolution of the Bromeliaceae. The extant base number for the family, $x = 25$ (Marchant, 1967; Goldblatt, 1980; Brown & Gilmartin, unpubl.), appears to be an obvious polyploid. The diploid n = 25 appears to represent the hexaploid level from an ancestral base number of $x = 8$ (Brown & Gilmartin, unpubl.).

Polyploidy from the extant base of $x = 25$ has been infrequently encountered in Bromeliaceae, and when noted, is mostly confined to subfamily Bromelioideae. Polyploids from Bromelioideae occur in *Bromelia* (two species), *Nidularium* (one species), *Pseudananas* (one species), and *Ananas comosus,* the pineapple. Polyploidy in Pitcairnioideae is reported from *Dyckia* (three species), and *Fosterella* (two species). In subfamily Tillandsioideae it has been reported in one species of *Guzmania,* and in several species from *Tillandsia* subgenus *Diaphoranthema.*

An interesting trend in polyploidy has recently been discovered in *Tillandsia* subgenus *Diaphoranthema* (Till, 1984; Brown & Gilmartin, unpubl.). In a revision of subgenus *Diaphoranthema,* Till recognizes 25 species for which 18 he reports at least one chromosome number. Assuming a base of $x = 25$, nine of these species (*T. aizoides* Mez in DC., *T. caliginosus* W. Till, *T. funebris* Castellanos, *T. gilliesii* Baker var. "*saxicola,*" *T. loliacea* Martius ex Schultes & Schultes, *T. rectangula* Baker, *T. recurvata* (L.) L., *T. tricholepis* Baker var. *macrophylla* L. B. Smith, and *T. usneoides*) have somatic (vegetative bud) chromosome numbers at the diploid level (i.e., 2n = ca. 50). Of particular interest are the 12 tetraploid (2n = ca. 100) taxa: *T. andicola* Gillies ex Baker, *T. angulosa* Mez, *T. bryoides* Grisebach ex Baker, *T. capillaris* Ruiz & Pavon, *T. castellanii* L. B. Smith, *T. erecta* Gillies ex Baker, *T. gilliesii* Baker ssp. *polysticha* W. Till & Hromadnik, *T. hirta* W. Till & Hromadnik, *T. loliacea, T. retorta* Grisebach ex Baker, *T. tricholepis* var. *tricholepis,* and *T. virescens* Ruiz & Pavon. Subgenus *Diaphoranthema* is characterized by a trend toward polyploidy.

The only tetraploid in *Tillandsia* documented with a meiotic chromosome count is *T. capillaris* (Brown & Gilmartin, unpubl.). Till reports tetraploid level numbers (i.e., 2n = 96) for this same species. *Tillandsia capillaris* is a complex of at least five described forms (Smith & Downs, 1977) of extreme xeric epiphytes or saxicols. True cleistogamy (see Lord, 1981, for definition) has recently been described from a Bolivian population of *T. capillaris* forma *hieronymii* (Gilmartin & Brown, 1985). Chromosome numbers were not available for that collection. Phenomena such as polyploidy and cleistogamy as is now known from *T. capillaris* may be important mechanisms in maintaining the five morphologies recognized by Smith and Downs (1977). Facultative apomixis and inbreeding in combination with polyploidy may contribute to the fixation of multiple morphologies within the *T. capillaris* complex. Studies of the other tetraploid species of subgenus *Diaphoranthema* are needed to determine if polyploidy correlates with specialized trends in reproductive biology.

KARYOTYPE BIMODALITY

Chromosome size bimodality within the Bromeliaceae was first recognized by Marchant (1967). He considered chromosome bimodality to be typical of Tillandsioideae, a tendency in Bromelioideae, and not present in the more primitive Pitcairnioideae. McWilliams (1974) corroborates Marchant's (1967) observation concerning the occurrence of bimodality, but states that there is always bimodality in the Tillandsioideae chromosome complement.

We have observed the bimodal karyotype numerous times within various *Tillandsia* and *Vriesea* species (Tillandsioideae), but we would disagree with statements that uniformly bimodal complements are characteristic for all members of Tillandsioideae. Our research does corroborate the reported small, generally equal sized chromosomes for Pitcairnioideae, and the bimodality tendency within parts of Bromelioideae.

Bromeliaceae karyotype evolution appears to have proceeded from the small, uniformly sized chromosome complements characteristic of Pitcairnioideae to the bimodal (two size classes) complements characteristic for many Tillandsioideae (Marchant, 1967; McWilliams, 1974). Studies of bimodal chromosome complements in selected Tillandsioideae taxa are now underway.

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