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# CHROMOSOME NUMBERS IN BROMELIACEAE

GREGORY K. BROWN[1] AND CARLOS A. PALACÍ

Department of Botany, University of Wyoming, Laramie, Wyoming 82071

HARRY E. LUTHER

Marie Selby Botanical Gardens, 811 South Palm Avenue, Sarasota, Florida 34236

ABSTRACT. Chromosome numbers are reported for 44 taxa from Bromeliaceae, including first reports for three genera (*Hohenbergia*, *Lymania*, *Quesnelia*), and first reports for 27 additional species. The reported numbers are all diploid ($2n = 50$), except for *Ananas ananassoides* ($2n = 75$), a triploid, *Tillandsia butzii* ($2n = 100$), a tetraploid, and *Fosterella villosula* ($2n = 150$), a hexaploid. These chromosome numbers support the proposed base chromosome number of $x = 25$ for extant Bromeliaceae. Hypotheses concerning the evolution of chromosome base number in the Bromeliaceae are evaluated in light of recent molecular evidence suggesting that the Rapateaceae and Bromeliaceae may be sister taxa.

## INTRODUCTION

Chromosome numbers have been published for approximately 220 of the nearly 3,000 bromeliad species, and Brown and Gilmartin (1986, 1989a) have summarized the systematic significance of these numbers. However, no chromosome numbers are available for nearly half of the genera (i.e., *Abromeitiella*, *Androlepis*, *Ayensua*, *Brewcaria*, *Brocchinia*, *Connellia*, *Cottendorfia*, *Deinacanthon*, *Disteganthus*, *Encholirium*, *Fascicularia*, *Fernseea*, *Greigia*, *Hohenbergiopsis*, *Mezobromelia*, *Navia*, *Neoglaziovia*, *Ochagavia*, *Pseudaechmea*, *Orthophytum*, *Ronnbergia*, *Steyerbromelia*, *Ursulaea*, *Wittrockia*).

Marchant (1967) was the first to suggest $x = 25$ as the base chromosome number for Bromeliaceae, and subsequent work continues to support that proposal (Goldblatt 1980, Brown et al. 1984, Varadarajan & Brown 1985, Brown & Gilmartin 1989a). This distinctive base chromosome number, together with results from recent morphological (Brown & Gilmartin 1988, 1989b) and molecular studies (Ranker et al. 1990, Clark et al. 1993, Duvall et al. 1993) reinforce the long-held notion (e.g., Smith 1934) that the Bromeliaceae is monophyletic.

The origin of the $x = 25$ base number for the bromeliads has been problematic, mainly because putative, closely related families (e.g., Velloziaceae) have chromosome base numbers of $x = 8$ or $x = 9$ (Dahlgren & Rasmussen 1983, Dahlgren et al. 1985, Gilmartin & Brown 1987, Goldblatt & Poston 1988). Hypotheses concerning the derivation of $x = 25$ have, consequently, been devised assuming a putative sister taxon with a base number of 8 or 9. Furthermore, the first published chromosome number from Bromeliaceae, still an unverified $n = 16$ for *Tillandsia usneoides* (Billings 1904), reinforced the bias for $x = 8$. McWilliams (1974), for example, suggested that an ancestor with $x = 8$ produced the $x = 25$ bromeliad lineage through successive rounds of polyploidy, followed by ascending aneuploidy. In contrast, Brown and Gilmartin (1989a) proposed the origin of a dibasic $x = 17$ lineage, via hybridization of $x = 8$ and $x = 9$ parental types, followed by a second hybridization with an $x = 8$ lineage, to produce $x = 25$. This latter hypothesis was parsimonious within the phylogenetic constraints of Dahlgren's Bromeliiflorae (Dahlgren et al. 1985). Moreover, two lines of indirect evidence seemed to support the Brown and Gilmartin (1989a) hypothesis. First, cladistic analyses of morphological characters show the Velloziaceae ($x = 9$) to be closely related to the Bromeliaceae (Gilmartin & Brown 1987), an affinity that had been suggested by Huber (1977). Second, a base chromosome number of $x = 17$ for *Cryptanthus* (Marchant 1967), accorded with the hypothetical dibasic hybrid-level in the Brown and Gilmartin (1989a) hypothesis.

This paper reports on an ongoing meiotic chromosome number survey within the Bromeliaceae, and evaluates the issue of base number evolution in light of recent molecular data indicating that Bromeliaceae and Rapateaceae may be sister taxa.

## MATERIALS AND METHODS

Floral buds were obtained from cultivated specimens at Marie Selby Botanical Gardens, Sarasota, Florida (SEL), or from the field. See Brown and Gilmartin (1989a) for a description of the bud collecting and chromosome squash protocols. Locations for voucher herbarium specimens are indicated in TABLE 1. All graphic

[1] Author for correspondence.

TABLE 1. Bromeliaceae chromosome number reports.

| Taxon | 2n= | Voucher | Collection origin |
|---|---|---|---|
| Bromelioideae | | | |
| *Aechmea bromeliifolia* (Rudge) Baker | 50 | Brown 3137 (RM) | Brazil, Goias |
| *Aechmea fulgens* Brongniart var. *discolor* (C. Morren) Brongniart ex Baker | 50 | SEL 87-0458 (SEL) | ex hort |
| *Ananas ananassoides* (Baker) L. B. Smith | 75 | Brown 3129 (RM) | Brazil, Goias |
| [a]*Araeococcus flagellifolius* Harms | 50 | SEL 78-0683 (SEL) | Venezuela |
| [a]*Araeococcus pectinatus* L. B. Smith | 50 | SEL 82-0531 (SEL) | Brazil, Roraima |
| [b]*Hohenbergia pennae* Pereira | 50 | SEL 83-0258 (SEL) | Brazil, ex hort |
| [b]*Lymania globosa* Leme | 50 | SEL 86-0428 (SEL) | Brazil, Bahia |
| [b]*Lymania smithii* R. W. Read | 50 | SEL 89-572 (SEL) | Brazil, Bahia |
| [b]*Quesnelia liboniana* (De Jonghe) Mez | 50 | SEL 83-0051 (SEL) | Brazil, Rio de Janeiro |
| Pitcairnioideae | | | |
| [a]*Fosterella villosula* (Harms) L. B. Smith | 150 | SEL 80-0854 (SEL) | Bolivia |
| *Pitcairnia andreana* Linden | 50 | SEL 75-0077-043 (SEL) | Colombia |
| [a]*Pitcairnia archeri* L. B. Smith | 50 | Brown 2727 (RM) | Colombia, Quibdo |
| [a]*Pitcairnia arcuata* (André) André | 50 | Brown 2865 (RM) | Ecuador, Morono-Santiago |
| [a]*Pitcairnia armata* Maury | 50 | SEL 84-0303 (SEL) | Venezuela, Amazonas |
| *Pitcairnia atrorubens* (Beer) Baker | 50 | SEL 78-2205 (SEL) | Nicaragua |
| [a]*Pitcairnia cosangaensis* Gilmartin | 50 | Brown 2857 (RM) | Ecuador, Morona-Santiago |
| [a]*Pitcairnia fusca* H. Luther | 50 | Brown 2902 (RM) | Ecuador, Pichincha |
| [a]*Pitcairnia imbricata* (Brongniart) Regel | 50 | Palací 1243 (RM) | Guatemala, San Felipe |
| *Pitcairnia maidifolia* (C. Morren) Decaisne | 50 | SEL 82-0542 (SEL) | Peru, San Martin |
| [a]*Pitcairnia palmoides* Mez & Sodiro | 50 | Brown 2898 (RM) | Ecuador, Pichincha |
| [a]*Pitcairnia smithiorum* H. Luther | 50 | SEL 89-0004 (SEL) | Peru, Loreto |
| Tillandsioideae | | | |
| [a]*Guzmania mucronata* (Grisebach) Mez | 50 | SEL 88-0005 (SEL) | Venezuela, Falcón |
| [a]*Guzmania patula* Mez & Wercklé | 50 | SEL 75-0090-029 (SEL) | Venezuela, Aragua |
| *Guzmania rhonhofiana* Harms | 50 | SEL 76-0044-041 (SEL) | Ecuador, Cotopaxi |
| [a]*Tillandsia acostae* Mez & Tonduz ex Mez | 50 | Peterson & Anable 7082 (WS) | Mexico |
| [a]*Tillandsia adpressa* André | 50 | Brown 2901 (RM) | Ecuador, Pichincha |
| *Tillandsia anceps* Loddiges | 50 | SEL 86-0885 (SEL) | Costa Rica, Puntarenas |
| [a]*Tillandsia arhiza* Mez | 50 | Brown 3127 (RM) | Brazil, Goias |
| [a]*Tillandsia butzii* Mez | 100 | SEL 80-1580 (SEL) | Mexico, Chiapas |
| *Tillandsia caput-medusae* E. Morren | 50 | Mazariego 26 (RM) | El Salvador, Santa Ana |
| [a]*Tillandsia* cf. *didisticha* (E. Morren) Baker | 50 | Brown 3117 (RM) | Brazil, Goias |
| *Tillandsia dodsonii* L. B. Smith | 50 | SEL 73-0004-033 (SEL) | Ecuador, Pichincha |
| [a]*Tillandsia dyeriana* André | 50 | SEL 82-0215 (SEL) | Ecuador, Esmeraldas |
| [a]*Tillandsia friesii* Mez | 50 | Palací 1165 (RM) | Argentina, Salta |
| [a]*Tillandsia hamaleana* E. Morren | 50 | SEL 80-1132 (SEL) | Ecuador, Pichincha |
| *Tillandsia monadelpha* (E. Morren) Baker | 50 | SEL 80-0676 (SEL) | Costa Rica, Puntarenas |
| [a]*Tillandsia muhriae* Weber | 50 | Palací 1192 (RM) | Argentina, Salta |
| | 50 | Palací 1200 (RM) | Bolivia, Tupiza |
| [a]*Tillandsia multicaulis* Steudel | 50 | Mazariego 36 (RM) | El Salvador, Santa Ana |
| *Tillandsia polystachia* (L.) L. | 50 | SEL 76-0026-066 (SEL) | Mexico, Jalisco |
| *Tillandsia venusta* Mez & Wercklé | 50 | SEL 76-0044-039 (SEL) | Ecuador, Cotopaxi |
| [a]*Tillandsia zecheri* Till var. *cafayatensis* Palací & G. Brown | 50 | Palací 1172 (RM) | Argentina, Salta |
| [a]*Vriesea heterandra* (André) L. B. Smith | 50 | Brown 2875 (RM) | Ecuador, Morona-Santiago |
| [a]*Vriesea malzinei* E. Morren | 50 | SEL 81-2346 (SEL) | Mexico |
| [a]*Vriesea* cf. *sanguinolenta* Cogniaux & Marchal | 50 | Palací 1222 (RM) | Costa Rica, Guanacaste |

[a] First chromosome number reported for species.
[b] First chromosome number reported for genus.

documentation of chromosomes is at the Rocky Mountain Herbarium (RM). Taxonomic nomenclature follows Smith and Downs (1974, 1977, 1979), as updated by Luther and Sieff (1991).

## RESULTS

We report chromosome counts for 44 taxa, including 30 first reports (TABLE 1) for Bromeliaceae.

### Bromelioideae

The chromosome number reports for *Hohenbergia*, *Lymania*, and *Quesnelia*, all $n = 25$, are the first documented for these genera. The chromosome numbers for *Aechmea bromeliifolia* and *Aechmea fulgens* var. *discolor* confirm previously published reports (Lindschau 1933; Lindschau 1933 and Marchant 1967, respectively). Triploidy has also been documented in *Ananas ananassoides*, a taxon previously reported as diploid ($2n = 50$, Collins 1960, Brown & Gilmartin 1989a). Triploids are known in *Ananas*, with repeated documentation in the cultivated pineapple, *Ananas comosus* (L.) Merrill (Heilborn 1921, Collins & Kerns 1931, Collins 1933).

### Pitcairnioideae

The chromosome numbers for *Pitcairnia andreana*, *P. atrorubens*, and *P. maidifolia* confirm previously published numbers (Lindschau 1933, and Brown et al. 1984; Marchant 1967, and Varadarajan & Brown 1985, respectively). We report polyploidy in the Pitcairnioideae from meiotic material for the second time, a hexaploid ($2n = 150$) in *Fosterella villosula*. The published chromosome numbers for three other species of *Fosterella* are diploid ($2n = 50$; Brown et al. 1984, Brown & Gilmartin 1989a) and hexaploid (*Lindmania penduliflora* = *F. penduliflora*; Marchant 1967).

### Tillandsioideae

Chromosome numbers for the following species agree with earlier reports: *Guzmania rhonhofiana* (Marchant 1967), *Tillandsia anceps* (Marchant 1967), *T. dodsonii* (Brown & Gilmartin 1989a), *T. monadelpha* (Marchant 1967, Brown & Gilmartin 1989a), and *T. venusta* (Brown et al. 1984). The tetraploid level in *Tillandsia butzii* is the third report of polyploidy from meiotic material in the Tillandsioideae; the first two were obtained from *T. capillaris* and *T. tricholepis* (Brown & Gilmartin 1989a). Tetraploidy ($2n = 100$) has been reported from mitotic chromosome preparations for four species of *Tillandsia* (*T. castellanii*, *T. gilliesii*, *T. hirta*, *T. loliacea*; Till 1984). Furthermore, putative tetraploids (e.g., $2n = 84, 89, 92, 96, 97$), also determined form mitotic material, have been reported for 15 additional *Tillandsia* subgenus *Diaphoranthema* species (Lindschau 1933, Tschischow 1956, Gauthe 1965, Till 1984). However, see Brown and Gilmartin (1986) for a discussion of possible problems associated with mitotic root tip chromosome reports from epiphytic bromeliads.

## DISCUSSION

The chromosome numbers reported here support Marchant's (1967) proposal that $x = 25$ is the base number for Bromeliaceae. The database of bromeliad chromosome numbers (Brown, unpubl., available on request) is now large enough that new data on chromosome numbers in the family will probably not change this view. We still lack chromosome numbers, however, for many genera.

The earliest hypotheses about the base chromosome number for Bromeliaceae (Lindschau 1933, Weiss 1965, Sharma & Ghosh 1971, McWilliams 1974) were guided by lowest-common-denominator derivations (e.g., $2n = 48$ interpreted as a hexaploid based on $x = 8$). In contrast, Brown and Gilmartin (1989a) formulated their model of chromosome number evolution based on the then-held notion of a potential sister taxon relationship between the Bromeliaceae and the Velloziaceae (e.g., Huber 1977, Dahlgren & Rasmussen 1983, Dahlgren et al. 1985, Gilmartin & Brown 1987, Ranker et al. 1990). Nevertheless, this model is no longer tenable. Recent molecular phylogenetic studies, using *rbc*L sequences, indicate the Rapateaceae to be the most likely sister taxon to Bromeliaceae, and place Velloziaceae in a distant clade (Clark et al. 1993, Duvall et al. 1993).

The only known chromosome number for Rapateaceae is $2n = 22$ for the genus *Maschalocephalus* (Mangenot & Mangenot 1957). Based on this single report, Sharma (1972) assigned $x = 11$ as the base number for the family, although *Maschalocephalus* is unique in being the only African genus in this otherwise South American assemblage of 16 genera. Therefore, we believe that comments about base chromosome numbers in the Rapateaceae, and their relationship to base number evolution in the Bromeliaceae, are premature and overly speculative. More information is needed about chromosome numbers from Rapateaceae before chromosomal evolution in Bromeliaceae can be addressed.

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