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# CHROMOSOME NUMBERS AND KARYOTYPES IN ASTERACEAE<sup>1</sup>

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## ABSTRACT

Chromosome numbers were determined from microsporocytes (meiotic counts) and root-tip cells (mitotic counts) in 201 collections of 51 genera and 119 specific and infraspecific taxa belonging to nine tribes of Asteraceae and *Acicarpha spathulata* R. Br. of Calyceraceae from Australia, Bolivia, Brazil, Chile, Mexico, and the United States. These include the first reports and new numbers for the basal members of the Barnadesieae and Mutisieae. First reports are provided for 45 taxa, including five genera, *Dasyphyllum* HBK ( $2n = 54$ ), *Dithyrostegia* A. Gray ( $2n = 14$ ), *Epitriche* Turcz. ( $2n = 10$ ), *Revelia* R. M. King & H. Rob. ( $2n = 22$ ), and *Stiffia* J. C. Mikan ( $2n = 54$ ). In addition, new chromosome numbers are established at the generic level in the genera *Barnadesia* Mutis ( $2n = 54$ ), *Eremanthus* Less. ( $2n = 34, 30$ ), *Macvaughiiella* R. M. King & H. Rob. ( $2n = 24$ ), and *Trichocline* Cass. ( $2n = 38$ ), and in 12 additional species. Remaining counts augment and agree with previously reported determinations. The base chromosome numbers of Calyceraceae and Asteraceae are discussed in published records and our original counts.

**Key words:** Asteraceae, Brazil, chromosome number, cytotaxonomy, genome size, karyotype, phylogeny.

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Chromosomal information has contributed extensively to our understanding of relationships within the diverse Asteraceae and has resulted in heightened awareness of groups in need of taxonomic reevaluation. Most previous studies on the chromosomes of this family were conducted on plants in temperate regions of the Northern Hemisphere, although there is more species diversity in Central America and South America.

Recent molecular studies have suggested that Barnadesieae is the most primitive tribe in the Asteraceae, followed by Mutisieae, while Calyceraceae is sister to Asteraceae (Jansen & Palmer, 1987, 1988; Kim & Jansen, 1995; Bayer & Starr, 1998; Kim et al., 2002; Panero & Funk, 2002). Most members of Barnadesieae and Mutisieae are concentrated in South America and are relatively poorly known cytologically. In this paper, we report original chromosome counts from 201 accessions representing 120 species and varieties, including first reports for 45 taxa of Asteraceae and one species of Calyceraceae.

## MATERIALS AND METHODS

A total of 201 accessions attributed to 51 genera and 119 specific and infraspecific taxa of nine tribes of Asteraceae and *Acicarpha spathulata* R. Br. of Calyceraceae were collected from Australia, Bolivia, Brazil, Chile, Mexico, and the United States. Chromosome counts were obtained from either floral buds fixed in a 3:1 ethanol-acetic acid fixative in the field or root tips obtained from seedlings grown from cypselae of known provenance in the greenhouse of Kobe University. Excised root tips about 1 cm in length were pre-treated with cold water at 0°C for 24 hours and fixed in 3:1 ethanol-acetic acid for 1–5 hours at 5°C. Haploid karyotypic idiograms are based on the means of 10 measurements for each chromosome.

Although Turner (1987) and Bremer (1994) have treated *Revelia* R. M. King & H. Rob. and *Cronquistia* R. M. King as synonyms of *Carphochaete* A. Gray, in the present study, the two are treated as separate genera with different chromosome numbers

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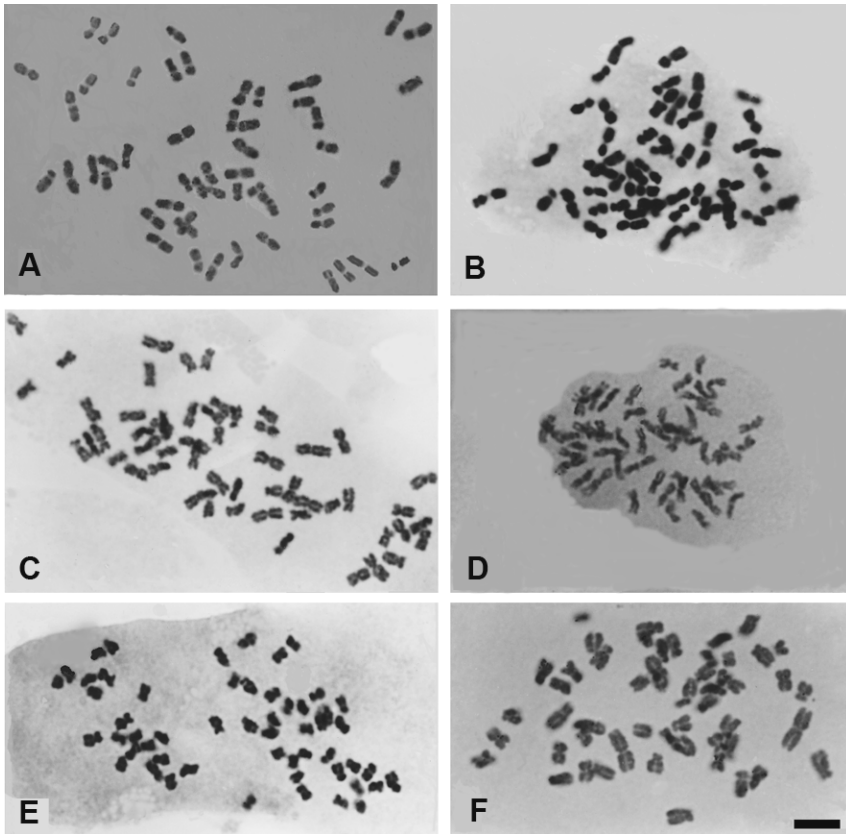


Figure 1. Photomicrographs of somatic metaphase chromosomes. Scale bar = 5  $\mu\text{m}$ . —A. *Dasyphyllum spinescens* ( $2n = 54$ ). —B. *Dasyphyllum brasiliense* ( $2n = 54$ ). —C. *Barnadesia caryophylla* ( $2n = 54$ ). —D. *Stiffia chrysanthia* ( $2n = 54$ ). —E. *Trixis praetans* ( $2n = 54$ ). —F. *Mutisia campanulata* ( $2n = 52$ ).

and habits. Voucher specimens have been deposited in the Centro de Pesquisas de Historia Natural Herbario Goro Hashimoto (GHSP, Brazilian specimens), KANA (Bolivian and Chilean specimens), MEL (Australian specimens), MEXU (Mexican specimens), KYO (Brazilian and Mexican specimens), and TI (Australian specimens). Indices consulted for previous chromosome number determinations include: Fedorov (1974), Moore (1973), Goldblatt (1981, 1984, 1985, 1988), Goldblatt and Johnson (1990, 1991, 1994, 1996, 1998, 2000, 2003), and <<http://www-asteraceae.cla.kobe-u.ac.jp>>. We have cited only these in order to save space and still provide a means of access to the primary literature.

#### RESULTS AND DISCUSSION

Chromosome numbers of 201 collections representing 51 genera and 119 specific and infraspecific taxa belonging to nine tribes of Asteraceae and *Acicarpha pathulata* of Calyceraceae were determined. Among

them, the chromosome numbers of 45 species and/or infraspecific taxa and five genera (*Dasyphyllum* Kunth [ $2n = 54$ ], *Dithyrostegia* A. Gray [ $2n = 14$ ], *Epitriche* Turcz. [ $2n = 10$ ], *Revealia* [ $2n = 22$ ], and *Stiffia* J. C. Mikan [ $2n = 54$ ]) have not been previously counted. Chromosome numbers for *Barnadesia* Mutis ex L. f. ( $2n = 54$ ), *Eremanthus* Less. ( $2n = 34, 30$ ), *Macvaughiiella* R. M. King & H. Rob. ( $2n = 24$ ), *Trichocline* Cass. ( $2n = 38$ ), and 14 additional species differ from those previously reported; new base chromosome numbers are established for those species. Among taxa reported here, three show infraspecific polyploidy (Appendix 1). Photomicrographs of the mitotic chromosomes of six taxa are displayed in Figure 1, and the idiograms of the mitotic chromosome of 17 taxa are displayed in Figure 2. The characteristics of karyotypes of 17 taxa are presented in Table 1.

The tribal arrangements of Asteraceae listed in Appendix 1 and Table 1 follow those of Panero and Funk (2002).

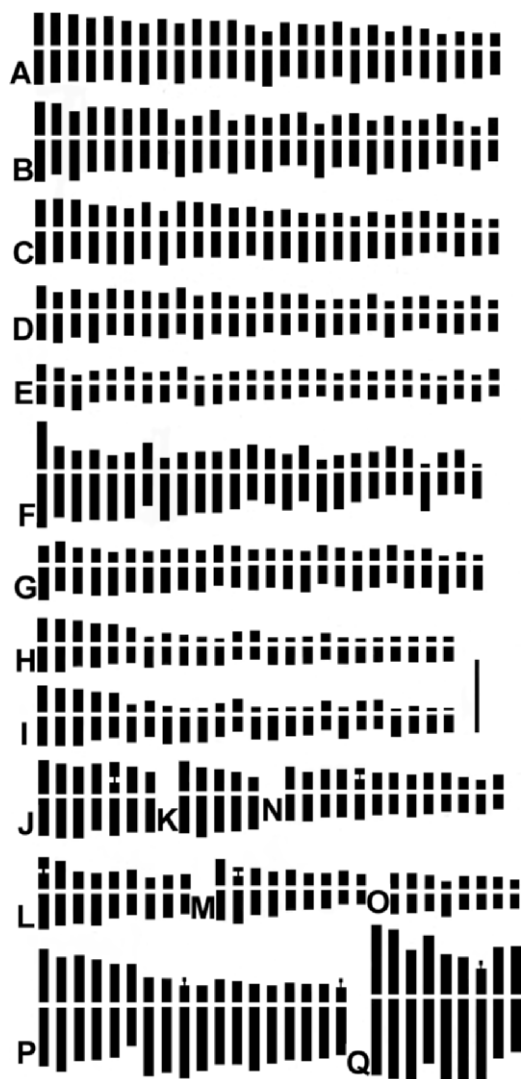


Figure 2. Haploid karyotypic idiograms. Scale bar = 5  $\mu$ m. —A. *Dasyphyllum spinescens* ( $n = 27$ ). —B. *Dasyphyllum brasiliense* ( $n = 27$ ). —C. *Barnadesia caryophylla* ( $n = 27$ ). —D. *Stiffia chrysantha* ( $n = 27$ ). —E. *Trixis praetans* ( $n = 27$ ). —F. *Mutisia campanulata* ( $n = 26$ ). —G. *Mutisia* sp. ( $n = 26$ ). —H. *Chaptalia integrifolia* ( $n = 24$ ). —I. *Chaptalia nutans* ( $n = 24$ ). —J. *Symphyotrichum graminifolium* ( $n = 7$ ). —K. *Epitriche demissus* ( $n = 5$ ). —L. *Aster squamata* ( $n = 9$ ). —M. *Notiastrum acuminatum* ( $n = 9$ ). —N. *Dyssodia papposa* ( $n = 13$ ). —O. *Thymophylla aurea* ( $n = 8$ ). —P. *Marshallia mohrii* ( $n = 18$ , diploid karyotypic idiogram). —Q. *Espejoa mexicana* ( $n = 9$ ).

#### CALYCERACEAE

*Acicarpha spathulata* has a chromosome number of  $2n = 8II$ , which is in accord with numbers previously reported.

#### ASTERACEAE

**Barnadesieae.** First reports are provided for seven specific and infraspecific taxa of *Dasyphyllum* and *Barnadesia caryophylla* (Vell.) S. F. Blake. In *Barnadesia*, chromosome numbers have been reported for eight species. They vary from  $n = 12$  (Olsen, 1980) to  $2n = 62$  (Cristobal, 1986). In *B. caryophylla*, we found a chromosome number of  $2n = 54$ . This is the first report of this number for this genus, and it matches or closely approximates previously reported numbers for other genera such as *Arnaldoa* Cabrera ( $n = 24$ – $27$  in Stuessy & Sagastegui, 1993) and *Chuquiraga* Juss. ( $n = 27$  and/or  $2n = 54$  in Diers, 1961; Wulff, 1990). In addition,  $2n = 54$  is reported here for the first time for seven *Dasyphyllum* taxa. Reports for taxa of *Dasyphyllum* and *Barnadesia* establish a new base chromosome number of  $x = 27$  for both genera here.

**Mutisieae.** First reports are provided for *Chaptalia graminifolia* (Dusen) Cabrera ( $2n = 48 + 0$ – $7Bs$ ), *C. runcinata* Kunth ( $2n = 48$ ), *Jungia sellowii* Less. ( $n = 20II$ ), *Mutisia campanulata* Less. ( $2n = 52$ ), two varieties of *Stiffia chrysantha* Mikan ( $2n = 54$ ), *Trichocline catharinensis* Cabrera ( $2n = 38$ ), and *Trixis praetans* (Vell.) Cabrera ( $2n = 54$ ). All of the genera examined have high chromosome numbers. Counts of  $2n = 54$  for the genera *Stiffia*, *Trixis* P. Browne, *Acourtia* D. Don (Vuilleumier, 1969; Pinkava & Keil, 1977; Powell & Powell, 1978; Ward, 1983; Carr et al., 1999; Strother & Panero, 2001), *Plazia* Ruiz & Pav. (Covas & Schnack, 1946), and *Proustia* Lag. (Covas & Schnack, 1946) agree with those of four genera of Barnadesieae. Our counts of  $2n = 54$ , as well as many previous reports of  $n = 27$  for *Trixis* species, differ from the report from Carr et al. (1999) for *T. inula* Crantz ( $2n = 28II$ ). Chilean and Brazilian *Mutisia* L. f. species have chromosome numbers of  $2n = 52$ , which agree with those of *M. acuminata* Ruiz & Pav. (Waisman et al., 1984; Carr et al., 1999), *M. clematis* L. f. (Powell & King, 1969), *M. coccinea* A. St.-Hil. (Gibbs & Ingram, 1982), *M. ledifolia* Decne. ex Wedd. (Waisman et al., 1984), and *M. orbignyana* Wedd. (Fernández Casas, 1981) and are different from previous counts for other species (Diers, 1961; Turner et al., 1979). Grau (1987) reported  $2n = 46$  for five Chilean *Mutisia* species. Thus, our count of  $2n = 52$  for Chilean *Mutisia* species is a new report. Previous chromosome counts for *Trichocline* species were reported to be  $n = 18$  (Covas & Schnack, 1947; Zardini, 1975) and  $n = 20$  (Turner et al., 1979). Our count for *Trichocline catharinensis* establishes a new base number,  $x = 19$ , at the generic level. Kim et al. (2002) showed that Mutisieae is polyphyletic based on

Table 1. Taxa, chromosome number, total haploid karyotypic length, range of chromosome size, ratio of chromosome size, mean arm ratio, and life form. TKL, total haploid karyotypic length; range, the longest chromosome to the shortest chromosome; ratio, the longest chromosome to the shortest chromosome; SE, standard error; SD, standard deviation; MAR, mean arm ratio (total long arm length to total short arm length); LF, life form; T, tree; S, shrub; L, liana; P, perennial; A, annual.

Taxon	2n	TKL (μm)			Range (μm)	Ratio	MAR	LF
		Total	SE	SD				
<i>Dasyphyllum spinescens</i>	54	185.46	10.04	22.45	4.44–2.48	1.79	1.46	T
<i>Dasyphyllum brasiliense</i>	54	185.32	9.29	20.78	5.03–2.44	2.06	1.49	T
<i>Barnadesia caryophylla</i>	54	161.40	5.86	13.11	4.02–1.92	2.10	1.53	S
<i>Stiffitia chrysantha</i>	54	126.52	2.96	6.62	3.10–1.72	1.80	1.55	S
<i>Trixis praestans</i>	54	92.58	2.64	5.91	2.20–1.34	1.64	1.71	S
<i>Mutisia campanulata</i>	52	176.66	3.88	8.68	6.78–1.88	3.61	2.17	L
<i>Mutisia</i> sp.	52	116.72	1.96	4.38	3.09–1.69	1.83	2.32	L
<i>Chaptalia integrifolia</i>	48	82.28	6.10	13.63	3.08–1.20	2.57	2.21	P
<i>Chaptalia nutans</i>	48	95.68	4.76	10.65	3.71–1.19	3.12	2.31	P
<i>Dithyrostegia amplexicaulis</i>	14	58.52	0.67	1.50	4.61–3.59	1.28	1.39	A
<i>Epitriche demissus</i>	10	37.84	0.80	1.78	4.34–3.07	1.41	1.77	A
<i>Aster squamatus</i>	18	50.38	2.58	5.77	3.89–2.09	1.86	1.42	P
<i>Noticastrum acuminatum</i>	18	41.86	1.30	2.91	3.58–1.55	2.31	1.43	P
<i>Marshallia mohrii</i>	36	202.64	6.68	14.93	7.50–4.10	1.83	2.13	P
<i>Espejoa mexicana</i>	18	147.16	4.98	9.13	9.66–6.72	1.44	1.61	A
<i>Dyssodia papposa</i>	26	38.98	1.06	2.38	3.17–1.79	1.77	1.32	A
<i>Thymophylla aurea</i>	16	28.70	0.64	1.44	2.08–1.53	1.36	1.11	A

the *ndhF* sequence variation. Panero and Funk (2002) supported the polyphyly of the old Mutisieae and proposed to allocate members of Cardueae and Mutisieae into the following group and subfamilies: “The *Stiffitia* group,” Mutisioideae, Gochnatioideae, Hecastocleioideae, Carduoideae, Pertyoideae, and Gymnarrhenioideae, based on the comparison of 13380 bp of cpDNA. “The *Stiffitia* group” follows the basal Barnadesioideae, a relationship consistent with the same chromosome numbers. The base chromosome number for Mutisieae, including “the *Stiffitia* group,” may be  $x = 27$ . The chromosome numbers  $2n = 52$ ,  $2n = 48$ , and  $2n = 38$  may have been derived through dysploidal reduction.

*Vernonieae*. First reports are provided for *Eremanthus bicolor* (DC.) Baker ( $2n = 30$ ) and three species of *Vernonia* Schreb. There are three unidentified specimens of *Eremanthus*; *Eremanthus* species 1 has a chromosome number of  $2n = 30$ , but species 2 and species 3 have chromosome numbers of  $2n = 34$  and/or  $2n = 17H$ . Turner et al. (1979) reported  $n = 15$  for Brazilian *E. elaeagnus* Sch. Bip. Jones (1982) reported  $2n = 36$  for Brazilian *E. reflexo-auriculatus* G. M. Barroso. Thus, three base

chromosome numbers ( $x = 15$ , 17, and 18) have been reported for *Eremanthus*. We report  $2n = 17H$  or  $2n = 34$  for six species and one unidentified specimen of *Vernonia*. The chromosome base numbers of New World *Vernonia* have been reported to be  $x = 17$ , 16, 15, 14, and 10 (Ruas et al., 1991; Dematteis, 1997). Dematteis (1998) and Dematteis and Fernandez (2000) reported  $2n = 32$  for all species of *Vernonia* they examined.

*Gnaphalieae*. The additional descending dysploidy of  $x = 13$ , 12, and 6 in *Angianthus* J. C. Wendl., of  $x = 14$ , 12, and 11 in *Erymophyllum* Paul G. Wilson, and of  $x = 14$  and 13 in *Podotheca* Cass. was found in a previous study (Watanabe et al., 1999a). The Australian members of Gnaphalieae we examined have lower chromosome numbers ( $n = 13$ , 12, 7, and 5), which are lower than those present on other continents ( $n = 14$ ; Watanabe et al., 1999a).

*Astereae*. First reports are provided for *Baccharis pentodonta* Malme and *B. triplinervis* Baker. All species of shrubby *Baccharis* L. examined are diploids based on  $x = 9$ . All of the previous counts for *Symphyotrichum graminifolium* (Spreng.) G. L. Nesom reported as *Aster squamatus* (Spreng.) Hieron. have

been  $n = 10$  or  $2n = 20$  (Schnack & Covas, 1947; Kamel, 1996), except those by Coleman (1968,  $n = 9-10$ ) and Spooner et al. (1995,  $n = 5$ ). The present study found chromosome counts of  $2n = 18 + 0-2Bs$ . The longest chromosome pair has a large trabant at the end of a short arm (Fig. 2L). Previous studies may have counted this trabant or B chromosome as an independent chromosome.

**Plucheeae.** *Pluchea sagittalis* (Lam.) Cabrera has  $n = 10II$ . As noted by Watanabe et al. (1999a), all members reported for this tribe, excluding some erroneous counts, have chromosome counts of  $2n = 20$  or polyploid numbers based on  $x = 10$ .

**Helenieae.** Two previous counts for *Thymophylla pentachaeta* (DC.) Small var. *hartwegii* (A. Gray) Strother (as *Dyssodia hartwegii* (A. Gray) B. L. Rob.) were  $n = 26$  (Johnston & Turner, 1962; De Jong & Longpre, 1963). This is the first chromosome number of  $2n = 26$  for this variety, although Strother (1989) has stated that all *Thymophylla* Lag. species have chromosome numbers based on  $x = 8$ . Strother (1989) reported  $2n = 16II$  and  $2n = 32$  for Texas *T. pentachaeta*. Our two Mexican accessions of this variety had counts of  $2n = 24$ . The monotypic *Espejoa mexicana* DC. has a chromosome number of  $2n = 18$ . *Marshallia mohrii* Beadle & F. E. Boynton has a chromosome number of  $2n = 36$ , which is a tetraploid based on  $x = 9$ .

**Heliantheae.** The first report,  $2n = 17II$ , is provided for *Verbesina clausenii* Sch. Bip. ex Baker and agrees with previous reports for other species of the genus.

**Eupatorieae.** First reports are provided for species of *Ageratina* Spach (1), *Carphochaete* (1), *Chromolaena* DC. (4), *Decachaeta* DC. (1), *Praxelis* Cass. (1), *Revealia* (1), and *Stevia* Cav. (9). Some species of *Chromolaena* are polyploids and apomicts; *C. kleinii* (Cabrera) R. M. King & H. Rob. is a diploid based on  $x = 10$  and is probably sexual. For the first time, hexaploidy ( $2n = 60$ ) is documented for *Chromolaena laevigata* (Lam.) R. M. King & H. Rob. Sundberg et al. (1986) reported  $n = 16$  for *D. pyramidalis* (B. L. Rob.) S. D. Sundb., C. P. Cowan & B. L. Turner (= *Erythradenia pyramidalis* (B. L. Rob.) R. M. King & H. Rob.). It is confirmed to have a chromosome number of  $2n = 32$ . A previous chromosome count for *Gyptis crassipes* (Hieron.) R. M. King & H. Rob. was reported as  $n = 30$  (as *Eupatorium lanigerum* Hook. & Arn.) by Coleman (1968). Diploidy ( $2n = 30$ ) is documented for the first time in this species. Our count of  $2n = 24 + 4-8Bs$  for *Macvaughiiella mexicana* (Sch. Bip.) R. M. King & H. Rob. is different from a previous count of  $n = ca. 13$  (King et al., 1976). Our accession of *Microspermum nummu-*

*lariaefolium* Lag. is a triploid with a chromosome number of  $2n = 36$ ; triploidy is documented for the first time in this species. *Praxelis missiona* (Malme) R. M. King & H. Rob., with a chromosome number of  $2n = 80$ , is an octoploid based on  $x = 10$ . The diploid chromosome number of  $n = 10$  has been reported only for Bolivian *P. clematidea* (Griseb.) R. M. King & H. Rob. by Wulff et al. (1996).

*Stevia* includes four basic life forms: woody shrubs, plants with woody caudices and herbaceous stems, rhizomatous perennials, and annuals, all of which have been found in Mexico. All Mexican species of shrubs or shrublets are sexual diploids with chromosome numbers of  $2n = 24$ , while all Mexican species of annual herbs are also sexual diploids, but their chromosome numbers vary from  $2n = 24$  to  $2n = 8$ . North and Central American perennial *Stevia* are diploids or agamospermous polyploids based on  $x = 11$  or  $12$  (Watanabe et al., 2001). The chromosome number of  $n = 17$  reported by Grashoff et al. (1972) for the Mexican perennial *S. purpusii* B. L. Rob. is probably a miscount. It is difficult to determine the chromosome number from the irregular meiotic chromosome configurations of odd polyploids. Our accession of Mexican *S. purpusii* has a chromosome number of  $2n = 36$  and is a triploid based on  $x = 12$ . Native South American species of *Stevia* are perennials, and mostly diploids based on  $x = 11$ . The chromosome number of  $n = 12$  for *S. organensis* Gardner reported by Coleman (1970) is possibly erroneous. Our accession collected from the same site as that of Coleman (1970) had a chromosome number of  $2n = 22$ . Colombian *S. lucida* Lag., with a chromosome number of  $n = 12$ , is a shrub and is basically a Central American species. Three polyploids reported from South America are also basically Central American (*S. elatior* HBK by Jansen et al., 1984; *S. ovata* Willd. by Turner et al., 1967; *S. serrata* Cav. by Powell & King, 1969). The occurrence of polyploidy in Peruvian *S. andina* B. L. Rob. ( $n = ca. 22$ , Turner et al., 1967) and Bolivian *S. bangii* Rusby ( $2n = 44 + 0-5Bs$ , present study) may represent sporadic origins (a single count, respectively) because their distribution is restricted to small areas instead of the widespread prevalence of agamospermous polyploids in North and Central American.

#### KARYOTYPES

Figure 2 contains haploid (except for *Marshallia* Schreb.) karyotypic idiograms. In Table 1, we report the mean total haploid karyotypic length with standard errors, standard deviations, ranges of longest and shortest chromosome, arm ratios for each karyotype, mean arm ratio (total long arm length to



total short arm length), and life form. The total haploid karyotypic length of *Dasyphyllum* and *Barnadesia* has been shown to be significantly longer than those of members of Astereae and Anthemideae, with  $n = 9$  reported in the literature (Table 1; Watanabe et al., 1999b). The karyotypes of members of *Dasyphyllum*, *Barnadesia*, *Stiffia*, *Trixis*, and *Mutisia* do not have the duplicated homologous chromosome sets that would suggest autopolyploid origin. Their karyotypes are well diverged even if they have polyploid origins. The base number for Barnadesieae and Mutisieae may be  $x = 27$ , but the possibility that they may be hexaploids based on  $x = 9$  cannot be discounted, as we mention later.

From our results (Figs. 1–2; Appendix 1; Table 1), it is apparent that there is a great diversity of karyotypes. For example, the karyotypes of *Barnadesia* and *Dasyphyllum* are unimodal and contrast with the bimodal karyotypes of *Mutisia campanulata* and *Trichocline catharinensis*, which have one pair of large chromosomes and 25 or 18 pairs of small chromosomes, respectively. *Mutisia campanulata* has three pairs of nearly telocentric chromosomes, and *Chaptalia* Vent. species *C. integrifolia* (Cass.) Baker and *C. mandonii* (Sch. Bip.) Burkart have 13 to seven pairs of nearly telocentric chromosomes, respectively. Lower chromosome numbers and asymmetric karyotypes of Mutisieae may have been derived through dysploidal reduction from a base of  $x = 27$  resulting from structural rearrangements. *Marshallia* is basal in the Helenieae (Baldwin et al., 2002) and has a base chromosome number of  $x = 9$ . It has an extraordinarily large genome size as shown in Figure 2P and Table 1. (This accession is an allotetraploid karyotypically, and its idiogram and total karyotypic length are given as “diploid.”) The smaller chromosome number and genome size (= total haploid karyotypic length) may have been selected in annuals such as *Thymophylla aurea* (A. Gray) Greene, as well as those in many other genera of Asteraceae (Watanabe et al., 1999a, b). The monotypic *Espejia* DC. is an annual and also has a large genome size (Fig. 2Q and Table 1). It is desirable to estimate the isozyme number or the state of ploidal level for both *Marshallia* and *Espejia* to determine whether they are “true” diploid states or not.

#### THE ANCESTRAL BASE CHROMOSOME NUMBER OF ASTERACEAE AND SOME RELATED LIFE FORMS

Among papers that have dealt with the ancestral base chromosome number of Asteraceae, most have suggested  $x = 9$ , largely because this is the modal number based on more than 30% of all counted species (Solbrig, 1977). Support for  $x = 9$  comes from

reports for taxa of Astereae and Anthemideae collected from temperate regions of the Northern Hemisphere, where researchers have sampled most intensively in the past. The sister family Calyceraceae has base chromosome numbers of  $x = 13, 15, 18$ , and 21 in three of four genera examined (Covas & Schnack, 1947; Rahn, 1960; Turner, 1978; Moore, 1981), in addition to  $n = 8$ , which was reported for two species of *Acicarpha* Juss. (Sugiura, 1936, 1937; Raven et al., 1965; Rodriguez Correia et al., 1977; Benko-Iseppon, 1992; present study). De Vore (1994; cited by Stuessy et al., 1996) treated *Acicarpha* as the most primitive genus within Calyceraceae. But *A. spathulata* ( $n = 8$ ), one of the five species of the genus, is a specialized succulent plant growing on the coastal sands. In Barnadesieae, the chromosome numbers have been reported for six of nine genera. Among them, the perennial monotypic genus *Schlechtendahlia* Benth. & Hook. f. has a chromosome number of  $n = 8$  (Cialdella & Lopez de Kresling, 1981; Hunziker et al., 1989), and the five remaining genera have chromosome numbers of  $n = 24, 25$  (*Doniophyton* Wedd., annual; Wulff, 1990), and  $n = 27$  for *Arnaldoa*, *Barnadesia*, *Chuiriraga*, and *Dasyphyllum*. Based on cladistic analysis of morphological characters, Bremer (1994) and Stuessy et al. (1996) noted that *Schlechtendahlia* and *Dasyphyllum* were primitive and basal in subfamily Barnadesioideae. Stuessy et al. (1996) treated the members of both sections of the subgenus *Dasyphyllum* as having the life form of arching shrubs. Among the accessions we examined, *Dasyphyllum trichophyllum* (Baker) Cabrera (sect. *Macrocephala*), *D. brasiliense* (Spreng.) Cabrera, *D. spinescens* (Less.) Cabrera, and *D. tomentosum* (Spreng.) Cabrera (sect. *Microcephala*), all are trees. Stuessy et al. (1996) mentioned that the arborescent life form in *Dasyphyllum* might be a derived feature. *Schlechtendahlia*, all genera of Calyceraceae, and most of Goodeniaceae are herbaceous perennials. Stuessy et al. (1996) regarded *Schlechtendahlia* and *Acicarpha* as basal and took  $x = 8$  as the original base number for both Asteraceae and Calyceraceae. Phylogenetic trees of Barnadesioideae by Bremer (1994) and Stuessy et al. (1996) are based on morphological characters and are influenced significantly by the life form. Molecular systematic data on the chloroplast *ndhF* sequences (Kim & Jansen, 1995) indicate that two clades including *Dasyphyllum* and *Schlechtendahlia* diverged at the base of subfamily Barnadesioideae. Gustaffson et al. (2001) and Funk et al. (2005) reported the more detailed molecular phylogenetic trees of the Barnadesioideae. Their trees show that the genera of *Barnadesia* and *Dasyphyllum* are at the basal position in the separate clades, and *Schlechtendahlia* is a derivative

in the *Dasyphyllum* clade. Both genera of *Barnadesia* and *Dasyphyllum* have a chromosome number of  $2n = 54$ , and *Schlechtendahlia* has a chromosome number of  $2n = 16$ . It is difficult to infer the dysploid reduction from  $2n = 54$  to  $2n = 18$  by the simple steps of chromosomal changes. Thus, we consider that the chromosome number of  $n = 8$  for *Schlechtendahlia* has been derived from the ancestral  $n = 9$  by the dysploid reduction, and the chromosome number of  $2n = 54$  for *Barnadesia* and *Dasyphyllum* is a hexaploid state based on the original base chromosome number,  $x = 9$ . Because their genome sizes (= total haploid chromosome length) are so large (Table 1), some tribes have higher base chromosome numbers than previously suspected (i.e.,  $x = 17$  for Cardueae and Vernonieae,  $x = 14$  for Gnaphalieae; Watanabe et al., 1999a). The base chromosome number in the clade comprising Heliantheae s.l.–Eupatorieae is  $x = 18$ . Estimated base chromosome numbers for helenioid tribes include  $x = 19$  for Madieae,  $x = 18$  for Helenieae s. str. and Perityleae, and  $x = 17$  for Bahieae (Baldwin et al., 2002). Dysploid reduction in chromosome number from the putatively high base number in Heliantheae s.l.–Eupatorieae (Watanabe et al., 1995; Ito et al., 2000) and other tribes, except for Astereae ( $x = 9$ ), Anthemideae ( $x = 9$ ), Inuleae ( $x = 11$ – $7$ ), Lactuceae ( $x = 9$ ), and Plucheeae ( $x = 10$ ), to the typical diploid levels appears to have occurred repeatedly in different sublineages, especially in groups rich in annuals (Stebbins, 1950; Robinson et al., 1981; Kadereit & Jeffrey, 1996; Watanabe et al., 1996, 1999; Baldwin et al., 2002).

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APPENDIX 1. New chromosome number counts and voucher data for species of Asteraceae and Calyceraceae. \*First report for species, \*\*first report for genus.

## CALYCERACEAE

- Acicarpha spathulata* R. Br. 2n = 8II. Brazil. Sao Paulo: Itanhaem, Nova Itanhaem, *Watanabe & Nagatani* 205 (GHSP, KYO).

## ASTERACEAE

### Barnadesiaceae

- \**Barnadesia caryophylla* (Vell.) S. F. Blake. 2n = 54. Brazil. Goiás: 11 km SW from Colinas do Sul to Niquelandia, *Watanabe & Nagatani* 232 (GHSP, KYO); 2n = 54. Brazil. Goiás: 13 km SW from Colinas do Sul to Niquelandia, *Watanabe & Nagatani* 234 (GHSP, KYO).
- \*\**Dasyphyllum brasiliense* (Spreng.) Cabrera var. *brasiliense*. 2n = 54. Brazil. Minas Gerais: 13 km SE from Carandai, *Watanabe & Nagatani* 43 & 46 (GHSP, KYO); 2n = 54. Brazil. São Paulo: cultivated in Jardim Botânico do Estado de São Paulo, *Watanabe & Nagatani* 258 (GHSP, KYO).
- \*\**Dasyphyllum brasiliense* (Spreng.) Cabrera var. *multiflorum* (Baker) Cabrera. 2n = 54. Brazil. Paraná: 54 km NE from Curitiba, *Watanabe & Nagatani* 133 (GHSP, KYO).
- \*\**Dasyphyllum flagellare* (Casar.) Cabrera. 2n = 54. Brazil. Minas Gerais: ca. 13 km from Corrego do Bom Jesus to Pedra de São Domingo, *Watanabe & Nagatani* 109 (GHSP, KYO).
- \*\**Dasyphyllum spinescens* (Less.) Cabrera. 2n = 54. Brazil. Minas Gerais: ca. 13 km from Corrego do Bom Jesus to

Pedra de São Domingo, *Watanabe & Nagatani* 108 (GHSP, KYO).

- \*\**Dasyphyllum tomentosum* (Spreng.) Cabrera var. *tomentosum*. 2n = 54. Brazil. Santa Catarina: E Catanduvas along BR282, *Watanabe & Nagatani* 144 (GHSP, KYO).
- \*\**Dasyphyllum tomentosum* (Spreng.) Cabrera var. *multiflorum* (Baker) Cabrera. 2n = 54. Brazil. Santa Catarina: 14 km N from Santa Cecilia, *Watanabe & Nagatani* 139 (GHSP, KYO).
- \*\**Dasyphyllum trichophyllum* (Baker) Cabrera. 2n = 54. Brazil. Minas Gerais: São Tome das Letras, *Watanabe & Nagatani* 96 (GHSP, KYO).

### Mutisieae

- \**Chaptalia graminifolia* (Dusen) Cabrera. 2n = 48 + 0–7Bs. Brazil. Paraná: waterfall of Mariquinha, 34 km from Ponta Grossa, *Watanabe & Nagatani* 174 (GHSP, KYO).
- Chaptalia integrifolia* (Cass.) Baker. 2n = 48. Brazil. São Paulo: 26 km SE from Cunha, *Watanabe & Nagatani* 24 (GHSP, KYO). 2n = 48. Brazil. Minas Gerais: 27 km SW from Barbacena to Ibertioga, *Watanabe & Nagatani* 61 (GHSP, KYO); 2n = 48. Brazil. Paraná: waterfall of Mariquinha, 34 km from Ponta Grossa, *Watanabe & Nagatani* 177 (GHSP, KYO); 2n = 48. Brazil. Santa Catarina: 13 km NE of São Joaquim, *Yahara et al.* B317 (GHSP, KYO).
- Chaptalia mandonii* (Sch. Bip.) Burkart. 2n = 48. Brazil. São Paulo: 26 km SE from Cunha, *Watanabe & Nagatani* 25 (GHSP, KYO).
- Chaptalia nutans* (L.) Polak. 2n = 48. Brazil. São Paulo: 17 km SE from Cunha to Parati, *Watanabe & Nagatani* 8 & 9 (GHSP, KYO); 2n = 48. Brazil. São Paulo: 26 km SE from Cunha, *Watanabe & Nagatani* 23 (GHSP, KYO); 2n = 48. Brazil. Santa Catarina: the W entrance of Campos Novos BR470, *Watanabe & Nagatani* 142 (GHSP, KYO).
- \**Chaptalia runcinata* Kunth. 2n = 48. Brazil. Paraná: waterfall of Mariquinha, 34 km from Ponta Grossa, *Watanabe & Nagatani* 185 (GHSP, KYO).
- \**Jungia sellowii* Less. 2n = 20II. Brazil. Santa Catarina: 13 km N of Urubici, *Yahara et al.* B291 (GHSP, KYO).
- \**Mutisia campanulata* Less. 2n = 52. Brazil. São Paulo: 3 km from Campode Jordao to Petra do Bau, *Watanabe & Nagatani* 113 (GHSP, KYO); 2n = 52. Brazil. São Paulo: ca. 10 km from Campos do Jordao to Santo Antonio do Pinhal through Lageado, *Watanabe & Nagatani* 114 (GHSP, KYO).
- Mutisia* sp. 2n = 52. Chile. *Ito* 021501-2 (KANA).
- \*\**Stiffia chrysanthi* Mikan var. *chrysanthi*. 2n = 54. Brazil. Rio de Janeiro: cultivated in Jardim Botânico do Estado de Rio de Janeiro, *Watanabe & Nagatani* s.n. (GHSP, KYO).
- \*\**Stiffia chrysanthi* Mikan var. *fravicans* Toredó ex Dedecca. 2n = 54. Brazil. São Paulo: cultivated in Jardim Botânico do Estado de São Paulo, *Watanabe & Nagatani* 257 (GHSP, KYO).
- \**Trichocline catharinensis* Cabrera var. *catharinensis*. 2n = 38. Brazil. Santa Catarina: 2.5 km SW of Lages, *Watanabe & Nagatani* 146 (GHSP, KYO).
- Trixis antimenorrhoea* (Schrunk) Mart. ex Baker. 2n = 54. Brazil. Minas Gerais: 67 km SW from Barbacena, *Watanabe & Nagatani* 72 (GHSP, KYO).
- \**Trixis praestans* (Vell.) Cabrera. 2n = 54. Brazil. São Paulo: 18 km SE from Cunha to Parati, *Watanabe & Nagatani* 11 (GHSP, KYO); 2n = 54. Brazil. São Paulo: 26 km SE from Cunha, *Watanabe & Nagatani* 28 (GHSP, KYO); 2n = 54. Brazil. Minas Gerais: ca. 10 km from corrego do

Bom Jesus to Pedra de São Domingo, *Watanabe & Nagatani 104* (GHSP, KYO).

### Vernonieae

\**Eremanthus bicolor* (DC.) Baker.  $2n = 30$ . Brazil. Goiás: 44 km NE from Niquelandia, *Watanabe & Nagatani 236* (GHSP, KYO).

*Eremanthus* sp. 1.  $2n = 30$ . Brazil. Goiás: 15 km N of GO118 from Brasília to Planaltina, *Watanabe & Nagatani 210* (GHSP, KYO).

*Eremanthus* sp. 2.  $2n = 34$ . Brazil. São Paulo: 2.5 km SE from Cunha to Parati, *Watanabe & Nagatani 15* (GHSP, KYO).

*Eremanthus* sp. 3.  $2n = 17$ II. Brazil. Rio de Janeiro: 4 km S of Petropolis, *Watanabe & Nagatani 35* (GHSP, KYO).

\**Vernonia florida* Gardner.  $2n = 34$ . Brazil. Paraná: 3 km W of São Luis do Puruna, *Yahara et al. B208* (GHSP, KYO).

\**Vernonia hypochaeris* DC.  $2n = 17$ II. Brazil. Santa Catarina: Morro do Quiriri, *Yahara et al. B134* (HGS, KYO, P);  $2n = 34$ . Brazil. Paraná: 3 km W of São Luis do Puruna, *Yahara et al. B235* (GHSP, KYO).

*Vernonia nitidula* Less.  $2n = 17$ II. Brazil. Santa Catarina: 10 km SW of Lages, *Yahara et al. B261* (GHSP, KYO).

*Vernonia polyanthes* Less.  $2n = 34$ . Brazil. São Paulo: 26 km SE from Guaratingueta to Cunha, *Watanabe & Nagatani 1* (GHSP, KYO);  $2n = 34+0-2$ Bs. Brazil. São Paulo: 26 km SE from Guaratingueta to Cunha, *Watanabe & Nagatani 3* (GHSP, KYO).

*Vernonia scorpioides* (Lam.) Pers.  $2n = 34$ . Brazil. Rio de Janeiro: Petropolis, 5 km S of Petropolis, *Watanabe & Nagatani 32* (GHSP, KYO);  $2n = 17$ II. Brazil. São Paulo: Nova Itanhaem, sandy beach, *Watanabe & Nagatani 206* (GHSP, KYO).

*Vernonia* sp. 1.  $2n = 34$ . Brazil. Goiás: 32 km W from Niquelandia to Uruacu, *Watanabe & Nagatani 237* (GHSP, KYO).

\**Vernonia* sp. 2.  $2n = 17$ II. Brazil. Paraná: E limit of Guarapuava, *Yahara et al. B166* (GHSP, KYO).

### Gnaphalieae

*Achyrocline alata* DC.  $2n = 14$ II. Brazil. Santa Catarina: 15 km N of Urubici, *Yahara et al. B302* (GHSP, KYO).

*Achyrocline satureioides* DC.  $2n = 14$ II. Brazil. Santa Catarina: 15 km N of Urubici, *Yahara et al. B303* (GHSP, KYO).

\**Angianthus micropodioides* (Benth.) Benth.  $2n = 12$ II. Australia. W Australia: 2 km W of Hines Hill township, *Short 4449* (MEL, TI).

\*\**Dithyrostegia amplexicaulis* A. Gray.  $2n = 14$ . Australia. W Australia: 12 km W of Pindar, *Short 4489* (MEL, TI).

\*\**Epitriche demissus* (A. Gray) P. S. Short.  $2n = 10$ . Australia. W Australia: 5 km from Morawa on rd. to Perenjori, *Short 4508* (MEL, TI).

\**Erymphyllum ramosum* subsp. *ramosum* (A. Gray) Paul G. Wilson.  $2n = 12$ II. Australia. W Australia: 138.9 km W from Balladonia, *Watanabe et al. 344* (MEL, TI).

*Leptorhynchos squamatus* (Labill.) Less.  $2n = 12$ II. Australia. Victoria: 36 km W of Mitre, *Watanabe et al. 303* (MEL, TI).

\**Podotheca unisetia* P. S. Short.  $2n = 26$ . Australia. W Australia: 7 km S of Bunjil along rd. to Latham, *Short 4512* (MEL, TI).

*Waitzia acuminata* Steetz.  $2n = 12$ II. Australia. W Australia: 18 km S of Binnu, *Short 4492 & 4493* (MEL, TI).

### Astereae

*Baccharis anomala* DC.  $2n = 18$ . Brazil. São Paulo: Cunha, 17 km SE from Cunha to Parati, *Watanabe & Nagatani 9* (GHSP, KYO);  $2n = 9$ II + BII. Brazil. Paraná: E of Guarapuava, *Yahara et al. B180* (GHSP, KYO);  $2n = 9$ II. Brazil. Santa Catarina: 13 km NE of São Joaquim, *Yahara et al. B310* (GHSP, KYO).

\**Baccharis pentodonta* Malme.  $2n = 9$ II. Brazil. Paraná: 3 km W of São Luis do Puruna, *Yahara et al. B211* (GHSP, KYO).

\**Baccharis triplinervis* Baker.  $2n = 18$ . Brazil. Santa Catarina: W entrance of Campos Novos BR470, *Watanabe & Nagatani 143* (GHSP, KYO).

*Noticastrum acuminatum* (DC.) Cuatrec.  $2n = 18$ . Brazil. Santa Catarina: 5 km S of Campo Alegre, *Yahara et al. B228* (GHSP, KYO);  $2n = 9$ II. Brazil. Santa Catarina: 10 km SW of Lages, *Yahara et al. B254* (GHSP, KYO).

*Symphotrichum graminifolium* (Spreng.) G. L. Nesom.  $2n = 18 + 0-2$ Bs. Brazil. Santa Catarina: Serra da Anta Gorda, 13 km N of Urubici, *Yahara et al. B289* (GHSP, KYO).

### Plucheeae

*Pluchea sagittalis* (Lam.) Cabrera.  $2n = 10$ II. Brazil. Santa Catarina: 10 km SW of Lages, *Yahara et al. B257* (GHSP, KYO).

### Helenieae

*Chrysactinia truncata* S. Watson.  $2n = 30$ . Mexico. Nuevo León: 3 km W from San Juan Bautista, *Yahara et al. 1458* (KYO, MEXU).

*Dyssodia papposa* (Vent.) Hitchc.  $2n = 26$ . Mexico. Coahuila: 15 km WNW of Coahuila–Nuevo Leon State border on Mex 57, *Yahara et al. 1467* (KYO, MEXU).

*Dyssodia tagetiflora* Lag.  $2n = 26$ . Mexico. Nuevo León: 29.4 km NW from Galeana, *Yahara et al. 1438* (KYO, MEXU).

*Espejoa mexicana* DC.  $2n = 18$ . Mexico. Guerrero: 1.5 km E of aeropuerto on Mex 200, *Yahara et al. 2001* (KYO, MEXU).

*Florestina tripteris* DC.  $2n = 20$ . Mexico. Nuevo León: 7.6 km E of Salda to General Bravo on hwy. 40D, *Yahara et al. 1460* (KYO, MEXU).

*Marshallia mohrii* Beadle & F. E. Boynton.  $2n = 36$ . U.S.A. Missouri: *Yahara & Mishima s.n.* (KYO).

*Palafoxia texana* DC.  $2n = 22$ . Mexico. Veracruz: Playa palma Sola, *Yahara et al. 1365* (KYO, MEXU).

*Porophyllum macrocephalum* DC.  $2n = 22$ . Mexico. Oaxaca: Village of Sta. Maria Petapa, *Yahara et al. 1372* (KYO, MEXU).

*Strotheria gypsophila* B. L. Turner.  $2n = 16$ . Mexico. Nuevo León: 3 km W from Hwy. 57, salida to El Refugio, *Yahara et al. 142* (KYO, MEXU).

*Thymophylla aurea* (A. Gray) Greene.  $2n = 16$ . Mexico. Coahuila: 8.5 km N of Bermejillo, *Yahara et al. 1497* (KYO, MEXU).

*Thymophylla gentryi* (M. C. Johnst.) Strother.  $2n = 16 + 0-1$ B. Mexico. Coahuila: 15 km W of Mex 30 and Mex 45 jct., *Yahara et al. 1505* (KYO, MEXU).

*Thymophylla pentachaeta* (DC.) Small var. *pentachaeta*.  $2n = 24$ . Mexico. Nuevo León: 2.1 km SE of Zaragoza, *Yahara et al. 1414* (KYO, MEXU);  $2n = 24$ . Mexico. Coahuila: 15 km WNW of Coahuila–Nuevo León State border on Mex 57, *Yahara et al. 1466* (KYO, MEXU).

*Thymophylla pentachaeta* (DC.) Small var. *hartwegii* (A. Gray) Strother.  $2n = 26$ . Mexico. Nuevo León: 79 km from Monterrey to Sabinas Hidalgo on 85 Libre, *Yahara et al. 463* (KYO, MEXU).

*Urbinnella palmeri* Greenm.  $2n = 16$ . Mexico. Durango: 49 km W of Durango City on Mex 40, *Yahara et al.* 1507 (KYO, MEXU).

# Heliantheae

*Galinsoga parviflora* Cav.  $2n = 16$ II. Brazil. Santa Catarina: 13 km N of Urubici, *Yahara et al.* B299 (GHSP, KYO).

*Jaegeria hirta* (Lag.) Less.  $2n = 18$ II. Brazil. Santa Catarina: 13 km N of Urubici, *Yahara et al.* B292 (GHSP, KYO).

*Tithonia speciosa* (Hook.) Hook. ex Griseb.  $2n = 17$ II. Brazil. Minas Gerais: 4 km SW from Marbacena to Ibertiega, *Watanabe & Nagatani* 52 (GHSP, KYO).

\**Verbesina clausenii* Sch. Bip. ex Baker.  $2n = 17$ II. Brazil. Santa Catarina: Morro do Quiriri, *Yahara et al.* B233 (GHSP, KYO).

# Eupatorieae

*Ageratina cardiophylla* (B. L. Rob.) R. M. King & H. Rob.  $2n = 68$ . Mexico. Michoacan: 9 km W from jct. to Zinapécuaro, *Yahara et al.* 72 (KYO, MEXU).

\**Ageratina hintonii* R. M. King & H. Rob.  $2n = 34 + 0-2$ Bs. Mexico. Guerrero: 64 km SW from Filo de Caballo, *Yahara et al.* 54 (KYO, MEXU).

*Ageratina* sp.  $2n = 34$ . Mexico. Michoacan: 38 km E of Morelia, *Yahara et al.* 73 (KYO, MEXU).

\**Carphochaete wislizeni* A. Gray.  $2n = 22$ . Mexico. Chihuahua: 31.7 km W from Parral on Mex 24, *Yahara et al.* 733 (KYO, MEXU).

\**Chromolaena horminoides* DC.  $2n = 30$ . Brazil. Goiás: Serra dos Pirineus. 13 km W from Pirenópolis, *Watanabe & Nagatani* 243 (GHSP, KYO).

\**Chromolaena kleinii* (Cabrera) R. M. King & H. Rob.  $2n = 10$ II. Brazil. Santa Catarina: 13 km N of Urubici, *Yahara et al.* B298 (GHSP, KYO).

*Chromolaena laevigata* (Lam.) R. M. King & H. Rob.  $2n = 60$ . Brazil. São Paulo: 21 km SE from Cunha to Pedra de Macela, *Watanabe & Nagatani* 19 (GHSP, KYO).

\**Chromolaena inopolepis* (Malme) R. M. King & H. Rob.  $2n = 10$ II + 10I, 6III + 4II + 4I. Brazil. Santa Catarina: 10 km SW of Lages, *Yahara et al.* B281 (GHSP, KYO).

\**Chromolaena pedunculosa* (Hook. & Arn.) R. M. King & H. Rob.  $2n = 10$ II + 10I, 8III + 2II + 2I. Brazil. Paraná: Serra da Esperanca, *Yahara et al.* B159 (GHSP, KYO);  $2n = 20$ II + 10I,  $2n = 30$ . Brazil. Santa Catarina: 10 km SW of Lages, *Yahara et al.* B262 & B276 (GHSP, KYO).

*Cronquistia pringlei* (S. Watson) R. M. King.  $2n = 24$ . Mexico. Chihuahua: 95.7 km SW from Parral on Mex 24, *Yahara et al.* 735 (KYO, MEXU).

\**Decachaeta haenkeana* DC.  $2n = 32$ . Mexico. Guerrero: 24 km S of Chilpancingo, *Yahara et al.* 60 (KYO, MEXU).

*Erythradenia pyramidalis* (B. L. Rob.) R. M. King & H. Rob.  $2n = 32$ . Mexico. Guerrero: 24 km S of Chilpancingo, *Yahara et al.* 59 (KYO, MEXU).

*Gyptis crassipes* (Hieron.) R. M. King & H. Rob.  $2n = 30$ . Brazil. Santa Catarina: 10 km SW of Lages, *Yahara et al.* B284 (GHSP, KYO).

*Macvaughiiella mexicana* (Sch. Bip.) R. M. King & H. Rob.  $2n = 24 + 4-8$ Bs. Mexico. Oaxaca: 7 km SW of El Cameron, *Yahara & Soejima* 372 (KYO, MEXU).

*Microspermum debile* Benth.  $2n = 24$ . Mexico. Guerrero: 64 km SW from Filo de Caballo, *Yahara et al.* 53 (KYO, MEXU).

*Microspermum nummulariaefolium* Lag.  $2n = 36$ . Mexico. Guerrero: 14.8 km N of jct. to Ixtateopan, *Yahara & Soejima* 239 (KYO, MEXU).

*Mikania* sp.  $2n = 34$ . Brazil. Minas Gerais: Conceição do Ibitipoca, Serra de Ibitipoca, *Watanabe & Nagatani* 84 (GHSP, KYO).

*Oxylobus adscendens* B. L. Rob. & Greenm.  $2n = 32$ . Mexico. Hidalgo: 8 km N from jct. to Mineral del Chico, *Yahara et al.* 9 (KYO, MEXU).

\**Praxelis missiona* (Malme) R. M. King & H. Rob.  $2n = 80$ . Brazil. São Paulo: 2 km N from Campos do Jordão, *Yahara et al.* B128 (GHSP, KYO).

*Piqueria pilosa* Kunth.  $2n = 24$ . Mexico. Mexico: 29 km W of Jalatlaca, *Yahara et al.* 90 (KYO, MEXU).

\**Revelia macrocephala* (Paray) R. M. King & H. Rob.  $2n = 22$ . Mexico. Guerrero: 76 km SW from Filo de Caballo, *Yahara et al.* 56 (KYO, MEXU).

\**Stevia alternifolia* Hieron.  $2n = 11$ II + 0-1B,  $2n = 22$ . Brazil. Paraná: 3 km W of Palmeira, *Yahara et al.* B190 (GHSP, KYO);  $2n = 11$ II. Brazil. Paraná: Rio dos Papagoios, *Yahara et al.* B216 (GHSP, KYO).

\**Stevia bangii* Rusby.  $2n = 44 + 0-5$ Bs. Bolivia. Laja: *Ito* 010209-2 (KANA).

*Stevia camachensis* Hieron.  $2n = 22$ . Bolivia. Comarapa to Matara: *Ito* ASA199-1 (KANA).

\**Stevia cinerascens* Sch. Bip. ex Baker.  $2n = 22$ . Brazil. Santa Catarina: 2.5 km SW of Lages, *Yahara et al.* B58 (GHSP, KYO);  $2n = 22$ . Brazil. Santa Catarina: 27 km S from Lages, *Yahara et al.* B66 & B67 (GHSP, KYO);  $2n = 11$ II,  $2n = 22$ . Brazil. Santa Catarina: 10 km SW of Lages, *Yahara et al.* B251 & B252 (GHSP, KYO).

\**Stevia clausenii* Sch. Bip. ex Baker.  $2n = 22$ . Brazil. Santa Catarina: 14 km E of Bom Joaquim da Serra, *Yahara et al.* B89 (GHSP, KYO);  $2n = 22$ . Brazil. Santa Catarina: 18 km E of Bom Joaquim da Serra, *Yahara et al.* B99 (GHSP, KYO).

*Stevia clinopodioides* Greenm.  $2n = 36 + 0-4$ Bs. Mexico. Nuevo León: Cerro Potosi, *Yahara et al.* 1440 (MEXU, KYO).

*Stevia coahuilensis* Soejima & Yahara.  $2n = 33$ . Mexico. Coahuila: 0.4 km E of Monterreal, *Yahara et al.* 1668 (KYO, MEXU);  $2n = 33$ . Mexico. Coahuila: 9.4 km E of Monterreal, *Yahara et al.* 1696 (KYO, MEXU);  $2n = 44$ . Mexico. Nuevo León: 3.3 km W of Dieciocho de Marzo, *Yahara et al.* 1794 (KYO, MEXU).

*Stevia commixta* B. L. Rob.  $2n = 22, 22+, 2-3$ Bs. Brazil. São Paulo: 2 km N of jct. from Campos do Jordao to Pedra do Bau, *Yahara et al.* B1, B3 & B5 (GHSP, KYO);  $2n = 22$ . Brazil. São Paulo: 15 km N from Campos do Jordão to Pedra do Bau, *Yahara et al.* B11 & B12 (GHSP, KYO).

*Stevia decussata* Baker.  $2n = 22$ . Brazil. Minas Gerais: Pico de São Domingo, *Yahara et al.* B18 (GHSP, KYO).

*Stevia hintoniorum* B. L. Turner.  $2n = 22$ . Mexico. Coahuila: 5.2 km E of Monterreal, *Yahara et al.* 1695 (Type 1) (KYO, MEXU);  $2n = 33$ . Mexico. Coahuila: 0.4 km E of Monterreal, *Yahara et al.* 1665 (KYO, MEXU);  $2n = 33 + 1$ B. Mexico. Coahuila: 4.7 km E of Monterreal, *Yahara et al.* 1678 (KYO, MEXU);  $2n = 44$ . Mexico. Nuevo León: 17 km W of Dieciocho de Marzo, *Yahara et al.* 1795 & 1796 (KYO, MEXU);  $2n = 44 + 1$ B. Mexico. Coahuila: 15.2 km E of Monterreal, *Yahara et al.* 1692 (Type 1) (KYO, MEXU).

*Stevia incognita* Grashoff.  $2n = 33 + 1-3$ Bs. Mexico. Coahuila: 11.3 km E of Monterreal, *Yahara et al.* 1704 (KYO, MEXU);  $2n = 44 + 0-2$ Bs. Mexico. Nuevo León: 17 km NE of San Antonio Pena Nevada, *Yahara et al.* 1569 (KYO, MEXU).

*Stevia jorullensis* Kunth.  $2n = 36$ . Mexico. Nuevo León: 4.8 km W of San Ishidro, *Yahara et al.* 1645 (KYO, MEXU);  $2n = 36$ . Mexico. Nuevo León: 5.8 km W of San



- Ishidro, *Yahara et al.* 1650 (KYO, MEXU);  $2n = 36$ . Mexico. Nuevo León: 15 km E of San Antonio de las Alazanas, *Yahara et al.* 1662 (KYO, MEXU);  $2n = 36$ . Mexico. Coahuila: 10.1 km E of Jame, *Yahara et al.* 1717 (KYO, MEXU);  $2n = 36$ . Mexico. Nuevo León: 11.6 km SE of Zaragoza, *Yahara et al.* 1814 (KYO, MEXU);  $2n = 36 + 0-1B$ . Mexico. Nuevo León: 6.9 km SE of Zaragoza, *Yahara et al.* 1808 (KYO, MEXU).
- Stevia leptophylla* Sch. Bip. ex Baker.  $2n = 22 + 0-1B$ . Brazil. Paraná: 6 km E of São Luis do Puruna, *Yahara et al.* B151 (GHSP, KYO);  $2n = 11II$ . Brazil. Paraná: E limit of Lapa, *Yahara et al.* B223 (GHSP, KYO).
- \**Stevia lundiana* DC.  $2n = 22, 22 + 1B$ . Brazil. São Paulo: 2 km N of Campos do Jordão to Pedra do Bau, *Yahara et al.* B2 & B4 (GHSP, KYO);  $2n = 22$ . Brazil. Santa Catarina: 2.5 km S from Lages, *Yahara et al.* B49 (GHSP, KYO);  $2n = 22$ . Brazil. Santa Catarina: 27 km S from Lages, *Yahara et al.* B75 (GHSP, KYO);  $2n = 11II$ ,  $2n = 22$ . Brazil. Santa Catarina: 15 km N of Urubici, *Yahara et al.* B300 (GHSP, KYO);  $2n = 22$ . Brazil. Santa Catarina: 13 km NE of São Joaquim, *Yahara et al.* B311 (GHSP, KYO).
- \**Stevia mitopoda* B. L. Rob.  $2n = 24$ . Mexico. Puebla: 21 km SE of Izcar de Matamoros on Mex 160, *Yahara et al.* 1022 (KYO, MEXU).
- \**Stevia myriadenia* Sch. Bip. ex Baker.  $2n = 11II$ ,  $2n = 22$ . Brazil. Santa Catarina: 15 km N of Urubici, *Yahara et al.* B308 & B309 (GHSP, KYO).
- Stevia nepetifolia* Kunth.  $2n = 33 + 3Bs$ . Mexico. Coahuila: 0.4 km E of Montereal, *Yahara et al.* 1667 (KYO, MEXU);  $2n = 33$ . Mexico. Coahuila: 4.7 km E of Montereal, *Yahara et al.* 1669 (Type 2) (KYO, MEXU);  $2n = 33 + 1B$ . Mexico. Coahuila: 5.2 km E of Montereal, *Yahara et al.* 1694 (Type 2) (KYO, MEXU);  $2n = 44 + 1-4Bs$ . Mexico. Nuevo León: 20 km NE from San Antonio Pena Nevada, *Yahara et al.* 1596 (KYO, MEXU).
- Stevia ophrophylla* B. L. Rob.  $2n = 11II$ ,  $2n = 22$ . Brazil. Paraná: E limit of Lapa, *Yahara et al.* B220 (GHSP, KYO).
- Stevia organensis* Gardner.  $2n = 22$ . Brazil. São Paulo: Pedra do Bau, *Yahara et al.* B8 & B148 (GHSP, KYO).
- Stevia ovata* Willd.  $2n = 22 + 0-2Bs$ . Mexico. Nuevo León: 6 km W of Cola de Caballo, *Yahara et al.* 1619 (KYO, MEXU);  $2n = 33 + 0-2Bs$ . Mexico. Coahuila: 10.1 km E of Jame, *Yahara et al.* 1715 (KYO, MEXU);  $2n = 33 + 3Bs$ . Mexico. Nuevo León: 69 km SE of Zaragoza, *Yahara et al.* 1806 (KYO, MEXU);  $2n = 33 + 2-3Bs$ . Mexico. Coahuila: 5.2 km E of Montereal, *Yahara et al.* 1693 (KYO, MEXU);  $2n = 33 + 3-8Bs$ . Mexico. Nuevo León: 8.2 km W of San Ishidro, *Yahara et al.* 1654 (KYO, MEXU);  $2n = 44 + 2Bs$ . Mexico. Nuevo León: 20 km NE from San Antonio Pena Nevada, *Yahara et al.* 1600 (KYO, MEXU).
- \**Stevia parvifolia* Hassl.  $2n = 11II$ ,  $2n = 22$ . Brazil. Santa Catarina: Morro do Quiriri, *Yahara et al.* B232 (GHSP, KYO).
- Stevia pilosa* Lag.  $2n = 33$ . Mexico. Nuevo León: 3.3 km W of Dieciocho de Marzo, *Yahara et al.* 1786 (KYO, MEXU);  $2n = 33$ . Mexico. Coahuila: 15 km E from San Antonio de las Alazanas, *Yahara et al.* 1663 (KYO, MEXU);  $2n = 33 + 0-1B$ . Mexico. Nuevo León: 20 km NE from San Antonio Pena Nevada, *Yahara et al.* 1576 (KYO, MEXU);  $2n = 44$ . Mexico. Coahuila: 4.7 km E of Montereal, *Yahara et al.* 1679 (KYO, MEXU);  $2n = 44$ . Mexico. Coahuila: 15.2 km E of Montereal, *Yahara et al.* 1691 (KYO, MEXU).
- Stevia porphyrea* McVaugh.  $2n = 44$ . Mexico. Nuevo León: 1 km W of San Ishidro, *Yahara et al.* 1640 (KYO, MEXU).
- Stevia potosina* Soejima Yahara & K. Watan.  $2n = 33$ . Mexico. Nuevo León: 15 km E of San Antonio de las Alazanas, *Yahara et al.* 1661 (KYO, MEXU);  $2n = 33$ . Mexico. Coahuila: 10 km E of Montereal, *Yahara et al.* 1800 (KYO, MEXU);  $2n = 33$ . Mexico. Nuevo León: 3.3 km W of Dieciocho de Marzo, *Yahara et al.* 1776 (KYO, MEXU);  $2n = 33$ . Mexico. Nuevo León: 12 km W of Dieciocho de Marzo, *Yahara et al.* 1786 (KYO, MEXU);  $2n = 33 + 0-1B$ . Mexico. Coahuila: 10.1 km E of Jame, *Yahara et al.* 1716 (KYO, MEXU).
- Stevia purpusii* B. L. Rob.  $2n = 36$ . Mexico. Morelos: Steep mtn. above Tepoztlán, *Yahara et al.* 2029 (KYO, MEXU).
- Stevia selloi* Sch. Bip. ex Baker.  $2n = 22$ . Brazil. Santa Catarina: 2.5 km SW of Lages, *Yahara et al.* B51 (GHSP, KYO);  $2n = 22$ . Brazil. Santa Catarina: 27 km S from Lages, *Yahara et al.* B65 (GHSP, KYO);  $2n = 11II$ . Brazil. Paraná: 3 km W of Palmeira, *Yahara et al.* B191 (GHSP, KYO).
- Stevia serrata* Cav. var. *serrata*.  $2n = 44$ . Mexico. Coahuila: 4.7 km E of Montereal, *Yahara et al.* 1671 (KYO, MEXU);  $2n = 44 + 1B$ . Mexico. Coahuila: 4.7 km E of Montereal, *Yahara et al.* 1670 (KYO, MEXU);  $2n = 44 + 1-2Bs$ . Mexico. Nuevo León: 20 km NE from San Antonio Pena Nevada, *Yahara et al.* 1585 (KYO, MEXU).
- Stevia setifera* Rusby ex B. L. Rob.  $2n = 22$ . Bolivia. Unduavi: *Ito 15-2st* (KANA).
- Stevia* sp. 2.  $2n = 22$ . Bolivia. Sta Cruz New Rd., near Siberia, *Ito 0102095-2* (KANA).
- \**Stevia tenuis* Hook. & Arn.  $2n = 22$ . Brazil. Santa Catarina: 14 km E of Bom Joaquim da Serra, *Yahara et al.* B97 (GHSP, KYO).
- Stevia tephra* B. L. Rob.  $2n = 33 + 1-2Bs$ . Mexico. Nuevo León: 1 km W of San Ishidro, *Yahara et al.* 1640 (KYO, MEXU);  $2n = 33 + 3Bs$ . Mexico. Nuevo León: 8.2 km W of San Ishidro, *Yahara et al.* 1656 (KYO, MEXU);  $2n = 33 + 0-1B$ . Mexico. Nuevo León: 45.4 km SW of Mex 58 & 85 jct. in Linares, *Yahara et al.* 1771 (KYO, MEXU);  $2n = 33 + 3-4Bs$ . Mexico. Nuevo León: 45.4 km SW of Mex 58 & 85 jct. in Linares, *Yahara et al.* 1772 (KYO, MEXU).
- Stevia tomentosa* Kunth.  $2n = 33 + 2Bs$ . Mexico. Nuevo León: 45.4 km SW of Mex 58 & 85 jct. in Linares, *Yahara et al.* 1770 (KYO, MEXU);  $2n = 33 + 3Bs$ . Mexico. Nuevo León: 8.2 km W of San Ishidro, *Yahara et al.* 1651 (KYO, MEXU);  $2n = 44 + 2-4Bs$ . Mexico. Nuevo León: 8.7 km SE of Zaragoza, *Yahara et al.* 1811 (KYO, MEXU).
- Stevia veronicae* DC.  $2n = 11II$ . Brazil. Paraná: E limit of Guarapuava, *Yahara et al.* B170 (GHSP, KYO);  $2n = 11II$ ,  $2n = 22$ . Brazil. Paraná: 3 km W of São Luis do Puruna, *Yahara et al.* B204 & B205 (GHSP, KYO);  $2n = 11II$ . Brazil. Santa Catarina: 10 km SW of Lages, *Yahara et al.* B250 (GHSP, KYO).



## Erratum

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Watanabe, K., T. Yahara, G. Hashimoto, Y. Nagatani, A. Soejima, T. Kawahara & M. Nakazawa. 2007. Chromosome numbers and karyotypes in Asteraceae. *Ann. Missouri Bot. Gard.* 94: 643–654.

In Appendix 1 on p. 653, under Eupatorieae, the second accession for *Chromolaena pedunculosa* (Hook. & Arn.) R. M. King & H. Rob. was erroneously listed as  $2n = 20\text{II} + 10\text{I}$ . The correct accession is  $2n = 10\text{II} + 10\text{I}$ . The authors regret the error.