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CHROMOSOME COUNTS OF COMPOSITAE FROM ECUADOR AND VENEZUELA[1]

David M. Spooner,[2] Diederik C. D. De Jong,[3] Byung-Yun Sun,[4] Tod F. Stuessy,[5] Karla M. Gengler,[5] Guy L. Nesom,[6] and Paul E. Berry[7]

Abstract

Forty-three chromosome counts of Compositae are reported from Ecuador and Venezuela. A first generic count is reported for *Stuckertiella* Beauverd (n = 11–12), and first counts also are reported for 15 species in *Ageratina* Spach, *Chromolaena* DC., *Coespeletia* Cuatrec., *Erigeron* L., *Espeletia* Mutis, *Gynoxys* Cass., *Hinterhubera* Sch. Bip., *Oritrophium* (HBK) Cuatrec., *Pentacalia* Cass., *Ruilopezia* Cuatrec., *Senecio* L., *Tanacetum* L., and *Vasquezia* Phil. Additional counts also are provided for 23 populations of previously counted taxa, two of which are new numbers. The taxonomic implications of certain of these counts are discussed.

During research expeditions to Ecuador and Venezuela in the past 15 years, we have collected numerous samples of Compositae. In addition to herbarium material, we have obtained floral buds for chromosomal studies. This paper gives the results of these studies, which are important for helping delimit taxa and reconstructing phylogeny in the family. These investigations extend previous chromosomal work by Keil & Stuessy (1975, 1977), Jansen & Stuessy (1980), and Jansen et al. (1984). This paper lists first counts for genera, species, and varieties, as well as confirmatory data for other taxa known from only one or a few reports. Discussion focuses on taxonomic and/or evolutionary implications.

Materials and Methods

The materials and methods involving conventional squash techniques for meiotic stages of nuclei in pollen parent cells are outlined in Keil & Stuessy (1975, 1977) and Jansen & Stuessy (1980). Either Snow's stain (Snow, 1963) or acetocarmine was used. Voucher specimens of Venezuelan collections are deposited at Instituto Botánico, Venezuela (VEN), and Ecuadorian collections are at Ohio State University (OS).

Results

The 42 new chromosome counts are listed in Table 1. First counts are reported for 1 genus and 17 species, and 23 additional counts are for previously reported taxa, 2 of which are new numbers. The new generic count is for *Stuckertiella* Beauverd. New species counts are in *Ageratina* Spach, *Chromolaena* DC., *Coespeletia* Cuatrec., *Erigeron* L., *Espeletia* Mutis, *Gynoxys* Cass., *Hinterhubera* Sch. Bip., *Oritrophium* (HBK) Cuatrec., *Pentacalia* Cass., *Ruilopezia* Cuatrec., *Senecio* L., *Tanacetum* L., and *Vasquezia* Phil.

Discussion

The discussion here is restricted to first or new counts and to significant comments, which is the approach used in previous papers (Keil & Stuessy, 1975, 1977; Jansen & Stuessy, 1980; Jansen et al., 1984). References for statements regarding ranges of chromosomal variation within genera or for frequently counted species will not be given; documentation for those counts comes from available chromosomal indices (Darlington & Wylie, 1955; Cave, 1958–65; Ornduff, 1967–69; Fedorov, 1969; Moore, 1970–77; Goldblatt, 1981–1988; Goldblatt & Johnson, 1990–1991).

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[2] USDA, ARS Department of Horticulture, University of Wisconsin, Madison, Wisconsin 53706, U.S.A.
[3] Department of Biology, Raymond Walters College, University of Cincinnati, Cincinnati, Ohio 45236, U.S.A.
[4] Department of Biology, Chonbuk National University, Chonju 560–756, Korea.
[5] Department of Plant Biology, Ohio State University, Columbus, Ohio 43210, U.S.A. Present address: The Natural History Museum of Los Angeles County, 900 Exposition Boulevard, Los Angeles, California 90007, U.S.A.
[6] Herbarium, University of Texas, Austin, Texas 78713, U.S.A.
[7] Missouri Botanical Garden, St. Louis, Missouri 63166, U.S.A.

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The referral of genera to particular tribes follows the classification of the Compositae in Heywood, Harborne, and Turner (1977). The sequence of tribes used within subfamilies is alphabetical, but tribal composition of each subfamily follows Bremer (1994), with recognition of tribe Tageteae, after Strother (1977). Chloroplast DNA and morphological cladistic analyses (e.g., Bremer, 1987; Jansen et al., 1992) are in reasonable agreement that the family should be divided into three subfamilies, Barnadesioideae, Asteroideae, and Cichorioideae. Most of the counts reported here come from Asteroideae.

ASTEROIDEAE

Anthemideae. Our count of $n = 12$ for *Tanacetum cinerariaefolium* is very unusual, considering the constancy of $x = 9$ throughout the genus. Heywood & Humphries (1977) also reported several very unusual chromosome numbers for *Tanacetum,* such as $2n = 24$, 34, and 56, but no literature is cited as documentation.

Astereae. Aster squamatus has been counted previously as $n = 10$ (Villa, 1978; Jansen & Stuessy, 1980; Dillon & Turner, 1982; Baltisberger, 1988). Our count of $n = 5$ establishes what appears to be the diploid level within this species. Dillon & Turner (1982) distinguished this South American species from the closely related North American taxon, *A. subulatus* Michx., emphasizing differences in characters of the involucre. *Aster subulatus* has repeatedly been found to be diploid ($n = 5$), except for one tetraploid count by Turner (1978) from Florida, and other reports of tetraploidy from Asia and Africa (Turner & Lewis, 1965; Matsuda, 1970; Miyagi, 1974). Our report of a new chromosome level for *A. squamatus,* therefore, suggests that it, too, has undergone infraspecific polyploidy, and that tetraploid cytodemes have evolved independently within each taxon.

Of the 27 species of *Erigeron* found in South America (Solbrig, 1962), 10 species have been counted (*E. andicola* DC., *E. ecuadoriensis* Hieron., *E. fernandezianus* (Colla) Solbrig, *E. karwinskianus* DC., *E. lanceolatus* Wedd., *E. leptopetalus* Phil., *E. leptorhizon* DC., *E. maximus* (D.Don) DC., *E. myosotis* Pers., and *E. rupicola* Phil.). Our count of n = ca. 27 for *E. apiculatus* is the first for the species and is at the hexaploid level. Another first count of $n = 36$–40 for *E. pinnatus* is apparently at the octaploid level. *Erigeron karwinskianus,* a pantropical weed native to Mexico and Central America (Solbrig, 1962), has previously been counted as diploid, triploid ($2n = 27$I), tetraploid, and hexaploid from populations in Mexico and Central America. Our count from South America (Ecuador) is also tetraploid. However, there is also one diploid report from Ecuador for this species (Olsen, 1980). This is the only diploidy reported in the genus *Erigeron* from South America. An interesting observation is that hexaploids and octaploids predominate in South America, whereas diploids largely prevail in North America and Central America. This geographical partitioning between ploidy levels suggests that the genus may have originated in North America, which might be expected based on the greater number and diversity of species in that region.

Only one chromosome count has been reported previously for *Hinterhubera* (*H. imbricata,* $n = 9$; Powell & Cuatrecasas, 1970), which comprises four species in the Andes. Our count of n = ca. 9 for *H. lagesgui* is consistent with the basic number $x = 9$ and is the first count for the species.

Oritrophium, a genus with 15 species mainly distributed in the Andes (Mabberly, 1987) and once treated as a section of *Erigeron* (Bentham & Hooker, 1873), has had, until now, only two chromosomally known species (*O. aciculifolium* Cuatrec., $n = 9$, Turner et al., 1967 and *O. hirtopilosum* (Hieron.) Cuatrec., $n = 18$, Dillon & Turner, 1982). Our new count of n = ca. 17 for *O. venezuelense* is presumably also a tetraploid. The three closely related genera *Aster, Conyza,* and *Erigeron* have basic numbers of $x = 9$, which is consistent with the base found in *Oritrophium.*

Eupatorieae. Ageratina is composed of five subgenera and about 248 species and has very diverse chromosome numbers (King & Robinson, 1987). Although variations are known to exist within particular species comprising subgenus *Ageratina* (Grashoff et al., 1972; King et al., 1976), the basic number is likely $x = 17$ (King & Robinson, 1987). Among our counts for three species belonging to subgenus *Ageratina,* two, *A. cuencana* (n = ca. 18) and *A. rhypodea* (n = ca. 18), are reported for the first time. *Ageratina azangaroensis,* however, is counted as $n = 12$ and $n = 16$–18 from two different populations from Ecuador. Previously reported chromosome numbers for this species were $n = 17$, with or without one or more fragments (King et al., 1976). Whether our count of $n = 12$ reflects an aberrant plant, a stabilized cytotype, or apomixis cannot be determined at this time. More sampling is needed.

Chromolaena has over 165 known species (King & Robinson, 1987); only 17 species have been counted (King & Robinson, 1970; King et al.,

Table 1. Chromosome counts of Compositae from Ecuador and Venezuela. First counts designated by **; new chromosome level by *.

Taxon	Gametic chromosome number[a]	Voucher[b]
ASTEROIDEAE		
ANTHEMIDEAE		
Chrysanthemum parthenium (L.) Bernh.	ca. 9	ECUADOR. Chimborazo: 6.8 km NE of Cajabamba, *SN 5825.*
Cotula australis (Less.) Hook. f.	9	ECUADOR. Loja: 50.6 km N of Loja, *SN 5909.*
***Tanacetum cinerariaefolium* Sch. Bip.	12	ECUADOR. Tungurahua: 21.9 km N of Riobamba, *SN 5941.*
ASTEREAE		
**Aster squamatus* (Spreng.) Hieron.	5	ECUADOR. Cañar: 7.7 km N of Cañar *SN 5787.*
Baccharis latifolia (Ruiz & Pav.) Pers.	18	ECUADOR. Pichincha: 2.2 km N of Tambillo, *SN 5787.*
Blakiella bartsiifolia (S. F. Blake) Cuatrec.	9	VENEZUELA. Mérida: Páramo Piedras Blancas, *BG 3959*
***Erigeron apiculatus* Benth.	ca. 27	ECUADOR. Tungurahua: 21.9 km N of Riobamba, *SN 5943.*
Erigeron karwinskianus DC.	ca. 18	ECUADOR. Azuay: 20.9 km S of Cuenca, *SN 5925.*
***Erigeron pinnatus* Turcz.	36–40	ECUADOR. Chimborazo: 6.8 km NE of Cajabamba, *SN 5824.*
Hinterhubera imbricata Cuatrec. & Aristeg.	9	VENEZUELA. Mérida: Páramo Piedras Blancas, *BG 3886.*
	ca. 10	VENEZUELA. Mérida: Páramo Piedras Blancas, *BG 3954.*
***Hinterhubera lagesgui* Wedd.	ca. 9	VENEZUELA. Mérida: Páramo Piedras Blancas, *BG 3953.*
***Oritrophium venezuelense* (Steyerm.) Cuatrec.	ca. 17	VENEZUELA. Mérida: Páramo Piedras Blancas, *BG 3873.*
EUPATORIEAE		
Ageratina azangaroensis (Sch. Bip. ex Wedd.) R. M. King & H. Rob.	12	ECUADOR. Chimborazo: 15.0 km SW of Cajabamba, *SN 5837.*
	16–18	ECUADOR. Cotopaxi: 16.2 km S of Machachi, *SN 5952.*
***Ageratina cuencana* (B. L. Rob.) R. M. King & H. Rob.	ca. 18	ECUADOR. Tungurahua: along path from W end of Baños to Chaupi, *SN 5800.*
Ageratina exerto-venosa (Klatt) R. M. King & H. Rob.	36–40	ECUADOR. Loja: 21.4 km NNW of Saraguro, *SN 5921.*
***Ageratina rhypodea* (B. L. Rob.) R. M. King & H. Rob.	ca. 18	ECUADOR. Loja: 13.9 km NE of Saraguro, *SN 5916*
***Chromolaena leptocephala* (DC.) R. M. King & H. Rob.	9	ECUADOR. Tungurahua: on path from W end of Baños to Chaupi, *SN 5804.*
Oxylobus glanduliferus (Sch. Bip.) A. Gray	16	VENEZUELA. Mérida: Páramo Piedras Blancas, *BG 3879.*
HELIANTHEAE		
Ambrosia peruviana Willd.	18	ECUADOR. El Oro: 1.8 km N of El Cambio, *SN 5859.*
***Coespeletia timotensis* (Cuatrec.) Cuatrec.	19	VENEZUELA. Mérida: Páramo Piedras Blancas, *BG 3966.*
	19	VENEZUELA. Mérida: Páramo Piedras Blancas, *BG 3883.*
***Espeletia batata* Cuatrec.	19	VENEZUELA. Mérida: Páramo Piedras Blancas, *BG 3874.*

Table 1. Continued.

Taxon	Gametic chromosome number[a]	Voucher[b]
Garcilassa rivularis Poepp. & Endl.	ca. 16	ECUADOR. Chimborazo: NW edge of Bucay, *SN 5854.*
Monactis flaverioides H.B.K.	30–32	ECUADOR. Pichincha: 2.2 km N of Tambillo, *SN 5786.*
	ca. 30	ECUADOR. Tungurahua: 38.4 km N of center of Riobamba, *SN 5945.*
***Ruilopezia floccosa* (Standl.) Cuatrec.	19	VENEZUELA. Mérida: Páramo Piedras Blancas, *BG 3965.*
Sigesbeckia jorullensis H.B.K.	ca. 16	ECUADOR. Loja: 50.6 km N of Loja, *SN 5911.*
Steiractina mollis S. F. Blake	14	ECUADOR. Cañar: 6.7 km S of Suscal, *SN 5931.*
***Vasquezia titicacensis* (Meyen & Walp.) S. F. Blake	20	ECUADOR. Cañar: 3.3 km N of Cañar, *SN 5927.*
INULEAE		
Gamochaeta americana (Mill.) Wedd.	14	VENEZUELA. Mérida: Páramo Piedras Blancas, *BG 3920.*
***Stuckertiella capitata* (Wedd.) Beauverd	11–12	ECUADOR. Chimborazo: 10.5 km S of Cajabamba, *SN 5830.*
SENECIONEAE		
***Gynoxys buxifolia* Cass.	ca. 36	ECUADOR. Chimborazo: 15.0 km SW of Cajabamba, *SN 5838.*
	ca. 12	ECUADOR. Cotopaxi: 12.6 km S of Machachi, *SN 5951.*
***Pentacalia sclerosa* (Cuatrec.) Cuatrec.	ca. 20	VENEZUELA. Mérida: Páramo Piedras Blancas, *BG 3906.*
Senecio formosus H.B.K.	40	VENEZUELA. Mérida: Páramo Piedras Blancas, *BG 3870.*
***Senecio teretifolius* (H.B.K.) DC.	20	ECUADOR. Chimborazo: 8.6 km NW of center of Riobamba, *SN 5938.*
TAGETEAE		
Tagetes zypaquirensis Humb. & Bonpl.	ca. 12	ECUADOR. Chimborazo: 9.7 km NW of center of Riobamba, *SN 5940.*
CICHORIOIDEAE		
LIABEAE		
Liabum floribundum Less.	18	ECUADOR. Chimborazo: 44.4 km SW of Cajabamba, *SN 5845.*
**Erato sodiroi* (Hieron.) H. Rob.	9	ECUADOR. Chimborazo: 34.1 km N of jct. rd. to Huigra, *SN 5934.*
MUTISIEAE		
Onoseris albicans (D. Don) Ferreyra	18	ECUADOR. Azuay: 54.2 km NNE of Saraguro, *SN 5923.*
Perezia multiflora (Humb. & Bonpl.) Less.	8	ECUADOR. Chimborazo: 10.5 km S of Cajabamba, *SN 5827.*

[a] Numbers represent bivalents.
[b] Ecuadorian collections by *Stuessy & Nesom* (*SN*); Venezuelan collections by *Berry & Gómez* (*BG*).

1976; Mathew & Mathew, 1983; Strother, 1983; Baker & Parfitt, 1986; Bernardello, 1986; Sundberg et al., 1986). Most previous reports suggest that the basic number of this genus is $x = 10$, although some variations have been found due to irregular meiosis (for *C. laevigata* (Lam.) R. M. King & H. Rob., $2n =$ ca. 56I, Sundberg et al., 1986; for *C. odorata* (L.) R. M. King & H. Rob., $2n = 58$, Ghosh, 1961, $n =$ ca. 31 + 4I, King et al., 1976). Our count of $n = 9$ with clear bivalents for *C. leptocephala* suggests that it is an aneuploid within the genus.

Heliantheae. *Coespeletia* (Espeletiinae), with eight species once included in *Espeletia* (Smith & Koch, 1935) but separated by Cuatrecasas (1976), has two chromosomally known species with $n = 19$ (*C. moritziana* (Sch.Bip. ex Wedd.) Cuatrec., *C. thyrsiformis* (Smith) Cuatrec.; Powell & Cuatrecasas, 1975). Our new counts of $n = 19$ for two individuals of *C. timotensis* (Cuatrec.) Cuatrec. are consistent with these reports. Another generic segregate, *Ruilopezia,* is known to have $n = 19$ in *R. bromelioides* (Cuatrec.) Cuatrec. (Powell & Powell, 1978) and $n = 19$ in a possible intergeneric hybrid between *R. floccosa* and *Espeletiopsis pannosa* (Standley) Cuatrec. (Powell & Cuatrecasas 1970; cited as *Espeletia floccosa* × *Espeletia pannosa*). Our count of $n = 19$ is the first for *R. floccosa.* In addition, *Espeletia batata* has been newly counted as $n = 19$. The counts for these species are consistent with the rest of Espeletiinae, which contains seven genera that include species previously placed in *Espeletia* Mutis ex Humb. & Bonpl. (Cuatrecasas, 1976). More than 50 species have been counted, all as $n = 19$ (Powell & King, 1969; Powell & Cuatrecasas, 1970, 1975). Despite the obvious morphological differences among these newly created genera, they appear to represent a monophyletic unit. The putative hybrid between two of these genera underscores their close affinity, as does the uniform chromosome number for all species of the subtribe counted to date. A more taxonomically meaningful approach might be to recognize sections and subgenera within a diverse single genus, *Espeletia.*

Our new count of $n = 20$ for *Vasquezia titicacensis* is consistent with previous reports (*V. achillioides* (Less.) Less., $n = 9$, Olsen, 1980; *V. anemonifolia* (HBK) S. F. Blake, $n = 19$, Powell & King, 1969; Jansen et al., 1984; *V. oppositifolia* (Lag.) S. F. Blake, $n = 20$, Dillon & Turner, 1982). Dillon & Turner (1982) suggested that this genus has a basic number of $x = 9$ or 10, in which case our report for *V. titicacensis* is also at the tetraploid level.

Inuleae. *Stuckertiella* is a genus with only two known species, both in S. America: *S. capitata* and *S. peregrina* Beauverd (Beauverd, 1913; Merxmüller et al., 1977). Our count of $n = 11$–12 for *S. capitata* is the first report for this genus. *Gamochaeta* is the closest generic relative, itself sometimes treated as a section of *Gnaphalium* (Beauverd, 1913). The basic chromosome number of *Gnaphalium* sensu lato is suggested as $x = 7$, a number which, along with $x = 9$ and 10, is predominant in Inuleae (Merxmüller et al., 1977). Our count might be interpreted as coming from a descending aneuploid from $n = 14$, a number also occurring in the tribe (Merxmüller et al., 1977).

Senecioneae. *Gynoxys,* with about 100 species, has only three chromosomally known taxa (*G. fuliginosa* (HBK) Cass., $n =$ ca. 40, Hunziker et al., 1989; *G. parvifolia* Cuatrec., $n =$ ca. 40; and *G. tomentosissima* Cuatrec., $n = 40$ + fragment, Turner et al., 1967). The basic number of this genus has been suggested to be $x = 10$ by Turner et al. (1967). Our new counts from two different populations in Ecuador for *G. buxifolia* are $n =$ ca. 12 and $n =$ ca. 36, which could indicate a basic number of $x = 12$, or perhaps dibasic with $x = 10$ and $x = 12$.

Our counts for *Senecio,* one of which is reported here for the first time (*S. teretifolius*), are consistent with the previously established basic number $x = 10$, although Turner and Lewis (1965) report three African species with $2n = 10$ ($x = 5$). Our count of $n =$ ca. 20 for *Pentacalia sclerosa* is consistent with previous numbers based on $x = 10$.

CICHORIOIDEAE

Liabeae. Our count of $n = 9$ for *Erato sodiroi* is a new level for the species, which has been previously counted as $n = 11$ (Strother and Panero, 1994). While our count and that of Olsen (1980) for *E. polymnioides* DC. support the suggestion by Robinson et al. (1985) that the basic number of this genus is $x = 9$, additional reports for *E. polymnioides* of $n =$ ca. 11 (Sundberg & Dillon, 1986) from material taken in Huánuco, Peru, and $2n =$ ca. 20 with possible multivalents from Ecuadorian material (Strother & Panero, 1994) could point to more complex chromosomal patterns within the genus.

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