Systematic Botany (2000), 25(1): pp. 15–25

Additional Chromosome Numbers of American Acanthaceae

THOMAS F. DANIEL
Department of Botany, California Academy of Sciences, Golden Gate Park,
San Francisco, California 94118

Communicating Editor: Anita Cholewa

ABSTRACT. Original meiotic chromosome counts are presented for 39 species in 15 genera of Acanthaceae from Belize, Costa Rica, Ecuador, Mexico, Panama, the United States, and Venezuela. These reports include the first counts for 20 species representing 10 genera of the family, including the first chromosome number documented for the genus *Poikilacanthus*. Counts for 15 species confirm numbers previously reported for them from different sources. New chromosome numbers are reported in two genera, *Carlowrightia* (n = 17 in *C. pectinata*) and *Justicia* (n = 24 in *J. galapagana*). New chromosome numbers are also reported in two species of *Justicia*, *J. comata* (n = 28) and *J. oerstedii* (n = 11). Systematic implications of these chromosome numbers are addressed where appropriate.

The Acanthaceae are a pantropical family with more than 4,000 species in some 230 genera. Major concentrations of species occur in southeastern mainland Asia, insular Malesia, India, Madagascar, tropical Africa, Brazil, Andean South America, and Mexico-Central America. Studies of phylogenetic relationships within the family are in their infancy. As a result, putative relationships are usually based on Lindau's (1895) outdated but complete classification of the family or Bremekamp's (1965) improved but incomplete infrafamilial classification. Like many other large and predominately tropical families of flowering plants, the Acanthaceae remain poorly known cytologically. Based on the summaries of chromosome counts cited below, chromosome numbers have been determined for approximately 468 species (or less than 12% of total species) in the family. In addition, one or more counts are known for only 67 of the 228 genera of Acanthaceae (i.e., 29%) recognized in Brummitt (1992). Counts have been determined for only a single species in 25 of these 67 genera.

During the past 20 years my research has focused on Acanthaceae in North America and Central America, a region in which about 500 species are known to occur. These species represent natural occurrences of taxa for three of the four traditionally recognized subfamilies of Acanthaceae (Lindau 1895): Acanthoideae, Mendoncioideae, and Nelsonioideae. Several species of the fourth subfamily, Thunbergioideae, are naturalized in this region. This study is a further contribution toward providing basic cytological information on American Acanthaceae. As in several previous studies on chromosomes of Acanthaceae (Daniel et al. 1984, 1990; Daniel and Chuang 1993), most of the plants studied here are from Mexico and Central America. Previous studies of chromosome numbers of plants from this region have helped to reassess the taxonomic status of some unispecific genera, suggest relationships among genera, and establish probable basic numbers for genera.

MATERIALS AND METHODS

Between 1982 and 1998, buds and herbarium vouchers of 60 species of Acanthaceae were collected from their native habitats in various countries of the Western Hemisphere. Some plants were grown at the San Francisco Conservatory of Flowers from seeds collected in the field (indicated by "cv" or "gh" following the field collection number). Buds were collected from these plants in the greenhouse and vouchers were made from the cultivated plants. My collection of *Justicia galapagana* (*Daniel s.n.cv*) was taken from a greenhouse-cultivated plant grown from seed collected on Santa Cruz Island in the Galapagos Islands (i.e., no collection was made in the field). Floral buds for chromosome studies were fixed in absolute ethanol:glacial acetic acid (3:1) for 24 hours and subsequently washed and stored in ethanol (70%) until analyzed. Anthers were macerated in ferric acetocarmine (1%) and counts were made from microsporocytes in various stages of meiosis. Chromosomes were studied under oil immersion on a phase contract microscope at a magnification of 1000x. Counts from at least two cells were made for most collections and all counts were verified by at least two persons. Preparations from which counts were obtained were recorded with camera lucida drawings. Voucher spec-

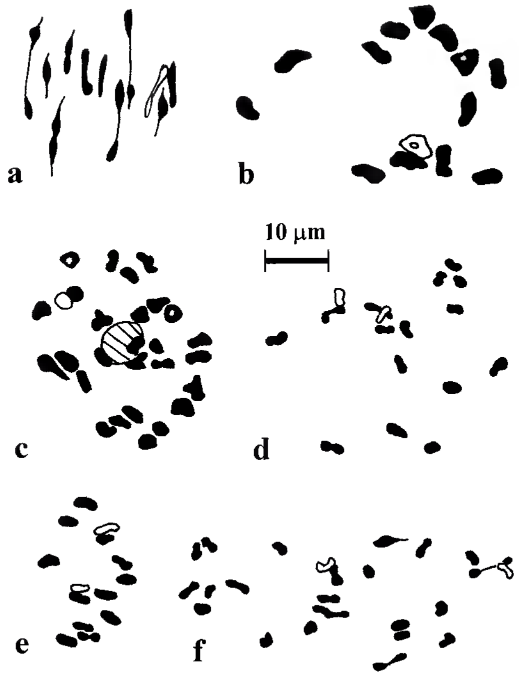

FIG. 1. Camera-lucida drawings of meiotic chromosome preparations. a. *Justicia oerstedii* (*Daniel et al. 6219*), $n = 11$ (metaphase I). b. *Aphelandra tonduzii* (*Daniel et al. 8105*), $n = 14$ (metaphase I). c. *Justicia comata* (*Daniel & Almeda 6356*), $n = 28$ (diakinesis I). d. *Carlowrightia pectinata* (*Daniel et al. 6846*), $n = 17$ (metaphase I). e. *Poikilacanthus macranthus* (*Daniel 6180gh*), $n = 14$ (metaphase I). f. *Justicia galapagana* (*Daniel s.n.cv*), $n = 24$ (metaphase I).

imens are deposited at CAS and the camera lucida drawings are attached to the specimens. Drawings of several critical preparations are reproduced here (Fig. 1). In the following discussion, all previously published chromosome counts are listed as n (gametic, haploid, meiotic) numbers irrespective of whether they were originally reported as sporophytic or gametophytic numbers. Voucher specimens, if they exist, documenting previous counts by other workers have not been examined. Previously reported approximate counts have generally been ignored unless they have been confirmed by my studies.

The concept of basic chromosome numbers was discussed by Rieger et al. (1976) and Dyer et al. (1970). In the discussion below, the basic number is typically postulated to be the only known haploid number or the lowest known haploid number of a euploid series.

RESULTS

Chromosome numbers determined for 39 species representing 15 genera of Acanthaceae from Belize, Costa Rica, Ecuador, Mexico, Panama, the United States, and Venezuela are summarized in Table 1. Based on the 60 species for which counts were attempted, this represents a success rate of about 65%. Typical problems encountered among those bud samples for which counts were not obtained included: buds either too old or too young, clumping of chromosomes during meiosis, dark cytoplasmic staining, and dark granules in the cytoplasm. In preparations from which counts were obtained pollen mother cells were observed to be particularly large (varying in diameter from 43–200 μm) whereas the chromosomes they contain are relatively small (varying in length from 2.4–16 μm at metaphase I).

DISCUSSION

Counts that Confirm Previous Chromosome Numbers. Counts obtained for the following 15 species agree with some or all chromosome numbers previously reported for the same species from different sources: *Anisacanthus andersonii* (agrees with Daniel et al. 1990), *Aphelandra gigantiflora* (agrees with Daniel and Chuang 1993), *A. guerrerensis* (agrees with Daniel and Chuang 1993, which was based on cultivated progeny of this same number), *A. sinclairiana* (agrees with Daniel in press and McDade 1984), *Asystasia gangetica* (see below), *Blechum pyramidatum* (= *B. brownei*; agrees with Daniel et al. 1984 and Grant 1955), *Carlowrightia arizonica* (agrees with Daniel et al. 1984), *C. hapalocarpa* (agrees with Daniel 1983), *C. parviflora* (agrees with Daniel et al. 1984 and 1990), *Dicliptera brachiata* (agrees with and confirms Grant's approximate count of $2n$ = ca. 80 reported in 1955), *Holographis pallida* (agrees with Daniel et al. 1990), *Justicia betonica* (agrees with most previous counts; see Daniel and Chuang 1998), *J. secunda* (agrees with Daniel et al. 1990), *Ruellia nudiflora* (agrees with previous counts; see Daniel et al. 1990), and *Tetramerium oaxacanum* (agrees with Daniel et al. 1990).

Asystasia gangetica is widely distributed in the Paleotropics, naturalized in parts of the United States (e.g., Florida and Hawaii), and cultivated throughout much of the world. It has often been studied by those counting chromosomes of Acanthaceae. A chromosome number of $n = 26$ has been reported previously on eight occasions for *A. gangetica* (including *A. coromandeliana* Nees; Narayanan

1951; Grant 1955; Ellis 1962; Kaur 1965; Valsala Devi and Mathew 1982; Saggoo and Bir 1983, 1986) and is the most commonly reported number for the species. Additional haploid numbers of 13 (Narayanan 1951; Mangenot and Mangenot 1957, 1962; Gadella 1977, 1982; Ugborogho and Adetula 1988), 14 (Subramanian and Govindarajan 1980; Govindarajan and Subramanian 1983), 22 (Narayanan 1951), 24 (Narayanan 1951), and 25 (De 1966; Sarkar et al. 1978) have also been reported for *A. gangetica*. Meiotic numbers of 13, 14, and 26 have also been reported for eight other species of the genus with 13 being most frequent (summarized by Federov 1969; Ornduff 1967; Moore 1973; Goldblatt 1984, 1985, 1988; Goldblatt and Johnson 1991). I have neither confirmed the identity of voucher specimens (where they were noted to exist) for the various counts in *Asystasia* nor resolved the taxonomy of the 50 or more species in this genus; however, some preliminary conclusions can be drawn based on the data available. A basic number of $x = 13$ is suggested for the genus. Euploidy (e.g., the presence of both $n = 13$ and $n = 26$ in both *A. gangetica* and *A. dalzelliana* Santapau) and presumed dysploidy, both ascending and descending (e.g., counts of 14, 22, and 25 in *A. gangetica*) are present within species. Both polyploidy and presumed dysploidy also appear to have been important within the genus; for example, the chromosome number of *A. travancorica* Bedd., is reported to be $n = 14$ (Narayanan 1951; presumably derived from ascending dysploidy) and the chromosome number of *A. mysurensis* (Roth) T. Anders. is reported to be $n = 26$ (Kaur 1965; a presumed polyploid). Once the genus and this species are better studied, it might be useful to seek correlations among morphology, chromosome numbers, and geography in *A. gangetica*.

New Chromosome Numbers for Species. Chromosome numbers obtained for three species (*Carlowrightia pectinata, Justicia comata,* and *J. oerstedii*) differ from counts previously reported for them. A representative meiotic preparation for each of these species is illustrated in Fig. 1. The count of $n = 17$ for *Carlowrightia pectinata* is somewhat perplexing. All previous counts for both this species (Daniel et al. 1990) and for other species of *Carlowrightia* (12 species representing each of the five sections recognized by Daniel in 1983; see summary of counts in Daniel et al. 1990; Daniel and Chuang 1993) are $n = 18$. In the material sampled here, several cells at various stages of meiosis all had $n = 17$. This suggests either an individual (or population) of *C. pectinata* with an aberrant chromosome number or a greater diversity in chromosome numbers both for this species and genus than previously suspected. Such presumed intraspecific dysploidy, though not common, is known in several other species of the family (see Daniel in press): *Elytraria imbricata* (Vahl) Pers. ($n = 11$ and 12), *Graptophyllum pictum* (L.) Griff. ($n = 20$ and 21), *Justicia ramosa* (Oerst.) V.A.W. Graham ($n = 11$ and 12; reported as *Siphonoglossa ramosa* Oerst.), and *J. sessilis* Jacq. ($n = 22$ and 23; reported as *S. sessilis* (Jacq.) Oerst.).

My count of $n = 28$ for *Justicia comata* differs from two previous counts of $n = 14$ (Grant 1955; Meagher 1973) for this species. Likewise, my counts of $n = 11$ for *J. oerstedii* do not agree with the prior count of $n = 22$ (Daniel et al. 1990) for the species. Euploidy has been noted in several other species of American Acanthaceae (e.g., *Holographis virgata* (Harv. ex Benth. & Hook.) T.F. Daniel; see Daniel et al. 1984), and it appears to be present in both of these species as well. Based on numbers so far known for these species, plants of *J. oerstedii* studied here would appear to be diploid whereas the collection of *J. comata* sampled would appear to be tetraploid.

First Chromosome Counts for Species. Chromosome number determinations for the following 20 species represent the first counts for them: *Aphelandra tonduzii* ($n = 14$), *Blechum costaricense* ($n = 17$), *Dicliptera iopus* ($n = 40$), *D. skutchii* ($n = 40$), *D. unguiculata* ($n =$ ca. 40), *Dyschoriste novogaliciana* ($n = 15$), *Justicia angustibracteata* ($n = 14$), *J. aurea* ($n =$ ca. 11), *J. candelariae* ($n = 14$), *J. costaricana* ($n = 14$), *J. galapagana* ($n = 24$), *J. herpetacanthoides* ($n = 14$), *J. isthmensis* ($n = 14$), *J. masiaca* ($n = 14$), *Odontonema microphyllum* ($n = 21$), *Poikilacanthus macranthus* ($n = 14$), *Pseuderanthemum floribundum* ($n = 21$), *P.* sp. ($n = 21$), *Ruellia standleyi* ($n = 17$), and *Stenandrium pilosulum* ($n = 26$). The chromosome numbers of all of these species, except for *Justicia galapanana* and *Poikilacanthus macranthus*, agree with one or more previously reported counts for other species in their respective genera. Because all other New World species of *Dicliptera* that have been analyzed (11 species) have $n = 40$, the approximate count for *D. unguiculata* likely reflects a true number of 40. Although a wide range of chromosome numbers has been noted in *Justicia* (summarized below), with $n = 14$ most commonly encountered, a haploid number of 11 has been previously reported in 12 species of the genus; the approximate count for *J. aurea* likely reflects a true number of 11. The count for *J. masiaca* was reported by Daniel et al. (1990) as a count for *Siphonoglossa longiflora* (Torr.) A. Gray. The distinctions between these taxa were addressed by

TABLE 1. Meiotic chromosome numbers of American Acanthaceae.

Taxon	*n*	Locality	Collection
Anisacanthus andersonii T.F. Daniel	18	MEXICO: Sonora	*Daniel et al. 8553*
Aphelandra gigantiflora Lindau	14	MEXICO: Chiapas	*Daniel 8368*
Aphelandra guerrerensis Wassh.	14	MEXICO: Oaxaca	*Daniel 5376*
Aphelandra sinclairiana Nees	14	COSTA RICA: Limón	*Daniel et al. 6233*
Aphelandra tonduzii Leonard	14	PANAMA: Chiriquí	*Daniel et al. 8105*
Asystasia gangetica T. Anderson	26	U.S.A: Hawaii	*Daniel & Butterwick 6640*
Blechum costaricense Oerst.	17	PANAMA: Veraguas	*Daniel et al. 8169*
Blechum pyramidatum (Lam.) Urb.	17	COSTA RICA: Puntarenas	*Daniel et al. 6216*
Carlowrightia arizonica A. Gray	18	MEXICO: Baja California Sur	*Daniel et al. 6845*
Carlowrightia hapalocarpa B.L. Rob. & Greenm.	18	MEXICO: San Luis Potosí	*Manktelow 715*
Carlowrightia myriantha Standl.	18	BELIZE: Corozal	*Daniel 8267*
Carlowrightia parviflora (Buckley) Wassh.	18	MEXICO: Coahuila	*Manktelow 704*
Carlowrightia pectinata Brandegee	17	MEXICO: Baja California Sur	*Daniel et al. 6846*
Dicliptera brachiata (Pursh) Spreng.	40	U.S.A.: Texas	*Daniel 6643cv*
Dicliptera iopus Lindau	40	COSTA RICA: Puntarenas	*Daniel et al. 6218*
Dicliptera skutchii Leonard	40	COSTA RICA: San José	*Daniel 6981cv*
Dicliptera unguiculata Nees	ca. 40	COSTA RICA: Puntarenas	*Daniel & Almeda 6367*
Dyschoriste novogaliciana T.F. Daniel	15	MEXICO: Nayarit	*Daniel 2051*
Holographis pallida Leonard & Gentry	26	MEXICO: Sonora	*Daniel et al. 8510*
Justicia angustibracteata Leonard	14	COSTA RICA: San José	*Daniel 6979cv*
Justicia aurea Schltdl.	ca. 11	PANAMA: Veraguas	*Daniel et al. 8171*
Justicia betonica L.	17	U.S.A.: Hawaii	*Daniel & Butterwick 6631*
Justicia candelariae (Oerst.) Leonard	14	COSTA RICA: Cartago	*Daniel & Almeda 6335*
Justicia candelariae (Oerst.) Leonard	14	COSTA RICA: Puntarenas	*Daniel & Almeda 6363*
Justicia comata (L.) Lam.	28	COSTA RICA: Puntarenas	*Daniel & Almeda 6356*
Justicia costaricana Leonard	14	COSTA RICA: Puntarenas	*Daniel & Almeda 6359*
Justicia galapagana Lindau	24	ECUADOR: Galapagos	*Daniel s.n.cv*
Justicia herpetacanthoides Leonard	14	MEXICO: Chiapas	*Breedlove & Daniel 71004*
Justicia isthmensis T.F. Daniel	14	PANAMA: Chiriquí	*Daniel et al. 8118cv*
Justicia masiaca T.F. Daniel	14	MEXICO: Sonora	*Daniel et al. 2546*
Justicia oerstedii Leonard	11	COSTA RICA: Puntarenas	*Daniel et al. 6219*
Justicia oerstedii Leonard	11	COSTA RICA: Puntarenas	*Daniel & Almeda 6368*

TABLE 1. Continued.

Taxon	*n*	Locality	Collection
Justicia secunda Vahl	14	VENEZUELA: Mérida	*King et al. 10544cv*
Odontonema microphyllum Durkee	21	PANAMA: Panamá	*Daniel et al. 8208cv*
Poikilacanthus macranthus Lindau	14	MEXICO: Chiapas	*Daniel 6180gh*
Pseuderanthemum floribundum T.F. Daniel	21	MEXICO: Oaxaca	*Daniel 5381*
Pseuderanthemum sp.	21	MEXICO: Oaxaca	*Daniel & Ton 6171*
Ruellia nudiflora (Engelm. & A. Gray) Urb.	17	BELIZE: Orange Walk	*Daniel 7033*
Ruellia standleyi Leonard	17	COSTA RICA: Cartago	*Almeda et al. 6858*
Stenandrium pilosulum (S.F. Blake) T.F. Daniel	26	MEXICO: Sonora	*Daniel et al. 8607*
Stenandrium pilosulum (S.F. Blake) T.F. Daniel	26	MEXICO: Sonora	*Daniel et al. 8614*
Tetramerium oaxacanum T.F. Daniel	18	MEXICO: Oaxaca	*Daniel & Ton 6175cv*

Daniel (1995a); both have a chromosome number of $n = 14$.

The count of $n = 14$ for *Aphelandra tonduzii* (Fig. 1) is somewhat surprising and perhaps revealing. While $n = 14$ is widespread in *Aphelandra* (in fact, 14 is the only haploid number known among the 19 species of the genus that have been both studied cytologically and vouchered; see McDade 1984; Daniel et al. 1990; Daniel and Chuang 1993), *A. tonduzii* shows many morphological similarities to *Stenandrium* ($x = 13$). Based on its herbaceous habit (vs. shrubby in most *Aphelandra*), relatively short and subactinomorphic corollas (vs. longer and strongly zygomorphic in most *Aphelandra*), stamens that are inserted in the distal 2/3 of the corolla tube and included within it (vs. inserted in the proximal 1/3 of the corolla tube and conspicuously exserted from it in most *Aphelandra*), I have often considered transferring this species, and several morphologically similar ones (e.g., *A. siebertii* Leonard), to *Stenandrium*. In fact, Wasshausen (1996) recently transferred a similar species in this complex, *A. arnoldii* Mildbr., to *Stenandrium*. I had assumed that obtaining a chromosome number of 13 (or a multiple of 13) in one or more of these Central American species would confirm their affiliation with the latter genus. Our counts from several cells of *A. tonduzii* are clearly $n = 14$. Now one must accept either that this species (and possibly those morphologically similar to it) truly belongs in *Aphelandra*, that the diversity of chromosome numbers found in *Stenandrium* includes at least one number that is not in a euploid series based on 13, or that *Aphelandra* and *Stenandrium* cannot be distinguished on the basis of chromosome numbers. Indeed, distinctions between these genera have never been adequately promulgated. Further morphological studies and additional chromosome counts of species in both genera are desirable.

Poikilacanthus comprises fewer than 15 species of perennial herbs and shrubs that occur in Mexico, Central America, and South America (Daniel 1991). This count of $n = 14$ (Fig. 1) for *P. macranthus* is the first chromosome number reported for the genus. The species has a widespread distribution, extending from southern Mexico to Panama; some of its morphological variation was discussed by Daniel (1991). Lindau (1895) included *Poikilacanthus* in subfamily Acanthoideae, tribe Isoglosseae, subtribe Porphyrocominae. The genus was distinguished from others in the family primarily on the basis of its pollen with four to eight pores and faceted exine. Raj (1961) noted that this type of pollen is not en-

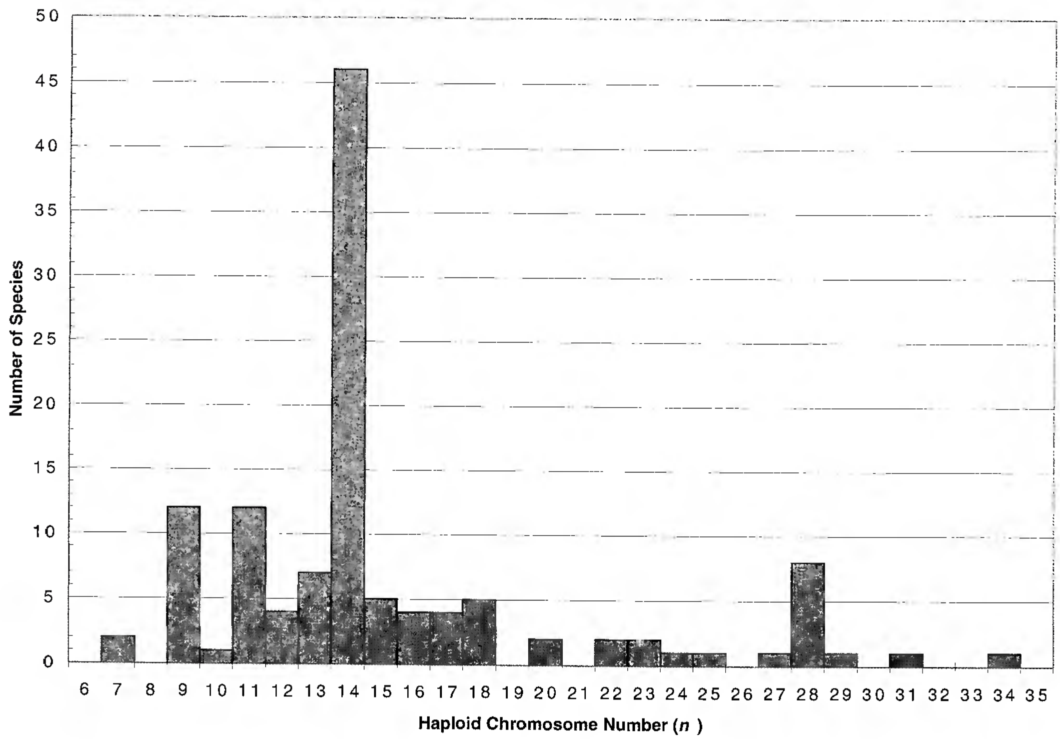

FIG. 2. Frequency histogram showing the distribution of haploid chromosome numbers reported for species of *Justicia*. See text for additional information.

countered elsewhere in the family. Bremekamp (1965) incorporated Lindau's Isoglosseae into the Justicieae but noted that the taxonomic position of *Poikilacanthus* in that tribe was unclear. Based on macromorphological and palynological evidence, Daniel (1998) concluded that the genus could be readily accommodated in the Justiciinae. Such a relationship was subsequently confirmed by data from chloroplast DNA sequences (McDade and Moody 1999). A chromosome number of n = 14 is the most commonly reported number in the related genus *Justicia* of that subtribe as well (see below).

***Chromosome Numbers in* Justicia.** *Justicia* is the largest genus in the family with between 400 and 600 species worldwide. My count of n = 24 for *Justicia galapagana* (Fig. 1) is the first report of this number in the genus. Daniel et al. (1984, 1990) noted that a wide range of chromosome numbers has been reported for species of *Justicia*, with n = 14 being the most common. Figure 2 shows the diversity and frequency of numbers reported for the genus. This summary is based on all non-approximate counts reported for species of *Adhatoda, Beloperone, Chaetothylax, Dianthera, Drejerella, Gendarussa, Ixtlania, Jacobinia, Justicia, Rhyticalymma, Rostellularia,* and *Siphonoglossa* in Federov (1969), Kaur (1969), Morton (1978), Ornduff (1967, 1968), Moore (1973, 1974, 1977), Goldblatt (1981, 1984, 1985, 1988), Goldblatt and Johnson (1990, 1991, 1994, 1996), and Daniel and Chuang (1998). All of these genera were treated as synonyms of *Justicia* by Graham (1988). To the extent possible, nomenclatural and taxonomic synonyms for species treated in these genera were resolved based on Graham (1988), Ensermu Kelbessa (1990), Daniel (1995b), and other sources. In some cases, nomenclatural combinations in *Justicia* have not been made for species whose chromosome number was reported in one or more of these genera. Because non-approximate chromosome numbers are known for 93 species of *Justicia* and 53 of these were included by Graham (1988) in an infrageneric classification of the genus, some preliminary comments on patterns of chromosome numbers within the genus are warranted. Graham (1988) did not discuss chromosome numbers, but counts have been reported for species representing 13 of the 16 sections she recognized (species treated by Graham as "peripheral" to her sections are not included). Chromosome numbers have been reported for only a single species in several sections (e.g., *Vasica, Cyrtanthera, Harnieria,* and *Tyloglossa*); thus patterns are not discernible within these taxa. A diversity of numbers is known for sections *Betonica* (three species: 13, 14, 17), *Chaetothylax* (four species: 11, 14, 22, 23), *Drejerella* (three species: 14, 15, 31), *Rhaphidospora* (four species: 13–16, 27, 34), and *Sarotheca* (five species: 11, 12, 14, 22, 24, 28). Section *Dianthera* comprises two subsections; counts of two species in subsection *Strobiloglossa* and two species in subsection *Dianthera* are all $n = 14$. A third count in subsection *Dianthera* is $n = 13$. The three species counted in subsection *Dianthera* are all morphologically similar taxa occurring in temperate North America. The count of $n = 13$ (*J. americana* (L.) Vahl) likely represents a dysploid derivative of an ancestor with $n = 14$, which number would appear to be widespread in the section. A meiotic number of 14 is the only number known in both sections *Plagiacanthus* (four species) and *Simonisia* (five species). According to Graham (1988) section *Rostellaria* comprises two subsections. In subsection *Rostellaria* a meiotic number of nine has been reported in all nine species studied. Although $n = 14$ and 18 have also been reported for one species (*J. simplex* D. Don) in this subsection and $n = 14$, 18, and 28 have also been reported for another (*J. procumbens* L.), the common occurrence of a relatively low number (i.e., nine) in all the species would appear to be significant. Among the seven species studied in subsection *Ansellia*, $n = 9$ has been reported in two. Meiotic numbers among the other five species in this subsection comprise seven (two species) and eleven (three species).

Subsequent to Graham's (1988) studies, Ensermu Kelbessa (1990) provided evidence to support the recognition of *Ansellia* at the sectional rank. He noted that in one species (*Justicia anagalloides* (Nees) T. Anderson), in which both $n = 9$ and $n = 18$ are known, the diploid number was found in small-flowered populations whereas a large-flowered population was found to be tetraploid. He also concluded that the counts of $n = 7$ reported for two species in this section represent the lowest numbers reported in the genus; that the occurrence of the unique chromosome number $n = 9$ in both sections *Rostellaria* and *Ansellia* supports their relationship as sister taxa; and that the variation in chromosome numbers of section *Ansellia* contrasts with the relative constancy of numbers in some other sections (in which evolution appears to have taken place at the same ploidal level).

Hilsenbeck (1990) used chromosome numbers, in conjunction with morphological and phytochemical data, to recircumscribe the American species of *Siphonoglossa*. He found that four species treated in *Siphonoglossa* with equally five-parted calyces, quercetin-based 0-glycosylated flavonols, and chromosome numbers of $n = 14$ (or multiples of 14) were more closely allied to species of *Justicia* than to other species of *Siphonoglossa*. Species of *Siphonoglossa* sensu stricto were noted to have four-parted calyces, apigenin-based C-glycosylflavones, and chromosome numbers of $n = 11$ (or euploid and presumed dysploid derivatives of 11). Although chemical constituents of only a few species of *Justicia* have been identified, four-parted calyces and chromosome numbers of $n = 11$ are both known in diverse species of *Justicia*. A four-parted calyx is found in at least six sections of the genus (Graham 1988) and $n = 11$ occurs in at least three sections (see above). As a result, both Graham (1988) and Daniel (1995b) have treated *Siphonoglossa* s.s. within *Justicia*. However, the correlated traits noted by Hilsenbeck (1990) in this assemblage likely delimit a clade within the genus.

The diversity of chromosome numbers so far reported for *Justicia* contrasts with the relative constancy of chromosome numbers reported for some other large genera (e.g., *Ruellia*; see Daniel et al. 1984). A basic number of $x = 7$ would appear to be highly probable for *Justicia*, as suggested by Piovano and Bernardello (1991), for several reasons: it is the lowest known number in the genus; multiples of seven are frequent and are known in 11 of the 13 sections for which at least one chromosome number has been reported; and $x = 7$ is the presumed basic number of the family (Grant 1955; Raven 1975; Piovano and Bernardello 1991; Daniel and Chuang 1993). Other possible basic numbers of *Justicia* include six (although not known in the genus or family), nine, and eleven. Multiples of each of these relatively low numbers are also known in the genus. Whatever the basic number of *Justicia*, given the diversity of numbers now known for the genus, it appears evident that both dysploidy and euploidy have been important components of evolution within the genus. While Graham's (1988) infrageneric classification provides a good beginning for resolving the taxonomy of *Justicia*, and some preliminary patterns involving chromosome numbers are evident in several of her supraspecific taxa, this large genus requires considerably more study.

Patterns of Chromosome Numbers and Suprageneric Relationships. Many of the same chromosomal patterns that were summarized by Daniel and Chuang (1993, 1998) and Daniel et al. (1984, 1990) for Acanthaceae continue to be confirmed by additional studies in the family. For example, widely divergent chromosome numbers are sometimes found within genera, euploidy and/or dysploidy are encountered at both the specific and generic levels, and haploid numbers for most taxa are relatively high (i.e., $n = 14$ or more). The diversity of basic numbers previously postulated for genera in the family (Piovano and Bernardello 1991; Daniel and Chuang 1998) is also reaffirmed. Given a probable basic number of $x = 7$ for the family, most of the counts reported here are relatively high. The high basic numbers suggested for most genera undoubtedly result from ancient polyploidizations. Species with the highest known chromosome numbers in the family, $n = 56$ in *Acanthus spinosus* L. (Sugiura 1939; Daniel and Chuang 1998) and $n = 68$ in *Sanchezia nobilis* Hook. f. (Singh 1951; Kaur 1970), would appear to represent evolution to the octoploid and decaploid levels respectively. Given the variation in chromosome numbers reported within numerous species and genera, it is likely that chromosomal alterations have been responsible for some of the proliferation in numbers of taxa in this large family. Thus, differences in chromosome numbers should prove useful in reconstructing probable phylogenies of Acanthaceae.

Bremekamp (1965) recognized 12 tribes within his narrow concept of Acanthaceae (i.e., the Acanthoideae of Lindau 1895). Chromosome numbers reported here represent only three of Bremakamp's tribes: Aphelandreae, Justicieae, and Ruellieae.

Nine of the genera studied here belong to the Justicieae: *Anisacanthus, Asystasia, Carlowrightia, Dicliptera, Justicia, Odontonema, Poikilacanthus, Pseuderanthemum,* and *Tetramerium.* It has been indicated previously (Daniel et al. 1990; Daniel and Chuang 1993, 1998) that diversity of chromosome numbers among several of these (and other) genera, combined with morphological data, suggest potential infratribal relationships with at least three suprageneric groups discernable among Neotropical taxa: *Pseuderanthemum, Odontonema,* and their relatives with $n = 21$; *Anisacanthus, Carlowrightia, Tetramerium,* and their relatives with $n = 18$; and New World *Dicliptera* with $n = 40$.

Three genera in which chromosome numbers were determined here, *Aphelandra, Holographis,* and *Stenandrium,* represent Bremekamp's Aphelandreae. *Aphelandra* appears to have $x = 14$ whereas *Holographis* and *Stenandrium* have $x = 13$ (Daniel et al. 1984, 1990). Morphological boundaries among these genera have yet to be adequately delimited and the chromosome number determined for *A. tonduzii* raises doubts about some of the correlations between taxonomy/morphology and cytology that have been promulgated previously (Daniel et al. 1984).

The remaining genera studied here, *Blechum, Dyschoriste,* and *Ruellia,* belong to the tribe Ruellieae. A basic number of $x = 17$ appears to be shared by both *Blechum* and *Ruellia* (Daniel et al. 1984; Daniel and Chuang 1998). Macromorphological similarities between these genera are well-known (Daniel et al. 1984; Daniel 1998) and *trnL-trnF* chloroplast DNA sequences (McDade and Moody 1999) strongly support a close phylogenetic relationship between them. *Blechum* and *Ruellia* undoubtedly shared a common ancestor with $x = 17$. They are readily distinguishable from one another on the basis of palynological and carpological characters (Daniel 1995c). Chromosome numbers have been reported for 11 species of *Dyschoriste.* Both $n = 15$ and $n = 30$ are common to species from the Old World and the New World with the former number reported for eight species. A basic number of $x = 15$ appears likely for *Dyschoriste.* Thus, chromosome number differences support molecular data (McDade and Moody 1999) in suggesting that *Dyschoriste* is less closely related to either *Ruellia* or *Blechum* than these latter genera are to one another.

Suprageneric classification of Acanthaceae is currently undergoing modification based largely on phylogenetic relationships as revealed by DNA sequence data (Hedrén et al. 1995; Scotland et al. 1995; McDade and Moody 1999). These studies (and others in preparation) reveal that several of the major taxonomic groupings recognized by Bremekamp (1965) based on morphology form monophyletic clades whereas others need to be reassessed. Correlations between chromosome numbers and some suprageneric groupings suggest that an expanded knowledge of chromosome numbers will be helpful in clarifying infrafamilial relationships in the Acanthaceae.

Chromosome numbers recently obtained in two genera of Acanthaceae for which chromosome numbers were previously unknown, *Poikilacanthus* (see above) and *Stenostephanus* (Daniel 1999), have helped to confirm their suspected systematic affinities. In order to be of greatest value for understanding relationships among Acanthaceae, efforts to obtain chromosome numbers in tribes and genera for which there are no counts should continue.

For example, chromosome numbers remain undetermined in Bremekamp's tribes Haselhoffieae, Louteridieae, Rhombochlamydeae, and Whitfieldieae. In addition, chromosome numbers have yet to be determined for 161 of the 228 genera of Acanthaceae recognized in Brummitt (1992). Chromosome number variation both within genera and species also needs further investigation and documentation. Some of the pitfalls of relying on single counts were noted by Darlington (1956; e.g., presence of unidentified B chromosomes) and increased sample size should be a priority in taxa where only one or a few counts have been made. Finally, sample sizes should be increased by analyzing taxa from geographic regions rich in Acanthaceae but underrepresented by studies of chromosome cytology involving them (e.g., southeastern Asian mainland, Malesia, southern Africa, Madagascar, Brazil, and Andean South America).

ACKNOWLEDGEMENTS. I am grateful to the following individuals who facilitated or assisted with the field studies: S. Acosta C., F. Almeda, B. Bartholomew, D. Breedlove, M. Correya, A. Gavazzi, M. González, V. Lee, J.-L. León de la Luz, J. Luteyn, L. McDade, G. Olalde, W. Trauba, I. Valdespino, T. and A.-L. Van Devender, A. Ton, and B. Winning. Frank Almeda and Mariette Manktelow kindly collected buds of several species for me. George Marcopulos, director of the San Francisco Conservatory of Flowers, generously provided greenhouse space in which to grow several of the species. Funding for field studies was provided by the American Philosophical Society, the In-House Research Fund of the California Academy of Sciences, Oceanic Society Expeditions, and the National Science Foundation (BSR-8609852). Logistical support in the field was enhanced by the Smithsonian Tropical Research Institute (Panama), Lamanai Outpost Lodge (Belize), El Colegio de la Frontera Sur (Mexico), the Fransican Mission at the Iglesia de Nuestra Señora de Guadalupe in Yecora (Mexico), and the Museo Nacional de Costa Rica (Costa Rica).

This contribution is dedicated to the memory of my friend and colleague, T.I. Chuang (1933–1994), who encouraged my interest in chromosomal cytology, made many counts of Acanthaceae, and co-authored four papers on chromosome numbers of Acanthaceae with me. His friendship, enthusiasm for botany, and research productivity continue to inspire me. His wife, Fei-Mei Chuang continues to provide expert technical assistance to me and others in our efforts to count chromosomes.

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