CHROMOSOMAL OBSERVATIONS ON THE ALZATEACEAE (MYRTALES)[1]

Frank Almeda[2]

ABSTRACT

Alzatea verticillata Ruiz & Pav. subsp. *amplifolia* S. A. Graham of the monotypic neotropical family Alzateaceae has a haploid chromosome number of $n = 14$. This first report for the family is unique as a putative base number among the 14 core families of the Myrtales. Given that $x = 12$ appears to be the basic number for the order, $n = 14$ could have arisen as an ascending dysploid or as a tetraploid derived from an ancestral base number of $x = 7$. A summary of probable basic chromosome numbers is given for all families currently recognized in the Myrtales except the Crypteroniaceae, which remains unknown cytologically.

Alzatea is a monotypic genus of shrubs or small trees restricted to low montane cloud forest habitats from Costa Rica and Panama south to Andean South America from Colombia to Bolivia. The placement of this genus in eight families in five orders since its discovery nearly 200 years ago (Graham, 1984) has stimulated considerable research in the last two decades aimed at assessing its relationships and taxonomic status. Several recent papers have brought to light data from macromorphology, anatomy, chemistry, embryology, palynology, DNA sequencing, and cladistic analysis that support the recognition of *Alzatea* as a distinct family within the angiosperm order Myrtales (Dahlgren & Thorne, 1984; Graham, 1984; Graham & Averett, 1984; Johnson & Briggs, 1984; Keating, 1984; Patel et al., 1984; Tobe & Raven, 1984; van Vliet & Baas, 1984; Conti et al., 1996; Conti et al., in press). I here add chromosome information for the Alzateaceae that fills a notable gap in the knowledge of cytology in the order.

MATERIALS AND METHODS

Flower buds were collected from a natural population in the field, fixed in modified Carnoy's solution (4 chloroform, 3 ethanol, 1 glacial acetic acid, v/v/v) for 24 hours, then transferred to 70% ethanol for refrigerated storage. Anthers were teased open and the contents squashed in 1% ferric aceto-carmine. Counts were made from pollen mother cells using a Zeiss light microscope with phase contrast and a 100× oil immersion objective. Drawings of meiotic configurations were made by camera lucida at a magnification of 1500×. The voucher collection for the count reported here is as follows:

Alzatea verticillata Ruiz & Pav. subsp. *amplifolia* S. A. Graham. $n = 14$. Panama. Chiriquí: Fortuna Dam area in the vicinity of Centro de Investigaciones Jorge Arauz, 1200 m, 8 Feb. 1996, *Almeda et al. 7545* (CAS).

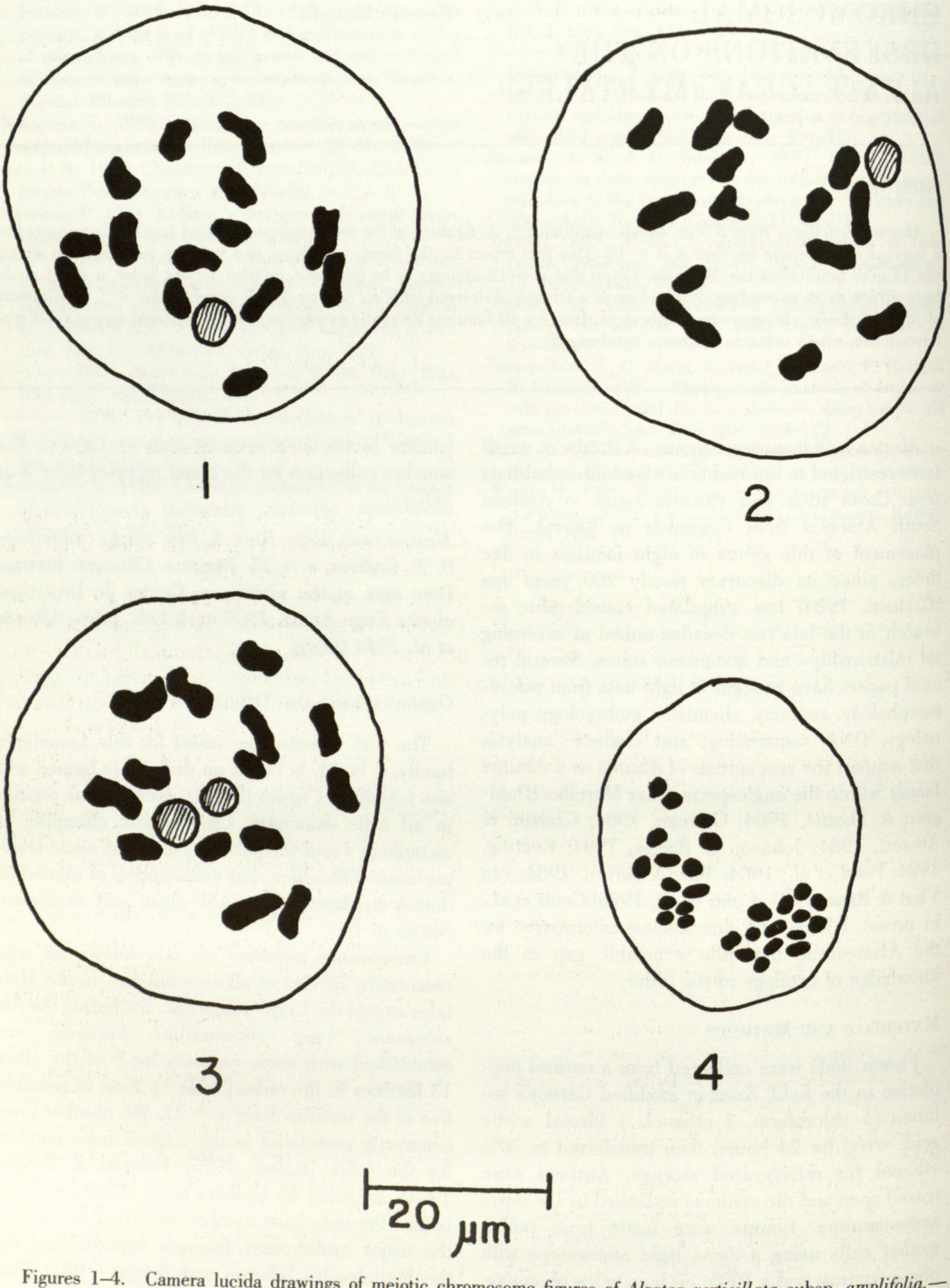
OBSERVATIONS AND DISCUSSION

The first chromosome count for this monotypic family, $n = 14$, is based on diakinesis figures and one telophase I figure (Fig. 1). Meiosis was regular in all cells examined. Chromosome clumping at metaphase I and telophase I presented some interpretation difficulties, but examination of numerous diakinesis figures provided clear and consistent counts of 14.

Chromosome numbers are now known for representative species of all core families in the Myrtales except the Crypteroniaceae. Excluding the Alzateaceae, base chromosome numbers are established with some certainty for 9 of the other 13 families in the order (Table 1). Four or possibly five of the families have $x = 12$, the number most commonly postulated as the original base number for the order (Raven, 1975; Johnson & Briggs, 1984). As noted by Graham et al. (1993), $x = 12$ is also the only base number occurring in each of the major evolutionary lineages hypothesized for the Myrtales by Johnson and Briggs (1984). The lowest base numbers in the order are $x = 8$ for the

[1] Fieldwork for this study was made possible, in part, by the G. Lindsay Field Research Fund of the California Academy of Sciences. I am grateful to Mireya Correa and the Smithsonian Tropical Research Institute for logistical support; I. Valdespino, T. F. Daniel, and J. L. Luteyn for assistance in the field; Fei-Mei Chuang for technical laboratory assistance; and Shirley Graham for helpful comments on the manuscript.

[2] Department of Botany, California Academy of Sciences, Golden Gate Park, San Francisco, California 94118, U.S.A.



Figures 1–4. Camera lucida drawings of meiotic chromosome figures of *Alzatea verticillata* subsp. *amplifolia*.—1–3. Diakinesis ($n = 14$).—4. Telophase I ($n = 14$).

Table 1. Base chromosome numbers of core families in the Myrtales.

Family	Base number (x)	References
Alzateaceae	14?	This paper
Combretaceae	12	Raven, 1975
Crypteroniaceae	?	—
Heteropyxidaceae	12	Fernandes, 1971
Lythraceae	8	Graham, pers. comm. in Raven, 1975; Tobe et al., 1986
Melastomataceae	9 or 12	Almeda, unpublished
Memecylaceae	7?	Favarger, 1952, 1962; Solt & Wurdack, 1980
Myrtaceae	11	Smith-White, 1959; Rye, 1979
Oliniaceae	10?	Goldblatt, 1976
Onagraceae	11	Raven, 1975
Penaeaceae	10	Dahlgren, 1968, 1971
Psiloxylaceae	12	Johnson & Briggs, 1984
Rhynchocalycaceae	10	Goldblatt, 1976; Johnson & Briggs, 1984
Trapaceae	12	Raven, 1975

Lythraceae and possibly $x = 7$ for the Memecylaceae (Table 1), both of which were very likely derived by descending dysploidy from the ancestral base. The chromosome number reported here for the Alzateaceae would not be discordant with what is known about base numbers in the order. The process by which it evolved, however, is open to speculation.

Accepting the premise that chromosome numbers higher than $n = 13$ are considered to be of polyploid derivation (Grant, 1963, 1981), then $n = 14$ for *Alzatea* could be interpreted as a tetraploid based on $x = 7$. Recent collections from South America have extended the geographic ranges for each of the two subspecies of *Alzatea*, and, not surprisingly, diminished the perceived morphological distinctions between them (Graham, 1995). Chromosome information for the nominate subspecies of *Alzatea* is needed before $x = 7$ can be ruled out as an extant base number for the family since intraspecific polyploidy is known in species of other myrtalean families such as the Lythraceae (Graham, 1989), Melastomataceae (Almeda, in press), Onagraceae (Berry, 1982; Raven & Tai, 1979), and Myrtaceae (Rye, 1979).

Given the range of base numbers in the Myrtales, another less parsimonious scenario that could account for the origin of $n = 14$ is descent from a tetraploid ($n = 16$) based on $x = 8$. A parallel example has been postulated by Graham (1992) to account for $x = 15$ in *Diplusodon* of the Lythraceae.

An alternative scenario that could also account for the origin of $n = 14$ would be dysploid increase from the ancestral base of $x = 12$. Given that ascending dysploidy is believed to be four times less common in the flowering plants than descending dysploidy (Jones, 1970; Goldblatt & Poston, 1988), one could argue that this scenario is less likely, but it certainly is not implausible.

A base number of 7 or 14 would serve to underscore the uniqueness of Alzateaceae but would provide no additional insights about relationships that have not already been demonstrated using other lines of evidence. Information amassed to date shows that the Alzateaceae and the Rhynchocalycaceae share a common ancestor that, in turn, is closest to the Penaeaceae, Oliniaceae, and Crypteroniaceae (Graham, 1984; Johnson & Briggs, 1984). Chromosome data are lacking for the latter family. The Penaeaceae and Rhychocalycaceae both have $x = 10$ (Table 1). The Oliniaceae are in need of additional study to confirm the few known counts that are also suggestive of $x = 10$ (Goldblatt, 1976). The fact that *Alzatea* is sister to the three families with $x = 10$ or 10? in the clade Alzateaceae–Rhynchocalycaceae–Penaeaceae–Oliniaceae (Conti et al., 1996) lends further support to descending dysploidy as the likely mechanism for chromosome number changes in *Alzatea*. Chromosome information can sometimes inform us in ways that morphological data cannot. In this instance, if $x = 14$ is ultimately established as the base number for *Alzatea*, it may prove to be the only family-level lineage in the order that originated via polyploidy.

Literature Cited

Almeda, F. In press. Chromosome numbers and their evolutionary significance in some neotropical and paleotropical Melastomataceae. BioLlania 12.

Berry, P. E. 1982. The systematics and evolution of *Fuchsia* sect. *Fuchsia* (Onagraceae). Ann. Missouri Bot. Gard. 69: 1–198.

Conti, E., A. Litt & K. J. Sytsma. 1996. Circumscription of Myrtales and their relationship to other rosids: Evidence from *rbc*L sequence data. Amer. J. Bot. 83: 221–233.

———, S. A. Graham, A. Litt, P. G. Wilson, B. G. Briggs, L. A. S. Johnson & K. J. Sytsma. In press. Interfamilial relationships in Myrtales: Molecular phylogeny and patterns of morphological evolution. Syst. Bot.

Dahlgren, R. 1968. Studies on Penaeaceae. Part II. The genera *Brachysiphon, Sonderothamnus,* and *Saltera.* Opera Bot. 18: 1–72.

———. 1971. Studies on Penaeaceae. Part VI. The genus *Penaea.* Opera Bot. 29: 1–58.

——— & R. F. Thorne. 1984. Myrtales: Circumscription, variation, and relationships. Ann. Missouri Bot. Gard. 71: 633–699.

Favarger, C. 1952. Recherches sur quelques Mélastomacées d'Afrique occidentale. Ber. Schweiz. Bot. Ges. 62: 5–65.

———. 1962. Nouvelles recherches cytologiques sur les Mélastomatacées. Ber. Schweiz. Bot. Ges. 72: 290–305.

Fernandes, A. 1971. Contribution à la connaissance du genre *Heteropyxis* Harv. Mitt. Bot. Staatssamml. München 10: 207–234.

Goldblatt, P. 1976. New or noteworthy chromosome records in the angiosperms. Ann. Missouri Bot. Gard. 63: 889–895.

——— & M. E. Poston. 1988. Observations on the chromosome cytology of Velloziaceae. Ann. Missouri Bot. Gard. 75: 192–195.

Graham, S. A. 1984. Alzateaceae, a new family of Myrtales in the American tropics. Ann. Missouri Bot. Gard. 71: 757–779.

———. 1989. Chromosome numbers in *Cuphea* (Lythraceae): New counts and a summary. Amer. J. Bot. 76: 1530–1540.

———. 1992. New chromosome counts in Lythraceae—Systematic and evolutionary implications. Act. Bot. Mex. 17: 45–51.

———. 1995. Two new species in *Cuphea* (Lythraceae), and a note on Alzateaceae. Novon 5: 272–277.

——— & J. E. Averett. 1984. Flavonoids of Alzateaceae (Myrtales). Ann. Missouri Bot. Gard. 71: 855–857.

———, K. Oginuma, P. H. Raven & H. Tobe. 1993. Chromosome numbers in *Sonneratia* and *Duabanga* (Lythraceae s.l.) and their systematic significance. Taxon 42: 35–41.

Grant, V. 1963. The Origin of Adaptations. Columbia Univ. Press, New York.

———. 1981. Plant Speciation, 2nd ed. Columbia Univ. Press, New York.

Johnson, L. A. S. & B. G. Briggs. 1984. Myrtales and Myrtaceae—A phylogenetic analysis. Ann. Missouri Bot. Gard. 71: 700–756.

Jones, K. 1970. Chromosome changes in plant evolution. Taxon 19: 172–179.

Keating, R. C. 1984. Leaf histology and its contribution to relationships in the Myrtales. Ann. Missouri Bot. Gard. 71: 801–823.

Patel, V. C., J. J. Skvarla & P. H. Raven. 1984. Pollen characters in relation to the delimitation of Myrtales. Ann. Missouri Bot. Gard. 71: 858–969.

Raven, P. H. 1975. The bases of angiosperm phylogeny: Cytology. Ann. Missouri Bot. Gard. 62: 724–764.

——— & W. L. Tai. 1979. Observations of chromosomes in *Ludwigia* (Onagraceae). Ann. Missouri Bot. Gard. 66: 862–879.

Rye, B. L. 1979. Chromosome number variation in the Myrtaceae and its taxonomic implications. Austral. J. Bot. 27: 547–573.

Smith-White, S. 1959. Cytological Evolution in the Australian Flora. Cold Spring Harbor Symp. Quant. Biol. 24: 273–289.

Solt, M. L. & J. J. Wurdack. 1980. Chromosome numbers in the Melastomataceae. Phytologia 47: 199–220.

Tobe, H. & P. H. Raven. 1984. The embryology and relationships of *Alzatea* Ruiz & Pav. (Alzateaceae, Myrtales). Ann. Missouri Bot. Gard. 71: 844–852.

———, P. H. Raven & S. A. Graham. 1986. Chromosome counts for some Lythraceae sens. str. (Myrtales), and the base number of the family. Taxon 35: 13–20.

Vliet, G. J. C. M. van & P. Baas. 1984. Wood anatomy and classification of the Myrtales. Ann. Missouri Bot. Gard. 71: 783–800.