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CHROMOSOMES OF SALVIA: SECTION AUDIBERTIA

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Chromosome numbers have previously been reported for 11 of the 19 species of *Salvia,* section Audibertia (Labiatae), and these have been surprisingly diverse for an assemblage of related species, most of which are shrubby. Furthermore, more than one chromosome number has been reported for several species. As a consequence of these diverse and conflicting reports the chromosome number of each of the 19 species of the section has been examined or re-examined by us. In addition we have examined meiosis of natural hybrids between *Salvia apiana* and *S. mellifera* because of its relevance to previous studies of introgression between these species (Epling, 1947; Anderson and Anderson, 1954).

Somatic chromosome numbers have been determined for the most part from sectioned root tips stained in gentian violet. A few additional determinations of somatic chromosome number have been made from squash preparations of anthers. Determinations of chromosome number and pairing at meiosis have been made using microsporocytes fixed in 1:3 acetic alcohol and squashed in acetocarmine. No meiotic irregularities have been observed in any of the species.

Chromosome numbers are summarized in table 1 in accord with the taxonomic treatment of Epling (1938). Collections cited are deposited at the University of California, Los Angeles.

All members of subsections Greeneostachys, Jepsonia, and Parishiella, comprising 14 species, have the same gametic chromosome number, n=15, as was reported for *S. apiana* and *S. mellifera* by Carlson and Stuart (1936). Reports of other numbers for some of these species are due to incorrect interpretation of sectioned material, as we have learned from re-examination of the slides on which they were based (see footnote, table 1). The two collections we have examined of *S. columbariae,* the only species of subsection Pycnosphace, had a gametic chromosome number of n=13 (fig. 1b) as was earlier reported by Yakovleva (1933). The bases for the reports of n=16, by Carlson and Stuart (1936), n=8 by Stewart (1939), and 2n=28 by Delestaing (1954) are not known, and the possibility of more than one chromosome number in this species can not be excluded. However, the known errors in determining chromosome number for other species leads us to question the validity of reports other than n=13 for this species.

Subsection Echinosphace is chromosomally and perhaps also morphologically the most variable within Audibertia. The annual *S. carduacea* (fig. 1a) and the shrub *S. californica,* an endemic of Baja California, both have n=16. Further evidence of the close relationship of these species is suggested by the well-developed lobate leaves of *S. californica,* when grown under cultivation at Los Angeles, which simulate the normal leaves of *S. carduacea.* On the other hand, *S. funerea,* an endemic of limestone crevices in the mountains near Death Valley, Inyo County, California, has n=32, and, judging from quadrivalents present at first metaphase, may be autotetraploid. However, genomes of *Salvia* species of section Audibertia are structurally similar as indicated below, and quadrivalents might be expected in an allotetraploid. On the other hand, only one plant could be examined and the possi-

Table 1. *Chromosome numbers in Salvia: section Audibertia.*

Subsection and species	n	2n	Locality	Previous report n	Previous report 2n	Previous report author
Echinosphace						
carduacea	16		East of Edison, Kern Co., Calif., *Lewis in 1956*		32	Scheel, 1931
				16		Yakovleva, 1933
				12		Stewart, 1939
californica		32	North-east of El Arco, Baja Calif., *Nelson in 1955*			
funerea	c.32	64	Hole-in-the-Rock Spring, Inyo Co., Calif., *Epling in 1935*.			
greatae		c.30	Near Clemens Well, Riverside Co., Calif., *H. & M. Lewis in 1955*.			
Pycnosphace						
columbariae	13		Temblor Range, San Luis Obispo Co., Calif., *Lewis in 1954*.		26	Yakovleva, 1933
				16	32	Carlson & Stuart, 1936
	13		Hellhole Canyon, San Diego Co., Calif., *Lewis in 1955*.	8		Stewart, 1939
					28	Delestaing, 1954
Greeneostachys						
spathacea		30	San Marcos Pass, Santa Barbara Co., Calif., *Lewis 1312*.		26[a]	Stewart, 1939
		30	Topanga Canyon, Los Angeles Co., Calif., *Lewis in 1940*.			
Parishiella						
mellifera		30	Torrey Pines, San Diego Co., Calif., *Epling in 1932*.	15		Carlson & Stuart, 1936
		30	Banning, Riverside Co., Calif.	16		Stewart, 1939; Epling, 1947
		30	West Los Angeles, Los Angeles Co., Calif.			
		30	Aguanga, Riverside Co., Calif.			
		30	Indian Canyon, Riverside Co., Calif.			
munzii		30	Otay Lake, San Diego Co., Calif., *Lewis in 1940* (6 plants examined)	16		Epling, 1940
					24[a]	Stewart, 1939
brandegei	15		Santa Rosa I., Santa Barbara Co., Calif., *Epling in 1940* (transplant).			
Jepsonia						
clevelandii		30	Japatul Valley, San Diego Co., Calif.		32	Stewart, 1939
		30	Otay Mt., San Diego Co., Calif., *Epling in 1936*.			
		30	Torrey Pines, San Diego Co., Calif., *Lewis in 1940*.			
leucophylla		30	Topanga Canyon, Los Angeles Co., Calif., *Ernst in 1947*.	12		Stewart, 1939
		30	Newhall, Los Angeles Co., Calif.			
		30	Pt. Mugu, Ventura Co., Calif.			
chionopeplica	15		Near San Augustín, Baja Calif., *Raven, Mathias & Turner 12251*.			
mohavensis	15		Joshua Tree National Monument, Riverside Co., Calif., *Raven 15497*.			
pachyphylla		30	Big Bear Valley, San Bernardino Co., Calif.			

TABLE 1. *Chromosome numbers in Salvia: section Audibertia. (continued)*

SUBSECTION AND SPECIES	n	2n	LOCALITY	PREVIOUS REPORT n	PREVIOUS REPORT 2n	PREVIOUS REPORT AUTHOR
dorrii (carnosa)						
subsp. *dorrii (pilosa)*		30	Re-examination of slide of Stewart		32[a]	Stewart, 1939
subsp. *gilmanii*		30	Re-examination of slide of Stewart		22[a]	Stewart, 1939
eremostachya		30	Palms-to-Pines Highway, Riverside Co., Calif., *Epling in 1937.*		24[a]	Stewart, 1939
sonomensis		30	Cuyamaca Lake, San Diego Co., Calif., *Epling in 1937.*		32[a]	Stewart, 1939
vaseyi	15		Palms-to-Pines Highway, Riverside Co., Calif., *Lewis in 1957.*			
apiana	15		Pala, San Diego Co., Calif., *Lewis in 1957.*	15		Carlson & Stuart, 1936
	15		Sentenac Canyon, San Diego Co., Calif., *Lewis in 1955.*	16 16	32[a]	Stewart, 1939 Epling, 1947
		30	Devil Canyon, San Bernardino Co., Calif.			
		30	Indian Canyon, Riverside Co., Calif.			
		30	Japatul Valley, San Diego Co., Calif.			
		30	San Marcos Pass, Santa Barbara Co., Calif.			
		30	Aguanga, Riverside Co., Calif.			

a. Slides kindly supplied by Dr. Stewart showed on re-examination a somatic chromosome number 2n=30.

bility exists that it was an autotetraploid but aberrant for the species as a whole, which may not be tetraploid. The remaining species of subsection Echinosphace, *Salvia greatae,* another exceedingly localized endemic in the mountains along the eastern margin of the Salton Sea, California, has a chromosome number that is anomalous for its subsection but widespread in the others, n=15. This count, however, is not as certain as the others reported in this paper and is based on examination of three premeiotic divisions in anther tissue of a bud too young for meiosis.

Among the subsections characterized by n=15, the morphological and ecological diversity which has led to species formation has not necessarily been associated with structural change or repatterning of the chromosomes. This is indicated by the nearly complete pairing of chromosomes at meiosis in hybrids between *Salvia apiana* (subsection Jepsonia; chromosomes in fig. 1c) and *S. mellifera* (subsection Parishiella) as shown in fig. 1d. These two species contrast strongly in floral morphology (for illustrations, see Epling, 1938, plates 18 and 29) and occur in mixed stands throughout an extensive area in southern California. Sporadic hybrids are found in this area, most of which are indistinguishable from first generation hybrids that have been grown in the garden. In addition, hybrid swarms have been found in localized areas in which the habitat has been disturbed (Epling, 1947; Anderson and Anderson, 1954).

We have examined meiosis in three natural hybrids of *S. apiana* and *S. mellifera* and the results are summarized in table 2. One hybrid came from a mixed population near the mouth of Big Tujunga Canyon, Los Angeles County *(Lewis in 1954)* which showed no evidence of hybridization, except for the individual examined. Consequently, the individual in question was undoubtedly a first generation hybrid. This plant regularly showed 15 pairs of chromosomes at first metaphase but at anaphase a high frequency of cells showed a bridge and accompanying fragment indicating that it was heterozygous for at least one paracentric

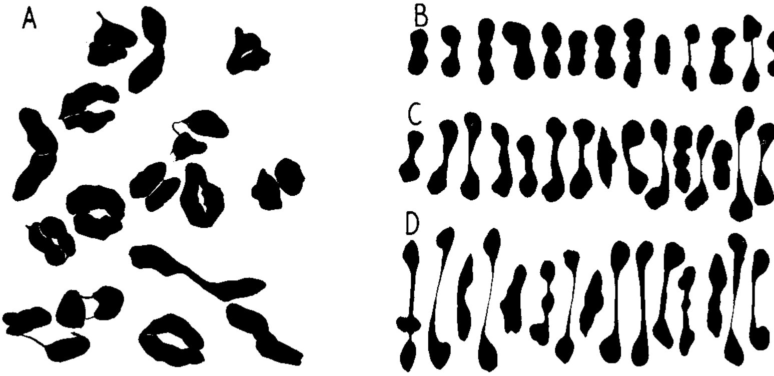

Fig. 1. Camera lucida drawings of meiotic chromosomes of *Selvia.*—a. *S. carduacea* (east of Edison), diakinesis, 16 pairs.—b. *S. columbariae* (Temblor Range), metaphase I, 13 pairs.—c. *S. apiana* (Sentenac Canyon), metaphase I, 15 pairs.—d. *S. apiana* × *mellifera* (Big Tujunga), metaphase I, 15 pairs. All drawings × 1700.

inversion. No other irregularities were observed. Inversion heterozygotes have not been detected in either of the parent species, or any of the other species of *Salvia.* This suggests that the genomes of *S. apiana* and *S. mellifera* may be characterized by this inversion. However, no evidence of an inversion was detected in the other two hybrid plants examined. Both of these hybrids *(Lewis 1246)* were morphologically equivalent to first generation hybrids but came from a natural stand of Coastal Sage on the U.C.L.A. campus which had been disturbed and where hybridization beyond the first generation was evident. Consequently, these may not have been primary hybrids. One of the hybrids from this population showed no irregularities whatsoever; the other showed one asynaptic or early dissociating pair. Whether the same pair was concerned in every instance could not be determined and the cause may have been either genetic or structural. Taken together, however, our observations from all three hybrids indicate that the genomes of these two morphologically very different species are structurally very similar.

TABLE 2. *Meiosis in microsporocytes of three natural hybrids between Salvia apiana and S. mellifera. Frequencies shown indicate the number of cells observed.*

	METAPHASE I		ANAPHASE-TELOPHASE I BRIDGE + FRAGMENT	
LOCALITY	15_{II}	$14_{II}+2_{I}$	ABSENT	PRESENT
Big Tujunga	15	0	64	36
U.C.L.A.-1	16	8	100	0
U.C.L.A.-2	18	0	40	0

The basic chromosome numbers in section Audibertia are high compared to those reported for some species of the genus and suggests that Audibertia is probably of polyploid origin. Unfortunately, however, chromosome numbers are known for very few of the related species in the large American subgenus Calosphace and the few that are known give no indication of the original basic number for Audibertia or of its origin. We suggest, however, that the original number was probably 16 and that 15 and 13 represent reductions, although the evidence is indirect. *Salvia columbariae,* the only species with n=13 is annual and surely derived from a shrubby ancestor with n=15. The close relationship of *S. colum-*

bariae to shrubs with n=15 is indicated by the spontaneous hybrids that it forms occasionally with *S.mellifera (S. × bernardina)* in areas where the two grow together. The evidence for the origin of the large group with n=15 from an original basic number of 16 is more tenuous. However, a comparison of the present pattern of distribution of species in subsection Echinosphace, to which all of the species with n=16 belong, compared to the subsections characterized by n=15 is suggestive (for distributions, see Epling, 1938). All of the species of the former are widely disjunct, which suggests that they are fragments of a relatively old group. In contrast, the 14 species in the three subsections with n=15 occupy overlapping or contiguous areas and the more closely related species replace one another geographically. This pattern suggests that the species in these groups are for the most part relatively young.

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