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The new chromosomal data and karyotypic variations in genus *Salvia* L. (Lamiaceae): dysploidy, polyploidy and symmetrical karyotypes

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Abstract. In this study, it was aimed to determine the chromosome number of 21 *Salvia* L. species, to determine chromosome morphology, to reveal karyotype analysis in detail and to contribute to the cytotaxonomy of *Salvia*. In this context, the results are as follows: (i) the first report for the number of chromosomes of ten species, namely *S. corrugata* Vahl. (2*n* = 16), *S. curviflora* Benth. (2*n* = 16), *S. darcyi* J.Compton, *S. greggii* A.Gray, *S. longifolia* Nutt., *S. vitifolia* Benth. (2*n* = 22), *S. subrotunda* A.St.-Hil. ex Benth. (2*n* = 44), *S. oppositiflora* Ruiz & Pav. (2*n* = 56), *S. stolonifera* Benth. and *S. atrocyanea* Epling (2*n* = 60); (ii) the karyotypic variations and new chromosome numbers different from previous reports for three species, namely *S. cardiophylla* Benth. (2*n* = 36), *S. cuspidata* Ruiz & Pav. (2*n* = 44) and *S. microphylla* Sessé & Moc. (2*n* = 46); (iii) the same chromosome numbers from previous reports for eight species, namely *S. campanulata* Wall. ex Benth. (2*n* = 16), *S. elegans* Vahl. (2*n* = 20), *S. involucrata* Cav., *S. mexicana* Sessé & Moc. (2*n* = 22), *S. apiana* Jeps., *S. leucophylla* Greene, *S. mellifera* Greene (2*n* = 30), and *S. splendens* Ker Gawl. (2*n* = 44); (iv) the detailed chromosome measurements and karyotype analyses for all species studied for the first time; (v) the symmetrical karyotypes for all studied species; (vi) the variations resulting from dysploidy or polyploidy and discussing their reasons.

Keywords: chromosomal alteration, karyotype asymmetry, sage, Turkey.

INTRODUCTION

The word Salvia that means sage in Turkish is derived from the Latin salvare, which means protect and heal because of its medicinal properties. The genus Salvia is placed in the family Lamiaceae and is one of the largest

genera of the family with nearly 1000 perennials, biennial or annual, often strongly aromatic species throughout the world (Sheidai and Alijanpoo 2011). This ratio corresponds to one quarter of the family. The Salvia species usually spread in tropical and temperate regions of the world. The species are mostly distributed in three different regions: Central and South America (about 500 species), West Asia (about 200 species) and East Asia (about 100 species) (Walker and Sytsma 2007). Turkey, which has 98 species in terms of the diversity of Salvia species, is an important gene center in Asia (Hedge 1982; Kahraman *et al.* 2011).

Aboveground organs of *Salvia* species have been used in cough, colds, teeth, stomach and abdominal pains and skin diseases since ancient times. Most of *Salvia* species are used as folk medicine because of their antioxidant, antidiabetic, antimicrobial, antitumor, antiplasmodial, antihypertensive and anti-inflammatory properties (Ulubelen 2003; Kamatou *et al.* 2008; Şenol *et al.* 2010). Some *Salvia* species have been reported to be used to prevent memory loss (Perry *et al.* 1996). In addition, *Salvia* species are frequently used in food, perfumery, cosmetics and pharmaceutical industries (Chalchat *et al.* 1998; Baylac and Racine 2003). Many *Salvia* species are easily cultured frequently due to their aromatic nature; and because of their beautiful appearance, they are grown as decorative ornamental plants in parks and gardens (Nakipoğlu 1993; Marin *et al.* 1996).

Many karyological reports showed that *Salvia* is a polybasic genus with diverse chromosome numbers in different regions of the world and the species are polyploid origins (Sheidai and Alijanpoo 2011). It was reported that the basic number is $x = 16$ for California species (Epling *et al.* 1962); is $x = 11$ for species of Russia and Europe (Patudin *et al.* 1975); is $x = 7$ for Mediterranean species (Afzal-Rafii 1976). According to the chromosome databases, comprehensive chromosomal reports exist in genus *Salvia*. Due to the high number of species and samples, there may be some cytotaxonomic uncertainties. The purpose of this work is to contribute to the cytotaxonomy of *Salvia* with the following questions: (1) The chromosome numbers of which species will be reported for the first time? (2) Are there species with karyotypic variations and new chromosome numbers different from previous reports? (3) What are the detailed chromosome measurements and karyotype analysis results for all species? (4) What are the karyotype asymmetry states for all species? Symmetrical or asymmetrical. (5) What are the chromosomal variations caused by polyploidy and dysploidy in genus *Salvia*? (6) What are the possible causes of polyploidy, dysploidy, and symmetrical/asymmetrical karyotypes?

MATERIALS AND METHODS

The seeds of the plants included in the study were provided by Mr. Robin Middleton, who cultivated many Salvia species in his personal botanical garden in England. Identification and confirmation of the specimens were performed by the third author of this study.

The cytogenetical study was conducted on root tips germinated on wet filter paper in Petri dishes. After germination, the fresh root tip meristems were pretreated in α-mono-bromonaphthalene at 4°C for 16 hours, fixed in glacial acetic acid and absolute alcohol (1:3) at 4°C for 24 hours, deposited in 70% ethanol at 4°C, and then hydrolyzed in 1 N HCl at room temperature for 12 minutes. Finally, they were squashed and stained in 2% aceto-orcein. Permanent slides were prepared using Standard liquid nitrogen method (Altay *et al.* 2017; Martin *et al.* 2019).

Karyotypes were determined using Image Analysis System (Bs200Pro) on a personal computer. 10 mitotic plates were assessed to determine the chromosome numbers. The following variables were measured: long arm (la), short arm (sa), total chromosome length (la + sa), arm ratio (la / sa), centromeric index [(sa / la + sa) × 100], total haploid length (THL), mean chromosome length (MCL), and relative length (RL%). Centromere positions and karyotype formulae of 17 *Salvia* species were determined. From the point of view of chromosome morphology, median (M, m), submedian (sm) and subtelocentric (st) chromosome pairs were observed (Levan *et al.* 1964). As centromere positions of the other taxa (*S. cardiophylla*, *S. cuspidata*, *S. oppositiflora*, and *S. atrocyanea*) could not be determined, their total chromosome length and haploid chromosome length were measured. Intrachromosomal asymmetry and interchromosomal asymmetry were determined with the parameters of M_{CA} (Peruzzi and Eroğlu 2013) and CV_{CL} (Paszko 2006), respectively. The intrachromosomal asymmetry increases by shifting of centromere position from the center to the end of the chromosome. In this case there is a transition from median/submedian chromosomes to subterminal/terminal chromosomes. The interchromosomal asymmetry depends on relative variation in chromosome length, namely it determines how different the chromosome lengths of a complement. Finally, a scatter diagram was drawn between M_{CA} and CV_{CL}.

RESULTS

Chromosomal data

Chromosome records of 21 taxa are herein provided (Figure 1), ten of which are reported for the first time,

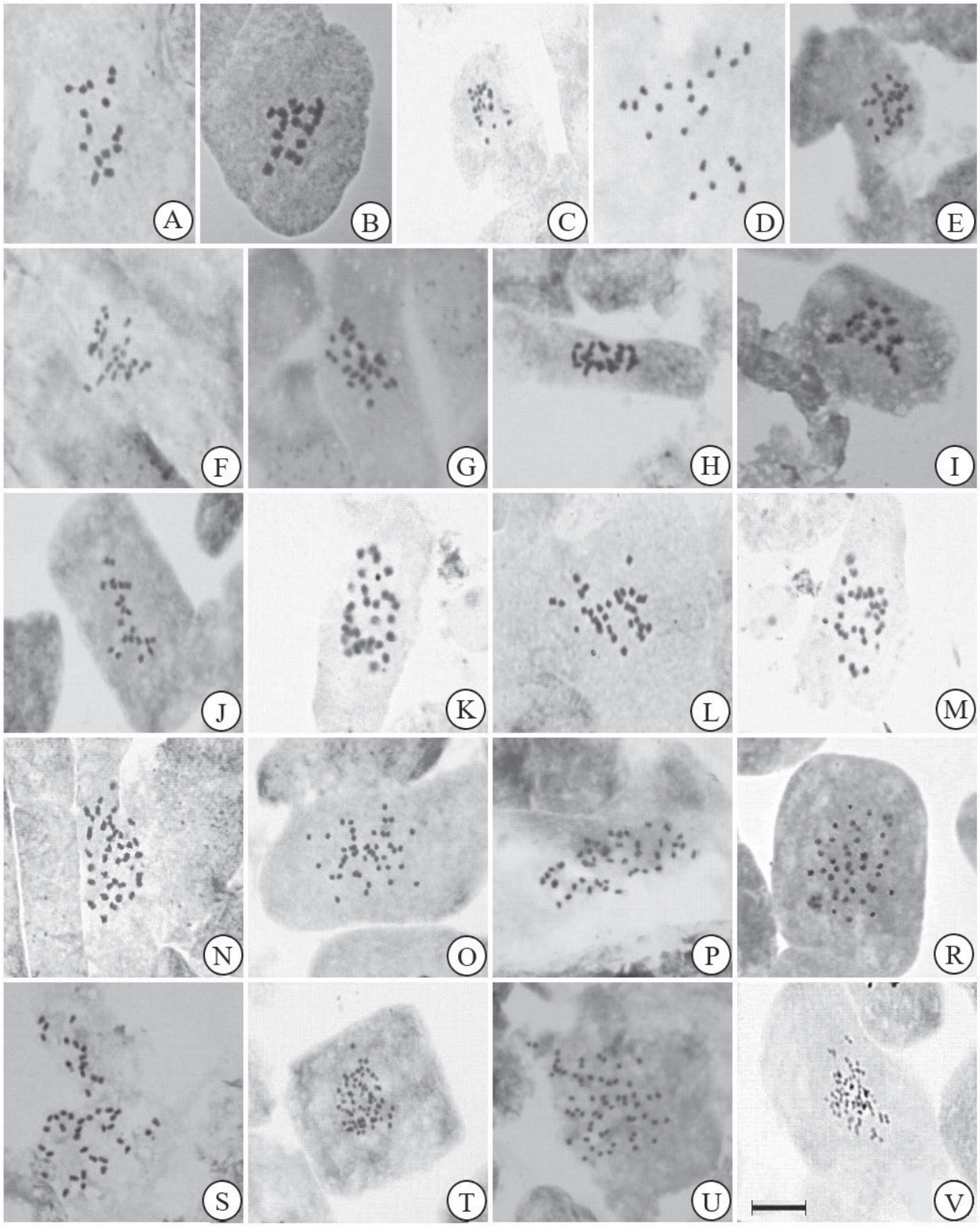

Figure 1. Mitotic metaphase chromosomes of *Salvia*: (A) *S. corrugata*, (B) *S. campanulata*, (C) *S. curviflora*, (D) *S. elegans*, (E) *S. darcyi*, (F) *S. greggii*, (G) *S. involucrata*, (H) *S. longifolia*, (I) *S. vitifolia*, (J) *S. mexicana*, (K) *S. apiana*, (L) *S. leucophylla*, (M) *S. mellifera*, (N) *S. cardiophylla*, (O) *S. cuspidata*, (P) *S. splendens*, (R) *S. subrotunda*, (S) *S. microphylla*, (T) *S. oppositiflora*, (U) *S. stolonifera*, (V) *S. atrocyanea* (scale bar: 10 μm).

Table 1. The chromosome counts of the investigated species in present and previous studies.

Species	Previous results		References	Present results	Explanation
	n	2*n*		2*n*	
S. corrugata				16	First report
S. campanulata	8	32	Saggoo and Bir 1986; Hu *et al.* 2016	16	Detailed measurements
S. curviflora				18	First report
S. elegans	10		Cherian and Kuriachan 1990	20	Detailed measurements
S. darcyi				22	First report
S. greggii				22	First report
S. involucrata	7	22 + 0-1B	Gill 1984; Alberto *et al.* 2003	22	Detailed measurements
S. longifolia				22	First report
S. vitifolia				22	First report
S. mexicana		22	Palomino *et al.* 1986	22	Detailed measurements
S. apiana	15, 16	32	Carlson and Stuart 1936; Stewart 1939	30	Detailed measurements
S. leucophylla		24, 30	Stewart 1939; Epling *et al.* 1962	30	Detailed measurements
S. mellifera		30, 32	Epling *et al.* 1962; Stewart 1939	30	Detailed measurements
S. cardiophylla		44 + 0-1B	Alberto *et al.* 2003	36	New count
S. cuspidata		22	Alberto *et al.* 2003	44	New count
S. splendens	8	32, 44 44 + 0-1B	Carlson and Stuart 1936; Haque and Ghoshal 1980; Gill 1984; Alberto *et al.* 2003	44	Detailed measurements
S. subrotunda				44	First report
S. microphylla	11	22	Haque and Ghoshal 1980; Alberto *et al.* 2003	46	New count
S. oppositiflora	–	–		56	First report
S. stolonifera	–	–		60	First report
S. atrocyanea	–	–		60	First report

three possess new chromosome numbers, and eight have the same results including previous reports. Ten different chromosome numbers (2*n* = 16, 18, 20, 22, 30, 36, 44, 46, 56, and 60) are also detected (Table 1). Among the studied taxa, the smallest and the largest chromosome shapes are 0.53 μm in *S. oppositiflora* and 3.28 μm in *S. campanulata*, respectively. The smallest and the highest values of total haploid chromosome length are 9.12 μm in *S. curviflora* and 36.92 μm in *S. stolonifera*, respectively (Table 2). In addition, the detailed chromosome measurements of all chromosome pairs are given in supplemental online material (Supplementary Tables 1–21).

Basic numbers and ploidy levels

There are six basic chromosome numbers within *Salvia*, namely $x = 7$ in only one species, $x = 8$ in two species, $x = 9$ in two species, $x = 10$ in six species, most common $x = 11$ in nine species, and $x = 23$ (probably dysploidy) in only one species. The ploidy levels are $2x$ (in 11 species), $3x$ (in three species), $4x$ (in four species), $6x$ (in two species), and $8x$ (in only one species) (Table 2). The monoploid ideograms generated by the basic chromosome numbers are given in Figure 2.

Karyotype formula and karyotype asymmetry

17 taxa possess median (m) and submedian (sm), whereas none subtelocentric (st) chromosomes and telocentric (t) chromosomes. Due to the uncertainty of centromere positions, the karyotype formulae of four taxa are not given, namely *S. cardiophylla*, *S. cuspidata*, *S. oppositiflora*, and *S. atrocyanea*. Four different formulae are observed, namely (1) M-m, (2) m, (3) m-sm, and (4) M-m-sm. The M_{CA} values for intrachromosomal asymmetry vary from 14.94 in *S. curviflora* to 26.01 in *S. corrugata* and are characterized by taxa with symmetric karyotypes consisting entirely of median and submedian chromosomes. The CV_{CL} values for interchromosomal asymmetry vary from 10.73 in *S. longifolia* to 22.13 in *S. mellifera* (Table 2).

Table 2. The karyological features of the studied *Salvia* taxa; karyotype formula (KF), shortest chromosome length (SC), longest chromosome length (LC), relative length (RL), total haploid chromosome length (THL), mean chromosome length (MCL), centromeric index (CI), coefficient of variation of chromosome length (CV_{CL}), mean centromeric asymmetry (M_{CA}), median point (M), median (m), submedian (sm).

Taxa	KF	SC (μm)	LC (μm)	RL (%) SC–LC	THL (μm)	MCL (μm)	CI (min–max)	CV_{CL}	M_{CA}
S. corrugata	8m + 8sm	1.55	2.44	10.58–16.66	14.65	1.83	31.55–41.38	15.84	26.01
S. campanulata	10m + 6sm	1.92	3.28	9.41–16.08	20.40	2.55	36.16–45.97	17.29	22.14
S. curviflora	2M + 16m	0.72	1.35	7.89–14.80	9.12	1.01	38.89–50.00	20.05	14.94
S. elegans	20m	1.21	2.16	7.48–13.35	16.18	1.62	37.13–45.22	17.06	18.55
S. darcyi	18m + 4sm	1.17	1.84	7.49–11.78	15.62	1.42	27.17–48.51	12.91	16.30
S. greggii	2M + 14m + 6sm	0.84	1.60	6.87–13.08	12.23	1.11	32.71–50.00	20.28	19.59
S. involucrata	2M + 14m + 6sm	1.03	1.76	7.05–12.04	14.62	1.33	30.00–50.00	16.00	20.90
S. longifolia	2M + 14m + 6sm	1.09	1.60	7.14–10.48	15.26	1.39	26.25–50.00	10.73	22.59
S. vitifolia	14m + 8sm	1.22	2.21	6.66–12.06	18.33	1.67	31.15–43.95	17.33	21.48
S. mexicana	20m + 2sm	0.97	1.70	6.37–11.16	15.23	1.38	35.37–44.88	15.94	17.32
S. apiana	28m + 2sm	1.07	1.93	4.87–8.79	21.95	1.46	33.86–46.34	16.17	17.31
S. leucophylla	26m + 4sm	0.95	1.81	5.01–9.55	18.96	1.26	35.00–43.28	17.62	20.83
S. mellifera	26m + 4sm	0.97	2.17	4.44–9.92	21.87	1.46	34.75–45.89	22.13	18.26
S. cardiophylla		0.82	1.61	3.70–7.26	22.19	1.23			
S. cuspidata		1.05	1.88	3.43–6.14	30.63	1.39			
S. splendens	28m + 16sm	0.72	1.38	3.23–6.20	22.26	1.01	27.27–45.79	18.23	23.67
S. subrotunda	2M + 26m + 16sm	0.75	1.42	3.18–6.01	23.62	1.07	25.96–50.00	15.32	21.92
S. microphylla	34m + 12sm	0.78	1.89	2.49–6.03	31.36	1.36	31.53–46.56	19.53	21.43
S. oppositiflora		0.53	1.21	2.31–5.27	22.98	0.82			
S. stolonifera	48m + 12sm	0.81	1.73	2.19–4.69	36.92	1.23	25.49–46.34	18.79	22.40
S. atrocyanea		0.62	1.51	2.23–5.43	27.80	0.93			

DISCUSSION

Table 1 shows the chromosome counts of the investigated species in present and previous studies. The chromosome numbers are the first report for ten species, namely *S. corrugata* (2*n* = 16), *S. curviflora* (2*n* = 16), *S. darcyi*, *S. greggii*, *S. longifolia*, *S. vitifolia* (2*n* = 22), *S. subrotunda* (2*n* = 44), *S. oppositiflora* (2*n* = 56), *S. stolonifera* and *S. atrocyanea* (2*n* = 60). The chromosome numbers are new counts different from previous reports for three species, namely *S. cardiophylla* (2*n* = 36), *S. cuspidata* (2*n* = 44) and *S. microphylla* (2*n* = 46). In literature, the chromosome numbers are 2*n* = 44 for *S. cardiophylla*, 2*n* = 22 for *S. cuspidata* and *S. microphylla* (Haque and Ghoshal 1980; Alberto *et al.* 2003). The chromosome numbers of the other eight species are the same as the previous reports, namely *S. campanulata* (2*n* = 16), *S. elegans* (2*n* = 20), *S. involucrata* and *S. mexicana* (2*n* = 22), *S. apiana*, *S. leucophylla*, and *S. mellifera* (2*n* = 30) and *S. splendens* (2*n* = 44) (Carlson and Stuart 1936; Epling *et al.* 1962; Haque and Ghoshal 1980; Palomino *et al.* 1986; Saggoo and Bir 1986; Cherian and Kuriachan 1990; Alberto *et al.* 2003).

It is already known that genus *Salvia* includes diploids and polyploids (Carlson and Stuart 1936; Epling *et al.* 1962; Haque and Ghoshal 1980; Gill 1984; Alberto *et al.* 2003; Hu *et al.* 2016). With chromosome data available at present, 11 species are diploids with 2*n* = 16, 18, 20, 22, and 46 (probably dysploidy) (c.52% of the species with available data) and 10 species are polyploids (c.48% of the species with available data). When previous and current chromosomal data are compared, four species, *S. campanulata*, *S. cuspidata*, *S. splendens*, and *S. microphylla*, show both diploid and polyploid status (c.19% of the species with available data). This suggests that intraspecific polyploidy may be common in genus *Salvia*. The polyploid nature are demonstrated by the prevalence of cells with 2*n* = 30, 36, 44, 56, and 60 chromosomes in 10 species. Polyploidy originates by autopolyploidy mechanism (genome duplication in a species) and allopolyploidy (genome duplication with hybridization between species) and has played a major role in the speciation and evolution of higher plants (Demirci Kayıran and Özhatay 2017). The polyploidy possibly caused by glacial, climatic changes, altitude and high latitudes may have contributed to *Salvia* specia-

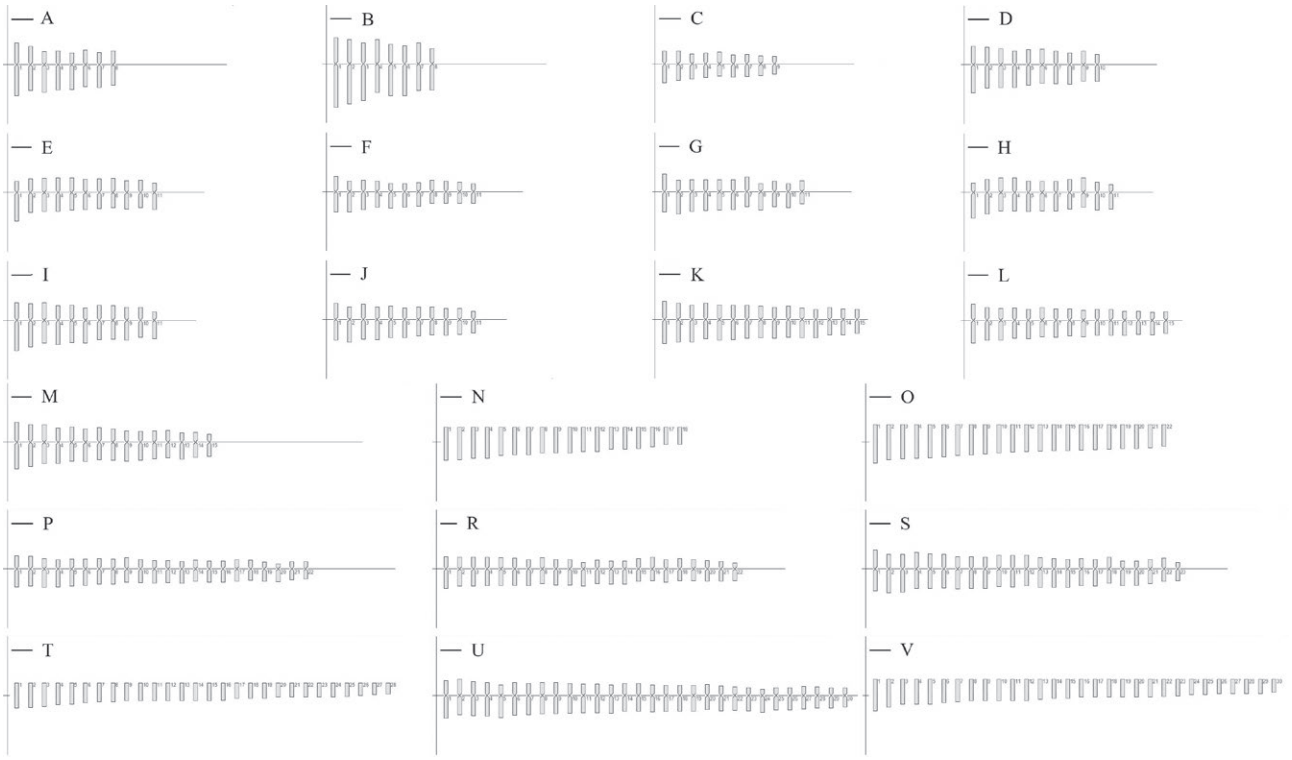

Figure 2. Ideograms of *Salvia*: (A) *S. corrugata*, (B) *S. campanulata*, (C) *S. curviflora*, (D) *S. elegans*, (E) *S. darcyi*, (F) *S. greggii*, (G) *S. involucrata*, (H) *S. longifolia*, (I) *S. vitifolia*, (J) *S. mexicana*, (K) *S. apiana*, (L) *S. leucophylla*, (M) *S. mellifera*, (N) *S. cardiophylla*, (O) *S. cuspidata*, (P) *S. splendens*, (R) *S. subrotunda*, (S) *S. microphylla*, (T) *S. oppositiflora*, (U) *S. stolonifera*, (V) *S. atrocyanea* (scale bars: 1 μm).

tion. Although *Salvia* is a polybasic genus with species of polyploid origin (Sheidai and Alijanpoo 2011), variations are observed resulting from dysploidy shows that different basic numbers with karyotypes that contain one or a few chromosomes more or less than that of the original, occur in a genus. *S. microphylla* has different basic number ($x = 23$) probably with dysploidy. These data indicate that the effects of dysploidy on the lineage diversification of *Salvia* should be investigated further.

In studied species, B-chromosomes, a special type of supernumerary chromosomes and are extra chromosomes other than basic A-chromosomes in diploid and polyploid species, have been reported. The karyotype formulae are 22 + 0-1B in *S. involucrata* and 44 + 0-1B in *S. cardiophylla* and *S. splendens* (Alberto *et al.* 2003). We have not observed B-chromosomes. As a matter of fact, while B-chromosomes do not exist in some individuals of the same population, the others may have different numbers. When the number of B-chromosomes is small, they cannot have a visible effect on the phenotype and their presence can be determined only by cytological examinations. In case of high numbers, they have a negative effect on the development and fertility of plants (Houben 2017).

A symmetric karyotype contains a high proportion of median and submedian chromosomes, unlike an asymmetric karyotype has a high rate of subterminal and terminal chromosomes (Peruzzi and Eroğlu 2013). In intrachromosomal asymmetry, the most symmetrical and asymmetrical karyotype are *S. curviflora* and *S. corrugata*, respectively. The relatively higher asymmetric karyotypes than other species may have been caused by chromosomal structural changes as centric fission or centric fusion observed in especially polyploid and dysploidy species. In interchromosomal asymmetry, the most symmetrical and asymmetrical karyotype are *S. longifolia* and *S. mellifera*, respectively. The relatively higher asymmetric karyotypes than other species may be the result of chromosome rearrangements and may also result in bimodality observed in *S. campanulata*, *S. splendens*, and *S. microphylla*. In these species, the bimodal karyotypes may occur due to loss of chromosomal segments following polyploidy. The symmetric and asymmetric karyotypes are different between intrachromosomal asymmetry and interchromosomal asymmetry with very low positive correlation (r = 0.157) (Figure 3). All studied *Salvia* species contain only median and submedian chromosomes and are symmetrical as a common condition

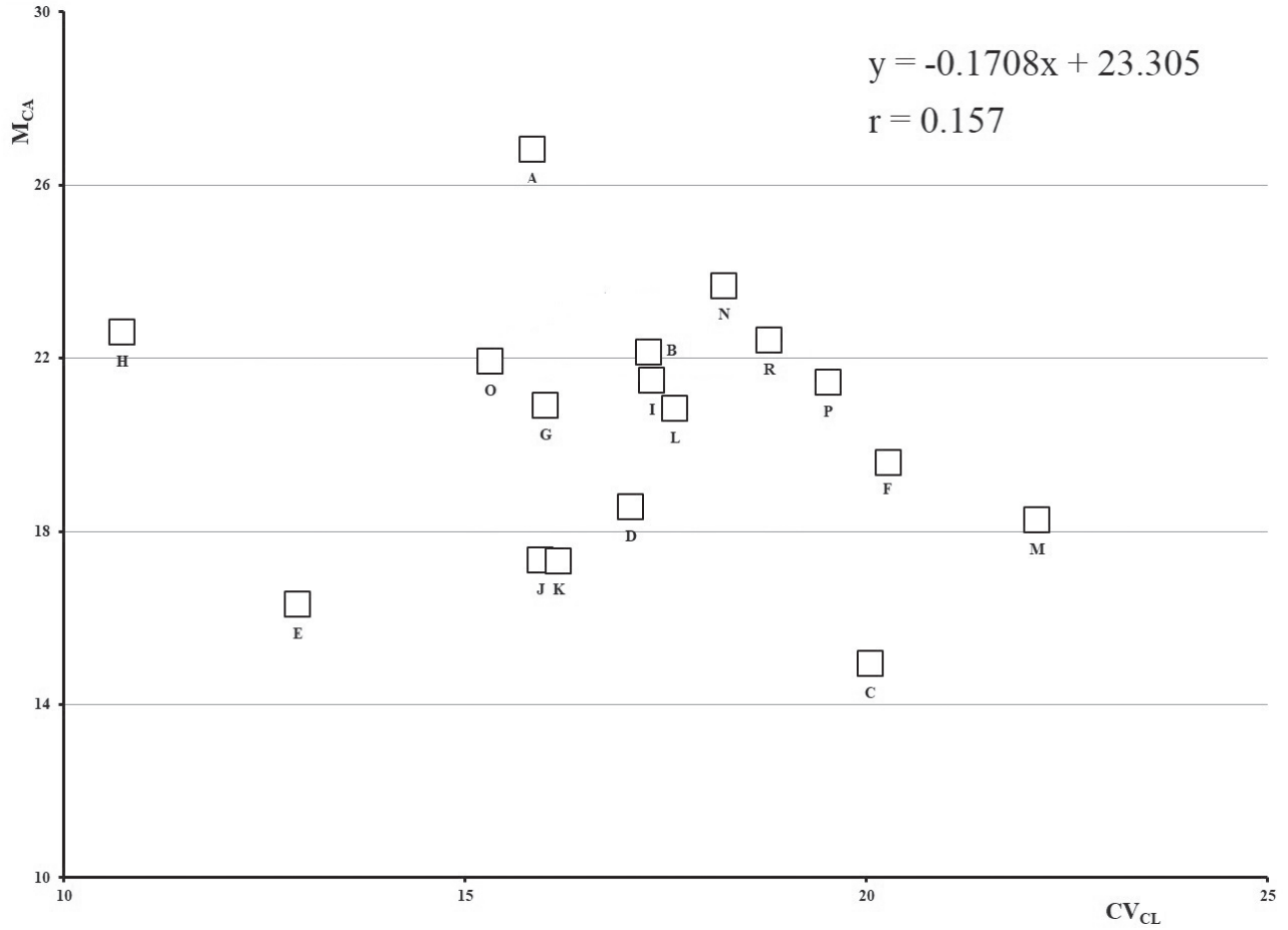

Figure 3. Scatter diagram between M_{CA} and CV_{CL}: (A) *S. corrugata*, (B) *S. campanulata*, (C) *S. curviflora*, (D) *S. elegans*, **(E)** *S. darcyi*, (F) *S. greggii*, (G) *S. involucrata*, (H) *S. longifolia*, **(I)** *S. vitifolia*, (J) *S. mexicana*, (K) *S. apiana*, (L) *S. leucophylla*, (M) *S. mellifera*, **(N)** *S. splendens*, (O) *S. subrotunda*, (P) *S. microphylla*, (R) *S. stolonifera*.

in genus *Salvia* (Sheidai and Alijanpoo 2011; Doğan *et al.* 2019). On the contrary, Hu *et al.* (2016) reported that *S. bulleyana* Diels, *S. digitaloides* Diels and *S. przewalskii* Maxim. had asymmetrical karyotypes.

In this study, it was aimed to determine the chromosome number of 21 *Salvia* species, to determine chromosome morphology, to reveal karyotype analysis in detail and to contribute to the cytotaxonomy of *Salvia*. In this context, the results are as follows: (i) the first report for the number of chromosomes of ten species, (ii) the karyotypic variations and new chromosome numbers different from previous reports for three species, (iii) the detailed chromosome measurements and karyotype analyses for all species studied for the first time, (iv) the symmetrical karyotypes for all studied species, (v) the variations resulting from dysploidy or polyploidy and discussing their reasons. On the other hand, the genus *Salvia* is one of the largest in the world with about 1000 species. The results of such studies provide important data supports for *Salvia* cytotaxonomy. It is an important issue that combining all supporting data with further comparative studies and integrating them into morphological data.

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