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Karyotype studies on the genus *Origanum* L. (Lamiaceae) species and some hybrids defining homoploidy

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Abstract. In this study, chromosome numbers and structures of some *Origanum* L. taxa growing in Turkey were identified. Using the Image Analysis System, the complements of plant accessions belonging to eight sections, namely *Amaracus* (Gleditsch) Vogel, *Anatolicon* Benth., *Brevifilamentum* Ietsw., *Longitubus* Ietsw., *Chilocalyx* (Briq.) Ietsw., *Majorana* (Miller) Ietsw., *Origanum*, and *Prolaticorolla* Ietsw. were determined, by classification with the cytogenetic method. The chromosome number of all taxa except *O. sipyleum* L. ($2n = 28$) and *O. rotundifolium* Boiss. ($2n = 28$) is $2n = 30$. In addition, the hybrids and their parental species have $2n = 30$ chromosome numbers. Also, the smallest chromosome length is 0.32 μm in *O. sipyleum*. The largest chromosome length is 2.02 μm in *O. minutiflorum* O.Schwarz & P.H.Davis. The smallest total haploid length is 10.08 μm in *O. vulgare* subsp. *hirtum* (Link) A.Terracc. and the largest value is 22.00 μm in *O. haussknechtii* Boiss. The smallest mean length is 0.33 μm in *O. vulgare* L. subsp. *hirtum* and *O. saccatum* P.H.Davis. The largest mean length is 0.74 μm in *O. sipyleum* L. The chromosome numbers obtained in this study support the speciation of *Origanum* members via homoploid hybridization. Finally, the somatic chromosome numbers of 10 taxa (including 2 hybrids), chromosome measurements of 22 taxa (including 2 hybrids), and ideograms of 19 taxa (including 2 hybrids) were for the first time performed in this study.

Keywords: chromosome, hybrid, karyotype, Lamiaceae, *Origanum*.

INTRODUCTION

The genus *Origanum* L. is placed in the family Lamiaceae, subfamily Nepetoideae, tribe Mentheae, subtribe Menthineae, contains 43 species and 20 hybrids (Ietswaart 1980, 1982; Govaerts *et al.* 2013; Dirmenci *et al.* 2018a, 2018b, 2019). Approximately, 21 species (24 taxa, including 13 endemic) and

13 hybrids are reported from the Turkey (Ietswaart 1982; Davis *et al.* 1988; Duman 2000; Dirmenci *et al.* 2018a, 2018b, 2019). Majority of the species are found in Mediterranean basin and 75% of them are only found in Eastern Mediterranean region. Some species are distributed in the Middle East (Syria and Lebanon), North Africa (Algeria, Libya and Morocco) and the Canary Islands (Ietswaart 1980, 1982). The genus *Origanum* contains ten sections, eight of them are distributed in Turkey (Ietswaart 1980). The species are mostly distributed along the Taurus Mountains in Turkey.

Recently, the use of the Image Analysis System in karyotyping of plant taxa having small and indistinguishable somatic chromosomes (Fukui 1986, 1998; Fukui and Iijima 1991; Iijima *et al.* 1991) has drawn the attentation for study chromosome morphology in *Origanum*. Literature studies belonging to the genus *Origanum* have revealed that there are too few karyotype analyses of this genus. The lack of sufficient data on the karyomorphology of the genus is probably due to the small size of its chromosomes. The chromosome numbers are $2n$ = 28, 30 and 32 (Ietswaart 1980; Gill 1970, 1981, 1981a 1984; Saggoo 1983; Magulaev 1984; Ayyangar and Vembu 1985; Krasnikov and Schaulo 1990; Wentworth *et al.* 1991; Khatoon and Ali 1993; Stepanov and Muratova, 1995; Dobea *et al.* 1997; Kıtıkı 1997; Balım and Kesercioğlu 1998; Albers and Pröbsting 1998; Lövkvist and Hultgård 1999; Yıldız and Gücel 2006; Dirmenci *et al.* 2018a, 2018b, 2019) in the genus *Origanum*.

The hybridization is a widespread phenomenon among *Origanum* species. It usually occurs in the regions where the distribution of the species overlaps. The overlappings can occur in natural habitat or botanical gardens. Because of interspecific hybridization, so far 19 hybrids have been identified in the genus. It was reported that the chromosome number of some hybrids was $2n$ = 30 (Bakha *et al.* 2017; Dirmenci *et al.* 2018a, 2018b, 2019). These results support the idea that the origin of the hybridization in *Origanum* is probably homoploidy.

The main aims of this study are to contribute to the cytotaxonomy of *Origanum* with the following marks: 1- to define the karyotypes of some *Origanum* specimens for the first time, 2- to verify the homoploidy in the *Origanum* genus, 3- to present the chromosomal differences of the *Origanum* species, 4- to observe the chromosome structure of the hybrids and their parents in *Origanum*.

MATERIALS AND METHODS

Plant materials used in this study were collected between 2013 and 2017 and collected specimens were deposited in Balıkesir University. Voucher numbers and collection information of the examined specimens were given in the appendix section. The seeds were germinated at room temperature. All karyological observations were carried out on root tips. Firstly, the root tips were pretreated for 16 h in α-monobromonaphthalene at 4°C, fixed in 3:1 absolute alcohol/glacial acetic acid, then hydrolyzed with 1 N HCl for 12 min at room temperature and stained with 2% aceto-orcein for 3 h at room temperature. Stained root tips were squashed in a drop of 45% acetic acid, and permanent slides were made by mounting in Depex (Martin *et al.* 2016). The five metaphase plates from each species were used to obtain chromosomal data using an Olympus microscope and the chromosomal data were measured with software image analyses (Bs200ProP). Chromosome lengths were made by nomenclature following Levan *et al.* (1964).

RESULTS

Sect. *Amaracus* (Gleditsch) Benth.

The chromosome numbers of *Origanumayliniae* Dirmenci & Yazıcı, *O. boissieri* Ietsw., *O. saccatum* P.H.Davis, and *O. solymicum* P.H.Davis are $2n$ = 30 (Figure 1A-D, Table 1). The smallest chromosome length is 0.39 µm in *O. saccatum* (no. TD4522). The largest chromosome length is 1.94 µm in *O. boissieri* (no. TD4319). The smallest total haploid length is 10.13 µm in *O. saccatum* (no. TD4522), and the largest value is 19.74 µm in *O. boissieri* (no. TD4319).

The chromosome morphologies of *Origanum ayliniae*, *O. boissieri*, *O. saccatum*, and *O. solymicum* are described for the first time in this study.

Sect. *Anatolicon* Benth.

The chromosome numbers of *Origanum hypericifolium* P.H.Davis is $2n$ = 30, and *O. sipyleum* L. has two different counts as $2n$ = 28 and 2n = 30 (Figure 1E-F, Table 1). The smallest chromosome length is 0.32 µm in *O. sipyleum* (no. TD4308). The largest chromosome length is 2.00 µm in *O. sipyleum* (no. TD4517). The smallest total haploid length is 10.46 µm in *O. sipyleum* (no. TD4522) and the largest value is 20.98 µm in *O. sipyleum* (no. TD4308).

The chromosomes morphologies of *Origanum hypericifolium* are described for the first time.

The chromosome number of *Origanum sipyleum* is mostly $2n$ = 30 in a biosystematic study performed by

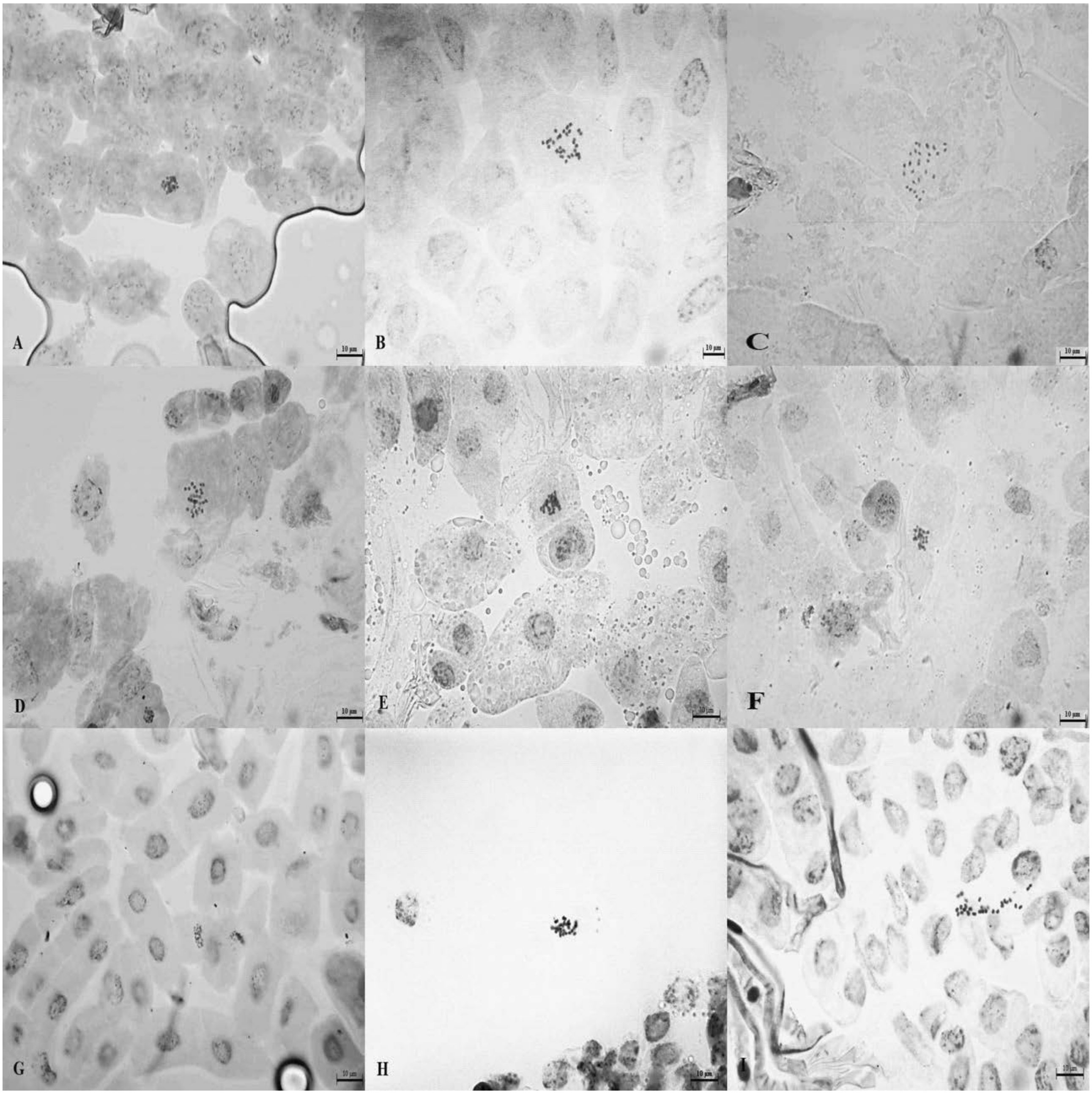

Figure 1A-I. Somatic metaphase chromosomes of *Origanum* taxa: **A)** *O. ayliniae* (TD4516) **B)** *O. boissieri* (TD4319); **C)** *O. saccatum* (TD4732); **D)** *O. solymicum* (TD4347); **E)** *O. hypericifolium* (TD4357); **F)** *O. sipyleum* (TD4727); **G)** *O. acutidens* (TD4956a); **H)** *O. brevidens* (TD4331); **I)** *O. haussknechtii* (TA2824). Scale bar: 10 µm.

Kıtıkı 1997 (Table 2). The diploid number of no. 4308 is $2n = 28$ as different from the literature (Table 2). While the number of chromosomes of *O. sipyleum* is included in the literature, the chromosome morphologies of the species have been demonstrated for the first time in this study.

Sect. *Brevifilamentum* Ietsw.

The chromosome numbers of *Origanum acutidens* (Hand.-Mazz.) Ietsw. (no. TD4956a), *O. brevidens* Bornm. Dinsm. (no. TD4331), *O. haussknechtii* Boiss. (no. TD2824), *O. husnucan-baseri* H.Duman, Aytaç & A.Duran, (no. TD4528), and *O. leptocladum* Boiss. (no. TD4345), $2n = 30$ (Figure 1G-K, Table 1). The chromo-

Table 1. Chromosome counts and size of species and hybrids of *Origanum* determined in the study.

Section	Taxa	Chromosome Number (2n)	Chromosome length (µm) min-max	Total haploid length (µm)	Mean chromosome length (µm)
Amaracus	*O. ayliniae* TD 4516	30	0.83-1.72	18.35	0.61
	O. boissieri TD 4319	30	0.78-1.94	19.74	0.65
	O. boissieri TD 4501	30	0.47-1.61	14.48	0.48
	O. solymicum TD 4347	30	0.45-1.59	16.22	0.54
	O. solymicum TD 4520	30	0.40-1.26	12.16	0.40
	O. saccatum TD 4342	30	0.53-1.75	17.17	0.55
	O. saccatum TD 4522	30	0.39-1.12	10.13	0.33
	O. saccatum TD 4732	30	0.60-1.46	14.77	0.49
Anatolicon	*O. hypericifolium* TD 4357	30	0.34-1.36	13.80	0.40
	O. sipyleum TD 4308	28	0.79-2.00	20.98	0.74
	O. sipyleum TD 4352	30	0.53-1.59	14.19	0.47
	O. sipyleum TD 4534	30	0.39-1.52	13.32	0.44
	O. sipyleum TD 4517	30	0.32-1.11	10.46	0.34
	O. sipyleum TD 4727	30	0.49-1.08	11.26	0.37
Brevifilamentum	*O. brevidens* TD 4331	30	0.50-1.63	14.67	0.49
	O. haussknechtii TD 2824	30	0.99-2.00	22.00	0.73
	O. husnucan-baseri TD 4528	30	0.56-1.79	14.88	0.49
	O. leptocladum TD 4345	30	0.49-1.63	15.27	0.50
	O. rotundifolium TD 3943	28	0.57-1.82	16.497	0.58
Chilocalyx	*O. bilgeri* TD 4343	30	0.38-1.58	14.25	0.47
	O. minutiflorum TD 4348	30	0.69-2.02	19.01	0.63
Longitubus	*O. amanum* TD 4514-a	30	0.73-1.91	16.92	0.56
Majorana	*O. majorana* TD 3984	30	0.50-1.58	17.25	0.57
	O. majorana TD 4356	30	0.43- 1.84	17.35	0.57
	O. majorana TD 4346	30	0.43-1.54	14.44	0.48
	O. onites TD 4355	30	0.50-1.77	15.93	0.53
	O. onites TD 4725	30	0.63-1.27	15.14	0.50
	O. onites TD 4532	30	0.43-1.26	13.45	0.44
	O. syriacum subsp. *bevanii* TD 4336	30	0.53- 1.58	16.26	0.54
	O. syriacum subsp. *bevanii* TD 4330	30	0.49-1.13	11.02	0.36
Origanum	*O. vulgare* subsp. *hirtum* TD 4733	30	0.58-1.14	13.22	0.44
	O. vulgare subsp. *hirtum* TD 4722	30	0.49-1.22	13.32	0.44
	O. vulgare subsp. *hirtum* TD 4359	30	0.40-1.07	10.08	0.33
	O. vulgare subsp. *vulgare* TD 4688	30	0.56-1.18	12.73	0.42
Prolaticorolla	*O. laevigatum* TD 4497	30	0.45-1.96	16.34	0.54
Hybrids	*O.* × *intermedium* TD 4726	30	0.46-1.14	11.62	0.38
	O. × *adae* TD 4518	30	0.72-1.40	15.47	0.51

some number of *O. rotundifolium* Boiss. (no. TD3943), $2n = 28$ (Figure 1L, Table 1). The smallest chromosome length is 0.49 µm in *O. leptocladum*. The largest chromosome length is 2.00 µm in *O. haussknechtii*. The smallest total haploid length is 14.67 µm in *O. brevidens* and the largest value is 22.00 µm in *O. haussknechtii*.

The chromosomes morphologies of *Origanum acutidens*, *O. brevidens*, *O. haussknechtii*, *O. husnucan-baseri*, *O. leptocladum*, and *O. rotundifolium* are described for the first time.

Sect. *Chilocalyx* (Briq.) Ietsw.

The chromosome numbers of *Origanum bilgeri* P.H.Davis (no. TD4343), *O. minutiflorum* O.Schwarz & P.H.Davis (no. TD4348) and *O. vogelii* Greuter & Burdet (no. TD4509) are $2n = 30$ (Figure 1M-O, Table 1). The smallest chromosome length is 0.38 µm in *O. bilgeri*. The largest chromosome length is 2.02 µm in *O. minutiflorum*. The smallest total haploid length is 14.25 µm in *O. bilgeri* and the largest value is 19.01 µm in *O. minutiflorum*.

Table 2. Chromosome counts of species and hybrids of *Origanum* according to references.

Section	Species	Chromosome numbers (2n)	References
Amaracus	*O. ayliniae*	30	(Dirmenci *et al.* 2018a)
	O. boissieri	30	(Dirmenci *et al.* 2018b, Kıtıkı *et al.*, 1997)
	O. calcaratum.	30	(Von Bothmer, 1970)
	O. dictamnus	30	(Lepper, 1970)
	O. solymicum	30	(in this study; Kıtıkı *et al.*, 1997)
	O. saccatum	30	(in this study; Kıtıkı *et al.*, 1997)
Anatolicon	*O. hypericifolium*	30	(in this study)
	O. sipyleum	30 28	(Kıtıkı *et al.*, 1997) (in this study)
Brevifilamentum	*O. acutidens*	30	(Dirmenci *et al.* 2019)
	O. brevidens	30	(in this study)
	O. haussknechtii	30	(in this study)
	O. husnucan-baseri	30	(in this study)
	O. leptocladum	30	(in this study)
	O. rotundifolium	28	(in this study)
Chilocalyx	*O. bilgeri*	30	(in this study)
	O. minutiflorum	30	(in this study)
	O. vogelii	30	(in this study)
Elongatispica	*O. elongatum*	30	(Bastida and Talavera, 1994; Bakha *et al.*, 2017)
	O. grosii	30	(Bakha *et al.*, 2017)
Longitubus	*O. amanum*	30	(in this study; Lepper 1970)
Majorana	*O. majorana*	30	(in this study; Harriman, 1975; Májovský, 1978; Fernandes and Leitão, 1984; Balim and Kesercioğlu, 1998)
	O. onites	30	(in this study; Von Bothmer, 1970; Miege and Greuter, 1973; Ietswaart, 1980; Montmollin, 1986; Kıtıkı *et al.*, 1997; Bakha *et al.*, 2017)
	O. syriacum subsp. *bevanii*	30	(in this study; Balim and Kesercioğlu, 1998; Yildiz and Gücel, 2006)
Origanum	*O. vulgare*	28	(Magulaev, 1984)
	O. vulgare	30	(Skalinska *et al.*, 1971; Krasnikov and Schaulo, 1990; Stepanov and Muratova, 1995; Lövkvist and Hultgård, 1999)
	O. vulgare	32	(Ayyangar and Vembu, 1985)
	O. vulgare subsp. *hirtum*	30	(Strid and Franzen, 1981; Markova and Goranova, 1995; Dirmenci *et al.* 2018b)
	O. vulgare subsp. *gracile*	30	(Astanova, 1981; Dirmenci *et al.* 2019)
	O.vulgare subsp. *virens*	30	(Fernandes and Leitão, 1984; Pastor *et al.* 1990; Bakha *et al.*, 2017)
	O. vulgare subsp. *viride*	30	(in this study; Strid and Franzen 1981)
	O. vulgare subsp. *viridulum*	30	(Strid and Franzen, 1981; Markova and Goranova, 1995)
	O. vulgare subsp. *vulgare*	28	(Magulaev, 1984)
	O. vulgare subsp. *vulgare*	30	(in this study; Gill, 1981, 1981a; Saggoo, 1983; Bir and Saggoo, 1984; Gill, 1984; Krasnikov and Schaulo, 1990; Wentworth *et al.*, 1991; Khatoon and Ali, 1993; Stepanov and Muratova, 1995; Dobea *et al.*, 1997; Albers and Pröbsting, 1998; Lövkvist and Hultgård, 1999)
	O. vulgare subsp. *vulgare*	32	(Ayyangar and Vembu, 1985)
Prolaticorolla	*O. compactum*	30	(Bakha *et al.*, 2017)
	O. laevigatum	30	(Balim and Kesercioğlu, 1998)
Hybrids	*O.* × *adae*	30	(Dirmenci *et al.* 2018a)
	O. × *font-queri*	30	(Bakha *et al.*, 2017)
	O. × *haradjanii*	30	(in this study)
	O. × *intermedium*	30	(in this study)
	O. × *munzurense*	30	(Dirmenci *et al.* 2019)
	O. × *sevcaniae*	30	(Dirmenci *et al.* 2018b)

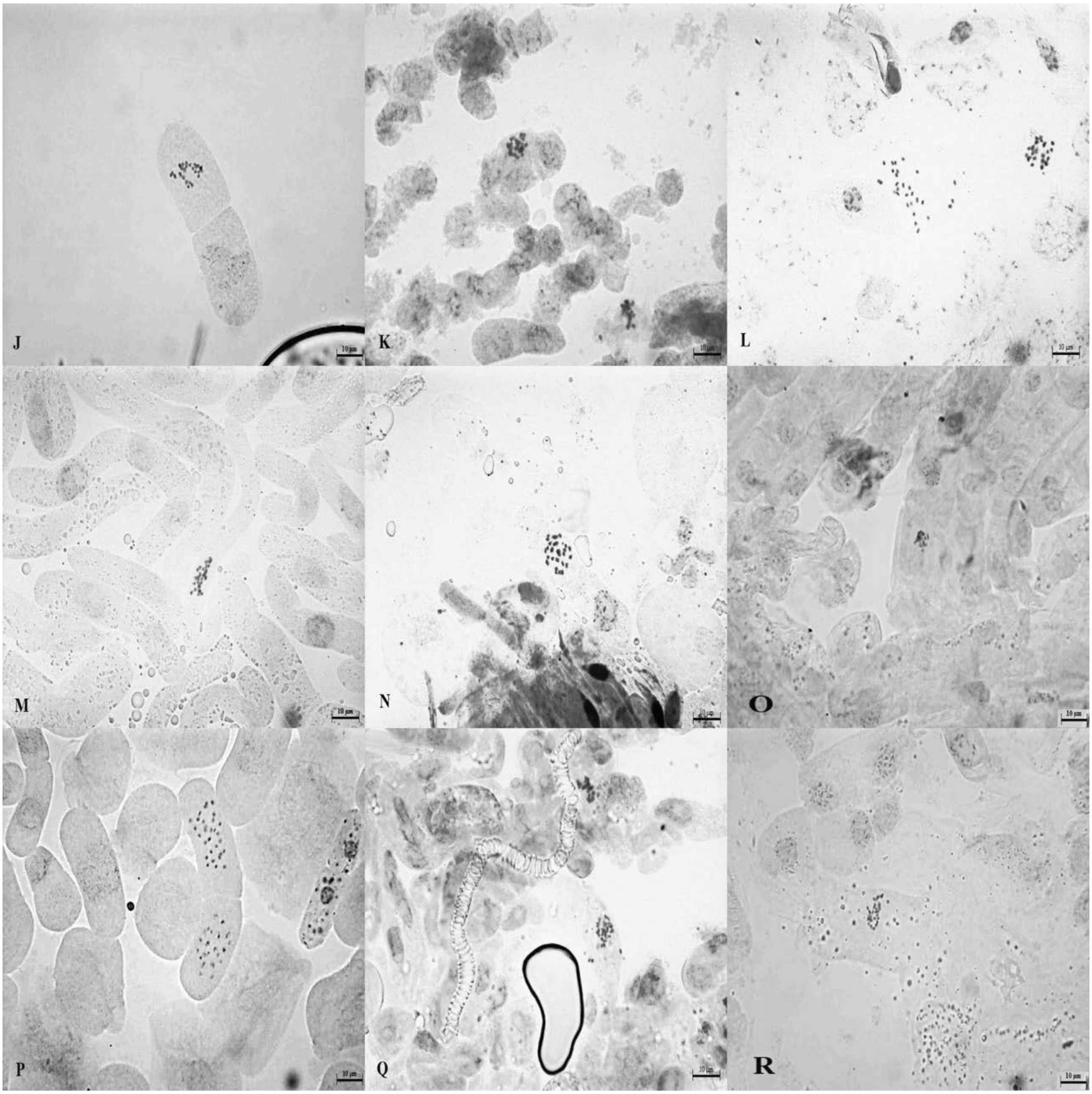

Figure 1J-R. Somatic metaphase chromosomes of *Origanum* taxa: **J)** *O. husnucan-baseri* (TD4528); **K)** *O. leptocladum* (TA4345); **L)** *O. rotundifolium* (TD3943); **M)** *O. bilgeri* (TD4343); **N)** *O. minutiflorum* (TD4348); **O)** *O. vogelii* (TD4509); **P)** *O. amanum* (TD4514a); **Q)** *O. majorana* (TD3984); **R)** *O. onites* (TD4725). Scale bar: 10 µm.

The chromosome morphologies of *O. bilgeri*, *O. minutiflorum*, and *O. vogelii* are described for the first time.

Sect. *Longitubus* Ietsw.

Sect. *Longitubus* contains only one species. The chromosome number of *Origanum amanum* Post (no. TD4514a) is $2n = 30$ (Figure 1P, Table 1). Ietswaart (1980) reported that the chromosome number of *O. amanum* was $2n = 30$ (Table 2). The chromosome

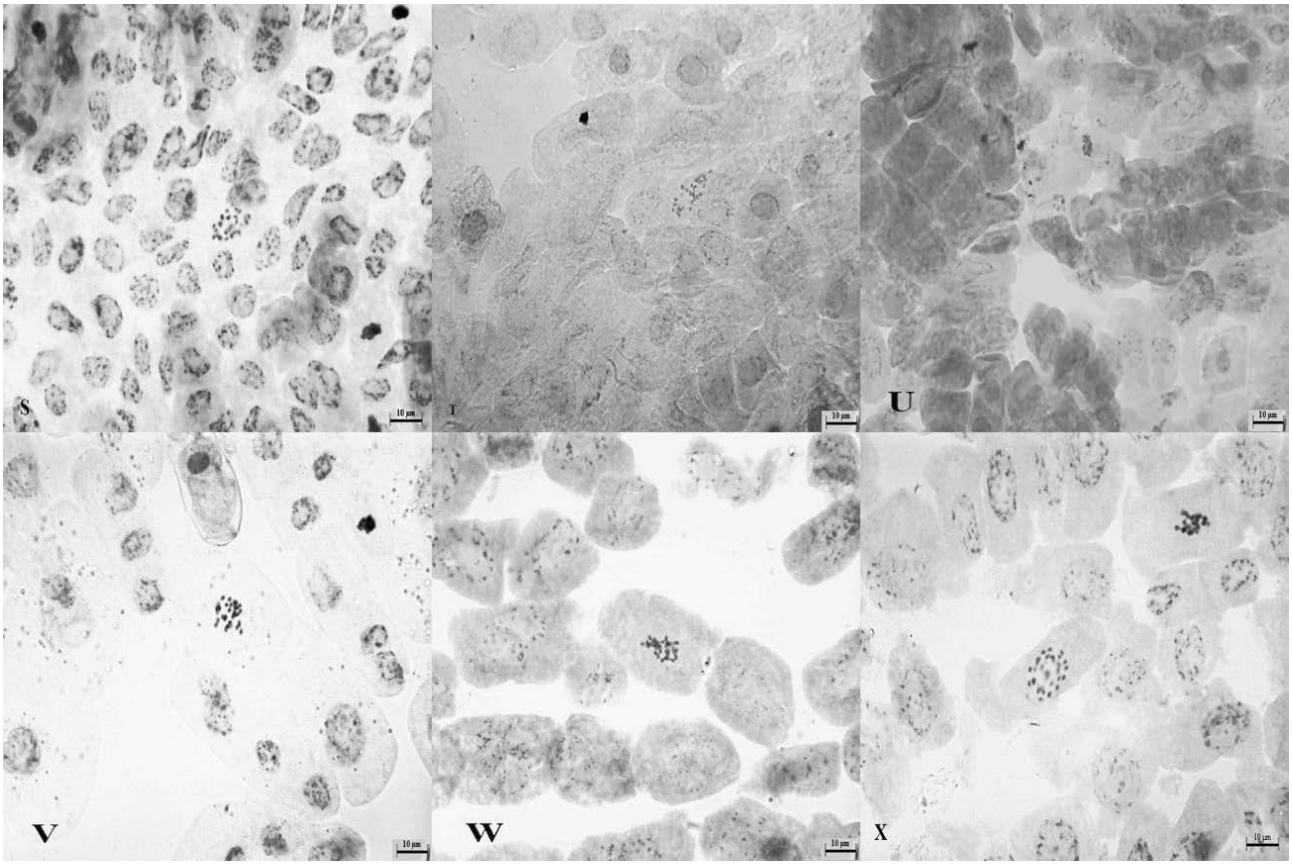

Figure 1S-X. Somatic metaphase chromosomes of *Origanum* taxa: **S)** *O. syriacum* subsp. *bevanii* (TD4336); **T)** *O. vulgare* subsp. *gracile* (TD4821); **U)** *O. vulgare* subsp. *hirtum* (TD4507); **V)** *O. vulgare* subsp. *viridulum* (TD4662a); **W)** *O. vulgare* subsp. *vulgare* (TD4688); **X)** *O. laevigatum* (TD4497). Scale bar: 10 µm.

lengths range from 0.73 to 1.91 µm. The chromosome morphologies of *O. amanum* are described for the first time.

Sect. *Majorana* (Mill.) Benth.

The chromosome numbers of *Origanum majorana* L. (no. TD3984), *O. onites* L. (no. TD4725), and *O. syriacum* L. subsp. *bevanii* (Holmes) Greuter & Burdet (no. TD4336) are $2n = 30$ (Figure 1Q-S, Table 1). The smallest chromosome length is 0.43 µm in *O. majorana* and *O. onites* (no. 4356, 4346, and 4532). The largest chromosome length is 1.84 µm in *O. majorana* (no. 4356). The smallest total haploid length is 11.02 µm in *O. syriacum* subsp. *bevanii* (no. 4330), and the largest value is 17.35 µm in *O. majorana* (no. 4356).

It was reported that the chromosome number of *Origanum onites* and *O. majorana* was $2n = 30$ (Ietswaart 1980; Kıtıkı 1997; Balım and Kesercioğlu 1998) (Table 2). The number of chromosomes we obtained overlapped with the literature. In addition to the chromosome numbers of taxa, chromosome measurements are also introduced to the scientific world.

Sect. *Origanum*

The chromosome numbers of *Origanum vulgare* L. subsp. *gracile* (K.Koch) Ietsw. (no. TD4821), *O. vulgare* subsp. *hirtum* (Link.) A.Terracc. (no. TD4507), *O. vulgare* subsp. *viridulum* (Matrin-Dones) Nyman (no. TD4662a), and *O. vulgare* subsp. *vulgare* (no. TD4688) are $2n = 30$ (Figure 1T-W, Table 1). The smallest chromosome length is 0.40 µm in *O. vulgare* subsp. *hirtum* (no. TD4359). The largest chromosome length is 1.22 µm in *O. vulgare* subsp. *hirtum* (no. TD4722). The smallest total haploid length is 10.08 µm in *O. vulgare* subsp. *hirtum* (no. TD4359) and the largest value is 13.32 µm in *O. vulgare* subsp. *hirtum* (no. TD4722).

It was reported that the chromosome numbers of *Origanum vulgare*, *O. vulgare* subsp. *hirtum*, *O. vulgare* subsp. *viride*, and *O. vulgare* subsp. *viridulum* are 2*n* = 28, 30 and 32 (Ietswaart 1980; Strid and Franzen 1981; Gill 1981a, 1984; Saggoo 1983; Bir and Saggoo 1984; Magulaev 1984; Ayyangar and Vembu 1985; Krasnikov and Schaulo 1990; Wentworth *et al.* 1991; Khatoon and Ali 1993; Stepanov and Muratova 1995; Markova and Goranova 1995; Dobea *et al.* 1997; Kıtıkı 1997; Albers and Pröbsting 1998; Lövkvist and Hultgård 1999; Dirmenci *et al.* 2018b) (Table 2).

The chromosome morphologies of *Origanum vulgare* subsp. *gracile* are described for the first time. In addition, the detailed chromosome lengths are given for *O. vulgare* subsp. *gracile*, *O. vulgare* subsp. *hirtum*, *O. vulgare* subsp. *viridulum*, and *O. vulgare* subsp. *vulgare*.

Sect. *Prolaticorolla* Ietsw.

Sect. *Prolaticorolla* contains only one species in Turkey. The chromosome number of *Origanum laevigatum* Boiss. is 2*n* = 30 (Figure 1X, Table 1). The chromosome lengths range from 0.45 to 1.96 µm (no. TD4497). The chromosome number of *O. laevigatum* is given for the first time.

The chromosome counts and morphologies of the hybrids and their parents

***Origanum* × *adae* Dirmenci & Yazıcı (*O. ayliniae* × *O. sipyleum*)**

The chromosome number of *Origanum* × *adae* is 2*n* = 30 (Table 1). The chromosome lengths range from 0.72 to 1.40 µm. The total haploid length is 15.47 µm (no. TD4518). The chromosome lengths of *O. ayliniae* range from 0.83 to 1.72 µm. The total haploid length is 18.35 µm (no. TD4516). The chromosome lengths of *O. sipyleum* range from 0.32 to 1.11 µm. The total haploid length is 10.46 µm (no. TD4517).

According to the karyological results, the chromosome numbers of *Origanum* × *adae*, *O. ayliniae*, and *O. sipyleum* are similar with *n* = 15 for the haplotype (Figure 2A-C). Karyological analyses support the idea that *Origanum* ×*adae*, is a natural hybrid, is generated from crossed homoploidy of *O. ayliniae* and *O. sipyleum*. The hybrid is generated by homoploid hybridization (all taxa have 2*n* = 30 chromosomes) (Dirmenci *et al.* 2018a).

The chromosome morphologies of *Origanum* ×*adae* and *O. ayliniae*, and *O. sipyleum* are described for the first time.

***Origanum* × *haradjanii* Rech.f. (*O. syriacum* subsp. *bevanii* × *O. laevigatum*)**

The chromosome number of *Origanum* × *haradjanii* is 2*n* = 30 (no. TD4335). The chromosome lengths of *O. syriacum* subsp. *bevanii* range from 0.53 to 1.58 µm. The total haploid length is 16.26 µm. (no. TD4336). The chromosome lengths of *O. laevigatum* range from 0.45 to 1.96 µm. The total haploid length is 16.34 *µm* (no. TD4497).

According to the karyological results, the chromosome numbers of *Origanum* × *haradjanii, O. laevigatum*, and *O. syriacum* subsp. *bevanii* are similar with *n* = 15 for the haplotype (Figure 2D-F). Karyological analyses support the idea that *O.* × *haradjanii*, is a natural hybrid, is generated from crossed homoploidy of *O. syriacum* subsp. *bevanii* and *O. laevigatum*. The hybrid is generated by homoploid hybridization (all taxa have 2*n* = 30 chromosomes).

The chromosome number of *O.* × *haradjanii* is first reported. In addition, the chromosome morphologies of *O. syriacum* subsp. *bevanii* and *O. laevigatum* are described for the first time.

***Origanum* × *intermedium* P.H.Davis (*O. onites* × *O. sipyleum*)**

The chromosome number of *Origanum* × *intermedium* is 2*n* = 30. The chromosome lengths range from 0.46 to 1.14 µm. The total haploid length is 11.62 µm (no. TD4726). The chromosome lengths of *O. sipyleum* range from 0.49 to 1.08 µm. The total haploid length is 11.26 µm (no. TD4727). The chromosome lengths of *O. onites* range from 0.49 to 1.08 µm. The total haploid length is 11.26 µm (no. TD4725).

According to the karyological results, the chromosome numbers of *Origanum* × *intermedium*, *O. onites*, and *O. sipyleum* are similar with *n* = 15 for the haplotype (Figure 2G-I). Karyological analyses support the idea that *O.* × *intermedium*, is a natural hybrid, is generated from crossed homoploidy of *O. onites* and *O. sipyleum*. The hybrid is generated by homoploid hybridization (all taxa have 2*n* = 30 chromosomes).

The chromosome number and morphologies of *Origanum* × *intermedium* are described for the first time.

***Origanum* × *sevcaniae* Dirmenci, Arabacı & Yazıcı (*O. vogelii* × *O. vulgare* subsp. *hirtum*)**

The chromosome number of *Origanum* × *sevcaniae* is 2*n* = 30 (no. TD4508). According to the karyological results, the chromosome numbers of *O.* × *sevcaniae*, *O. vogelii* and *O. vulgare* subsp. *hirtum* are similar with *n* = 15 for the haplotype (Figures 2J-L). Karyological analyses support the idea that *Origanum* × *sevcaniae*, is a natural hybrid, is generated from crossed homoploidy of *O. vogelii* and *O. vulgare* subsp. *hirtum*. The hybrid is generated by homoploid hybridization (all taxa have 2*n* = 30 chromosomes) (Dirmenci *et al.* 2018b).

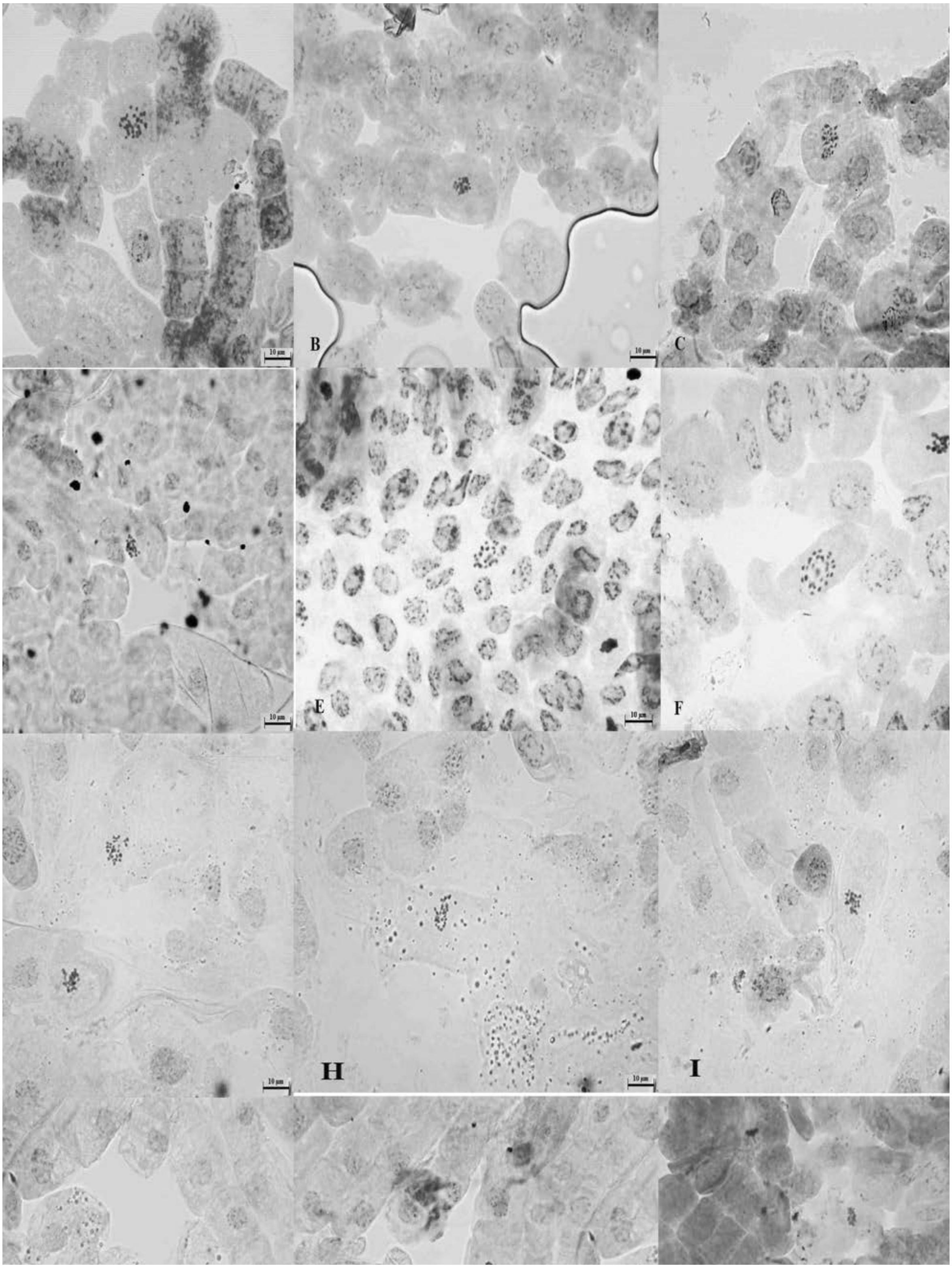

Figure 2A-L. Somatic metaphase chromosomes of hybrids and their parents: **A)** *O.* × *adae* (TD4518); **B)** *O. ayliniae* (TD4516); **C)** *O. sipyleum* (TD4517); **D)** *O.* × *haradjanii* (TD4335); **E)** *O. syriacum* subsp. *bevanii* (TD4336); **F)** *O. laevigatum* (TD4497); **G)** *O.* × *intermedium* (TD4726); **H)** *O. onites* (TD4725); **I)** *O. sipyleum* (TD4727); **J)** *O.* × *sevcaniae* (TD4508); **K)** *O. vogelii* (TD4509); **L)** *O. vulgare* subsp. *hirtum* (TD4507). Scale bar: 10 µm.

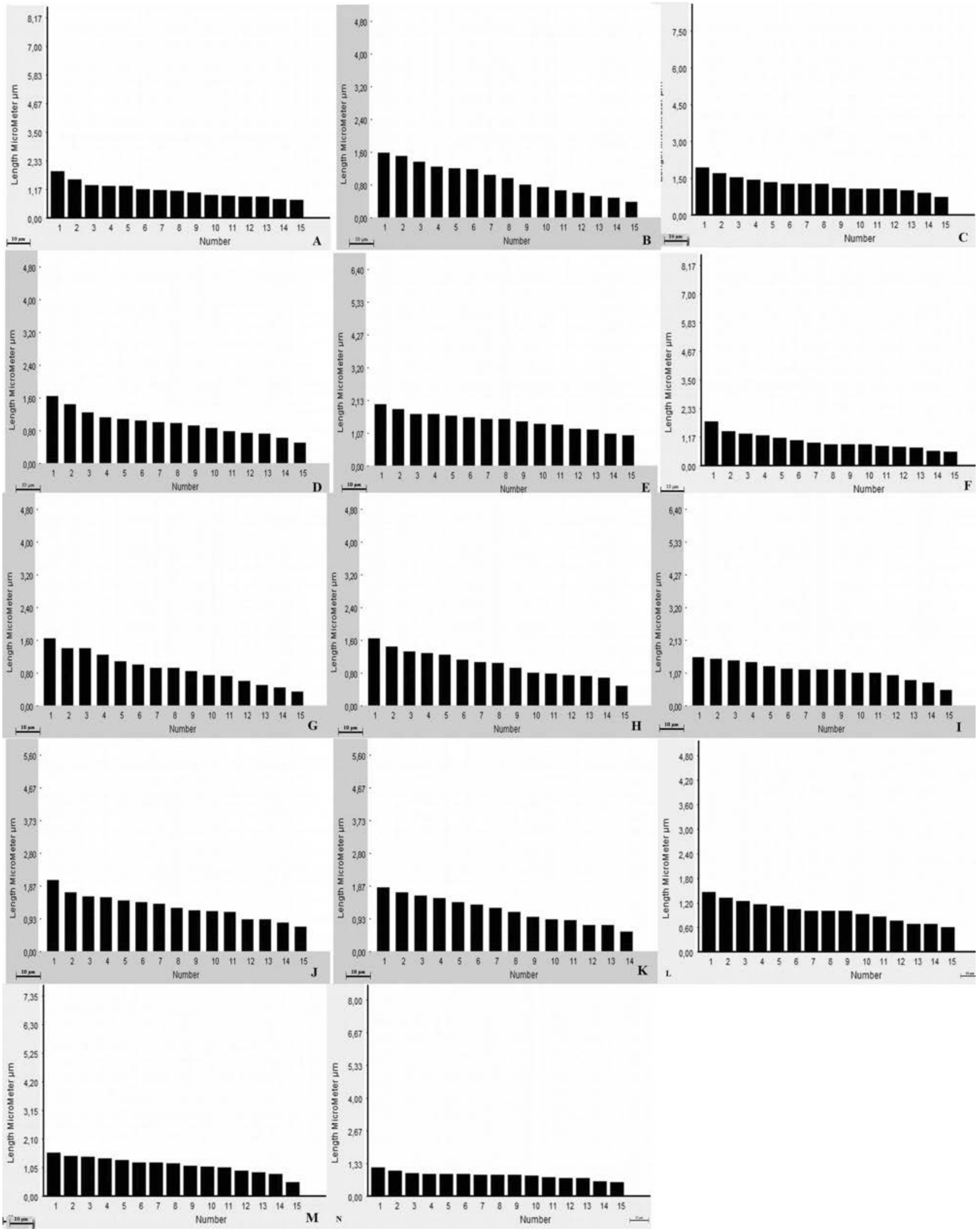

Figure 3A-N. Ideograms of *Origanum* taxa: **A)** *O. amanum* (TD4514a); **B)** *O. bilgeri* (TD4343); **C)** *O. boissieri* (TD4319); **D)** *O. brevidens* (TD4331); **E)** *O. haussknechtii* (TA2824); **F)** *O. husnucan-baseri* (TD4528); **G)** *O. hypericifolium* (TD4357); **H)** *O. leptocladum* (TD4345); **I)** *O. majorana* (TD3984); **J)** *O. minutiflorum* (TD4348); **K)** *O. rotundifolium* (TD3943); **L)** *O. saccatum* (TD4732); **M)** *O. solymicum* (TD4347); **N)** *O. vulgare* subsp. *vulgare* (TD4688). Scale bar: 10 µm.

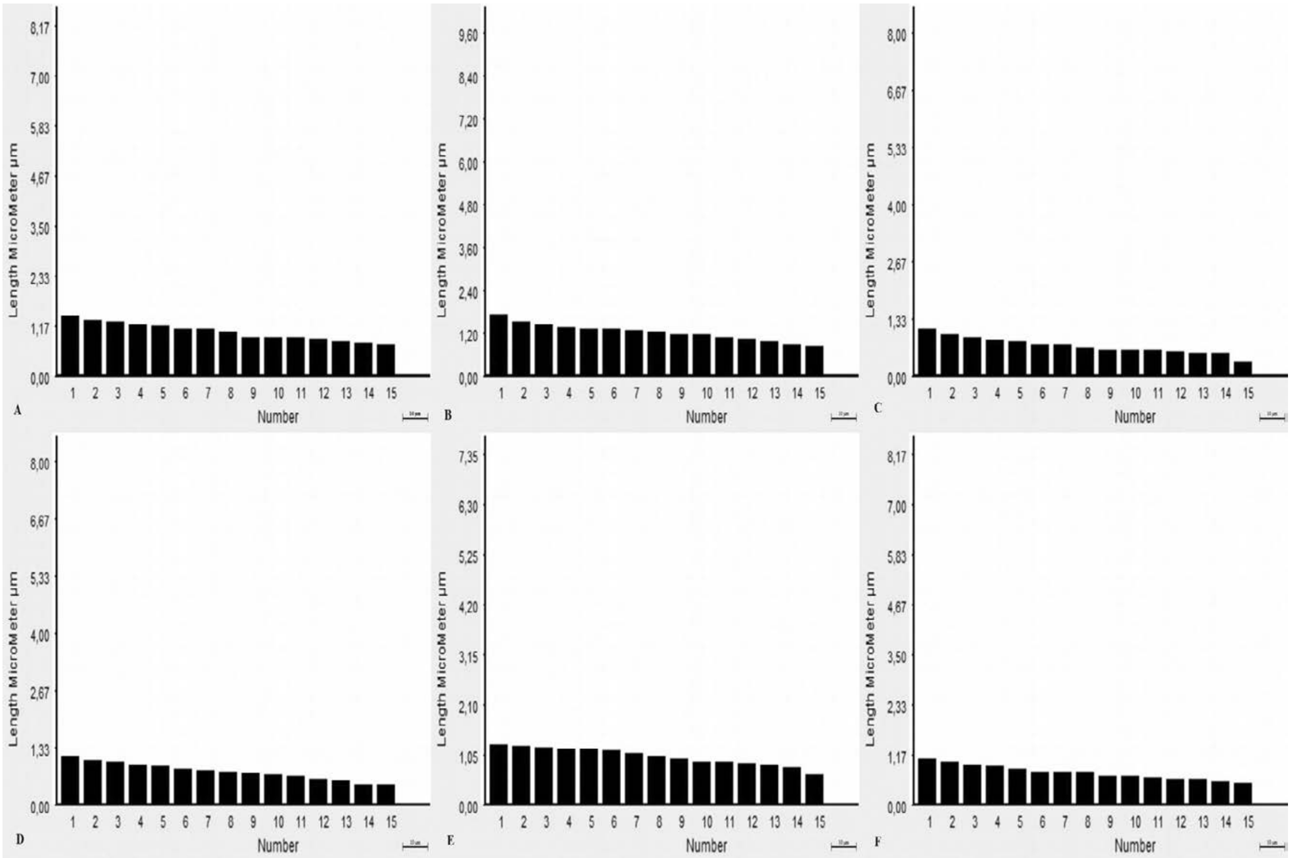

Figure 4A-F. Ideograms of hybrids and their parents: **A)** *O.* × *adae* (TD4518); **B)** *O. ayliniae* (TD4516); **C)** *O. sipyleum* (TD4517); **D)** *O.* × *intermedium* (TD4726)**; E)** *O. onites* (TD4725); **F)** *O. sipyleum* (TD4727). Scale bar: 10 µm.

The ideograms, which were drawn by Software Image Analysis (Bs200ProP) loaded on a personal computer are given in Figure 3A-N and Figure 4A-F.

DISCUSSION

Counting of chromosomes has been a very useful approach (particularly at the generic level) for researchers investigating evolutionary relationships (Levin and Wilson 1976; Stace 1991; Goldblatt 2007; Guerra 2008; Stuessy 2009; Contreras and Ruter 2011). Indeed, the chromosome numbers can affect inbreeding depression and the potential for introgression of traits through interspecific hybridization, among other factors that can alter breeding strategy (Fehr 1991; Contreras and Ruter 2011).

Measuring of chromosome size correlated with evolutionary age provides to estimate genome size using the chromosomal data (Mehra and Bawa 1972; Contreras and Ruter 2011).

According to the Index to Plant Chromosome Numbers (IPCN, http://www.tropicos.org/Project/IPCN) (Goldblatt and Johnson 1979-2017) and Chromosome Counts Database (CCDB, version 1.45, http://ccdb.tau.ac.il/home/) (Rice *et al.* 2015), there are the chromosome numbers of more than 1500 taxa of 140 genera belonging to Lamiaceae family (Chen *et al.* 2018). In Lamiaceae, the chromosome numbers between genera and even species are highly variable from $2n = 10$ to $2n = 240$. Allopolyploidy and autopoliploidy are the main reasons for variations. The basic numbers are $x = 5$, 7, 8, and 10. Secondly, basic numbers can be assumed to be $x = 13$, 14, 15, 17, and 19 (Singh 1995; Mabberley 1997). Singh (1995) considered that $x = 17$ arised as the result of the combination of $x = 8$ and $x = 9$ (Miura *et al.* 2005). Extensive cytological studies have revealed the presence of diploid, tetraploid, hexaploid and octoploid species in the family Lamiaceae. In family, the diversification may be attributed to the presence of polyploidy and aneuploidy (Rather *et al.* 2018).

In the genus *Origanum*, it was reported that the main diploid numbers were $2n = 28$, 30, and 32 and the basic number was $x = 15$ (IPCN, http://www.tropicos.org/Project/IPCN) (Goldblatt and Johnson 1979-2017) and Chromosome Counts Database (CCDB, version 1.45, http://ccdb.tau.ac.il/home/) (Rice *et al.* 2015). The chromosome counts of the investigated species in present and previous studies are given in Table 2.

In Table 1 and Table 2, the chromosome number of all sections is $2n = 30$ except some *Origanum sipyleum* specimens (because some of the specimens have $2n = 30$) in sect. *Anatolicon* and *O. rotundifolium* in the sect. *Brevifilamentum* with $2n = 28$. The smallest chromosome length is 0.32 µm in *Origanum sipyleum* (no. TD4517). The largest chromosome length is 2.02 µm in *O. minutiflorum* (no. TD4348). The smallest total haploid length is 10.08 µm in *O. vulgare* subsp. *hirtum* (no. TD4359) and the largest value is 22.00 µm in *O. haussknechtii* (no. TA2824). The smallest mean length is 0.33 µm in *O. vulgare* subsp. *hirtum* and *O. saccatum* (no. TD4359; TD4522, respectively). The largest mean length is 0.74 µm in *O. sipyleum* (no. TD4308). The chromosome lengths range from 0.75 to 6.00 µm. The chromosome lengths were measured between 0.33 and 0.74 in this karyological study of the genus *Origanum*. In the genus *Origanum*, the centromeric position could not be clearly observed because the chromosomes were generally very small compared to family members. On the other hand, total chromosome length could be measured.

The chromosome number as $2n = 30$ is typical in some genera of Lamiaceae family (*Clinopodium* L., *Micromeria* Benth., *Satureja* L., *Thymus* L. etc.). Some *Thymus* species have the same chromosome number (Jalas & Kaleva 1967; Vaarama 1948). In addition, some species have different basic numbers as $x = 6$, 7, 9, 14, 21, 27, and 24 in the genus (Darlington and Wylie 1955; Vaarama 1948). The secondary basic numbers, namely $x = 14$ and 15 probably originate from $x = 7$. The most common numbers are $2n = 28$, 30, 56, and 60, while $2n = 84$ and 90 are rarely. Jalas (1967) showed that although the chromosome numbers of distinct *Thymus* subsections were different, both subsections *Vulgares* L. and *Piperella* Willk. had the same chromosome number with $2n = 30$.

In genus *Micromeria* s.str., the chromosome number of most species was reported as $2n = 30$ (Martin *et al.* 2011). On the other hand, *Micromeria* s.l. has various somatic chromosome numbers as $2n = 20$, 22, 26, 30, 48, 50, and 60. Similarly, *Clinopodium* s.str. has various somatic chromosome numbers as $2n = 18$, 20, 22, 24, and 48 (IPCN, http://www.tropicos.org/Project/IPCN) (Goldblatt and Johnson 1979-2017) and Chromosome Counts Database (CCDB, version 1.45, http://ccdb.tau.ac.il/home/) (Rice *et al.* 2015).

Morton (1962) reported that the basic numbers were $x = 6$, 7, 8, 9, 10, 11, and 15 in *Satureja*. Harley and Brighton (1977) reported that the genus *Mentha* had various chromosome counts ranging from $x = 6$ to $x = 54$. This means that we can see diploid-octoploid members in this genus.

As mentioned before, the genus *Origanum* is a member of the Mentheae tribe and the Menthinae subtribe (Harley *et al.* 2004). The chromosome numbers of Menthinae subtribe vary from $2n = 12$ (*Hyssopus*) to $2n = 144$ (*Mentha*). The chromosome numbers were $2n = 30$ in most of the *Thymbra* L., *Satureja*, and *Micromeria* (s.str.) species belonging to the tribe Menthinae. In addition, the chromosome numbers of some species in *Thymus*, *Mentha* and *Prunella* L. were $2n = 30$ (Harley *et al.* 2004).

Ietswaart's hypothesis with regard to the origin of the genus *Origanum* suggests that *Origanum* might have emerged in the Pliocene, and that formerly, the tribe *Saturejeae* genera (*Clinopodium* sl., *Micromeria*, *Satureja*, *Thymus,* etc.) were probably the main genera from which *Origanum* could be derived (see Ietswaart 1980: pp. 7-14 and 21-24, Figure 2). When we analyzed the closest genera mentioned in the discussion part, homoploid hybridization was the main ploidy type in *Origanum*. The emergence of other sections has been diversified by hybridization between the main sections and hybridization of some *Thymus* and *Origanum* species (in part including *Satureja*, *Micromeria* s.str. and *Clinopodium* sl. species) (Ietswaart 1982). According to this hypothesis, the genera mentioned above are important regarding chromosome number compatibility. However, *Thymbra*, *Prunella*, and *Clinopodium* (partly) are morphologically very different from *Origanum* species. On the other hand, *Satureja, Thymus, Micromeria* s.str., and *Clinopodium* (partly) are morphologically closer. It may have been derived from one or more of these genera and then continued to speciation via hybridization in time. The compatibility of chromosome numbers between species supports Ietswaart's hypothesis (1980).

Although the hybridization is widespread, the generation of a unique and isolated hybrid lineage is probably very rare. New hybrid lineages must establish reproductive isolation and a unique ecological niche to overcome genetic swamping and competition from parental species (Goulet *et al.* 2017). A new hybrid lineage may be formed through allopolyploidy or homoploid hybrid speciation. Allopolyploid lineages may be formed by the fusion of unreduced gametes, genome doubling following hybridization, or via a triploid bridge (Ramsey and Schemske 1998; Goulet *et al.* 2017). Homoploid hybrid speciation forms a new unreproductive hybrid lineage

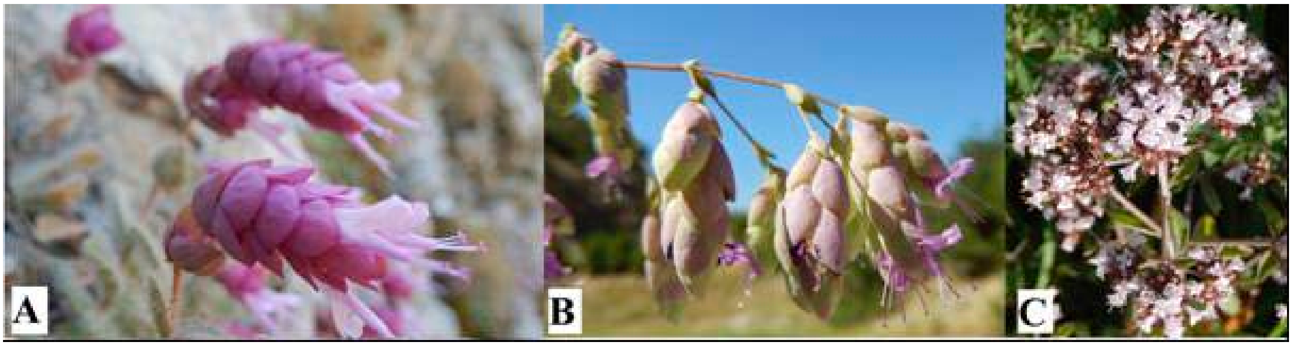

Figure 5. Inflorescence of *O. ayliniae* (A), *O. sipyleum* (B), *O. vulgare* subsp. *vulgare* (C) (photo by Tuncay Dirmenci).

with the same ploidy level with its parents (Goulet *et al.* 2017). It should be shown that both the hybrid origin of the species and the hybridization having reproductive isolation to verify a homoploid hybrid speciation (Schumer *et al.* 2014). While homoploid hybrid speciation is often concentrated on the demonstration of genetic divergence of hybrids and their origin and a pronounced ecological separation, the number of examples showing the strong link between hybridization and isolated species is very few (Stebbins 1947; Chapman and Burke 2007; Schumer *et al.* 2014; Yakimowski and Rieseberg 2014).

Hybridization is a common phenomenon in the genus *Origanum* (Dirmenci *et al.* 2018a, 2018b, 2019). The sections *Amaracus*, *Majorana*, and *Origanum* (*O. vulgare* s.l.) can be considered as the ancestral sections in the genus. Later, speciation via homoploid hybridization has an important role in speciation in the genus. This is important evidence that species hybridize easily in different sections, or that species in one section have intermediate characteristics between two different sections. According to Ietswaart (1980) and our morphological observations, sect. *Anatolicon* species have transition characters between the species of sect. *Amaracus* and *Origanum* (Figures 5A-C, 6A-F). Thus, sect. *Amaracus* is characterized by its branches. The firstorder branches are usually present, but the second-order branches are seldom present. Leaves are usually leathery, spikes large and usually nodding (Figure 5A), bracts partly purple, calyces 1 or 2-lipped, corollas saccate and all stamens greatly exserted from corolla (Figure 6A, D). In the sect. *Anatolicon,* branches of the first order are always present, while the second-order branches are sometimes present. Leaves may be leathery or not. Spikes are medium sized, usually nodding, bracts partly or slightly purple (5B), calyces usually 2-lipped, corollas not saccate and all stamens exserted from corolla (Figure 6B, E). The first- and second-order branches of the sect. *Origanum*

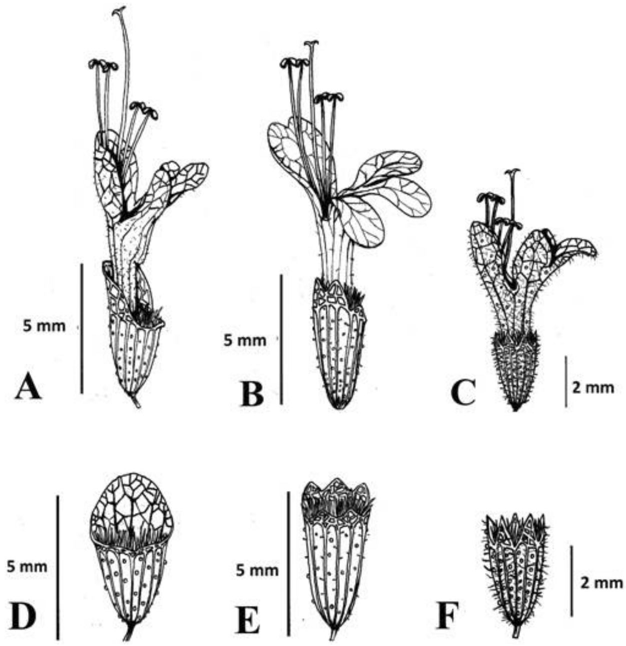

Figure 6. Flower and calyx of *O. ayliniae* (A, D), *O. sipyleum* (B, F), *O. vulgare* subsp. *hirtum* (C, F) (figures A, D, B, F from Dirmenci et al 2018a and C, F from Dirmenci *et al.* 2018b).

are always present, while the third-order branches are usually present. Leaves are usually herbaceous, spikes dense and small to medium-sized, bracts green or purple (5C), calyces actinomorphic and with 5 equal teeth, corollas not saccate and stamens subincluded or slightly protruding (Figure 6E, F).

These morphological transitions are important evidence that the genus may have intrageneric speciation via hybridization. Besides, recent studies and the chromosome numbers of hybrids and ancestors occurring in this study are the cytological evidence supporting this hypothesis. *Origanum* hybrids originate via homoploidy. The chromosome numbers of *Origanum* × *adae*, *O.* ×

intermedium, *O.* × *haradjanii*, *O.* × *munzurense* Sorger & Kit Tan, *O.* × *sevcaniae, O.* × *font-queri* and their parents were 2*n* = 30 (Bakha *et al.* 2017; Dirmenci *et al.* 2018a, 2018b, 2019).

Finally, it is clear that the cytologic findings obtained in this study combined with the previously obtained morphological, palynological and molecular studies (continuing) will contribute significantly to answering the questions about the origin and diversity of the genus *Origanum*.

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APPENDIX

Origanum acutidens*;** Tunceli: Between Ovacık and Tunceli, 21-22. km, Aşağıtorunoba village, Munzur stream, near bridge, c. 1200 m, Dirmenci 4956a, T.Arabacı & M.Açar; ***Origanum amanum*;** Osmaniye, Düziçi district, Düldül mountain, between Mando Taşı and Hüseyinoluk Çeşme, 03.10.2015, Dirmenci 4514a & T.Arabacı; ***Origanum ayliniae: Aydın: Kuşadası, Dilek Yarımadası National Park, Radar, 3922 ft, 08.10.2015, Dirmenci 4516; ***Origanum bilgeri*; Antalya:** Gündoğmuş, between Hanboğazı and Oğuz yayla, 1. km, 4775 ft, 24.10.2014, Dirmenci 4343; ***Origanum boissieri*:** *İçel*: 15 km *Çamlıyayla* district to Saimdibi place, 6045 ft, 18.09.2014, Dirmenci 4319, T.Arabacı & T.Yazıcı; ***Origanum brevidens:*** Osmaniye: 1-2 km from Yarpuz to Yağlıpınar, 5030 ft, 19.09.2014, Dirmenci 4331, T.Arabacı & T.Yazıcı; ***Origanum haussknechtii***; Erzincan, 15. km from Kemaliye to Arapkir, 1000 - 1100 m, 22.08.2013, T.Arabacı 2824; ***Origanum husnucan-baseri*;** Antalya: between Alanya and Hadim, 1-2 km to Gökbel Yayla, 4500 ft, 09.10.2015, Dirmenci 4528, T.Arabacı & T.Yazıcı; ***Origanum hypericifolium:*** Denizli: Honaz district, Honaz mountain, İncekara stream, 1300 m, 07.11.2014, Dirnmenci 4357 & T.Yazıcı; ***Origanum laevigatum*:** Osmaniye: Düziçi, above Kuşçu village, 03.10.2015, Dirmenci4497 & T.Arabacı; ***Origanum leptocladum*;** Karaman: between Ermenek and Kazancı, above Görmeli village, 1. km, 870 m, 24.10.2014, Dirmenci 4345, T.Arabacı & T.Yazıcı; ***Origanum majorana*;** Mersin: Güzeldere, 252 m, 13.07.2013, Dirmenci 3984, T.Arabacı & T.Yazıcı; İçel: between Anamur and Gazipaşa, 15-20. km, 300 m 26.10.2014, Dirmenci 4356 & T.Yazıcı; Karaman: Ermenek, 2 km from Kazancı to Abanoz Yayla, 1238 m, 24.10.2014, Dirmenci 4346, T.Arabacı & T.Yazıcı; ***Origanum minutiflorum*:** Antalya: Kemer, Üçoluk, above Tülek, 4470 ft, 25.10.2014, Dirmenci 4348 & T.Yazıcı; ***Origanum onites***: Denizli: Taşocağı, 527 m, 26.10.2014, Dirmenci 4355 & T.Yazıcı; ibid, 11.10.2015, Dirmenci 4532 & T.Yazıcı; Denizli: between Buldan and Güney, 13 from road disjunction to Güney, Dirmenci 4725 & T.Yazıcı; Denizli: ***Origanum rotundifolium*: Artvin: between** Artvin and Ardanuç, 600-700 m, 27.08.2013, Dirmenci 3943, B.Yıldız & T.Arabacı; ***Origanum saccatum:*** Antalya, 1 km from Gündoğmuş to *Çayırözü* village, 3715 ft, 24.10.2014, Dirmenci 4342, T.Arabacı & T.Yazıcı; Antalya: 38 km from Alanya to Hadim, Kuşkayası, 3814 ft, 09.10.2015, Dirmenci 4522 T.Arabacı & T.Yazıcı; ibid., Dirmenci 4732 & T.Arabacı; ***Origanum sipyleum:*** Denizli: 5 km from Serinhisar to Denizli, 1066 m, 19.08.2014, Dirmenci 4308; ibid., 26.10.2014, Dirmenci 4352; Denizli: Taşocağı, 1808 ft, Dirmenci 4534 & T.Yazıcı; Aydın: Kuşadası, Dilek Peninsuna National Park, Radar, 3922 ft, 08.10.2015, Dirmenci 4517; Denizli: Denizli: between Buldan and Güney, 13 from road disjunction to Güney, Dirmenci 4727 & T.Yazıcı; ***Origanum solymicum:*** Antalya: Kemer, 4 km from Kesmeboğazı *to* Kuzdere village, 1470 m, 25.10.2014, Dirmenci 4347 & T.Yazıcı; Antalya: Kemer, 7 km from Kesmeboğazı to Karçukuru Yayla, 1506 ft, 09.10.2015, Dirmenci 4520 & T.Yazıcı;; ***Origanum syriacum* subsp. *bevanii*:** Hatay: between Antakya and Samandağ, around St. Symeone church, 20.09.2014, Dirmenci 4336, T.Arabacı & T.Yazıcı; Osmaniye: Düziçi, between Kuşçu village and Düldül mountain, 19.09.2014, Dirmenci 4330 & T.Arabacı; ***Origanum vogelii*;** Niğde: Ulukışla, Horoz village, Fenk Boğazı, 4800 ft, 02.10.2015, Dirmenci 4509 & T.Yazıcı; ***Origanum vulgare* subsp. *gracile*:** K.Maraş: Göksun, between Yeşilköy and Kınıkkoz villages, 400-450 m, 04.08.2017, Dirmenci 4821 & T.Arabacı; Tunceli: 20-21 km from Ovacık to Tunceli, c. 1200 m, 11.08.2017, Dirmenci 4958, T.Arabacı & M.Açar; ***Origanum vulgare* subsp. *hirtum*:** Antalya: Antalya: between Alanya and Hadim, 1 km to Gökbel Yayla, Dirmenci 4733, T.Arabacı & T.Yazıcı; Denizli: Taşocağı, 527 m, Dirmenci 4722 & T.Yazıcı; Denizli: Honaz district, North face of Honaz mountain, Arpacık Yayla road, 4160 ft, 07.11.2014, Dirmenci 4359 & T.Yazıcı; Niğde: Ulukışla, Horoz village, Fenk Boğazı, 4800 ft,, 02.10.2015, Dirmenci 4507 & T.Yazıcı; ***Origanum vulgare*** **subsp. *viridulum*:** Giresun: 33 km from Şebinkarahisar to Tamdere, nort of Eğribel pass, Dirmenci 4662a & T.Arabacı; ***Origanum vulgare*** **subsp. *vulgare*:** 22 km from Şavşat to Ardahan, Dirmenci 4688 & T.Arabacı; ***Origanum*** × ***adae*:** Kuşadası, Dilek Yarımadası National Park, Radar, 3922 ft, 08.10.2015, Dirmenci 4518; ***Origanum*** × ***haradjanii*:** Hatay: between Antakya and Samandağ, around St. Symeone church, 20.09.2014, Dirmenci 4335, T.Arabacı & T.Yazıcı; ***O.*** × ***intermedium*:** Denizli: Denizli: between Buldan and Güney, 13 from road disjunction to Güney, Dirmenci 4726 & T.Yazıcı; ***Origanum*** × ***munzurense*:** Tunceli: Between Ovacık and Tunceli, 21-22. km, Aşağı Torunoba village, Munzur stream, near bridge, c. 1200 m, Dirmenci 4957a, Arabacı & Açar; ***Origanum*** × ***sevcaniae*:** Niğde: U Ulukışla, Horoz village, Fenk Boğazı, 4800 ft, 02.10.2015, Dirmenci 4508 & T.Yazıcı.