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Contribution to knowledge about genome size in members of the family Asteraceae from Turkey: first assessments in 17 taxa, with chromosome counts for nine taxa

Huseyin Inceer* and Nursen Aksu Kalmuk

Karadeniz Technical University, Faculty of Science, Department of Biology, 61080 Trabzon, Turkey
* correspondence: inceer@ktu.edu.tr

ABSTRACT:
In this study, we report genome size (C-values) estimated using flow cytometry for 18 taxa of Asteraceae from Turkey, 17 of which are here assessed for the first time. The studied taxa belong to the genera *Achillea* (one species), *Anthemis* (one subspecies), *Tanacetum* (four taxa) and *Crepis* (12 taxa). Additionally, chromosome numbers of nine taxa of *Crepis* are provided, four counts being new reports and the remainder confirming previous data. The 2C-values of the studied taxa range from 2.08 to 11.06 pg, which represent more than fivefold variation. The systematic and evolutionary significance of genome size is discussed within the framework of the results obtained in this study.

Keywords:
Achillea, *Anthemis*, Compositae, *Crepis*, flow cytometry, *Tanacetum*

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INTRODUCTION

Genome size, or the C-value, is known as the DNA content of the unreplicated gametic chromosome complement of an organism (Swift 1950). It is an important trait with reflections in molecular biology, systematics, ecology and population biology (Pellicer *et al.* 2018, and references therein). Genome size within a species is supposedly stable (Swift 1950; Greilhuber 2005), but some studies revealed significant intraspecific variation (Smarda & Bures 2010). In angiosperms, genome size is available for only 3% of the species and spans four orders of magnitude, from 0.12 pg/2C in *Genlisea aurea* A.St.-Hil. and *G. tuberosa* Rivadavia, Gonella & A. Fleischm. to 304.4 pg/2C in *Paris japonica* (Franch. & Sav.) Franch. (reviewed in Pellicer *et al.* 2018). Polyploidy and activation of transposable elements are seen as the main factors promoting genome size variation across plant lineages (Pellicer *et al.* 2018), although increasing evidence highlights the importance of chromosome rearrangements for generating genome size differences (Vitales *et al.* 2019).

The Asteraceae (Compositae) is one of the largest of plant families, with ca. 24,000 species. It has a worldwide distribution (Funk *et al.* 2009) and includes many useful economically important horticultural and crop plants. It has been the subject of many karyological and genome size studies (reviewed in Semple & Watanabe 2009; Garcia *et al.* 2014). However, information about genome size in the Asteraceae is still relatively scarce, as it covers only approximately 6% of the genera, 3% of the species and 32.56% of the tribes (Vallès *et al.* 2013). The present study aims at expanding this knowledge by contributing new data on genome size together with chromosome counts for some members of the family Asteraceae from Turkey.

MATERIALS AND METHODS

Plant material. Plant materials of taxa belonging to the genera *Achillea* L., *Anthemis* L., *Crepis* L. and *Tanacetum* L. of the family Asteraceae were collected from natural populations in Turkey (Table 1). Vouchers are deposited in the herbarium at the Karadeniz Technical University, Department of Biology (KTUB). The names of the

Table 1. Data collection in Turkey and voucher numbers of the studied taxa.

Taxon	Locality	Voucher
Achillea biserrata Bieb.	A7 Gumushane: Zigana Mountain, 1700 m a.s.l., 20.vi.2016	Inceer 1201
Anthemis rosea Sm. subsp. *carnea* (Boiss.) Grierson*	C2 Antalya: Kepez, 180 m a.s.l., 24.iv.2015	Inceer 1141
Tanacetum albipannosum Hub.-Mor. & Grierson*	A7 Gumushane: Zigana Mountain, 1300 m a.s.l., 01.vii.2018	Inceer 1208
T. polycephalum Sch. Bip. subsp. *argyrophyllum* (K. Koch) Podlech	A7 Gumushane: Tekke, Kecikale, 1562 m a.s.l., 01.vii.2018	Inceer 1209
T. aucherianum (DC.) Sch. Bip.	A7 Gumushane: Tekke, Kecikale, 1565 m a.s.l., 01.vii.2018	Inceer 1210
T. coccineum (Willd.) Grierson subsp. *chamaemelifolium* (Somm. & Lev.) Grierson	A9 Artvin: Savsat, 1900 m a.s.l., 21.vii.2018	Inceer 1216
Crepis alpestris (Jacq.) Tausch	A2 Bursa: Uludag, 2045 m a.s.l, 08.viii.2012	Aksu 139
C. amanica Babcock*	C7 Sanliurfa: Between Akcakale and Ceylanpinar, 400 m a.s.l., 10.vi.2014	Inceer 1087
C. armena DC.*	A8 Bayburt: Kop Mountain, 2410 m a.s.l., 10.vii.2011	Aksu 61
C. aurea (L.) Cass. subsp. *olympica* (K. Koch.) Lamond*	A2 Bursa: Uludag, 2040 m a.s.l., 15.viii.2014	Aksu 218
C. dioritica Schott & Kotschy ex Boiss.*	C5 Nigde: Bolkar Mountains, 2620 m a.s.l., 05.vii.2013	Inceer 1035
C. multiflora Sm.	B1 Balikesir: Sarimsakli, 130 m a.s.l., 26.iv.2014	Inceer 1082
C. palaestina (Boiss.) Bornm. subsp. *babcockii* Inceer & Aksu Kalmuk*	C3 Antalya: Manavgat, 10 m a.s.l., 29.iv.2014	Inceer 1086
C. purpurea (Willd.) M. Bieb.	A4 Ankara: Between Ankara and Ayas, near Aysanti Pass, 1165 m a.s.l., 29.vi.2013	Inceer 1011
C. reuteriana Boiss. & Heldr.	A1 Canakkale: Dardanos, 25 m a.s.l., 15.v.2015	Aksu 226
C. sahendi Boiss. & Buhse	B8 Erzurum: Palandoken Mountain, 2685 m a.s.l., 13.vii.2014	Inceer 1100
C. stojanovii Georgiev	B3 Eskisehir: Between Eskisehir and Seyitgazi, 1030 m a.s.l., 25.vi.2014	Inceer 1098
C. willdenowii Czerep.	A8 Bayburt: Kop Mountain, 2120 m a.s.l., 22.vii.2012	Aksu 138

* endemic to Turkey

investigated taxa, accession numbers and collection information are given in Table 1.

Germination of achenes and chromosome counts. Mature achenes obtained from five different individuals per population were germinated in Petri dishes at 22–23°C. Germinated seedlings with well-developed root tips about 1 cm long were pre-treated with 0.05% colchicine solution for 2–5 h at room temperature. They were fixed in absolute ethanol-glacial acetic acid (3:1) for at least 24 h at 4°C, hydrolysed in 1M HCl at 60°C for 10 min and then rinsed in deionised water for 2–3 min. Staining was carried out in 1% aqueous lacto-propionic orcein for 12–18 h at room temperature, squashes were made in 45% acetic acid and the preparations were mounted in Entellan (Inceer *et al*. 2018a). Permanent slides were observed with a Leica DM 4000B microscope at a magnification of 1000×. Best metaphase plates were photographed using a Leica DFC 490 digital camera. Chromosome counts were carried out on five metaphase plates from five individuals per taxon.

Nuclear genome size estimation. Young leaves were taken from three specimens in natural populations for flow cytometric analysis. Nuclear DNA content was assessed by flow cytometry as follows. Leaf fragments of the sample plant and the standard plant were chopped using a razor blade in 1mL of a woody plant buffer [0.2 M Tris HCl, 4 mM $MgCl_2.6H_2O$, 2 mM EDTA, $Na_2.2H_2O$, 86 mM NaCl, 10 mM $K_2S_2O_5$, 1% PVP-10, 1% (v/v) Triton X-100, pH 7.5; Loureiro *et al*. 2007] supplemented with 50 µg mL^{-1} propidium iodide and 50 µg mL^{-1} DNAse-free RNAse, filtered through a 30-µm mesh and stored on ice in the dark until measurement. Due to differences in genome size of the analysed taxa, two reference standards (*Pisum sativum* L. 'Ctirad'; 2C = 9.09 pg DNA, Doležel *et al*. 1998; *Lycopersicon esculentum* Mill. 'Swanson'; 2C = 2.00 pg DNA,

Table 2. Genome size (C-value) and somatic chromosome number (2*n*).

Taxon	2*n*	2C (pg)	2C (Mbp)	1C (pg)	CV (%)	Standard plant
Achillea biserrata	18[a]	6.69±0.24*	6542.82	3.35	2.87	*Pisum sativum*
Anthemis rosea subsp. *carnea*	?	8.33±0.39*	8146.74	4.17	3.99	*P. sativum*
Tanacetum albipannosum	18[b]	8.53±0.37*	8342.34	4.27	4.53	*P. sativum*
T. polycephalum subsp. *argyrophyllum*	18[b]	8.50±0.26	8313	4.25	2.80	*P. sativum*
T. aucherianum	18[b]	7.25±0.14*	7090.5	3.63	3.69	*P. sativum*
T. coccineum subsp. *chamaemelifolium*	18[a]	9.57±0.26*	9359.46	4.79	4.06	*P. sativum*
Crepis alpestris	8**	6.19±0.48*	6053.82	3.10	1.95	*Lycopersicon esculentum*
C. amanica	8*	2.13±0.05*	2083.14	1.07	1.28	*L. esculentum*
C. armena	8*	6.07±0.42*	5936.46	3.04	1.32	*L. esculentum*
C. aurea subsp. *olympica*	10*	2.08±0.04*	2034.24	1.04	2.30	*L. esculentum*
C. dioritica	8	6.28±0.28*	6141.84	3.14	1.65	*L. esculentum*
C. multiflora	8[d]	6.26±0.39*	6122.28	3.13	1.02	*L. esculentum*
C. palaestina subsp. *babcockii*	8[c]	8.44±0.60*	8254.32	4.22	1.33	*L. esculentum*
C. purpurea	10*	3.99±0.30*	3902.22	2.00	1.45	*L. esculentum*
C. reuteriana	8**	11.01±0.50*	10767.78	5.51	1.87	*L. esculentum*
C. sahendi	10**	3.60±0.14*	3520.8	1.80	1.80	*L. esculentum*
C. stojanovii	8[d]	11.06±0.30*	10816.68	5.53	1.43	*L. esculentum*
C. willdenowii	10**	4.31±0.26*	4215.18	2.15	1.60	*L. esculentum*

CV – coefficient of variation; mean value ± standard deviation; 1 pg = 978 Mbp (Doležel *et al.* 2003); *new to science, **first report from Turkey; [a]Inceer & Hayirlioglu-Ayaz (2007); [b]Inceer *et al.* (2012); [c]Inceer & Aksu Kalmuk (2018); [d]Babcock (1947b).

Inceer *et al.* 2016) were used for flow cytometric analysis. Three independent samples were extracted, filtered and measured on the same day. Measurements were made on three consecutive days using a BD Accuri™ C6 instrument. Usually 10.000 nuclei per sample were analysed for nuclear DNA content and absolute values (Inceer *et al.* 2016). DNA content was then calculated from mean values of G1 peaks according to the following formula:

$$Sample\ 2C\ DNA\ content = \frac{(sample\ G1\ peak\ mean) \times (standard\ 2C\ DNA\ content)}{standard\ G1\ peak\ mean}$$

RESULTS AND DISCUSSION

Genome size data are provided for 18 species and subspecies of Asteraceae from Turkey (Table 2), these data representing the first genome size assessments for 17 of them. Coefficients of variation range from 1.02 to 4.53% (with a mean value of 2.27%) indicating reliable and reproducible estimates. The obtained 2C-values represent a fivefold range of variation from 2.08 to 11.06 pg (both in *Crepis*, Table 2) and fall within the range of variation known for their respective genera (http://www.asteraceaegenomesize.com, accessed on 30 August 2019; Garnatje *et al.* 2011; Garcia *et al.* 2014).

We also carried out chromosome counts for nine Asteraceae taxa corresponding to the same populations used for the genome size survey, four of them being the first reports for the considered taxa (Table 2; Fig. 1).

***Crepis*.** This genus is known as a model for the study of evolution and systematics of the flowering plants due to the low mitotic chromosome numbers encountered in the mostly diploid species, ranging from $2n = 6$ to $2n = 12$. Moreover, most *Crepis* species are diploid, and numerous chromosomal studies have been conducted up to now on the genus (Babcock 1947a, b; Siljak-Yakovlev & Cartier 1982; Kamari 1992; Dimitrova & Greilhuber 2000, 2001; Enke *et al.* 2015; Inceer *et al.* 2018a). A decreasing tendency in the base number x (6→3) is distinct in diploid species of the genus (Babcock 1947a; Dimitrova & Greilhuber 2000). It is generally accepted that the primitive *Crepis* complement is $2n = 2x = 12$ and that lower basic numbers were derived as a result of unequal (asymmetric) reciprocal translocations between nonhomologous chromosomes (Babcock

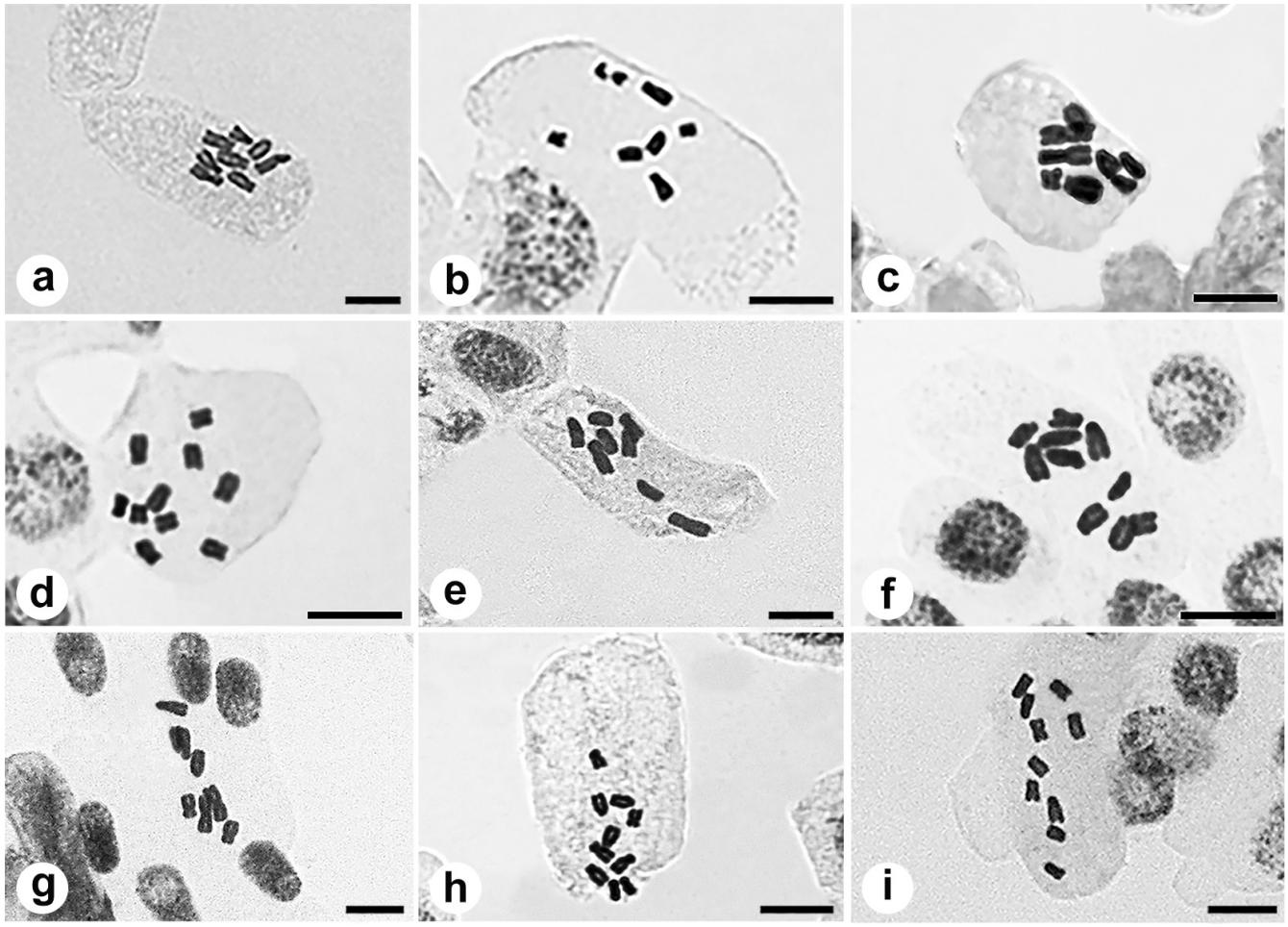

Fig. 1. Somatic metaphases in *Crepis* **(a-i)**: **a.** *C. alpestris* (2*n* = 8), **b**. *C. amanica* (2*n* = 8), **c**. *C. armena* (2*n* = 8), **d**. *C. aurea* subsp. *olympica* (2*n* = 10), **e**. *C. dioritica* (2*n* = 8), **f**. *C. purpurea* (2*n* = 10), **g**. *C. reuteriana* (2*n* = 8), **h**. *C. sahendi* (2*n* = 10), **i**. *C. willdenowii* (2*n* = 10), scale bars = 10 μm.

1947a). Thus, a reduction in chromosome number plays an important role in *Crepis* speciation (Babcock 1947a; Dimitrova & Greilhuber 2000). Our chromosome counts indicate that the studied taxa of *Crepis* are diploid with 2*n* = 2*x* = 8 and 10 (Table 2, Fig. 1). Similar chromosome counts are also reported in other members of *Crepis* from Turkey (Inceer *et al*. 2016, 2018a) and other territories (Babcock 1947b; Watanabe 2018, and references therein).

To our knowledge, the chromosome numbers of *C. amanica* Babcock (2*n* = 8), *C. armena* DC. (2*n* = 8), *C. aurea* (L.) Cass. subsp. *olympica* (K. Koch.) Lamond (2*n* = 10) and *C. purpurea* (Willd.) M. Bieb. (2*n* = 10) are new to science (Fig. 1). Furthermore, the chromosome counts of *C. alpestris* (Jacq.) Tausch (2*n* = 8), *C. reuteriana* Boiss. & Heldr. (2*n* = 8), *C. sahendi* Boiss. & Buhse (2*n* = 10) and *C. willdenowii* Czerep. (2*n* = 10) are the first reports for Turkish populations (Fig. 1). Our results support previous reports for these species from other territories (Babcock 1947b; Watanabe 2018, and references therein). The present chromosome count for *C. dioritica* Schott & Kotschy ex Boiss. (2*n* = 8) is the third chromosome count for this Turkish endemic species and is consistent with previous reports (Babcock 1947b; Lamond 1975).

Our results show that *C. aurea* subsp. *olympica* (2*n* = 10) has the smallest genome size (with 2.08 pg/2C), whereas *C. stojanovii* Georgiev (2*n* = 8) has the largest one (with 11.06 pg/2C). On the other hand, previously published data for diploid *Crepis* show a slightly wider range, viz., from 1.08 pg/2C in *C. hellenica* Kamari subsp. *hellenica* to 14.11 pg/2C in *C. bupleurifolia* (Boiss.) Freyn & Sint. (Enke *et al.* 2015; Inceer *et al*. 2018a).

The 2C-value in taxa having 2*n* = 8 chromosomes with a basic chromosome number of *x* = 4 varies from 2.13 pg in *C. amanica* to 11.06 pg in *C. stojanovii*. The 2C-value in taxa having 2*n* = 10 chromosomes with a basic chromosome number of *x* = 5 ranges from 2.08 pg in *C. aurea* subsp. *olympica* to 4.31 pg in *C. wildenowii*. The mean 2C-value in the here studied taxa having 2*n* = 8 chromosomes is 7.18 ± 2.94 pg, whereas the mean 2C-value in those having 2*n* = 10 chromosomes is 3.5 ± 0.99 pg. This means that relative genome size is greater in taxa with 2*n* = 8 chromosomes

than in ones with $2n = 10$ chromosomes. Preliminary results showed a negative but not significant correlation between genome size and chromosome number in *Crepis* (Enke *et al.* 2011), but further analyses on an extended sampling and using methods that incorporate phylogenetic information are needed to address this correlation.

Crepis sahendi resembles *C. armena*, from which it is distinguished by having a receptacle with setiform paleae longer than mature achenes (Lamond 1975). The present results show that these species also differ in both their chromosome number and their genome size (Table 2).

Classical karyological methods studies of chromosome characteristics using coloured squashes made of meristematic parts of plants frequently failed to distinguish closely related taxa which have the same chromosome number, as was the case for *C. praemorsa* (L.) Tausch subsp. *praemorsa* and *C. praemorsa* (L.) Tausch subsp. *dinarica* (Beck) P.D. Sell ($2n = 8$) (Siljak-Yakovlev & Cartier 1982). Among the studied taxa of *Crepis*, *C. amanica* is allied to *C. pulchra* L., from which it is distinguished by having distinctively ribbed achenes and a coarser pappus (Lamond 1975). Both species share a chromosome number of $2n = 8$, but their genome size differs substantially, with 2.13 pg/2C for *C. amanica* (Table 2) and 9.56-12.22 pg/2C for *C. pulchra* (Dimitrova & Greilhuber 2000; Inceer *et al.* 2018a).

Another taxon closely related to *C. pulchra* is *C. palaestina* (Boiss.) Bornm. subsp. *babcockii* Inceer & Aksu Kalmuk ($2n = 8$), which was recently described from Turkey and is distinguished by the shape of its achenes (Inceer & Aksu Kalmuk 2018). The two taxa have $2n = 8$, but *Crepis palaestina* subsp. *babcockii* has a genome size of 8.44 pg/2C, while the genome size of *C. pulchra* ranges from 9.56 to 12.22 pg/2C (Dimitrova & Greilhuber 2000; Inceer *et al.* 2018a).

Similarly, *C. multiflora* Sm. is phylogenetically close to *C. dioscoridis* L., from which it is very distinct in size and form of the involucre, size of the corolla and anther tube, size and form of the achenes and habit of the plant (Babcock 1947b). The two species have the same chromosome number ($2n = 8$), but different genome size [6.26 pg/2C for *C. multiflora* (Table 2) and 9.58 pg/2C for *C. dioscoridis* (Inceer *et al.* 2018a)].

***Tanacetum*.** The karyology of *Tanacetum* has been extensively studied, with chromosome counts known for a considerable number of species (Olanj *et al.* 2015; Watanabe 2018, and references therein). The basic chromosome number of the genus is $x = 9$, which is the most common number in the Anthemideae tribe, and in the Asteraceae as a whole (Semple & Watanabe 2009). Ploidy levels in *Tanacetum* range up to $10x$, and it is believed that polyploidy is an important evolutionary force within the genus (Inceer *et al.* 2012; Olanj *et al.* 2015). All *Tanacetum* taxa investigated here are diploid with $2n = 2x = 18$ (Table 2; Inceer & Hayirlioglu-Ayaz 2007; Inceer *et al.* 2012).

The 2C-value in diploid species of *Tanacetum* varies from 3.84 pg in *T. parthenium* (L.). Sch. Bip. to 13.19 pg in *T. pinnatum* Boiss. (Olanj *et al.* 2015). Our present results show that the 2C-value of the studied taxa of *Tanacetum* ranges from 7.25 pg in *T. aucherianum* (DC.) Sch. Bip. to 9.57 pg in *T. coccineum* (Willd.) Grierson subsp. *chamaemelifolium* (Somm. & Lev.) Grierson. These results are in agreement with previous data on diploid *Tanacetum* taxa (Olanj *et al.* 2015).

The present results show that the here measured 2C-value of *T. polycephalum* Sch. Bip. subsp. *argyrophyllum* (K. Koch) Podlech (8.50 pg/2C; Table 2) is smaller than the previously published value (9.26 pg/2C, $2n = 18$; Olanj *et al.* 2015). This difference in the given taxon´s 2C-values may be due to the use of different types of flow cytometers. In addition, different standards or geographical and environmental factors can cause intraspecific variation in genome size, as in *Artemisia* L. (Torrell & Vallès 2001) and *Crepis* (Inceer *et al.* 2018a).

According to Grierson (1975), *Tanacetum albipannosum* Hub.-Mor. & Grierson is closely related to *T. aucherianum*, from which it is distinguished by having no broad hyaline margins in the involucral bracts. Moreover, these closely related species share the same chromosome number (Inceer *et al.* 2012). Our present results show that genome size differs between these species (Table 2), *T. albipannosum* presenting greater genome size (8.53 pg/2C) than its relative, *T. aucherianum* (7.25 pg/2C).

CONCLUSION

The present paper supplements information about genome size with new datasets on plants of the family Asteraceae in Turkey, where knowledge about genome size of the family´s members is still limited (Garcia *et al.* 2005; Inceer *et al.* 2016, 2018a, b). This study revealed a number of closely related species presenting substantially different genome sizes. Thus, our results suggest that genome size data can be useful in addition to morphological characters for supporting taxonomic circumscription.

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REZIME

Botanica SERBICA

Prilog poznavanju veličine genoma predstavnika familije Asteraceae u Turskoj: prve procene za 17 taksona, sa brojem hromozoma za 9 taksona

Huseyin Inceer i Nursen Aksu Kalmuk

U ovoj studiji je dat prikaz veličine genoma procenjenog uz upotrebu tečnog citometra za 18 taksona iz familije Asteraceae u Turskoj, od čega za njih 17 prvi put. Istraživani taksoni pripadaju rodovima *Achillea* (jedna vrsta), *Anthemis* (jedna podvrsta), *Tanacetum* (četiri taksona) i *Crepis* (12 taksona). Dodatno, dat je broj hromozoma za devet taksona iz roda *Crepis*, pri čemu četiri predstavljaju nove podatke, dok ostali potvrđuju predhodno utvrđene. 2-C vrednosti istraživanih taksona su u rasponu od 2.08 do 11.06 pg, što predstavlja više od petostrukog variranja. Sistematski i evolutivni značaj veličine genoma je diskutovan unutar okvira rezultata prikazanih u ovoj studiji.

Ključne reči: *Achillea*, *Anthemis*, Compositae, *Crepis*, tečna citometrija, *Tanacetum*