Chromosome counts in Asian *Artemisia* L. (Asteraceae) species: from diploids to the first report of the highest polyploid in the genus

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This work comprises 24 reports of chromosome numbers in 24 *Artemisia* L. species from Asia. Ten are included in the subgenus *Dracunculus* Besser and the rest belong to other subgenera. Seven counts are new reports, 14 are consistent with scarce previous ones, and three contribute new ploidy levels. That carried out in *A. medioxima* reports the highest ploidy level ever counted for the genus (16x). There is only one species with x = 8 as the basic chromosome number. In the remaining x = 9-based species, ploidy levels range from 2x to 16x, illustrating the great role played by polyploidy in the evolution of the genus. © 2007 The Linnean Society of London, Botanical Journal of the Linnean Society, 2007, 153, 301–310.

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INTRODUCTION

*Artemisia* L. is the largest genus of the tribe Anthemideae and one of the largest of the Asteraceae. It contains more than 500 taxa, a variable number depending on the author (Vallès & Garnatje, 2005, and references cited therein). *Artemisia* are distributed mainly in the Northern Hemisphere, especially in West and Central Asia, although some have a worldwide distribution. Many representatives of the genus have been used traditionally as medicines, food, forage, ornamentals, etc. (Pareto, 1985; Marco & Barberá, 1990; Heinrich et al., 1998; Wright, 2002).

Palaeontological data suggest that the origin of *Artemisia* was most probably in the mountain regions of north-western Asia in the mid-Cenozoic (Ling, 1982; Wang, 2004). The most important centre of diversity is temperate Asia, although there are dispersed foci of speciation in temperate and cold regions of Eurasia and North America (Ling, 1982). The finding of different ploidy levels in these and other Artemisiinae species in Asia also supports the hypothesis of this origin of speciation.

The infrageneric classification of *Artemisia* has been the subject of many taxonomic rearrangements. It was divided classically into four groups treated as sections or subgenera: *Absinthium* DC., *Artemisia* (originally named *Abrotanum* Besser), *Dracunculus* DC., and *Seriphidium* (Besser) Rouy (Besser, 1829, 1832, 1834, 1835; Candolle, 1837). Rydberg (1916) created a new section (* Tridentatae*), including species previously within the subgenus *Seriphidium*, which was subsequently separated as an independent subgenus (McArthur, Pope & Freeman, 1981). Afterwards, Ling (1982, 1991a, b, 1995a, b) proposed the segregation of *Seriphidium* (Besser ex Hook) Fourr. as an independent genus, which was accepted by Bremer & Humphries (1993) and Bremer (1994) in their cladistic revisions of the Anthemideae and Asteraceae, respectively. However, molecular studies based on chloro-
plast DNA (cpDNA) restriction site variation and internal transcribed spacers (ITS) of nuclear ribosomal DNA (Kornkven, Watson & Estes, 1998; Torrell et al., 1999; Watson et al., 2002; Vallès et al., 2003) have refuted this separation. Several other small genera, such as Filifolium Kitam., Kaschgaria Poljakov, Neopallasia Poljakov, and Turaniphytum Poljakov, are very close to Artemisia, or have been segregated from it (Rydberg, 1916; Poljakov, 1961; Ling & Ling, 1978; Ghafoor, 1992; Bremer & Humphries, 1993).

The relevance of karyological and cytogenetic studies to the knowledge of the systematics and evolution of the genus was noted long ago (Weinedel-Liebau, 1928; Ehrendorfer, 1964; Korobkov, 1972). From the earliest studies to the present, numerous chromosome counts (for around 350 taxa, i.e. over 50% of the genus, including species and subspecies) and cytogenetic data have been reported (Vallès & Garnatje, 2005, and references cited therein). The genus has two basic chromosome numbers: \( x = 9 \), present in all the subgenera, and the less frequent \( x = 8 \), present in Absinthium, Artemisia, and Dracunculus (Solbrig, 1977; Schweizer & Ehrendorfer, 1983; Oliva & Vallès, 1994; McArthur & Sanderson, 1999). A centric (Robertsonian) chromosome fusion may have been the cause of this descending dysploidy, reducing the basic chromosome number from \( x = 9 \) to \( x = 8 \) (Vallès & Siljak-Yakovlev, 1997). Both basic numbers show polyploid series, with known levels up to dodecaploid for \( x = 9 \) and hexaploid for \( x = 8 \) (Ehrendorfer, 1964, 1980; Estes, 1969; Persson, 1974; McArthur & Pope, 1979; Oliva & Vallès, 1994; McArthur & Sanderson, 1999). Moreover, different studies on Artemisia have shown that the nuclear DNA content increases with ploidy level, although the monoploid genome size decreases with increasing polyploidy (Torrell & Vallès, 2001; Garcia et al., 2004). It is clear that there exists a wide knowledge of Artemisia from the karyological and cytogenetic viewpoint, but these chromosomal data are still limited or unavailable for many widespread species.

The present study covers most of the Artemisia subgenus, with a particular emphasis on the subgenus Dracunculus, which is distributed largely in Eurasia and North America. The main traits which differentiate this group from the other subgena are the presence of heterogamous capitula, with outer female florets and central hermaphrodite but functionally male florets. This morphology induced Cassini (1817) to name the species of this subgenus as a new genus, Oligosporus Cass., which was later returned to Artemisia (Besser, 1829, 1832, 1834, 1835; Candolle, 1837). The inclusion of this group within Artemisia has been confirmed by molecular phylogenetic data (Vallès et al., 2003). The main objective of this work is to enlarge the chromosomal data in the genus and to shed light on the role of polyploidy in its diversification.

MATERIAL AND METHODS

Root-tip meristems were obtained from wild-collected achenes germinated on wet filter paper in Petri dishes at room temperature in the dark. Seedlings were pre-treated with 0.05% aqueous colchicine at room temperature for 2.5–3 h. Material was fixed in absolute ethanol and glacial acetic acid (3 : 1) for 2–4 h at room temperature and stored in the fixative at 4 °C. Samples were hydrolysed in 1 M HCl for 5–8 min at 60 °C, stained with 1% aqueous aceto-orcein for 2–12 h, and squashed on slides in 45% acetic acid–glycerol (9 : 1). The best metaphase plates were photographed with a digital camera (AxioCam MRC5 Zeiss) mounted on a Zeiss Axiosplan microscope, and images were analysed with Axio Vision Ac software version 4.2. Herbarium vouchers of most species are deposited in the herbarium of the Centre de Documentació de Biodiversitat Vegetal de la Universitat de Barcelona (BCN), and some others are in the Komarov Botanical Institute, St Petersborg (LE).

To assess the existence of previously published chromosome counts in the studied species, we used the most common indexes of plant chromosome numbers (cited in Vallès, Torrell & García-Jacas, 2001a), previous publications (Vallès et al., 2005; Garcia et al., 2006; and references cited therein), and the chromosome number databases Index to Plant Chromosome Numbers (Missouri Botanical Garden, http://mobot.org/W3T/Search/ipcn.html) and Index to Chromosome Numbers in the Asteraceae (Watanabe, 2002; http://www-asteraceae.cla.kobe-u.ac.jp/index.html).

RESULTS AND DISCUSSION

Some authors have proposed different series of sections and subsections in Artemisia (Rydberg, 1916; Poljakov, 1961; Korobkov, 1981; Ling, 1991a, b, 1995a, b), but a global treatment of the entire genus at these levels has not yet been achieved; therefore, we consider here only the classical main subdivisions. The localities are given with the use of Russian (‘krai’, region; ‘oblast’, province; ‘raion’, district) and Mongolian (‘aimag’, province, written ‘aimak’ in Russian language works; ‘sum’, village, written ‘somon’ in Russian language works) administrative divisions. Seven of the chromosome counts reported here are new, 14 confirm previous ones, and three report new ploidy levels.

SUBGENUS ABSINTHIUM DC

Artemisia caespitosa Ledeb. Russia, Republic of Tuva: Barun-Khemchinskii raion, plateau, right side of the Great Ienissei, in front of the Tais outfall, grassy semi-desert with other Artemisia species, A.A. Korobkov, 11.ix.2003 (LE-Korobkov). \( 2n = 18 \) (Fig. 1).
This is the first count for this species, an endemic of Mongolia and southern Russia. It is a diploid based on the most common basic chromosome number in the genus, x = 9.

**Artemisia davazamczii Sh. Darimaa & Kamelin**

Mongolia, Umnu (south) Gobi aimag: Bulgan sum, East Gurvan Saikhan mountains, canyon near Brigat, rocky slopes, *Sh. Darimaa, Sh. Tsooj & J. Vallès*, 1.ix.2004 (BCN 34488). 2n = 36 (Fig. 2).

Again we present a new count for this recently described species (Kamelin et al., 1992), endemic to Mongolian and Russian Altai.

**Artemisia sericea Web. ex Stechm.**

Mongolia, Bulgan aimag: Sansar sum, north-east slope of Khugunkhaan mountain, steppe near *Betula* and *Pinus* forest, 2000 m, *Sh. Darimaa, Sh. Tsooj & J. Vallès*, 25.viii.2004 (BCN 34486). 2n = 90 (Fig. 3).

This is the fourth count for the species, but the first for a Mongolian population. We report a decaploid x = 9-based cytotype. Previous studies, all in Russian populations, have presented mostly diploid or tetraploid cytotypes (Kawatani & Ohno, 1964; Stepanov, 1994), although Krogulevich & Rostovtseva (1984) reported 2n = 88. We consider that this last count corresponds to a hypo-aneploid decaploid population. We do not believe that this occurrence could be a result of dysploidy as all previous counts are based on x = 9 and it would be illogical to consider the count to be an 11-ploid based on x = 8. The different ploidy levels of this species confirm the relevance of ploidy polymorphism in the genus (Vallès & Garnatje, 2005; Vallès et al., 2005; and references cited therein).

**Artemisia xerophytica Krasch.**

Russia, Republic of Tuva: Erzinskii raion, north side of Tere-Khol lake, Tsuger-Ellis, sandy dunes with rare shrubs of *Caragana, A.A. Korobkov*, 13.ix.2003 (LE-Korobkov). 2n = 18 (Fig. 4).

According to our data, this is the first count of the chromosome number of this species, which occupies semi-desert steppes and dunes and has been traditionally used for sand stabilization and to make windbreaks.

**SUBGENUS ARTEMISIA L.**

**Artemisia blepharolepis Bunge**

Mongolia, Umnu (South) Gobi aimag: Bulgan sum, 1 km north of the sum, desert steppe, *Sh. Darimaa, D. Samjid, Sh. Tsooj & J. Vallès*, 26.viii.2004 (BCN 34490). 2n = 18 (Fig. 5).

This is the first count for this species, endemic to Mongolia and northern China. This taxon has been located in the subgenus *Artemisia* by most authors working on Mongolian flora (Grubov, 1982; Dariimaa, 1989), although Ling, Humphries & Shultz (2006) have included it in the subgenus *Dracunculus*, with which it shares some morphological characters. Further work is needed to clarify its relationships; molecular phylogenetic research on the subgenus *Dracunculus* (J. Pellicer, T. Garnatje & J. Vallès, unpubl. data) could throw light on this point in due course.

**Artemisia freyniana (Pamp.) Krasch.**

Russia, Primorskii krai: Khassanski raion, cape Gamov, pass to Vityaz bay, rocky ridge, meadows with shrubs, *A.A. Korobkov*, 15.x.2004 (LE-Korobkov). 2n = 18 (Fig. 6).

This is the first chromosome count for this endemic of Mongolia and eastern Russia.

**Artemisia insulana Krasch.**

Russia, Kamchatskaya oblast: Bering island, windy tundra with shrubs, V.V. Yakuvov, 20.viii.2003 (LE-Korobkov). 2n = 18 (Fig. 7).

This is the second report for the species, an endemic of eastern Russia. It agrees with one from the Komandorskie islands (Korobkov, 1981).

**Artemisia medioxima Krasch. ex Poljakov**

Russia, Khabarovskii krai: Baninskii raion, Tummin river basin, upper Akur river valley, base of rocky slopes, *Larix* and *Betula* forest, *A.A. Korobkov*, 21.x.2004 (LE-Korobkov). 2n = 144 (Fig. 8).

This is the second chromosome count for this species. The previous one (2n = 4x = 36) corresponds to a Mongolian population (Garcia et al., 2006). This is the first report of the 16x ploidy level in *Artemisia* and the subtribe Artemisiinae, and is the highest chromosome number ever counted in this plant group, which is confirmed by a high nuclear DNA content assessed by flow cytometry (J. Pellicer, T. Garnatje & J. Vallès, unpubl. data). To date, the highest ploidy level described for *Artemisia* L. was a unique case of a dodecaploid (x = 9, 2n = 108) counted in a Russian population of *A. macrantha* Ledeb. (Malakhova, 1990). However, chromosome numbers up to 2n = 171, 180, 198 have been described in the Asteraceae, in genera such as *Leucanthemum* L. and *Senecio* L. (Dowrick, 1952; Hedberg & Hedberg, 1977). Some *Artemisia* species have long ploidy series, such as, for instance, *A. dracunculus* L., with 2n = 18, 36, 54, 72, 90 (Kawatani & Ohno, 1964; Rousi, 1969; Vallès et al., 2001a). Polyploidy is a relevant evolutionary mechanism in plants (Bretagnolle et al., 1998, and references cited therein) and is especially active in some Anthemideae groups (Solbrig, 1977; Vallès et al., 2001a, b; and references cited therein). The present exceptional finding...
indicates the great genetic plasticity of the genus *Artemisia*. It also reinforces the importance of polyploidy as a process contributing to the diversification of these species in their areas of expansion. In this particular case, the plants inherit a herb-dominated community on open rocky slopes in a site being colonized after fire. The plants are clearly larger than those of other *A. medioxima* populations and present an extraordinary development of vegetative leaf rosettes. The ease of pioneer colonization might have caused a predominance of vegetative multiplication, which is often associated with a high ploidy level.

**Artemisia palustris** L.

Mongolia, Uvur-Khangai aimag: Khotont sum, 10 km east, margins of cultivated fields in steppe area, *Sh. Darimaa, Sh. Tsooj & J. Valles*, 26.viii.2004 (BCN 34847). 2n = 18 (Fig. 9).

This is the third count for this species and confirms the diploid cytotype based on x = 9 found previously by Volkova & Boyko (1986) and Wang et al. (1998) in Russian and Chinese populations, respectively. Our report is the first carried out on a Mongolian population.

**Artemisia selengensis** Turcz. ex Besser

Mongolia, Selenge aimag: Shaamar sum, 3 km west of Burk Tolze hills, near river Orkhon, 700 m, *Sh. Darimaa, Sh. Tsooj, J. Valles & E. Yatamsuren*, 9.ix.2004 (BCN 34489). 2n = 36 (Fig. 10).

The chromosome number of this widely distributed species has been counted by several authors (Shimotomai, 1946; Kawatani & Ohno, 1964; Lee, 1972; Volkova & Boyko, 1986; Hoshi et al., 2003) in Japanese, Russian, French (in material coming from a botanical garden), and Korean populations. Nevertheless, no data on any Mongolian population have been reported until now. The tetraploid x = 9-based cytotype agrees with the results from other geographical areas.

**Artemisia subulata** Nakai

Russia, Primorskiy krai: Ussuri river valley, near Kirovskii, slope of the valley of a creek, community with other *Artemisia* and herbs, A.A. Korobkov, 9.ix.2004 (LE-Korobkov). 2n = 54 (Fig. 11).

This record is the first for the species, distributed widely in Japan, Korea, and eastern Russia. This hexaploid level again supports polyploidization as an evolutionary factor contributing to speciation in the genus.

**Artemisia sylvatica** Maxim.

Russia, Primorskiy krai: Nadezhinskii raion, Razdolnaya river valley, near town Terekhovk, base of the coastal rocks, effusive block degradation, shrub community, A.A. Korobkov, 10.x.2004 (LE-Korobkov). 2n = 16 (Fig. 12).

Our report agrees with the two previously carried out by Volkova & Boyko (1986) and Probatova & Sokolovskaya (1988) in Russian populations. The species is a diploid based on x = 8, the other basic chromosome number of the genus, present in the subgenera *Absinthium*, *Artemisia*, and *Dracunculus* and less frequent than x = 9 (Solbrig, 1977; Schweizer & Ehrendorfer, 1983; Oliva & Vallès, 1994; McArthur & Sanderson, 1999).

**Artemisia umbrosa** Turcz. ex DC.

Russia, Primorskiy krai: Khassanskiy raion, cape Gamov, base of coastal rocks, community dominated by Poaceae and *Artemisia*, A.A. Korobkov, 16.x.2004 (LE-Korobkov). 2n = 50 (Fig. 13).

To our knowledge, this is the third count for the species. Two previous counts were by Hoshi et al. (2003) and Garcia et al. (2006) with different results for Russian (2n = 50) and Mongolian (2n = 54) populations, respectively. The Russian counts suggest aneuploidy from 2n = 6x = 54 (basic number x = 9), although both basic numbers (x = 8 and 9) are present in the *A. vulgaris* L. complex to which *A. umbrosa* belongs (Vallès & Garnatje, 2005). The records of 2n = 50 could be considered to indicate the presence of diplody if these changes were established widely in many populations of the species; however, we prefer the term aneuploidy because diplody would indicate a new basic chromosome number for the genus and, in this case, only two populations account for this number. The chromosome number 2n = 54 has also been reported in an eastern Russian population of *Artemisia dubia* Wall., which is another member of this complex (Volkova & Boyko, 1986).

**Subgenus Dracunculus** Besser

*Artemisia bargusinensis* Spreng.

Russia, Republic of Tuva: Pii-Khemskii raion, 60 km north–north-east of Turan, sloping grasslands with steppe, V. Nikitin, V. Byalt & A. Sytin (det. A.A. Korobkov), 11.viii.2002 (LE-Korobkov). 2n = 36 (Fig. 14).
This count agrees with the earlier counts, also on Russian populations, by Korobkov (1972) and Zhukova & Petrovsky (1987).

**Artemisia changaica** Krasch.
Mongolia, Arkhangai aimag: Taryat sum, Khorgo-Terkh National Park, larch forest above lake Terkhen Sagan nur, Sh. Dariimaa, Sh. Tsooj & J. Vallès, 27.viii.2004 (BCN 34487). $2n = 36$ (Fig. 15).
This is also the first count for this species.

**Artemisia depauperata** Krasch.
Russia, Republic of Tuva: Erzinskii raion, calcareous mountains beside Tes-Khem river, among small stones, A.A. Korobkov, 18.ix.2003 (LE-Korobkov). $2n = 36$ (Fig. 16).
This is the third count for this species, agreeing with Krogulevich (1978) and Garcia *et al.* (2006), reporting on Russian and Mongolian populations, respectively.

**Artemisia desertorum** Spreng.
Russia, Primorskii krai: Nadezhdinskii raion, Razdolnaya river valley, near Terekhovka, steep rocky slope on the right side of the valley, meadows in oak forest, A.A. Korobkov, 10.x.2004 (LE-Korobkov). $2n = 36$ (Fig. 17).
To our knowledge, this is the second count for this species. It agrees with a count on a Russian population by Volkova & Boyko (1985).

**Artemisia desertorum Spreng.**
Russia, Primorskii krai: Nadezhdinskii raion, Razdolnaya river valley, near Terekhovka, steep rocky slope on the right side of the valley, meadows in oak forest, A.A. Korobkov, 10.x.2004 (LE-Korobkov). $2n = 36$ (Fig. 17).
To our knowledge, this is the second count for this species. It agrees with a count on a Russian population by Volkova & Boyko (1985).

**Artemisia limosa** Koidz.
Russia, Sakhalin island: Magutan volcano, north of Yuzhno-Sakhalinsk, Y.S. Smirnov, 20.ix.2000 (LE-Korobkov 00-03). $2n = 18$ (Fig. 18).
There is a previous count for this Sakhalin endemic (Sokolovskaya, Probatova & Rudyka, 1985), where the

Figures 16–24. Somatic metaphases. Fig. 16. *Artemisia depauperata* ($2n = 36$). Fig. 17. *A. desertorum* ($2n = 36$). Fig. 18. *A. limosa* ($2n = 18$). Fig. 19. *A. manshurica* ($2n = 36$). Fig. 20. *A. oxycephala* ($2n = 18$). Fig. 21. *A. sphaerocephala* ($2n = 18$). Fig. 22. *A. subdigitata* ($2n = 36$). Fig. 23. *A. tomentella* ($2n = 36$). Fig. 24. *A. schrenkiana* ($2n = 18$). Scale bars, 10 μm.
diploid was described. Our results agree with this previous study.

*Artemisia manshurica* Kom.

Russia, Primorski krai: Muraviev-Amurskii peninsula, summit of the pass, steep slopes at the narrow crest, meadows with shrubs in a *Malus* forest, A.A. Korobkov, 21.x.2004 (LE-Korobkov). $2n = 36$ (Fig. 19).

To our knowledge, this is the fourth count for this species. All the earlier reports are from Chinese and Russian populations (Sokolovskaya *et al.*, 1985; Wang *et al.*, 2000; Hoshi *et al.*, 2003), and that presented here agrees with them.

*Artemisia oxycephala* Kitag.

Mongolia, Tuv (central) aimag: Mungunmort sum, 10 km south of the sum, Sh. Dariimaa, Sh. Tsooj, J. Vallès & E. Yatamasuren, 7.ix.2004 (BCN 34491). $2n = 18$ (Fig. 20).

Our result is the first on a Mongolian population of this species, showing the existence of the diploid cytotype based on $x = 9$. A previous count for this species reported the tetraploid level in plants from China (Wang, 2000; $2n = 36$).

*Artemisia sphaerocephala* Krasch.

Mongolia, Bulgan aimag: Dashin Shellen sum, 10 km north-west of the sum, near the Institute of Folk Medicine, steppe with *Caragana*, Sh. Dariimaa, Sh. Tsooj & J. Vallès, 24.viii.2004 (BCN 34485). $2n = 18$ (Fig. 21).

This is the third count for this desert steppe species traditionally used for windbreaks and sand stabilization. Ours is the first for Mongolian material, the two previous counts being on plants from Chinese populations and reporting the same chromosome number (Yan *et al.*, 1989; Qiao, Yan & Zhang, 1990).

*Artemisia subdigitata* Mattf.

Mongolia, Umnur (south) Gobi aimag: Bulgan sum, eastern Gurvan Saikhan mountains, canyon near Brigat, rocky slopes, Sh. Dariimaa, Sh. Tsooj & J. Vallès, 1.ix.2004 (BCN 34846). $2n = 36$ (Fig. 22).

Our count, the first for a Mongolian population, agrees with two reported from China by Yan *et al.* (1989) and Qiao *et al.* (1990). We have not found any diploid count for this taxon in the literature.

*Artemisia tomentella* Trautv.

Russia, Republic of Tuva: close to Erzin city, small population in a degraded field, A.A. Korobkov, 16.ix.2003 (LE-Korobkov). $2n = 36$ (Fig. 23).

This is the third count for this Central Asian endemic. The previous reports (Filatova, 1971; Magulaev, 1976) indicated the diploid and tetraploid cytotypes based on $x = 9$, and the present result confirms the latter.

**Subgenus Seriphidium** Besser

*Artemisia schrenkiana* Ledeb.

Russia, Republic of Tuva: Chegl-Kholskii raion, depression of the salt lakes Shara-Hur and Dus-Khol, 10 km west of Agar-Dag-Taiga mountain chain, saline soil on the shores of the lakes, A.A. Korobkov, 17.ix.2003 (LE-Korobkov) $2n = 18$ (Fig. 24).

To our knowledge, this is the second count for this species, endemic in Kazakhstan, Mongolia, and Russia. This report confirms the previous one (Filatova, 1975).

**CONCLUDING REMARKS**

All the species studied have chromosome numbers based on $x = 9$, except one, which is based on $x = 8$. This confirms the existence of two basic numbers in the genus (Vallès & Garnatje, 2005, and references cited therein) and further demonstrates the dominance of $x = 9$ in the genus, tribe, and family (Solbrig, 1977; Schweizer & Ehrendorfer, 1983; Oliva & Vallès, 1994; Vallès & Siljak-Yakovlev, 1997; Garcia *et al.*, 2006; and references cited therein). In this paper, we have reported many ploidy levels, ranging from $2x$ to the hitherto unknown $16x$, the highest known ploidy level in the genus, a finding which accounts for its great cytogenetic diversity. Polyploidy is considered by many authors as an important evolutionary mechanism in plants (Bretagnolle *et al.*, 1998; Soltis & Soltis, 1999; Soltis *et al.*, 2004). Most of the *Artemisia* that colonize extreme and arid habitats are polyploids. This fact supports the hypothesis that polyploids have more tolerance of extreme environmental conditions (Otto & Whitten, 2000). The high frequency of polyploids in the plants examined here (more than 50% of the studied populations) leads us to consider that *Artemisia* is continuously developing genetic and ecological evolutionary mechanisms leading to diversification and speciation, particularly in Asia, which is regarded as the main centre of diversification of the genus.

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