

Biogeography of the Genus *Linaria* (Plantaginaceae) Based on Chromosome Number Data

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Abstract

The biogeography of genus *Linaria* was revealed by the available chromosome counts from all over the world. Chromosome numbers of 92 taxa of the genus *Linaria* are included in an on-line karyological database. Furthermore, information about chromosome numbers taken from 374 literature sources was used in this paper. Each database record includes name of taxon, data on chromosome and data on the origin of the material and species-area distribution. Each database also provides a reported chromosome number and place of publication. More than half of the available species in chromosome data are diploid or consist of both diploid and polyploid populations and a few numbers of the species are polyploid. For the first time, in this study, mitosis and meiosis chromosome numbers of 13 populations belonging to three species, namely *L. lineolata* Boiss (2n = 2x = 12), *L. fastigiata* Chav. (2n = 2x = 12) and *L. dalmatica* (L.) Mill. (2n = 2x = 12), were determined by examining anthers. In addition, pollen stainability has been documented in *Linaria* populations in Iran.

Keywords: Chromosome numbers, Karyological database, *Linaria*, Pollen stainability, Polyploidy, Scrophulariaceae

Introduction

Toadflaxes (*Linaria* Miller) is the largest genus of the tribe Antirrhineae (Sutton, 1988). The tribe Antirrhineae as revised by Sutton (1988), consists of 27 genera representing 328 species. *Linaria* posses 200 species world wide, and it is widely distributed throughout the Northern hemisphere with its centre of distribution in the Mediterranean basin and eastern Asia (Hong, 1983). *Linaria* has about 30 species in Iran (Davis, 1982; Sutton, 1988), and comprises annual or perennial herbs with heteromorphic shoots. Flowers are arranged in bracteate racemes and have an accurate personate corolla. *Linaria* species have profuse glandular hairs with unicellular or insert stalks of varying length and heads usually composed of 1-4 cells. Small seeds of *Linaria* are enclosed in capsules, and may or may not be surrounded by an encircling wing. *Linaria* recognized with seven sections (*Diffuse*, *Linaria*, *Pelisseriana*, *Speciosae*, *Supinae*, *Macrocentrum* and *Versicolores*), mainly based on seed morphology (In the form and seed), and only useful reliable characters in the separation of these species are the morphology of seed surface and capsule. In this paper, we used cytotaxonomic

studies, that can be a powerful tool for investigating different evolutionary trends such as breeding system or polyploidy and hybridization. Cytological studies of *Linaria* species can provide useful information for the assessment of taxonomic relationships (Stace, 2000). The reported chromosome numbers species *Linaria* mainly are 2n = 12, with the exception of one octoploid *L. pelisseriana* (2n = 4x = 48). Valdes and Cabezudo (1977) determined basic numbers x = 6 for most of species of *Linaria* under review. *L. chalepensis* and *L. canadensis* var. *texana* with 2n = 24 (Heitz, 1927, Raven, 1963) and *L. helenica* with 2n = 24, 26 (Contandriopoulos and Yannitsaros, 1975) are tetraploid. The *L. cymbalaria* with seven pairs (East, 1933) and *L. sagittata* with nine pair bivalents in meiosis stage (Dalgaard, 1986) are exceptions in this genus and other species have six pair bivalents in meiosis stage. The small chromosomal variation exists within genus *Linaria* as the members of *L.* sect. *Supinae* subsect. *Supinae* which have been so far cytologically investigated are only diploids with x = 6 and 2n = 12 (Heitz, 1926, 1927a, b; Love and Kjellqvist, 1974; Cardona and Contandriopoulos, 1980; Sutton, 1988; Mayol et al., 1998). It should be mentioned that, the most species have more similar genome sizes. Due to the small chromosomal variation in

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Linaria, it is possible to use genome size value to separate some taxa in *Linaria*. An analysis indicates that members of *L.* sect. *Pelisseriana* present the highest value of genome size, as compared to *L.* sect. *Versicolores* present the lowest among other sections of *Linaria* (Castro et al., 2012). The present work aimed to increase the knowledge about cytogenetics and biogeography of the species and comparison of the basic chromosome numbers and polyploidy levels among the different species, which are distributed throughout the world. Such findings would help us to promote our understanding about the relationships between chromosomal criteria and taxonomic delimitation.

Materials and Methods

Description of Database

There are numerous databases on chromosome numbers available on-line. In this study, on-line database gathers data from published indices to plant chromosome numbers from 1926 onwards (1926-2009). The data are presented as they were published, without any attempt to make a taxonomic revision of the analysed plant material. The database currently contains 92 species taken from 374 literature sources. Also, there are numerous on-line or book reference based databases available describing the distribution of species. This on-line database or book reference gathers data from published indices on plant distribution from 1827 onwards (1827-2011). Records in the database includes the following data: (1) Name of the taxon (include the name of taxon as published in the original source, the standardized name) (2) Data on the voucher specimen (includes the collector(s) name(s), date of the collection, specimen number and the herbarium collection where it is deposited, species-area distribution, Voucher specimens are deposited in BASU, Hamedan, Iran) and (3) chromosomes (includes mitotic or meiotic chromosome number; ploidy level, detailed data on the locality where material was collected, along with its position in the World Geographical Scheme for Recording Plant Distributions (Brummitt, 2001)). Some chromosome records based online databases and literature are presented in table 1.

[see (<http://www.tropics.org/Project/IPCN>); (<http://www.rjb.csic.es/snapdragons/Paginas/Especie>); (<http://www.magrama.gob.es/es/biodiversidad/temas/inventarios>); (<http://www.botanicalkeys.co.uk/flora/content/species.asp>); (<http://www.floravascular.com>); (<http://www.binran.ru>); (vargas@rjb.csic.es)]

Table 1. List of *Linaria* species investigated for chromosome number and pollen fertility showing name species, chromosome number, locality, altitude (m), collector, no. voucher and % of pollen sterility.

Species	Voucher number	Locality	Alt. (m)	Collector	Percentage of sterility	2 n
<i>L. dalmatica</i>	27675 BASU	Hamedan, Toyserkhan, after Shahrestane	1940	RANJBAR and NOURI	11.67	-
<i>L. dalmatica</i>	33895 BASU	Arak to Malayer	1660	RANJBAR and NOURI	3.49	12
<i>L. fastigiata</i>	25021 BASU	Azerbaijan-e gharbi, Bookan toward Miandoab	1870	RANJBAR	3.35	12
<i>L. fastigiata</i>	27029 BASU	Lorestan. Dourud, beginning of Forest Park of Gahar.	1660	RANJBAR	1.73	12
<i>L. fastigiata</i>	27749 BASU	Kermanshah, Songor, 10 km after Songor	1600	RANJBAR and NOURI	8.45	12
<i>L. fastigiata</i>	29025 BASU	Kordestan, 5 km before of Salavat abad neck	1892	RANJBAR and NOURI	5.87	-
<i>L. fastigiata</i>	27213 BASU	Kermanshah, Songor toward qorveh, Kotchkineh village	2062	RANJBAR	18.31	12
<i>L. fastigiata</i>	27632 BASU	Kermanshah, Songor, Bavleh village	1840	RANJBAR and NOURI	23.29	12
<i>L. fastigiata</i>	27535 BASU	Hamedan, Babanazar village	1600	RANJBAR and NOURI	33.05	12
<i>L. fastigiata</i>	27188 BASU	Kermanshah, Songor toward Qorveh	2050	RANJBAR and NOURI	23.61	12
<i>L. fastigiata</i>	27081 BASU	Kordestan, Salavat Abad neck	1550	RANJBAR and NOURI	-	12
<i>L. fastigiata</i>	30150 BASU	Hamedan to Malayer, Karkan village	1840	RANJBAR	5.24	12
<i>L. fastigiata</i>	26573 BASU	Azerbaijan-e gharbi, Piranshahr toward Oshnaviyeh	1860	RANJBAR and NOURI	-	12
<i>L. fastigiata</i>	33045 BASU	Hamedan, Alvand Mt, Haydarreh village	1600	RANJBAR	14.35	12
<i>L. lineolata</i>	27473 BASU	Arak, Komeyjan to Vafs, 7 km after Vafs	715	RANJBAR	7.52	-
<i>L. lineolata</i>	25734 BASU	Azerbaijan-e gharbi, Mahabad	1890	RANJBAR	56.63	-
<i>L. lineolata</i>	30626 BASU	Zanjan, Nader Abad village, Deh-jalal neck, 8 km before Soltanieh	1940	RANJBAR	50.30	12
<i>L. lineolata</i>	29133 BASU	Hamedan to Zanjan.Qeydar to Khorkhoreh, 10 km after Qeydar.	1892	RANJBAR and NOURI	16.36	-

Cytogenetics

In angiosperms, with the beginning of the first meiotic division, the pollen mother cells are isolated from each other and from the tapetum by the thick layer of callose (Echlin and Godwin, 1968) and they become progressively enveloped in the layer of callose (β -1, 3-glucan) which characterizes a well-defined stage of pollen grain ontogeny (Waterkeyn, 1962; 1964). The thickness of the callose layer in different species is variable and *Linaria* species have a thick layer of callose in meiotic small cells (figures 1O).

The innermost cell layer of the anther wall in angiosperm species is tapetum layer, (Chaudhury, 1993; Wilson et al., 2001; Kapoor et al., 2002; Sorensen et al., 2002; 2003; Higginson et al., 2003). In *Linaria* species mitotic cells of this layer are different in shape, size and, presence or absence of the vacuole and its number (figures 1Q and R). The tapetum cells are usually bigger and normally have more than one nucleus per cell.

In this study, the mitotic chromosome numbers in anthers of 11 *L. fastigiata* populations, one *L. dalmatica* population and one *L. lineolata* population were studied. Randomly, selected flowers at the appropriate stage were collected for mitotic studies and fixed in 96% ethanol, chloroform and propionic acid (6: 3: 2) for 24 h at room temperature, and then washed and preserved in 70% ethanol at 4 °C until used. Microsporocytes were prepared by squashing and stained with 2% aceto-carmine. Chromosome numbers were counted in five individuals of each population during prophase. The mitotic chromosome association was evaluated in at least twenty cells. Mitotic stages were photographed by a BX-51 Olympus microscope equipped with a 3030 digital camera.

Pollen Fertility

Pollen fertility was studied in 10 populations of *Linaria fastigiata*, two populations of *L. dalmatica* and four populations of *L. lineolata*. Randomly flowers of dry plant were selected and then, pollen fertility results, presented in table 1, obtained using the aceto-carmine method. To determine pollen fertility, darkly stained pollen grains were recorded as fertile and viable, and unstained or very lightly stained ones were considered as sterile or non-viable. Pollen fertility was calculated by dividing the number of viable pollen grains over the total number of grains counted in the scope of view and then, averaging them for all plants in that species.

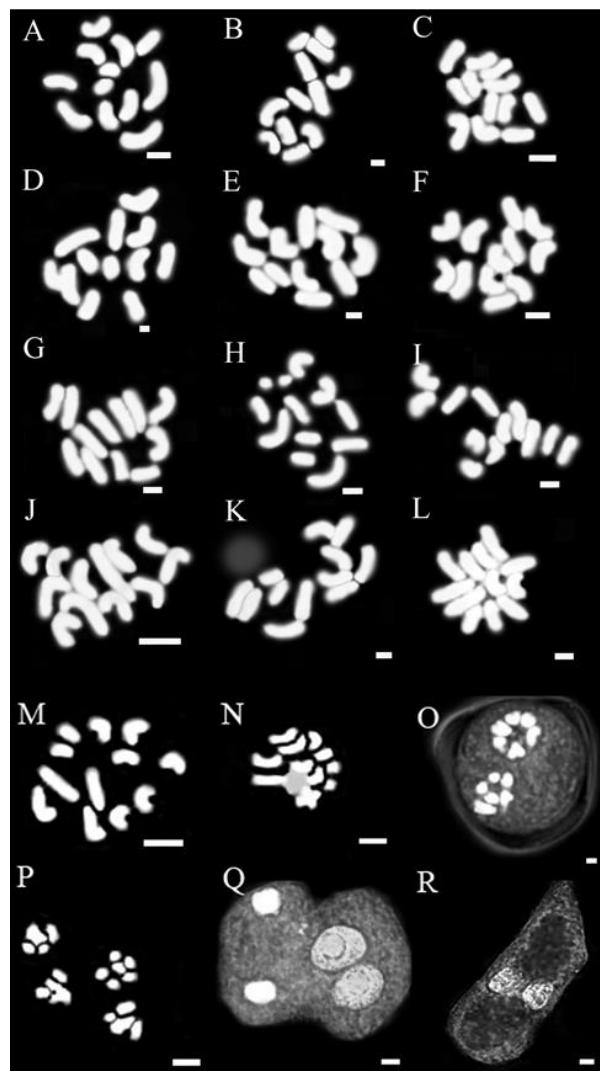


Figure 1. Representative meiotic and mitotic cells in different species of *Linaria* studied. $2n = 2x = 12$. (A) Prophase mitotic in *L. fastigiata* 27188, scale bar = 2 μ m, (B) Prophase mitotic in *L. fastigiata* 27213, scale bar = 2 μ m, (C) Prophase mitotic in *L. fastigiata* 27632, scale bar = 2 μ m, (D) Prophase mitotic in *L. fastigiata* 27749, scale bar=20 μ m, (E) Prophase mitotic in *L. fastigiata* 27081, scale bar = 1 μ m, (F) Prophase mitotic in *L. fastigiata* 27029, scale bar = 50 μ m, (G) Prophase mitotic in *L. fastigiata* 27535, scale bar = 2 μ m, (H) Prophase mitotic in *L. fastigiata* 26573, scale bar = 50 μ m, (I) Prophase mitotic in *L. fastigiata* 25021, scale bar = 20 μ m, (J) Prophase mitotic in *L. fastigiata* 33045, scale bar = 2 μ m, (K) Prophase mitotic in *L. fastigiata* 30150, scale bar = 1 μ m, (L) Prophase mitotic in *L. lineolata* 30626, scale bar = 2 μ m, (M) Prophase mitotic in *L. dalmatica* 33895, scale bar = 2 μ m, (N) Prophase mitotic in *L. fastigiata* 27188, scale bar = 50 μ m, (O) Telophase I meiotic with thick callose layer in *L. fastigiata* 27188, scale bar = 20 μ m, (P) Telophase II meiotic in *L. dalmatica* 33895, scale bar = 2 μ m, (Q) Telophase I mitotic without vacuoles in *L. fastigiata* 27188, scale bar = 50 μ m, (R) Telophase I mitotic with two vacuoles in *L. fastigiata* 27188, scale bar = 50 μ m.

Result and discussions

Chromosome Data Analysis

In this paper, the current databases have been described reporting for only 92 species out of 200 total species, counted for the genus *Linaria* throughout the world. Chromosome numbers so far reported for *Linaria* are $x = 6$, $x = 7$, $x = 9$, $x = 12$, $x = 13$, but the highest frequent chromosome number reported is $2n = 12$ (figures 2, 3B). European taxa are more intensively studied rather than those in other geographical areas. In this study, karyological data for diploidy and polyploidy percentages of the genus *Linaria* are represented as follows: 89% diploid, ca. 11% polyploid: among diploids, 82% ($x = 6$), 2% ($x = 7$) and 3% are ($x = 9$). In *Linaria* species, 3% are polyploid with $x = 12$ and only 1% probably aneuploid with $x = 13$ (figure 3B). Base chromosome number 7 was reported only for three species namely *L. cymbalaria* ($x = 7$), *L. triphylla* ($2n = 14$) and *L. rubrifolia* ($2n = 14$). Three species, namely *L. sagittata* ($2n = 18$), *L. ramosissima* ($2n = 18$) and *L. lamarckii* ($2n = 18$) have the base chromosome number 9 and 13 was accounted only for two species, namely *L. odorata* ($x = 13$) and *L. hellenica* ($2n = 26$). Sporophytic count was reported 15 only for one species, namely *L. melanogramma* ($2n = 15$) and the questionable $2n = 6$ only for one species, namely *L. nivea* Boiss. and Reut ($2n = 6$), which is collected from Spain that is cited in IOPB (Goldblatt 1984). Tetraploid level ($n = 12$) for *L. Simplex* was reported by Ghaffari et al. (2007). According to information, this is the first tetraploid chromosome count for *Linaria* species. However the chromosome number was reported for *L. simplex* only $2n = 12$ in ICPN index and in all over the world.

Also, we collected some *Linaria* material from the mountainous regions of Iran and resulted from analysis of mitotic chromosome anthers are summarized in table 1. The meiotic chromosome numbers were studied in 2 populations of *L. dalmatica* pertaining to *L. sect. Specioae*, 12 populations of *L. fastigiata* and 4 populations of *L. lineolata* belongs to *L. sect. Linaria*. All taxa have a chromosome number $2n = 12$ (figure 1). Also in Iranian species, we observed that meiotic cells were smaller and have a thick layer callose and mitotic cells were larger with different forms and sizes (figures 1O, Q and R) surrounded by 1–3 vacuoles. It is evident that after South European, Northern parts of Africa and Middle-East in Asia have more species of *Linaria* respectively. Iberica is a connective bridge between the three continents. It seems that the primary centres of diversity are

probably in Iberica with maximum species of the genus. All basic chromosome numbers ($x = 6, 7, 9, 12$ and 13) of *Linaria* are in southern Europe in the margin of the Mediterranean Sea (Luque and Lifante, 1992). In this article, we cannot separate species of the genus *Linaria* based on chromosome number in the different areas of the world, mainly due to difference between areas in these two cases (figure 2).

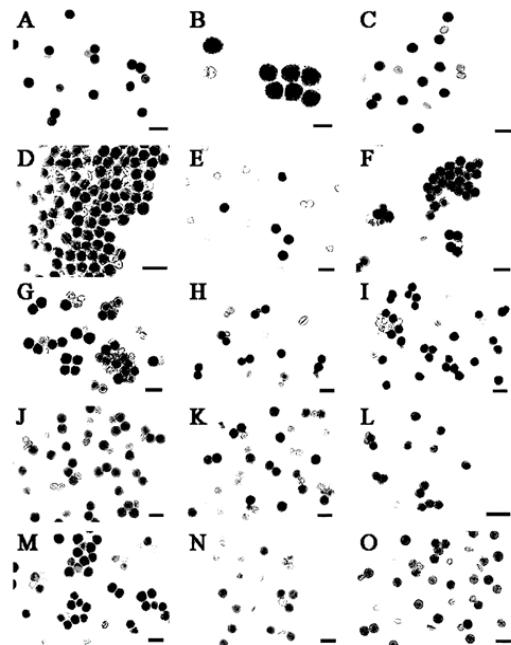


Figure 2. Fertility PMC. Cells in different species of *Linaria*. (A) *L. fastigiata* 25021, scale bar: 10 μ m, (B) *L. fastigiata* 33045, scale bar: 20 μ m, (C) *L. dalmatica* 33895, scale bar: 200 μ m, (D) *L. lineolata* 25734, scale bar: 10 μ m, (E) *L. fastigiata* 27535, scale bar: 20 μ m, (F) *L. fastigiata* 27029, scale bar: 200 μ m, (G) *L. lineolata* 30626, scale bar: 20 μ m, (H) *L. lineolata* 29133, scale bar: 200 μ m, (I) *L. fastigiata* 27632, scale bar: 20 μ m, (J) *L. fastigiata* 27213, scale bar: 20 μ m, (K) *L. fastigiata* 27188, scale bar: 200 μ m, (L) *L. lineolata* 27473, scale bar: 10 μ m, (M) *L. dalmatica* 27675, scale bar: 20 μ m, (N) *L. fastigiata* 29025, scale bar: 20 μ m, (O) *L. fastigiata* 27749, scale bar: 20 μ m.

There are $n = 6$ in all ten geographical zones ((Europe-Asia: South-Center Europe, Northern parts of Europe-Siberia, South West Asia, Far East), (America: Northern parts of America, Canada, southern parts of America), (Africa: South-center, North) and Australia), $n = 7$ in the Northern hemisphere New World and the Mediterranean margin, $n = 9$ in the Mediterranean margin and Southwest Asia of Old World and ploidy levels of $n = 12, 13$ in the Mediterranean margin, Southwest Asia and the Northern hemisphere New World. We have proposed that speciation in *Linaria* cannot be very old and with the exception of $n = 6$, other chromosome numbers already have been

engendered and until now an opportunity for distribution of the genus has not been found. However, there are 82% of diploid species with $x = 6$ and less than 20% with other levels ($x = 3, 7, 9, 12, 13, 15$) in this genus (figure 3).

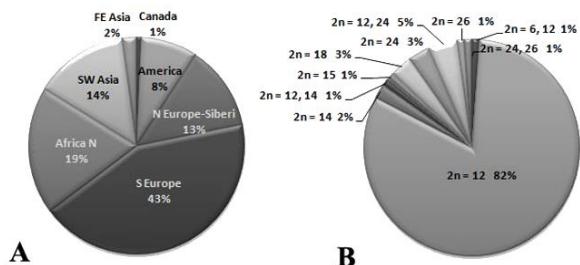


Figure 3. (A). Percent frequency variable chromosome numbers in all over world, (B). Percent distribution species within the genus *Linaria* from all over the world for the species have chromosome report.

Pollen Fertility

For the plant taxonomists pollen fertility is valuable in attempting to distinguish putative hybrids from the parent plants and is also useful to determine the degree of fertility in those plants that are grown under unfavourable conditions (Lawrence, 1969). Several investigators have presented evidence indicating a correlation between the percentage of normal pollen grains and the ultimate fertility of hybrid plants (Poole, 1931). However, pollen fertility can generally high in both diploids and tetraploids and cannot distinguish diploid from polyploid (Qureshi et al., 2009). The assumption of these estimates is that pollen grains that are potentially fertile (its mean that they have no problem of sterility because of meiotic abnormality) will absorb the stain and the sterile ones will appear hollow in the microscope (figure 4). Pollen stainability has measured since 1.73 up to 56.63 in 16 diploid populations include 10 populations of *L. fastigiata* that pollen stainability has measurements consist of: (1.73, 3.35, 5.24, 5.87, 8.45, 14.35, 18.31, 23.29, 23.61, 33.05) with average 13.72% of this species. Two populations of *L. dalmatica*, which pollen stainability has measurements consist of: (3.49, 11.67) with average 7.58% of this species and in four populations of *L. lineolata* pollen stainability has measurements consist of: (7.52, 16.36, 50.30, 56.63) with average 32.70% of this species, all investigated species were diploid (table 1). In spite of our interest to do a review for polyploids population, we couldn't find any polyploid population in Iran.

Note: We have prepared two analyses, one based on the distribution of all *Linaria* species in the

world (Fig 4), and another based on the distribution of species that have reported chromosome numbers which are presented in the literature (Fig 3).

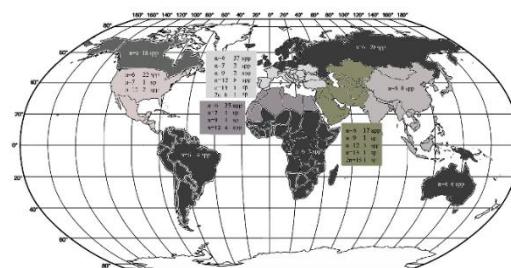


Figure 2. Map ploidy distribution within the genus *Linaria* in all over the world ($n = 6, n = 7, n = 9, n = 12, n = 13, 2n = 6, 2n = 15$), for all regions that name species have reported.

Distribution of the Genus *Linaria*

Interpretations of the cytogenetic differences between Old and New World of *Linaria* have not varied widely. In this paper, distribution of genus *Linaria* studied in ten zones (Europe-Asia: South-Center Europe, Northern parts of Europe-Siberia, South West Asia, Far East), (America: Northern parts of America, Canada, southern parts of America), (Africa: South-center, North) and Australia. Europe-Asia has 130 species of the genus *Linaria*: (28 species in Northern parts of Europe-Siberia, 8 species in the Far East, 23 species in South West Asia and 71 species in South-Center Europe). It is also continental America has 47 species: (18 species in Canada, 4 species in southern parts of America, 25 species in Northern parts of America) and continental Africa has 43 species: (2 species in South Africa and 41 species in Northern parts of Africa). The latter continental Australia has 6 species of this genus (figure 2). Also Mediterranean region has presently 135 species (South-Center Europe (71 spp.), Northern parts of Africa (41 spp.) and South West Asia (23 spp.). Distributions of *Linaria* species that have chromosome reports studied in 7 zones: South-Center Europe, Northern parts of Europe-Siberia, South West Asia, Far East, Northern parts of America, Canada and Northern parts of Africa. Among taxa that have chromosome number records, 56% in Europe-Siberia (Northern parts of Europe-Siberia (13%) and South-Center Europe (43%)); 16% in Asia (Far East (2%) and South West Asia (14%)), 9% in continental America (America (8%) and Canada (1%)) and 19% of species occur in Northern parts of Africa (segmentations of geographic areas in figure 3A are according to author). It should also be mentioned that Mediterranean region (South-Center Europe (43%), Northern parts of Africa (19%) and South

West Asia (14%) have 76% of the chromosome number records.

Biogeography

The geographical distribution of the taxa belonging to the genus *Linaria* was obtained from online databases and atlases mainly based on their localities taken from floras and literatures that mapped here (Hamdi and Assadi, 2011; Boissier, 1888; Borgmann, 1964; Davis, 1982; Dumortier, 1827-1830; Hansen and Sunding, 1993; Hooker, 1884; Kuprianova, 1950; Parsa, 1949; Press and Short, 1994; Saez Bernal, 2009; Sanchez-Gullon et al., 2006; Valdes, 1978-1986; Vicioso, 1946) (figure 4). Cytological evidences have not indicated a distinction between Old and New World of *Linaria*. Based on a recent survey (table 2, figure 3B) of the 92 old species for which chromosome numbers have been determined, counts of $x = 6$ have been reported for 83 species, $n = 7$ for 3 species, $n = 9$ for 3 species, $n = 12$ for 9 species and $n = 13$ for 2 species that some of these are questionable due to discrepancies in samples from the same species and among authors. Among 7 geographic zones for the genus *Linaria* that have reported chromosome numbers in the literature, 71 species occur in southern parts of Europe which 80.28% of species with $n = 6$, 2.81% of species with $n = 7$, 2.81% of species with $n = 9$, 11.26% of species with $n = 12$ and 1.40% of species with $n = 13$. 41 species of the genus *Linaria* occur in Africa, including 85.36% of species with $n = 6$, 2.43% of species with $n = 7$, 2.43% of species with $n = 9$ and 9.75% of species with $n = 12$. Among the 23 bechanted species of *Linaria* in Asia, 73.91% of species with $n = 6$, 4.34% of species with $n = 9$, 13.04% of species with $n = 12$, 4.34% of species with $n = 13$ and 4.34% of species with $2n = 15$. New world species having $n = 6, 7$ and 9 and higher chromosome numbers are derived from species with $n = 12$. 25 species of *Linaria* occur in America, including 88% of species with $n = 6$, 4% of species with $n = 7$ and 8% of species with $n = 12$. 28 species of the genus *Linaria* arise in the centre and Northern parts of Europe and Siberia, that all of the species have $n = 6$. 8 species of *Linaria* bechance in the Far East, which $n = 6$ have been reported for all of them. 18 species of *Linaria* arise in Canada and $n = 6$ have been reported for all of them. Among three geographic zones for the genus *Linaria* with no reported chromosome numbers, two species occur in southern parts of Africa (with $n = 6$ in zones which have chromosome number report), four species of the genus *Linaria* occur in southern parts of America

(with $n = 6$ for all of the species in zones which have chromosome number reports), and 6 species of the genus *Linaria* occur in Australia (with $n = 6$ for all of the species in zones which have chromosome number report).

Chromosome Evolution in *Linaria*:

Linaria distributed primarily in regions of the Northern hemisphere. The Mediterranean basin only encompasses 1.6% of the earth's surface (Melendo et al., 2003). A remarkable spatial and temporal complexity made the Mediterranean basin an ideal geographic framework for this approach. The complex Iberian orography may have allowed partial differentiation of lineages in allopatry that may have been the framework for *Linaria* and many other southern European plant groups (Feliner, 2011). The *Linaria* distribution centre is placed on the Iberian Peninsula of South Western Europe and it is probably evolved from the Mediterranean in response to various selection pressures toward different regions of the World (Valdes, 1970). There is no regular pattern in the distribution of the genus, as in this research, we cannot separate species of *Linaria* based on either distribution section and chromosome number in the world, because there is not difference between areas in these two cases. The commonly reported base chromosome in the genus are 6, 7 and 9, with a polyploid series of tetraploid being developed on $x = 6$. There are a few previous reports of tetraploid numbers based on $x = 6$. The chromosome number $n = 12$ was reported for eight species, namely *L. kocianovichii*, *L. miller*, *L. hellenica*, *L. chalepensis*, *L. pelisseriana*, *L. canadensis* var. *texana* (L.), *L. angustissima* and *L. arcusangeli* that most of the species are annual and only one species is perennial, since annual species have higher selfing rates than perennials. Generally, polyploidy is one of the prominent and significant forces in plant evolution (Leitch and Bennett, 1997; Otto and Whitton, 2000; Soltis and Soltis, 2000; Wendel, 2000; Liu and Wendel, 2003). It is a process of genesis and maintenance of plant diversity play a role in Scrophulariaceae s.l. in the Iberian Peninsula, but apparently is not among the main mechanisms of current speciation in now *Linaria* places in Plantaginaceae. (Castro, 2011). However, sociological studies of the *Linaria* species growing in Iran, also indicate that polyploidy are not a common phenomenon within this genus (Ghaffari 2006, Ghaffari et al. 2007). In studies conducted so far in *Linaria*, all polyploid species are in the Mediterranean margin and only one species is in the New World (table 2).

Table 2. Chromosome number reports in the genus *Linaria* (* = diploid, ** = aneuploid, *** = polyploid, 4* = haploid, 5* = hybrid)

Species	Section	A reference article reports Chromosome number	Locality species	Locality species that chromosome number reported	2N
<i>Linaria acutiloba</i> Fisch. ex Rchb.	?	http://www.binran.ru	Asia	Asia: Russia, East Siberia	12*+ 0-4B
<i>L. aeruginea</i> (Gouan) Cav.	<i>Supinae</i>	Chater et al. 1972, Cardona and Contandriopoulos 1980, Love and Kjellqvist 1974	N Europe	SW Europe	12*
<i>L. albifrons</i> (Sibth. and Sm.) Spreng	<i>Diffusae</i>	Chater et al. 1972, Snogerup 1985, Diaz Lifante et al. 1992	Asia, Europe, Africa, Australia	SW Europe	12*
<i>L. algarviana</i> Chav.	<i>Versicolores</i>	http://www.rjb.csic.es/snapdragons ; http://www.floravascular.com , Chater et al. 1972, Viano 1974, Viano 1973	Europe	SW Europe	12*
<i>L. alpina</i> (L.) Mill.	?	http://www.rjb.csic.es/snapdragons ; Chater et al. 1972, Murin and Paclova 1986, Dobeau et al. 1996, Heitz 1927a, Favarger and Huynh 1964, Lovka et al. 1971, Fernandes et al. 1977	Asia, Europe	C and S Europe	12*
<i>L. amethystea</i> (Lam.) Hoffmanns. and Link	<i>Supinae</i>	Chater et al. 1972, Pastor et al. 1988, Fernandes et al. 1977, Valdes 1969, Van Loon and De Long 1978	Europe, Africa	SW Europe, Africa	12*
<i>L. amoī</i> campo ex Campo and Amo	<i>Supinae</i>	http://www.rjb.csic.es/snapdragons , Chater et al. 1972, Valdes 1969, 1970b	Europe, Africa	SW Europe	12*
<i>L. angustissima</i> (Loisel.) Borbás	<i>Linaria</i>	http://www.rjb.csic.es/snapdragons ($2n = 12$), http://www.floravascular.com ($2n = 12$), Chater et al. 1972 ($2n = 12$), Uhrikova et al. 1983 ($2n = 12$), Majovsky 1974 ($2n = 24$)	Europe, America, Asia	Mediterranean region, SW Asia	12*, 24***
<i>L. anticaria</i> Boiss. and Reut.	?	http://www.rjb.csic.es/snapdragons ; Luque and Lifante 1991, Heitz 1926; 1927a, Valdes 1970b	Europe	SW Europe	12*
<i>L. arcuangelii</i> Atzei and Comarda	?	Bacchetta 2001 ($2n = 12$), Atzei and Camarda 1984 ($2n = 24$)	Europe	Europe: Mediterranean	12*, 24***
<i>L. arenaria</i> DC.	?	http://www.magrama.gob.es/gob.es/es , Serrano Perez and Carvajal Villaverde 2004	Europe	SW Europe	12*
<i>L. arvensis</i> (L.) Desf.	<i>Supinae</i>	http://www.rjb.csic.es/snapdragons , Chater et al. 1972, Heitz 1927a, Löve and Kjellqvist 1974, Van Loon and Dejong 1978	Europe, Africa, Asia	S, W and C Europe, NW Africa, SW Asia	12*
<i>L. balbata</i> Dieter	?	Matsura et al. 1935	Asia: Japan	Asia: Japan	12*
<i>L. bipartita</i> (Vent.) Willd.	<i>Macrocantrum</i> or <i>Versicolores</i>	Verma and Dhillon 1967, Heitz 1926, Chandran and Bhavanandan 1983, Nazeer et al. 1980	Asia, Africa	N African: W Morocco	12*+ 0-1B
<i>L. broussonnetii</i> Chav.	<i>Versicolores</i> ?	East 1933	Africa, America	America: Massachusetts	12*
<i>L. bubanii</i> Font Quer	<i>Supinae</i>	Chater et al. 1972, Montserrat Marti 1981-1982	Europe	SW Europe	12*
<i>L. caesia</i> DC. ex Chav.	<i>Supinae</i>	http://www.rjb.csic.es/snapdragons , Valdes 1970b, 1973, Chater et al. 1972, Van Loon and De Long 1978	Europe	SW Europe	12*
<i>L. canadensis</i> (L.) Dum. Cours.	<i>Macrocantrum</i> or <i>Versicolores</i>	Kapoor et al. 1987 ($2n = 12$) (report for <i>Nuttallanthus canadensis</i> (L.) D. A. Sutton, Raven 1963 ($2n = 24$))	America: Mexico and Texas, Hawaii Asia cult.	America	12*, 24***
<i>L. capraria</i> Moris and De Not.	?	http://www.rjb.csic.es/snapdragons , Heitz 1927a, 1927b, Signorini et al. 2001	Europe	S Europe	12*
<i>L. cavanillesii</i> Chav	<i>Diffusae</i>	Boscaiu et al. 1997	Europe	SW Europe	12*
<i>L. chalepensis</i> (L.) Mill.	<i>Macrocentrum</i>	http://www.floravascular.com , http://www.rjb.csic.es/snapdragons , Heitz 1926, 1927b, Ghaffari 2006, Chater et al. 1972	Europe, Asia, Africa, Australia	Mediterranean region	24***
<i>L. clementei</i> Haenseler ex Boiss.	<i>Versicolores</i>	http://www.floravascular.com , Chater et al. 1972, Viano 1979	Europe	SW Europe	12*
<i>L. corifolia</i> Desf.	?	http://www.rjb.csic.es/snapdragons , Viano 1972	Asia	SW Asia, Russia	12*
<i>L. cymbalaria</i> (L.) Mill.	?	East 1933, Chatterjee et al. 1989	America: Mexic Europe	America: Massachusetts	14**

<i>L. dalmatica</i> (L.) Mill.	<i>Linaria</i>	Vujnovic and Wein 1996, Gervais 1981, Heitz 1926, Valdes 1970b, Chuang and Heckard 1992	America, SW Asia, S, C Europe, far East, Australia	America: Canada, SE, SC Europe, SW Asia	12*
<i>L. debilis</i> Kuprian	<i>Linaria</i>	Rostovtseva et al. 1981	Asia	Asia: Siberia	12*
<i>L. diffusa</i> Hoffmanns. and Link	<i>Supinae</i>	http://www.rjb.csic.es/snapdragons, Fernandes et al. 1977, Chater et al. 1972	Europe	N, C and SW Europe	12*
<i>L. elegans</i> Cav	<i>Versicolores</i>	http://www.rjb.csic.es/snapdragons, http://www.floravascular.com, Heitz 1926, Chater et al. 1972	N Europe, Asia, Africa	Mediterranean region, SW Asia	12*
<i>L. faucicola</i> Leresche and Levier	?	Valdes 1978	Europe	SW Europe	12*
<i>L. flava</i> (Poirer) Desf.	?	Verlaque et al. 1992	Europe, Africa	Europe: Zurich	12*
<i>L. genistifolia</i> (L.) Mill.	<i>Speciosae</i>	http://www.rjb.csic.es/snapdragons, Buttler 1981, Jasiewicz and Mizianty 1975, Kiehn et al. 1991, Van Loon and Setten 1982, Dobeal et al. 1997, Javourkova-Jarolimova 1992, Heitz 1926, Valdes 1970b, Van Loon and Van Setten 1982	Europe, Asia: Far East, America	SE Europe, Asia: Anatolia, Russia	12*
<i>L. glacialis</i> Boiss.	<i>Supinae</i>	Küpfer 1968	Europe	SW Europe	12*
<i>L. glauca</i> (L.) Chaz.	<i>Supinae</i>	Baltisberger and Charpin 1989, Valdes 1978	Europe	SW Europe	12*
<i>L. haelava</i> (Forssk.) Delile	?	Diaz Lifante et al. 1992	Africa, SW Asia, Australia	Mediterranean	12*
<i>L. hellenica</i> Turrill	?	http://www.rjb.csic.es/snapdragons (2n = 24, 26), Contandriopoulos and Yannitsaros 1975 (2n = 24, 26)	Europe	SW Europe	24**, 26***
<i>L. heterophylla</i> Desf.	?	East 1933, Rossitto et al. 1983, Devesa et al. 1984, Silvestre 1991, Galland 1988	Europe, Africa, Asia, America: Massachusetts	America: Massachusetts	12*
<i>L. hirta</i> (L.) Moench.	<i>Diffusae</i>	http://www.rjb.csic.es/snapdragons, http://www.floravascular.com, Viano 1973; 1974, Löve and Kjellqvist 1974, Chater et al. 1972, Luque and Lifante 1991	Europe, Africa, Asia	C, S Europa and Mediterranean, NW Africa, SW Asia	12*
<i>L. huteri</i> Lange	<i>Supinae</i>	Chater et al. 1972, Viano 1973	Europe	Europe and Mediterranean	12*
<i>L. incarnata</i> Spreng.	<i>Versicolores</i>	http://www.rjb.csic.es/snapdragons, http://www.floravascular.com, Chater et al. 1972, Silvestre 1991, Valdes 1969; 1970b, Fernandes et al. 1977	Europe, N Africa, America	SW Europe and Mediterranean	12*
<i>L. japonica</i> Miq.	<i>Diffusae</i>	Karol Marhold 2008, Probatova and Sokolovskaya 1981	Asia: Russia, Far East	Asia: Russia, Far East	12*
<i>L. kocianovichii</i> Asch.	?	Murin et al. 1999	Europe	S, C Europe	24***
<i>L. lamarckii</i> Rouy	?	Caixinhas et al. 1991	Europe	SW Europe	18**
<i>L. Lineolata</i> Boiss.	<i>Linaria</i>	http://www.rjb.csic.es/snapdragons, Heitz 1927a	Asia	SW Asia	12*
<i>L. macroura</i> (Bieb.) Link	<i>Linaria</i>	http://www.rjb.csic.es/snapdragons, East 1933, Heitz 1926	Asia, Europe America: Massachusetts	America: Massachusetts, SE Europe, Asia: Russia	12*
<i>L. maroccana</i> Hooker fil.	<i>Versicolores</i>	http://www.rjb.csic.es/snapdragons, East 1933, Heitz 1926	N Africa, Europe, Americae: Massachusetts, Australia	America: Massachusetts, N Africa:	12*
<i>L. melampyroides</i> Kuprian.	<i>Linaria</i>	Probatova 2006	Asia: Siberia	Asia: Moscow, Leningrad	12*
<i>L. melanogramma</i> Rech. f. and al.	?	Aryavand 1983	Asia	Asia: Iran	15** or 5*
<i>L. meyeri</i> Kuprian.	<i>Linaria</i>	Gagnidze 2006	Asia	Asia: Moscow, Leningrad	12*
<i>L. michauxii</i> Chav.	<i>Linaria</i>	http://www.rjb.csic.es/snapdragons, Aryavand 1977	Asia	Asia: Iran.	12*
<i>L. micrantha</i> (Cav.) Hoffmanns. and Link	<i>Supinae</i>	http://www.rjb.csic.es/snapdragons, Löve and Kjellqvist 1974, Fernandes et al. 1977, Chater et al. 1972, Valdes 1978	N Europe, Africa, Asia	S Europe, Mediterranean, SW Asia, N Africa	12*
<i>L. miller</i> Gard	?	http://www.rjb.csic.es/snapdragons	Europe, Asia, Africa	Europe, Asia, Africa	12*, 24***

<i>L. nivea</i> Boiss. and Reut.	<i>Speciosae</i>	http://www.floravascular.com ($2n = 12$), Chater et al. 1972 ($2n = 12$), Elena Rossello et al. 1984, 1986 ($2n = 12$), Viano 1975 ($2n = 6$)	N Europe, Africa, Asia	Mediterranean region and Europe, Africa, SW Asia	12* 6? ^{4*}
<i>L. oblongifolia</i> Boiss. and Reuter	<i>Supinae</i>	Chater et al. 1972, Viano 1979, Valdes 1969	N Europe	SW Europe	12*
<i>L. odorata</i> M. Bieb.	<i>Linaria</i>	Chatterjee et al. 1989	Europe, Asia	Asia: Himalayan	26***
<i>L. oligantha</i> Lange	<i>Supinae</i>	Chater et al. 1972, Valdes 1978	Europe	SW Europe	12*
<i>L. orbensis</i> Carretero and Boira	<i>Supinae</i>	Chater et al. 1972, Mayol and Rosello 1998	Europe	SW Europe	12*
<i>L. pallidiflora</i> (Lam.) Valdés	<i>Linaria?</i>	http://www.floravascular.com	Europe: Slovenská	SW Europe	12*
<i>L. panticii</i> Janka ex Nyman	?	East 1933	Asia: Alaska, America: Massachusetts	Americae: Massachusetts	12*
<i>L. pedunculata</i> (L.) F. Dieter.	<i>Versicolores</i>	http://www.rjb.csic.es/snapdragons , http://www.floravascular.com , Chater et al. 1972, Vogt and Oberprieler 1994, Viano 1975; 1979	Europe, N Africa	Mediterranean Europe, NW Africa	12*
<i>L. pelisseriana</i> (L.) Miller	<i>Pelisseriana e Supinae</i>	http://www.rjb.csic.es/snapdragons , http://www.botanicalkeys.co.uk/flora , http://www.floravascular.com , Ward et al. 2009, Chater et al. 1972, Strid and Franzen 1981, Verlaque et al. 1997, Larsen and Laegaard 1971, Dahlgren et al. 1971, Strid 1981	Europe, Africa, Asia, Australia, America	C and E Mediterranean region, W Europe, N. Africa	24***
<i>L. peloponesiaca</i> Boiss. and Heldr.	?	Baltisberger 1987, Baltisberger and Baltisberger 1995, Strid and Franzen 1981	Europe	S. Europe	12*
<i>L. peltieri</i> Batt.,	?	http://www.rjb.csic.es/snapdragons , Reese 1957	Europe, Africa	SW Europe, N. Africa	12*
<i>L. perezii</i> J.Gay	?	East 1933	Europe, America: Massachusetts	Americae: Massachusetts	12*
<i>L. platycalyx</i> Boiss.	<i>Supinae</i>	Chater et al. 1972, Aparicio Martinez 1993	Europe, Africa	SW Europa	12*
<i>L. polygalifolia</i> Hoffmanns. and Link	<i>Supinae</i>	http://www.rjb.csic.es/snapdragons , Chater et al. 1972, Castroviejo and Lago 1990, Valdés 1973, Viano 1974, Fernandes and Queiros 1971, Fernandes et al. 1977, Lago Canzobre and Castroviejo 1993	Europe, America	S, W, SW and NW Europa	12*
<i>L. pseudolaxiflora</i> Lojac.	?	http://www.rjb.csic.es/snapdragons , Bartolo et al. 1981	Africa, Europe	Europe: Madrid	12*
<i>L. pseudoviscosa</i> Murb.	<i>Versicolores</i>	http://www.rjb.csic.es/snapdragons , Viano 1975	Africa	N and C Africa	12*
<i>L. purpurea</i> (L.) Mill.	<i>Linaria?</i>	http://www.botanicalkeys.co.uk/flora , Colombo et al. 1978, Heitz 1926, Valdes 1970b, Fernandes et al. 1977	N Europe, America, Africa	S Europa	12*
<i>L. ramosissima</i> Wall.	?	Verma and Dhillon 1967	Asia	Asia	18**
<i>L. reflexa</i> Desf.	<i>Diffusae</i>	Goldblatt 1984	Africa, Europe, Asia	W Mediterranean	12*
<i>L. repens</i> (L.) Mill.	<i>Speciosae</i>	http://www.rjb.csic.es/snapdragons , http://www.floravascular.com , http://www.botanicalkeys.co.uk/flora , Chater et al. 1972, Mateu and Mansanet 1982, Boscaiu et al. 2000, Heitz 1926, Valdés 1969; 1970b, Löve and Kjellqvist 1974, Fernandes et al. 1977, Laane and Lie 1985	N Europe, America, Asia	W, NW and C Europe	12*
<i>L. reticulata</i> Desf.	?	East 1933	Africa, America: Massachusetts	America: Massachusetts	12*
<i>L. rubrifolia</i> Robill and Cast. ex DC.	<i>Chaenorhinum</i>	Cardona 1991	Africa, Europe	Mediterranean	14**
<i>L. sagittata</i> (Poir.) Steud., Syn. <i>Kickxia heterophylla</i> (Schousb) Dandy	?	Vilhelm Dalgaard 1986, Podlech 1986, Aldridge and Ortega 1976	Africa: Sahara, Europe: Canary Islands, Asia: Macaronesia, America: Macaronesia, America	America: Massachusetts, Asia: Macaronesia, and SW, N Africa, Europe: Eastern	18**

				Canary Islands and Sahara	
<i>L. salzmannii</i> Boiss	<i>Versicolores</i>	http://www.rjb.csic.es/snapdragons, http://www.floravascular.com, Viano 1974, Chater et al. 1972	Europe	SW Europe	12*
<i>L. saxatilis</i> (L.) Hoffmanns. and Link	<i>Supinae</i>	http://www.rjb.csic.es/snapdragons, Chater et al. 1972, Baltisberger and Charpin 1989, Caixinhas et al. 1991, Heitz 1926, 1927a, East 1933, Valdés 1969, 1970b, Fernandes et al. 1977	Europe, Africa	C, N and SW Europe	12*
<i>L. simplex</i> Desf.	<i>Supinae</i>	http://www.rjb.csic.es/snapdragons, Chater et al. 1972, Snogerup 1985, Valdes 1969; 1970b; Ghaffari and Tajik 2007	SW Asia, Europe, Africa	S Europe, N Africa, SW Asia, S Russia	12*
<i>L. spartea</i> (L.) Hoffmanns. and Link	<i>Macrocentrum Versicolores</i>	http://www.rjb.csic.es/snapdragons, http://www.floravascular.com, Viano 1973; 1974, Heitz 1927a, Fernandes et al. 1977, Chater et al. 1972, Love and Love 1982, Diosdado et al. 1993	N Europe, America	C, SW Europe	12*
<i>L. striatella</i> Kuprian	<i>Linaria</i>	http://www.rjb.csic.es/snapdragons, Aryavand 1983	Asia	C. and SW Asia, Russia	12*
<i>L. supina</i> (L.) Chaz.	<i>Supinae</i>	http://www.rjb.csic.es/snapdragons, http://www.botanicalkeys.co.uk/flora, Heitz 1927a, Valdes 1973, Fernandez Casas et al. 1980a, Fernandez Casas and Perez-Chao 1978, Fernandez et al. 1977, Cardona 1977	Europe, Africa, SW Asia America	SW Europe	12*
<i>L. tenuis</i> Spreng.	<i>Versicolores</i>	Diaz Lifante et al. 1992	Africa, Asia: Middle East	Mediterranean: N Negev	12*
<i>L. texana</i> Scheele	?	Ward 1983	America	America: New Mexico and southern Colorado	12*
<i>L. tingitana</i> Boiss. and Reuter	?	http://www.rjb.csic.es/snapdragons, Humphries et al. 1978	Europe, Africa	SW Europe, NW Africa	12*
<i>L. triornithophora</i> (L.) Willd.	<i>Pelisseriana</i>	http://www.rjb.csic.es/snapdragons, http://www.floravascular.com, Chater et al. 1972, Vazquez et al. 2001, Heitz 1926, Queiros and Santos 1977, Van Loon and Dejong 1978	Europe	SW Europe	12*
<i>L. triphylla</i> (L.) Miller	<i>Diffusae</i>	http://www.rjb.csic.es/snapdragons ($2n = 12$), http://www.floravascular.com ($2n = 12$), Chater et al. 1972 ($2n = 12$), East 1933 ($2n = 12, 14$), Heitz 1926; 1927b ($2n = 12$), Valdes 1969; 1970b ($2n = 12$), Viano 1973; 1974 ($2n = 12$), Darlington and Wylie 1955 ($2n = 12, 14$).	Europe, Africa, SW Asia, America: Massachusetts	America: Massachusetts, W and S Mediterranean, Asia: Russia	12* 14**
<i>L. tristis</i> (L.) Mill.	<i>Supinae</i>	http://www.rjb.csic.es/snapdragons, Heitz 1926, 1927a, Chater et al. 1972, Galland 1988, Favarger et al. 1979, Vogt and Oberprieler 1994, Aparicio Martinez 1993, Valdés 1969	Europe, N Africa	NW Africa, S and SW Europe	12*
<i>L. tursica</i> valdes and Cabezudo	<i>Supinae</i>	http://www.rjb.csic.es/snapdragons, Valdes and Cabezudo 1977, Chater et al. 1972	Europe	SW Europe	12*
<i>L. ventricosa</i> Cosson and Bal.	<i>Speciosae</i>	http://www.rjb.csic.es/snapdragons, Fernandes et al. 1977, Humphries et al. 1978	N Africa, SW Europe	NW Africa	12*
<i>L. verticillata</i> Boiss.	<i>Supinae</i>	Lioren Saez and Manuel Crespo 2004, Chater et al. 1972, Luque and Lifante 1991	Europe, Africa: (Nevada)	SW Europe, N Africa	12*
<i>L. viscosa</i> Dum. Courset	<i>Versicolores</i>	http://www.rjb.csic.es/snapdragons, http://www.floravascular.com, Chater et al. 1972, Löve and Kjellqvist 1974, Fernandes et al. 1977, Valdes 1969; 1970b, Viano 1979; 1973	Europe, Africa	SW Europe, NW Africa, Canaries Trigales	12*
<i>L. vulgaris</i> Miller	<i>Linaria</i>	http://www.rjb.csic.es/snapdragons, http://www.floravascular.com, http://www.botanicalkeys.co.uk/flora, Dmitrieva and Parfenov 1985, Dmitrieva 1986, Van Loon and Setten 1982, Laane et al. 1999, Van Den Brand and Wieffering 1979, Arohonka 1982, Subramanian and Pondmudi 1987, Probatova et al. 2001, Chuang and Heckard 1992, Dempsey et al. 1994, Montgomery et al. 1997, Javourkova-Jarolimova 1992, Mesicek 1992, East 1933, Chater et al. 1972, Heitz 1926; 1927a, Valdés 1969, Fernandes et al. 1977, Van Loon and Van Setten 1982	S, C Europe, Australia, Asia: Far East, Alaska, Western Siberia, America	S, C Europe, SW Asia, Russia, Far East, N Africa	12*

It might be hypothesized that regions with highly diversified floras, such as the Iberian Peninsula, could be characterized by more polyploid species than the other regions. It seems that the natural hybridization is another significant force in plant evolution of this genus (Ranjbar et al. 2012, Ranjbar and Mahmoudi 2013a, 2013b, Ranjbar and Mahmoudian 2015, Ranjbar et al. 2014, Ranjbar et al. 2015). With a narrow scope (between *Linaria vulgaris* P. Mill. and *L. dalmatica* (L.) P. Mill in U.S. intermountain West (Ward et al., 2009), historical hybridization between closely related *Linaria* species, and the high number of species in the Mediterranean (104 spp.), suggests that this group is likely to have undergone a rapid diversification (Sutton, 1988). Nevertheless, spontaneous hybridization between *Linaria* species within the native Eurasian range of the genus has previously been reported. Considering the palaeogeography of this region and the potential broad-scale effects on gene regulation and developmental processes, the tertiary Iberian orogeny and the subsequent glaciations may have led to important changes in climate and topography (Thompson, 1999), which may have provided opportunities for the establishment of polyploids through hybridization and other mechanisms in the contact zones between existing species. Only about 1% of *Linaria* species represented $n = 13$ and $2n = 15$ which may possess a hybrid origin among species which are available in the Mediterranean margin. There is *L. hellenica* ($2n = 26$) which is likely a hybrid between $n = 6$ and $n = 7$ or is an aneuploid ($n = 12+1$) from a tetraploid species with $n = 12$ (figure 5).

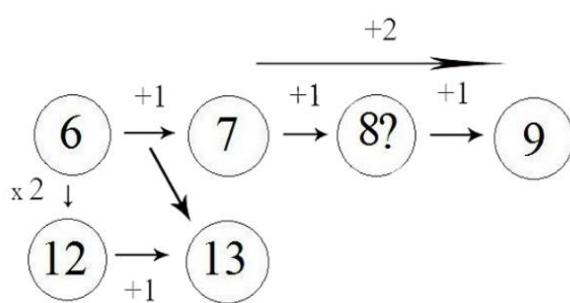


Figure 5. The proposed evolutionary pattern within the genus *Linaria* based on chromosome numbers.

Also *L. melanogramma* by Aryavand 1983 reported in Iran with $2n = 15$ that the questioners can be a hybrid of $n = 6$ and $n = 9$ (*L. ramosissima*, $2n = 18$ in Asia, is likely to occur in Bangladesh) (figure 5). The third factor of speciation by changes in the chromosome numbers is common in flowering plants and an almost characteristic occurrence in

angiosperms. Aneuploidy and diploidy are the common phenomena in plants resulted from the loss or gain of one or a few numbers of chromosomes. According to Abou-el-Enain (2002), aneuploidy is an evolutionary process producing variations in plants. Although there are numerous examples of progressive loss of chromosomes in plants, the factors driving unemployed have been far less investigated than those of polyploidy. In *Linaria* genus these unemployed species are sporadically distributed among geographically disparate Old and New World species. A species with $n = 7, 9$ are both derived by descending aneuploidy from higher numbers and argues that $n = 7, 9$ could be produced by ascending aneuploidy. Origin of species with $n = 7$ which are annuals is likely $n = 6$ and origin of species with $n = 9$ which are perennials is likely $n = 8$ that possibly could not stand out through evolutionary process. Finding occasional plants in various populations with aneuploid chromosome numbers belonging to this genus indicates that aneuploid gametes not only are produced, but actually are functional. However the transmittance $n = 6, 7$ and 9 there is in all zones. No species having $n = 13$ are known from the New World and no species having $n = 7$ are known from Asia, even though this is the most common number in the New World and Mediterranean region. It is likely appeared that multiple origins of aneuploidy in *Linaria* have occurred, perhaps via non disjunction in $n = 6$ crosses, hybridization between $n = 6$ and $n = 7$ species, or aneuploid addition from $n = 13$, as in the case of the $n = 12$ species, so that species with $n = 7$ are derived through enabled loss. Due to the high detail it is appeared that in spite of marked morphological differentiation, species divergence within *Linaria* is relatively recent and reproductive isolation has not yet fully evolved (Ward et al., 2009). However, it can be concluded that the variation in chromosome number in the genus can be referred to the diversity in environmental constraints (Ranjbar et al., 2010b; 2011a). On the other hand, these variations represent a complex evolutionary pattern between the taxa (figure 5). Using flow cytometry, it has been possible to characterize the geographical distribution of cytotypes (within species or between closely related species), with the main advantage, in comparison with related techniques (e.g., Chromosome counting) and in a relatively short period of time. It seems that, to shed further light on the origin of polyploidy *Linaria* species, more complete cytogenetic and also molecular evidence will be necessary. In addition, more accessions should be cytogenetically studied and a directed

analysis through genomic (GISH) and fluorescent in situ hybridization (FISH) would supply interesting and important information.

References

1. Abou-El-Enan M. M. (2002) Chromosomal criteria and their phylogenetic implications in the genus *Onobrychis* Mill. sect. *Lophobrychis* (Leguminosae), with special reference to Egyptian species. *Bot. J. Linn. Soc.* 139(4): 409-414.
2. Aparicio Martinez A. (1993) Planes de recuperación de especies vegetales amenazadas en el Parque Natural de la Sierra de Grazalema (Cádiz-Málaga). *Acta Bot. Malac.* 18: 199-221.
3. Arohonka T. (1982) Chromosome counts of vascular plants of the island Seili in Nauvo, southwestern Finland. *Turun Yliopiston Julkaisuja*. 3: 1-12.
4. Aryavand A. (1977a) Reports [In Love, A. (ed.), IOPB Chromosome number reports LVII]. *Taxon*. 26(4): 443-444.
5. Aryavand A. (1977b) Reports [In Love, A. (ed.), IOPB Chromosome number reports LVIII]. *Taxon*. 26(5/6): 561-562.
6. Aryavand A. (1983) Contribution al etude cytotaxonomique des *Crucifères* de l'Iran III. *Bull. Soc. Neuchateloise Sci. Nat.* 106: 123-130.
7. Atzei, A. D. and Camarda, I. (1984) *Linaria arcusangeli* Atzei et Camarda species nova de île de Sardaigne. *Webbia*. 38: 591-599.
8. Bacchetta G. (2001) Numeros cromosomáticos de plantas occidentales, 863-879. *Anales Jard. Bot. Madrid*. 58(2): 341-342.
9. Baltisberger M. (1987) Chromosomenzahlen einiger Pflanzen aus Albanien. *Ber. Geobot. Inst. E. T. H. Stiftung Rübel*. 53: 47-63.
10. Baltisberger M. and Charpin A. (1989) Chromosomenzählungen von Gilbert Bocquet. *Ber. Geobot. Inst. E. T. H. Stiftung Rübel*. 55: 246-251.
11. Baltisberger M. and Baltisberger E. (1995) Cytological data of Albanian plants. *Candollea*. 50(2): 457-493.
12. Bartolo G., Brullo S. and Pavone P. (1981) Numeros cromosomáticos de plantas occidentales: 138-156. *Anales Jard. Anales Jard. Bot. Madrid* 38: 288-299.
13. Bennett M. D. (1972) Nuclear DNA content and minimum generation time in herbaceous plants. *Proc. R. Soc. London B.* 181: 109-135.
14. Bennett M. D. (1987) Variation in genomic form in plants and its ecological implications. *New Phytol.* 106 (Suppl.): 177-200.
15. Boissier E. (1888) *Flora Orientalis*. vol. 4 pp: 297-492.
16. Borgmann E. (1964) Anteil der polyploiden in der Flora des Bismarckgebirges von Ostneuguinea. *Z. Bot.* 52: 118-173.
17. Boscaiu M., Riera J., Estrelles E. and Güemes J. (1997) Numeros cromosomáticos de plantas occidentales, 751-776. *Anales Jard. Bot. Madrid*. 55(2): 430-431.
18. Boscaiu M., Riera J., Estrelles E. and Güemes J. (2000) Numeros cromosomáticos de plantas occidentales, 827-848. *Anales Jard. Bot. Madrid*. 58(1): 163-164.
19. Brummitt R. K. (2001) World Geographical Scheme for Recording Plant Distributions: Edition 2. Biodiversity Information Standards TDWG. Retrieved 2006. 11-27.
20. Buttler K. P. (1981) *Linaria genistifolia* (L.) Miller seit 30 Jahren bei Grossauheim. *Hess. Flor. Briefe*. 30(4): 54.
21. Caixinhas L., Vasconcelos T., Monjardino J., Barao A. D., Ricardo C. P. and Martins J. N. (1991) Situation actuelle de la banque de germplasme des espèces endémiques du Portugal. *Bot. Chron. (Patras)* 10: 603-608.
22. Cardona M. A. (1977) Numeros cromosómicos para la flora española, 40-44. *Lagascalia*. 7(2): 212-216.
23. Cardona M. A. and Contandriopoulos J. (1980) In numeros cromosómicos para la flora Espaçola. 121-182. *Lagascalia*. 9: 249-284.
24. Cardona A. (1991) IOPB chromosome data 3. *Int. Organ. Pl. Biosyst. (Zurich)* 17: 7-8.
25. Castro M. O. E. (2011) Incidence of polyploidy and genome evolution in Scrophulariaceae s.l. universidade de Coimbra.
26. Castro M., Castro S. and Loureiro J. (2012) Genome size variation and incidence of polyploidy in Scrophulariaceae sensu lato from the Iberian Peninsula.
27. Castroviejo S. and Lago E. (1990) Una *Linaria* (Scrophulariaceae) de la Costa

- Gallega mal interpretada. Nova Acta Ci. Compostelana, Biol. 1: 5-10.
28. Chandran R. and Bhavanandan K. V. (1983) In IOPB chromosome numbers reports LXXIX. Taxon. 32: 320.
29. Chater A. O., Valdes B. and Webb D. A. (1972) *Linaria*. In Tutin T. G., Heywood V. H., Burges N. A.; Moore, D. M.; Valentine, D. H.; Walters, S. H.; Webb, D. A., eds. Flora Europea 3. Cambridge: Cambridge University Press. 226-236.
30. Chatterjee A., Ghosh S. and Roy S. C. (1989) A cytological survey of eastern Himalayan plants III. Cell Chromosome Res. 12: 22-29.
31. Chaudhury A. (1993) Nuclear genes controlling male fertility. Plant Cell. 5: 1277-1283.
32. Chuang T. I. and Heckard L. R. (1992) Chromosome numbers of some North Americaee Scrophulariaceae, mostly Californian. Madroño 39(2): 137-149.
33. Colombo P., Colombo R., Marzeno C. and Pavone P. (1978) Numeri cromosomici per la Flora Italiana. 517-525. Inform. Bot. Ital. 10: 406-413.
34. Contandriopoulos J. and Yannitsaros A. (1975) Distribution geographique, ecologie et cytotoxonomie du *Linaria hellenica* Turrill (Scrophulariaceae). (The geographical distribution, ecology and cytotoxicity of *Linaria hellenica* Turrill (Scrophulariaceae)). Candollea. 30 (2): 293-300.
35. Dahlgren R., Karlsson T. and Lassen P. (1971) Studies on the Flora of the Balearic Islands. I. Chromosome numbers in Balearic Angiosperns. Bot. Not. 124: 249-268.
36. Dalgaard, V. (1986) Estudios cromosómicos sobre fanerogamas de Macaronesia. Anales Jard. Bot. Madrid 43(1): 83-111.
37. Darlington C. D. and Wylie A. P. (1955) Chromosome atlas of flowering plants.
38. Davis P. H. (1982) Scrophulariaceae. pp. 458-748 in: Davis, P. H. (ed.), Flora of Turkey and the Aegean Islands 5. Edinburgh.
39. Dempsey R. E., Gornall R. J. and Bailey J. P. (1994) Contributions to a cytological catalogue of the British and Irish flora, 4. Watsonia. 20: 63-66.
40. Devesa J. A., Talavera S. and Galiano E. F. (1984) Chromosome Number Reports LXXXII. Taxon. 33: 126-134.
41. Diaz Lifante Z., Luque T. and Barbara C. S. (1992) Chromosome numbers of plants collected during Iter Mediterraneum II in Israel. Boccone. 3: 229-250.
42. Diosdado J. C., Santa-Barbara C., Vioque J., Juan R. and Pastor J. (1993) Numeros cromosomaticos para la flora Espanola. 691-719. Lagascalia. 17: 173-184.
43. Dmitrieva S. A. (1986) Chisla khromosom nekotorych vidov rastenij Berezinskogo Biosfernogo Zapovednika. Zapov. Belorussii Issl. 10: 24-28.
44. Dobeá C., Kiehn M. and Vitek E. (1996) Beiträge zur Gefäßpflanzen-Flora von Österreich: Chromosomenzählungen III. Verh. Zool. Bot. Ges. Wien. 133: 301-318.
45. Dobeá C., Hahn B. and Morawetz W. (1997) Chromosomenzahlen zur Gefäßpflanzen-Flora Österreichs. Linzer Biol. Beitr. 29(1) 5-43.
46. Dumortier, B. C. J. 1827-1830) Florula Belgica. Tournay. 51.
47. East E. M. (1933) Genetic observations on the genus *Linaria*. Harvard University, Bussey Institution, Jamaica Plain, Massachusetts Received January. 9.
48. Echlin P. and Godwin H. (1968) The ultrastructure and ontogeny of pollen in *Helleborus Foetidus* L. II. Pollen grain development through the callose special wall stage. J. Cell Sci. 3: 175-186.
49. Elena Rossello J. A.; Zapatero M. A. G. and Andres F. N. (1984) Numeros cromosomicos de algunos oroendemismos Ibericos. Jornades Fitosociol. 4: 199.
50. Elena Rossello J. A., Gonzalez Zapatero M. A. and Navarro Andres F. (1986) Notas cariologicas sobre algunos oroendemismos ibericos. Lazaroa. 8: 91-96.
51. Favarger C. and Huynh K. L. (1964) In IOPB Chromosome number reports II. Taxon. 13: 201-209.
52. Favarger C., Galland N. and Kupper P. (1979) Recherches cytotoxonomiques sur la flore orophile du Maroc. Nat. Monspel., Ser. Bot., 29: 1-64.
53. Feliner G. N. (2011) Southern European glacial refugia: A tale of tales. Taxon. 60: 365-372.
54. Fernandes A. and Queirós M. (1971a) Contribution à la connaissance cytotoxonomique des Spermatophyta du Portugal Compositae. BoI. Soc. Brot. ser. 2, 45: 5-121.

55. Fernandes A. and Queirós M. (1971b) Contribution à la connaissance cytotaxinomique des Spermatophyta du Portugal IV. Leguminosae. BoI. Soc. Brot. ser. 2, 45: 177-225.
56. Fernandes A. and Queiros A. and Santos M. F. (1977) Contribution, la connaissance cytotaxonomique de Spermatophyta de Portugal Scrophulariaceae. Bot. Soc. Brot., 51: 37-90.
57. Fernandez Casas J. and Perez-Chao J. L. (1978) In Numeros cromosomicos para la flora Espanola 1-44. Lagascalia. 7: 191-216.
58. Fernandez Casas J., Sorolla A. P. and Susanna A. (1980a) Numeros cromosomaticos de plantas occidentales, 48-54. Anales Jard. Bot. Madrid 36: 401-405.
59. Gagnidze R. (2006) Chromosome numbers of some species of the Georgian flora. Bot. Zhurn. (Moscow and Leningrad) 91(12): 1928-1929.
60. Gagnidze R. (2006) IAPT/IOPB chromosome data 2. Taxon. 55(3): 757.
61. Galland N. (1988) Recherche sur l'origine de la flore orophile du Maroc etude caryologique et cytogeographique. Trav. Inst. Sci. Univ. Mohammed V, Sér. Bot. 35: 1-168.
62. Gervais C. (1981) Liste annotée de nombres chromosomiques de la flore vasculaire du nord-est de l'Amérique. II. Naturaliste Canad. 108: 143-152.
63. Ghaffari S. M. (2006) New or rare chromosome counts of some angiosperm species from Iran. Iran. J. Bot. 11(2): 185-192.
64. Ghaffari S. M. and Tajik F. (2007) Chromosome Counts of Some Angiosperm Species from IRAN (III). Rostaniha. vol. 8 (2).
65. Goldblatt P. (1984) Index to Plant Chromosome Numbers, 1979-1981. Monogr. Syst. Bot. Missouri Bot. Gard. 8: 1-427.
66. Hamdi M. M. and Assadi M. (2011) Flora of Iran. vol. 68. Research Institute of Forests and Rangelands. Tehran.
67. Hansen A. Y. and Sunding P. (1993) Flora of Macaronesia. Check-list of vascular plants. 4 revised edition. Sommerfeltia 17: 1-295 pp.
68. Heitz E. (1926) Der Nachweis der Chromosomen. Vergleichende Studien über ihre Zahl, Grösse und Form Pflanzenreich, I. Zeitschrift für Botanik 18: 625-681.
69. Heitz E. (1927) Über multiple und aberrante Chromosomenzahlen. Abhandlungen aus dem Gebiete der Naturwissenschaften, Hamburg. 21: 45-47.
70. Heitz E. (1927) Chromosomen und Gestalt bei *Antirrhinum* und verwandten Gattungen. Planta. 7: 392-410.
71. Higginson T., Li S. F. and Parish R. W. (2003) AtMYB103 regulates tapetum and trichome development in *Arabidopsis thaliana*. Plant. J., 35: 177-192.
72. Hong D. Y. (1983) The distribution of the Scrophulariaceae in the Holarctic with special reference to the floristic relationships between Eastern Asia and Eastern North Americae. Annals of the Missouri Botanical Garden. 70: 701-712.
73. Hooker J. D. (1884) The Flora of British India. Published: (1973). The Flora of British India 4(11): 306-307.
74. Humphries C. I., Murray B. G., Bocquet G. and Vasudevan K. (1978) Chromosome numbers of Phanerogams from Morocco and Algeria. Bot. Not. 131: 391-406.
75. Jasiewicz A. and Mizianty M. (1975) Chromosome numbers of some Bulgarian plants. Fragm. Florist. Geobot. 21: 277-288.
76. Javurkova-Jarolimova V. (1992) Reports. [In Mesicek J. and Javurkova-Jarolimova V. (eds.), List of Chromosome Numbers of the Czech Vascular Plants]. Academia, Praha.
77. Kapoor B. M., Ramcharitar S. and Gervais C. (1987) Liste annotée de nombres chromosomiques de la flore vasculaire du nord-est de l'Amérique. Naturaliste Canad. 114: 105-116.
78. Kapoor S., Kobayashi A. and Takatsujii H. (2002) Silencing of the tapetum-specific zinc finger gene TAZ1 causes premature degeneration of tapetum and pollen abortion in petunia. Plant Cell. 14: 2353-2367.
79. Kiehn M., Vitek E., Hellmayr E., Walter J., Tschenett J., Justin C. and Mann M. (1991) Beiträge zur Flora von Österreich: Chromosomenzählungen. Verh. Zool. Bot. Ges. Wien 128: 19-39.
80. Kuprianova L. A. (1950) *Linaria*. - pp. 178-225 in Schishkin, B. K. and Bobrov, E. G. (ed.), Flora SSSR 22. Moskva and

- Leningrad.
81. Laane M. M. and Lie T. (1985) Fremstilling av kromosompreparater med enkle metoder. *Blyttia*. 1985: 7-15.
 82. Lago Canzobre E. and Castroviejo S. (1993) Estudio citotaxonómico de la flora de las costas gallegas. *Cadernos. Área Ci. Biol.* 3: 1-215.
 83. Larsen K. and Laegaard S. (1971) Chromosome studies of the Sicilian flora. *Bot. Tidsskr.* 66: 249-268.
 84. Lawrence H. M. (1969) Taxonomy of Vascular Plants. Mac Millan, New York. pp: 737-775.
 85. Leitch I. J. and Bennett M. D. (1997) Polyploidy in angiosperms. *Trends in Plant Science* 2: 470-476.
 86. Liu B. and Wendel J. F. (2003) Epigenetic phenomena and the evolution of plant allopolyploids. *Molecular Phylogenetics and Evolution*. 29: 365-379.
 87. Love A. and Kjellqvist E. (1974) Cytotaxonomy of Spanish plants. IV. Dicotyledons: Caesalpinae-Asteraceae. *Lagascalia* 4: 153-211.
 88. Love A. and Love D. (1982) In IOPB chromosome number reports LXXVII. *Taxon*. 31: 777.
 89. Lovka M., Susnik F., Love A. and Love D. (1971) Reports. [In Love, A. (ed.), IOPB Chromosome Number Reports XXXIV]. *Taxon*. 20: 785-797.
 90. Luque T. and Lifante Z. D. (1991) Chromosome numbers of plants collected during Iter Mediterraneum I in the SE of Spain. *Bocconeia*. 1: 303-364.
 91. Majovsky J. (ed.) (1974) Index of chromosome numbers of Slovakian flora (Part 3). *Acta Fac. Rer. Natur. Univ. Comen. Bot.* 22: 1-20.
 92. Marhold K. and Feliner G. N. (2008) IAPT/IOPB chromosome data 5 chromosome data 1. *Taxon*. 55: 444.
 93. Mateu I. and Mansanet J. (1982) Numeros cromosomicos de plantas occidentales. 164-168. *Anales Jard. Bot. Madrid*. 38(2): 515-518.
 94. Mayol M. and Rosello J. A. (1998) Numeros cromosomaticos de plantas occidentales. 780-785. *Anales Jard. Bot. Madrid*. 56(1): 119.
 95. Mehra P. N. and Vasudevan K. N. (1972) In IOPB Chromosome number reports XXXVI. *Taxon*. 21: 333-346.
 96. Melendo M., Gimenez E., Cano E., Gomez-Mercado F. and Valle F. (2003) The endemic flora in the south of the Iberian Peninsula: taxonomic composition, biological spectrum, pollination, reproductive mode and dispersal. *Flora*. 198: 260-276.
 97. Mesicek J. (1992) In Mesicek, J. and Javurkova-Jarolimova, V., List of Chromosome Numbers of the Czech Vascular Plants. Academia, Praha.
 98. Montgomery L., Khalaf M., Bailey J. P. and Gornal K. J. (1997) Contributions to a cytological catalogue of the British and Irish flora, 5. *Watsonia*. 21: 365-368.
 99. Montserrat Marti J. M. (1981-1982) Números cromosómicos de plantas occidentales, 77-83. *Anales Jard. Bot. Madrid*. 38(1): 249-252.
 100. Murin A., Svobodova Z., Majovsky J. and Ferakova V. (1999) Chromosome numbers of some species of the Slovak flora. *Thaiszia* 9(1): 31-40.
 101. Murin A. and Paclova L. (1986) Karyological study of the Slovak flora IX. *Acta Fac. Rerum Nat. Univ. Comeniana*, Bot. 33: 45-48.
 102. Nazeer M. A., Subramanyam G. V. and Ohri D. (1980) B-chromosome in *Linaria bipartita* Wilid. *Curr. Sci.* 49: 448-449.
 103. Otto S. P. and Whitton J. (2000) Polyploidy: Incidence and evolution. *Annual Reviews of Genetics*. 34: 401-437.
 104. Parsa A. (1949) Flora de l. Iran vol. IV, *Verbascum* 323-334 and *Celsia* 347-361. Tehran.
 105. Pastor J., Fernandez I. and Diez M. (1988) Numeros cromosómicos para la flora Espanola. 528-543. *Lagascalia* 15: 124-129.
 106. Podlech D. (1986) Chromosomenstudien en Pflanzen des Saharo-Sindischen Trockengebietes. *Mitt. Bot. Staatssamml. München*. 22: 5-20.
 107. Poole C. F. (1931) Pollen Grain Studies as an Indication of Fertility in Hybrids. August. 3.
 108. Press J. R. and Short M. J. (1994) Scrophulariaceae. – Flora of Madeira. 574 pp. The Natural History Museum. London.
 109. Probatova N. S. and Sokolovskaya A. P. (1981) Kariologicheskoe issledovanie sosudistykh rastenij ostrovov Dalnevostocnogo gosudarstvennogo morskogo sapovednika. Sb. Cvetkaye

- Rastenija Ostrovov Dalnevostochnogo Morskogo Sapovednika. 92-114.
110. Probatova N. S., Rudyka E. G. and Shatalova S. A. (2001) Chromosome numbers in some plant species from the environs of Vladivostok city (Primorsky Region). Bot. Zhurn. (Moscow and Leningrad). 86(1): 168-172.
111. Probatova N. S. (2006) Chromosome numbers of vascular plants from nature reserves of the Primorsky Territory and the Amur River basin. Bot. Zhurn. (Moscow and Leningrad). 91(7): 1117-1134.
112. Qureshi S. J., Khan M. A., Arshad M., Rashid A. and Ahmad M. (2009) Pollen Fertility (Viability) Status in Asteraceae Species of Pakistan. Trakia Journal of Sciences. vol. 7, No. 1, pp 12-16.
113. Ranjbar M., Hajmoradi F. and Karamian R. 2012. An overview on cytogenetics of the genus *Onobrychis* (Fabaceae) with special reference to *O. sect. Hymenobrychis* from Iran. Caryologia. 65: 187-198.
114. Ranjbar M. and Mahmoudi A. (2013a) Chromosome numbers and biogeography of the genus *Scutellaria* L. (Lamiaceae). Caryologia. 66: 205-214.
115. Ranjbar M. and Mahmoudi A. (2013b) Cytomorphological study of *Scutellaria platystegia* (Lamiaceae) in Iran. Feddes Repert. 124: 1-15.
116. Ranjbar M., Karami S. and Rostami M. (2014) Cytogenetic study and meiotic behaviour on 13 populations of *Fibigia* (Brassicaceae) in Iran. Webbia. 69: 269-280.
117. Ranjbar M. and Mahmoudian B. (2015) An overview on cytogenetics of the genus *Astragalus* subgenus *Hypoglottis* (Fabaceae). Caryologia. 68: 109-124.
118. Ranjbar M., Pakatchi A. and Babataheria Z. (2015) Chromosome number evolution, biogeography and phylogenetic relationships in *Salvia* (Lamiaceae). Webbia. 70: 293-312.
119. Reese G. (1957) Ober die Polyploidiespektren in der nordsaharischen WU stenfplanzen. Flora. 144(4): 598-634.
120. Rossitto M., Ottonello D. and Fici S. (1983) Numeri cromosomici per la Flora Italiana: 993-1002. Inform. Bot. Ital. 15: 188-194.
121. Rostovtseva T. S., Krasnborov I. M. and Krasnikova S. A. (1981) Chisla khromosom nekotorych vidov flory Sibiri. Sb. Novye Dannye Fitogeografii Sibiri. 215-220.
122. Saez L. and Bernal M. (2009) *Linaria* Mill. In: Castroviejo, S. and al. (eds.). Flora Iberica. vol. 13: 232-324. Real Jardin Botanico. C.S.I.C. Departamento de Publicaciones del CSIC. Madrid.
123. Sanchez-Gullon E., Valdes B., Macias-Fuentes F. J. and Weickert P. (2006) Notas para la flora de la provincia de Huelva (SO de España). Lagascalia 26: 187-196.
124. Sarkar A. K., Chakraverty M., Saha N. C. and Das S. K. (1976) In IOPB Chromosome number reports LIV. Taxon. 25: 631-649.
125. Sarkar A. K., Chakraverty M., Das S. K., Pal C. R. and Hazara D. (1980) In IOPB Chromosome number reports LXVII. Taxon. 29: 347-367.
126. Serrano Perez M. and Carvajal Villaverde R. (2004) *Linaria arenaria* DC. In Bañares A. Blanca G., Güemes J., Moreno J. C. and Ortiz S. (eds.). Atlas y Libro Rojo de la Flora Amenazada de Espana. 382-383. Dirección General de Conservación de la Naturaleza. Madrid.
127. Shetty B. V. and Subramanyam K. (1971) In IOPB Chromosome number reports XXXIV. Taxon. 20: 785-797.
128. Signorini M. A., Foggi B. and Mori B. (2001) Mediterranean chromosome number reports 11 (1264-1270). FL. Medit. 11: 473-478.
129. Silvestre S. (1991) Números cromosómicos de plantas occidentales, 639-648. Anales Jard. Bot. Madrid. 49: 95.
130. Snogerup B. (1985) Chromosome Number Reports LXXXIX. Taxon. 34: 727-730.
131. Soltis D. E. and Soltis P. S. (1999) Polyploidy: recurrent formation and genome evolution. Trends in Ecology and Evolution. 14: 348-352.
132. Sorensen A., Guerineau F., Canales-Holzeis C., Dickinson H. G. and Scott R. J. (2002) A novel extinction screen in *Arabidopsis thaliana* identifies mutant plants defective in early microsporangial development. Plant. J. 29: 581-594.
133. Stace C. (2000) Cytogeny and

- Cytogenetics as a fundamental taxonomic resource for the 20th and 21st centuries. *Taxon.* 49: 451-477.
134. Strid A. and Franzen R. (1981) In Chromosome number reports LXXIII. *Taxon.* 30: 829-842.
135. Subramanian D. and Pondmudi R. (1987) Cytotaxonomical studies of south Indian Scrophulariaceae. *Cytologia.* 52: 529-541.
136. Sutton D. A. (1988) A revision of the tribe Antirrhineae (Scrophulariaceae). Cambridge University Press. London and Oxford. (Rev Antirrh.) 497.
137. Thompson J. D. (1999) Population differentiation in Mediterranean plants: insights into colonization history and the evolution and conservation of endemic species. *Heredity.* 82: 229-236.
138. Uhrikova A., Ferakova V. and Schwarzova T. (1983) In IOPB chromosome number reports LXXX. *Taxon.* 32: 507-508.
139. Valdes B. (1969) Taxonomia experimental del genero *Linaria* III. Cariologia de algunas especies de *Linaria*, *Cymbalaria Chaenorrhinum*. Boletin de la Real Sociedad Espanola de Historia Natural, Seccion Biologia. 67: 243-256.
140. Valdes B. (1970b) Taxonom an experimental del genero *Linaria*. V. Hibridacion interespecifica. *Acta Phytotaxonomica Barcinonensis.* 4: 5-24.
141. Valdes B. (1973) Numeros cromosomicos de algunas plantas espanolas, I. Lagascalia. 3(2): 211-217.
142. Valdes, B. and Cabezudo B. (1977) *Linaria tursica* Valdes and Cabezudo. sp. nov. Lagascalia. 7: 9-12.
143. Valdes B. (1978) In numerous cromosomicas para la flora Espanola. 45-83. Lagascalia. 8: 105-125.
144. Valdes B. (1986) Notas taxonomicas y corologicas sobre la flora de Andalucia Occidental. 141-257. 160-257. Notas breves: 214. *Linaria tartessiana* (Vicioso) Valdes, comb. nova. Lagascalia. 14: 157.
145. Valdes B. (1987) Scrophulariaceae. In: Flora Vascular De Andalucia Occidental. 2. Valdes, B., S. Talvera and E.F. Galiano (Eds.). Ketres, Barcelona, pp: 486-547.
146. Van Den Brand C., Meel F. C. and Wieffering J. H. (1979) In IOPB chromosome number reports LXIV. *Taxon.* 28: 395-397.
147. Van Loon J. C. and De Long A. (1978) Reports [In Lave, A. (ed.), IOPB Chromosome number reports LIX]. *Taxon.* 27(1): 56-61.
148. Van Loon J. C. and Setten A. K. V. (1982) IN: IOPB Plant chromosome number reports. *Taxon.* 31: 589-592.
149. Vazquez F. M., Ramos S., Doncel E., Blanco J. and Balbuena E. (2001) IOPB chromosome data 17. *Newslett. Int. Organ. Pl. Biosyst.* (Pruhonice). 33: 26.
150. Verlaque R., Contandriopoulos J. and Aboucaya A. (1992) IOPB chromosome data 4. *Int. Organ. Pl. Biosyst. Newslett.* (Zurich). 18/19: 9-10.
151. Verlaque R., Reynaud C. and Aboucaya A. (1997) Mediterranean chromosome number reports 7 (843-854). *Fl. Medit.* 7: 240-246.
152. Verma S. C. and Dhillon S. S. (1967) In IOPB Chromosome number reports XI. *Taxon.* 16: 215-222.
153. Viano J. (1971) Contribution a letude caryosystematique du genre *Linaria*. *Caryologia* 24: 183-201.
154. Viano J. (1972) Contribution to the Karyological Study of the *Linaria* of Turkey. *Adansonia.* 12: 461-8.
155. Viano J. (1973) Resultats caryologiques de quelques especes de *Linaria* et *Chaenorrhinum* recoltees au Sud de la Penôsule Iberique. *Bol. Soc. Brot. ser.* 247: 325-331.
156. Viano J. (1974) Resultats caryologiques de quelques especes de *Linaria* et *Chaenorrhinum* recoltees au Sud de la Peninsule iberique. *Bol. Soc. Brot.*, vol. 47, 2e ser.
157. Viano J. (1975) IOPB. Chromosome number reports XLIX. *Taxon.* 24 (4): 508.
158. Viano J. (1979) Investigations au MEB du test des graines du genre *Linaria*. *Candollea* 34: 341-355.
159. Viano J. (1979) In numerous cromosomicos para la flora Espanola. 84-120. Lagascalia. 9: 115-130.
160. Viano J. (1979) Numeros cromosomicos para la flora espanola. Lagascalia. 95-98. 9(1): 120-121.
161. Vicioso C. (1946) Notas sobre la flora Espanola. *Anales del Jardin Botanico de Madrid.* 6: 5-92.

162. Vij S. P. and Kashyap S. K. (1975) In IOPB Chromosome number reports XLVIII. *Taxon*. 24: 367-372.
163. Vogt R. and Oberprieler C. (1994) Chromosome numbers of North African phanerogams. IV. *Candollea*. 49(2): 549-570.
164. Vujnovic K. and Wein R. W. (1996) The biology of Canadian weeds: *Linaria dalmatica* (L.) Mill. *Canadian Journal of Plant Science*. 77: 483-491.
165. Ward S. M., Fleischmann C. E., Turner M. F. and Sing S. E. (2009) Hybridization between Invasive Populations of Dalmatian Toadflax (*Linaria dalmatica*) and Yellow Toadflax (*Linaria vulgaris*). *Invasive Plant Science and Management*. 2: 369-378.
166. Ward D. E. (1983) Chromosome counts from New Mexico and southern Colorado. *Phytologia*. 54: 302-309.
167. Ward D. E. (1983) In: IOPB chromosome number reports LXXX. *Taxon*. 32: 510-511.
168. Waterkeyn F. (1962) Les parois microsporocytaires de nature callosique. *Cellule*. 62: 225-255.
169. Waterkeyn F. (1964) Callose microsporocytaire et callose pollinique. *Pollen Physiology and Fertilization* (ed. H. F. Linskens), pp. 52-58. Amsterdam. North Holland Publishing Co. 42.
170. Wendel J. F. (2000) Genome evolution in polyploids. *Plant Molecular Biology*. 42: 225-249.
171. Wilson Z. A., Morroll S. M., Dawson J., Swarup R. and Tighe P. J. (2001) The *Arabidopsis* Male Sterility 1 (MS1) gene is a transcriptional regulator of male gametogenesis, with homology to the PHD finger family of transcription factors. *Plant J.* 28: 27-39.

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