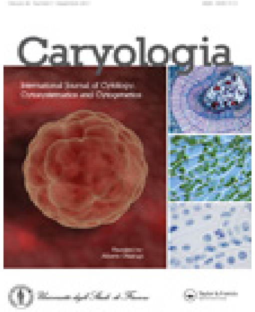

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Chromosome numbers and biogeography of the genus *Scutellaria* L. (Lamiaceae)

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Chromosome numbers and biogeography of the genus *Scutellaria* L. (Lamiaceae)

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A survey on chromosome counts of different sections belonging to the genus *Scutellaria* L. (Lamiaceae) throughout the world is presented and the relationships between chromosome data of its sections and their biogeography are also discussed here. In addition, meiotic chromosome numbers of 20 populations belonging to eight species growing in Iran, namely *S. tomentosa* ($2n$ = 2x = 22), *S. theobromina* ($2n = 2x = 22$), *S. araxensis* ($2n = 2x = 22$), *S. platystegia* ($2n = 2x = 22$), *S. nepetifolia* ($2n = 2x = 22$), *S. farsistanica* ($2n = 2x = 22$), *S. persica* ($2n = 2x = 22$) and *S. pinnatifida* ($2n = 2x = 22$) were determined. With exception of *S. pinatifida*, all chromosome counts are reported for the first time, and are consistent with proposed base number of $x = 11$.

Keywords: biogeography; chromosome number; meiosis; *Scutellaria*

Introduction

The family Lamiaceae comprises about 3500 species in 258 genera worldwide. Many of its species have great importance due to their economic value (Duarte and Lopes 2007). Many species of the family are aromatic plants and often used in folk medicine, as herb spices or fragrance (Werker et al. 1985). *Scutellaria* L. is a genus belonging to the subfamily Scutellarioideae and grows both in Old and New Worlds (Cantino et al. 1992). With 425 currently recognized species, it is one of the large genera within Lamaiceae, but when the possible synonyms are considered the actual number of species is closer to 360 (Paton 1990a). *Scutellaria* and its active principles possess a wide range of pharmacological actions, such as antitumor, anti-angiogenesis, hepatoprotective, antioxidant, anticonvulsant, antibacterial and antiviral activities (Shang et al. 2010). All members of the genus are recognized as a monophyletic clade, so their genetic distances from *Stachys*, *Lamium* and *Marubium* account for 2.7%, suggesting that this group should be classified as a tribe, e.g. Scutellarieae (Wink and Kaufmann 1995).

The Irano-Turanian region, particularly Central Asia and Afghanistan, is the centre of maximum diversity for the genus. However, Eastern Mediterranean and the Andes are the second centers of its speciation (Paton 1990a). In *Flora Iranica* the genus is represented by 40 species, of which only 22 species grow in Iran and 10 species are endemic (Rechinger 1982). They are distributed all over the country, mainly in mountainous to sub-mountainous areas, but with a few in wet places and also in forests. *Scutellaria* species are typically characterized by the shape of calyx with two undivided lips and the presence of a scutellum on the upper lip. The calyx shows variable characters in different species, and the scutellum may be absent or the calyx may be inflated in the upper lip.

The latest global taxonomic review and infrageneric classification of *Scutellaria* was presented by Paton (1990a). He comprehensively studied *Scutellaria* and its allied genera and showed that the features related to inflorescence, calyx, corolla and nutlets are the most important and taxonomically reliable characters in distinguishing species (Paton 1990a, 1990b, 1992). He also divided *Scutellaria* into two subgenera, namely *Scutellaria* (Neveski ex Juz.) Juz. emend. Paton, which is characterized by one-sided or rarely spiral inflorescence and opposite flowers not subtended by leaves or by leaf-like bracts; and *Apelthanthus* (Neveski ex Juz.) Juz. emend Paton, characterized by 4-sided inflorescence, opposite and decussate flowers subtended by cucullate bracts. *S.* subgen. *Scutellaria* was divided into five sections, namely *Scutellaria* (Rech.) Paton, *Anaspis* (Rech.) Paton, *Salazaria* (Torrey) Paton, *Perilomia* (Kunth) Epling emend. Paton and *Salviifoliae* (Boiss.) Edmondson. Subgenus *Apelthanthus* was divided into two sections, namely *Apeltanthus* Nevski ex Juz. and *Lupulinaria* Hamilton. Based on this classification, the Iranian *Scutellaria* species will be recognized in *S.* sect. *Scutellaria* and *S.* sect. *Anaspis* of *S.* subgen. *Scutellaria*, and *S.* sect. *Lupulinaria* of *S.* subgen. *Apeltanthus*.

Most cytological studies of the genus *Scutellaria* have concerned chromosome counts, but there is some report on the relationships between chromosomal criteria and biogeography. The first cytological observation of the genus was the chromosome number count of $2n = 26$ in *S. insignis* reported by Lee (1967). At least 14 different chromosome numbers have been found for the genus: $2n = 14$ (*S. sibthorpii*), $2n = 16$ (e.g. *S. chodja-kasiani*), $2n = 18$ (e.g. *S. intermedia*), $2n = 20$ (e.g. *S. repens*), $2n = 22$ (e.g. *S. grandiflora*), $2n = 24$ (e.g. *S. discolor*),

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2*n* = 26 (e.g. *S. indica*), 2*n* = 28 (e.g. *S. alpina*), 2*n* = 30 (e.g. *S. altissima*), 2*n* = 32 (e.g. *S. hastifolia*), 2*n* = 34 (e.g. *S. hirta*), 2*n* = 44 (*S. lateriflora*), 2*n* = 60 (e.g. *S. churchilliana*) and 2*n* = 88 (*S. lateriflora*) (Sharma 1970; Vij and Kashyap 1975, 1976 Rostovtseva 1977; Gill and Morton 1978; Murin 1978; Astanova 1981; Montmollin 1982, 1986; Singh 1984; Yildiz and Gücel 2006). Due to the large chromosomal variation in the genus, the present work aimed at increasing the knowledge about the cytogenetics and biogeography of the species, and at comparing the base chromosome numbers and polyploidy levels between different sections, which are distributed throughout the world. Such findings would help us to promote our understanding about the relationships between chromosomal criteria and taxonomic delimitation.

This article follows previous studies conducted on cytological researches in Iran (Ranjbar et al. 2009, 2010a, b, c, 2011a, b, 2012, Sheidai et al. 2010).

Materials and methods

Description of database

Some chromosome records from online databases (http://www.tropics.org/Project/IPCN) and the literature are presented in Table 1. Each record in the database includes the following data: name of taxon as published in the original source, the standardized name (authorship of the name is corrected, as well as possible typing errors, and the currently accepted name); data on chromosomes includes mitotic or meiotic chromosome number, ploidy level, the name of person who counted chromosomes and the locality where plant materials have been collected.

Cytogenetics

The meiotic chromosome numbers were studied in five populations of *S. pinnatifida*, five populations of *S. platystegia*, three populations of *S. araxensis*, three populations of *S. theobromina* and only one population from each of *S. tomentosa*, *S. farsistanica*, *S. persica* and *S. nepetifolia*. Voucher specimens are deposited in BASU, Hamedan, Iran. Randomly selected flowers in the ideal stage for meiotic studies were collected 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% acetocarmine. Chromosome numbers were determined in five individuals of each population during diakinesis. The meiotic chromosome association was evaluated in at least 20 diakinesis cells. Meiotic stages were photographed by a BX-51 Olympus (Nagano, Japan) microscope equipped with a 3030 digital camera.

Results and discussion

Chromosome data analysis

The current databases represent the reports for only 86 species (93 taxa including subspecies) from total of 425 species that are estimated for the genus *Scutellaria* throughout the world (Paton 1990a). There are records for approximately 21% of species with known chromosome numbers. The abundance of the species is not consistent with their geographical distributions (Figure 1). Asian taxa are more intensively studied than the taxa growing in other geographical areas. About 300 species of the genus occur in Asia (Boissier 1879; Juzepczuk 1954; Edmondson 1982; Rechinger 1982; Tatsu-Nami-Sō 1984; Huang 1994), and as much as 68% of the chromosome number records originate from this continent. Even within Asia the data are not equally distributed: 36% of the Asian records originate from E and SE Asia, 22% in central and northern Asia and 10% in W and SW Asia (Brummitt 2001). This is somewhat proportional to the number of species: 112 species occur in E and SE Asia, 148 in the center and N; and 40 in W and SW Asia. Of about 90 taxa in North America, 55 taxa occur in Europe and eight taxa in Africa (Rionchardson 1972; Paton 1992; Joshee et al. 2010). that represented only 14.2%, 17.14% and 0.95% chromosome counts, respectively. Thus, an unequal spread of the records throughout the distribution area of the genus is apparent. However, the hypothesis is needed to be confirmed by deeper karyogeographical explorations. As the genus *Scutellaria* is a subcosmopolitan genus (Paton 1992), our estimated statistics represent the same pattern as expected by Kučera et al. (2005) for the genus *Cardamine*.

Another comparison can be made of the percentages of taxa that are entirely diploid, those that are both diploid and polyploid, and those that are entirely polyploid. For the genus *Scutellaria*, we have found 67.03% diploid, 7.69% diploid and polyploid, and 24.27% entirely polyploid taxa. Karyological data for entire diploidy (basic chromosome numbers) and polyploidy percentages are represented as follows (Figure 2): x = 7, 0.95% (one taxon); x = 8, 9.52% (10 taxa), x = 9, 1.90% (two taxa), x = 10, 9.52% (10 taxa), x = 11, 12.38% (13 taxa), x = 12, 11.43% (11 taxa) and x = 13, 22.86% (24 taxa). The highest frequent chromosome number is 2*n* = 88, reported for *S. lateriflora* L. (Gill and Morton 1978) from N America (Canada).

Cytogenetics

Chromosome numbers of *S.* sect. *Scutellaria*, *S.* sect. *Anaspis* and *S.* sect. *Salazaria* of *S.* subgen. *Scutellaria* and *S.* sect. *Lupulinaria* of *S.* subgen. *Apelthanthus* have been previously reported (Paton 1990a). Results from analyses of chromosome data, summarized in Table 1, represent about 85.42% of the studied species belonging to *S.* sect. *Scutellaria*, 12.50% to *S.* sect. *Lupulinaria* and the remaining taxa (about 2%) to *S.* sect. *Anaspis*

Table 1. *Scutellaria* species analyzed in the present study.

Taxon	Section	Reference	Origin	2*n*	Ploidy level
S. adenostegia Briq.	*Lupulinaria*	Singh 1984	Central Asia	22	2
S. adenostegia Briq.	*Lupulinaria*	Singh 1979	Central Asia	20	2
S. albida L.	*Scutellaria*	Markova and Goranova 1995	Mediterranean area	32	4
S. albida subsp. *albida*	*Scutellaria*	Bothmer 1985	Aegean area	34	4*
S. albida subsp. *vacillans* (Rech. f.) Bothmer	*Scutellaria*	Bothmer 1985	Aegean area	34	4*
S. albida subsp. *velenovskyi* (Rech. f.) Greuter & Burdet	*Scutellaria*	Markova and Goranova 1995	Mediterranean area	34	4*
S. alpina L.	*Scutellaria*	Andreev 1982; Baltisberger 1988	Italy	22	2
S. alpina L.	*Scutellaria*	Singh 1984	Europe	28	4
S. altissima L.	*Scutellaria*	Singh 1984	Europe	30	4**
S. altissima L.	*Scutellaria*	Lövkvist and Hultgard 1999	Sweden	34	4*
S. amabilis H. Hara	*Scutellaria*	Sawanomukai et al. 2003	Japan	26	2
S. angustifolia subsp. *angustifolia*	*Scutellaria*	Olmstead 1990	America	24	2
S. angustifolia subsp. *micrantha*	*Scutellaria*	Olmstead 1990	America	24	2
S. antirrhinoides Benth.	*Scutellaria*	Olmstead 1990	America	24	2
S. austrotaiwanensis C. X. Xie & T. C. Huang	*Scutellaria*	Hsieh and Huang 1997	Taiwan	26	2
S. baicalensis Georgi	*Scutellaria*	Probatov and Sokolovskaya 1990; Shatokhina 2006	Russia	32	4
S. baicalensis Georgi	*Scutellaria*	Cheng 2010	Japan	18	2
S. balearica Barceló	*Scutellaria*	Castro 2005	Balearic Islands	22	2
S. barbata D. Don.	*Scutellaria*	Hsieh and Huang 1995; Sawanomukai et al. 2003	Taiwan, Japan	26	2
S. bolanderi A. Gray	*Scutellaria*	Olmstead 1990	America	24	2
S. brachyspica Nakai H. Hara	*Scutellaria*	Sawanomukai et al. 2003	Japan	26	2
S. brittonii Porter	*Scutellaria*	Olmstead 1990	America	22	2
S. bucharica Juz.	*Lupulinaria*	Astanova 1984	Tadjikistan	20	2
S. californica A. Gray	*Scutellaria*	Olmstead 1990	America	24	2
S. cardiophylla Engelm. & A. Gray	*Scutellaria*	Pittman 1987	Europe	24	2
S. chodja-kasiani Kamelin	*Scutellaria*	Astanova 1981	Tadjikistan	16	2
S. churchilliana Fernald	*Scutellaria*	Gill 1981, Gill and Morton 1978	Canada	60	
S. colebrookiana Benth.	*Scutellaria*	Saggoo 1983; Bir and Saggoo 1985	India	26	2
S. columnea All.	*Scutellaria*	Baltisberger et al. 1993	Mediterranean area	34	4*
S. columnea All.	*Scutellaria*	Van Loon and Setten 1982	Europe	32	4
S. dependens Maxim.	*Scutellaria*	Sawanomukai et al. 2003	Japan	28	4
S. dependens Maxim.	*Scutellaria*	Probatova 2006	Russia	32	4
S. discolor Colebr.	*Scutellaria*	Krishnappa and Basavaraj 1982	India	26	2
S. discolor Colebr.	*Scutellaria*	Sharma 1970; Sudarmono and Conn 2010	India, Indonesia	24	2
S. galericulata L.	*Scutellaria*	Arohonka 1982; Dempsey et al. 1994	Finland	30	4**
S. galericulata. L.	*Scutellaria*	Lövkvist and Hultgard 1999	Sweden	28, 30	4
S. galericulata L.	*Scutellaria*	Gill 1981; Pogan et al.1980; Vachova and Ferakova 1980; Gill and Morton 1978	Canada	32	4
S. galericulata L.	*Scutellaria*	Dmitrieva 2000	Byelarus	30, 32	4
S. gontscharovii Juz.	*Lupulinaria*	Astanova 1981a	Tadzhikistan	22	2
S. grandiflora Sims.	*Lupulinaria*	Krasnoborov et al. 1980	Russia	20, 22	2
S. grandiflora Sims.	*Lupulinaria*	Rostovtseva 1977; Kranborov and Rostovtseva 1975	Russia	22	2
S. grossa Wall. ex Benth.	*Scutellaria*	Saggoo 1983; Bir and Saggoo 1984; Saggoo and Bir 1981	India, Himalaya	34	4*
S. grossa Wall.	*Scutellaria*	Gill 1984	Himalaya	20	2
S. guilielmii A. Gray	*Scutellaria*	Sawanomukai et al. 2003	Japan	28	4
S. hastifolia L.	*Scutellaria*	Arohonka 1982; Murin 1978	Finland, Slovakia	32	4
S. hirta Sibth. & Sm.	*Scutellaria*	Montmollin 1982, 1986	Greece	34	4*

(*Continued*)

Table 1. (*Continued*)

Taxon	Section	Reference	Origin	2*n*	Ploidy level
S. indica L.	*Scutellaria*	Xu et al. 1992; Hsieh and Huang 1995	Japan, Taiwan	26	2
S. indica var. *indica*	*Scutellaria*	Sawanomukai et al. 2003	Japan	26	2
S. indica var. *parvifolia* Makino	*Scutellaria*	Sawanomukai et al. 2003	Japan	26	2
S. indica var. *satokoae* Wakasugi & Naruh.	*Scutellaria*	Naruhashi et al. 2004	Japan	26	2
S. indica var. *satokoae*	*Scutellaria*	Naruhashi et al. 2004	Japan	26	2
S. insignis Nakai	*Scutellaria*	Lee 1967	Korea	26	2
S. intermedia Popov	*Lupulinaria*	Astanova 1981	Tadjikistan	18	2
S. intermedia Popov	*Lupulinaria*	Singh 1984	Central Asia	20	2
S. intermedia Popov	*Lupulinaria*	Singh 1979	Central Asia	22	2
S. iyoensis Nakai	*Scutellaria*	Sawanomukai et al. 2003	Japan	26	2
S. kiusiana H. Hara	*Scutellaria*	Sawanomukai et al. 2003	Japan	26	2
S. krasevii Kom. & I. Schischk. ex Juz.	*Scutellaria*	Probatova 2006	Russia	16	2
S. laeteviolacea var. *Laeteviolacea*	*Scutellaria*	Sawanomukai et al. 2003	Japan	26	2
S. laeteviolacea var. *maekawae* H. Hara	*Scutellaria*	Sawanomukai et al. 2003	Japan	26	2
S. lateriflora L.	*Scutellaria*	Love and Love 1982	Canada	80	8
S. lateriflora L.	*Scutellaria*	Gill 1981	Canada	44	4
S. lateriflora L.	*Scutellaria*	Gill 1980	Canada	44, 80	4, 8
S. lateriflora L.	*Scutellaria*	Gill and Morton 1978	Canada	44, 88	4, 8
S. leonardii Epling	*Scutellaria*	Gill 1981, Gill 1980	Canada	20	2
S. mexicana (Torr.) A. J. Paton	*Salazaria*	Paton 1990a	America	50	5
S. microdasys Juz.	*Lupulinaria*	Zakirova and Nafanailova 1992	Kazakhstan	16	2
S. minor Huds.	*Scutellaria*	Buttler 1989; Fernandes and Leitão 1984; Lövkvist and Hultgard 1999	Sweden	28	4
S. minor Huds.	*Scutellaria*	Morton 1973	Europe	32	4
S. multicaulis subsp. *multicaulis* Boiss.	*Lupulinaria*	Ghaffari 1988	Iran	22	2
S. muramatsui H. Hara	*Scutellaria*	Sawanomukai et al. 2003	Japan	26	2
S. nana A. Gray	*Scutellaria*	Olmstead 1990	America	24	2
S. novae-zealandia Hook. f.	*Scutellaria*	Paton 1990a	New Zealand	60	6
S. orientalis L.	*Lupulinaria*	Sekovski and Jovanovska 1983	Europe	22	2
S. orientalis var. *demnatensis* Batt.	*Lupulinaria*	Galland 1988	Morocco	22	2
S. orientalis subsp. *hispanica* Boiss.	*Lupulinaria*	Galland 1991	Morocco	22	2
S. orientalis subsp. *pinnatifida* J. R. Edm.	*Lupulinaria*	Markova and Goranova 1995	Mediterranean area	22	2
S. ovata subsp. *mexicana* Epling	*Scutellaria*	Zhao 1996	Mexico	c.16	2
S. ovata Hill	*Scutellaria*	Pittman 1987	America	20	2
S. parvula Michx.	*Scutellaria*	Gill 1981	Canada	20	2
S. pekinensis var. *transitra* (Makino) H. Hara ex H. W. Li	*Scutellaria*	Sawanomukai et al. 2003	Japan	28	4
S. petiolata Hemsl. & Lace	Anaspis	Khatoon and Ali 1993	Pakistan	16	2
S. pinnatifida Hamilt.	*Lupulinaria*	Aryavand 1977, Ghaffari 2008	Iran	22	2
S. polyphylla Juz.	*Scutellaria*	Shatokhina 2006	Russia	32	4
S. rivularis Benth.	*Scutellaria*	Saggoo 1983	India	20	2
S. repens Buch.-Ham. ex D. Don.	*Scutellaria*	Gill 1974, 1984; Vij and Kashyap 1976a	Himalaya, India	20	2
S. rubicunda Hornem.	*Scutellaria*	Baltisberger 1991	Albania	34	4*
S. rubropunctata var. Rubropunctata	*Scutellaria*	Sawanomukai et al. 2003	Japan	26	2
S. sapphirina (Barneby) Olmstead	*Scutellaria*	Olmstead 1990	America	24	2
S. saxatilis Riddell	*Scutellaria*	Pittman 1987	America	30	4**
S. scandens Buch.-Ham. ex D. Don.	*Scutellaria*	Saggoo 1983	India	22, 26	2
S. scandens Buch.-Ham. ex D. Don.	*Scutellaria*	Gill 1984	Himalaya, India	26	2
S. scandens Buch.-Ham. ex D. Don.	*Scutellaria*	Saggoo and Bir 1981	India	22	2
S. scordifolia Fisch. ex Schrank	*Scutellaria*	Krogulevich 1978	Siberia–China	60	6
S. shikokiana Makino	*Scutellaria*	Sawanomukai et al. 2003	Japan	28	4
S. sibthorpii (Benth.) Hal.	*Scutellaria*	Yildiz and Gücel 2006	Cyprus	14, 28	2, 4

(*Continued*)

Table 1. (*Continued*)

Taxon	Section	Reference	Origin	2*n*	Ploidy level
S. sieberi Benth.	*Scutellaria*	Montmollin 1982, 1986; Bothmer 1985	Greece	34	4*
S. siphocampyloides Vatke	*Scutellaria*	Olmstead 1990	America	24	2
S. slametensis Sudarmono & Conn	*Scutellaria*	Sudarmono and Conn 2010	Indonesia	24	2
S. sporadum Bothmer	*Scutellaria*	Bothmer 1985	Greece	34	4*
S. strigillosa Hemsl.	*Scutellaria*	Sokolovskaya et al. 1986; Nishikawa 1985; Probatova and Sokolovskaya 1990	Japan, USSR	32	4
S. strigillosa Hemsl.	*Scutellaria*	Sawanomukai et al. 2003	Japan	30	4**
S. strigillosa Hemsl.	*Scutellaria*	Probatova et al. 1998; Shatalova 2000	Russia	16	2
S. taipeiensis T. C. Huang, A. Hsiao & M. J. Wu	*Scutellaria*	Huang et al. 2003	Taiwan	26	2
S. tashiroi Hayata	*Scutellaria*	Hsieh and Huang 1995	Taiwan	26	2
S. taiwanensis C. Y. Wu	*Scutellaria*	Hsieh and Huang 1995	Taiwan	26	2
S. ternejica Prob.	*Scutellaria*	Probatova 2006	Russia	16	2
S. tsusimensis H. Hara	*Scutellaria*	Sawanomukai et al. 2003	Japan	26	2
S. tuberosa Benth.	*Scutellaria*	Olmstead 1990	California	24	2
S. tuminensis Nakai	*Scutellaria*	Probatova and Sokolovskaya 1990	Russia	16	2
S. ussuriensis (Regel) Kudô	*Scutellaria*	Probatova et al. 1991	Russia	32	4
S. vacillans Rech.	*Scutellaria*	Papanicolaou 1984	Greece	34	4*
S. violacea Heyne ex Benth. in Wall.	*Scutellaria*	Vembu 1984; Vembu and Sampathkumar 1999	India	24	2
S. violacea Heyne ex Benth. in Wall.	*Scutellaria*	Saggoo 1983; Bir and Saggoo 1985; Saggoo and Bir 1986	India, Himalaya	26	2
S. violacea var. *hispidior* Hook. F.	*Scutellaria*	Saggoo and Bir 1982	India	26	2
S. violacea var. *violacea*	*Scutellaria*	Saggoo and Bir 1982	India	26	2
S. wightiana Benth.	*Scutellaria*	Saggoo 1983; Bir and Saggoo 1985	India	26	2
S. wightiana Benth.	*Scutellaria*	Cherian and Kuriachan 1981	India	24	2
S. yezoensis Kudo	*Scutellaria*	Probatova et al. 1989	Japan	16	2
S. yezoensis Kudo	*Scutellaria*	Sawanomukai et al. 2003	Japan	30	4**

*Hyperpolyploidy; **hypopolyploidy.

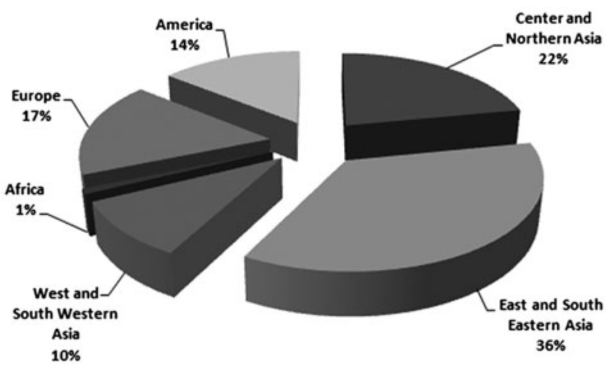

Figure 1. Geographical distribution of chromosome number records in the genus *Scutellaria* (the geographical division of the world follows Brummitt 2001).

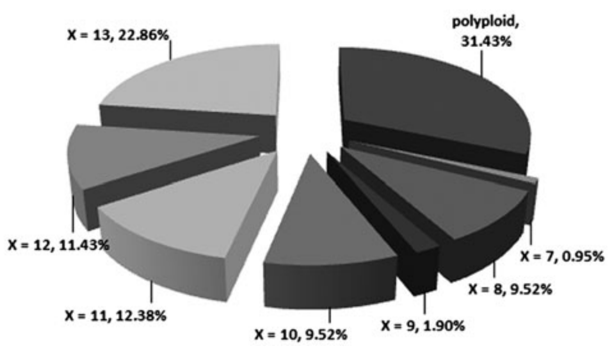

Figure 2. Assignment of the chromosome number records in the genus *Scutellaria*.

and *S.* sect. *Salazaria* based on Paton's classification (Paton 1990a).

Biogeography

Geographical distribution of the taxa belonging to the genus *Scutellaria* was obtained from online databases (http://ww2.bgbm.org/euroPlusMed/query.asp) and atlases mainly based on their localities taken from Floras and literatures and mapped here. For readability the localities, species numbers and prevailing chromosome counts of the sections are presented (Figure 3).

Scutellaria sect. *Scutellaria* (Rech.) Paton

Members of *S.* sect. *Scutellaria* are characterized by opposite or spiral flowers that are inserted in the leaf axis or leaf-like bracts, forming a one-sided inflorescence or rarely radiating out from the inflorescence axis in all directions. The section is probably the most primitive infrageneric taxon within the genus *Scutellaria*. The other sections of *S.* subgen. *Scutellaria* are probably evolved

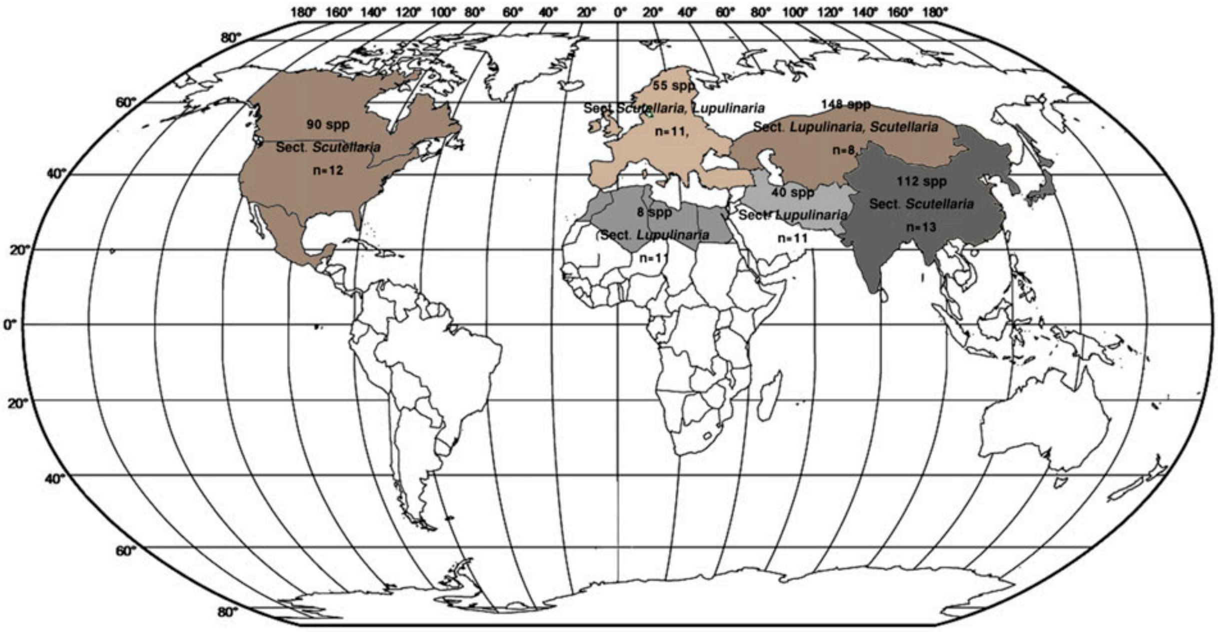

Figure 3. Centers of diversity of the *Scutellaria* species (the approximate numbers of species and prevailing base chromosome numbers in the sections from each region are presented inside each area).

Table 2. *Scutellaria* sect. *Lupulinaria* species analyzed in this study with their respective chromosome numbers, locations, and voucher specimens.

Taxon	Locality	Altitude (m)	Voucher specimen	*x*
S. araxensis Grossh.	W Azerbaijan: Bazargan toward Ghosh, protect area of Yaram ghiyeh	1745	BASU 26822	11
S. araxensis Grossh.	W Azerbaijan: Bazargan toward Ghosh, protect area of Grik	1415	BASU 26214	11
S. araxensis Grossh.	W Azerbaijan: 5 km after Shoot toward Chaldoran	1945	BASU 26100	11
S. farsistanica Rech.	Fars: Estahban	1720	BASU 24693	11
S. nepetifolia Benth.	Hamedan: Toysercan road, 5 km after Ski	1761	BASU 27446	11
S. persica Bornm.	E Azerbaijan: Mahabad toward Sardasht	1580	BASU 25500	11
S. pinnatifida Hamilt.	W Azerbaijan: Khoy toward Chaldoran, Khezerllo village	1495	BASU 26111	11
S. pinnatifida Hamilt.	W Azerbaijan: Mahabad	1368	BASU 25742	11
S. pinnatifida Hamilt.	W Azerbaijan: Oshnavieh toward Orumieh	1690	BASU 25428	11
S. pinnatifida Hamilt.	Kordestan: Salvatabad village, 5 km to Sanandaj	1805	BASU 28517	11
S. pinnatifida Hamilt.	W Azerbaijan: mountain around Bazargan	1415	BASU 26704	11
S. platystegia Juz.	E Azerbaijan: Zonuz	1630	BASU 26180	11
S. platystegia Juz.	E Azerbaijan: Siahroud toward Kaleibar, after Masan village, before Kalaleh village	1430	BASU 26224	11
S. platystegia Juz.	E Azerbaijan: Ahar toward Varzaghan, 20 km to Varzaghan	1620	BASU 26890	11
S. platystegia Juz.	E Azerbaijan: Kaleibar toward Ahar, 50 km after Kaleibar	1495	BASU 26370	11
S. platystegia Juz.	E Azerbaijan: Before Zonuz	1435	BASU 25760	11
S. theobromina Rech.	W Azerbaijan: 10 km from Orumieh toward Movana, Movana biforcate	1515	BASU 25838	11
S. theobromina Rech.	W Azerbaijan: 15 km after Bukan toward Mahabad	1530	BASU 25824	11
S. theobromina Rech.	W Azerbaijan: Piranshahr toward Oshnavieh, 15 km to Oshnavieh	1525	BASU 26554	11
S. tomentosa Bertol.	Esfahan: Kashan toward Mashhad Ardehal	1761	BASU 24420	11

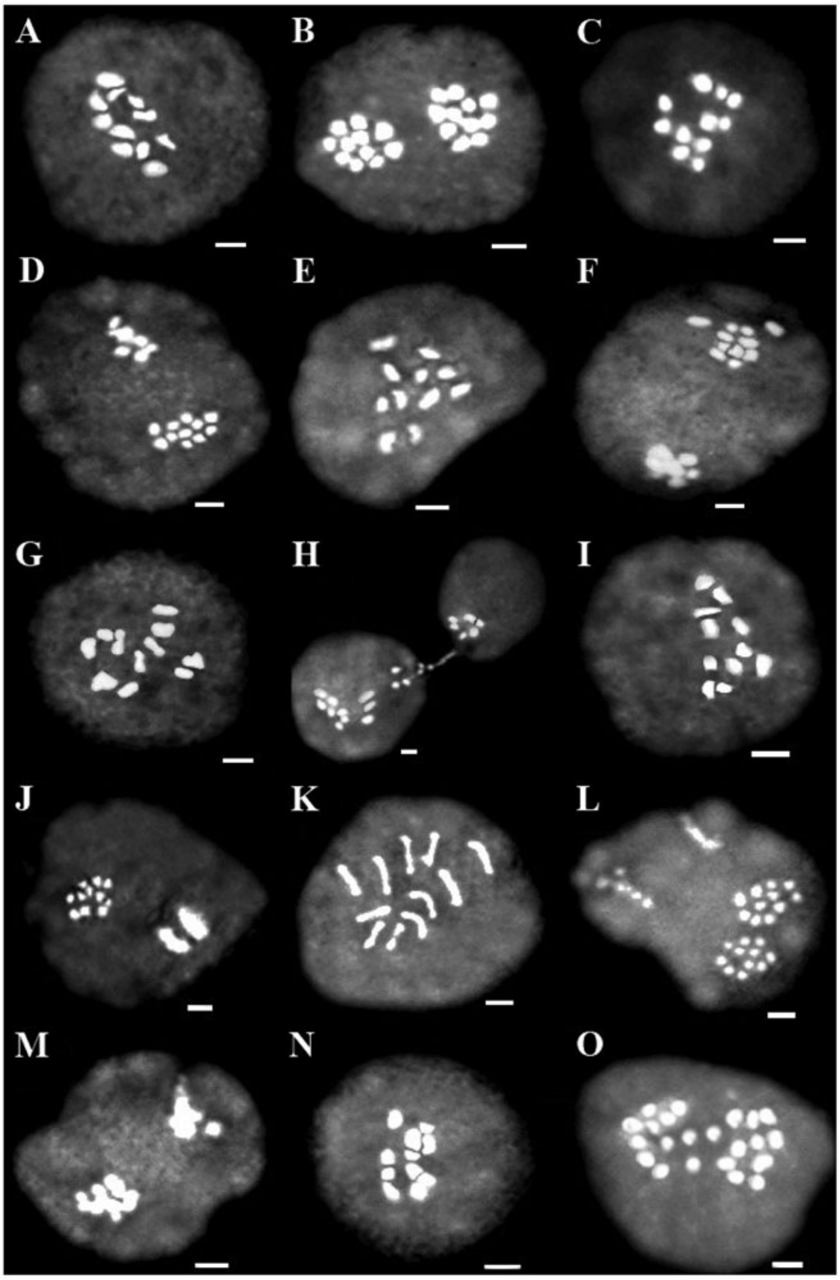

Figure 4. Representative meiotic cells of three *Scutellaria* species. (A–D) *S. araxensis*: (A) diakinesis (26100); (B) telophase I (26100); (C) diakinesis (26214); (D) asynchronous nuclei (26822). (E–M) *S. platystegia*: (E) diakinesis (25760); (F) telophase I with forward chromosome (25760); (G) diakinesis (26180); (H) cytomixis (26180); (I) diakinesis (26224); (J) asynchronous nuclei (26224); (K) diakinesis (26370); (L) asynchronous nuclei (26370); (M) asynchronous nuclei (26890). (N, O) *S. farsistanica*: (N) diakinesis (24693); (O) anaphase I with laggard chromosome (24693). Scale bars: 2 μm.

from *S.* sect. *Scutellaria* in response to various selection pressures in different regions of the world. It is the most widespread taxon, with about 240 species throughout the natural range of *Scutellaria* with unequal numbers in the Old and New Worlds (Paton 1990a). As *Scutellaria* is a subcosmopolitan section, most cytogenetic studies have been done on this section. Our results confirmed that there are different chromosome numbers in *S.* sect. *Scutellaria* ($2n$ = 16, 18, 20, 22, 24, 26, 28, 30, 32, 34, 44, 60, 80 and 88). (Probatov and Sokolovskaya 1990) These numbers probably represent aneuploid members that establish communities surrounding the diploid and polyploid species. The diploid numbers $2n$ = 24 and $2n$ = 26 are known in most of the taxa belonging to the section. Therefore, x = 2 and x = 13 are the prevailing basic numbers in the section. The basic chromosome number x = 13 is dominant in E and SE Asia and x = 12 in America. Meanwhile, chromosome numbers $2n$ = 44, 80 and 88 are rare and reported only for *S. lateriflora*. The other sections of *S.* subgen. *Scutellaria* are not widespread and there are few chromosome reports on these sections. *S.* sect. *Salazaria* is distributed in S Utah, S Arizona,

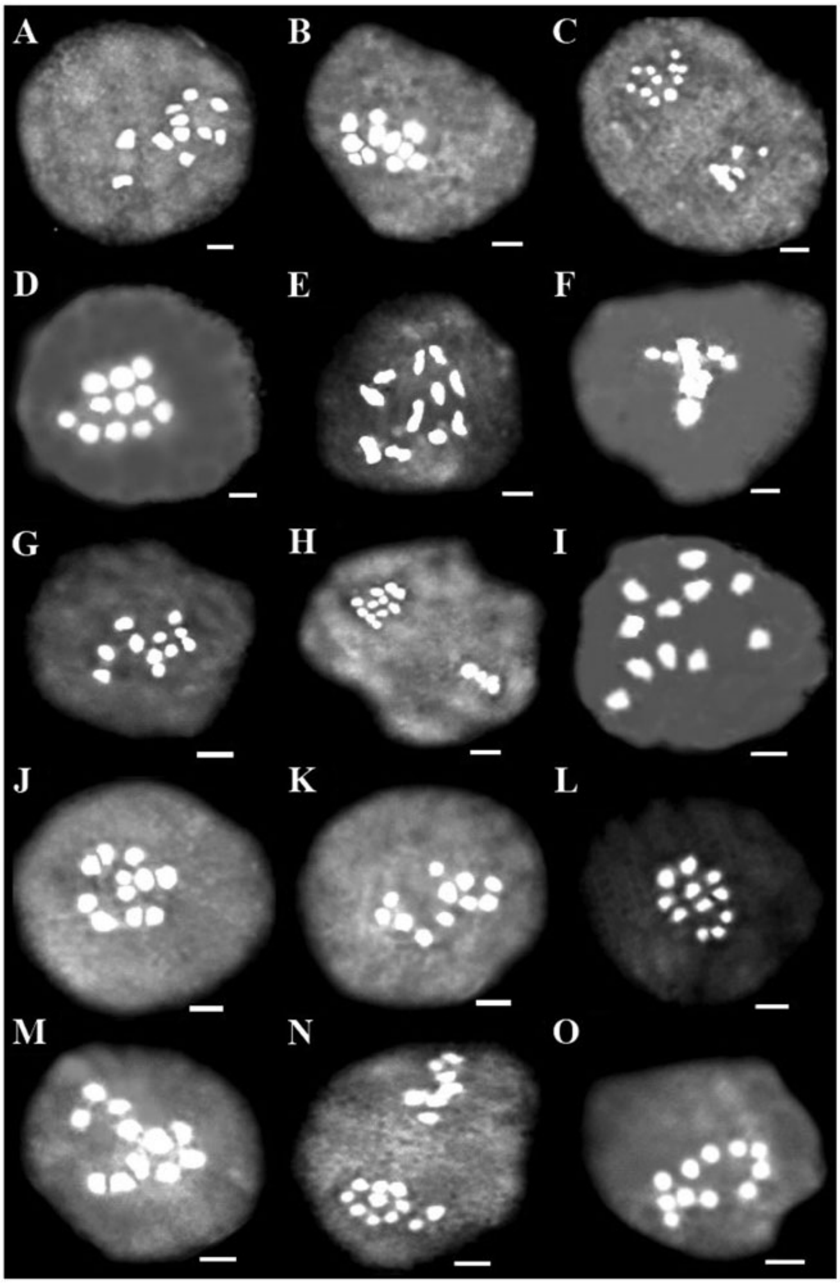

Figure 5. Representative meiotic cells of four *Scutellaria* species. (A) *S. tomentosa*: diakinesis (24420). (B, C) *S. persica*: (B) diakinesis (25500); (C) asynchronous nuclei (25500). (D–H) *S. theobromina*: (D) diakinesis (26554); (E) diakinesis (25838); (F) metaphase I with precocious chromosome migration to the pole (25838); (G) diakinesis (25824); (H) asynchronous nuclei (25824). (I) *S. nepetifolia*: diakinesis (27446). (J–O) *S. pinnatifida*: (J) diakinesis (25428); (K) diakinesis (26704); (L) diakinesis (25742); (M) diakinesis (28517); (N) asynchronous nuclei (28517); (O) diakinesis (26111). Scale bars: 2 μm.

New Mexico, Texas, California, Baja California and Chihuahua. The diploid chromosome number $2n = 50$ is reported for *S. mexicana* of *S.* sect. *Salazaria* (Paton 1990a). About 15 species of *S.* sect. *anaspis* are found in S Iran, Afghanistan, C Asia and Xizang (Tibet), of which *S. petiolata* shows a diploid number of $2n = 16$. (Aryavand 1977; Khatoon and Ali 1993) About 11 species of *S.* sect. *Perilomia* are found in the Andes from Colombia to Chile and no counts have been reported on this section (Paton 1990a). Chromosome numbers $2n =$ 24–34 have been reported for *S.* subgen. *Scutellaria* by Paton (1990a). This study is based on the published counts represent the known chromosome numbers $2n =$ 16–88.

Scutellaria sect. *Lupulinaria* A. Hamilton

S. sect. *Lupulinaria* are prostrate or erect suffruticose herbs and characterized by petiolate lower leaves, similar in form to the upper leaves, and dense or loose inflorescence. About 130 species of the section are found in the mountainous and upland regions in N Africa and Eurasia, usually over 1000 m elevation. The section was divided into two subsections, namely *S.* subsect. *Lupulinaria* (Hamilton) Paton and *S.* subsect. *Cystaspis*. (Juz.) Paton. Most studies on the section related to *S.* subsect. *Lupulinaria* (Paton 1990a). There are different chromosome numbers for the taxa belonging to the section ($2n$ = 16, 18, 20 and 22). Probably most of them are euploids or aneuploids. The chromosome number $2n = 22$ is known for the most of taxa in diploid level. Therefore, $x = 11$ is the prevailing basic chromosome number in the section and $x = 8$, $x = 9$ and $x = 10$ are less frequent. (Morton 1973; Aryavand 1977; Krogulevich 1978; Cherian and Kuriachan 1981; Montmollin 1982; Sekovski and Jovanovska 1983; Papanicolaou 1984; Vembu 1984; Nishikawa 1985; Saggoo and Bir 1986; Sokolovskaya et al. 1986; Galland 1988; Ghaffari 1988; Probatova et al. 1989; Probatova and Sokolovskaya 1990; Probatova et al. 1991; Galland 1991; Xu et al. 1992 ; Zakirova and Nafanailova 1992; Zhao 1996; Dempsey et al. 1994; Probatova et al. 1998; Vembu and Sampathkumar 1999; Shatalova 2000; Dmitrieva 2000; Huang et al. 2003; Naruhashi et al. 2004; Castro 2005; Cheng 2010; Sudarmono and Conn 2010).

We report here the chromosome numbers of 20 populations of eight species belong to *S.* sect. *Lupulinaria*, which were collected from different localities in Iran (Table 2). Our results showed that all populations were diploid and possessed $2n = 2x = 22$ chromosome number, consistent with the proposed base number of $x = 11$ (Figures 4 and 5). On the basis of published counts for *S.* sect. *Lupulinaria* together with the reports presented here, we have verified that $x = 11$ is the most common number for this section. The chromosome numbers $2n$ = 16–24 have been reported for *S.* subgen. *Apelthanthus* by Paton (1990a). The chromosome numbers $2n$ = 16–22 for the subgenus result from the published counts and the present study.

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