

# KARYOLOGICAL INVESTIGATIONS OF SELECTED ANGIOSPERMS FROM GEORGIA AND AZERBAIJAN

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Chromosome numbers of eleven angiosperm species, five dicots and six monocots from Georgia and Azerbaijan are reported. The chromosome number of *Cruciata coronata* (Rubiaceae) is provided for the first time (2n = 22). Additionally, karyotypes are presented for five species, those of *Danae racemosa* (Ruscaceae), *Paris incompleta* (Trilliaceae), and *Ruscus hyrcanus* (Ruscaceae) for the first time. The new data are compared with previous karyological information, and both are discussed in a biosystematic context.

Key words: Chromosome number, karyotype, karyosystematics, polyploidy, Georgia, Azerbaijan.

# INTRODUCTION

Karyological features are appreciated as very important taxonomic characters which do not simply provide an additional character but often allow conclusions about evolutionary events in the group of interest (e.g., Greilhuber and Speta, 1978; Greilhuber, 1982; Cerbah et al., 1998). In recent decades, vast amounts of data on chromosome numbers have been collected (Stace, 2000). However, these data are very unevenly distributed over plant groups and over geographical areas. In many taxa more than one ploidy level is reported; nowadays it is generally acknowledged that at least several counts per species are desirable. Although most frequently used for (karyo)systematic purposes, the chromosome number alone is often not sufficient to unambiguously trace the evolutionary history of the group. In such cases, more detailed information about the karyotype is necessary.

We report chromosome numbers of eleven angiosperm species from Georgia and Azerbaijan. One species is counted for the first time, and other data are first reports for certain ploidy levels. For three of those species the karyotypes are presented for the first time. The new data are compared with previous karyological information, and both are discussed in a biosystematic context.

## MATERIALS AND METHODS

Eleven species were collected in Georgia (G) and Azerbaijan (A) in May 2001 by G.M. Schneeweiss and A. Tribsch. Vouchers are deposited in the Schönswetter and Tribsch herbarium (S&T) in the Botanical Institute of the University of Vienna (WU), the Natural History Museum of Vienna (W) and the Oberösterreichisches Landesmuseum of Linz (LI). The specimens were analyzed karyologically (Tab. 1). Chromosomes were obtained either from flower buds fixed in the field or from root tip meristems obtained from plants transferred to and grown in the Botanical Garden of the University of Vienna (HBV).

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TABLE 1. Plant	material for	cytological	investigations

Taxon	Locality	Coordinates	Deposition
Brassicaceae			
<i>Alliaria petiolata</i> (Bieb.) Cavara & Grande	G: Minor Caucasus, Trialetic Mountains, Bakuriani; 1750–1850 m	E 43°31'18" N 41°45'39"	WU (S&T 6924)
Alyssum hirsutum Bieb.	G: Minor Caucasus, Trialetic Mountains, Kura Valley, between Akaltsikhe and Atsquri; 950–1100 m	E 43°09'58" N 41°41'11"	WU (S&T 6987)
Alyssum strigosum Banks & Soland.	G: Minor Caucasus, Trialetic Mountains, Kura Valley, between Akaltsikhe and Atsquri; 950–1100 m	E 43°09'58" N 41°41'11"	WU (S&T 6975)
Hyacinthaceae			
<i>Bellevalia paradoxa</i> (Fisch. & C. A. Mey.) Boiss.	G: Minor Caucasus, Trialetic Mountains, Tskhatsqaro ugheltekhili S of Bakuriani; 2100–2500 m	E 43°31'02" N 41°42'04"	LI (S&T 6671)
<i>Othocallis rosenii</i> (C. Koch) F. Speta	G: Minor Caucasus, Trialetic Mountains, Tskhatsqaro ugheltekhili S of Bakuriani; 2100–2500 m	E 43°31'02" N 41°42'04"	WU (S&T 6687)
Poaceae			
Dactylis hyrcana (Tzvel.) Musajev	A: Talysh, Hyrcanian Forest Reservation Qirqan qorugu (10-12 km SW Länkäran), 200–300 m	-	WU (S&T 6825)
Rubiaceae			
<i>Cruciata coronata</i> (Sibth. & Smith) Ehrend.	G: Minor Caucasus, Trialetic Mountains, Kura Valley, between Akaltsikhe and Atsquri; 950–1100 m	E 43°09'58" N 41°41'11"	WU (S&T 6985)
Phuopsis stylosa (Trin.) Hook. f.	A: Talysh, Hyrcanian Forest Reservation Qirqan qorugu (ca. 10-12 km SW Länkäran); 200–250 m	E 48°43'51" N 38°40'15"	W (S&T 6817)
Ruscaceae			
Danae racemosa (L.) Moench	A: Talysh, Hyrcanian Forest Reservation Qirqan qorugu (10-12 km SW Länkäran); 200–300 m	E 48°43'45" N 38°39'49"	WU (S&T 6809)
Ruscus hyrcanus Woronow	A: Talysh, Hyrcanian Forest Reservation Qirqan qorugu (SW Länkäran); 130–250 m	E 48°45'30" N 38°40'00"	W (S&T 6784)
Trilliaceae			
Paris incompleta Bieb.	G: Minor Caucasus, Trialetic Mountains, between Bakuriani and Tskhatsqaro ugheltekhili; 1750–1900 m	E 43°30'34" N 41°44'07"	WU (S&T 6704)

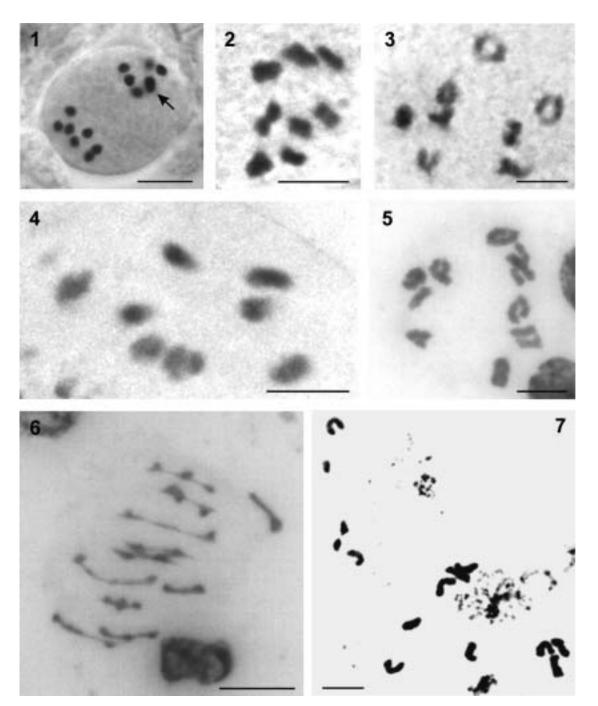
Flower buds were directly fixed in 3:1 ethanol:acetic acid, stored for several days at room temperature and then at -20°C until use. Root tips were pretreated with 0.1% colchicine for 24 h at 4°C in darkness and fixed in 3:1 ethanol:acetic acid for 24 h at room temperature and then stored at -20°C until use. Feulgen staining with Schiff's reagent was performed following the standard protocol. Briefly, material was hydrolyzed in 5N HCl for 20 min at room temperature, washed with tap water and stained with Schiff's reagent (SIGMA, Germany) in darkness for 1 h. Squash preparations were made in a drop of 45% acetic acid. Preparations with a minimum five well-spread metaphases were analyzed with a light microscope (Polyvar, Reichert-Jung). The number of plates chosen for chromosome number determination varied from 4 to 10.

The chromosomes in the karyotypes were ordered by decreasing length. Chromosome type terminology follows that of Levan et al. (1964). Photographs were taken on Technical Pan 100 ASA film (Kodak). Photos were scanned and karyotypes cut out using Corel Photo-Paint 7.0.

# **RESULTS AND DISCUSSION**

#### DICOTYLEDONS

Alliaria petiolata (Brassicaceae) possesses 2n = 14 small chromosomes (1–1.5 µm; Fig. 1). Individually they are almost unidentifiable during both mitotic and meiotic divisions. Among the populations of *A. petiolata* counted so far, based on x = 7, diploids (2n = 14) and hexaploids (2n = 42) are known. The



**Figs. 1–7**. Meiotic (1–6) and mitotic (7) chromosomes. **Fig. 1**. *Alliaria petiolata* (n = 7; arrow indicates two overlapping chromosomes). **Figs. 2–3**. *Alyssum hirsutum* (n = 8). **Fig. 4**. *Alyssum strigosum* (n = 8). **Fig. 5**. *Phuopsis stylosa* (n = 10; note two overlapping bivalents). **Fig. 6**. *Cruciata coronata* (n = 11). **Fig. 7**. *Dactylis hyrcana* (2n = 14). Bar = 5  $\mu$ m.

deviating counts of 2n = 36 presented by Gadella and Kliphuis (1963, and references therein) require confirmation. Diploids are known from Western Asia (Naqshi and Javeid, in: Löve, 1976; Maassoumi, 1980), whereas hexaploids are reported for Western and Central Europe and from introduced populations in North America (e.g., Queirós, 1973; Hill, in: Stace, 1989; Dobeš et al., 1997; Montgomery et al., 1997). Our data strengthen this geographical pattern, and the accession from Minor Caucasus analyzed here is so far the westernmost diploid *A. petiolata*. Investigations of material from Southeast Europe and Turkey would be necessary to (1) determine the borders of the distribution areas of the two cytotypes, (2) check the likely occurrence of tetraploids, and (3) allow a better judgement of whether these cytotypes can be distinguished as separate (intraspecific) taxa.

Alyssum hirsutum (Brassicaceae) is a diploid species (2n = 16; Figs. 2, 3). Its chromosomes are small  $(1-2 \mu m)$ , most of them being meta- and submetacentrics. Meiosis is regular, and in metaphase I eight bivalents (mostly rod-shaped) can be seen. We present the first record of diploid A. hirsutum, previously reported to be hexaploid (2n = 48,Il'yn'ska, 1986) and hypohexaploid (2n = 46, Ančev, in: Löve, 1981) based on x = 8, a number present in many genera of the tribe Alysseae (Contandriopoulos, 1969). The occurrence of diploid and polyploid cytotypes within one species is known for other annual taxa of Alyssum, such as A. alyssoides (L.) L. (e.g., Contandriopoulos, 1969) and A. desertorum Stapf (= A. turkestanicum Regel & Schmalh.; e.g., Podlech and Dieterle, 1969; Polatschek, 1968; 1971). The East Mediterranean and Southwest Asian A. hirsutum is closely related to A. strigosum (see below) and A. simplex Rudolphi [syn. A. minus (L.) Rothm.] but differs morphologically by the presence of long simple hairs on the silicule.

Alyssum strigosum (Brassicaceae) is also a diploid species with 2n = 16 (e.g., Al-Shehbaz, in: Löve, 1982; Díaz Lifante et al., 1992; Fig 4). The chromosome size and pairing behavior of this species are very similar to that of *A. hirsutum* discussed above. *A. strigosum* is widespread and frequent from the Eastern Mediterranean region to Southwest Asia, where it partly replaces the closely related circummediterranean diploid *A. simplex* (e.g., Ančev, in: Löve, 1975; Maassoumi, 1980; Luque and Díaz Lifante, 1991).

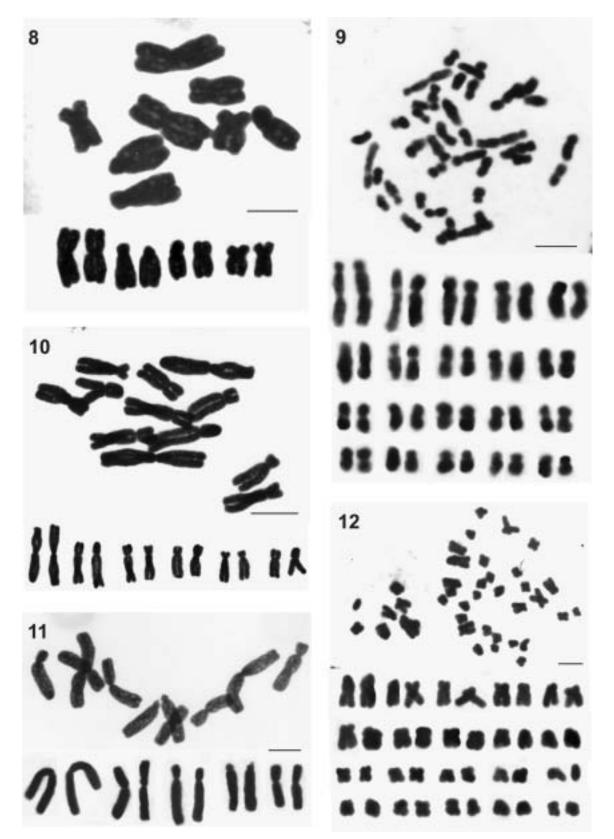
*Cruciata coronata* (Rubiaceae) possesses 2n = 22 chromosomes which are very small (1–1.5 µm) and similar in size and shape (Fig. 6). Meiosis is very regular. Mostly 11 bivalents are observed, each with one or occasionally two chiasmata. This is the first chromosome number report for *C. coronata. Cruciata* is sometimes treated as a section of the large genus *Galium*, with which it shares the chromosomal base number of x = 11 (e.g., Ehrendorfer, in: Moore, 1982). *C. coronata* belongs to the Southwest Asian *C. coronata* agg., comprising several not always clearly separable taxa (Ehrendorfer, 1962). The closely related *C. taurica* (Pall.) Ehrend. is reported to be tetraploid with 2n = 44 (Ehrendorfer, in: Moore, 1982). However, putatively hybridogenic

forms between *C. coronata* and *C. taurica* have also been reported (Ehrendorfer, 1962), leaving the correlation of morphological and karyological separation to be corroborated.

Phuopsis stylosa (Rubiaceae) is a diploid with 2n = 20 chromosomes (Fig. 5). Despite their relatively small size,  $(2-2.5 \,\mu\text{m})$ , most of the chromosomes can be identified as metacentrics and submetacentrics. Meiosis is very regular, with 10 bivalents, mostly rod-shaped with two chiasmata. Phuopsis is a monotypic genus restricted to Southwest Asia. Recent molecular investigations have shown that Phuopsis nests within Crucianella (Natali et al., 1995, 1996), supporting earlier treatments of Phuopsis stylosa as Crucianella stylosa (Sugiura 1937, 1939). The chromosome number report for Phuopsis presented here confirms those by Fagerlind (1934, 1937). A deviating count of n = 9 (Sugiura, 1937) was later corrected by the same author to n = 11 (Sugiura, 1939), a number also found by Homeyer (1936). The chromosome number of x = 11 would support the relationship of *Phuopsis* and *Crucianella*, since the latter possesses the same chromosome base number (e.g., Homeyer, 1936; Ehrendorfer, in: Moore, 1982; Queirós, 1986). It remains to be seen whether the genus *Phuopsis* really has two base chromosome numbers (x = 10 and x = 11). Possibly the earlier reports of x = 11 result from misinterpretation due to the small size of the chromosomes, or were biased by expectations of that chromosome number inferred from the taxonomic relationship.

#### MONOCOTYLEDONS

Bellevalia paradoxa (Hyacinthaceae) is a diploid species with 2n = 8 chromosomes (Fig. 8). The chromosomes are long, ranging from 5 µm to 9 µm. The analyzed individual of *B. paradoxa* is a diploid, but polyploids are also known in this species, as in other species of the genus (Özhatay et al., 1991). Karyotypes of several species of the genus published so far (e.g., Özhatay et al., 1991; Tzanoudakis et al., 1991) reveal uniform karyotype morphology. Each chromosome pair is easily distinguishable by chromosome morphology alone. The karyotype consists of one metacentric pair, two submetacentric pairs and one subtelocentric pair. No satellites are visible, although, as in other species, it is very likely that the second chromosome pair bears a NOR (Özhatay et al., 1991). B. paradoxa and other species of the genus morphologically resemble Muscari species, but differ significantly karyologically. Bellevalia has a chromosome base number of x = 4, while *Muscari* 



**Figs. 8–12.** Mitotic chromosomes and karyotypes. **Fig. 8.** *Bellevalia paradoxa* (2n = 8). **Fig. 9.** *Danae racemosa* (2n = 40). **Fig. 10.** *Othocallis rosenii* (2n = 12). **Fig. 11.** *Paris incompleta* (2n = 10). **Fig. 12.** *Ruscus hyrcanus* (2n = 40). Bar = 5  $\mu$ m.

reveals x = 9 (Speta, 1998a). Additionally, the chromosomes of *Bellevalia* are much larger than those of *Muscari*. The report of 2n = 18 for *B. paradoxa* by Saito and Matsuzawa (1969) is thus very likely due to confusion with a *Muscari* species.

Dactylis hyrcana (Poaceae) is a diploid species (2n = 14; Fig. 7). The chromosomes of *D. hyrcana* are small  $(1.5-3.5 \,\mu\text{m})$ , but within the complement several groups of morphological types of chromosomes can be distinguished: larger metacentrics and submetacentrics and smaller subtelocentrics. Our record is the second for D. hyrcana; it confirms the chromosome number reported by Sokolovskaya and Probatova (1979). D. hyrcana belongs to the group of diploid races within the polyploid complex of the D. glomerata aggregate. The diploids are disjunctly distributed over the whole range from the Macaronesian Islands to China (Stebbins and Zohary, 1959). D. hyrcana is an endemic species of deciduous woods in Talysh (Azerbaijan, Iran), morphologically well characterized by a dense indumentum of short but soft hairs in the upper part of the panicle (Tsvelev, 1983). There are two conflicting concepts about the taxonomic treatment of the diploids: (1) diploids are always treated as taxa separate from polyploids, whether or not they are distinguishable morphologically, ecologically or geographically (e.g., Stebbins and Zohary, 1959; Jones et al., 1961; Borrill and Carroll, 1969); and (2) ploidy level alone is not sufficient to treat races as different taxa, so that taxa with more than one ploidy level do occur (e.g., Doroszewska, 1963; Speranza and Cristofolini, 1987; Ortiz and Rodriguez-Oubiña, 1993). Individuals with different ploidy levels often grow sympatrically (Zohary and Nur, 1959; Borrill and Lindner, 1971, Ortiz and Rodriguez-Oubiña, 1993), and some tetraploids have been shown to be of autopolyploid origin (Borrill and Lindner, 1971; Lumaret and Barrientos, 1990), supporting the second concept.

Analysis of somatic chromosome number in *Danae racemosa* (Ruscaceae) revealed that the species possesses 2n = 40 chromosomes (Fig. 9). The karyotype, presented here for the first time, is bimodal, with several bigger and the rest smaller chromosomes (2–6 µm). The first pair is large and metacentric, five are medium-sized and mostly submetacentric, and 14 are smaller and predominantly metacentric. Secondary constrictions (SCs) are clearly visible on at least one chromosome pair (pair no. 1). This is the second count for *D. racemosa*, and it confirms the report of Satô (1942). *Danae* has the same chromosome number as *Ruscus* (e.g., Satô, 1942; Vijayavalli, 1986), to which it is closely related

(Jang and Pfosser, 2002). The karyotypes of the two genera are somewhat similar, as also indicated by Sen (1975). However, while in *Danae* the SCs are clearly visible on the longest chromosome pair, they are not detectable in *Ruscus*.

Othocallis rosenii (syn. Scilla rosenii; Hyacinthaceae) is diploid with 2n = 12 chromosomes (Fig. 10). They are big (6–10  $\mu$ m), the largest pair being metacentric and the remaining ones submetacentrics to subtelocentrics. The karyotype consists of one pair of the largest, metacentric chromosomes, two pairs of submetacentrics and three pairs of smaller subtelocentrics. All chromosome pairs are easily distinguishable by their morphology. Despite the very stable basic chromosome number x = 6 (with polyploids occurring: Greilhuber, 1982), karyotypes of other Othocallis species, particularly O. siberica and O. amoena, reveal strong intraindividual polymorphism in the size of homologous chromosomes due to localization of heterochromatin blocks (Greilhuber and Speta, 1978). The population of O. rosenii analyzed in the present study also reveals polymorphism in the length of chromosome pairs 1 and 2 (Fig. 10). The genus Othocallis comprises about 20 species, distributed mainly in Southwest Asia (Speta, 1998a). Formerly it was included in Scilla, but recently has been split from that genus based on morphological and karyological characters (Speta, 1998b) also supported by molecular data (Pfosser and Speta, 1999).

Paris incompleta (Trilliaceae) is a diploid species with 2n = 10 chromosomes (Fig. 11). The karyotype of P. incompleta is presented here for the first time. The karyotype consists of one pair of metacentric chromosomes, two pairs of submetacentrics, one pair of subtelocentrics and one pair of telocentrics. The chromosomes are relatively large (7.0–11.5  $\mu$ m). One of the subtelocentric pairs (no. 4) carries a satellite, indicating the presence of at least one active NOR pair. This is the third count for P. incompleta; it confirms earlier reports of Tifonova in Fedorov (1969) and Gagnidze et al. (1985). Karyotypes of other Paris species (Miyamoto et al., 1992) reveal considerable variation in the length and type of chromosomes of corresponding pairs in related species, mostly in regard to chromosome pairs 4 and 5. In the present study, polymorphism in chromosome length and heterochromatin distribution was also observed between individuals within the same species, for almost all chromosome pairs, especially pair 1. Intraindividual polymorphism in the relative length of homologous chromosomes was also detectable in the karyotype of the specimens analyzed in the present study.

Karvological analysis of Ruscus hyrcanus (Ruscaceae) revealed the presence of 2n = 40 chromosomes in somatic cells (Fig. 12). The karyotype of *R. hyrcanus* is presented here for the first time and consists of one metacentric pair, the biggest, five smaller submetacentric pairs, and 14 pairs of small, mostly metacentric and submetacentric chromosomes. The chromosomes are medium-sized  $(2-5 \,\mu\text{m})$ . This is the second count for R. hyrcanus, and it confirms the report of Abramova in Fedorov (1969). In the Hyrcanian region (Azerbaijan, Iran) this species replaces the very closely related, widespread *R. aculeatus*, which also has 2n = 40 (e.g., Capineri et al., 1978; Popova and Česchmedjiev, in: Löve, 1978). The karyotype of *R. aculeatus* (2n = 40) published by Capineri et al. (1978) exhibits chromosome types similar to those of *R. hyrcanus*.

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### REFERENCES

- BORRILL M, and CARROLL CP. 1969. A chromosome atlas of the genus *Dactylis* (Part two). *Cytologia* 34: 6–17.
- BORRILL M, and LINDNER R. 1971. Diploid-tetraploid sympatry in Dactylis (Gramineae). New Phytologist 70: 1111–1124.
- CAPINERI R, D'AMATO G, and MARCHI P. 1978. Numeri cromosomici per la flora Italiana: 534–583. *Informatore Botanico Italiano* 10: 421–465.
- CERBAH M, COULAUD J, and SILJAK-YAKOVLEV S. 1998. rDNA organization and evolutionary relationships in the genus *Hypochaeris* (Asteraceae). *Journal of Heredity* 89: 312–318.
- CONTANDRIOPOULOS J. 1969. Contribution à l'étude cytotaxonomique des Alysseae Adams de Grèce. *Berichte der Schweizerischen Botanischen Gesellschaft* 79: 313–334.
- DÍAZ LIFANTE Z, LUQUE T, and SANTA BARBARA C. 1992. Chromosome numbers of plants collected during Iter Mediterraneum II in Israel. *Bocconea* 3: 229–250.
- DOBEŠ C, HAHN B, and MORAWETZ W. 1997. Chromosomenzahlen zur Gefäßpflanzen-Flora Österreichs. *Linzer Biologische Beiträge* 29: 5–43.
- DOROSZEWSKA A. 1963. An investigation on the diploid and tetraploid forms of *Dactylis glomerata* L. subsp. *woronowii* (Ovczinn.) Stebbins et Zohary. *Acta Societatis Botanicorum Poloniae* 32: 113–130.
- EHRENDORFER F. 1962. Notizen zur Systematik und Phylogenie von *Cruciata* Mill. und verwandten Gattungen der Rubia-

ceae. Annalen des Naturhistorischen Museums in Wien 65: 11–20.

- FAGERLIND F. 1934. Beiträge zur Kenntnis der Zytologie der Rubiaceen. *Hereditas* 19: 223–232.
- FAGERLIND F. 1937. Embryologische, zytologische und bestäubungsexperimentelle Studien in der Familie Rubiaceae nebst Bemerkungen über einige Polyploiditätsprobleme. *Acta Horti Bergiani* 11: 195–470.
- FEDOROV A. 1969. Chromosomnyie čisla cvetkovych rastenij (Chromosome numbers of flowering plants). Nauka, Leningrad.
- GADELLA TWJ, and KLIPHUIS E. 1963: Chromosome numbers of flowering plants in the Netherlands. *Acta Botanica Neerlandica* 12: 195–230.
- GAGNIDZE RI, GVINIASCHVILI CN, PATARAIA MG, and DZINDZOLIA LD. 1985. Chromosome numbers in some high-elevation species from the Big Caucasus. *Botanicheskij Zhurnal* 70: 1698–1699 (In Russian).
- GREILHUBER J. 1982. Trends in der Chromosomenevolution von *Scilla* (Liliaceae). *Stapfia* 10: 11–51.
- GREILHUBER J, and SPETA F. 1978. Quantitative analyses of Cbanded karyotypes, and systematics in the cultivated species of the *Scilla siberica* group (Liliaceae). *Plant Systematics and Evolution* 129: 63–109
- HOMEYER H. 1936. Beiträge zur Kenntnis der Zytologie und Systematik der Rubiaceen. *Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie* 67: 237–263.
- IL'YN'SKA AP. 1986. Cytotaxonomic analysis of representatives from the section *Alyssum, Psilonema* (Meyer) Hook. in Benth. et Hook. and *Meniocus* (Desv.) Hook. of the genus *Alyssum* L. of the Ukrainian flora. *Ukrainskyj Botanichnyj Zhurnal* 43: 26–30 (In Ukrainian).
- JANG CG, and PFOSSER M. 2002. Phylogenetics of Ruscaceae sensu lato based on plastid *rbcL* and *trnL-F* DNA sequences. *Stapfia* 60: 333–348.
- JONES K, CARROLL CP, and BORRILL M. 1961. A chromosome atlas of the genus *Dactylis* L. *Cytologia* 26: 333–343.
- LEVAN A, FREDGA K, and SANDBERG A. 1964. Nomenclature for centromeric position on chromosomes. *Hereditas* 52: 201– 220.
- LÖVE Á. 1975. IOPB chromosome number reports XLIX. *Taxon* 24: 501–516.
- LÖVE Á. 1976. IOPB chromosome number reports LIV. *Taxon* 25: 631–649.
- LÖVE Á. 1978. IOPB chromosome number reports LXI. *Taxon* 27: 375–392.
- LÖVE Á. 1981. IOPB chromosome number reports LXXIII. *Taxon* 30: 829–861.
- LÖVE Á. 1982. IOPB chromosome number reports LXXVI. *Taxon* 31: 574–598.
- LUMARET R, and BARRIENTOS E. 1990. Phylogenetic relationships and gene-flow between sympatric diploid and tetraploid plants of *Dactylis glomerata* (Gramineae). *Plant Systematics and Evolution* 169: 81–96.
- LUQUE L, and DÍAZ LIFANTE Z. 1991. Chromosome numbers of plants collected during Iter Mediterraneum I in the SE of Spain. *Bocconea* 1: 303–364.

- MAASSOUMI AAR. 1980. Cruciferes de la flore d'Iran etude caryosystematique. Ph.D. dissertation, University Louis Pasteur, Strasbourg.
- MIYAMOTO J, KURITA S, ZHIJIAN G, and HEN L. 1992. C-banding patterns in eighteen taxa of the genus *Paris* sensu Li, Liliaceae. *Cytologia* 57: 181–194.
- MONTGOMERY L, KHALAF M, BAILEY JP, and GORNALL RJ. 1997. Contributions to a cytological catalogue of the British and Irish flora, 5. *Watsonia* 21: 365–368.
- MOORE DM. 1982. Flora Europaea check-list and chromosome index. Cambridge University Press, Cambridge (U.K.).
- NATALI A, MANEN J-F, and EHRENDORFER F. 1995. Phylogeny of the Rubiaceae-Rubioideae, in particular the tribe Rubieae: evidence from a non-coding chloroplast DNA sequence. *Annals of the Missouri Botanical Garden* 82: 428–439.
- NATALI A, MANEN J-F, KIEHN M, and EHRENDORFER F. 1996. Tribal, generic and specific relationships in the Rubioideae-Rubieae (Rubiaceae) based on sequence data of a cpDNA intergene region. In: Robbrecht E, Puff C, and Smets E [eds.], *Proceedings of the 2nd International Rubiaceae Conference. Opera Botanica Belgica* 7: 193–203.
- ORTIZ S, and RODRIGUEZ-OUBINA J. 1993. *Dactylis glomerata* subsp. *izcoi*, a new subspecies from Galicia NW Iberian Peninsula. *Annales Botanici Fennici* 30: 305–311.
- ÖZHATAY N, JOHNSON M, and MATHEW B. 1991. Chromosome numbers of Turkish *Bellevalia* species, including a new hexaploid from European Turkey. *Botanika Chronika* 10: 813–818.
- PFOSSER M, and SPETA F. 1999. Phylogenetics of Hyacinthaceae based on plastid sequences. *Annals of the Missouri Botanical Garden* 86: 852–875.
- PODLECH D, and DIETERLE A. 1969. Chromosomenstudien an afghanischen Pflanzen. *Candollea* 24: 185–243.
- POLATSCHEK A. 1968. Cytotaxonomische Beiträge zur Flora Iranica I. Annalen des Naturhistorischen Museums in Wien 72: 581–586.
- POLATSCHEK A. 1971. Cytotaxonomische Beiträge zur Flora Iranica III. Annalen des Naturhistorischen Museums in Wien 75: 173–182.
- QUEIRÓS M. 1973. Contribuação para o conhecimento citotaxonómico das Spermatophyta de Portugal IX. Cruciferae. Boletim da Sociedade Broteriana, 2a série 47: 315–335.
- QUEIRÓS M. 1986. Notas cariológicas em Rubiaceae Portuguesas. Boletim da Sociedade Broteriana, 2a série 59: 233–243.
- SAITO K, and MATSUZAWA Y. 1969. Studies on the occurrence of polyploidy and its contribution to the flower plants breed-

ing. VII. On the natural polyploidy and phylogenetic evolution in the horticultural species of *Muscari. Japanese Journal of Breeding* 20: 57–62.

- SATO D. 1942. Karyotype alteration and phylogeny in Liliaceae and allied families. *Japanese Journal of Botany* 12, 57–161.
- SEN S. 1975. Cytotaxonomy of Liliales. *Feddes Repertorium* 86: 255–305.
- SOKOLOVSKAYA AP, and PROBATOVA NS. 1979. Chromosome numbers of some grasses (Poaceae) in the U. S. S. R. flora. III. *Botanicheskij Zhurnal* 64: 1245–1258 (in Russian).
- SPERANZA M, and CRISTOFOLINI G. 1987. The genus *Dactylis* L. in Italy. 2. The diploid entities. *Webbia* 41: 213–224.
- SPETA F. 1998a. Hyacinthaceae. In: Kubitzki K [ed.], The families and genera of vascular plants Volume III: Flowering plants, Monocotyledons, Lilianae (except Orchidaceae), 261–285. Springer, Heidelberg.
- SPETA F. 1998b. Systematische Analyse der Gattung *Scilla* L. s. l. (Hyacinthaceae). *Phyton (Austria)* 38: 1–141.
- STACE C. 1989. IOPB chromosome data 1. *IOPB Newsletter* 13: 15–22.
- STACE C. 2000. Cytogeny and cytogenetics as a fundamental taxonomic resource for the 20th and 21st centuries. *Taxon* 49: 451–477.
- STEBBINS GL, and ZOHARY D. 1959. Cytogenetic and evolutionary studies in the genus *Dactylis* I: Morphology, distribution, and interrelationships of the diploid subspecies. *University* of California Publications in Botany 31: 1–32.
- SUGIURA T. 1937. A list of chromosome numbers in angiospermous plants, III. *The Botanical Magazine (Tokyo)* 51: 425–426.
- SUGIURA T. 1939. Studies on the chromosome numbers in higher plants III. *Cytologia* 10: 205–212.
- TSVELEV NN. 1983. *Grasses of the Soviet Union* Part II. Amerind Publishing, New Dehli.
- TZANOUDAKIS D, IATROU G, KYPRIOTAKIS Z, and CHRISTODU-LAKIS D. 1991. Cytogeographical studies in some Aegean Liliaceae. *Botanika Chronika* 10: 761–775.
- VIJAYAVALLI B. 1986. Cytological studies on the Liliaceae and a few allied families from South India. Ph.D. dissertation, University of Kerala, Trivandrum (India).
- ZOHARY D, and NUR U. 1959. Natural triploids in the orchard grass, *Dactylis glomerata* L., polyploid complex and their significance for gene flow from diploid to tetraploid levels. *Evolution* 13: 311–317.