

From the Botany School, Oxford
GENETIC SYSTEMS IN ALLIUM
I. CHROMOSOME VARIATION

By

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With 9 Figures in the Text

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A. Introduction

The genus *Allium* comprises bulbous plants having a distinct smell of onions and garlic. Some of the species are well cultivated plants for use as vegetables, condiments and decoration in the home gardens. So far, about 170 forms have been cytologically examined. There are three basic members, 7, 8 and 9; with polyploidy ranging up to $13x$ (DARLINGTON and WYLLIE, 1955; OWNBEY and ASSE, 1955; ASSE 1959). I have studied 44 species (Table 1) including 21 new counts. The present survey of the number and morphology of chromosomes in *Allium* species has been undertaken in preparation for the study of genetic systems in the genus.

B. Materials and Methods

Different species of *Allium* which have been used in the present studies are listed in Table 1. Seeds and bulbs were obtained from different Botanic gardens and wild material was also used wherever possible. The bulbs of Turkish *Alliums* were collected and kindly passed on to me by Dr. P. DAVIS (Edinburgh). The seeds of *Allium hirsutum* were obtained through the courtesy of Professor L. K. MANN, Davis, California, and my thanks are due to both of them.

Root tips for the study of mitotic chromosomes were obtained from potted plants and were pretreated with saturated solution of paradichlorobenzene for three and a half hours at room temperature. After twenty four hours fixation in 1:3 acetic alcohol, the root tips were hydrolysed in NHCl for six minutes at 60°C and then stained with leucobasic fuchsin. The squashes were prepared in 45% acetic acid. The slides were made permanent by using euparal as the mounting medium (DARLINGTON and LA COUR, 1962). Measurements for chromosome size were made after making camera lucida drawings. The smallest and the longest chromosomes in a complement have been referred as S and L.

C. Chromosome Morphology

Symmetrical chromosomes with median-submedian centromeres are most common in the genus. This is particularly true of the species with $x=7$ except *A. macranthum* and *A. bidwelleae*. Species with $x=8$ include about 60% forms, each having a complement consisting of exclusively

Table 1. *New chromosome counts and the source of Allium species*

Species	2n = RT	PMC	Source	Earlier reference **
<i>Allium cernuum</i> . . .	14	7	Montreal B.G.*	LEVAN, 1935
<i>fuscum</i>	14	7	Egridir, Turkey	DIANNELIDIS, 1951 (2n = 16)
<i>hirsutum</i>	14	7	Mt. Carmel, Israel	FEINBRUN, 1950
<i>subhirsutum</i> . . .	14	7	Kew B.G.	KURITA, 1960
<i>ursinum</i>	14	7	Oxford B.G.	LEVAN, 1935
<i>neapolitanum</i> . . .	14	7	Holland, De Jager	LEVAN, 1935
	21			KEFALLINO, 1955
	28			KEFALLINO, 1955
	35			KEFALLINO, 1955
<i>macranthum</i>	28	14	Oxford B.G.	LEVAN, 1934
<i>beesianum</i>	16	—	Villa Taranto B.G.	—
<i>cepa</i>	16	8	Cultivated	D'AMATO, 1948
<i>cyathophorum</i> . . .	16	8	Oxford B.G.	LEVAN, 1935
<i>darwasicum</i>	16	8	Villa Taranto B.G.	—
<i>fistulosum</i>	16	8	Cultivated	LEVAN, 1935
<i>giganteum</i>	16	8	Cultivated	MENSINKAI, 1940
<i>heldreichii</i>	—	8	Oxford B.G.	LEVAN, 1935
<i>kochii</i>	16	8	Oxford B.G.	LEVAN, 1935
<i>lilacinum</i>	16	8	Mussoorie, Himalayas	—
<i>longicuspis</i>	16	—	Villa Taranto, B.G.	—
<i>margaritaceum</i> . . .	16	8	Oxford B.G.	MENSINKAI, 1940
<i>monanthum</i>	—	8	Villa Taranto, B.G.	—
<i>monadelphum</i> . . .	16	—	Villa Taranto, B.G.	—
<i>olympicum</i>	16	8	Kastamonu, Turkey	—
<i>pallens</i>	16	8	Kizilcahman, Turkey	—
<i>paniculatum</i> (hybrid)	16	8	Egridir, Turkey	—
	16 + B	—	Egridir, Turkey	—
	16	8	Oxford B.G.	LEVAN, 1935
<i>pulchellum</i>	16	8	Oxford B.G.	LEVAN, 1935
<i>schoenoprasum</i> . . .	16	8	Villa Taranto B.G.	LEVAN, 1936
<i>stipitatum</i>	16	8	Villa Taranto B.G.	LEVAN, 1935
<i>suaveolens</i>	—	8	Munich B.G.	—
<i>touricola</i>	16	8	Elmali, Turkey	—
<i>vavilovi</i>	16	—	Moscow B.G.	—
<i>flavum</i>	16	8	Oxford B.G.	LEVAN, 1935
<i>var. minor</i>	24	—	Oxford B.G.	—
<i>carinatum</i>	24	—	Oxford B.G.	LEVAN, 1937
<i>chinense</i>	24	—	Cultivated	—
	32	—	Cultivated	—
<i>suworowi</i>	32	—	Villa Taranto B.G.	LEVAN, 1935
<i>ampeloprasum</i> . . .	32	—	Cultivated	LA COUR, 1945

* B.G. = Botanic Garden.

** From DARLINGTON and WYLIE, 1955.

Table 1 (Continued)

Species	2n = RT	PMC	Source	Earlier reference**
<i>globosum</i> . . .	32	16	Villa Taranto B.G.*	—
<i>mutabile</i> . . .	32	—	Villa Taranto B.G.	—
<i>senescens</i> . . .	—	16	Oxford B.G.	ONO, 1935
<i>urceolatum</i> . .	32	—	New York B.G.	—
<i>wallichianum</i> .	32	—	Villa Taranto	—
<i>winklerianum</i>	32	—	Copenhagen B.G.	—
<i>vineale</i>	40	—	Oxford B.G.	FERNANDES <i>et al.</i> , 1948
<i>babingtonii</i> . .	48	—	Oxford B.G.	MAUDE, 1940
<i>oreoprasum</i> . .	48	—	Villa Taranto B.G.	—
<i>cilicicum</i> . . .	56	—	Villa Taranto B.G.	—

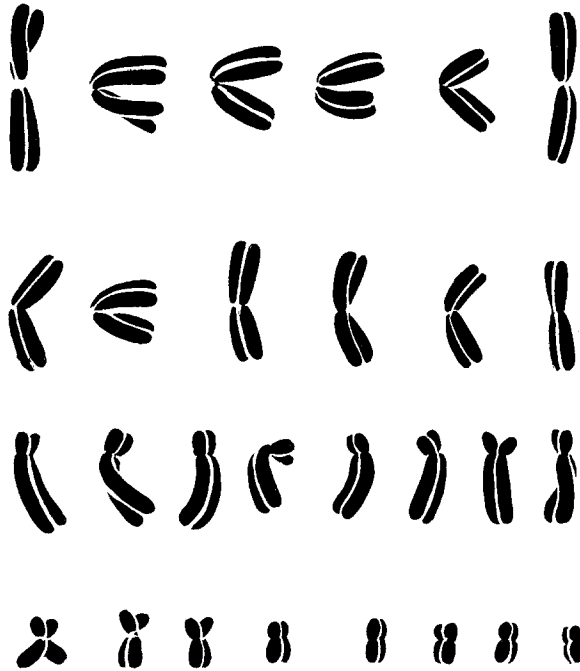


Fig. 1. Mitotic complement of *Allium macranthum* showing size differentiation of chromosomes.
All drawings $\times 1350$

symmetrical chromosomes. The remaining 40% forms have usually varying numbers of asymmetrical chromosomes which very often also carry the nucleolar organisers. Telocentric chromosomes are known only in a few species such as *A. zebdanense* ($x=9$).

Unlike *Hyacinthus* and *Uvularia*, a well-marked size differentiation of chromosomes within the complement is not common in *Allium*. It is

known only in $4x$ *A. macranthum* (LEVAN 1934) and *A. bidwelleae* (MENSINKAI 1940). The chromosome complement in each of these two species consists of twelve long, eight short and eight medium-sized chromosomes. The centromere position in the long and short chromosomes is median and in the medium ones as subterminal (Fig. 1).

Although in most of the species there is a lack of distinct size differentiation of chromosomes in the complement, still the longest chromosome always stands out from the shortest one. The relative size of the former to the latter within a complement varies from one species to another (Table 2). LEVAN (1935) has pointed out that species with $x=7$ have usually larger chromosomes than those with $x=8$ and 9; but *A. fuscum* ($x=7$) seems to be an exception to this. He has also found that in *A. nutans* the nucleolar chromosomes undergo a reduction in size with a change from diploidy to triploidy as I have observed the same situation in *A. neapolitanum* (Fig. 2). I have also found that in the triploid *A. flavum* var. *minor* and $7x$ *A. cilicicum* the whole complement consists of smaller chromosomes (Figs. 3b, 4) as in *Chrysanthemum* polyploids (DOWRICK 1952). This does not imply that all diploids species of *Allium* have necessarily larger chromosomes than the polyploids. Smaller chromosomes are previously known in diploid forms such as *A. schoenoprasum* (Fig. 3a), *A. saxatile*, *A. yunnanense* (LEVAN 1932); *A. decipiente* (MENSINKAI 1940) and also in *A. fuscum* (Fig. 5) as I have found.

Table 2. *Chromosome size in Allium species*

Species	2n =	S	L	Mean Chr. size μ
		μ	μ	
<i>Allium cernuum</i> . . .	14	9	14	11.6
<i>fuscum</i>	14	5	11	7.8
<i>hirsutum</i> . . .	14	9	14	11.3
<i>subhirsutum</i> . .	14	8	16	11.8
<i>neapolitanum</i> .	14	8	15	10.8
	21	5	13	11.2
<i>macranthum</i> . .	28	4	15	9.2
<i>beesianum</i> . . .	16	6	10	8.3
<i>fistulosum</i> . . .	16	7	11	9.3
<i>kochii</i>	16	7	12	9.4
<i>longicuspis</i> . .	16	8	14	11.1
<i>monadelphum</i> .	16	6	10	7.2
<i>olympicum</i> . . .	16	7	13	9.8
<i>schoenoprasum</i>	16	6	9	7.4
<i>vavilovi</i>	16	8	13	10.8
<i>aggregatum</i> . .	24	8	15	11.2
<i>flavum</i>				
var. <i>minor</i> . .	24	5	9	6.1
<i>chinense</i>	24	8	15	10.8
	32	7	16	10.4
<i>ampeloprasum</i>	32	6	10	7.9
<i>globosum</i>	32	7	11	9.6
<i>mutabile</i>	32	7	12	10.0
<i>suworowi</i>	32	6	10	8.3
<i>winklerianum</i> .	32	7	13	10.3
<i>wallichianum</i> .	32	5	10	7.2
<i>babingtonii</i> . .	48	7	17	11.3
<i>oreoprasum</i> . . .	48	5	12	8.0
<i>cilicicum</i>	56	4	10	7.3

The size differentiation of chromosomes in the complement of *A. macranthum* and *A. bidwelleae* is of great interest particularly owing to the fact that in the genus *Allium* there is no other species to show this situation. DARLINGTON (1963) considers it as a "ployploid drop" which

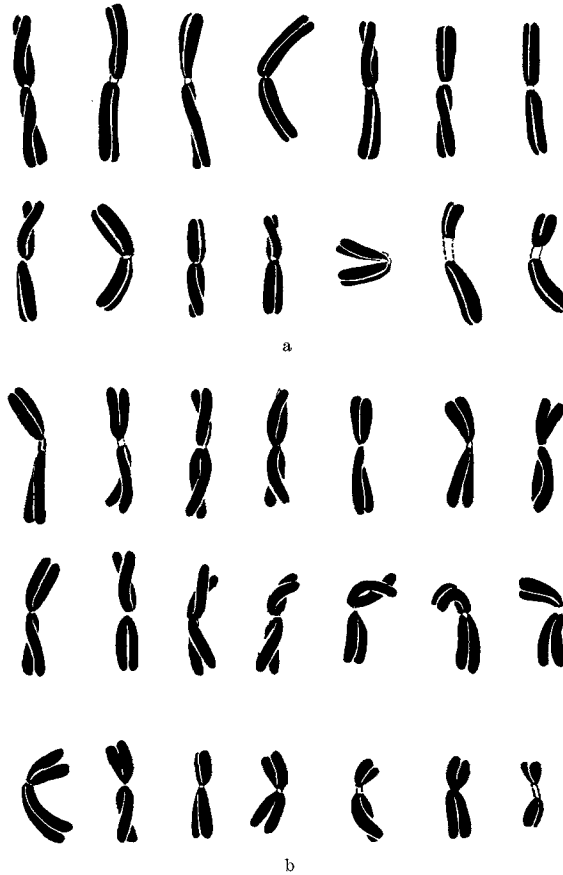


Fig. 2a and b. Mitotic complement of *A. neapolitanum*. a Diploid. b Triploid showing the reduction in the size of one of the nucleolar chromosomes having attenuated centromere

represents a case of natural selection and adaptation in the polyploids. Such species can well afford to lose bits of chromosomes as there is duplication of the material in the complement. This situation i.e. size differentiation of chromosomes in the complement in the polyploids may also be achieved through the medium of translocations as suggested by STEBBINS (1957).



Fig. 3a and b. Mitotic complements of (a) *A. schoenoprasum* ($2x = 16$), (b) *A. flavum* var. *minor* ($3x = 24$)

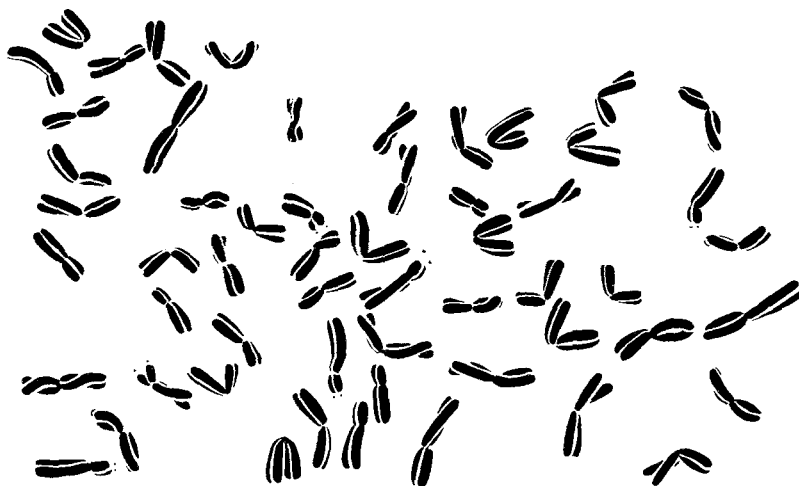


Fig. 4. Mitotic complement of *A. cilivicum* ($7x = 56$), a polyploid species with small chromosomes

D. Nucleolar Chromosomes

The number and morphology of the nucleolar chromosomes varies in different species. In most of the diploid species the mitotic complement includes only one pair but there are some cases with two pairs also. The latter number is considered as the secondary balanced condition (MENSINKAI 1940). In the polyploids the number of nucleolar chromosomes is usually correlated with the level of ploidy. As such, most of the tetraploids have four nucleolar chromosomes but this correlation does not hold good for all polyploids as there are ten nucleolar chromosomes in the hexaploid *A. ampeloprasum* (KHOSHOO, ATAL and SHARMA, 1960), and 6 in $7x$ *A. cilicicum* (Fig. 4). In the tetraploid *A. macranthum* however, the nucleolar chromosomes have not been detected.



Fig. 5. Mitotic complement of *A. fuscum*, a diploid species with small chromosomes including two pairs of the nucleolar ones

In the genus *Allium* mainly six types of nucleolar chromosomes can be described (Fig. 6). All of them vary in their morphology according

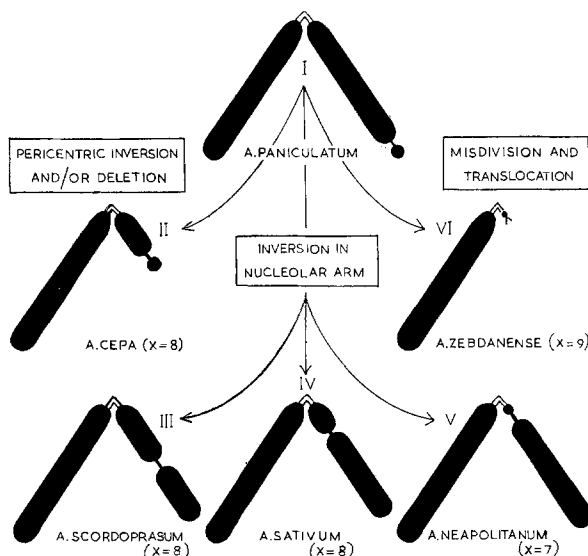


Fig. 6. Diagram showing six possible types of nucleolar chromosomes in the genus *Allium* and also the structural changes involving their origin from the basic type

to the relative position of the centromere and the nucleolar constriction. I have named them according to the type species and they are as follows:

I. Paniculatum type. This is characteristic of the section *Codonoprasum* and has been observed in 33% species with $x=7$ and 8. I suggest

that this metacentric chromosome with a satellite constitutes the basic type of the nucleolar chromosomes in the genus.

II. Cepa type. It is typical of *A. cepa*, the common onion. It has a subterminal centromere and a satellite on the short arm. It is commonly found in the species having $x=8$ or 9 and never in species with $x=7$. Such an asymmetrical chromosome can arise through a pericentric inversion as in *Vichoreae* (STEBBINS, 1958) or by means of a simple inversion following deletion in the nucleolar arm of the metacentric chromosome of the *paniculatum* type.

III. Scordoprasum type.

IV. Sativum type.

The section *Porrum* is characterised by the nucleolar chromosomes of both *Sativum* and *Scordoprasum* types which are usually found in the same diploid complement as in *A. sativum* (BATTAGLIA, 1963 b). The centromere position is median-submedian in both cases but the nucleolar constriction is proximal to the centromere in the former and median-submedian in the latter.

Presumably both of these have also arisen by means of an inversion in the nucleolar arm of the *Paniculatum* type.

V. Neapolitanum type. It is characteristic of some species of the section *Molium*. It is marked by a "compound constriction" which appears to be attenuated owing to the close proximity of the centromere to the nucleolar constriction (LA COUR, 1950). It is not so commonly known in the other genera. The only known cases other than *Allium* are *Crocus* (MATHER, 1932), *Poa* (MÜNTZING, 1948) and *Campanula* (DARLINGTON and LA COUR, 1950).

VI. Zebdanense type. These are telocentric nucleolar chromosomes known in *A. zebdanense* and *A. pendulinum*, both species with $x=9$. LEVAN (1932, 1935) has suggested that these telocentrics have arisen from the metacentrics through the process of misdivision which presum-

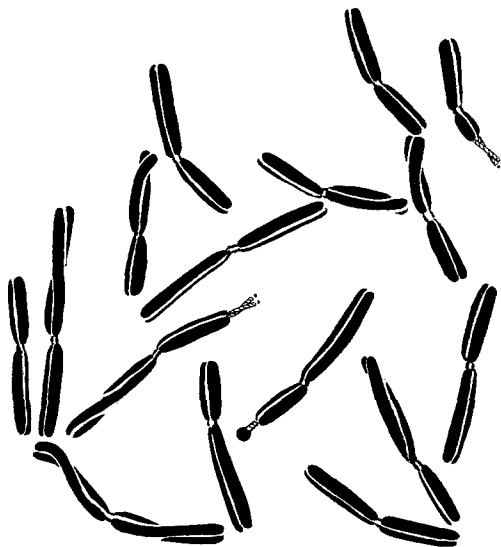


Fig. 7. Mitotic complement of *A. stipitatum* with three nucleolar chromosomes which also carry alloccyclic segments in the nucleolar arms

ably involves a nucleolar chromosome of the *Neapolitanum* type or *Paniculatum* type. But in the latter case it would also require a translocation of the nucleolar segment to the centromeric end of the telocentric.

E. Heterozygosity in Nucleolar Chromosomes

During mitosis the nucleolar constriction serves as a very good marker which enables us to detect any shift in the relative position of



Fig. 8

Fig. 8. Mitotic complements of *A. pallens* showing heterozygosity in one pair of nucleolar chromosomes $\times 1350$



Fig. 9

Fig. 9. Mitotic complement of *A. paniculatum* showing heterozygosity for the centromere position in the pair of nucleolar chromosomes. Also there is one B-chromosome in the complement $\times 1350$

the centromere. I have found clones of *A. stipitatum*, *A. paniculatum* and *A. pallens* which are heterozygous for the pair of nucleolar chromosomes (Figs. 7—9). A similar situation has also been previously reported in *A. schoenoprasum* (LEVAN 1936), *A. moschatum* (BILLERI, 1954), *A. cepa* (NODA, 1952; BATTAGLIA 1963a) and *A. sativum* (BATTAGLIA, 1963b). The existence of heterozygous clones in the sexually reproducing outbreeding species is an important source of genetic variation in the population. But, in the vegetatively reproducing species such as *A. sativum* they just reveal the occurrence of structural changes in the chromosomes which is the only source of variation in a clone.

Heterozygosity in the nucleolar chromosomes has been reported in many species and genera (DYER, 1963; Table 9). In Tomato more than 50% of the spontaneous mutations have been found to occur in the nucleolar chromosomes (JAIN, I. A. R. I., New Delhi, personal discussions). Morphological variability and structural heterozygosity of nucleolar chromosomes in *Allium* is also presumably due to their susceptibility to spontaneous mutations as in Tomato.

F. Heterochromatin in *Allium*

Alloocyly which is revealed by the cold treatment as in *Trillium*, is not found in *Allium*. LEVAN (1946) observed short heterochromatic segments in *Allium* species (Table 3) revealed by pretreating root tips

Table 3. *Allium* species showing heterochromaty

Species	2n	Reference	Species	2n	Reference
<i>cernuum</i> . .	14	LEVAN, 1946	<i>schoenoprasum</i> .	16	LEVAN, 1946
<i>bouddhae</i> . .	16	KURITA, 1958	<i>scordoprasum</i> .	16	KURITA, 1958
<i>carinatum</i> . .	16	LEVAN, 1946	<i>stipitatum</i> . . .	16	VED BRAT
<i>cepa</i>	16	LEVAN, 1946; KURITA, 1958	<i>wakegi</i>	16	KURITA, 1958
<i>fistulosum</i> . .	16	LEVAN, 1946	<i>porrum</i>	32	LEVAN, 1946
<i>nutans</i>	16	LEVAN, 1946	<i>odorum</i>	32	LEVAN, 1946

with mercuric nitrate, fixed with Navashin's solution and stained with crystal violet. KURITA (1958) has also found heterochromaty in *A. cepa* and *A. bouddhae* as revealed by 8-hydroxyquinoline pretreatment followed by acetic alcohol fixation and orcein staining. I have also found alloocyly in *A. stipitatum* after pretreating the root tips for 3½ hours with paradichlorobenzene, then fixing in 1:3 acetic alcohol and staining with Feulgen method twenty four hours later. In this case the alloocyly also reveals the heterozygosity (Fig. 7) as in *A. cepa* (TJIO and LEVAN, 1956), *Hyacinthus litwinowii* and *Cestrum* (DYER, 1963). The allocylic segments of *A. stipitatum* are not revealed very clearly with colchicine pretreatment which causes chromosome contraction.

G. B-Chromosomes

Supernumerary B-chromosomes are known in some species of *Allium* (Table 4). I have found that in *A. paniculatum* B-chromosomes persist in the sporogenous tissue and never undergo pairing with the other chromosomes during meiosis. The size and centromere position of B-chromosomes in *Allium* species are quite variable. They may be more or less half the size of the normal chromosomes as in *A. paniculatum* (Fig. 9) and *A. stracheyi* (SHARMA and AIYANGER, 1961) or they may appear

like acentric fragments as in *A. cernuum*. OWNBEY and ASSE (1955) have mentioned the presence of B-chromosomes in *A. canadense* alliance, a group of North American species; but they have not given any detail about their form and frequency.

Table 4. *Allium* species with B-chromosomes

Species	2n =		Reference
	A	B	
<i>alleghehiense</i>	14	1—4	LEVAN, 1932
<i>cernuum</i>	14	0—1	LEVAN, 1932
		0—11	GRUN, 1959
<i>stracheyi</i>	14	0—10	SHARMA and ATIYAN-GER, 1961
<i>cepa</i>	16	0—1	NODA, 1952
<i>paniculatum</i>	16	0—1	VED BRAT
<i>pulchellum</i>	16	0—1	TSCHERMAK-WOESS and SCHIMAN, 1960
<i>sphaerocephalum</i>	16	0—1	KURITA, 1956
<i>schoenoprasum</i>	16	0—1	KURITA, 1956
<i>porrum</i>	32	0—5	VOSA, unpublished

H. Basic Numbers

There are three basic chromosome numbers, i.e. 7, 8 and 9, in the genus *Allium*. LEVAN (1932, 1935) has suggested their origin in the form of an ascending series. MENSINKAI (1940) has also put forward an alternative view according to which the basic numbers seven and nine have both arisen from eight. His argument is based on his data showing that most of the species in the genus fall in the category of $x = 8$.

I suggest that any consideration of the basic numbers in a genus like *Allium* with more than 500 species would be more appropriate if it were based on the relevant taxonomic group which inhabit a particular centre of distribution. Thus, amongst the old world species sections *Codonoprasum* (mainly European and West Asiatic bulbous species) and *Molium* (typically Mediterranean species represented by *A. neapolitanum*) which consist of species with all basic numbers, are worth consideration in this respect.

In the section *Codonoprasum* most of the forms have basic chromosome number eight and there are only two species, i.e. *A. fuscum* ($x = 7$) and *A. pseudoflavum* ($x = 9$) atypical in the group. In the former species a form with $x = 8$ has also been reported from Greece by DIANNELIDIS (1951) whereas my own observations are based on material collected from Turkey. Taxonomically both *A. fuscum* and *A. pseudoflavum* are very closely allied to *A. paniculatum* and ARARATIAN and TONIAN (1945) have also suggested merging all three species into one.

In *A. paniculatum* and *A. fuscum* all chromosomes are symmetrical with median-submedian centromeres but there are two nucleolar chromosomes in the former and four in the latter which shows a "secondary balanced" condition (MENSINKAI, 1940). *A. fuscum* is also an inbreeder with a high chiasma frequency (2.76 chiasmata per bivalent). This adaptive compromise i.e. adjustment in the regulation of variability by restriction on recombination through breeding system and promotion of variability through high chiasma frequency in *A. fuscum* with $x=7$ is also suggestive of its derived condition in the genus which comprises mainly outbreeding species.

The other group of species worth mentioning is the section *Molium* which consists of Mediterranean species and also represented by the three basic numbers. EID (1963) has studied the chromosome morphology of *A. neapolitanum* ($x=7$), *A. reosum* ($x=8$) and *A. zebdanense* ($x=9$). The chromosome complement in *A. neapolitanum* consists of only metacentric chromosomes whereas in the latter two species there are also telocentrics. EID has suggested that in the section *Molium* all the three basic numbers form an ascending series owing to the fact that the telocentrics have arisen through misdivision of the metacentric chromosomes. Thus, the foregoing account of the sections *Codonoprasum* and *Molium* reveals that the three basic numbers in different taxonomic groups of the genus *Allium* have arisen in independent orders.

The situation concerning the New World species of *Allium* is quite simple. Except two (*A. schoenoprasum* and *A. tricoccum* both with $x=8$) all North American species have basic number seven and constitute a big group of species which are more closely linked together with each other than with the Old World species. STEARN (personal communications) has suggested that the two groups, i.e. the New and the Old World species, represent a case of parallel evolution from the proto-*Allium* which was of the rhizomatous kind and the purely bulbous forms represent an adaptation to environments with a marked seasonal variation of the Mediterranean nature.

Summary

1. *Allium* species show very little variation in the symmetry of their chromosomes within as well as between their complements.
2. In tetraploid *A. macranthum* and *A. bidwelleae*, the complement shows a distinct size differentiation of chromosomes into three groups (Fig. 1).
3. There are mainly six types of nucleolar chromosomes in the genus (Fig. 6). In some species they also carry heterozygosity (Figs. 7—9).
4. In *A. stipitatum* the heterozygous nucleolar chromosomes also show allocyclic which is revealed at the room temperature.

5. Species with supernumerary B-chromosomes are all diploids except *A. porrum*.

6. There are three basic numbers, i. e. 7, 8 and 9, in the genus. North American species have seven as the basic chromosome number. Most of the Eurasian species have $x=8$ and a few $x=7$ and 9.

7. In the section *Molium*, a group of Mediterranean species, the basic numbers 8 and 9 have arisen from seven in the form of an ascending series, i. e. 7-----8-----9. In the section *Codonoprasum* which includes European and West Asiatic species, the basic number eight has given rise to both seven and nine.

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