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GENETIC SYSTEMS IN *ALLIUM*

III. MEIOSIS AND BREEDING SYSTEMS

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1. INTRODUCTION

REGULATION of variability in a species is mainly determined by its chromosome behaviour and reproductive method. Their genotypic control and adaptive nature has been pointed out by Darlington (1932, 1939) and by Mather (1943). Their co-adaptation is vital for the genetic balance of a breeding group. Consequently, a forced change in the breeding system of a species upsets its chromosome behaviour during meiosis as in rye (see Rees, 1961) or it may lead to selection for a change in chromosome structure securing immediate fitness as in cockroaches (Lewis and John, 1957; John and Lewis, 1958). In nature, coordination between chromosome structure and behaviour, and the breeding system fulfils the need for compromise between long term flexibility and immediate fitness. This is achieved through the control of crossing over within the chromosomes and recombination between them. The sex differences in meiosis, however, have a special significance in this respect and I have discussed the same earlier (1965*b*). Thus, the meiotic mechanism provides recombination within the genotype and the breeding systems extend the same to the population. The present study is an attempt to find out the working correlations between the two components of the genetic systems in the genus *Allium.*

2. MATERIALS AND METHODS

Most of the *Allium* species used in the present studies were obtained from Botanic Gardens but wild material was examined where possible (table 1, Ved Brat, 1965*a*).

Meiosis was studied from the pollen mother cells after squashing in acetic orcein (Vosa, 1961). Acetic carmine and Feulgen staining were also used after overnight fixation in 1 : 3 acetic alcohol.

The positions and frequencies of chiasmata were scored from at least twelve cells in each case according to Frankel (1940) using arbitrary classification into three groups, proximal (P), distal (D) and median (M). The distal chiasma was marked terminal (T) when completely terminalised.

Observations on breeding systems were made on plants growing in the Genetic Garden of the Botany School and isolated plants in the greenhouse. Bagging and selfing was done to confirm the pollination mechanism. Pollinating insects were caught from the genetic garden, and identified but they also find their way into the greenhouse when open.

3. MEIOSIS

(a) *Chiasma frequencies and failure of pairing*

Meiosis in pollen mother cells has been studied in eighteen diploid and three tetraploid species (table 1). *A. macranthum* (4*x*) has the highest chiasma frequency showing a direct correlation with chromosome size within the complement (Levan, 1934). The chiasma frequency is lowest in " hybrid " clones of *A. paniculatum* and *A. suaveolens* with 0-4 and 0-2 univalents per cell respectively. Presumably the lack of pairing is due to heterozygosity although gene controlled asynapsis is also known in *A. amplectans* (Levan, 1940).

TABLE 1

Chiasma frequencies and breeding systems in Allium *species*

Species	Abbreviation	2n = 14	16	28	32	Chiasmata per bivalent	Recombination Index *	Breeding system
suaveolens . .	Su	...	+	...	...	1·56	20·50	●
monanthum .	M	...	+	...	...	1·73	21·85	●
paniculatum .	P	...	+	...	...	1·53	20·27	
(hybrid)	P	...	+	...	...	1·80	22·40	◆
	P	...	+B	...	...	1·82	22·58	
heldreichii . .	He	...	+	...	...	1·82	22·55	●
olympicum . .	O	...	+	...	...	1·85	22·83	●
flavum . .	F	...	+	...	...	1·85	22·87	●
pallens . .	Pa	...	+	...	...	1·87	23·00	●
kochii . .	K	...	+	...	...	1·87	23·00	●
touricola . .	T	...	+	...	...	1·91	23·27	●
hirsutum . .	H	+	...	...	...	1·92	20·42	●
cyathophorum .	C	...	+	...	...	1·95	23·60	●
ursinum . .	U	+	...	...	...	1·96	20·75	●
subhirsutum .	S	+	...	...	...	1·96	20·75	●
lilacinum . .	L	...	+	...	...	1·97	23·83	●
darwasicum .	D	...	+	...	...	2·03	24·30	⚲
schoenoprasum .	Sc	...	+	...	...	2·19	25·50	⚲
stipitatum . .	St	...	+	...	...	2·47	27·75	○
fuscum . .	Fu	+	...	...	...	2·76	26·33	⚲
ampeloprasum .	A	...	...	...	+	1·89	46·35	●
senescens . .	Se	...	...	...	+	2·06	49·00	⚲
macranthum .	Ma	...	...	+	...	3·02	56·30	⚲

* Recombination Index = Chiasma frequency per cell + half the somatic number of chromosomes (Darlington, 1937).

● = Outbreeder ◆ = Versatile
⚲ = Inbreeder ○ = Sterile

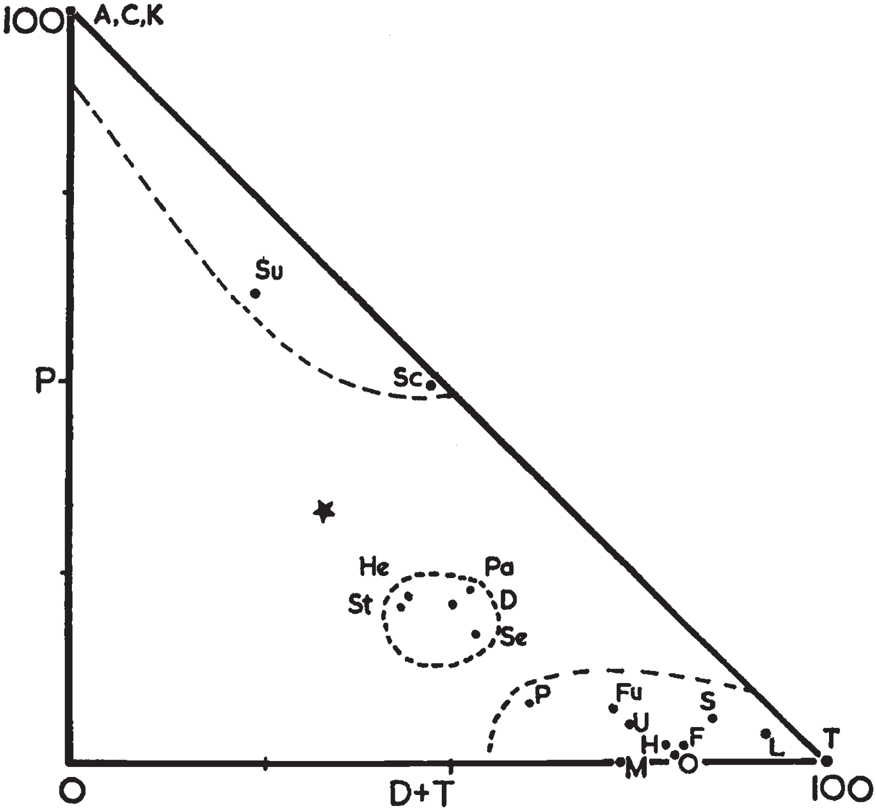
A seasonal failure of meiosis was observed in *A. kochii* which flowers practically throughout the year. During winter the sporogenous tissue degenerates during premeiotic development unlike other times when the meiosis is regular.

(b) *Regional distribution of chiasmata*

Except *A. macranthum*, all species (table 1) are without any size differentiation of chromosomes within the complement. The regional distribution of chiasmata along the chromosome arms varies in most of the species (text-fig. 1) which constitute three main groups, each subdivided as follows:

(i) *Species with proximal localisation of chiasmata*

(*a*) All chiasmata proximal to the centromere as in *A. cyathophorum*, *fistulosum*, *kochii*, *ampeloprasum*, *porrum* and *victorialis* (Levan, 1934; Matsuura and Süto, 1935).



Text-fig. 1.—Graph showing regional distribution of chiasmata along chromosome arm in different species of *Allium*. The ★ sign indicates the point of equal distribution of chiasmata in the proximal, median and distal-terminal regions. For abbreviations of the species see table 1, page 326.

(*b*) Species with at least 50 per cent. proximal chiasmata, very few (5 per cent.) median and the remaining ones distal-terminal as I have found only in *A. schœnoprasum* (plate I, fig. 2). A somewhat similar situation is also found in *A. suaveolens* (text-fig. 2) with at least 50 per cent. proximal chiasmata but the remaining ones evenly distributed in both median and distal-terminal regions.

(ii) *Species with distal localisation*

(*a*) All chiasmata distally localised as in *A. touricola* (text-fig. 3*a*).

(*b*) 90 per cent. chiasmata distally localised and the remaining 10 per cent. formed in proximal and median regions as in *A. lilacinum* (text-fig. 3*b*).

(*c*) At least 50 per cent. distally localised chiasmata as in most of *Allium* species (text-figs. 3*c*, *d*, *e*, *f*).

(iii) *Species with random distribution of chiasmata*

(*a*) Chiasma formation restricted in frequency, usually one per arm as in *A. heldreichii*, *darwasicum*, *pallens* and *senescens*.

(*b*) Chiasmata randomly distributed with more than one contact point along the chromosome arm as in *A. macranthum* and *A. stipitatum* (text-figs. 4*b*, *c*).

TEXT-FIG. 2.—First metaphase of meiosis in p.m.c. of *A. suaveolens*, a species with partially proximal localisation of chiasmata and low frequency due to failure of pairing. All drawings × 1350.

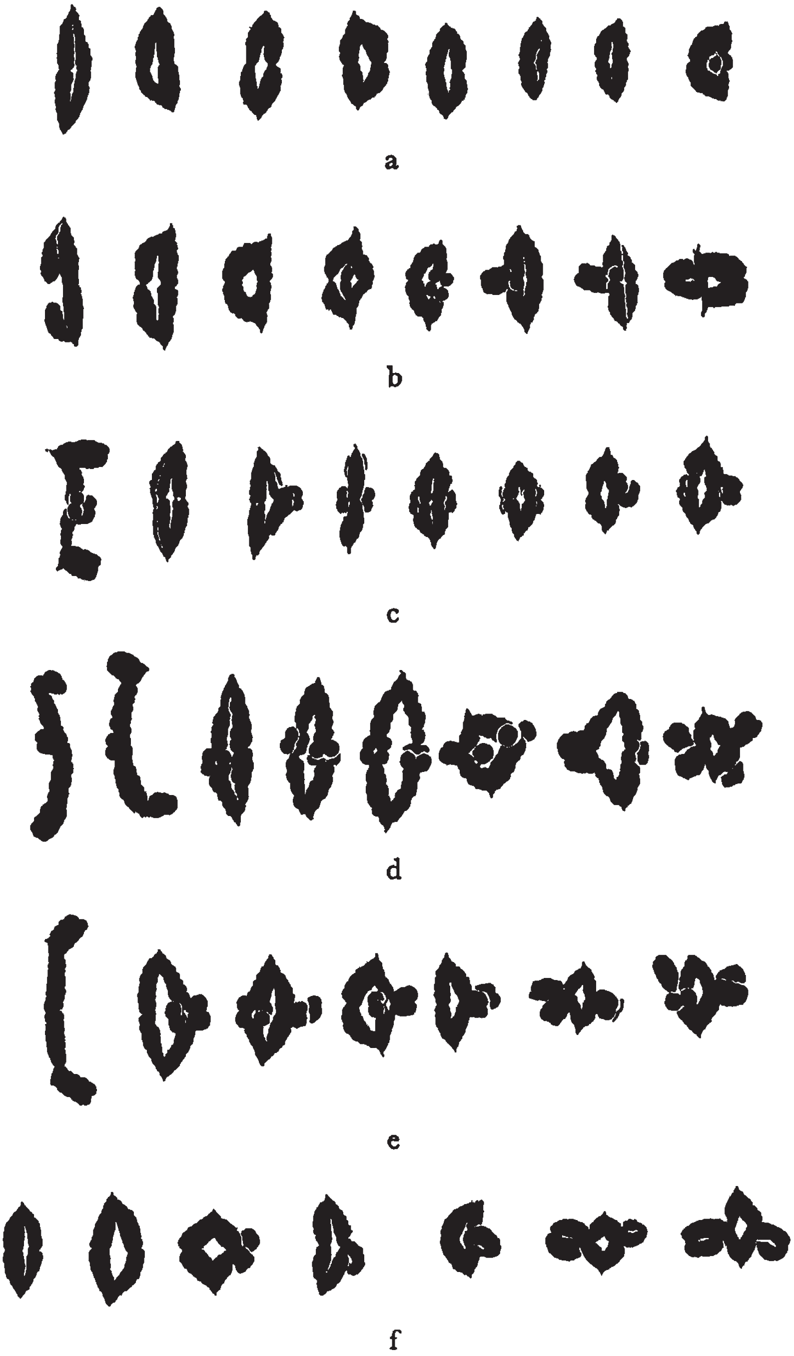
Owing to the size differentiation of chromosomes in the complement, the regional distribution of chiasmata in *A. macranthum* needs separate consideration. The long chromosomes and the long arms of the medium-sized chromosomes form randomly distributed chiasmata. Short chromosomes form distal chiasmata like the short arms of the medium ones.

(c) *Control of crossing-over*

The amount of crossing-over in a species is determined by the number and position of chiasmata along the chromosome arms revealing thereby the order of pairing (Darlington, 1940) in different species (table 2).

(i) Where the proximal localisation is complete, crossing-over is confined to the regions near the centromere with the result that chiasma frequency never exceeds more than two per bivalent, *i.e.* one per arm. The chromosome arms are differentiated into a pairing region which normally undergoes chiasma formation and, accordingly, crossing-over, and a differential region behaving like a super gene. Thus, the restriction on recombination is qualitative as well as quantitative as in *A. fistulosum*, *A. kochii*, *A. cyathophorum* (plate I, figs. 1, 3) and *A. ampeloprasum*.

In the case of incomplete localisation, restrictions on crossing-over obtains in different ways in various species. In *A. schœnoprasum*

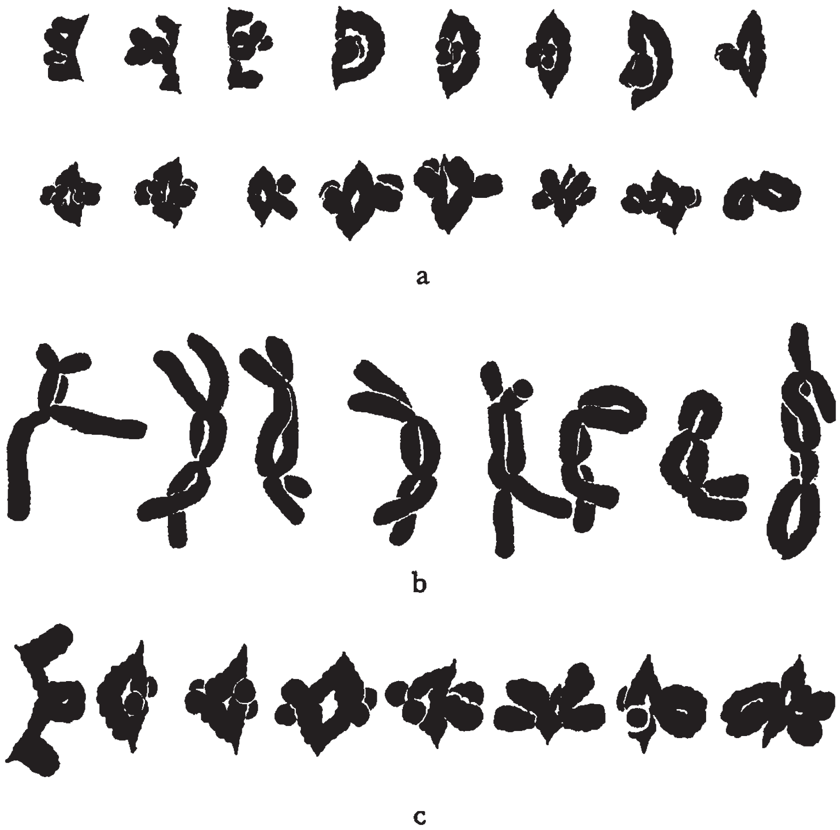


TEXT-FIG. 3.—First metaphase of meiosis in the p.m.c.'s of *Allium* species with distal localisation of chiasmata.

a. *A. touricola* b. *A. lilacinum* c. *A. olympicum*
d. *A. monanthum* e. *A. hirsutum* f. *A. fuscum*

X 2

50 per cent. of the chiasmata are proximal, 48 per cent. are distal-terminal and only 2 per cent. median. The proximal chiasmata, as a matter of fact, are formed in 60 per cent. of the total bivalents. This also includes 28 per cent. bivalents each with at least one distal chiasma arising from a secondary contact point. The remaining 40 per cent. bivalents mainly form distal chiasmata and vary from 1-4 per cell. Thus in *A. schœnoprasum* pairing starts either distally or proximally but in the latter case distal secondary contact points obtain a higher chiasma frequency unlike *A. fistulosum* and *A. cyathophorum*, species with complete proximal localisation.



TEXT-FIG. 4.—Drawings showing meiotic chromosomes in the p.m.c.'s of *Allium* species with free pairing.

a. Metaphase in *A. senescens*.
b. Diplotene in *A. stipitatum*
c. Metaphase in *A. stipitatum*

In *A. suaveolens* incomplete localisation accompanies a lower chiasma frequency. Here, unlike *A. schœnoprasum*, 65 per cent. chiasmata are confined to proximal region and remaining 35 per cent. distributed in the median and distal-terminal regions. Bivalents forming proximal chiasmata vary from 2-6 per cell. Thus, restriction on recombination arises from localisation as well as low chiasma frequency However, variation in the position of chiasma has compensatory effects.

(ii) Functionally, distal pairing is similar to the previous case but here the distal region of the chromosome arm behaves as the pairing one. Presumably mechanical limits controlling the torsion and thus the secondary contact points towards the centric regions are more effective in delimiting the number of chiasmata to one per arm unlike procentric pairing in *A. schœnoprasum.* I have observed complete distal localisation of *Tradescantia* or *Œnothera* type only in *A. touricola* (text-fig. 3*a*), but in most cases it is incomplete (table 2) and text-figs. 3*c-f*).

TABLE 2

Order of pairing in Allium *species*

Proximal		Random	Distal	
Complete	Partial		Complete	Partial
cyathophorum	*schœnoprasum*	*darwasicum*	*touricola*	*cepa* *
fistulosum *	*suaveolens*	*heldreichii*	*lilacinum*	*monanthum*
kochii	...	*pallens*	...	*paniculatum*
ampeloprasum	...	*stipitatum*	...	*flavum*
porrum *	...	*macranthum*	...	*subhirsutum*
victorialis *	...	*senescens*	...	*ursinum*
...				*fuscum*
				olympicum

* Known cases (Levan, 1940; Matsuura and Süto, 1935).

(iii) Alternatively, there are some species of *Allium* with free pairing resulting in a random distribution of chiasmata. However, if the frequency is low, their position varies from one bivalent to the other and for a given bivalent in different cells as in *A. heldriechii* (plate 2, fig. 3). But if chiasma frequency is high, complete pairing giving free recombination as in *A. macranthum* (plate 2, fig. 5) does not leave much scope for variation in chiasma position.

(iv) The asymmetrical nucleolar chromosomes having subterminal centromeres can be identified during meiosis. Quite frequently the nucleolar arms fail in forming a chiasma as in *A. fistulosum* (Zen, 1961). Evidently it restricts recombination and this disadvantage in crossing-over arises from the nucleolus which stands in the way during pachytene pairing as in *Fritillaria* (Darlington, 1935) and *Eremurus spectabilis* (Upcott, 1936).

(d) *Structural hybridity*

(i) *Interchanges.* Diploids showing multiple associations of more than two chromosomes are known in *A. ammophilum* and *A. cernuum* (Levan, 1935 and 1939). These are presumably spontaneous mutations having arisen in experimental cultures as also in *A. fistulosum*

(Zen, 1961). However, in cultivated varieties of *A. scordoprasum* they are a regular feature (Takenka, 1960) and the frequency and the number of chromosomes involved in a multiple varies from 4-10 in different varieties.

(ii) *Inversions.* Pachytene pairing has never been studied in any *Allium.* Bridges and fragments presumably arisen from inversion crossing have been reported (table 3) but they can arise due to various causes (see John and Lewis, 1965). Also small inversions cannot be detected owing to suppression of crossing-over. However, a high frequency of inversion crossing-over as in wild *A. paniculatum* raises the hybridity potential of the population. The new chromosomes which arise from bridge-fragment configuration increase the amount of variability but their selection is subject to the healing of broken ends and viability of the new genotypes carrying them. The role of inversions can also vary according to the nature of chiasma localisation (see White, 1958).

TABLE 3

Inversion crossing-over in Allium *species as inferred from bridges and fragments*

Species	Bridges and fragments (per cent.)	Reference
cilicicum	10	Mensinkai, 1940
nigrum	10	,,
sewerzowi	10	,,
bidwelleæ	10	,,
paniculatum	16	Ved Brat
cepa × *fistulosum*	...	Emsweller and Jones, 1938
boddhæ var. *viviparum* × *boddhæ* .	...	Kurita, 1961

4. FLORAL BIOLOGY AND REPRODUCTIVE METHODS

Recombination is essentially a function of sexual reproduction. In higher plants the breeding systems also change with certain modifications in the pollination mechanism of the species. Very often these adaptations are revealed by the floral biology. In *Allium* the flowers have a typically *Lilliaceous* pattern, *i.e.* trimerous with two whorls of more or less epipetalous stamens having longitudinal introrse dehiscence of anthers. The stigma is usually pointed (*A. cepa*) but sometimes tripartite (*A. triquetrum*). Accordingly, sexually reproducing species are mostly cross-pollinated. Only a few are self-pollinated and versatile (table 4).

The outbreeders are usually protandrous with the inner whorl of stamens maturing first. Pollination is aided by locally observed insects like *Bombus lucorum*, *Bombus lapidarium* and *Apis mellifera* var. *carnica.* The cymose inflorescence is particularly suited to attract insects but inevitably their localised activity and repeated visits also result in a small amount of selfing.

TABLE 4

Breeding systems in Allium *species (enlarged and classified from Fryxell, 1957)*

	Sexual			Asexual	
	Outbreeder	Versatile	Inbreeder	Viviparous	Apomictic
2x	$x = 7$ *hirsutum* * *neapolitanum* * *subhirsutum* * $x = 8$ *cepa* *cyathophorum* * *fistulosum* *flavum* *heldreichii* * *kochii* *lilacinum* * *monanthum* * *multibulbosum* *nutans* *olympicum* * *pallens* * *pulchellum* * *schœnoprasum* *suaveolens* * *touricola* * *ursinum*	... $x = 8$ *paniculatum* † $x = 9$ *triquetrum* *	$x = 7$ *fuscum* * $x = 8$ *darwasicum* * *schœnoprasum* *	... $x = 8$ *ascalonicum* *longicuspis* * *sativum* *scordoprasum* *viviparum* *carinatum* (*flavum*) *	$x = 7$ *moly* $x = 8$ *odorum* $x = 9$ *zebdanense*
3x	...	...	...	$x = 8$ *carinatum*	$x = 7$ *amplectens* (?)
4x	$x = 8$ *ampeloprasum* *	...	$x = 7$ *macranthum* * $x = 8$ *senescens*	$x = 7$ *canadense* $x = 8$ *oleraceum* *vineale*	$x = 7$ *amplectens* *canadense* $x = 8$ *angulosum* *senescens* *odorum* *nutans*
6x	...	...	...	$x = 8$ *ampeloprasum* * *babingtonii* *roseum*	$x = 8$ *oreoprasum*

* Personal observations. † With B-chromosomes.

I have observed versatile pollination in only two species. *A. triquetrum* is more often cross pollinated but late in the season protoandry does not remain well marked. The stigma matures comparatively later facilitating selfing from the last dehiscing anthers of the same flower. Selfing effected thus results in 1-2 seeds per capsule. In *A. paniculatum* different populations show a remarkable variation in the size of anthers and thus floral biology (Levan, 1937) which affects and also reflects the pollination mechanism which I have also observed in my cultures.

Obligatory selfing occurs only in tetraploid *A. macranthum* in which the flowers remain closed till stamens and carpels mature and pollination is effected. In the other inbreeding forms like *A. fuscum* and *A. schœnoprasum* the essential parts mature simultaneously and selfing is aided by the insects and the longitudinal introrse dehiscence of the anthers.

A majority of *Allium* species are out-breeders but very few are known to be self-incompatible. Extremely polymorphic species like *A. schœnoprasum* and *A. senescens* are known to exist both in out-breeding and in inbreeding forms (table 4). Owing to the bulb-forming habit, vegetative reproduction is an essential feature of the genus. Where sexual reproduction fails, the clone may also reproduce by different forms of apomixis and vivipary. This exists at all levels of ploidy (table 4). In the *A. paniculatum* group, formation of bulbils is directly correlated with polyploidy and hybrid nature of the complex (Levan, 1937). But Geitler (1944) has reported bulbil formation in diploid *A. carinatum* and I have found it in diploid *A. flavum*. These two cases do not fit in with the views of Levan although both species belong to the group he studied. Instead, they indicate a case of pre-adaptation in the complex. Evidently, these diploids are not obligatory bulbiferous forms as they also set seeds from normal flowering. The obligatory forms are usually seed sterile and the only information available about the development of their gametes is as follows:

Weber (1929) has studied the development of female gametophytes in some species of *Allium*. In *A. sativum* var. *vulgare*, the E.M.C. develops only up to first division of meiosis but in var. *ophioscordon* it proceeds up to the first division of the embryo sac indicating the occurrence of meiosis but inviability of the gametophyte. In *A. scordoprasum*, *carinatum* and *oleraceum* the embryo sac completes its development but fertilisation fails. However, in the latter two species polyploidy which results in errors of segregation during meiosis is partly responsible for the inviability of the pollen. Weber has also reported fertilisation in *A. moly* var. *bulbiferum* and *A. zebdanense* in which the embryo never matures. But the former reproduces by bulbils and the latter apomictically (Gustafsson, 1947).

An interesting case of sterility owing to genotypic unbalance has been shown in *A. ascalonicum* (Darlington and Haque, 1955). It usually reproduces vegetatively including by bulbils. Normal flowering is very rare and anther development is marked by the errors of differentiation resulting in spontaneous premeiotic chromosome breakage and asynapsis. Thus, there is complete male sterility. The events on the female side are not known.

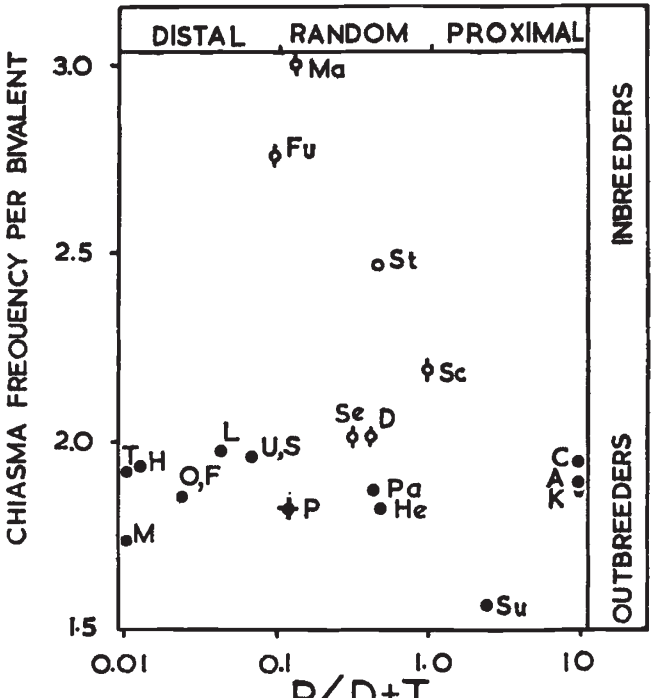
In *Allium* most of the apomictics are polyploids and so far only three diploid apomictic forms, *i.e. A. zebdanense*, *A. odorum* and *A. moly* are known. Correlation between polyploidy and apomixis has been pointed out by Gustafsson (1947) but this is not necessarily a casual one. It is instead more a case of pre-adaption (Darlington, 1956; Lewis and John, 1963). Pseudogamy in the diploid as well as tetraploid *A. odorum* may indicate that polyploids with asexually reproducing diploid progenitors have a better chance of success.

5. RECOMBINATION SYSTEMS

According to the breeding habit and chromosome behaviour, a species can recombine in three ways. The recombination system may be open or restricted when the rule is sexual reproduction. It is closed in a mitotic system particularly if it is an obligatory one. Twenty-five species of *Allium* are known to reproduce asexually (table 4), all with dead ends. Very little information is available about female meiosis in the apomicts. The only case studied so far is *A. odorum* (Hakansson and Levan, 1957) with endoduplicational meiosis which does not involve any recombination. Thus, the only source of genetic variability is gene mutation and structural changes which are easily preserved by the essentially mitotic system. During meiosis in the pollen mother cells this is shown by the formation of multivalents involving more than the expected number of chromosomes and also inversion bridges as in *A. carinatum*, *A. oleraceum* and *A. odorum* (Levan, 1937; Hakansson and Levan, 1957). This is also the case in *A. scordoprasum* ($2x = 16$) which reproduces usually by bulbils. This garlic bears only a few flowers and meiosis is normal in pollen mother cells (Levan, 1935). In the Japanese cultivated varieties, however, meiosis is marked by the formation of multiples involving 4-10 chromosomes (Takenka, 1960). The size and frequency of multiple associations varies from one variety to the other and determines the varietal differences. Takenka thinks that interchanges in *A. scordoprasum* var. *viviparum* have proved of a selective advantage for the origin of new cultivated varieties.

Amongst sexually reproducing species the breeding systems seem to be correlated with chiasma frequencies (table 1, text-fig. 5), a co-adaptation according to selection for optimum recombination. The inbreeders tend to have higher chiasma frequencies than the outbreeders as previously also observed in *Agropyron*, *Sorghum*, *Collinsia*, *Gilia* and in *Chorthippus* (see table 47, Lewis and John, 1963). These correlations have been hypothesised on the basis of expectation by Darlington (1939) and discussed in detail by Stebbins (1950). Evidently they are compensatory in nature. Factors which promote recombination in the breeding system are often associated with restrictive practices in the chromosomal mechanism. Owing to the high variability potential in the outbreding species of *Allium* a small amount of selfing which results from the localised activity of insects does not significantly affect the amount of recombination generated. On the contrary occasional out-crossing in the inbreeders has special significance. It provides an infrequent heterozygosity for which a high recombination index is ideal for exploitation (Lewis and John, 1963).

In the outbreeding species the rate of outcrossing directly determines the amount of variability generated. Also in the chromosomal mechanism meiosis is supplemented by mutation as in *A. cepa* with 93 per cent. out-crossing (see Fryxell, 1957) and several mutations involving nucleolar chromosomes (Battaglia, 1963). These mutations are known to occur mainly in the nucleolar arm and presumably the nucleolar handicap during pachytene pairing favours their establishment. Zen (1961) has also reported two mutants, one for a deletion and another for translocation in a population of 102 plants of *A. fistulosum*. So far, these mutations do not affect fertility, they are bound to raise the amount of variability in the population.



TEXT-FIG. 5.—Diagram showing relationship between frequency and regional distribution of chiasmata and the breeding systems in different species of *Allium*. The values for complete localisation are arbitrary. The regional frequencies of chiasmata are the same as in fig. 1. For specific abbreviations see table 1, page 326.

Outbreeder ●, Inbreeder ♁, Versatile ✦, Sterile ○.

In addition to chromosome mechanism and the breeding systems there are also other factors like habit and habitat which determine the amount of variability in a population (see Grant, 1958). Recently

Rees and Ahmad (1963), Sun and Rees (1964) have shown an adaptive compromise between high chiasma frequency and reduced potential variability in the annuals of outbreeding *Lolium* populations and different species of rye. Such factors have not been studied in *Allium*. Similarly, B-chromosomes increasing the amount of variability in a population (Darlington, 1956) are also important and some *Allium* species are known to carry them (see Ved Brat, 1965). An interesting suggestion but based on too meagre data is presented by *A. paniculatum*. Two clones one with and the other without a B-chromosome were examined for meiosis, which was abnormal in the latter. A similar situation is shown by locust populations where B-chromosomes were reponsible for the restoration of stability (Lewis and John, 1959).

6. SUMMARY

1. In twenty-one species of *Allium* chiasma frequency in P.M.C. varies from 1·53 to 3·02 per bivalents. The lowest frequencies occur in *A. paniculatum* and *A. suaveolens* with some univalents at metaphase-I of meiosis.

2. Regional distribution of chiasmata in different species has been found as follows:

(i) Six species with complete proximal localisation and two with incomplete.
(ii) Only one species with complete distal localisation and ten with incomplete.
(iii) Six species with random distribution of chiasmata.

These are evidently derived from procentric, proterminal and random contact points followed by incomplete pachytene pairing.

3. Reproductive methods, both sexual and asexual, have been surveyed in 53 forms which include 18 polyploids. The asexual forms consist of 60 per cent. polyploids. Only *A. stipitatum* which is sterile reproduces vegetatively. The remaining three diploids and eight polyploids are apomicts while seven diploids and seven polyploids are viviparous. Apomixis is correlated with polyploidy owing to preadaptation.

4. The sexual forms include 21 outbreeders, 5 inbreeders and only two with versatile reproduction. The outbreeders are protandrous. Pollination in both forms is aided by insects except in the cliestogamous *A. macranthum* (4*x*).

5. Restriction on recombination in the chromosomal mechanism is effected mainly through low chiasma frequency whether localised or random.

6. The sexual forms show an adaptive compromise between their chromosome behaviour and breeding systems. The outbreeders tend to have lower chiasma frequencies than the inbreeders which also include tetraploid *A. macranthum* with highest chiasma frequency going with obligatory selfing.

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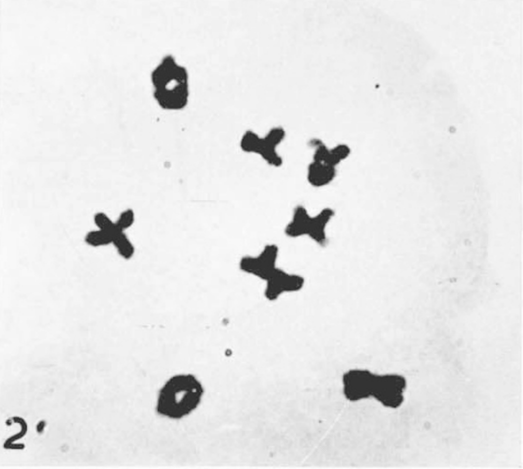
Plate I

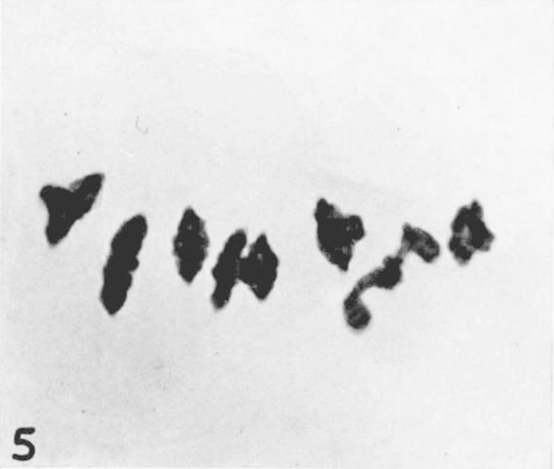
Microphotographs of metaphase-I of meiosis on p.m.c.'s of *Allium* species. × 1350.

1. *A. cyathophorum*
2. *A. schœnoprasum*
3. *A. kochii*
4. *A. lilacinum*
5. *A. olympicum*
6. *A. ursinum*


1


4


2

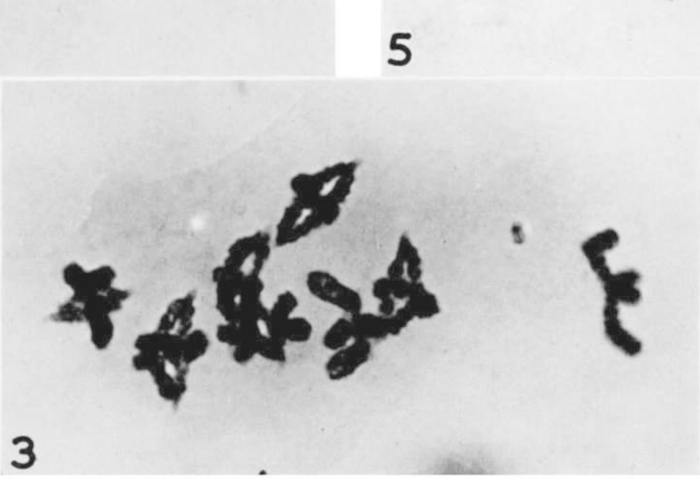

5


3

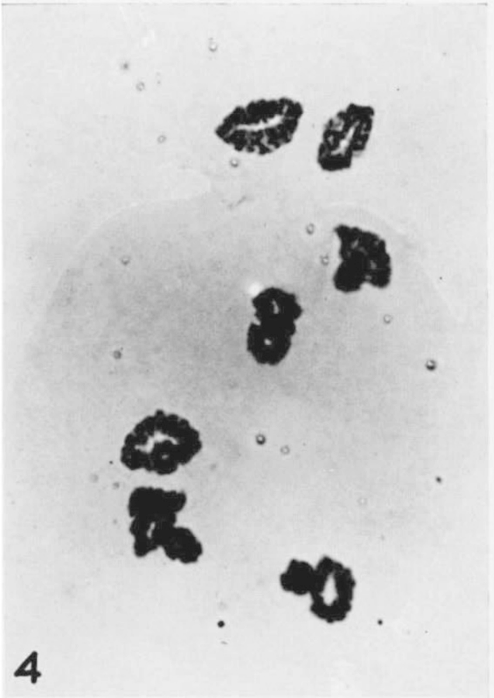

6

1

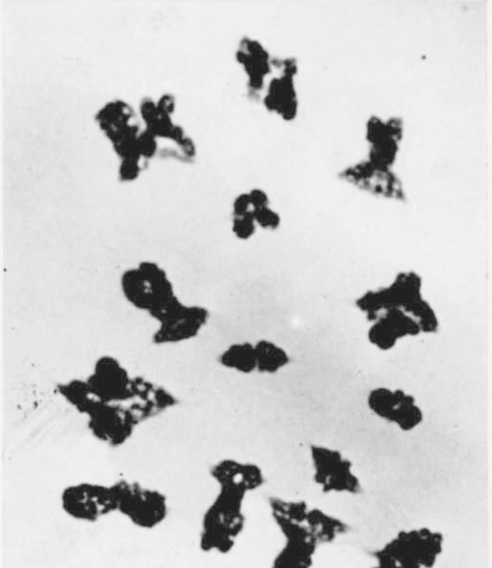
2



3



4



5

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