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CYTOGENETICAL STUDIES ON *PAPAVER SOMNIFERUM* L. AND *PAPAVER SETIGERUM* DC. AND THEIR HYBRID

by

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I. INTRODUCTION

It is known from ancient times that opium, morphine and other alkaloids have been obtained from the opium poppy, *Papaver somniferum* L., from the beginning of its cultivation. As regards the origin of this cultivated species, nothing definite is known, except for some attempts made in the field of systematics and archeology. The earliest data according to HEER (1865) refer to the times of lacrustine dwellings in Switzerland in the beginning of the stone age. The poppy plant has evidently come to Switzerland from other countries, very likely from East-Asia Minor, India and partly from Egypt, together with the culture of some cereals (BAZILEVSKAJA 1928). FRITZEL has found a subfossil from Aygalades near Marseille, which resembled to *P. somniferum nigrum* and concluded that *nigrum* came there without human help during the glacial period. KARL and FRANZ BERTSCH (1947) attribute that *P. somniferum nigrum* originated in the west and to Switzerland it would have gone along the River Rhone from France. They held the view that the primitive form of *Papaver* is the black type – *P. somniferum nigrum*, having violet flowers, black seeds and open capsules. This type is distinct from the '*album* type'; for *album* is nondehiscent, with white flowers and with white or nearly white seeds.

DE CANDOLLE (1896, p. 319) is the first to state that *Papaver setigerum* DC. – an indigenous species of the western Mediterranean region – should be considered as progenitor of *P. somniferum*. He

states "On ne peut pas dire qu'elle (*P. somniferum*) existe à l'état vraiment sauvage, mais les botanistes s'accordent à la considérer comme une modification du Pavot appelé *Papaver setigerum*, qui est spontané dans la région de la mer Méditerranée, notamment en Espagne, en Algérie, en Corse, en Sicile, en Grèce et dans l'isle de Chypre". HEGI (1918) quite agrees with DE CANDOLLE while BAZILEVSKAJA (1928) does not think *P. setigerum* DC. could be the progenitor. It is obvious that only species existing at that time should have been taken for cultivation and *P. setigerum* DC., as its area shows, has never occurred more eastwardly than Cyprus. The geological history of the Eastern Mediterranean countries shows no change from the beginning of the quarternary period. Therefore, it is not likely that *P. setigerum* DC. should have been found in the eastern part of the Mediterranean region in historical times; that it should have been cultivated there and then have died out.

The section Mecones of the genus *Papaver* comprises five species. One of them, the easternmost in distribution (Egypt, Iran, Baluchistan) *P. Decaisnei* Hochst. et Steud. morphologically occupies a position apart, forming a transition to the neighbouring section Orthorhoeadales. The other species form a rather close group of morphologically related types. Two of them being east Mediterranean species – *P. glaucum* Boiss. et Hausskn. and *P. gracile* Auch. – are morphologically very close to *P. somniferum*, in particular to its races cultivated at present in Asia Minor. The third west Mediterranean species *P. setigerum* DC. is so near to *P. somniferum*, that it is often considered as one of its varieties. Karyologically, however, they differ in their chromosome number, the former having $2n = 44$ whilst *P. somniferum* has $2n = 22$.

The purpose of the present study is to find arguments for the question how far *P. somniferum* L. and *P. setigerum* DC. are related and if the view held by some taxonomists beginning from DE CANDOLLE that *P. setigerum* DC. is the progenitor of *P. somniferum* L. is wellfounded. This investigation covers mainly the cytogenetics of these species and their hybrids and segregants in the second generation.

II. MATERIALS AND METHODS

Materials have been obtained as indicated in table 1:

TABLE 1 *

S. no.	Culture no.	Species	Source	Country	2n
1	5713/5812/5902	*Papaver somniferum* L.	Hortus botanicus, LUIK	Belgium	22
2	5718/5817/5908	,, ,,	Botanischer Garten, BERN	Switzerland	22
3	5720/5819/5910	,, ,,	Estaçao Agronomica Nacional, found at SACAVEM	Portugal	22
4	5721/5820/5911	,, ,,	Estaçao Agronomica Nacional, found at SINTRA-ALGUEIRAS	Portugal	22
5	5712/5811/5901	,, ,,	Jardim Botanico da Universidade, LISBON in an uncultivated field in limy soil; about 50 m. above sea-level	Portugal	20
6	5715/5814/5903	*Papaver setigerum* DC.	Botanic Garden, MALTA	Malta Island Mediterra-nean	44
7	5904	,, ,,	through Southern Research Station, Maple, Ontario, Canada originally from Chelsea Physic Gardens, Botan. Garten Tübingen and Hortus Botanicus Leiden	various countries	44
8	5905	,, ,,	through Southern Research Station, Maple, Ontario, Canada; originally from Jardin Botanique, Rouen.	various countries	44

*) The materials mentioned in table 1 were kindly left at my disposal by Dr A. KOOPMANS, to whom my thanks are due.

Culture no. 6 obtained from Malta has been received as a variety of *Papaver somniferum* L., but later it has turned out that this culture could be *Papaver setigerum* DC. Recently seeds of *Papaver setigerum* DC. (culture nrs 5904 and 5905) have been obtained from the Southern Research Station, Maple, Ontario, Canada. Culture no. 5905 has been found to be quite identical with the culture from Malta in all respects whilst the other culture differed only in the colour of the flower, being red. The somatic number of these three cultures is 44. Moreover, for confirmation the culture from Malta was identified as *Papaver setigerum* DC. through the courtesy of the Director of the Royal Botanic Gardens, Kew to whom my thanks are due.

All the cultures listed in table 1 together with their F_1s and F_2s (table 2) were grown in the Experimental Garden of the Genetical Institute at Haren (Gron.), Netherlands [1]).

In table 2 the crosses made amongst the cultures and the F_2s studied are listed.

The somatic number of the cultures mentioned in table 1 were determined from the root tips. The seeds were sown in petridishes and the young seedlings at the sixth day after sowing, were pretreated in α-bromonaphthalene (saturated aqueous solution) for two hours before they were fixed in acetic alcohol (1 : 3). After one hour fixation, the materials were kept overnight in absolute alcohol. The squash technique was found to be highly suitable. The seedlings were hydrolized in 1 N HCl for 12 minutes at 58°C and then stained in basic fuchsin for at least two hours. Then they were rinsed well in tapwater for about 15 minutes and squashed in 45 percent acetic acid. The preparation was kept in a freezer at −12° overnight for freezing. The following day, the coverslip was gently taken out with the help of a blade and both the slide and the coverslip were placed in absolute alcohol (already cooled to about −12°C) kept in a dish, in such a way that the material was facing down, and left in the freezer. Thirty minutes after, they were recombined in euparal. Then the preparation was allowed to dry on a warming plate.

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[1]) Due to unfavourable spring conditions (8 weeks without any rain) during 1959, the cultures suffered to a great extent, while a hailstorm on July 11, 1959 brought much damage to the full-grown plants.

TABLE 2. *Parents involved in the cross* *

S. no.	Chromosome nos. of the parents	Culture nos.	Parents	Culture no. of the F_1	F_2's studied with culture no.
1	44 × 22	5715 × 5713	Malta × Luik	5855/5943	5973
2	,,	5715 × 5718	Malta × Bern	5856/5942	5974
3	,,	5715 × 5720	Malta × Sacavem	5858/5938	5976
4	,,	5715 × 5721	Malta × Sintra-Algueiras	5859/5939	5977
5	44 × 20	5715 × 5712	Malta × Lisbon	5854/5941	5972
6	22 × 44	5713 × 5715	Luik × Malta (Reciprocal)	5768/5928	5970
7	22 × 22	5713 × 5718	Luik × Bern	5932	—
8	,,	5713 × 5720	Luik × Sacavem	5933	—
9	,,	5713 × 5721	Luik × Sintra-Algueiras	5934	—
10	,,	5718 × 5720	Bern × Sacavem	5953	—
11	,,	5718 × 5721	Bern × Sintra-Algueiras	5954	—
12	,,	5720 × 5721	Sacavem × Sintra-Algueiras	5959	—
13	22 × 20	5713 × 5712	Luik × Lisbon (Reciprocal)	5852/5927	5969
14	20 × 44	5712 × 5715	Lisbon × Malta (Reciprocal)	5919	—
15	20 × 22	5712 × 5713	Lisbon × Luik	5847/5918	5964/5861
16	,,	5712 × 5718	Lisbon × Bern	5849/5923	5966
17	,,	5712 × 5720	Lisbon × Sacavem	5850/5925	5967
18	,,	5712 × 5721	Lisbon × Sintra-Algueiras	5851/5926	5968

*) For the sake of convenience the cultures are named after the location from where they have been obtained.

Materials for meiotic studies were fixed in acetic alcohol (1 : 3) and kept in the freezer. The buds were then washed in absolute alcohol by keeping overnight and squashes in basic fuchsin were made as described above.

To determine the percentage of fertility the flowers were collected in the mornings as soon as they opened. One percent aqueous iodine in potassium iodide was used for staining the pollengrains. Pollen-

grains that were full and stained blue or nearly blue were counted as fertile whilst the shrivelled and the empty ones were considered as sterile pollengrains. For the parents and F_1s, ten flowers from ten plants were taken to determine the mean for that line, while for the F_2s, each segregant was treated separately and the percentage determined.

All the microscopic investigations were made with Carl Zeiss binocular microscope by using ocular × 10 in conjunction with oil immersion × 95. Microphotographs were taken in Ilford film.

III. REVIEW OF EARLIER DATA

No authentical record has been found as to the nomenclature of *Papaver somniferum* L., eventhough it has been referred after the work of LINNÉ (1753). The species name '*somniferum*' has not been mentioned by LINNÉ in his classifications (1737, 1748, 1749 and 1753) neither in the contemporary work of VAN ROYEN (1740). The only reference that could be seen after LINNÉ is, in the classification of DE CANDOLLE (1815, 1821) who mentioned *P. somniferum* L. and has given the name to 'pavot-porte-soie' as *Papaver setigerum*, a plant that has been found by M. Requien in the Levant (East-Mediterranean) and by him cultivated at Avignon in Southern France. DE CANDOLLE has observed many distinguishing characters sufficient enough to retain this plant as a separate species from *Papaver somniferum* L., differing from the opinion of earlier taxonomists. Mention of '*setigerum*' only as a variety of *Papaver somniferum* L. has been made by ELKAN (1839), in his monograph on the genus *Papaver*. An exhaustive taxonomical study of this genus has been published by FEDDE (1909, 1936) who has given a detailed description of each species with all the synonyms.

According to this author, the genus *Papaver* comprises 99 species grouped in 9 sections, of which under the section 4 – Mecones, are listed 5 species namely (1) the cultivated species *Papaver somniferum* L., (2) *Papaver setigerum* DC., (3) *Papaver glaucum* Boiss. et Hausskn., (4) *Papaver gracile* Auch. and (5) *P. Decaisnei* Hochst. et Steud. The latter two species are differentiated from the others by their obovate, oblongate capsules whereas the former three having globular or subglobular capsules. Further distinction amongst these three species is

based on *P. somniferum* L. and *P. setigerum* DC. having sparsely or full bristles and leaves deeply or lightly incised, while *P. glaucum* Boiss. et Hausskn. has glabrous peduncles with pinnately formed leaves. *P. somniferum* L. is characterized by lightly incised leaves, with the peduncle hairy or sparsely bristled, and 8–12 stigmatic rays, whereas in *P. setigerum* DC. the leaves are deeply incised, with fully bristled peduncle and 7–8 stigmatic rays.

At this juncture it is worthwhile to point out that the shape of the capsule as illustrated by FEDDE (1909, p. 339, Fig. 37) is quite different from the shape of the capsule of *P. setigerum* DC. (Fig. 2, p. 12) studied here. In fact, the close resemblance is to the capsule of *P. glaucum* Boiss. et Hausskn.

BASILEVSKAYA (1928, 1931) divides the principal botanical-systematical groups of the Opium poppy *P. somniferum* L. into 7 subspecies (geographical cultivated species) based on the following characters namely (1) type of capsule (dehiscent or non dehiscent), (2) shape of the capsule, (3) vigour of the plant, (4) branchiness and (5) leafiness of the stem. Analogous systematic studies have been made by PIEPER (1940) and DANERT (1958).

The first report on the hybridisation amongst different species of *Papaver* is found in the records "Die Pflanzenmischlinge" of FOCKE (1881). He mentions *P. hortense* Hussen. (apparently *P. somniferum* L.), *P. officinale* and *P. setigerum* DC. as the principal species in this genus, of which *P. setigerum* DC. is considered to be the wild type of *P. hortense* Hussen. The hybrid between *P. hortense* Hussen. and *P. setigerum* DC. has been found to resemble more like *P. setigerum* DC. whilst the F_2 progeny has given more plants resembling *P. hortense* Hussen. except for the presence of the hairs of the other parent. No report has been made about the fertility of this hybrid, eventhough it can be inferred that it would have been nearly sterile, from his statement that he could obtain only a few seeds to raise an F_2 progeny.

A series of investigations are recorded by HOFFMAN between 1872 and 1884 in which reference is made to flower and seed characters of the opium poppy among several other species of this family. DE VRIES (1890) has concluded from his studies on the inheritance of the flower colour, spot at the base of the petal and the margin of the petal, that crosses in both directions gave the same results.

KAJANUS (1919) and FRUWIRTH (1924) have found in their studies on the intraspecific hybrids of *P. somniferum* L. that the F_1 plant between laciniate and entire petals, showed an intermediate character. FRUWIRTH (1924) and PROCHASKA (1926) do not find any positive correlation between the colour at the base of the petal and the colour of the seedcoat whilst LEAKE and PERSHAD (1920) and PRZYBOROWSKI (1922) have reported a direct correlation. The latter has recorded that the colour of the seedcoat is conditioned by three polymeric factors namely V, I and G. Direct correlations between the size of the capsule, number of seeds and the number of anthers have been noticed by PROCHASKA. Number of stigmatic rays and number of anther filaments are also positively correlated. The form of the capsule and colour of the corolla are not found by him to be correlated.

Detailed genetic studies on *P. somniferum* L. made by MIYAKE and IMAI (1927) have been summarised as follows: The bristles on the flowerstalk are produced by duplicate factors, though they may exhibit some fluctuation in the manifestation of their phenotype and give more or less a higher ratio of the smooth stalk in the segregating population. The crapy petal behaves as a simple recessive to the normal, but its segregating ratio is always lower than the requirement. The serrate petal acts as a dominant over the entire, with modifiers affecting the degree of serration. The common double flower is a recessive character to the single. According to them, the genetic constitution of the common flower colour is as follows: (1) Red flower RRDD; (2) purple flower rrDD; (3) red flower with white centre RRdd; (4) white flower rrdd. Strong linkage between the factors I and R is found, the factor I suppresses the production of the red flower with white centre, thus forming a dominant white flower.

Linkage groups have been observed by NEWTON (1929) in *Papaver Rhoeas* L. and by PHILP (1933) in his studies on the genetics of *Papaver commutatum* Fisch. and its hybrid with *Papaver Rhoeas* L.

Since FOCKE, a rather more detailed information about the interspecific cross between *P. somniferum* L. and *P. setigerum* DC. is available from the works of BLARINGHEM (1925). He has observed that the hybrid resembled more of *P. setigerum* DC. and gave only very few seeds, quite agreeing with FOCKE. The hybrid has been found to be very weak, early flowering and producing a large number

of flowers with less and sterile anthers. He argues that if *P. setigerum* DC. and *P. somniferum* L. are the same as recognised by BATTANDIER et TRABUT, there should be only mendelian segregation; but the fact was, it behaved in a quite different way. He further states that *P. setigerum* DC. could give seeds without pollination after emasculation. The germination of the hybrid seeds has been found to be rather poor. He attributes that this poor setting of the seed after hybridization is due to incompatibility. On the contrary, according to the investigations of VESSELOVSKAYA (1933), crosses of *P. somniferum* L. and *P. setigerum* DC. give rise to perfectly normal fertile hybrids with viable seeds. But these studies have not given any indication as to the exact relation of these two species.

The earliest illustration of chromosomes of *P. somniferum* L. reproduced here (Fig. 1) has been given by TAHARA (1915). He has

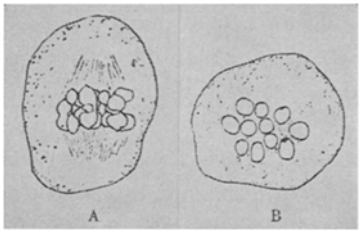

Fig. 1. Earliest illustration of chromosomes of *P. somniferum* L. (After TAHARA 1915).

counted the meiotic chromosomes of *P. somniferum* L. as eleven. Later workers, LJUNGDAHL (1922), YASUI (1921–1941) and KUZMINA (1935) have confirmed that the somatic number of *P. somniferum* L. and *P. setigerum* DC. are 22 and 44 respectively. DARLINGTON and WYLIE (1955) mention 44 being the somatic number for *P. somniferum* L. besides 22, as given by FURUSATO (1940), and 22 for *P. setigerum* DC. as reported by SUGIURA (1940). Tetraploidy of *P. somniferum* L. is never met with, nor is there any report of an autotetraploid of this species. Similarly, a haploid *P. setigerum* has not yet been recorded. It can be presumed that the above mentioned workers namely FURUSATO and SUGIURA, perhaps would have been wrong in their identification of the two species. Nobody else has confirmed their reports yet.

The investigations of YASUI and KUZMINA are of interest. YASUI has undertaken studies on the cytogenetics of artificially raised interspecific hybrids amongst *P. somniferum* L., *P. lateritum* C., *P. orientale* L., *P. bracteata* Lindl. and *P. nudicaule* L. From her studies, she (1940) has given the hypothesis that *P. somniferum* L. is an amphitriploid having $((3 + 4) = 7 + 4) = 11$ chromosomes. This hypothesis seems to me highly imaginative and I propose to discuss the same in a later chapter. SUGIURA (1940) has stated erroneously that *P. setigerum* DC. has $n = 11$. This worker has inclined to believe YASUI's hypothesis by stating that *somniferum* has 11 meiotic chromosomes consisting of $4 + 4 + 3 = 11$, where 4 and 3 are the basic chromosome numbers in the *Papaveraceae*.

The purpose of the cytological investigations of the cultivated poppy undertaken by KUZMINA is to ascertain the cytological peculiarities of *P. somniferum* L. and its related species, as well as the possible cytological distinctions within the limits of *P. somniferum* L. According to her, such data characterizing the degree of genetical nearness of the respective species and races, serve to throw light on their evolutional connection; they determine further work in the field of hybridisation and plant breeding. It is indicated in her studies, that *P. setigerum* DC. is genetically near to *P. somniferum* L., but can not be its direct ancestor as, in comparison to the latter, it possesses a double number of chromosomes, while it has been proved experimentally that the evolution of polyploid relations proceeds from lower to higher numbers. Reversion, according to her, would only mean return to the initial forms with few chromosomes.

IV. OBSERVATIONS

1. *Morphology of the parents*

The main distinguishing characters of the parents under study are given as follows:

a. *Papaver setigerum* DC. (Malta): (fig. 2). Plants about 35 cm high, weak stemmed, branching – 7 to 11 in number; Flowers – terminal, peduncle hairy; Calyx – hairy or not; Corolla – petals 4, about 3 cm long and about 3 cm wide at the margin of the petal, entire, light purple, very dilute purple towards the margin of the petal almost white, dark purple spot at the base of the petal; Stamina

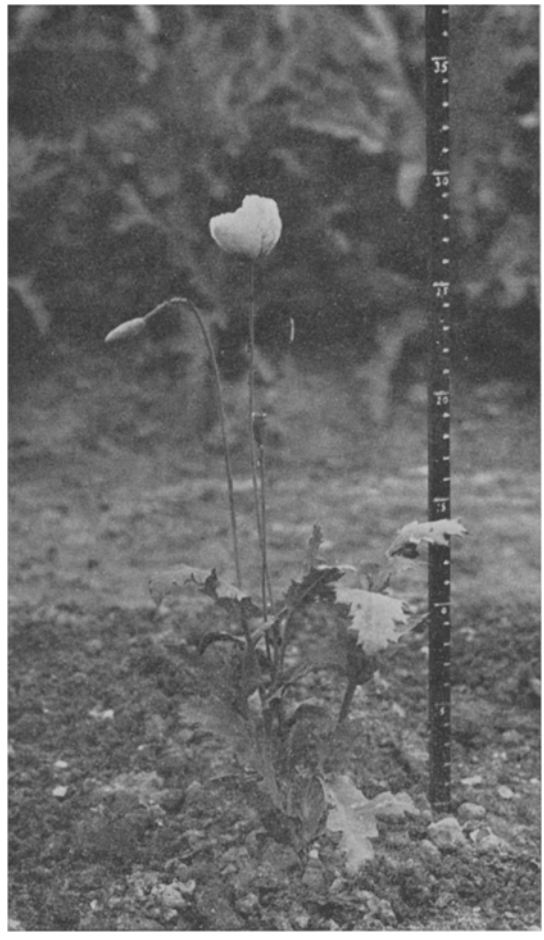

Fig. 2. *Papaver setigerum* DC. Malta.

– filament – light purple; Anther – light purple, 8–10 in number; Ovary-stigmatic rays 4–6; Capsule – dehiscent, small in size and obovate-oblong in shape; Seeds – black and small in size.

b. *Papaver somniferum* L. (Luik): (fig. 3). Plants about 100–115 cm high, branching – 3 to 9 in number; Leaves about 16 to 22 cm long and 10 to 15 cm wide; Flowers – terminal, peduncle hairy or not; Calyx – hairy or not; Corolla – 4 petals, about 8 cm long and about 8 cm wide at the margin of the petal, entire, purple

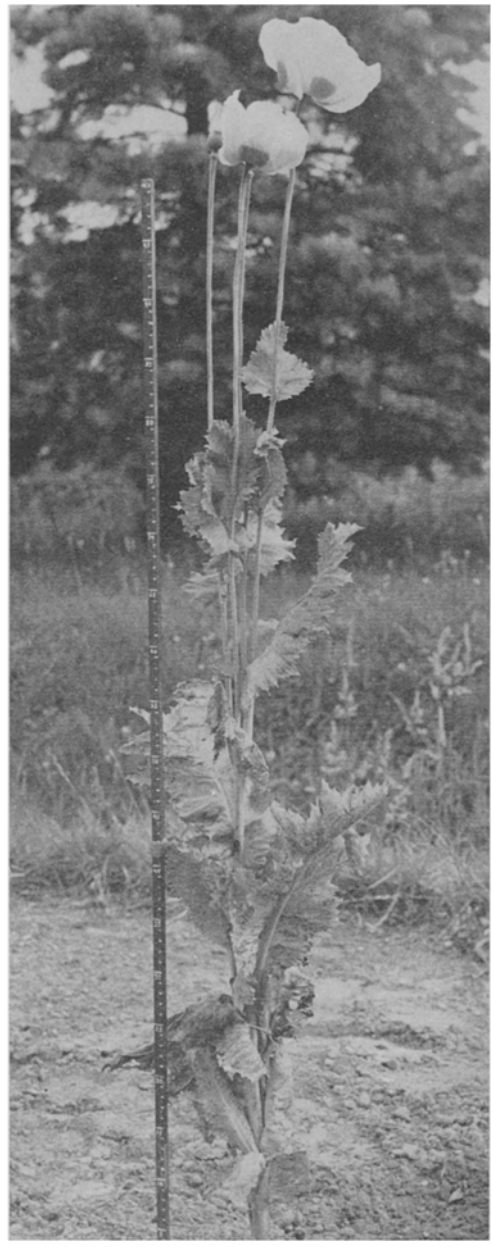

Fig. 3. *Papaver somniferum* L. Luik.

Fig. 4. *Papaver somniferum* L. Bern.

with a comparatively darker purple spot at the base of the petal; Stamina-filament – white; Anther – light yellow, many in number; Ovary-stigmatic rays 8–12; Capsule – dehiscent, larger in size and globose in shape; Seeds – grey and medium in size.

c. *Papaver somniferum* L. (Bern): (fig. 4). Plants about 85 to 100 cm high, non branching; Leaves about 12 to 17 cm long and 10 to 15 cm wide; Flowers – terminal, peduncle hairy; Calyx – hairy or not; Corolla – 4 petals, about 8 cm long and about 6 cm wide at

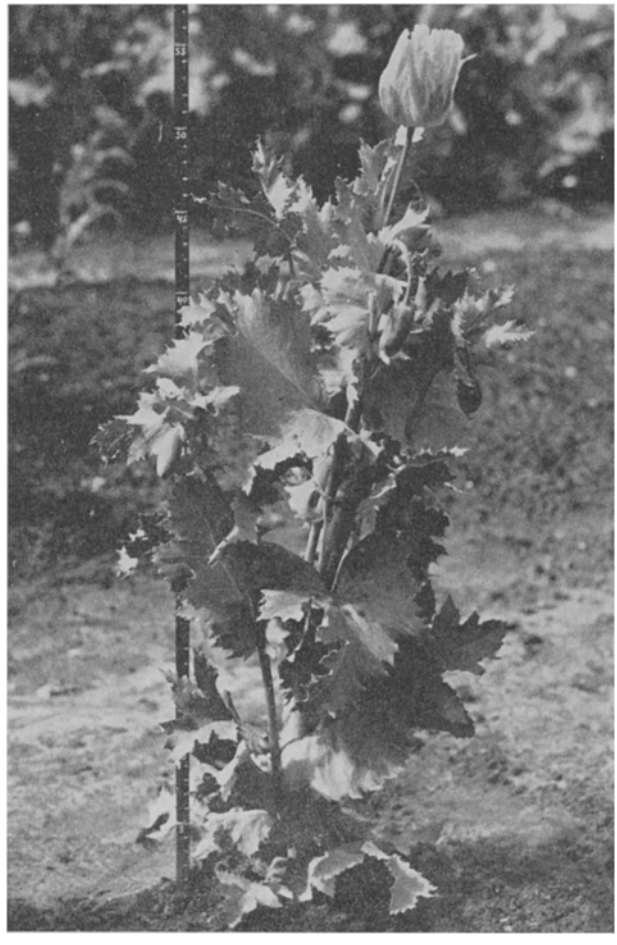

Fig. 5. *Papaver somniferum* L. Sacavem.

Fig. 6. *Papaver somniferum* L. Sintra-Algueiras.

Fig. 7. *Papaver somniferum* L. Lisbon.

the margin of the petal, entire, light red with a tinge of red at the base of the petal; Stamina-filament – white; Anther – yellow, many in number; Ovary-stigmatic rays 10–14; Capsule – dehiscent, larger in size and ovato-oblong in shape; Seeds brown and larger in size.

d. *Papaver somniferum* L. (Sacavem): (fig. 5). Plants about 55 to 65 cm high, branching – 5 to 8 in number; Leaves about 8 to 12 cm

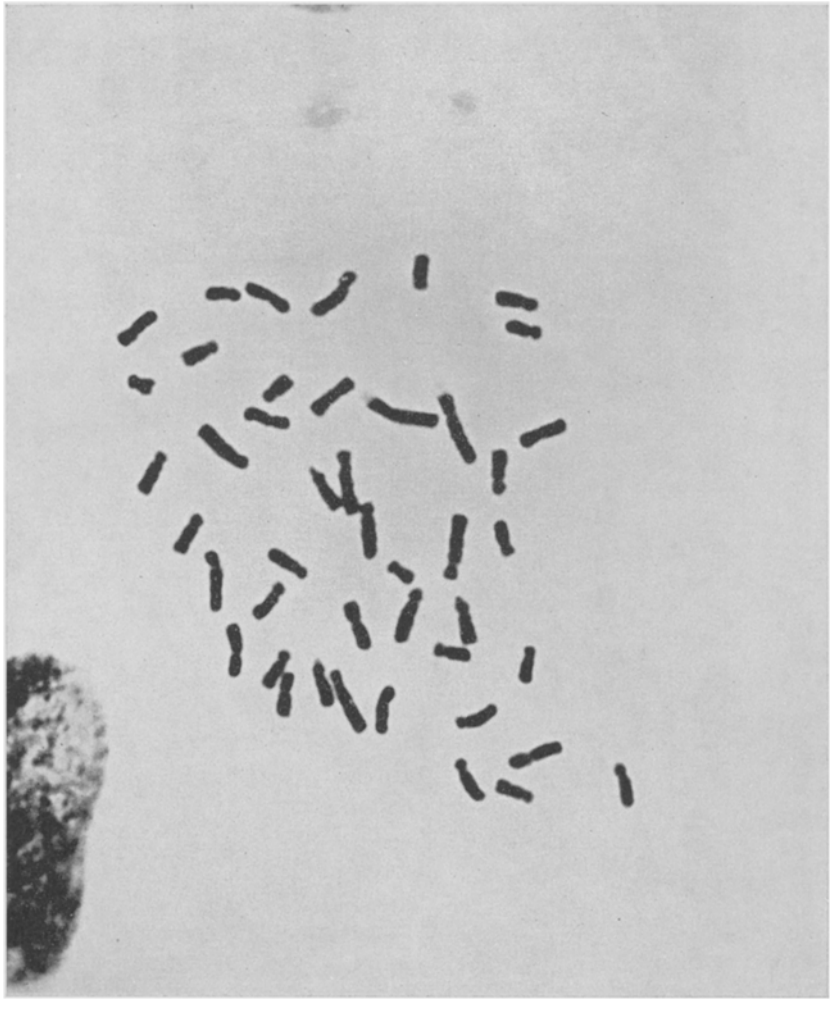

Fig. 8. Chromosome portrait of Malta. × 2116.

long and 6 to 10 cm wide; Flowers – terminal, peduncle hairy; Corolla – 4 petals, about 6 cm long and about 6 cm wide at the margin, entire, red, with a light purple spot at the base of the petal; Stamina-filament – white; Anther – yellow, many in number; Ovary-stigmatic rays 8–12 in number; Capsule – oblong, dehiscent, medium in size; Seeds – black and medium in size.

e. *Papaver somniferum* L. (Sintra-Algueiras): (fig. 6). Plants about 55–68 cm high, branching 5–8 in number; Leaves about 8 to 14 cm

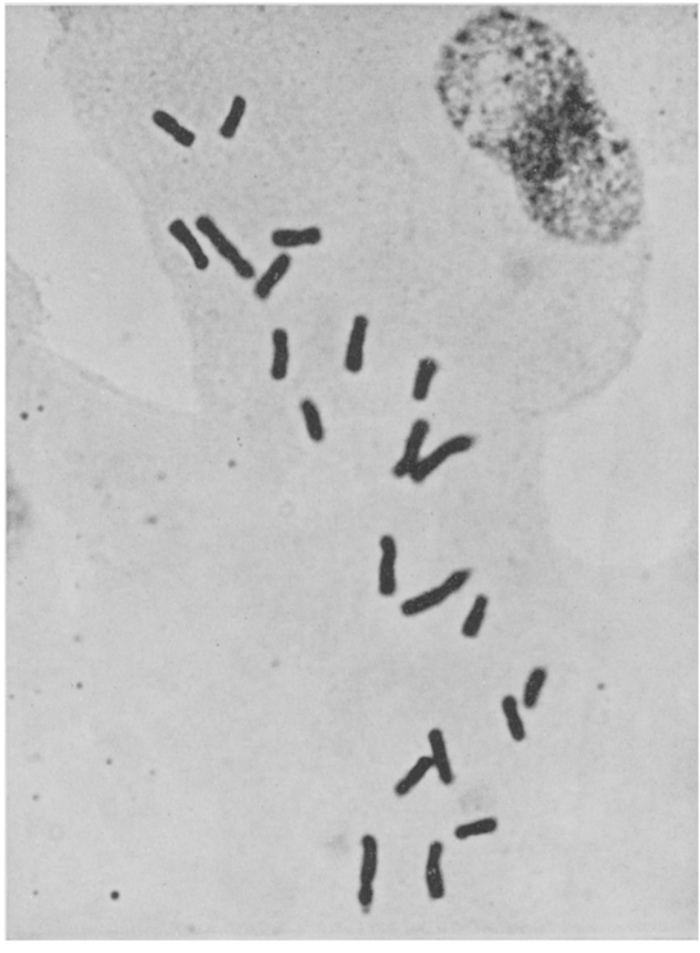

Fig. 9. Chromosome portrait of Luik. × 2116.

long and 5 to 8 cm wide; Flowers – terminal, peduncle hairy; Calyx – hairy or not; Corolla – 4 petals, about 6 cm long and about 6 cm wide at the margin of the petal, laciniate, red with a light purple colour at the base of the petal; Stamina-filament – high purple; Anther – yellow, many in number; Ovary-stigmatic rays 8–12; Capsule – dehiscent, medium in size and subglobular in shape; Seeds – black and small in size.

f. *Papaver somniferum* L. (Lisbon): (fig. 7). Seedlings and rosettes are very characteristic. Plants about 45 to 55 cm high, branching 10–14 in number; Leaves about 10 to 14 cm long and 2 to 5 cm wide;

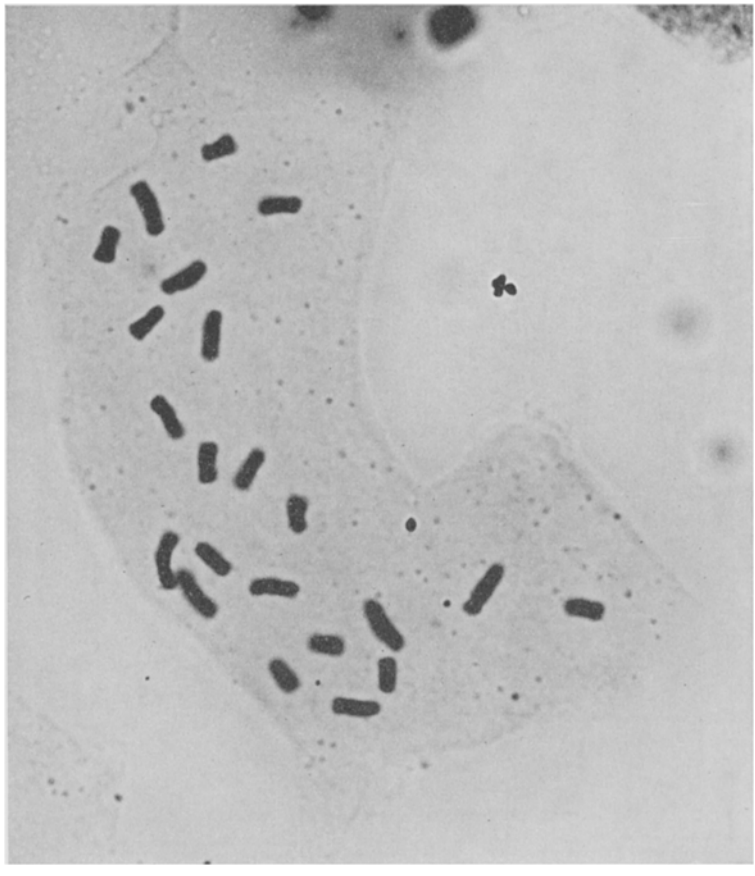

Fig. 10. Chromosome portrait of Bern. × 2116.

Flowers – terminal, peduncle glabrous; Calyx-hairy or not; Corolla – 4 petals, about 6 cm long and about 6 cm wide at the margin of the petal, entire, white with a dark purple spot at the base of the petal; Stamina-filament – dark purple; Anther – yellow, many in number; Ovary-stigmatic rays 7–10; Capsule – oblong, dehiscent, medium in size; Seeds – black and small in size.

2. *Mitosis*

a. The *mitotic studies* have been made from root tip squashes stained in basic fuchsin. The mitosis is normal in all the types.

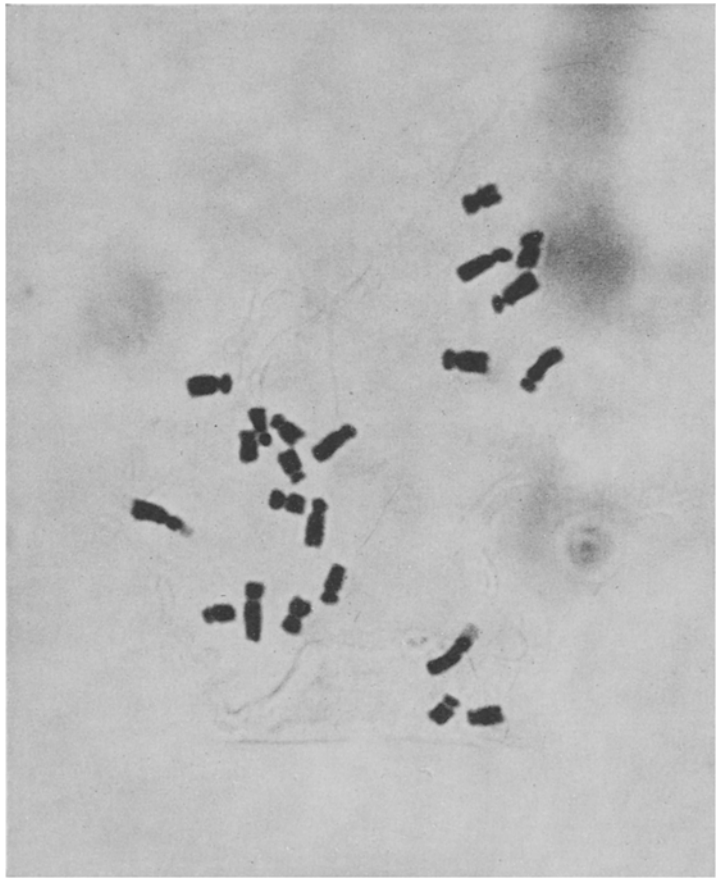

Fig. 11. Chromosome portrait of Sacavem. × 2116.

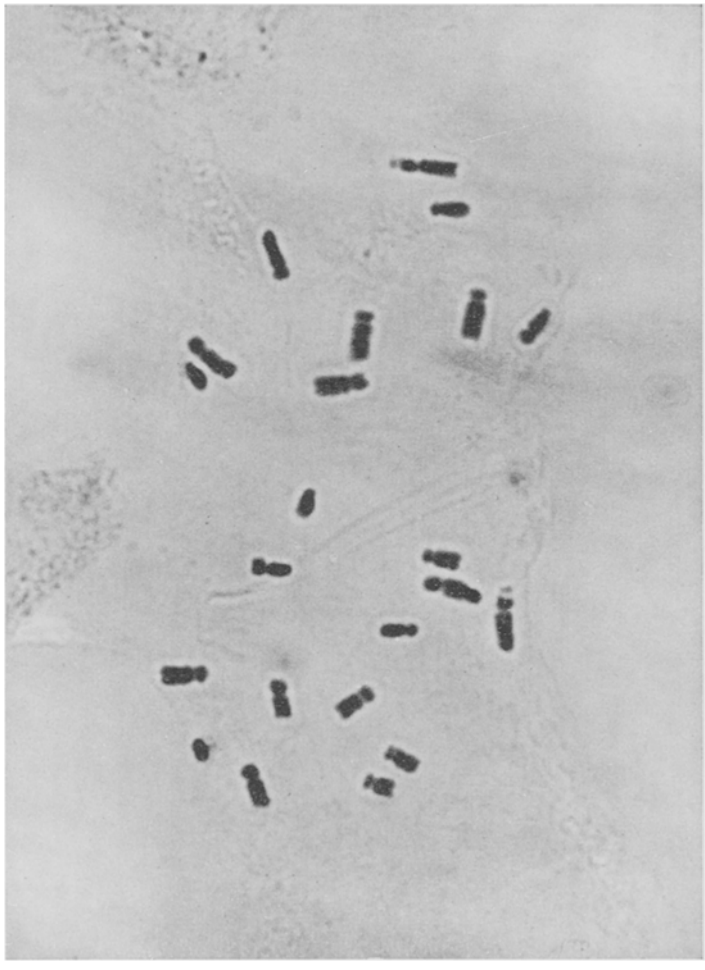

Fig. 12. Chromosome portrait of Sintra-Algueiras. × 2116.

b. *Karyotype*. Critical analysis of the karyotype of these types has been done so as to investigate how far the karyotypes of these types are related to one another. The somatic number has been found to be 44 for Malta, 22 for Luik, Bern, Sacavem and Sintra-Algueiras and 20 for Lisbon (figs 8 to 13). The length of all the chromosomes of each karyotype has been determined in terms of μ. The length in combination with the position of the centromere has been used as

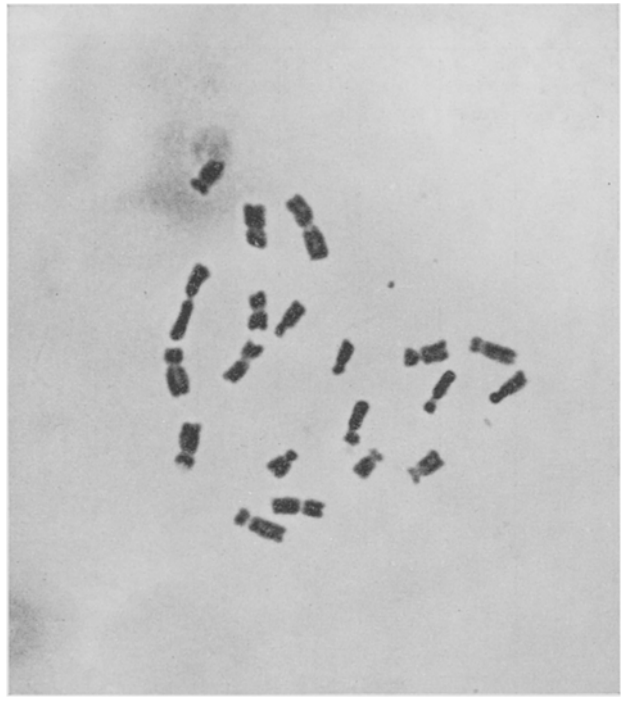

Fig. 13. Chromosome portrait of Lisbon. × 2116.

the criterion to pick out the homologous chromosomes in each karyotype. So for each of the six types described above, the whole lot of somatic chromosomes can be classified into groups of morphologically identical chromosomes. The reasons for which in groups 7, 17, 28 and 33 chromosomes with different lengths of the long arms are taken together will be discussed later. In table 3 the total length and the length of the long arm of the chromosomes of the different groups and the number of chromosomes present in each group are given for the six types studied. Accordingly, except in Luik where 11 pairs have been traced out, in the other types the following number of groups have been distinguished, viz. Bern 10, Sacavem 9, Sintra-Algueiras 10, Lisbon 12 and Malta 17. Each group may possess one to eight chromosomes as the case may be and this has been indicated in the karyogram (fig. 14a–c). Later, each group from one type has been compared to the corresponding groups in other types

TABLE 3

Groups	Length in μ		Number of chromosomes					
	Long arm	Total	Malta	Luik	Bern	Sacavem	Sintra-Algueiras	Lisbon
7	3.2 + 4.5	5.3	2	2				
31	2.8	5.0						1
23	3.2	4.9		2				
17	2.6 + 3.7	4.5			2		2	
32	2.2	4.4						1
18	2.1	4.2	1					
19	3.1	4.1	2					
28	1.3 + 3.1	4.0				2		
20	2.8	3.9	2					
8	2.7	3.8	3	2				
13	2.5	3.6		2		2	2	
24	2.6	3.5		2				
9	2.1	3.5	2		3			
33	2.1 + 2.8	3.5						2
10	1.9	3.4	2					2
34	2.7	3.3						1
14	2.4	3.3		2	2		4	
21	1.8	3.1	3					
1	2.1	3.0	1	2	2	4	2	
11	2.1	2.9	2					2
4	1.7	2.9	2	2	2			2
12	1.9	2.8	2	2				
6	1.9	2.7	8			2	2	
15	1.8	2.7		2				1
25	1.6	2.7		2				
35	1.3	2.7						1
26	1.6	2.6			2			
5	1.8	2.5	2			1	2	2
16	1.6	2.5			2	2	3	
2	1.6	2.2	6		2	4	2	3
27	1.3	2.2			3			
3	1.4	2.0	2		2	2	2	2
29	1.3	1.9				3		
22	1.1	1.7	2					
30	—	1.5					1	
Total number of chromosomes			44	22	22	22	22	20
Length of the longest chromosome in μ			5.3	5.3	4.5	4.0	4.5	5.0
Length of the shortest chromosome in μ			1.7	2.7	2.0	2.0	2.0	2.0
Average length of the chromosome in μ			3.0 ± 0.79	3.5 ± 0.74	2.9 ± 0.34	2.7 ± 0.49	2.9 ± 0.42	3.0 ± 0.32
Number of SAT-chromosomes			2	2	2	2	2	2

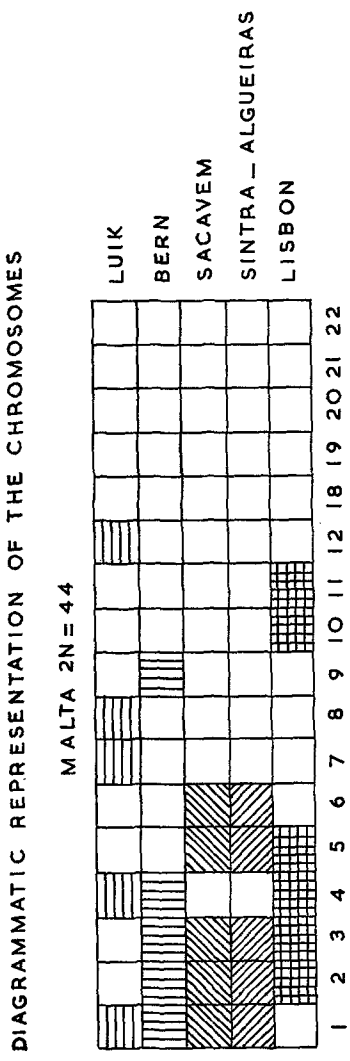

Fig. 14a. Karyogram of Malta and Luik.

to determine whether they are identical in morphology. By this method, it has been found possible to show that out of 17 groups observed in Malta, 12 groups are comparable to similar groups in the other types. Similarly 8 groups in Luik, 8 groups in Bern, 7 in Sacavem, 9 groups in Sintra-Algueiras and 7 groups in Lisbon are comparable to the other identical groups in the other types. These results are diagrammatically represented in fig. 14d. Besides, it is observed that there are some groups present in every type for which no comparable groups exist in the other types. The numbers of such groups having no identical groups found in the other types are, 5, 3, 2, 2, 1 and 4 in Malta, Luik, Bern, Sacavem, Sintra-Algueiras and Lisbon respectively.

The longest chromosomes are found in Malta and Luik and they happen to be the SAT-chromosomes. The shortest chromosomes are found to be present in Malta with a length of 1.7 μ whilst for Luik the smallest length is 2.7 μ; for others 2.0 μ. The mean length of the chromosomes of each group is indicated in table 3. No more

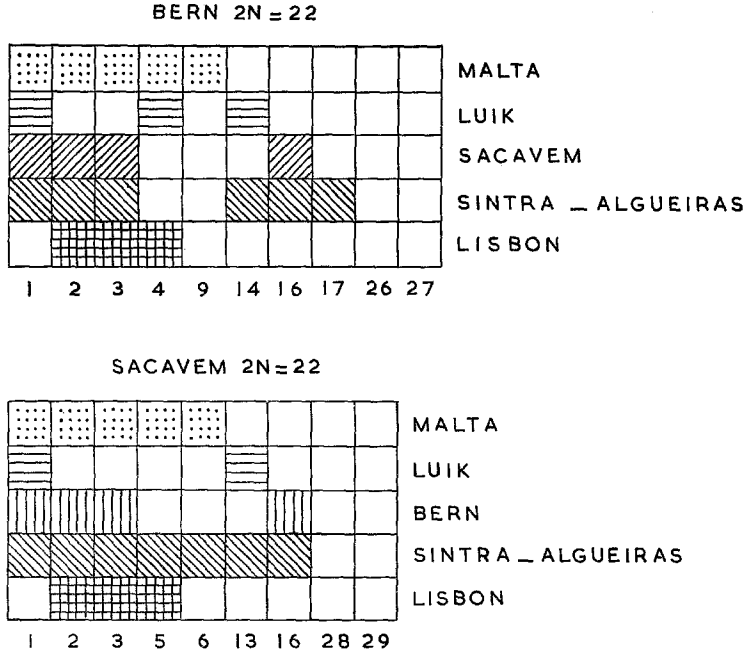

Fig. 14b. Karyogram of Bern and Sacavem.

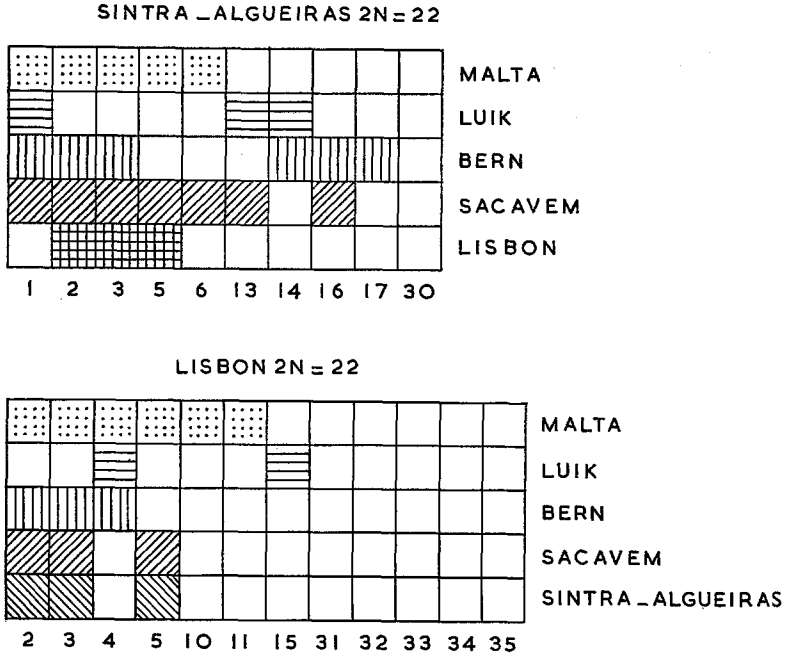

Fig. 14c. Karyogram of Sintra-Algueiras and Lisbon.

than two SAT-chromosomes are found in these types. This observation is quite in contrast to the observations recorded by YASUI (1940), which will be discussed in a later chapter. However, in fig. 8 apart from the two SAT-chromosomes seen, there are 3 chromosomes with a very small knoblike structure in their short arms, simulating satellites. As these have not been observed frequently in the metaphase plates examined and it is not certain whether they are really satellites, I refrain from including these under SAT-chromosomes. Perhaps this may be due to the fixation or to the pressure applied while squashing.

3. *Meiosis*

A. *Parents*. The meiosis is normal in all the types studied, except for some pecularities observed which are described separately.

i) Malta: At diakinesis, the pairing of chromosomes as bivalents has been observed. Some of these bivalents interlock themselves in groups of two each, giving an appearance of 'quadrivalents'. This

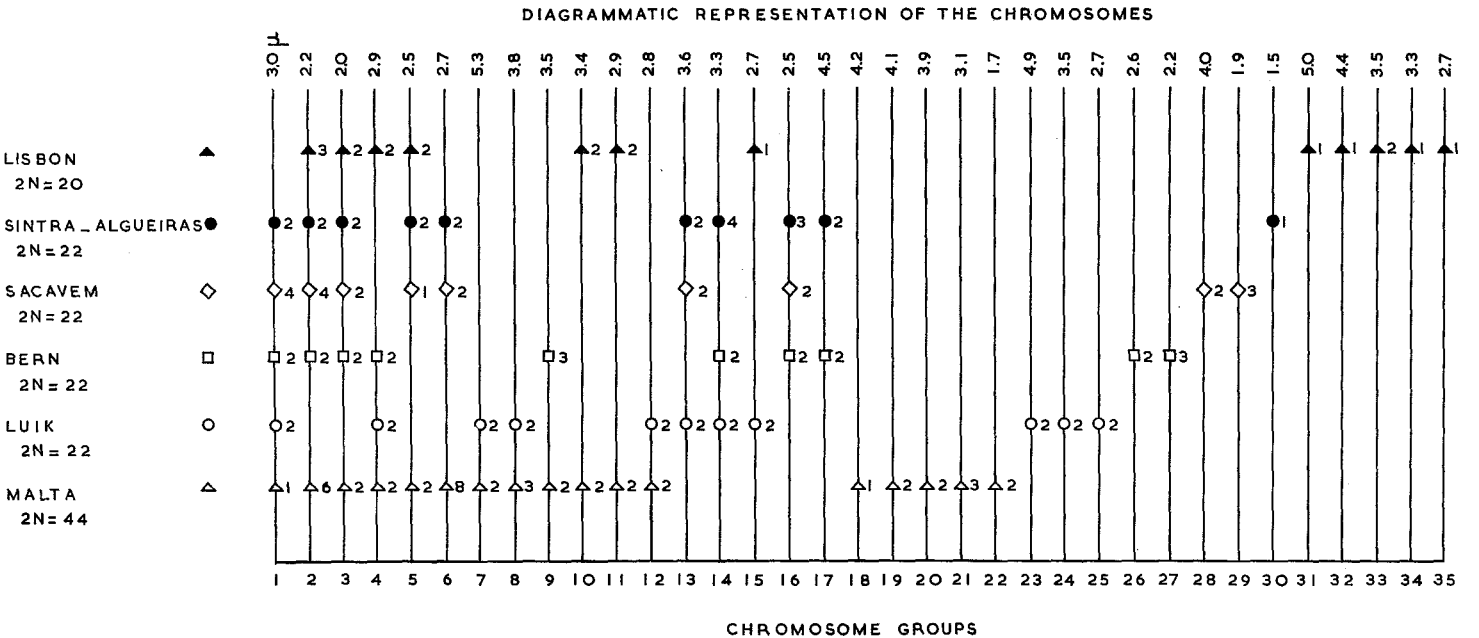

Fig. 14d. Digrammatic representation of chromosomes (karyogram).

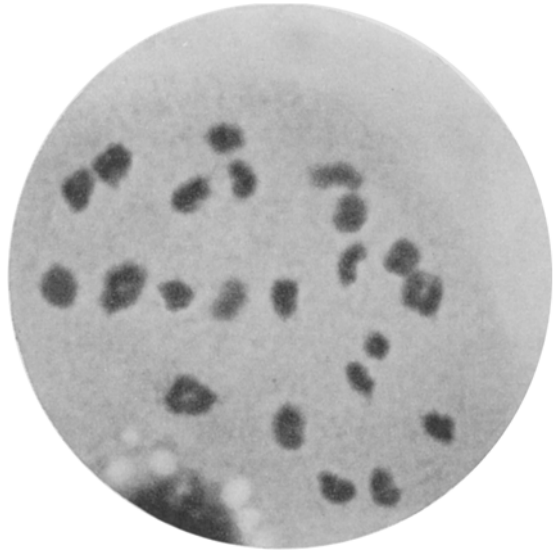

Fig. 15. Diakinesis in Malta 22_{II}. × 1411.

association does not continue until M–I as these interlocked bivalents separate themselves and behave as normal bivalents in the late diakinesis (fig. 15). There are 12 ring bivalents, 2 rod bivalents and 8 bivalents having end to end attachment. The frequency of these interlockings expressed in percentage is given in table 4.

TABLE 4. *Association in Malta*

S. No.	Associations *	Number of cells	Percentage
1	$4\text{‹}_{IV}\text{›} + 14_{II}$	10	10.5
2	$3\text{‹}_{IV}\text{›} + 16_{II}$	30	31.5
3	$2\text{‹}_{IV}\text{›} + 18_{II}$	45	47.4
4	$1\text{‹}_{IV}\text{›} + 20_{II}$	5	5.3
5	22_{II}	5	5.3
	Total	95	100.0

*) The interlocked bivalents are represented by the symbol 'IV' eventhough this symbol is used to denote a quadrivalent. Since it is not a true quadrivalent, it is shown within inverted commas. This method is adopted throughout – 'IV' for two interlocked bivalents, 'VI' for three interlocked, 'VIII' for 4 interlocked and 'X' for 5 interlocked bivalents.

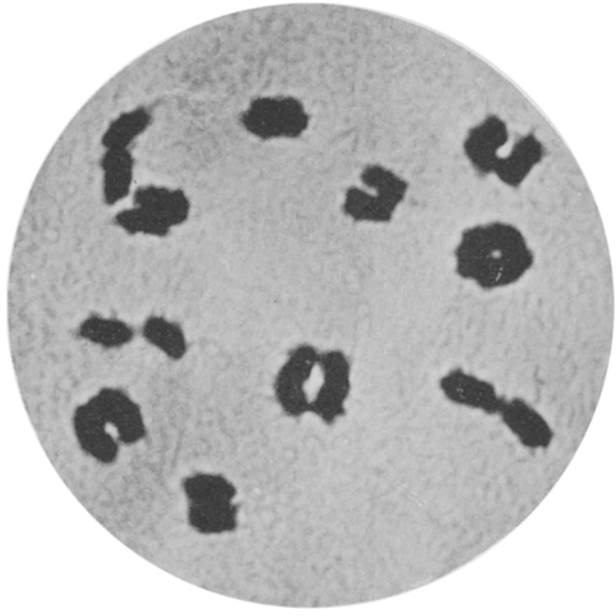

Fig. 16. Diakinesis in Luik 11_{II}. × 2116.

Disjunction of the bivalents is quite normal except for some few heterotypic bridges. In 16 percent of the M–I one to three bivalents behave as laggards and come to the equator late for disjunction. Towards the late anaphase the bridges disappear with the result that neither micronuclei nor any bridges have been observed in the interphase. The distribution of chromosomes in M–II has been found to be 22 + 22. A–II and T–II are normal except for a few equational bridges, the frequency of which is only 9.6 percent. The chromosomes that gave bridges later join the other chromosomes for the formation of normal tetrads. No micronuclei in tetrads have been observed.

ii) Luik: The eleven bivalents observed (fig. 16) at diakinesis are associated in the following manner: three ring bivalents with two terminal chiasmata each; four open rings with one terminalised and one non-terminalised chiasma each; three bivalents having one terminal chiasma each and one bivalent with side by side pairing involving two terminal and one interstitial chiasmata. No interlocking of bivalents has been observed. Fifty seven percent of the M–I are normal while twenty-two percent shows precocious division

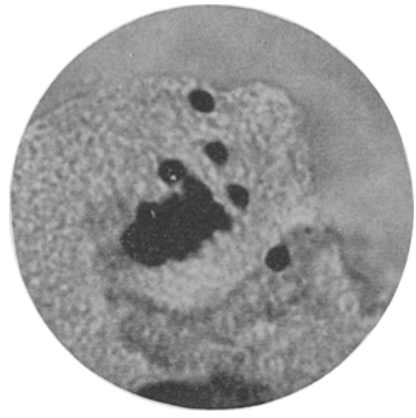

Fig. 17. M-I in Luik showing precocious division. × 1411.

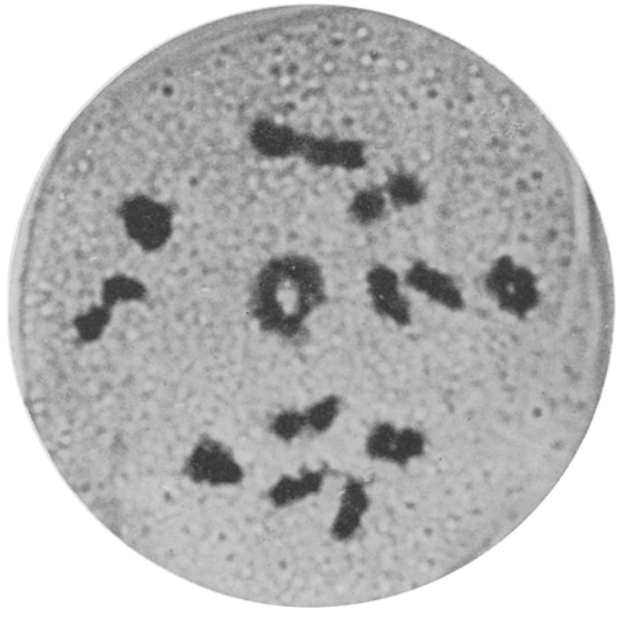

Fig. 18. Late diakinesis showing early 'detachment' of some bivalents. × 2116.

(fig. 17) and in ten percent one to two bivalents behave as laggards. One cell has been observed with precocious division of one bivalent and one bivalent behaving as a laggard. Disjunction of the bivalents with end to end attachment occurs even at the early diakinesis, so

much so, these pairs of daughter chromosomes can be mistaken for univalents (fig. 18). In A–I eighty percent of the cells has shown clean disjunction, whilst fourteen percent with one bridge, five percent with two bridges and one percent with three bridges. M–II is normal with eleven chromosomes each. Eighty-eight percent of the cells with M–II are normal; but in twelve percent there is precocious equational division of one dyad. Equational bridges to the extent of twelve percent have been observed in A–II, whilst eighty percent of the A–II have clean separation. All these laggards migrate to the poles to join with other chromosomes before tetrad formation is completed. Micronuclei in tetrads have not been observed.

iii) Bern. With the exception of the following peculiarities the meiosis otherwise is normal. The frequency of the interlocking association of the bivalents at diakinesis, expressed in percentage is given in table 5.

TABLE 5. *Associations in Bern*

S. No.	Associations	Number of cells	Percentage
1	$4_{\text{'IV'}} + 3_{II}$	1	0.8
2	$3_{\text{'IV'}} + 5_{II}$	7	5.7
3	$2_{\text{'IV'}} + 7_{II}$	82	66.0
4	$1_{\text{I'V'}} + 9_{II}$	25	20.2
5	11_{II}	9	7.3
	Total	124	100.0

Except for one 'quadrivalent' (association between one ring and one rod bivalents), the other 'quadrivalents' are formed always between two ring bivalents (fig. 19). The end to end attached (one terminal chiasma) bivalents are often found to separate in the late diakinesis. Seven percent of the cells examined shows eleven bivalents only at diakinesis. This is perhaps due to the separation of the 'quadrivalents' as bivalents towards the early M–I.

Even though higher association other than bivalents is formed, towards the late diakinesis all of them behave as normal bivalents. Only 13 percent of the M–I shows precocious division (11 percent for one bivalent and 2 percent for two bivalents) and in 7 percent one

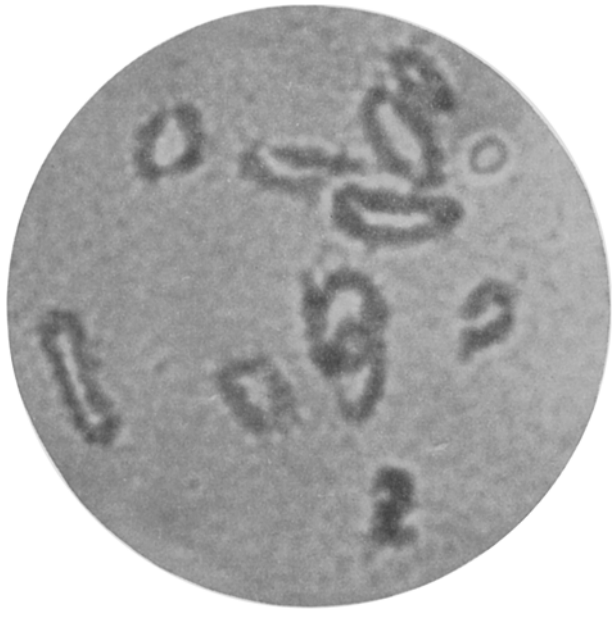

Fig. 19. Diakinesis in Bern $1_{\text{'IV'}} + 9_{\text{II}}$. × 2116.

TABLE 6. *Associations in Sacavem*

S. No.	Associations	Number of cells	Percentage
1	$3_{\text{'IV'}} + 5_{\text{II}}$	18	14.8
2	$2_{\text{'IV'}} + 7_{\text{II}}$	79	64.8
3	$1_{\text{'IV'}} + 9_{\text{II}}$	20	16.4
4	11_{II}	5	4.0
	Total	122	100.0

bivalent disjoins later, whilst the remaining 80 percent are normal. The frequency of bridges in A–I is only 19 percent for one bridge and 6 percent for two bridges. Only one cell with three bridges has been noticed out of 173 A–I analysed. Distribution of chromosomes in M–II is 11 + 11. In A–II, clean equational division is seen, except for 5 percent of the cells where one bridge is observed. Restitution nuclei have not been found in any of the tetrads.

iv) Sacavem. Some of the bivalents are found to associate in

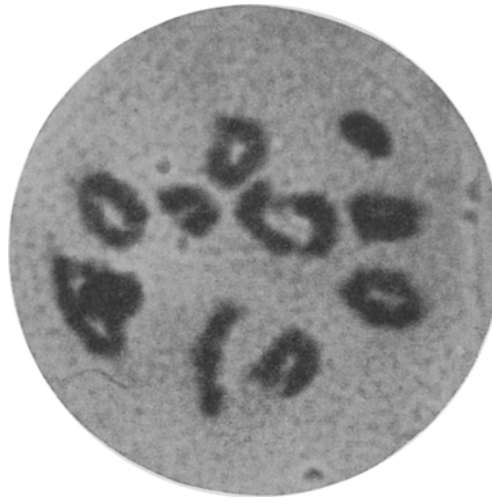

Fig. 20. Diakinesis in Sacavem $1_{'IV'} + 9_{II}$. × 2116.

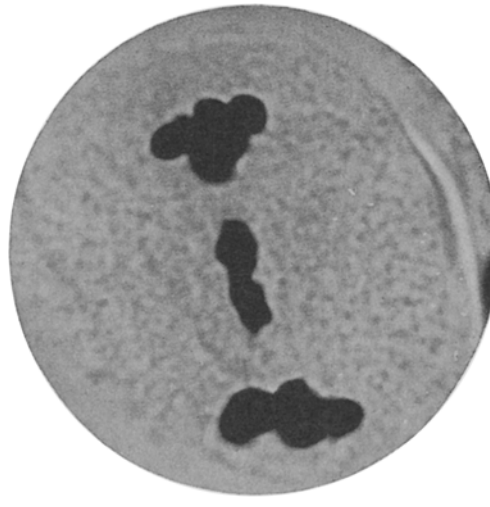

Fig. 21. Disjunction bridge in Sacavem. × 2116.

groups of two by interlocking, the frequency of which is given p. 33 (table 6).

The interlocked bivalents that are formed are invariably between two ring bivalents (fig. 20) except for one, where the interlocking is

always between one ring and one rod bivalents. Towards the late diakinesis the interlocked bivalents get separated as bivalents and in the succeeding stages they behave normally. No precocious division has been observed in M–I, but in 12 percent one bivalent is found to migrate late to the equator for disjunction. Fifteen percent of the A–I shows a disjunction bridge of one bivalent only (fig. 21); and perhaps this bivalent is the one which comes late to the equator for disjunction. The distribution of chromosomes in M–II is 11 + 11. Six percent of the interphase shows one chromosome lying by the side of one of the two nuclei; and perhaps this is due to the extreme lateness in reaching the pole before telophase nuclei are formed. But in M–II this chromosome behaves normally with the other chromosomes for the equational division, as no abnormalities have been observed. Ninetyfour percent of A–II shows clean separation whilst 6 percent shows bridges ranging from one to two. However, tetrad formation is normal without any micronuclei.

v) Sintra-Algueiras. This type has differed a little from the other

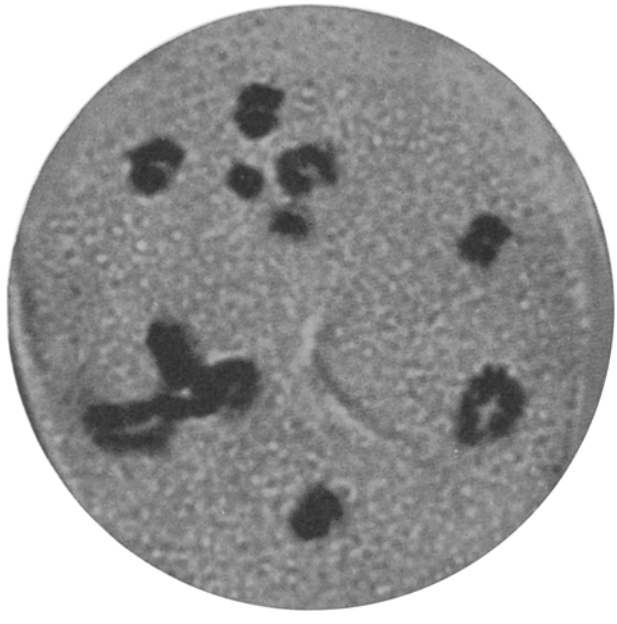

Fig. 22. Diakinesis in Sintra-Algueiras $1_{\text{'VIII'}} + 7_{II}$. Note one bivalent with end to end attachment has terminalized. × 2116.

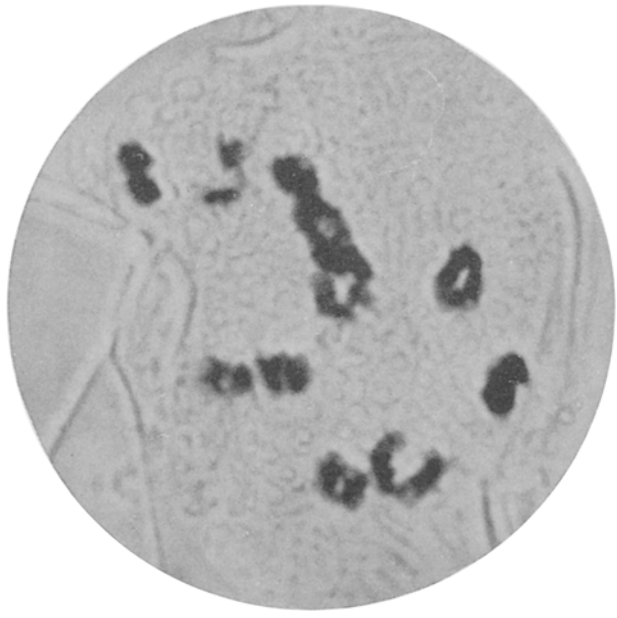

Fig. 23. Diakinesis in Sintra-Algueiras $1_{\text{'VI'}} + 8_{II}$. The 'sexivalent' is a chain of three ring bivalents. × 2116.

TABLE 7. *Associations in Sintra-Algueiras*

S. No.	Associations	Number of cells	Percentage
1	$1_{\text{'VIII'}} + 7_{II}$	3	1.7
2	$1_{\text{'VI'}} + 1_{\text{'IV'}} + 6_{II}$	6	3.5
3	$4_{\text{'IV'}} + 3_{II}$	2	1.2
4	$3_{\text{'IV'}} + 5_{II}$	10	5.9
5	$2_{\text{'IV'}} + 7_{II}$	62	36.5
6	$1_{\text{'IV'}} + 9_{II}$	49	28.8
7	11_{II}	38	22.4
	Total	170	100.0

parents, as higher associations other than interlocking of two bivalents are observed (figs. 22 and 23). Eventhough the percentage of these higher associations is very low, this indicates that the degree of affinity amongst the bivalents perhaps is greater. The percentage of

the frequency of the associations at diakinesis is presented in the preceding table 7.

The 'octavalent' and 'sexivalent' observed as chains of rings are the result of the additions of the ring bivalents to the 'quadrivalents' that are formed by the interlocking of two ring bivalents. When the 'octavalent' is present, no 'quadrivalents' are seen. Even that 'quadrivalent' between one ring and one rod bivalent which has been always observed, has not been found along with this 'octavalent'. One bivalent has been found to behave as a laggard in 24 percent of the M–I, examined. Occasionally (only three percent) two bivalents are seen behaving so. Precocious division of one bivalent with a frequency of 12 percent, has been observed. In A–I 91 percent of the cells is found to disjoin normally while nine percent shows one to two bridges. However, the distribution of chromosomes in M–II has been 11 + 11, as expected. In M–II about 26 percent of the cells show laggards of one to two chromosomes, while the rest are found to behave normally. Equational bridges amount only to about 11 percent. Normal tetrads without any restitution nuclei are formed.

vi) Lisbon. The meiosis is normal. Unlike in the other types no interlocking of bivalents to form higher 'associations' has been observed (fig. 24). Thin threads have been found to connect three bivalents as one group and another three as a second group whereas the rest – 4 bivalents are lying free in the cytoplasm. This pecularity is observed only in this type. Out of the 10 bivalents, three form rings with two terminal chiasmata each, three open rings with one terminalised and one non terminalised chiasmata each and the rest having one chiasma each (end to end attachment). Sixty five percent of the cells show in M–I precocious division of one to two bivalents (generally the end to end attached bivalents), whilst in 18 percent of the metaphase stages one ring bivalent behaves as a laggard (fig. 25). In most of the cases 3 to 4 bivalents (having one terminal chiasma) terminalise earlier when the other bivalents are still in the centre for disjunction. This early terminalisation can be seen even in the early diakinetic stage, so much so, these daughter chromosomes can be mistaken for univalents. The one to two lagging bivalents observed in M–I give disjunction bridges (one to two). M–II shows 10 chromosomes each. A–II is also normal except in a few cells 1–1 bridge is observed. Tetrad formation is normal.

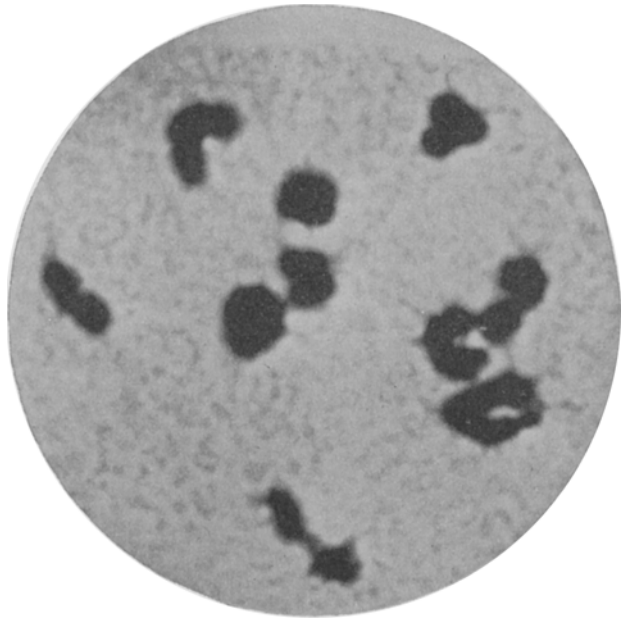

Fig. 24. Diakinesis in Lisbon 10_{II}. Note the fine threadlike structure connecting some of the bivalents. × 2116.

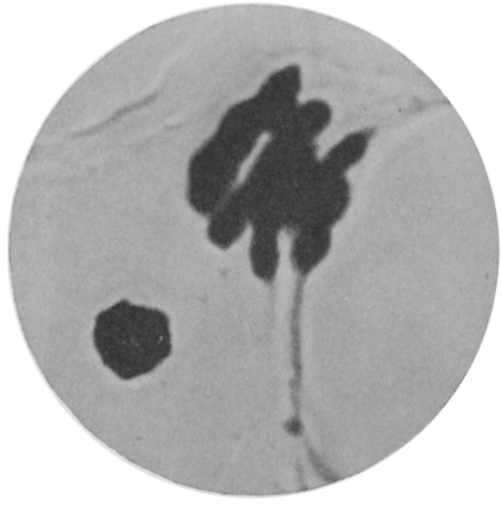

Fig. 25. M-I in Lisbon showing one ring bivalent as a laggard. × 2116.

B. *The F_1 Hybrids.* The hybrids are grouped based on the number of chromosomes of the parents concerned in the crosses. Thus the groupings are as follows:

a. Tetraploid × Diploid – 44 ♀ × 22 ♂ Malta with Luik, Bern, Sacavem, Sintra-Algueiras

b. Tetraploid × 'Nullisomic' 44 ♀ × 20 ♂ Malta with Lisbon

c. 'Nullisomic' × Diploid 20 ♀ × 22 ♂ Lisbon with Luik, Bern, Sacavem, Sintra-Algueiras

d. Diploid × Diploid 22 ♀ × 22 ♂

i) Luik with Bern, Sacavem, Sintra-Algueiras

ii) Bern with Sacavem, Sintra-Algueiras

iii) Sacavem with Sintra-Algueiras

The meiotic analysis of these groups is given separately as differences have been noticed between groups. Practically no differences in meiotic behaviour have been observed amongst the hybrids within one group; if otherwise, mention will be made when treating each group. Here, it is worthwhile to state that in groups a and b the hybrids are the result of an interspecific cross with different chromosome numbers; in group c, the F_1s are between two parents of the same species differing in chromosome number while group d consists of intraspecific hybrids of parents having the same chromosome number.

a. *Interspecific crosses (44 × 22)* – F_1 $2n = 33$

i) Malta × Luik $2n = 33$

ii) Malta × Bern $2n = 33$

iii) Malta × Sacavem $2n = 33$

iv) Malta × Sintra-Algueiras $2n = 33$

v) Luik × Malta (reciprocal) $2n = 33$

These hybrids show a constancy in the manner of pairing at diakinesis. It has been observed that $1_{III}' + 11_{II} + 8_{I}$ occur in all the cells examined (fig. 26c). The hybrid Malta × Sintra-Algueiras, however, differs a little from the other hybrids; apart from the pairing as one 'trivalent', eleven bivalents and eight univalents, different other types of associations are met with (fig. 27). The frequency of these associations calculated in percentage is indicated in table 8.

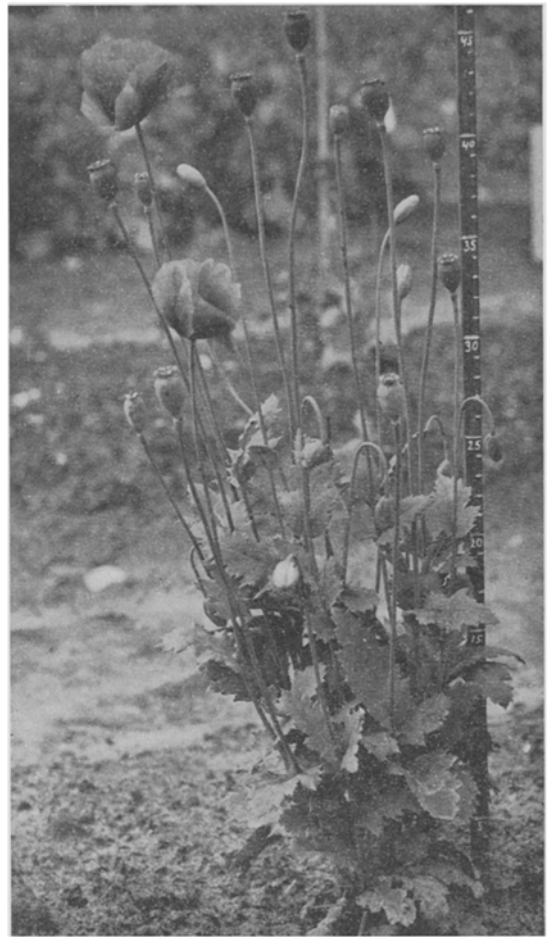

Fig. 26a. Malta × Bern. F_1-hybrid. Note the F_1 is more like Malta.

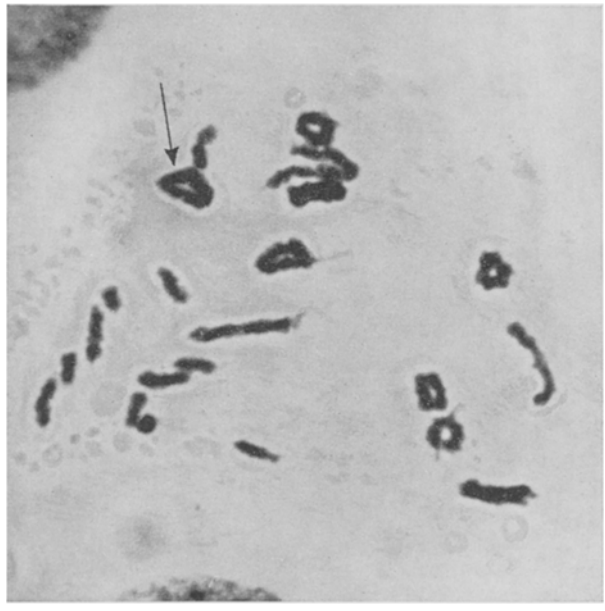

Fig. 26b. Malta × Bern showing $1_{\text{'III'}} + 11_{\text{II}} + 8_{\text{I}}$. The 'trivalent' is between a ring bivalent and an univalent. Univalents are rodlike. × 1411.

It can be seen from the above table that the percentage of higher associations is very low while the percentage of the univalents is higher. However, the minimum number of univalents noticed (three only) indicates that a certain degree of autosyndesis takes place apart from the allosyndesis between the chromosomes of Malta and Sintra-Algueiras. But the cells with $12_{\text{II}} + 9_{\text{I}}$ give a positive indication that all the higher associations tend to separate into either as bivalents or as univalents in late diakinesis. In a few cases 11 univalents are noticed. This may perhaps be due to the precocious division of one bivalent. The 11 bivalents also observed in the other hybrids are perhaps due to the result of pairing between the 11 chromosomes of Malta with the 11 chromosomes of the other parent concerned in the cross, or due to autosyndesis amongst the chromosomes of either parent. The formation of a 'trivalent' is not typical as it is between a bivalent and an univalent wherein the univalent always gets separated from the bivalent even before M–I.

One to two bivalents seem to disjoin precociously. At metaphase

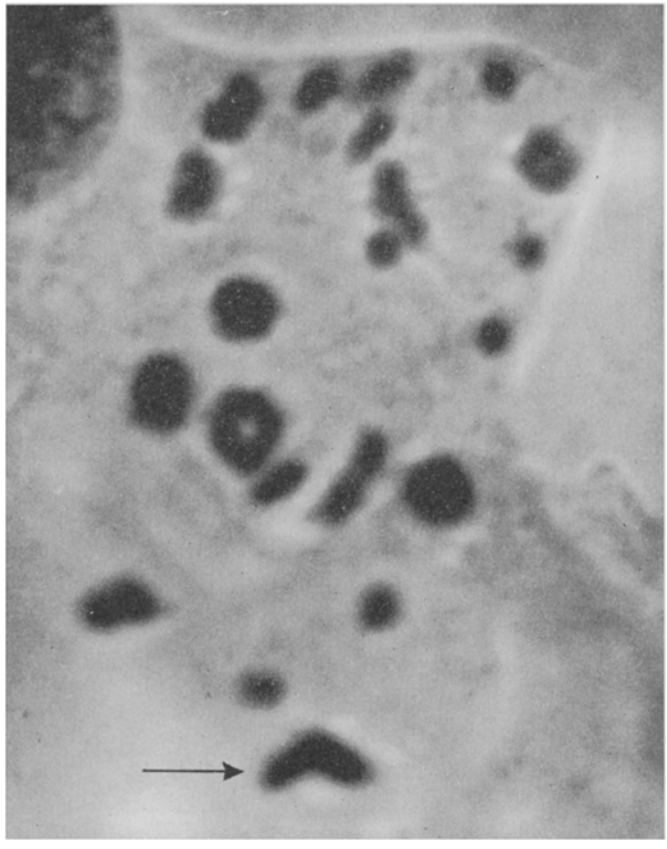

Fig. 26c. $1_{\cdot III'} + 11_{II} + 8_{I}$. Note the univalents are spherical. × 2116.

the bivalents migrate to the equator for disjunction, whilst the univalents remain scattered in the cytoplasm away from the centre. Figure 28 shows the side view of M–I where the 9 univalents can be seen lying in the cytoplasm, away from the equator. Once all the bivalents have disjoined, the univalents move to the equator for the homeotypic division. Only a very few cells show no division of the univalents. Hence in the M–I both hetero- and homeotypic divisions are found to occur (fig. 29). In A–I the disjoined chromosomes and the homeotypically divided chromosomes migrate to the poles without any lagging. In a few cases the equational bridges caused by the division of the univalents are seen, but they break off

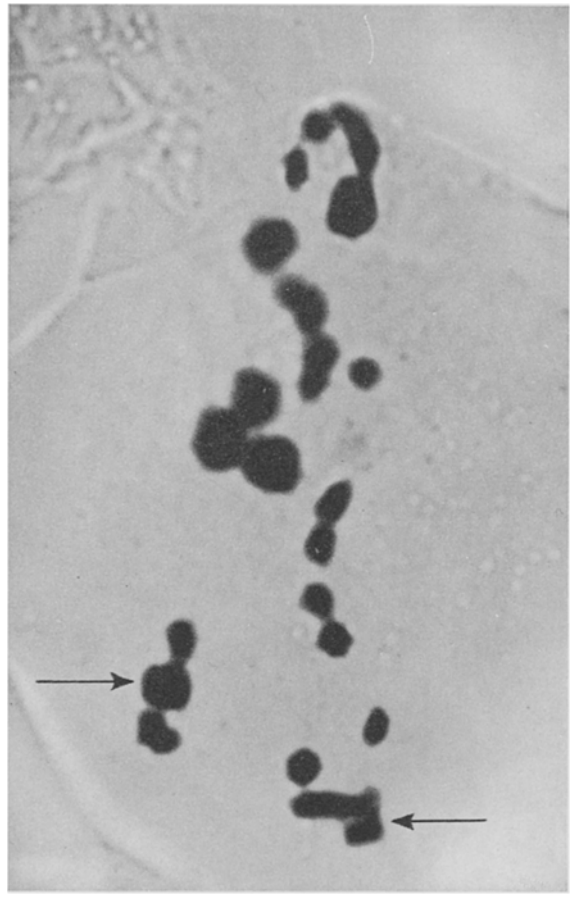

Fig. 27. Malta × Sintra-Algueiras $2'_{III} + 12_{II} + 3_{I}$. × 2116.

to join the telophase nuclei. Disjunction bridge has not been observed as complete terminalisation can be attained during the time the univalents divide. The distribution of chromosomes in the poles as a result of heterotypic and homeotypic division of the twelve bivalents and nine univalents in A–I, is (12 + 9) and (12 + 9). The interphase does not show any micronuclei in all the hybrids except in the F_1 Malta × Sintra-Algueiras where some irregularities are noticed. In this cross sixty-two percent of the interphase is normal with two nuclei, while in the rest one to four

TABLE 8. *Associations in the F_1-hybrid between Malta and Sintra-Algueiras* (96 PUCs) (*cross IV*)

S. No.	Association					Total chromosomes	Percent
	'VI'	'IV'	'III'	II	I		
1	1	2	2	2	9	33	6.3
2	1	2	—	5	9	33	6.3
3	—	3	1	5	8	33	6.3
4	—	3	—	9	3	33	6.3
5	—	3	—	5	11	33	6.3
6	—	1	2	9	5	33	6.3
7	—	—	2	12	3	33	12.5
8	—	1	1	9	8	33	12.5
9	—	—	1	11	8	33	30.9
10	—	—	—	12	9	33	6.3

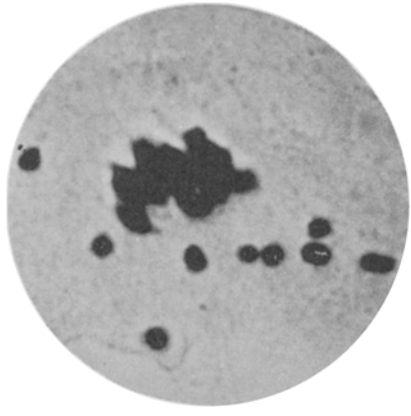

Fig. 28. M-I showing the bivalents in the equator and univalents (9) in the periphery. × 1411.

chromosomes are found left in the cytoplasm. Evidently this is due to the failure of the chromosomes derived from the division of the univalents in A–I, to get included in the nuclei. The bridge observed in A–I can be traced even in M–II in 78 percent of the cells examined.

The A–II is highly irregular in all the hybrids. Only the 12 chromo-

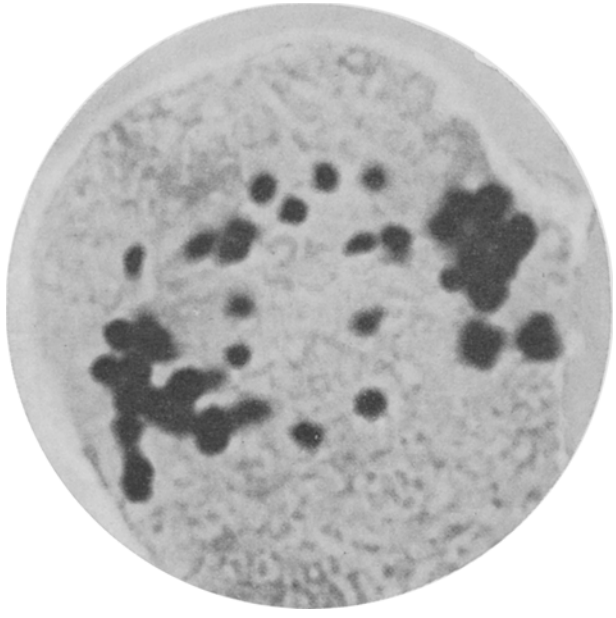

Fig. 29. Homeotypic division of univalents in A-I. × 2116.

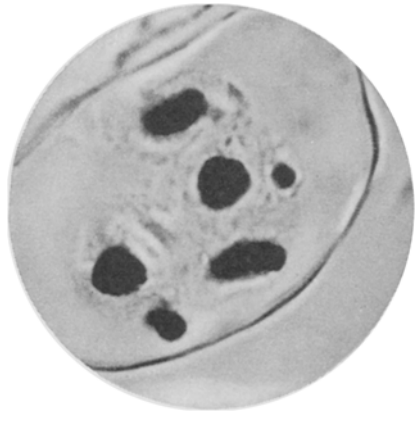

Fig. 30. Tetrad with two micronuclei. × 1411.

somes divide equationally and might migrate to the poles in the normal way. But the nine chromosomes resulted from the homeotypic division of the univalents in A–I, are found to lie in the equator instead of migrating to either of the poles. Towards the beginning of

telophase, some of these chromosomes behave as laggards and are left in the cytoplasm rather than being included into one of the nuclei. Later, these laggards form themselves into micronuclei ranging from one to six in a tetrad (fig. 30), making the tetrads non-functional pollengrains. The distribution of chromosomes as a result of A–II cannot be determined exactly as it has been found difficult to distinguish the identity of some of the chromosomes. The frequency of tetrads with micronuclei is given in table 9.

TABLE 9. *Percentage of normal tetrads and of tetrads with micronuclei*

F_1 44 × 22	Number of tetrads	Normal tetrads	Tetrads with micronuclei				Total tetrads with micro-nuclei	Mean fertility
			1	2	3	4		
Malta × Bern	62	12.9	45.2	27.4	11.3	3.2	87.1	$\bar{x}$ 10.34 ± 5.09
Malta × Sacavem	78	14.1	47.5	20.5	12.8	5.1	85.9	$\bar{x}$ 3.33 ± 3.11
Malta × Sintra-Algueiras	50	40.0	44.0	14.0	—	2.0	60.0	$\bar{x}$ 3.51 ± 2.85
Malta × Luik	46	30.4	43.5	19.6	2.2	4.3	69.6	$\bar{x}$ 7.53 ± 6.47
Luik × Malta	50	44.0	32.0	18.0	6.0	—	56.0	$\bar{x}$ 6.69 ± 8.18

b. *Interspecific crosses (44 × 20)* – F_1 2n = 32 (fig. 31)

i) Malta × Lisbon 2n = 32

ii) Lisbon × Malta (reciprocal) 2n = 32.

The meiotic behaviour of these hybrids differs a little from the other F_1's mentioned under group a, as these have shown constantly at diakinesis 2 'trivalents', 10 bivalents and 6 univalents. No higher association other than the 'trivalents' has been observed. The formation of 10 bivalents indicates that perhaps the 10 chromosomes of Lisbon pair with 10 of Malta or autosyndesis occurs amongst the chromosomes of either of the parents. Apart from the 10 bivalents, the appearance of 2 'trivalents' gives a positive evidence of auto-

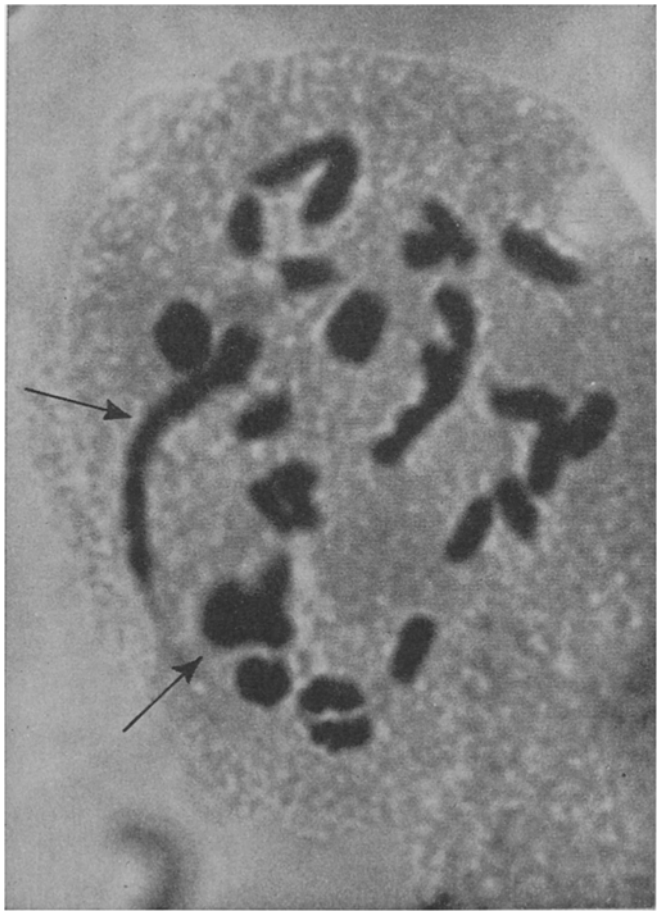

Fig. 31. Diakinesis. $2_{\text{'III'}} + 7_{II} + 12_{I}$. × 2116.

syndesis to some degree. The number of univalents being six, is almost constant at diakinesis but towards M–I often another six to ten solitary chromosomes are found besides these univalents, either due to precocious division of three bivalents or due to the 'detachment' of the chromosomes that gave 'trivalents' (fig. 32a, b). The M–I shows cases of precocious division of the bivalents and disappearance of the 'trivalents'. Only in a few cases (8 percent) the univalents are found to migrate at random to the poles while the rest have homeotypic division in A–I. The percentage of the frequency

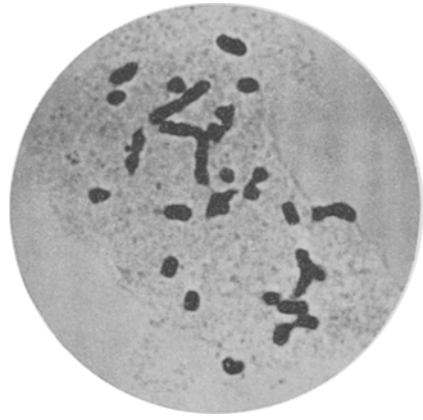

Fig. 32a. $8_{II} + 16_{I}$. showing early terminalisation in five bivalents. × 1058.

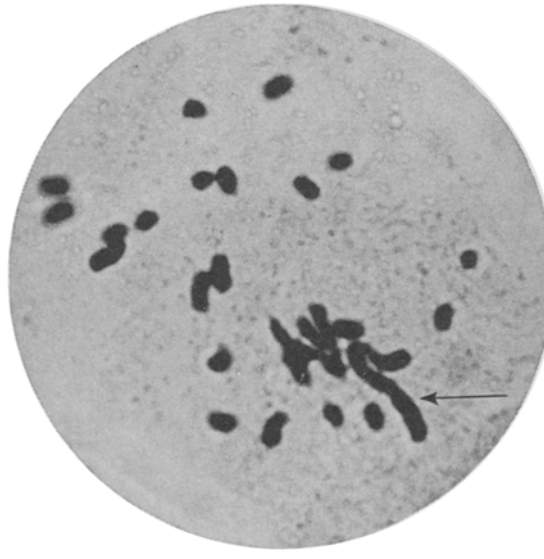

Fig. 32b. Showing early terminalisation in many bivalents. Note the 'trivalent' in the form of a chain. × 1411.

of migration observed in a few cells is: 5 + 1 – 10.0%, 4 + 2 – 46.6% and 3 + 3 – 43.4 percent. Evidently this migration has also influenced a little the frequency of the distribution of the chromosomes in A–I.

The bivalents disjoin normally. When all the bivalents have

completely disjoined, the univalents migrate to the equator for the homeotypic division. In late anaphase, equational bridges caused by the univalents, range from five to one, the frequency of which is mentioned in the following table 10.

This bridge can be traced out even in M–II in the 41 percent of the M–II examined (fig. 33). Here, the bridge appears to be only a connecting strand between the two dyads at their proximal ends. A–II is highly irregular as bridges and laggards are observed. The

TABLE 10. *Frequency of bridges in the hybrid Malta × Lisbon and its reciprocal* in A-I (106 cells)

Hybrid	Normal	Bridges					
		5	4	3	2	1	Total
i Malta × Lisbon	57.5	1.9	5.6	14.2	18.9	1.9	42.5
ii Lisbon × Malta	59.0	—	2.6	17.3	20.1	1.0	41.0

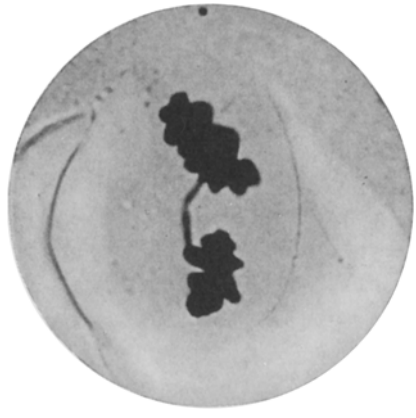

Fig. 33. M-II connected with a bridge. × 1411.

frequency of these bridges calculated in percentage is presented in table 11.

As the daughter chromosomes of the univalents do not divide, but behave only as laggards in A–II, the bridges observed at this stage are from the equational division of the chromosomes derived from disjunction. However, towards the late anaphase the bridges disappear, but some of the laggards instead of migrating to the poles and joining the telophase nuclei, remain in the cytoplasm and form

TABLE 11. *Frequency of bridges observed in anaphase II* (95 cells)

Hybrid	Normal	Bridges							
		*5-3	3–2	3–1	2–2	2–1	1–1	1–0	Total
i Malta × Lisbon	10.5	26.3	10.5	5.3	26.3	5.3	—	15.8	89.5
ii Lisbon × Malta	8.7	—	14.3	7.2	12.4	15.7	16.3	25.4	91.3

*) These numbers indicate the bridges observed in the equational division in A-II.

TABLE 12. *Frequency of normal tetrads and tetrads with micronuclei in the hybrid Malta × Lisbon and its reciprocal*

Hybrid	Number of tetrads	Normal tetrads	Tetrads with micronuclei			Total tetrads with micro-nuclei	Mean fertility
			1	2	3		
Malta × Lisbon	80	41.2	36.2	18.8	3.8	58.8	$\bar{\times}$ 6.48 ± 4.66
Lisbon × Malta	96	18.8	56.3	18.8	6.1	81.2	$\bar{\times}$ 0.77 ± 0.86

themselves into micronuclei. It is rather difficult to determine the exact number of chromosomes included in the telophase nuclei, as most of the chromosomes lose their identity. Only 41 percent has given normal tetrads whilst in the rest, micronuclei ranging from one to three, and of different sizes have been observed, the frequency of which is presented in table 12. These micronuclei together with the tetrads having chromosomes less than the absolute minimum required for the functioning of the normal pollengrains, have contributed to the formation of sterile pollen grains.

c. *Intraspecific crosses (20 × 22)*

i) Lisbon × Luik 2n = 21
ii) Lisbon × Bern 2n = 21
iii) Lisbon × Sacavem 2n = 21
iv) Lisbon × Sintra-Algueiras 2n = 21
v) Luik × Lisbon (reciprocal) 2n = 21

The meiosis of these hybrids is quite interesting and differs much from the meiotic behaviour of other hybrids treated under groups a

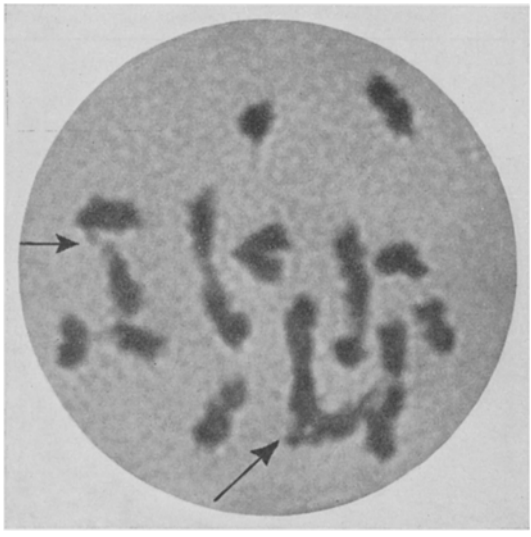

Fig. 34. Lisbon × Luik $2_{\text{III}'} + 5_{\text{II}} + 5_{\text{I}}$. × 2116.

and b. The course of meiosis is the same in all the hybrids of this group. However, differences are noticed in the pairing of chromosomes which vary much from one hybrid to the other, at diakinesis. Hence the diakinetic stage of each hybrid is described separately.

i) Lisbon × Luik (fig. 34). In an examination of 100 diakinetic stages, various types of synapsis as mentioned in table 13, are met with.

In all these higher associations very weak pairing is seen as the chiasmata formed are only terminal. Even in the 'decavalent' this type of synapsis is observed, as this invariably breaks off into bivalents or into univalents. In most of the cells either due to precocious terminalisation of the bivalents or due to 'detachments' that occur in the higher associations, the number of univalents range from 2 to 17.

ii) Lisbon × Bern. This hybrid gives still more combinations in synapsis than the other hybrid described above. The many types of associations seen at diakinesis, the frequency of which is estimated in percentage, are given in the following table 14.

From the above table it is seen that higher associations other than bivalents are frequent. These have been found to be temporary,

TABLE 13. *Associations in the hybrid Lisbon × Luik* (100 PMCs)

S. No.	Association						Total chromosomes	Percentage
	'X'	'VI'	'IV'	'III'	II	I		
1	1	—	—	—	4	3	21	3
2	—	1	2	—	3	1	21	8
3	—	1	1	—	2	7	21	3
4	—	2	—	—	1	7	21	3
5	—	1	—	—	6	3	21	5
6	—	1	—	1	5	2	21	6
7	—	1	1	1	3	2	21	6
8	—	—	—	2	5	5	21	8
9	—	1	1	—	—	11	21	1
10	—	—	2	1	3	4	21	3
11	—	—	2	—	5	3	21	7
12	—	—	1	—	8	1	21	4
13	—	—	1	—	5	7	21	3
14	—	—	1	2	3	5	21	3
15	—	—	1	—	6	5	21	6
16	—	—	1	1	4	6	21	1
17	—	—	—	—	10	1	21	8
18	—	—	—	—	8	5	21	3
19	—	—	—	—	7	7	21	6
20	—	—	—	—	5	11	21	6
21	—	—	—	—	4	13	21	1
22	—	—	—	—	2	17	21	6

as towards metaphase most of them have separated and behave as typical bivalents (fig. 35). Only one out of 100 cells has given one 'decavalent'. One fifth of the total number of cells has shown only one univalent, indicating that at least one chromosome often fails to pair. However, even this chromosome is observed to pair, as in 17 percent of the cells no univalent has been met with.

iii) Lisbon × Sacavem. Unlike the other hybrids, this hybrid gives only a very few types of associations during diakinesis. The frequency estimated in percentage is indicated in table 15.

The 'sexivalent' which has been observed in 35 percent of the cells, has not been found in either of the parents at diakinesis (fig. 36). Thirty percent of the diakinesis stages show associations not higher than bivalents, thereby indicating that the higher associations are having only mere 'attachments' not involving in the type of synapsis

TABLE 14. *Associations in the hybrid Lisbon × Bern* (100 PMCs)

S. No.	Association						Total number of chromosomes	Percentage
	'X'	'VI'	'IV'	'III'	II	I		
1	1	—	—	—	3	5	21	1
2	—	2	1	—	2	1	21	1
3	—	2	1	—	1	3	21	1
4	—	2	—	1	2	2	21	2
5	—	2	—	—	3	3	21	2
6	—	1	2	1	1	2	21	1
7	—	1	2	—	3	1	21	1
8	—	1	2	—	2	3	21	1
9	—	1	1	2	2	1	21	1
10	—	1	1	1	4	—	21	3
11	—	1	1	1	3	2	21	7
12	—	1	1	—	4	3	21	3
13	—	1	1	—	5	1	21	5
14	—	1	—	3	2	2	21	2
15	—	1	—	2	4	1	21	3
16	—	1	—	2	3	3	21	2
17	—	1	—	1	5	2	21	7
18	—	1	—	1	4	4	21	4
19	—	1	—	—	7	1	21	7
20	—	1	—	—	6	3	21	5
21	—	—	3	1	3	—	21	4
22	—	—	3	1	2	2	21	1
23	—	—	2	1	5	—	21	7
24	—	—	2	1	4	2	21	12
25	—	—	2	1	2	6	21	2
26	—	—	2	—	6	1	21	1
27	—	—	1	3	4	—	21	1
28	—	—	1	2	5	1	21	1
29	—	—	1	2	4	3	21	1
30	—	—	1	2	2	7	21	1
31	—	—	1	1	7	—	21	2
32	—	—	1	1	4	6	21	1
33	—	—	1	—	7	3	21	3
34	—	—	1	—	6	5	21	1
35	—	—	—	1	6	6	21	1
36	—	—	—	1	5	8	21	1
37	—	—	—	—	9	3	21	1

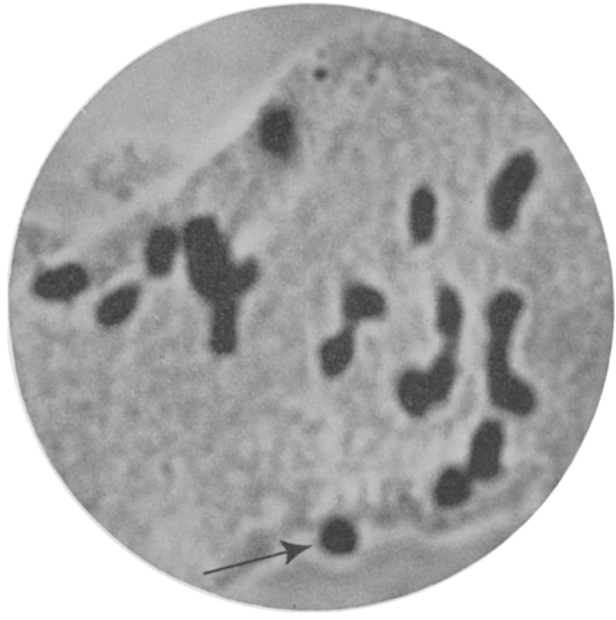

Fig. 35. M-I in Lisbon × Bern. 6_{II} + 8 dyads + one univalent. × 2116.

TABLE 15. *Associations in the hybrid Lisbon × Sacavem* (100 PMCs)

S. No.	Association					Total number of chromosomes	Percentage
	'VI'	'IV'	'III'	II	I		
1	1	—	1	3	6	21	35
2	—	2	—	2	5	21	9
3	—	2	1	4	2	21	10
4	—	1	3	3	2	21	8
5	—	1	2	4	3	21	8
6	—	—	—	9	3	21	9
7	—	—	—	8	5	21	21

generally found in the 'trivalent' or in the 'quadrivalent'. The minimum number of univalents (2) has been observed in 43 percent of the cells.

iv) Lisbon × Sintra-Algueiras. Only three types of associations are met with, namely $3_{'IV'} + 4_{II} + 1_I$, $1_{'III'} + 8_{II} + 2_I$ and $8_{II} + 5_I$ (fig. 37), whose frequency percentages are 22.0, 27.4 and 50.6 re-

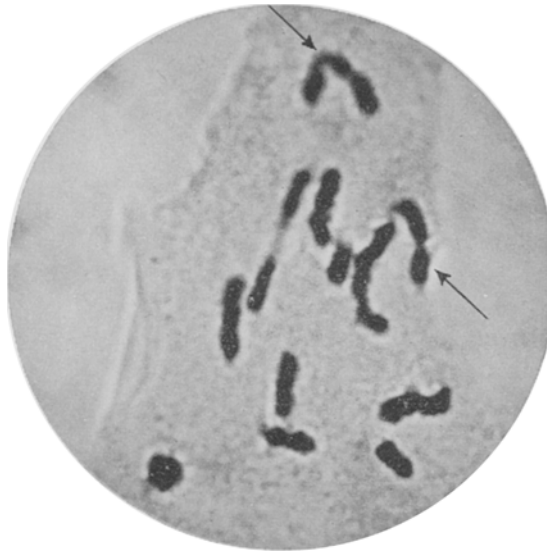

Fig. 36. Diakinesis in Lisbon × Sacavem $1_{\text{'VI'}} + 1_{\text{'III'}} + 3_{\text{II}} + 6_{\text{I}}$. × 1411.

Fig. 37. Diakinesis in Lisbon × Sintra-Algueiras $8_{\text{II}} + 5_{\text{I}}$. × 2116.

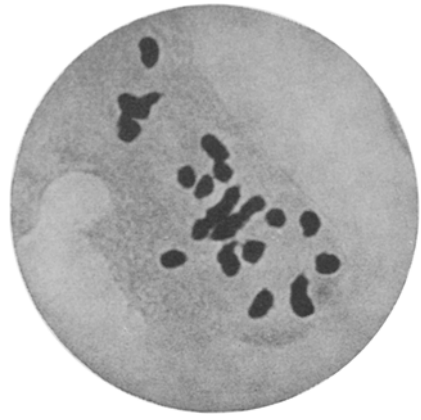

Fig. 38. Metaphase-I. × 1058.

TABLE 16. *Associations in the hybrid Luik × Lisbon* (100 PMCs)

S. No.	Association						Total number of chromosomes	Percentage
	'VI'	'IV'	'IV' + I *	'III'	II	I		
1	1	2	—	—	3	1	21	14
2	1	1	—	—	5	1	21	8
3	—	3	—	—	4	1	21	6
4	—	2	—	—	6	1	21	20
5	—	1	1	—	6	—	21	3
6	1	—	—	—	7	1	21	3
7	—	1	—	—	8	1	21	31
8	—	—	1	—	8	—	21	3
9	—	1	—	1	7	—	21	6
10	—	—	—	3	5	2	21	6

*) An univalent is found to associate with two interlocked bivalents.

spectively. The presence of one univalent in all the cells shows that this particular chromosome does not have any tendency to pair. Here also, the higher associations break off into bivalents towards the late diakinesis (fig. 38).

v) Luik × Lisbon (Reciprocal). This reciprocal hybrid behaves in a quite different way than the other way cross, at diakinesis. When 22 types of pairing have been observed in the hybrid, the reciprocal gives only 10 types of combinations in synapsis. In table 16 the pairing combinations are given.

The bridges (fig. 39), observed due to the delay in terminalisation of the bivalents in A–I, have influenced the distribution of chromosomes in the dyads (table 17). The behaviour of the univalent has not been precisely observed as the univalent can not be identified in the midst of the dyads resulted from the precocious division of some of the bivalents. The frequency of the distribution of chromosomes estimated from M–II is mentioned in table 18 (fig. 40a–c).

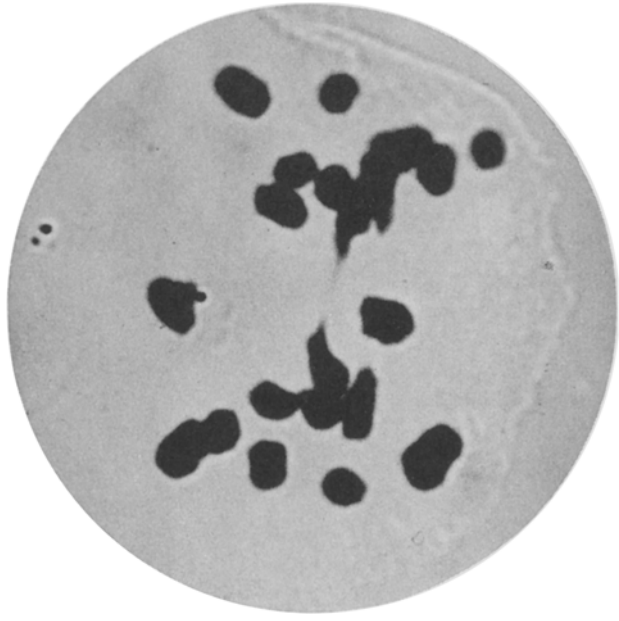

Fig. 39. Anaphase-I with one disjunction bridge. × 2116.

TABLE 17. *Frequency of bridges in the hybrids*

S. No.	Hybrid	Normal	Bridges				Total %	Total cells
			1	2	3	4		
1	Lisbon × Luik	43.0	44.0	12.0	0.5	0.5	57.0	197
2	Lisbon × Bern	47.4	30.6	15.0	4.1	2.9	52.6	173
3	Lisbon × Sacavem	27.1	36.8	21.1	13.5	1.5	72.9	133
4	Lisbon × Sintra-Algueiras	66.9	29.2	3.2	0.7	—	33.1	157
5	Luik × Lisbon	41.0	36.0	15.0	7.0	1.0	59.0	100

TABLE 18. *Frequency of distribution of chromosomes as a result of A-I* (100 cells)

S. No.	Hybrid	11 + 10	12 + 9	13 + 8
1	Lisbon × Luik	44	44	12
2	Lisbon × Bern	45	44	11
3	Lisbon × Sacavem	59	36	5
4	Lisbon × Sintra-Algueiras	82	13	5
5	Luik × Lisbon	73	27	—

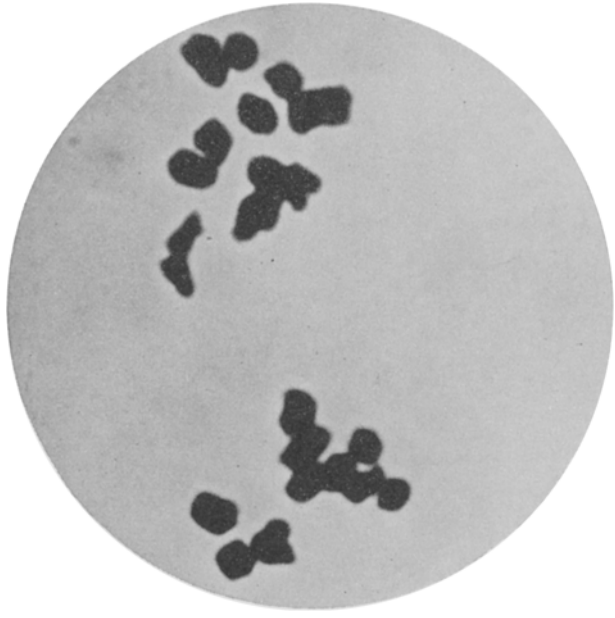

Fig. 40a. Distribution of dyads in A-I. 10 + 11. × 2116.

Apart from the high frequency of unequal distribution of 12 + 9 and 13 + 8, it has been observed that in many cases one chromosome is left in the cytoplasm rather than being included into one of the interphase nuclei (fig. 41). Perhaps this chromosome may be the univalent observed in the diakinesis. In addition to this, the bridge in the heterotypic division is found to have been retained in the M–II and in some cases even until late telophase II. The frequencies of these abnormalities are presented in table 19.

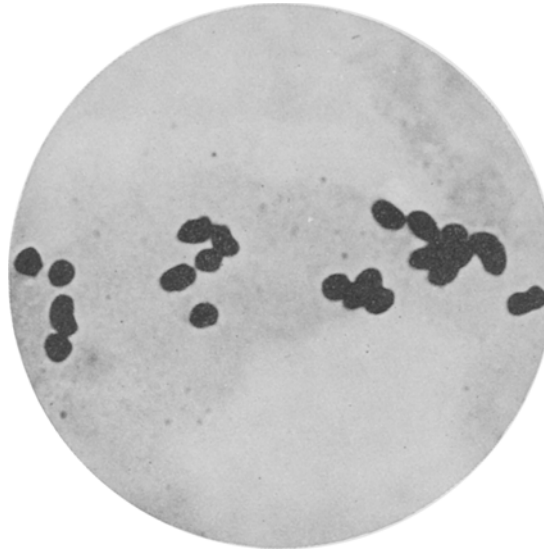

Fig. 40b. Distribution of dyads in A-I. 12 + 9. × 1411.

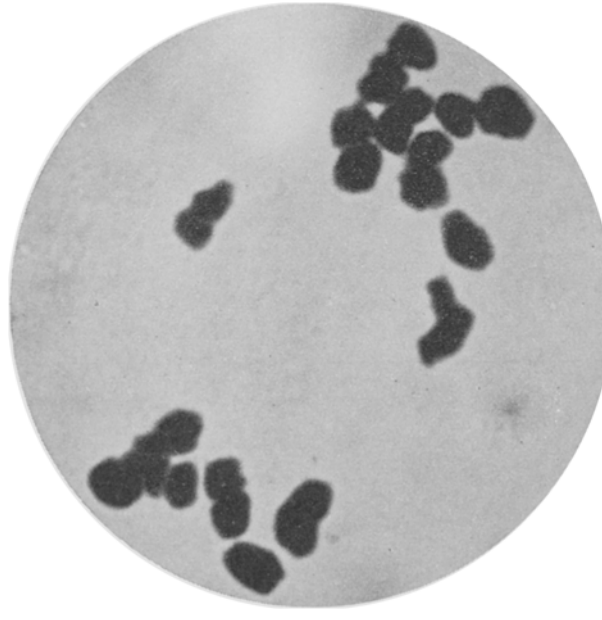

Fig. 40c. Distribution of dyads in A-I. 13 + 8. × 2116.

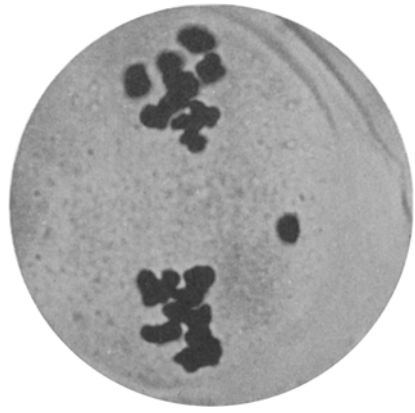

Fig. 41. Interphase showing the univalent in the cytoplasm. × 1411.

TABLE 19. *Frequency of abnormalities found in interphase and M-II* (100 cells)

S. No.	Hybrid	Percentage of interphases with one micronucleus observed	Percentage of M-II connected with the bridge of A-I
1	Lisbon × Luik	25	51
2	Lisbon × Bern	30	40
3	Lisbon × Sacavem	—	28
4	Lisbon × Sintra-Algueiras	24	29
5	Luik × Lisbon	22	48

TABLE 20. *Frequency of bridges observed in A-II*

S. No.	Hybrid	Normal	Bridges						
			4–0	3–3	2–2	2–1	2–0	1–1	1–0
1	Lisbon × Luik	50.0	—	—	—	0.9	—	14.6	34.5
2	Lisbon × Bern	44.9	0.8	—	3.1	4.7	2.3	14.7	29.5
3	Lisbon × Sacavem	63.0	—	1.0	—	4.0	3.0	13.0	16.0
4	Lisbon × Sintra-Algueiras	68.0	—	—	—	—	—	4.0	28.0
5	Luik × Lisbon	54.0	—	—	—	2.1	—	16.4	27.5

M–II is found to be normal in all the hybrids. But the A–II shows equational bridges in all the hybrids. The percentage of these bridges resulting from the homeotypic division is given in table 20.

The disturbances met with in A–II have directly contributed to the occurrence of many restitution nuclei in tetrads. These bridges in most of the cases are found to retain till late telophase. When once the cytokinesis begins, the daughter chromosomes connected by the equational bridges break off and form themselves into micronuclei, as they fail to get included into the nuclei of the tetrads due to the inordinate delay. The percentage of the frequency of the restitution nuclei observed in the tetrads has been estimated and presented in table 21.

TABLE 21. *Frequency of normal tetrads and tetrads with micronuclei*

F_1 20 × 22	Number of tetrads	Normal tetrad %	Tetrads with micronuclei					Mean fertility
			1	2	3	4	Total %	
Lisbon × Bern	117	76.0	19.7	4.3	—	—	24.0	$\bar{\times}$ 1.3 ± 0.81
Lisbon × Sacavem	103	68.9	24.3	5.8	1.0	—	31.1	$\bar{\times}$ 2.36 ± 1.81
Lisbon × Sintra-Algueiras	145	31.0	27.6	35.9	3.5	2.0	69.0	$\bar{\times}$ 3.43 ± 1.77
Lisbon × Luik	185	69.6	30.4	—	—	—	30.4	$\bar{\times}$ 1.99 ± 1.18
Luik × Lisbon	100	81.0	9.0	6.0	3.0	—	19.0	$\bar{\times}$ 3.99 ± 2.26

Amongst the normal tetrads, most of them are unequal in size, probably due to the varying number of chromosomes present. The final distribution of chromosomes in tetrads is rather difficult to estimate as most of the chromosomes lose their identity. These micronuclei evidently have formed into sterile pollengrains.

d. *Intraspecific crosses of parents having the same chromosome*

number – (22 × 22)

i)	Luik × Bern	2n = 22
ii)	Luik × Sacavem	2n = 22
iii)	Luik × Sintra-Algueiras	2n = 22
iv)	Bern × Sacavem	2n = 22
v)	Bern × Sintra-Algueiras	2n = 22
vi)	Sacavem × Sintra-Algueiras	2n = 22

These intraspecific hybrids do not show any particular pecularities in the pairing behaviour of their chromosomes at diakinesis. Some of the bivalents are found to interlock, giving a 'quadrivalent'. These interlocked bivalents, however, towards late diakinesis, separate out as bivalents and behave normally. The various types of interlocking of these bivalents are mentioned in table 22.

Only in the hybrids having Sintra-Algueiras as one parent, interlockings of more bivalents to give the configuration of an 'octovalent' or a 'sexivalent', have been observed; but the frequency of these is very low. Most of the interlockings are between two ring bivalents. Interlocking between one ring and one rod bivalent is met with in all cases. In table 23 the different types of bivalents are listed.

The univalents are completely absent, thereby indicating that the chromosomes of the two parents do pair. The stages from M–I to the tetrad formation are completely normal. Only in a very few cases whose frequency is negligible, bridges in A–I and A–II have been observed. The distribution of chromosomes in M–II has been found to be 11 + 11 as expected. Tetrad formation is normal and no micronuclei have been observed.

C. *F_2 progeny*. The karyology of the F_2's obtained from the interspecific hybrids under groups a and b and the hybrid Lisbon × × Luik (group c) has been studied. The segregation of characters including the fertility in F_2's is dealt with in a separate chapter. The meiosis of the F_2's of the hybrids in group d has not been studied as in the hybrids no abnormalities worth mentioning, have been observed. Those hybrids behave in meiosis in the same way as their parents. Moreover, the segregation of characters such as, height of the plant, number of branches, colour of the petal etc. are of varietal nature, involving neither meiotic abnormalities nor chromosomal differences.

TABLE 22. *Associations in the intraspecific hybrids*

Association \ Hybrid	Luik × Bern	Luik × Sacavem	Luik × Sintra-Algueiras	Bern × Sacavem	Bern × Sintra-Algueiras	Sacavem × Sintra-Algueiras
$1_{\text{'VIII'}} + 1_{\text{'IV'}} + 5_{II}$	—	—	5.1	—	—	—
$1_{\text{'VIII'}} + 7_{II}$	—	—	5.1	—	—	—
$1_{\text{'VI'}} + 1_{\text{'IV'}} + 6_{II}$	—	—	5.1	—	2.5	—
$1_{\text{'VI'}} + 8_{II}$	—	—	5.1	—	4.0	—
$3_{\text{'IV'}} + 5_{II}$	17.0	15.0	5.1	14.3	12.3	4.7
$2_{\text{'IV'}} + 7_{II}$	20.5	10.0	21.2	19.8	17.5	28.6
$1_{\text{'IV'}} + 9_{II}$	31.6	25.0	46.4	37.5	24.4	47.6
11_{II}	30.9	50.0	6.9	28.4	39.3	19.1

TABLE 23. *Different types of bivalents in the intraspecific hybrids*
(Average from 10 PMCs)

Hybrid \ Types of bivalent	Ring	Rod	End to end attached
Luik × Bern	7	—	4
Luik × Sacavem	7	1	3
Luik × Sintra-Algueiras	6	1	4
Bern × Sacavem	7	—	4
Bern × Sintra-Algueiras	6	1	4
Sacavem × Sintra-Algueiras	6	1	4

In the other F_2s, materials for the study of microsporogenesis have been collected based on the colour of the petal. The segregants namely Light Purple and Red have been studied in all the F_2s, eventhough there have occurred three more colours such as Reddish Purple, Purple and Pink. Due to extreme drought conditions during the summer season of 1959, it has been found to be very difficult to obtain materials for the diakinetic stage, as the meiosis is completed in a short time during the early hours of the morning. However, with much difficulty the materials from segregants Light Purple and Red have been obtained as these segregants have produced comparatively more buds for the choice.

The meiosis of the F_2s mentioned in table 24 is described in the following pages.

Except for the differences observed in the diakinetic stage regarding

TABLE 24

Group	F_2	Colour	Plant number	2n
a	Luik × Malta	i Light Purple	5970 e.7	34
		ii Red	5970 d.9	30
	Malta × Luik	i Light Purple	5973 e.4	35
		ii Red	5973 d.31	33
	Malta × Bern	i Light Purple	5974 a.13	35
		ii Red	5974 d.21	33
	Malta × Sacavem	i Light Purple	5976 b.15	35
		ii Red	5976 b.11	32
	Malta × Sintra-Algueiras	i Light Purple	5977 b.35	34
		ii Red	5977 b.47	36
b	Malta × Lisbon	i Light Purple	5972 f.5	33
c	Lisbon × Luik	i Light Purple	5861 c.50	24
		ii Red	5861 c.22	21

synapsis and the number of univalents, the description of which is given in the following pages, the stages from M–I up to the formation of tetrads in all the F_2s are similar. The interlocked bivalents, towards late diakinesis, detach themselves into bivalents and behave normally along with the other bivalents in the M–I and A–I. Like in the F_1s, the univalents divide in the A–I after the disjunction of the bivalents is completed. Heterotypic bridges have not been observed in late A–I as there has been enough time for the bivalents to terminalise completely. Hence the homeotypic division of the univalents in A–I after the disjunction of the bivalents, rather helps in giving sufficient time for the bivalents to terminalise completely, which otherwise would have shown bridges. Like in the F_1s the univalents do not divide completely, but they are found to be stretched from both ends, giving the shape of a dumbbell. The homeotypically divided univalents get themselves included into the telophase nuclei.

A–II is highly irregular in all the F_2s studied. The dyads resulting from the heterotypic division, have a normal equational division, whilst the daughter chromosomes of the univalents lie scattered in the cytoplasm. Some of the chromosomes fail to get included into the tetrad nuclei. The other chromosomes give a few equational bridges, the frequency of which is found to be negligible. After

TABLE 25. *Frequency of the normal tetrads and tetrads with micronuclei in the F_2s*

Group	Plant number	Colour group	Normal tetrad	Tetrad with micronuclei						
				1	2	3	4	5	6	7
a										
(44 × 22)	5970 e.7	Light Purple	—	43.0	29.0	14.6	8.6	—	2.4	2.4
	5970 d.9	Red	—	48.0	21.4	18.6	10.7	1.3	—	—
	5973 e.4	Light Purple	12.5	35.7	20.3	15.6	—	8.6	7.3	—
	5973 d.31	Red	10.4	29.8	21.7	19.3	10.7	4.4	—	3.7
	5974 a.13	Light Purple	2.3	40.3	20.1	14.7	7.5	10.1	5.0	—
	5974 d.21	Red	—	47.1	27.3	20.1	5.5	—	—	—
	5976 b.15	Light Purple	—	35.8	27.1	22.5	10.6	2.0	2.0	—
	5976 b.11	Red	7.3	33.6	19.7	17.5	7.6	7.2	4.1	3.0
	5977 b.35	Light Purple	3.7	42.5	20.9	14.7	10.2	4.5	3.5	—
	5977 b.47	Red	—	39.3	32.5	20.3	5.7	2.2	—	—
b										
(44 × 20)	5972 f.5	Light Purple	—	47.2	25.4	15.6	10.9	0.9	—	—
c										
(20 × 22)	5861 c.50	Light Purple	94.0	4.0	2.0	—	—	—	—	—
	5861 c.22	Red	30.9	35.3	28.2	2.8	2.8	—	—	—

complete homeotypic division they form the tetrad nuclei. Some of the daughter chromosomes of the univalents that do not join the tetrad nuclei, form themselves into many micronuclei whose frequency is indicated in table 25 for all the F_2s studied.

The exact distribution of chromosomes in the tetrad is difficult to estimate as most of the chromosomes lose their identity. The micronuclei later develop as pollen grains.

Luik × Malta.

5970 e.7. Light Purple $2n = 34$ (fig. 42). At diakinesis 4 ring bivalents having two terminal chiasmata each, one bivalent with one terminal chiasma and two interlocked bivalents; the interlockings being one between two ring bivalents and the other between one ring and one rod bivalents, are met with. Besides, univalents are observed ranging from ten to six, thereby indicating that the six chromosomes do not pair at all even heteromorphically.

5970 d.9. Red $2n = 30$ (fig. 43). The frequent occurrence of the synaptic configurations is $3_{\text{'IV'}} + 7_{II} + 4_I$; $1_{\text{'IV'}} + 11_{II} + 4_I$ and $1_{\text{'III'}} + 11_{II} + 5_I$. These 'quadrivalents' are the result of interlocking

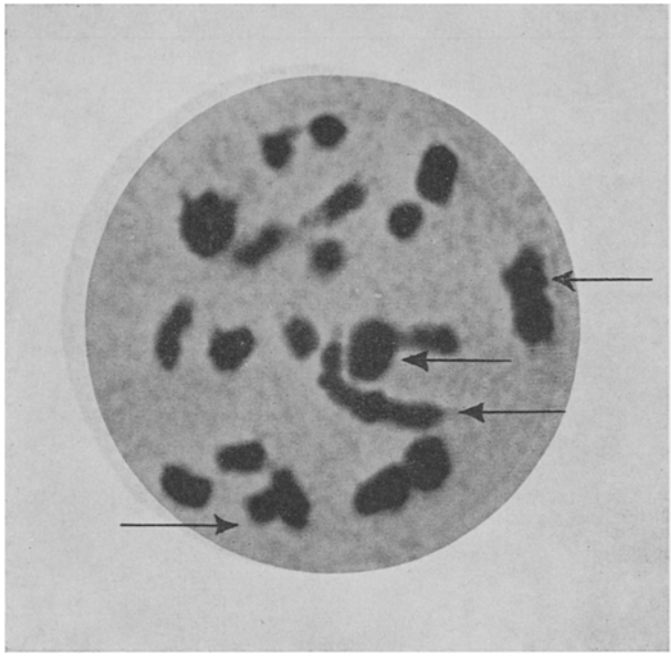

Fig. 42. Diakinesis in 5970 e.7 $3_{\text{'IV'}} + 1_{\text{'III'}} + 6_{II} + 7_{I}$. × 2116.

between two ring bivalents. The number of univalents is reduced to four as the minimum, thereby indicating that these four chromosomes fail to pair even heteromorphically.

Malta × Luik.

5973 e.4. Light Purple 2n = 35 (fig. 44). The most common configuration observed in the diakinetic stage is $1_{\text{'IV'}} + 12_{II} + 7_{I}$. Occasionally one more interlocking is found between two ring bivalents. There are 12 ring bivalents including those which enter into interlocking, one rod bivalent and two bivalents having end to end attachment, besides seven univalents. Only in one cell five univalents are noticed, the other two univalents have very loosely attached themselves to one bivalent giving a 'quadrivalent'. But in all the other cells examined, the number of univalents remains constant (7).

5973 d.31. Red 2n = 33 (fig. 45). This segregant shows $2_{\text{'IV'}} + 9_{II} + 7_{I}$ in synapsis in all the cells examined. The 'quadrivalents' are due to the result of interlocking between two ring bivalents in

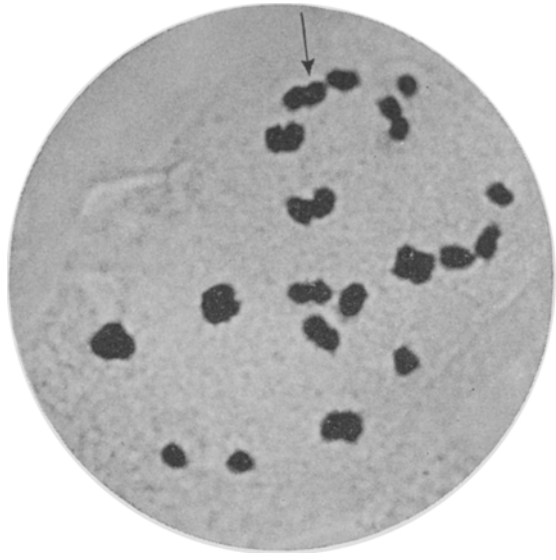

Fig. 43. Diakinesis in 5970 d.9 $1_{'III'} + 11_{II} + 5_{I}$. × 1411.

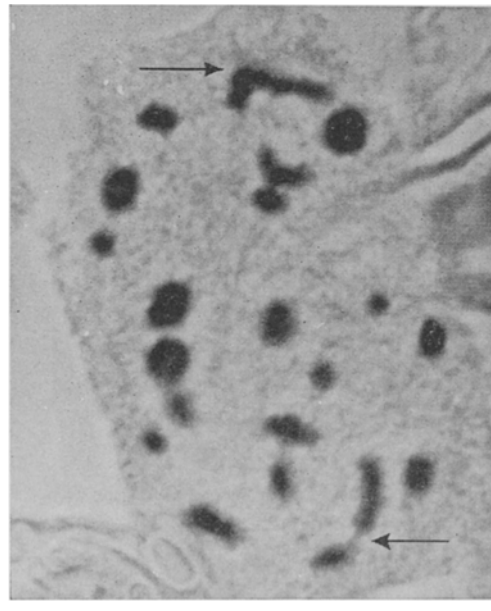

Fig. 44. Diakinesis in 5973 e.4 $1_{'IV'} + 12_{II} + 7_{I}$. Note the bivalent formed by the SAT-chromosomes. × 1411.

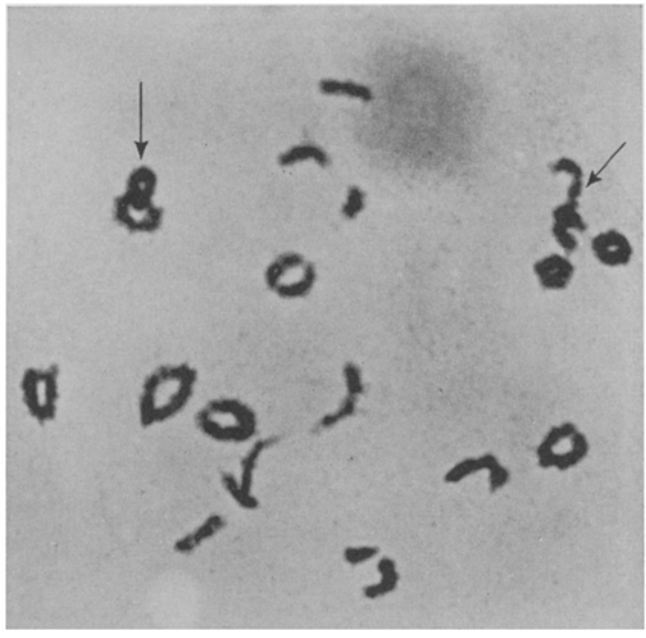

Fig. 45. Diakinesis in 5973 d.31 $2_{\text{'IV'}} + 9_{II} + 7_I$. Note one bivalent has almost terminalised. × 1411.

one case and in the other it is between one ring and one rod bivalents. Besides, there are seven ring bivalents with two terminal chiasmata and two bivalents with end to end attachment. The number of univalents is constant throughout. The interlocked bivalents separate themselves at late diakinesis.

Malta × Bern.

5974 a.13. Light Purple. 2n = 35 (fig. 46). Three types of associations are met with, namely $2_{\text{'IV'}} + 11_{II} + 5_I$; $1_{\text{'IV'}} + 12_{II} + 7_I$ and $1_{\text{'VI'}} + 1_{\text{'IV'}} + 9_{II} + 7_I$; the last mentioned having a high frequency of about 80 percent. There are three bivalents having end to end attachment, one rod and 10 ring bivalents. Out of these ten ring bivalents, two ring bivalents interlock to give the appearance of a 'quadrivalent' while one rod bivalent together with a ring of four chromosomes gives the configuration of a 'sexivalent'. However, these higher associations break off into bivalents and behave as

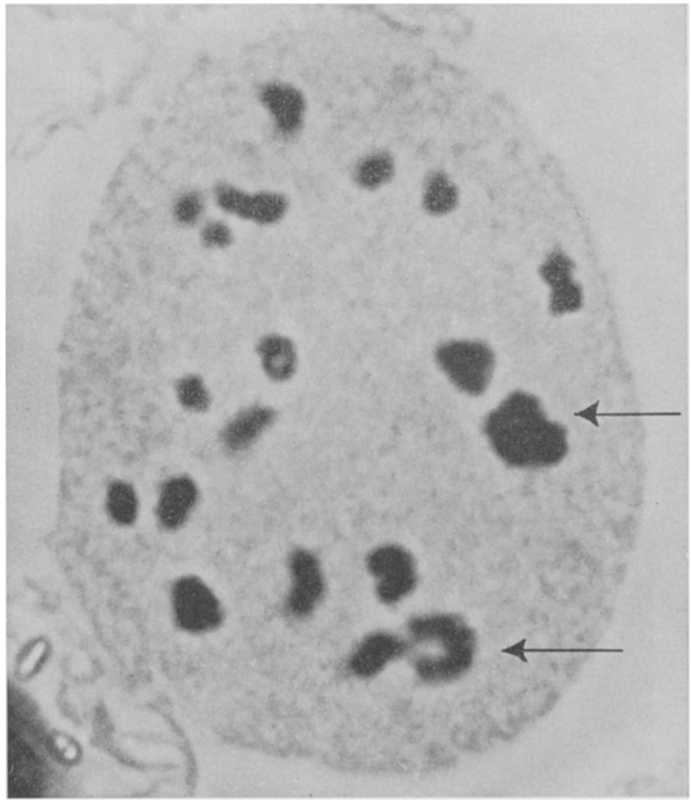

Fig. 46. Diakinesis in 5974 a.13 $1_{'VI'} + 1_{'IV'} + 9_{II} + 7_{I}$. × 2116.

normal bivalents in the other stages. Except in a few cells, where 5 univalents are seen, in all the other cells the number has been seven throughout. In the late diakinesis two to three bivalents are seen terminalising.

5974 d.21. Red 2n = 33 (fig. 47). This segregant differs a little from the others; most of the cells have shown at diakinetic stage, twelve bivalents and nine univalents. However, in about 30 percent of the cells, interlocking of two ring bivalents has been detected. The number of univalents has been found to be eleven in some cells. This may be due to the precocious terminalisation of one bivalent. There are 9 ring bivalents of which two give the interlocking in a

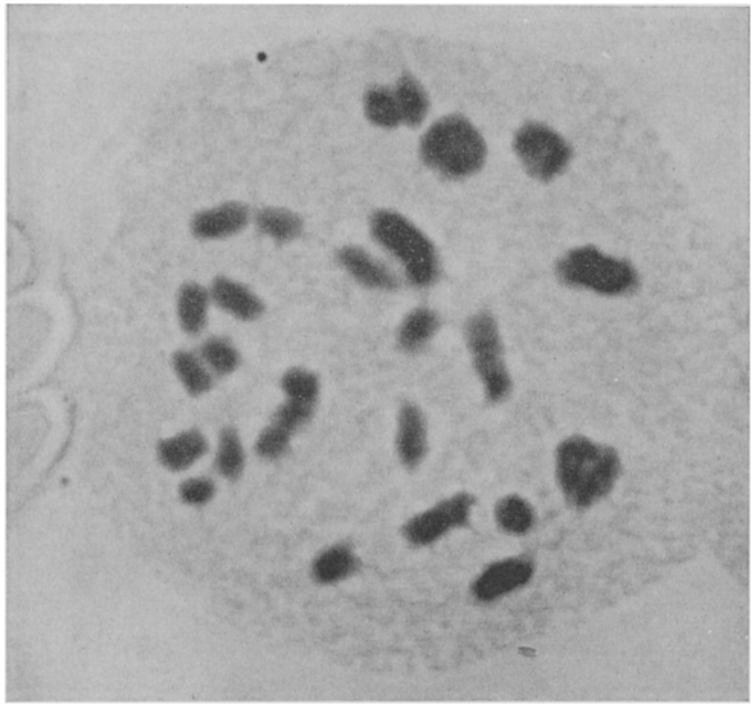

Fig. 47. Diakinesis in 5974 d.21 $12_{II} + 9_{I}$. × 2116.

few cases, one rod bivalent and one bivalent having end to end attachment. As in the other F_2's the interlocked bivalents separate themselves out and behave normally in all the stages beginning from M–I.

Malta × Sacavem.

5976 b.15. Light Purple 2n = 35 (fig. 48). The configurations observed in this plant vary much, as indicated in table 26.

Besides the interlocking of bivalents to give 'quadrivalent', one to two bivalents have been noticed in 17.9 percent of the cells examined. However, one fifth of the total number of cells shows fourteen bivalents and seven univalents. The minimum number of univalents has been six, but its frequency is very low, whereas about 50 percent of the cells shows as much as 9 univalents. The extra two univalents over 9, in 25 percent of the cells, are probably due to

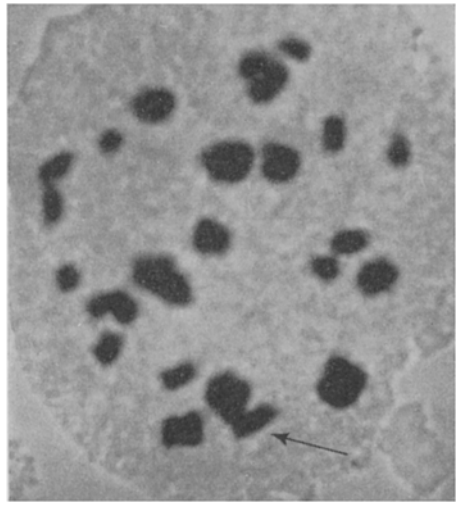

Fig. 48. Diakinesis in 5976 b.15 $1_{\text{'IV'}} + 11_{II} + 9_I$. × 1411.

TABLE 26. *Association at diakinesis in the F_2 Malta × Sacavem*

Association	Percentage
$1_{\text{'IV'}} + 2_{\text{'III'}} + 8_{II} + 9_I$	12.6
$2_{\text{'IV'}} + 9_{II} + 9_I$	10.4
$2_{\text{'IV'}} + 8_{II} + 11_I$	25.3
$1_{\text{'IV'}} + 11_{II} + 9_I$	26.4
$1_{\text{'III'}} + 13_{II} + 6_I$	5.3
$14_{II} + 7_I$	20.0

a failure of pairing or due to precocious terminalisation of one bivalent. Ring bivalents from 8 to 10 are met with, of which two bivalents interlock each other. The bivalents with one terminal chiasma vary from five to three in number.

5976 b.11. Red 2n = 32 (fig. 49). All the cells show only 11 bivalents and 10 univalents. Of the 11 bivalents, 8 are ring bivalents with two terminal chiasmata each and three with one terminal chiasma each. Often only eight univalents out of the 10 observed, are seen lying away from the equator. Hence the other two univalents which are often found lying almost at right angles to the equator

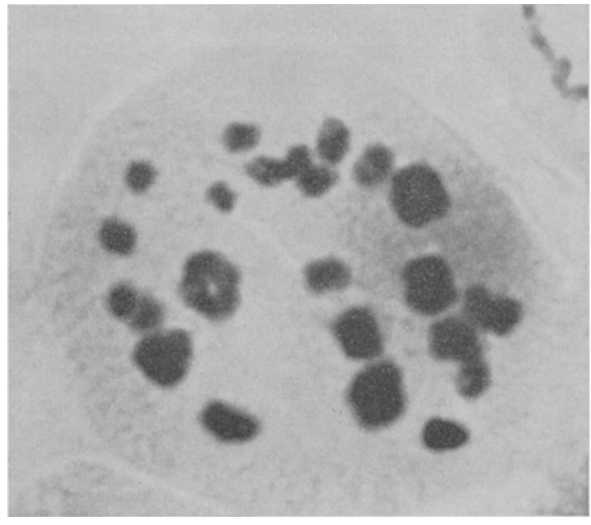

Fig. 49. Diakinesis in 5976 b.11 $11_{II} + 10_{I}$. × 2116.

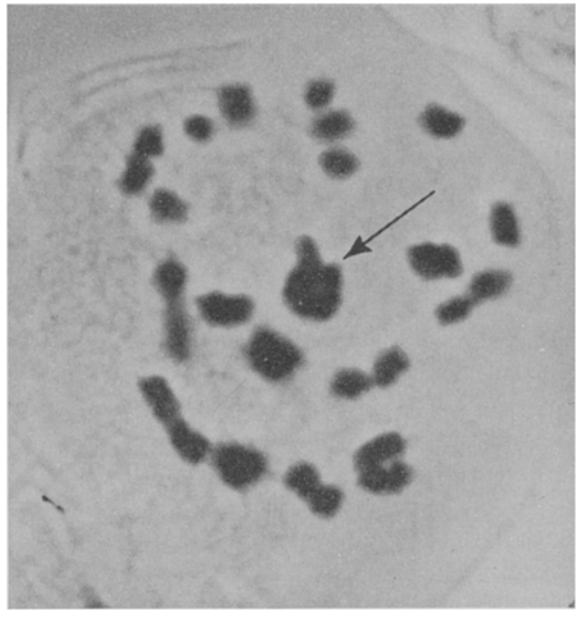

Fig. 50. Diakinesis in 5977 b.35 $1_{\text{'IV'}} + 11_{II} + 8_{I}$. × 2116.

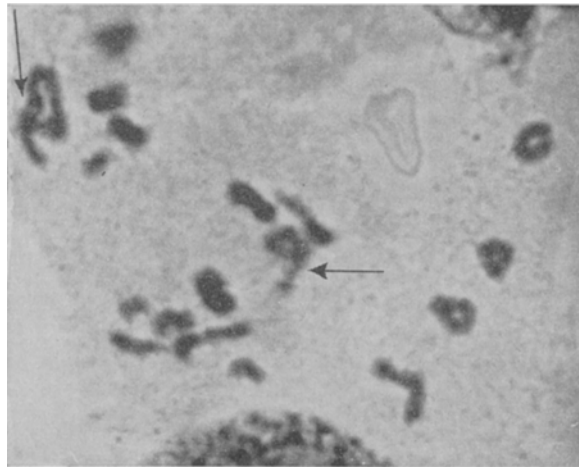

Fig. 51. Diakinesis in 5977 b.47 $2_{\text{IV}} + 12_{\text{II}} + 4_{\text{I}}$. × 1411.

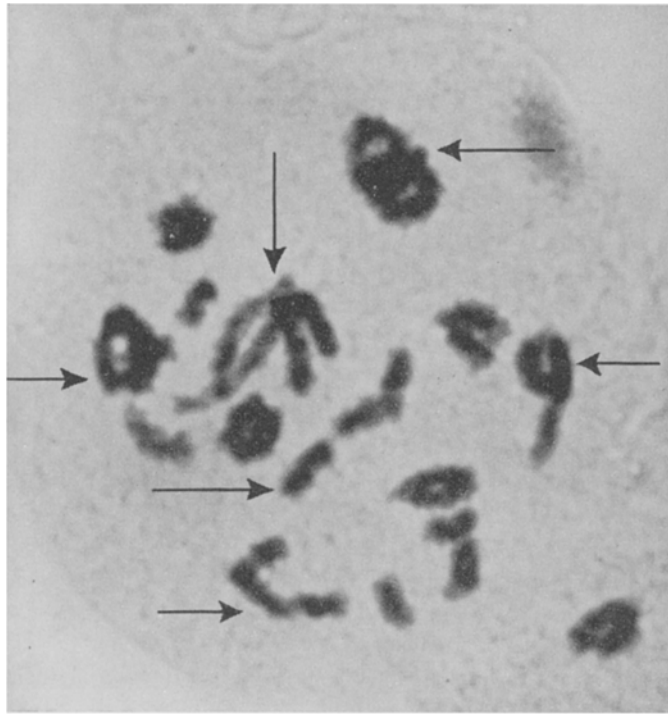

Fig. 52. Diakinesis in 5972 f.5 $3_{\text{IV}} + 3_{\text{III}} + 4_{\text{II}} + 4_{\text{I}}$. × 2116.

may be due to precocious division of a bivalent with one terminal chiasma. No interlocking of bivalents has been observed.

Malta × Sintra-Algueiras.

5977 b.35. Light Purple 2n = 34 (fig. 50). The most frequent associations observed during synapsis are $14_{II} + 6_I$ and $1'_{IV'} + 11_{II} + 8_I$. In one cell it has been found $4'_{IV'} + 8_{II} + 2_I$ to occur. As the frequency is so low, this type of pairing can not be considered as the normal type of pairing of this F_2. Otherwise no interlockings have been noticed.

5977 b.47. Red 2n = 36 (fig. 51). Only one type of pairing has been observed namely $2'_{IV'} + 12_{II} + 4_I$. There are 8 ring bivalents and two rod bivalents. One interlocking is between two ring bivalents whilst the two rod bivalents give the second interlocking association. No bivalent with one terminal chiasma has been found. The minimum number of univalents is four.

Malta × Lisbon.

5972 f.5. Light Purple 2n = 33 (fig. 52). At diakinesis the association has been found to be $3'_{IV'} + 3'_{III'} + 4_{II} + 4_I$. The three 'quadrivalents' are formed by the following interlockings: (1) between two rings, (2) between one ring and one open ring bivalent and (3) between one ring and one rod bivalents. Two 'trivalents' out of the three, are due to the formation of a chain of three chromosomes, whilst the third one is between a ring bivalent and the univalent. The four bivalents are ring bivalents having two terminal chiasmata each. These higher associations namely 'quadrivalents' and 'trivalents' break off into bivalents or as univalents at the late diakinetic stage as in M–I neither interlocking bivalents nor chains have been observed. The number of univalents being four is found to be constant.

Lisbon × Luik.

5861 c.50. Light Purple 2n = 24 (fig. 53). This F_2 segregant shows a higher somatic number than its parents. At diakinetic stage, the synaptic pairs observed are ten bivalents and four univalents. Of the ten bivalents seven are ring bivalents whilst the others have one terminal chiasma each. In fig. 52 the terminalisation of one bivalent can be seen. The number of univalents appears to be four in all the cells examined. The behaviour of the univalents in A–I and A–II is the same as in those of the other F_2s.

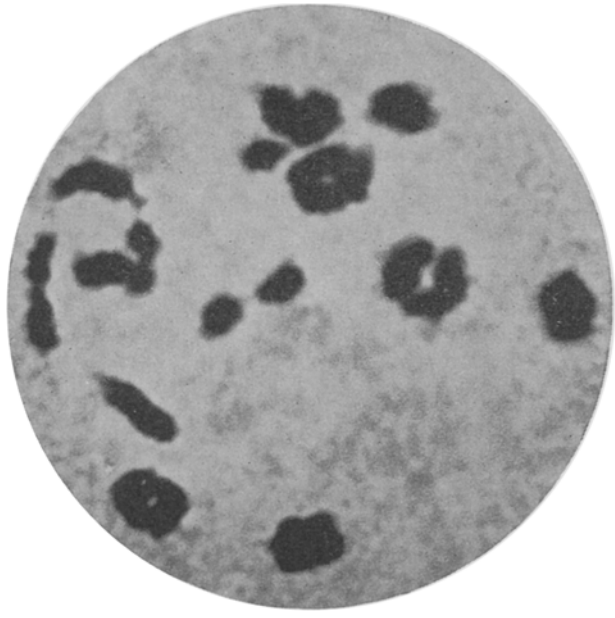

Fig. 53. Diakinesis in 5861 c.50 $10_{II} + 4_{I}$. × 2116.

5861 c.22. Red 2n = 21 (fig. 54). In most of the cells examined it has been found that the chromosomes pair as $1'_{IV'} + 1'_{III'} + 4_{II} + 6_{I}$. However, there are cells at the early M–I having only $5_{II} + 11_{I}$, thereby indicating that all the higher associations above bivalents have separated themselves as bivalents or as univalents. Moreover, it is possible that some of the bivalents having one terminal chiasma have terminalised even at the late diakinesis. The number of univalents has considerably increased from the number observed in the F_1.

4. *Investigations on the inheritance of characters*

Coupled with karyological studies conducted in the parents, their F_1s and F_2s, investigations on the height, branching, length and width of the leaf, colour of the petal, colour and number of filaments and colour of the seed coat have been undertaken to find out whether the segregations observed are of mendelian character. In this connection it is worthwhile to bear in mind that the parents involved in the crosses are a diploid and a tetraploid or two diploid types having different somatic number. Hence any strict mendelian segre-

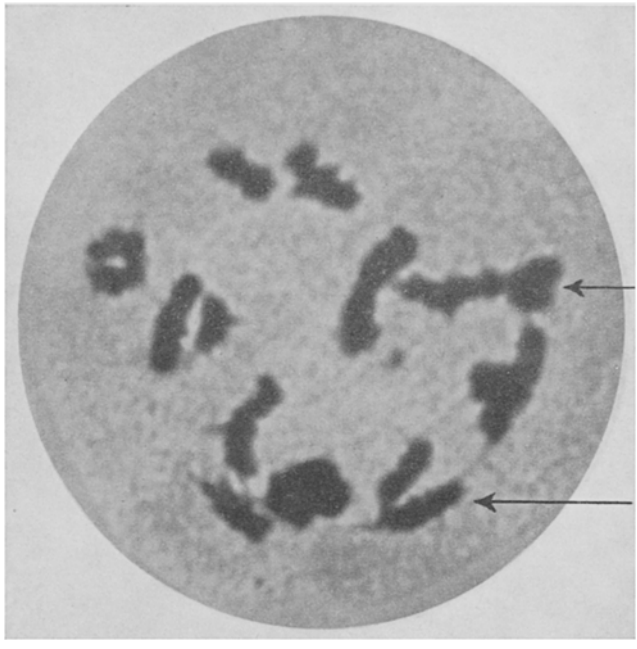

Fig. 54. Diakinesis in 5861 c.22 $1_{\text{'IV'}} + 1_{\text{'III'}} + 4_{II} + 6_{I}$. × 2116.

gation can not be expected, eventhough a nearest approach to such a segregation can be indicated from the data obtained from these studies. These results will be discussed in the following chapter.

The height of the plants has been measured from the base to the tip of the first terminal flower, while length and width of the leaf have been taken from a leaf of comparable leaf position – fifth leaf from the base. With the help of the Horticultural Chart of the Royal Horticultural Society (London) the colour of the petal has been broadly classified as Light Purple, Purple, Reddish Purple, Red, Pink and White, eventhough there occur various diluted forms under these main groups. The same principle has been applied with regard to the colour of the filament and the seed coat. The results are tabulated and presented in tables 27 to 32.

5. *Pollengrains of the parents*

It has been thought worthwhile to estimate the diameter of the pollengrains of these six types, during the study of their pollen

TABLE 27. *Mean height in cm.*

S. No.	Hybrids	Parents ♀ $\overline{\times}$	Parents ♂ $\overline{\times}$	F_1 $\overline{\times}$	F_2 $\overline{\times}$
1	Malta × Luik	26.6 ± 6.62	110.5 ± 7.97	38.0 ± 7.72	38.9 ± 10.5
2	Malta × Bern	26.6 ± 6.62	92.8 ± 8.16	55.2 ± 7.32	37.8 ± 14.1
3	Malta × Sacavem	26.6 ± 6.62	63.6 ± 4.29	29.4 ± 4.85	33.2 ± 12.4
4	Malta × Sintra-Algueiras	26.6 ± 6.62	63.0 ± 4.29	35.5 ± 4.22	33.4 ± 11.3
5	Luik × Malta	110.5 ± 7.97	26.6 ± 6.62	52.3 ± 8.48	30.8 ± 10.1
6	Malta × Lisbon	26.6 ± 6.62	47.8 ± 2.04	49.4 ± 6.72	39.8 ± 16.7
7	Lisbon × Malta	47.8 ± 2.04	26.6 ± 6.62	59.6 ± 3.50	*
8	Lisbon × Luik	47.8 ± 2.04	110.5 ± 7.97	94.7 ± 3.53	55.4 ± 28.3
9	Lisbon × Bern	47.8 ± 2.04	92.8 ± 8.16	95.3 ± 3.67	53.3 ± 25.7
10	Lisbon × Sacavem	47.8 ± 2.04	63.6 ± 4.29	53.5 ± 13.94	46.1 ± 20.3
11	Lisbon × Sintra-Algueiras	47.8 ± 2.04	63.0 ± 4.29	65.9 ± 5.81	54.8 ± 19.8
12	Luik × Lisbon	110.5 ± 7.97	47.8 ± 2.04	78.6 ± 8.81	68.4 ± 19.8
13	Luik × Bern	110.5 ± 7.97	92.8 ± 8.16	98.5 ± 10.59	*
14	Luik × Sacavem	110.5 ± 7.97	63.6 ± 4.29	87.2 ± 6.81	*
15	Luik × Sintra-Algueiras	110.5 ± 7.97	63.0 ± 4.29	84.4 ± 6.78	*
16	Bern × Sacavem	92.8 ± 8.16	63.6 ± 4.29	51.3 ± 3.27	*
17	Bern × Sintra-Algueiras	92.8 ± 8.16	63.0 ± 4.29	57.8 ± 5.98	*
18	Sacavem × Sintra-Algueiras	63.6 ± 4.29	63.0 ± 4.29	62.9 ± 9.45	*

*) Not studied.

fertility, with a view to find out whether there exist any differences between the two species *P. setigerum* DC. and *P. somniferum* L. (the chromosome number being 44 and 22 respectively) and also any intraspecific differences. The details regarding fertility for the hybrids and their F_2s are mentioned in a separate chapter under fertility. The meàn diameter of the pollen grains and the range of variation are given in table 33.

Excepting in Malta and Bern, in the other types the maximum number of pollengrains falls in the group 10.0. Malta and Bern show the maximum number under the group 11.0. The range of variation in Bern, Sintra-Algueiras and Lisbon is limited while Sacavem

TABLE 28. *Mean number of branches*

S. No.	Hybrids	Parents ♀ $\overline{X}$	Parents ♂ $\overline{X}$	F_1 $\overline{X}$	F_2 $\overline{X}$
1	Malta × Luik	7.7 ± 1.56	4.5 ± 2.01	7.4 ± 2.37	11.7 ± 5.9
2	Malta × Bern	7.7 ± 1.56	2.5 ± 1.20	9.0 ± 3.05	6.6 ± 4.7
3	Malta × Sacavem	7.7 ± 1.56	6.4 ± 1.26	7.2 ± 1.62	8.4 ± 5.5
4	Malta × Sintra-Algueiras	7.7 ± 1.56	6.1 ± 1.10	9.3 ± 2.21	10.2 ± 4.8
5	Luik × Malta	4.5 ± 2.01	7.7 ± 1.56	16.4 ± 8.82	7.8 ± 4.8
6	Malta × Lisbon	7.7 ± 1.56	12.5 ± 1.35	12.1 ± 3.28	7.6 ± 4.6
7	Lisbon × Malta	12.5 ± 1.35	7.7 ± 1.56	17.1 ± 3.50	*
8	Lisbon × Luik	12.5 ± 1.35	4.5 ± 2.01	13.6 ± 3.37	4.4 ± 1.6
9	Lisbon × Bern	12.5 ± 1.35	2.5 ± 1.20	6.4 ± 2.36	3.0 ± 2.2
10	Lisbon × Sacavem	12.5 ± 1.35	6.4 ± 1.26	4.2 ± 1.23	4.4 ± 3.1
11	Lisbon × Sintra-Algueiras	12.5 ± 1.35	6.1 ± 1.10	6.4 ± 2.27	4.5 ± 1.8
12	Luik × Lisbon	4.5 ± 2.01	12.5 ± 1.35	2.5 ± 1.78	4.9 ± 2.5
13	Luik × Bern	4.5 ± 2.01	2.5 ± 1.20	1.8 ± 1.23	*
14	Luik × Sacavem	4.5 ± 2.01	6.4 ± 1.26	5.6 ± 1.51	*
15	Luik × Sintra-Algueiras	4.5 ± 2.01	6.1 ± 1.10	5.9 ± 1.85	*
16	Bern × Sacavem	2.5 ± 1.20	6.4 ± 1.26	3.4 ± 2.10	*
17	Bern × Sintra-Algueiras	2.5 ± 1.20	6.1 ± 1.10	1.7 ± 0.82	*
18	Sacavem × Sintra-Algueiras	6.4 ± 1.26	6.1 ± 1.10	5.5 ± 1.58	*

*) Not studied.

shows the maximum range from 7.5 to 15.0. Malta and Luik occupy the middle position in between the two extremes.

6. *Male sterility*

On a cursory examination of some of the F_2 segregants for their pollen fertility, it has been found that segregants having red and light purple flowers show a tendency to a lower fertility level than the plants having purple or reddish purple flowers. In addition to this, in the F_2 some segregants are found to produce capsules full of seeds, some with half filled capsules and some with a very poor,

TABLE 29. *Mean length of the leaf in cm.*

S. No.	Hybrids	Parents		F_1	F_2
		♀ ×	♂ ×	×	×
1	Malta × Luik	4.5 ± 1.65	19.9 ± 6.24	4.8 ± 1.03	5.9 ± 2.2
2	Malta × Bern	4.5 ± 1.65	15.9 ± 2.47	7.7 ± 1.33	6.4 ± 2.5
3	Malta × Sacavem	4.5 ± 1.65	10.2 ± 1.55	4.5 ± 1.90	5.8 ± 2.5
4	Malta × Sintra-Algueiras	4.5 ± 1.65	9.9 ± 2.60	6.0 ± 0.94	6.1 ± 2.7
5	Luik × Malta	19.9 ± 6.24	4.5 ± 1.65	6.0 ± 1.05	5.4 ± 2.1
6	Malta × Lisbon	4.5 ± 1.65	12.9 ± 1.28	6.9 ± 1.52	6.4 ± 3.7
7	Lisbon × Malta	12.9 ± 1.28	4.5 ± 1.65	7.4 ± 1.26	*
8	Lisbon × Luik	12.9 ± 1.28	19.9 ± 6.24	12.7 ± 2.71	12.9 ± 3.8
9	Lisbon × Bern	12.9 ± 1.28	15.9 ± 2.47	13.5 ± 3.75	15.1 ± 1.7
10	Lisbon × Sacavem	12.9 ± 1.28	10.2 ± 1.55	11.1 ± 1.79	10.5 ± 3.7
11	Lisbon × Sintra-Algueiras	12.9 ± 1.28	9.9 ± 2.60	10.5 ± 1.84	11.0 ± 3.9
12	Luik × Lisbon	19.9 ± 6.24	12.9 ± 1.28	14.6 ± 2.37	13.0 ± 3.6
13	Luik × Bern	19.9 ± 6.24	15.9 ± 2.47	16.8 ± 5.55	*
14	Luik × Sacavem	19.9 ± 6.24	10.2 ± 1.55	11.4 ± 2.75	*
15	Luik × Sintra-Algueiras	19.9 ± 6.24	9.9 ± 2.60	12.0 ± 2.47	*
16	Bern × Sacavem	15.9 ± 2.47	10.2 ± 1.55	17.4 ± 1.17	*
17	Bern × Sintra-Algueiras	15.9 ± 2.47	9.9 ± 2.60	16.6 ± 1.90	*
18	Sacavem × Sintra-Algueiras	10.2 ± 1.55	9.9 ± 2.60	10.5 ± 1.27	*

*) Not studied.

almost nil seed setting. With a view to fully investigate this problem of segregation of fertility in correlation with the colour of the flower, it has been decided to determine the mean fertility of each segregant in every F_2 studied. For this investigation, the method adopted is very simple. The anthers have been collected from the flowers in the mornings, the day the flower opened. Then they have been teased out and stained in one percent iodine in potassiumiodide solution and kept for a few minutes before the preparation is ready for analysis, Counts of 500, both fertile and sterile pollengrains are taken, from which the percentage of fertility for the plant has been determined.

TABLE 30. *Mean width of the leaf in cm.*

S. No.	Hybrids	Parents		F_1	F_2
		♀ $\bar{X}$	♂ $\bar{X}$	$\bar{X}$	$\bar{X}$
1	Malta × Luik	2.3 ± 0.67	11.6 ± 2.27	2.8 ± 0.42	3.3 ± 1.4
2	Malta × Bern	2.3 ± 0.67	11.9 ± 2.23	4.5 ± 1.08	3.8 ± 1.6
3	Malta × Sacavem	2.3 ± 0.67	7.9 ± 1.52	1.8 ± 0.92	3.7 ± 1.7
4	Malta × Sintra-Algueiras	2.3 ± 0.67	6.3 ± 1.33	2.6 ± 0.51	3.7 ± 1.5
5	Luik × Malta	11.6 ± 2.27	2.3 ± 0.67	3.5 ± 0.52	3.2 ± 1.6
6	Malta × Lisbon	2.3 ± 0.67	4.2 ± 0.92	3.3 ± 0.48	3.8 ± 2.4
7	Lisbon × Malta	4.2 ± 0.92	2.3 ± 0.67	4.1 ± 0.57	*
8	Lisbon × Luik	4.2 ± 0.92	11.6 ± 2.27	10.6 ± 2.50	7.7 ± 2.6
9	Lisbon × Bern	4.2 ± 0.92	11.9 ± 2.23	10.4 ± 2.54	9.3 ± 3.3
10	Lisbon × Sacavem	4.2 ± 0.92	7.9 ± 1.52	5.2 ± 1.39	6.7 ± 1.8
11	Lisbon × Sintra-Algueiras	4.2 ± 0.92	6.3 ± 1.33	5.1 ± 1.45	7.0 ± 2.6
12	Luik × Lisbon	11.6 ± 2.27	4.2 ± 0.92	9.2 ± 1.99	8.1 ± 1.6
13	Luik × Bern	11.6 ± 2.27	11.9 ± 2.23	11.9 ± 2.08	*
14	Luik × Sacavem	11.6 ± 2.27	7.9 ± 1.52	8.1 ± 1.79	*
15	Luik × Sintra-Algueiras	11.6 ± 2.27	6.3 ± 1.33	8.1 ± 2.37	*
16	Bern × Sacavem	11.9 ± 2.23	7.9 ± 1.52	7.9 ± 1.10	*
17	Bern × Sintra-Algueiras	11.9 ± 2.23	6.3 ± 1.33	8.6 ± 1.64	*
18	Sacavem × Sintra-Algueiras	7.9 ± 1.52	6.3 ± 1.33	6.8 ± 1.40	*

*) Not studied.

Fertility means for each colour group in every F_2 and for all the F_2's together have been estimated. Mean fertility for each F_2 taking all colour groups together has also been calculated in order to compare with the fertility means of the hybrids and their parents. The result of all these investigations have been tabulated and presented in tables 34 to 37 (fig. 55a–e and 56).

V. DISCUSSION

Karyotype. DELAUNAY (1926) has formulated the concept of karyotype as a group of species resembling each other in the number,

TABLE 31. *Colour of the petal and filament*

S. No.	Hybrids	Parents ♀ Colour of the petal and of its base	Parents ♀ Colour and number of filaments	Parents ♂ Colour of the petal and of its base	Parents ♂ Colour and number of filaments	F_1 Colour of the petal and of its base	F_1 Colour and number of filaments	F_2*
1	Malta × Luik	LP/DP	DP/N	P/LP	W/L	R/DP	DP/N	
2	Malta × Bern	LP/DP	DP/N	R/LR	W/L	R/DP	DP/N	
3	Malta × Sacavem	LP/DP	DP/N	R/LR	W/L	R/DP	DP/L	
4	Malta × Sintra-Algueiras	LP/DP	DP/N	R/LR	W/L	R/DP	DP/L	
5	Luik × Malta	P/LP	W/L	LP/DP	DP/N	LP/LP	DP/N	
6	Malta × Lisbon	LP/DP	DP/N	W/DP	DP/L	LP/DP	DP/N	
7	Lisbon × Malta	W/DP	DP/L	LP/DP	DP/N	LP/DP	DP/L	
8	Lisbon × Luik	W/DP	DP/L	P/LP	W/L	Pk/DP	DP/L	
9	Lisbon × Bern	W/DP	DP/L	R/LR	W/L	Pk/LP	DP/L	
10	Lisbon × Sacavem	W/DP	DP/L	R/LR	W/L	CR/LP	DP/L	
11	Lisbon × Sintra-Algueiras	W/DP	DP/L	R/LR	W/L	CR/DP	DP/L	
12	Luik × Lisbon	P/LP	W/L	W/DP	DP/L	Pk/LP	DP/L	
13	Luik × Bern	P/LP	W/L	R/LR	W/L	CR/LP	W/L	
14	Luik × Sacavem	P/LP	W/L	R/LR	W/L	CR/LP	W/L	
15	Luik × Sintra-Algueiras	P/LP	W/L	R/LR	W/L	CR/LP	W/L	
16	Bern × Sacavem	R/LR	W/L	R/LR	W/L	CR/LP	W/L	
17	Bern × Sintra-Algueiras	R/LR	W/L	R/LR	W/L	R/LP	LP/L	
18	Sacavem × Sintra-Algueiras	R/LR	W/L	R/LR	W/L	R/LP	W/L	

CR = Carmine Red
R = Red
LR = Light Red
Pk = Pink
W = White

LP = Light Purple
P = Purple
DP = Dark Purple

N = Number of filaments 10 or less
L = Number of filaments more than 10

*) The colour segregation of the F_2 is given in table 36.

TABLE 32. *Colour and segregation of the seed coat in F_2*

S. No.	F_2	Colour			Total	Parents		F_1
		Black	Brown	Grey		♀	♂	
1	Malta × Luik	48	25	18	91	Black	Grey	Black
2	Malta × Bern	46	25	18	89	Black	Brown	Black
3	Malta × Sacavem	54	26	32	112	Black	Brown	Black
4	Malta × Sintra-Algueiras	83	8	27	118	Black	Grey	Black
5	Luik × Malta	67	1	15	83	Grey	Black	Black
6	Malta × Lisbon	28	9	19	56	Black	Black	Black

size and form of their chromosomes. Later it has been shown that the karyotypes differ from species to species in many ways, which are described in the classic work of LEVITZKY (1931a, b), by HEITZ (1926, 1928, 1932), DARLINGTON (1937) and others. These distinguishing features are as follows: (a) chromosome number, (b) form and relative size of different chromosomes of the same set, (c) presence (or absence) and size of the satellites and secondary constrictions and (d) distribution of euchromatin and heterochromatin regions in the chromosomes. From a detailed comparison of the somatic complements of different species with regard to the above characteristics, structural changes may be inferred with some certainty as has been studied in genera such as *Fritillaria* (DARLINGTON 1930), *Crepis* (BABCOCK and CAMERON 1934), *Pisum* (SANSOME 1938 and BLIXT 1959) and others. These differences within a somatic complement indicate solely the range of structural change and the consequent differentiation. Besides, these morphological characteristics have been taken as a criterion to distinguish each of the pairs of homologous chromosomes of a species.

Most of the karyological studies on these two species, namely *P. setigerum* and *P. somniferum*, relate only to the determination of the chromosome number (TAHARA 1915; LJUNGDAHL 1922; YASUI 1927, 1937a, b, 1940; KUZMINA 1935; SUGIURA 1936, 1938, 1940; FURUSATO 1940; and KOOPMANS 1956). However, KUZMINA and YASUI have studied the karyotype of *P. somniferum* L. in detail.

With regard to the somatic number of *P. somniferum* L. ($2n = 22$) the present study fully agrees with the observations recorded by the previous workers except FURUSATO (1940). KOOPMANS has

TABLE 33. *Mean diameter of the pollen grains 10 × 10 ocular division*

S. No.	Parents \ Diameter	7.5	8.0	8.5	9.0	9.5	10.0	10.5	11.0	11.5	12.0	12.5	13.0	13.5	14.0	14.5	15.0	Total	Mean $\bar{\times}$
1	Malta	—	—	—	4	14	72	74	96	57	45	42	38	38	20	—	—	500	11.5 ± 0.76
2	Luik	11	11	24	50	97	248	28	22	9	—	—	—	—	—	—	—	500	9.7 ± 1.05
3	Bern	—	—	—	—	5	63	160	183	65	20	4	—	—	—	—	—	500	10.8 ± 0.79
4	Sacavem	2	2	5	19	25	209	119	48	17	7	4	4	3	13	6	17	500	10.6 ± 1.25
5	Sintra-Algueiras	—	—	—	—	4	281	128	66	12	9	—	—	—	—	—	—	500	10.3 ± 0.89
6	Lisbon	—	1	4	39	74	376	6	—	—	—	—	—	—	—	—	—	500	9.8 ± 0.93

TABLE 34. *Frequency of different fertility groups in F_2-progenies*

S. No.	Fertility group / F_2	5	15	25	35	45	55	65	75	85	95	Total	Mean fertility $\overline{\times}$
1	Malta × Bern	20	16	21	19	21	7	14	15	11	5	149	42.3 ± 26.7
2	Malta × Sacavem	47	21	9	10	13	15	18	13	11	2	159	36.5 ± 28.7
3	Malta × Sintra-Algueiras	48	27	18	4	9	3	6	6	3	5	129	26.2 ± 26.2
4	Malta × Luik	40	45	21	12	11	9	6	7	3	1	155	26.3 ± 22.3
5	Luik × Malta	41	27	19	13	5	7	6	4	3	1	126	25.3 ± 22.6
6	Malta × Lisbon	31	20	5	4	4	3	4	12	7	5	95	21.3 ± 42.2

TABLE 35. *Frequency of different fertility groups in F_2-progenies*

S. No.	Fertility group / F_2	5	15	25	35	45	55	65	75	85	95	Total	Mean fertility $\overline{\times}$
1	Lisbon × Luik	29	6	6	1	2	1	3	3	1	1	53	22.0 ± 25.7
2	Lisbon × Bern	15	9	3	1	—	—	2	3	—	—	33	20.5 ± 22.9
3	Lisbon × Sacavem	44	22	5	3	5	8	3	1	6	4	101	25.8 ± 27.9
4	Lisbon × Sintra-Algueiras	38	18	4	2	7	4	11	6	8	4	102	33.2 ± 31.1
5	Luik × Lisbon	30	19	4	2	1	1	7	6	4	2	76	28.1 ± 29.1

TABLE 36. *Mean fertility value for the colour groups in the F_2*

S. No.	Colour group / F_2	Luik × Malta	Malta × Luik	Malta × Bern	Malta × Sacavem	Malta × Sintra-Algueiras	Malta × Lisbon	Mean fertility $\overline{\times}$
1	Light Purple	16.8	17.9	26.3	14.5	24.1	20.7	20.1 ± 4.2
2	Red	23.0	25.1	39.1	26.7	21.4	39.0	29.1 ± 7.7
3	Pink	15.0	21.7	47.0	52.1	21.7	65.0	40.2 ± 11.1
4	Reddish Purple	49.0	43.9	53.6	52.3	48.9	55.0	50.5 ± 3.2
5	Purple	69.0	50.6	50.6	62.3	40.6	66.1	56.5 ± 11.1

TABLE 37. *Mean fertility of the Parents, F_1s and F_2s*

S. No.	Hybrids	Mean fertility of the parents		Mean fertility of the F_1 $\overline{\times}$	Mean fertility of the F_2 $\overline{\times}$
		♀ $\overline{\times}$	♂ $\overline{\times}$		
1	Malta × Luik	83.9 ± 9.77	81.5 ± 4.18	7.5 ± 6.47	26.3 ± 22.3
2	Malta × Bern	83.9 ± 9.77	92.8 ± 1.86	10.3 ± 5.09	42.3 ± 26.7
3	Malta × Sacavem	83.9 ± 9.77	83.3 ± 2.02	3.3 ± 3.11	36.5 ± 28.7
4	Malta × Sintra-Algueiras	83.9 ± 9.77	80.3 ± 1.37	3.5 ± 2.85	26.2 ± 26.2
5	Luik × Malta	81.5 ± 4.18	83.9 ± 9.77	6.7 ± 8.18	25.3 ± 22.6
6	Malta × Lisbon	83.9 ± 9.77	91.6 ± 1.15	6.5 ± 4.66	21.3 ± 42.2
7	Lisbon × Malta	91.6 ± 1.15	83.9 ± 9.77	0.8 ± 0.86	*
8	Lisbon × Luik	91.6 ± 1.15	81.5 ± 4.18	2.0 ± 1.18	22.0 ± 25.7
9	Lisbon × Bern	91.6 ± 1.15	92.8 ± 1.86	1.3 ± 0.81	20.5 ± 22.9
10	Lisbon × Sacavem	91.6 ± 1.15	83.3 ± 2.02	2.4 ± 1.81	25.8 ± 27.9
11	Lisbon × Sintra-Algueiras	91.6 ± 1.15	80.3 ± 1.37	3.4 ± 1.77	33.2 ± 31.1
12	Luik × Lisbon	81.5 ± 4.18	91.6 ± 1.15	3.9 ± 2.26	28.1 ± 29.1
13	Luik × Bern	81.5 ± 4.18	92.8 ± 1.86	74.6 ± 8.46	*
14	Luik × Sacavem	81.5 ± 4.18	83.3 ± 2.02	79.8 ± 7.43	*
15	Luik × Sintra-Algueiras	81.5 ± 4.18	80.3 ± 1.37	77.7 ± 2.85	*
16	Bern × Sacavem	92.8 ± 1.86	83.3 ± 2.02	73.1 ± 4.51	*
17	Bern × Sintra-Algueiras	92.8 ± 1.86	80.3 ± 1.37	88.1 ± 1.65	*
18	Sacavem × Sintra-Algueiras	83.3 ± 2.02	80.3 ± 1.37	83.6 ± 4.81	*

* not studied

reported the number 2n = 22 in various types of *P. somniferum* L. but has also mentioned a type obtained from Malta received as *P. somniferum L.*, which showed a somatic number of 2n = 44. This material in which 2n = 44 has been reported, has been given for further study to the author who finds that this type is morphologically distinct from *P. somniferum* L. and belongs to *P. setigerum* DC. This has been confirmed by comparing with the typical *P. setigerum* DC. obtained from Canada and by the Director of the Royal Botanic Gardens, Kew.

Likewise, FURUSATO (1940) who mentioned 2n = 44 perhaps would have also been mistaken in the identification of the two

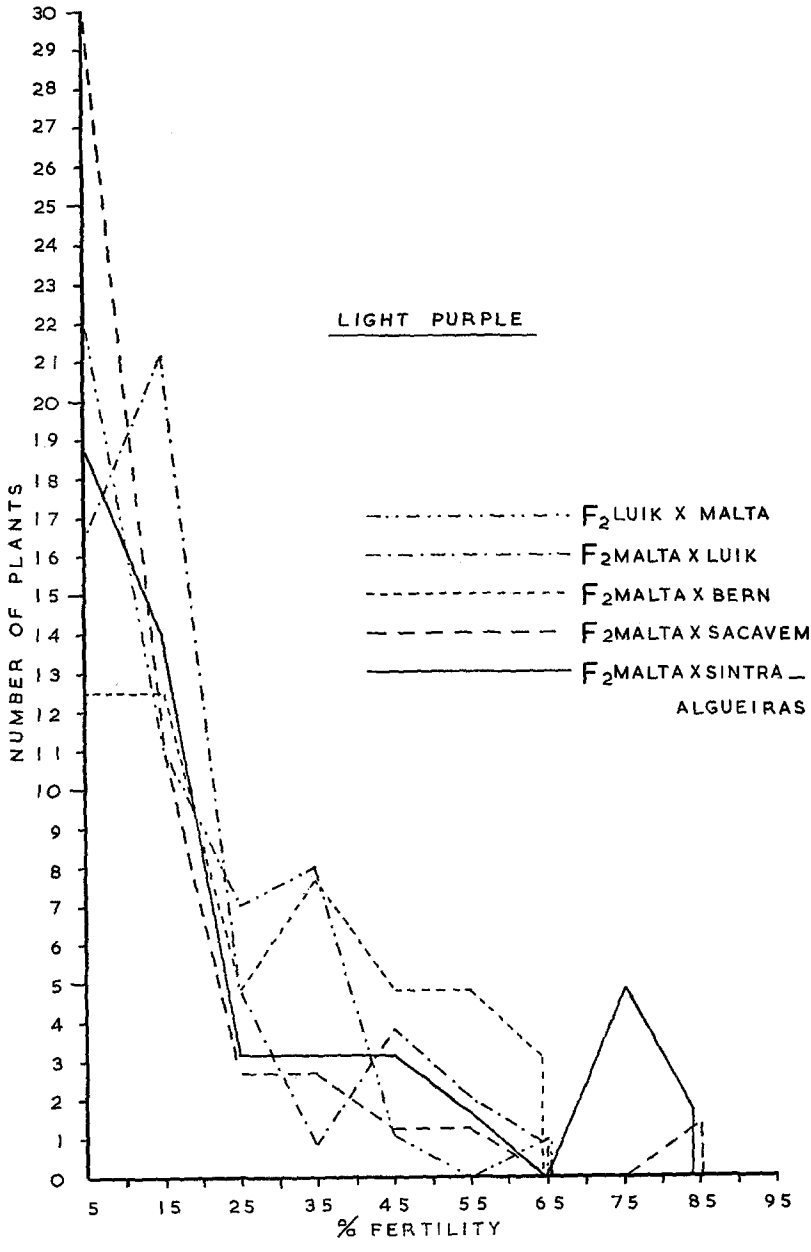

Fig. 55a. Frequency curve showing number of plants in the various fertility groups.

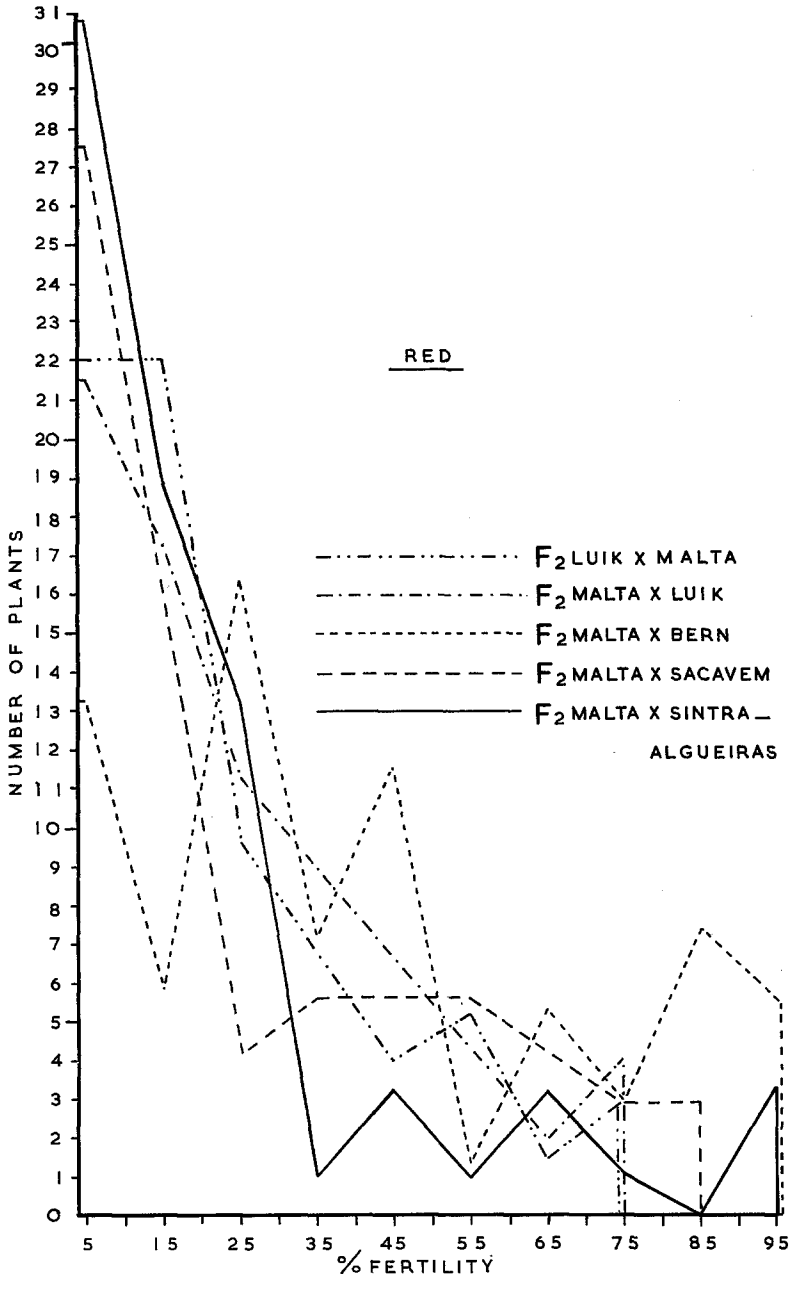

Fig. 55b. Frequency curve showing number of plants in the various fertility groups.

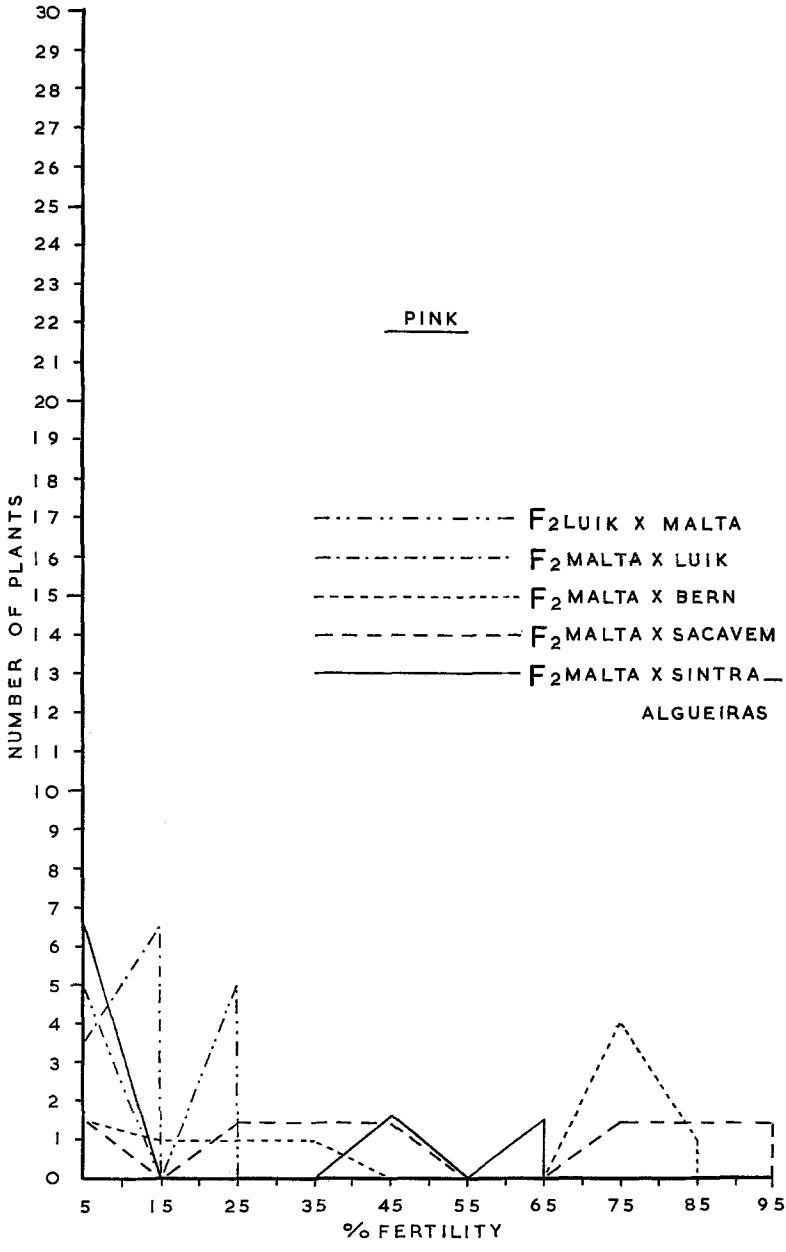

Fig. 55c. Frequency curve showing number of plants in the various fertility groups.

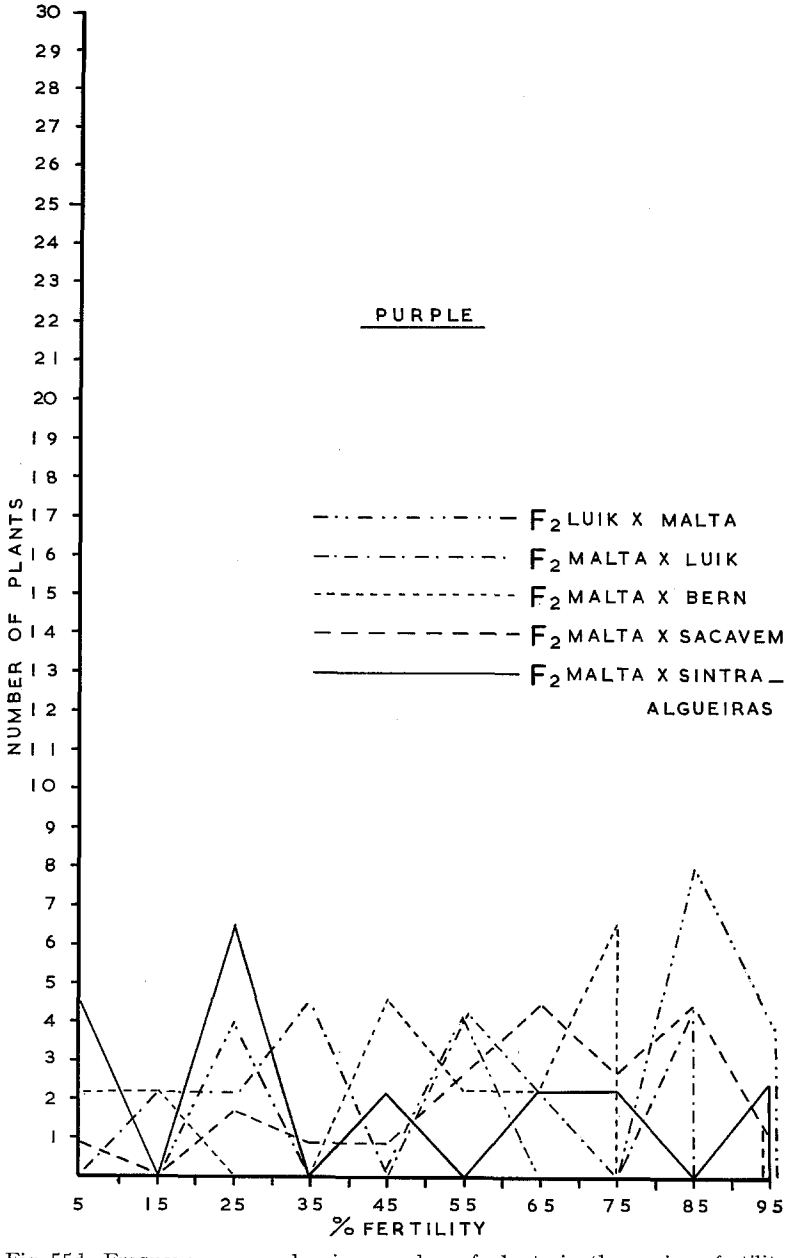

Fig. 55d. Frequency curve showing number of plants in the various fertility groups.

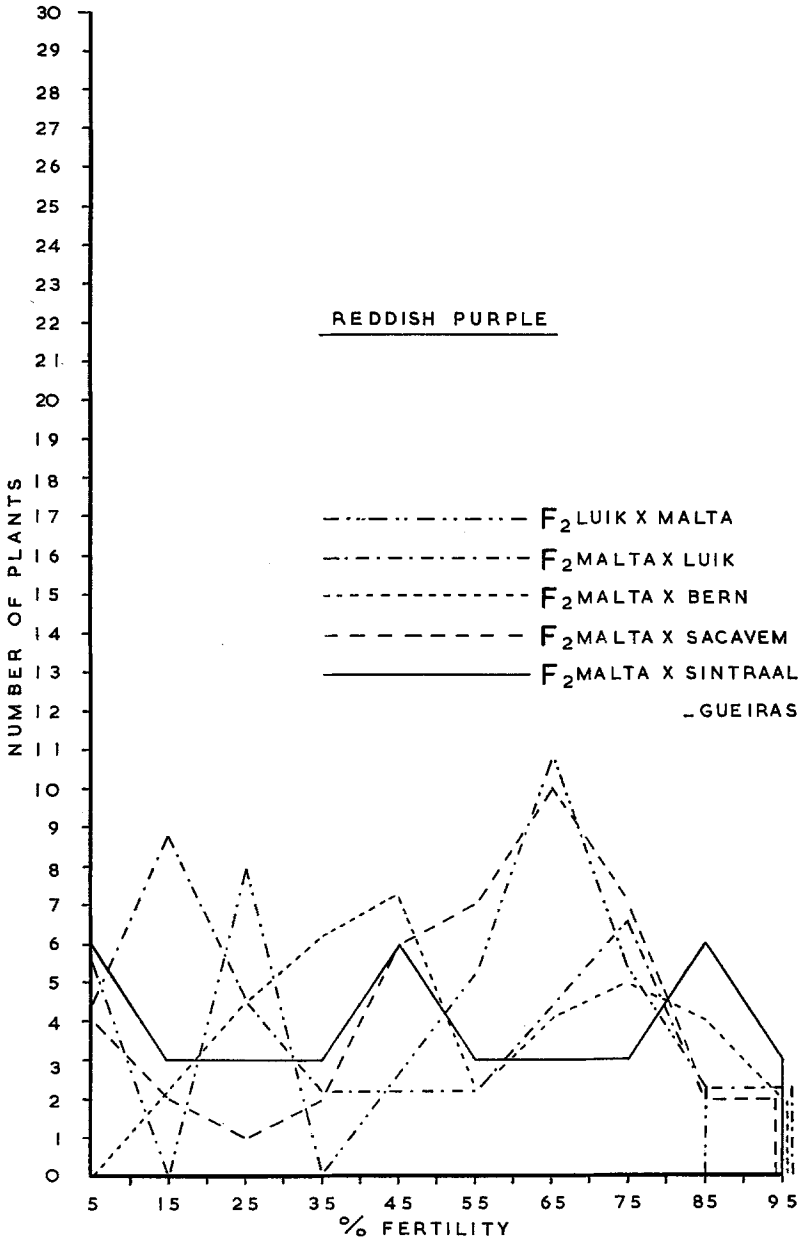

Fig. 55e. Frequency curve showing number of plants in the various fertility groups.

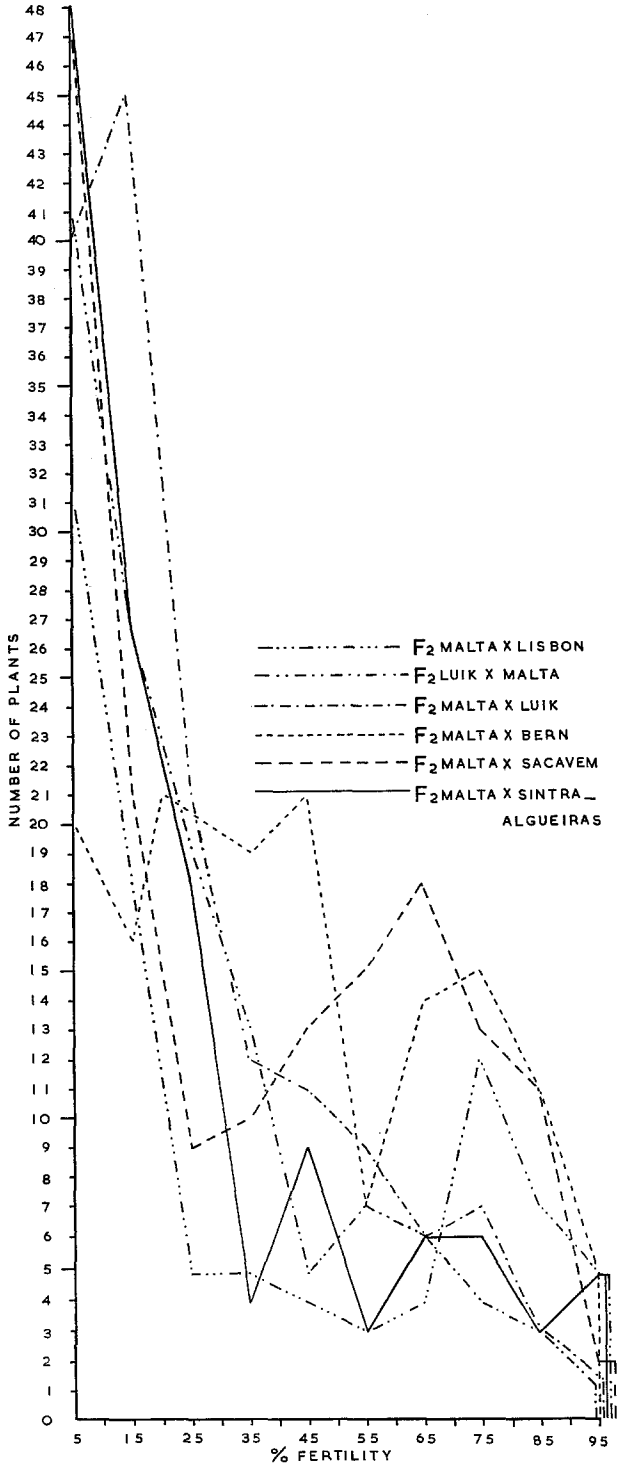

Fig. 56. Showing mean fertility of the F_2 progeny.

species. SUGIURA (1940) has mentioned eleven as the meiotic number of *P. setigerum* DC. – a very doubtful statement. It can not be taken for certain whether SUGIURA studied really *P. setigerum* DC., as neither description of the type nor an illustration has been given. Moreover, it has been found that there are some forms of *P. somniferum* L. closely resembling the other species. It is highly desirable, when such contradicting observations are made, to give a brief description of the type together with an illustration.

The contradicting data obtained by FURUSATO, SUGIURA and KOOPMANS, with regard to these two species seem doubtful, the writer believes that this is the result of inaccurate identification of the species.

KUZMINA (1935) finds in her studies of the karyotypical evolution in the species *P. somniferum* L. from semi-wild to cultivated types (Asian types), that the dehiscent poppies (Poppy of Madrid) form a distinct and rather a "homogeneous group set against all other cultivated subspecies". The same type of homogeneous or symmetrical karyotype has been found in the types in *P. somniferum* L. and *P. setigerum* DC., which form the dehiscent poppies.

Now we shall discuss the karyotypes of these types studied in the present paper except the type from Lisbon which will be discussed separately. Amongst the types of *P. somniferum* L. Luik has eleven homologous pairs with submedian chromosomes, whilst in the others varying degrees of structural changes have been observed.

In Bern we see under groups 9 and 29 (table 3, p. 24) three identical chromosomes each. We shall compare the length of the extra chromosome (the 3rd chromosome) in groups 29 and 9, – the length being $2.1 + 1.4 = 3.5\ \mu$ and $0.9 + 1.3 = 2.2\ \mu$ respectively. The short arm of the chromosome in group 9 ($0.9\ \mu$) suggests that there might have happened a deletion to the extent of $1.2\ \mu$ in length of the long arm of the otherwise homologous chromosome of group 29.

A simple translocation perhaps would have happened between the chromosomes in groups 5 and 29 in Sacavem while in Sintra-Algueiras such a translocation occurred perhaps between the chromosomes in the groups 16 and 30. This chromosome in group 30, happens to be telocentric after the simple translocation.

Malta shows in all the groups (except 1, 8, 18 and 21) 2, 6 or 8 submedian chromosomes as indicated in table 3, thereby suggesting

that perhaps there is a high amount of homology amongst the chromosomes in these groups. Eventhough there occur in one group four, six or eight chromosomes without any structural variation, this does not mean that they are really homologous. In the groups 8 and 21 one extra chromosome is found while the homologous chromosome is lacking in groups 1 and 18. This has been due to the structural changes happened, which can be explained in the following way. Let us take the length of the chromosomes from groups 1 and 18. They are

$$2.1 + 0.9 = 3.0\ \mu \text{ in group 1}$$
$$2.1 + 2.1 = 4.2\ \mu \text{ in group 18.}$$

This indicates that a breakage might have occurred and a part of the chromosome lost in one of the arms of a median chromosome in the group 18; or otherwise they form a homologous pair. The chromosomes in the groups 8 and 21 can also be explained in a similar manner.

Such structural variations like deficiency, deletion or fragmentation, following its breakage have been frequently reported (DARLINGTON 1937, SWANSON 1957). The deleted portion will not survive if it lacks a centromere, as it will be immovable in anaphase. Such a deficiency can arise by a single break in a chromosome followed by a healing of the broken end as observed by MCCLINTOCK (1932, 1938, 1941a, b) in *Zea Mays*. Such deletions involving loss of genic material can cause deleterious effect on the organism.

The evidence of such structural variations obtained from karyotype analysis, however, is incomplete and indirect; they may even be misleading unless this is supported by a detailed evidence from meiotic studies.

Now coming to YASUI's observations (1940) based on the karyotype analysis of one race of *P. somniferum* L., she opines that the "karyotype of *P. somniferum* L. seems not to be simple because *P. somniferum* L. consisting of a number of races, seems to have several different karyotypes among them". From the studies on the karyotypes of the four races reported in this paper, it can be stated that the karyotypes do not differ much one from the other, eventhough structural variations caused by deletions and simple translocations occur. Identical chromosomes are found to be present in these types as indicated in the karyogram (fig. 14d). Consequently, the genomes of these types in relation to *P. setigerum* DC. are given below:

Malta	Luik	Bern	Sacavem	Sintra-Algueiras	Lisbon
M_1	M_1M_1	M_1M_1	$M_1M_1M_1M_1$	M_1M_1	$M_2M_2M_2$
$M_2M_2M_2M_2M_2M_2$*)	M_4M_4	M_2M_2	$M_2M_2M_2M_2$	M_2M_2	M_3M_3
M_3M_3	M_7M_7	M_3M_3	M_3M_3	M_3M_3	M_4M_4
M_4M_4	M_8M_8	M_4M_4	M_5	M_5M_5	M_5M_5
M_5M_5	$M_{12}M_{12}$	$M_9M_9M_9$	M_6M_6	M_6M_6	$M_{10}M_{10}$
$M_6M_6M_6M_6M_6M_6M_6M_6$	L_1L_1	L_2L_2	L_1L_1	L_1L_1	$M_{11}M_{11}$
M_7M_7	L_2L_2	B_1B_1	B_1B_1	$L_2L_2L_2L_2$	L_3
$M_8M_8M_8$	L_3L_3	B_2B_2	S_1S_1	$B_1B_1B_1$	Lb_1
M_9M_9	L_4L_4	B_3B_3	$S_2S_2S_2$	B_2B_2	Lb_2
$M_{10}M_{10}$	L_5L_5	$B_4B_4B_4$		SA_1	Lb_3Lb_3
$M_{11}M_{11}$	L_6L_6				Lb_4
$M_{12}M_{12}$					Lb_5
M_{13}					
$M_{14}M_{14}$					
$M_{15}M_{15}$					
$M_{16}M_{16}M_{16}$					
$M_{17}M_{17}$					

*) The symbols given above, for example $M_2M_2M_2M_2M_2M_2$, do not mean that these six chromosomes are really homologous. It only indicates that they are identical in their length and position of the centromere. (M = Malta, L = Luik, B = Bern, S = Sacavem, SA = Sintra-Algueiras, Lb = Lisbon).

From this, it is concluded that amongst the somatic complements of these types, there is a high resemblance though not perfect. YASUI too has observed in a race two chromosomes viz 'XI_1 and XI_2' having no exactly homologous partner, as has been observed in the types studied. Besides, YASUI finds a satellite for every chromosome: the total being 22 satellites as mentioned in her table 1 (Cytologia vol 10, pp. 553, 1940). This does not agree with the observation recorded here, in which only two satellites are found for each karyotype, including the tetraploid species *P. setigerum* DC. In a private communication to me by letter she states "I have found each chromosome having a small terminal constriction, which I have called 'satellite'. Some of these chromosomes should be so-called SAT-chromosomes, but others do not attach the nucleolus, though they concern the extrusion of the nucleoli or separation of the substance from the chromosomes". As no clear distinction is made between the

SAT-chromosome and "the so-called SAT-chromosomes", her observations regarding this, cannot stand the test of validity.

Interlocking of bivalents or the 'quadrivalents' at diakinesis.

Apart from the normal pairing of homologous chromosomes observed at diakinesis, there is yet another type of pairing consisting of groups of bivalents in the first metaphase and the dyads in the second metaphase lying close together. This is not due to any chiasma formation, but is considered to be due to an attraction similar to somatic pairing. This is called secondary pairing which has been observed by KUWADA (1910) in *Oryza*, TAHARA (1910) in *Morus*, ISHIKAWA (1911) in *Dahlia*, CRANE and DARLINGTON (1927) in *Rubus*, RYBIN (1927) in *Nicotiana*, LAWRENCE (1929, 1931a, c) in *Dahlia*, MEURMAN (1929) in *Aucuba*, DARLINGTON and MOFFETT (1930) and MOFFETT (1931) in *Pyrus*. LAWRENCE has discussed the secondary association in detail and has considered this association as the basis for the homology of the chromosomes. According to DARLINGTON and LAWRENCE the secondary association is the union of the homologous chromosomes of small size in metaphase which failed to form multivalents in the meiotic prophases. This type of secondary association is entirely different from the type of association recorded in this paper. Further, this is different from what HÅKANSSON (1931) has described as amphibivalent to the association of two bivalents in the form of a ring or a chain of four chromosomes during the M–I of some *Pisum* crosses. Two, three, four or more bivalents interlock themselves giving the configuration of a 'quadrivalent', a 'sexivalent' or an 'octavalent' as the case may be. These interlocked bivalents can not be considered as true quadrivalents or sexivalents etc., because of the definition given for a quadri-, sexi-, or octavalent by KNIGHT (1948) quoted from DARLINGTON: "an association of chromosomes held together by chiasmata during the period from diplotene to metaphase of the first meiotic division". The 'quadrivalents', 'sexivalents' or 'octavalents' observed here do not satisfy the conditions cited above, because these associations appear in the late prophase and during late diakinesis they separate themselves to bivalents which behave in the normal way in M–I. Moreover, no chiasmata have been observed so as to hold the chromosomes together. These types of associations have not been recorded for other species studied

in the other sections of the genus *Papaver* (LJUNGDAHL, 1922, 1924; YASUI 1927, 1936, 1937, 1941, 1943 and KOOPMANS 1954, 1955). This shows that this mode of association is perhaps peculiar to the species in the section *Mecones*. But this cannot be stated with certainty as in the other species of this Section namely *P. glaucum* Boiss. et Hausskn., *P. gracile* Auch. and *P. Decaisnei* Hochst et Steud. no karyological studies have yet been made.

We propose the name pseudoquadrivalent, pseudosexivalent or pseudooctovalent as the case may be, for these types of associations between bivalents which enter into an interlocking in the prophase and separate out as bivalents in the late diakinesis.

The exact cause for the formation of these interlockings is not precisely known. YASUI (1940) too has observed the same phenomenon in *P. somniferum* L. and has held the view that the nucleolus may not be the main cause of bivalent association. However, it seems evident to the author, that this type of associations are perhaps genetically controlled by five polymeric factors. If we take the types Lisbon and Luik, at diakinesis no such associations are met with. But the hybrids between them exhibit these associations; the maximum being five bivalents interlock to form a pseudodecavalent. Similarly the crosses of Lisbon and Luik with the other races of *P. somniferum* L. show this tendency to form pseudoquadrivalents or pseudosexivalents. This phenomenon can be best explained on the basis of the following hypothesis. We shall assume that five polymeric genes namely P_1P_1, P_2P_2, P_3P_3, P_4P_4 and P_5P_5 (the symbol P is taken to denote pseudo-) control this tendency of the bivalents to interlock. The factors P_1 and P_2 themselves can not produce this peculiar tendency under their own power, whereas P_3, P_4 and P_5 can exhibit this phenomenon independently. However, P_1 and P_2 can interact together or in combination with P_3 or P_4 can create this condition. But P_1, P_2 and P_3 behave as epistatic factors for P_5 so much so in their presence P_5 can not make the bivalents to form pseudoquadri-, pseudosexi- or pseudooctavalent. Based on the above assumption, the genotypes of the parents and their hybrids with regard to this particular behaviour can be expressed as follows:

	Parent or the hybrid	Genotype	Whether pseudo-quadri-, pseudo-sexi-, pseudo-octa or pseudo-decavalent are formed or not	Reference table
1	Lisbon	$P_1P_1\ p_2p_2\ p_3p_3\ p_4p_4\ p_5p_5$	No	see text
2	Luik	$p_1p_1\ P_2P_2\ p_3p_3\ p_4p_4\ p_5p_5$	No	see text
3	Bern and Sacavem	$p_1p_1\ p_2p_2\ P_3P_3\ p_4p_4\ p_5p_5$	Yes	5 and 6
4	Sintra-Algueiras	$p_1p_1\ p_2p_2\ p_3p_3\ P_4P_4\ p_5p_5$	Yes	7
5	Malta	$p_1p_1\ p_2p_2\ p_3p_3\ p_4p_4\ P_5P_5$	Yes	4
6	Lisbon × Luik	$P_1p_1\ P_2p_2\ p_3p_3\ p_4p_4\ p_5p_5$	Yes	13 and 16
7a	Lisbon × Bern	$P_1p_1\ p_2p_2\ P_3p_3\ p_4p_4\ p_5p_5$	Yes	14 and 15
b	Lisbon × Sacavem			
8	Lisbon × Sintra-Algueiras	$P_1p_1\ p_2p_2\ p_3p_3\ P_4p_4\ p_5p_5$	Yes	see text
9	Lisbon × Malta	$P_1p_1\ p_2p_2\ p_3p_3\ p_4p_4\ P_5p_5$	No	see text
10a	Luik × Bern	$p_1p_1\ P_2p_2\ P_3p_3\ p_4p_4\ p_5p_5$	Yes	22
b	Luik × Sacavem			
11	Luik × Sintra-Algueiras	$p_1p_1\ P_2p_2\ p_3p_3\ P_4p_4\ p_5p_5$	Yes	22
12	Luik × Malta	$p_1p_1\ P_2p_2\ p_3p_3\ p_4p_4\ P_5p_5$	No	see text
13	Bern × Sintra-Algueiras	$p_1p_1\ p_2p_2\ P_3p_3\ P_4p_4\ p_5p_5$	Yes	22
14a	Malta × Bern	$p_1p_1\ p_2p_2\ P_3p_3\ p_4p_4\ P_5p_5$	No	see text
b	Malta × Sacavem			
15	Malta × Sintra-Algueiras	$p_1p_1\ p_2p_2\ p_3p_3\ P_4p_4\ P_5p_5$	Yes	8

Thus we see a case of anisomeric polymery in which the factors donot have quite the same effect, but can still intensify one another, whereas in the isomeric polymery all factors are equivalent and each factor in its turn intensifies the same character to a limited degree (SIRKS, 1956).

RILEY and CHAPMAN (1958) have shown that in hexaploid common wheat, control of the purely bivalent forming, diploid-like, meiotic behaviour is influenced by a gene, or genes, on one particular chromosome. In the absence of this chromosome, pairing can take place

between equivalent, homologous chromosomes in each of the there genomes, so that wheat ceases to behave as a classical autosyndetic allopolyploid.

Heteromorphic pairing: From a critical analysis of the karyotype, it has been found that in some groups there exist chromosomes having no homologous partner, while in some other groups more than two chromosomes are found. Normally one will expect the formation of multivalents amongst the chromosomes in the groups 2, 6, 8 and 21 in Malta, 9 and 27 in Bern, 1, 2, and 29 in Sacavem, 14 and 16 in Sintra-Algueiras and 2 in Lisbon (cf table 3, p. 24). Likewise, a single chromosome without a homologous partner observed in some other groups, will in the normal course behave as an univalent. But in meiosis, neither multivalents nor univalents are found to occur; only bivalents are found. This suggests that in the groups having more than two chromosomes – for example, eight chromosomes in group 6 and six chromosomes in the group 2 in Malta – instead of pairing as octa- or sexivalent, they form only 4 or 3 bivalents. Some of these bivalents, perhaps enter into an interlocking later to give pseudoquadri- or pseudosexivalents; the probable cause of which has been discussed in the foregoing pages. Further, as no univalents are observed in any of these parental types, it is evident that these single chromosomes pair with the extra chromosomes present in the other groups. For example, pairing may occur between the chromosome in group 1 and the third chromosome in group 18 in Malta. This assumption is justified by the fact that two to three bivalents having end to end attachment have been observed in these types; that is to say that there is some extent of pairing between heteromorphous chromosomes, at one of their ends. Such heteromorphic pairing has been observed by HOLLINGSHEAD and BABCOCK (1930) in *Crepis*, PHILP and HUSKINS (1931) in *Matthiola* and NAVASHIN (1932) in *Crepis*.

More than fifty percent of the synaptic pairs are either ring bivalents with two terminal chiasmata each or open rings with one terminalised and one non-terminalised chiasmata each. This suggests that the homology is only between the ends of the two chromosomes that pair, thereby indicating that segmental interchanges might have occurred in the course of evolution of the karyotypes. Moreover,

interstitial chiasma is found to occur very rarely; so much so the terminalisation coefficient per bivalent is nearly one in the parents and one in their F_1 hybrids as shown in the tables 38 and 39.

Although the meiosis is regular in the parents, bridges are noticed. That these are only disjunction bridges formed as a result of the late arrival of the longer chromosomes at the equator, is inferred from the absence of fragments, absence of micronuclei in the interphase and sterility (HRISHI 1952). Likewise, precocious separation of some of the bivalents indicates the occurrence of a terminal chiasma between two short homologous chromosomes (PAINTER 1927, LARTER 1932).

TABLE 38. *Terminalisation coefficient of chiasmata of the parents calculated from 10 cells*

S. No.	Type	2n	Number of bivalents	Total number of chiasmata	Average number of chiasmata per bivalent	Total number of interstitial chiasmata
1	Malta	44	220	412	1.87	7
2	Luik	22	110	156	1.42	1
3	Bern	22	110	170	1.55	6
4	Sacavem	22	110	197	1.79	2
5	Sintra-Algueiras	22	110	183	1.66	—
6	Lisbon	20	100	139	1.39	5

TABLE 38. *Continued*

S. No.	Type	Average number of interstitial chiasmata per bivalent	Total number of terminal chiasmata	Average number of terminal chiasmata per bivalent	Terminalisation coefficient	Maximum number of chiasmata in any bivalent
1	Malta	0.03	405	1.84	0.98	3
2	Luik	0.01	155	1.41	0.99	2
3	Bern	0.06	164	1.49	0.97	4
4	Sacavem	0.02	195	1.77	0.99	3
5	Sintra-Algueiras	—	183	1.66	1.00	2
6	Lisbon	0.05	134	1.34	0.96	3

TABLE 39. *Terminalisation coefficient of chiasmata of the F_1s calculated from 10 cells*

S. No.	F_1	2n	Total number of univalents	Average number of univalents per cell	Number of * bivalents	Total number of chiasmata	Average number of chiasmata per bivalent	Total number of interstitial chiasmata	Average number of interstitial chiasmata per bivalent	Total number of terminal chiasmata	Average number of terminal chiasmata per bivalent	Terminalisation coefficient	Maximum number of chiasmata in any bivalent
1	Malta × Luik	33	100	10	115	175	1.52	—	—	175	1.52	1.00	2
2	Malta × Bern	33	90	9	120	185	1.54	3	0.02	182	1.52	0.98	2
3	Malta × Sacavem	33	90	9	120	190	1.58	—	—	190	1.58	1.00	2
4	Malta × Sintra-Algueiras	33	90	9	120	200	1.67	—	—	200	1.67	1.00	2
5	Luik × Malta	33	90	9	120	165	1.38	—	—	165	1.38	1.00	2
6	Malta × Lisbon	32	80	8	120	198	1.65	—	—	198	1.65	1.00	2
7	Lisbon × Malta	32	80	8	120	175	1.46	—	—	175	1.46	1.00	2
8	Lisbon × Luik	21	10	1	100	153	1.53	—	—	153	1.53	1.00	2
9	Lisbon × Bern	21	50	5	80	98	1.23	—	—	98	1.23	1.00	2
10	Lisbon × Sacavem	21	10	1	100	112	1.12	—	—	112	1.12	1.00	2
11	Lisbon × Sintra-Algueiras	21	10	1	100	172	1.72	—	—	172	1.72	1.00	2
12	Luik × Lisbon	21	10	1	100	160	1.60	—	—	160	1.60	1.00	2
13	Luik × Bern	22	—	—	110	145	1.32	—	—	145	1.32	1.00	2
14	Luik × Sacavem	22	—	—	110	150	1.36	—	—	150	1.36	1.00	2
15	Luik × Sintra-Algueiras	22	—	—	110	147	1.34	—	—	147	1.34	1.00	2
16	Bern × Sacavem	22	—	—	110	180	1.64	—	—	180	1.64	1.00	2
17	Bern × Sintra-Algueiras	22	—	—	110	185	1.68	—	—	185	1.68	1.00	2
18	Sacavem × Sintra-Algueiras	22	—	—	110	175	1.59	—	—	175	1.59	1.00	2

* The poeudo-trivalent has been considered as one bivalent + one univalent.

Is Papaver setigerum an allotetraploid of P. somniferum? With the discovery of the prevalence of structural changes, the phylogenetical and autosyndetic relationships of chromosomes have been well inferred (SANSOME and PHILP 1939). In autopolyploids only autosyndesis can take place whereas in allopolyploids both auto- and allosyndesis can occur. For example, in the hybrid between *Papaver striatocarpum* (2n = 70) and *P. nudicaule* (2n = 14), LJUNGDAHL (1924) has found that 21 bivalents are formed. She has assumed that these bivalents resulted from internal pairing amongst the *striatocarpum* complement (autosyndesis) and pairing of the complement of *nudicaule* with 7 of the *striatocarpum* chromosomes (allosyndesis). Similar examples can be found in *Primula kewensis* while autosyndesis occurs in the allopolyploid *Nicotiana digluta* (CLAUSEN and GOODSPEED 1925) which contains two sets of *N. tabacum* chromosomes and two sets of *N. glutinosa* chromosomes. Twentyfour *Tabacum* bivalents and 12 *glutinosa* bivalents are formed. KIHARA (1929, 1930b and 1931a) in his studies on the conjugation of homologous chromosomes in the genus hybrid *Triticum* × *Aegilops*, has found from the existence of bivalents, the positive occurrence of autosyndesis within the different sets of chromosomes. EMME (1936) reports such complete pairing by autosyndesis in the hybrid between *Solanum longipedicellata* (2n = 48) and *S. rybinii* (2n = 24).

In the following interspecific crosses namely *Papaver somniferum* L. × *P. nudicaule* L. (YASUI 1927), *P. bracteata* Lindl. × *P. orientale* L. (YASUI 1936), *P. somniferum* L. × *P. bracteata* Lindl. (YASUI 1937), and *P. bracteata* Lindl. × *P. lateritium* (YASUI 1941), partial pairing between the chromosomes of the two parents involved in these different crosses, to form a few bivalents and one to three bivalents, has been reported. But YASUI has failed to mention whether such pairing has been due to autosyndesis or allosyndesis. In the crosses between *P. setigerum* DC. and *P. somniferum* L. (Malta with other types-groups a and b) investigated here, always one 'trivalent' (two 'trivalents' in the case of Malta × Lisbon), eleven bivalents and eight univalents are found to occur. The formation of the eleven bivalents is perhaps due to allosyndesis between the eleven chromosomes of either of the parents.

The 'trivalent' is not typical. During late diakinesis this pseudotrivalent separates out as a bivalent and an univalent as also has

been observed by YASUI (1937) in a trigenomic hybrid of *Papaver*. If so, then it remains to decide how this twelfth bivalent has arisen? This is perhaps possible only by autosyndesis between two chromosomes in the complement of Malta. It is highly probable that the third chromosome in the pseudotrivalent, that later behaves as the univalent, belongs to the karyotype of Malta, having a very weak homology. In the competition to form the chiasmata amongst these three chromosomes, often the third chromosome with a weak homology at one of its ends, is eliminated, so much so, a ring bivalent between the other two chromosomes is formed. And with this bivalent the third chromosome sticks on with one of its ends till late diakinesis. Further, the eight chromosomes which do not pair in the hybrids and behave as univalents naturally belong to Malta.

Hence mainly allosyndesis occurs and to a very low degree autosyndesis between the genomes of P. setigerum DC. and P. somniferum L. This evidently indicates that P. setigerum DC. is an allotetraploid of P. somniferum L.

The Univalents – their behaviour and the evolutionary consequences in the tetraploid-diploid crosses.

The behaviour of the univalents in the hybrids and in the F_2s reported here, is conspicuous and peculiar. The question why the univalents divide at the heterotypic division in such hybrids, has been considered quite obscure (GAJEWSKI 1949). Further, the rules governing their movements during meta- and anaphases, orientation and division are far from being understood, eventhough many reports on the description of this behaviour are found in literature (DARLINGTON 1928, ERLANSON 1929, AASE 1930, THOMPSON and ROBERTSON 1930, CLAUSEN 1931, MORINAGA 1931, VAKAR 1932). A critical analysis of this particular phenomenon will no doubt throw some light on the question of the mechanics of evolution.

When the bivalents have already orientated for disjunction in M–I, the univalents are found scattered in the periphery of the spindle. Some univalents may also be found near the center of the spindle, but they are not quite well arranged. At anaphase this difference is still more striking. The bivalents disjoin and the dyads move to the poles. All the univalents slowly migrate to the equator, so much so, at this stage two anaphasal groups of bivalent halves

towards the poles and in the equator a more or less ring like configuration of univalents, have been observed. At late anaphase the univalents begin to stretch. Some of the univalents are found to stretch to many times their initial length while others seem to remain unchanged. At the end of anaphase and the beginning of telophase, the picture of the univalents appears to be very irregular. Sometimes the size of the two halves of the univalents is very unequal and it simulates a fragmentation more than a division of the univalent. The number of univalents going to the poles is regular. In a few cases in the hybrid and in the reciprocal cross between Malta and Lisbon, the univalents are found to migrate to the poles at random without any division and this migration happens before the disjunction of the bivalents. The stretching and movement of the univalents are much delayed and are often found to prolong until telophase. However, these daughter chromosomes of the univalents are found included into one of the nuclei except in the cross Malta × Sintra-Algueiras where in 38 percent of the interphase one to four chromosomes are seen left in the cytoplasm.

From the above description of the behaviour of univalents in relation to the bivalents in A–I the following conclusions can be drawn:

(a) The congression, orientation and disjunction of the bivalents are quite normal.
(b) The disjunction of the bivalents is quite independent of the behaviour of the univalents.
(c) The univalent behaviour in the heterotypic division mainly depends on two factors: their ability to migrate to the equator and their ability for proper orientation and division.

Regarding the question of movement GAJEWSKI (1949) has discussed two types of movements namely in transverse and longitudinal directions. For the longitudinal movement, forces of attraction or repulsion between poles and centromeres are responsible whereas for the transverse movement ÖSTERGREN (1945) suggests that some transverse equilibria on the spindle must exist. However, from the rather slow and unsteady movement of the univalents to the poles after division, it seems evident to the author, that the spindle mechanism has some part to play. The spindle formed in A–I is especially intended for a heterotypic division, the fibres of

which exhibit much turgor as they have to exert a great force sufficient enough to make the bivalents disjoin and move to the poles. After the exertion of such a force, the spindle mechanism perhaps loses its turgor, so much so, when the univalents enter for the homeotypic division, which in the normal course is not expected, it fails to cope up with the function for which it is intended.

In the hybrid between Malta and Sintra-Algueiras the fact that some of the univalents do not reach the poles, is perhaps due to the unbalanced timing of the univalent division and of the telophasal and interphase changes in the P.M.C.'s. KIHARA (1930) has stated that if the regression (the transition to the stage of interphase) begins earlier, when the univalents are still on the poles, we obtain two nuclei; but if the univalents are nearer the equator, micronuclei are formed. It has been reported that in general the movement of the univalent is delayed in asynaptic hybrids more than in hybrids with a greater number of bivalents (GAJEWSKI 1949). Perhaps, the presence of the bivalents and their influence on the spindle formation is a stimulus to the movements and division of the univalents. In all hybrids the congression, separation and movement to the poles of the univalents are always delayed when compared with the bivalents. What is early anaphase for bivalents is still metaphase for the univalents. Likewise, the anaphase of the univalents corresponds to the telophase of the dyads. In other words, there is a difference of one stage in the behaviour of the bivalents and univalents in meiosis, that is to say that more time is required to complete both these hetero- and homeotypic divisions.

The splitting of the univalents and their actual separation into two parts are two separate processes (GAJEWSKI 1949). AASE (1930) has stated "if, however, the movement to the poles is delayed and the anaphase split occurs, it affects simultaneously all the univalents wherever they lie on the spindle. An univalent lying at the equator will actually divide, adding a half to each pole. A dividing univalent lying off the equator will add both its halves to the nearer pole". This statement indicates that the univalent divides irrespective of its position in the spindle. But in the hybrids and in the F_2s investigated here, the univalents are found to divide completely and each half moving to one ploe. Regarding the kind of orientation of the univalents in the spindle, it can not be precisely stated as the

univalents are small in size and spherical in shape due to extreme contraction. According to KOLLER (1938) and DARLINGTON (1939), usually the misorientated univalents do not divide at all or are misdivided by transverse division at the centromere. However, in the material investigated all the univalents are found to divide completely which indicates that the univalents are orientated in the spindle in the normal way.

Now, we shall go back to the second anaphase where high irregularity is met with in the congression and anaphase movement of these daughter chromosomes of the univalents. These daughter chromosomes are found to lie in the equational plate along with the chromosomes derived from the heterotypic division. These chromosomes divide homeotypically and migrate to the poles without any abnormalities, while the daughter chromosomes of the univalents lag behind. However, some of the chromosomes reach the poles to join the telophase nuclei and the rest form themselves into micronuclei of various sizes. This lagging behaviour is perhaps due to the misorientation of these chromosomes in the spindle, which have already undergone the homeotypic division in the first anaphase.

How far does this peculiar behaviour of the univalents influence the mechanism of evolution? *Two consequences arise from this kind of behaviour of the unpaired chromosomes namely, 1) this type of behaviour and the number of univalents present directly contribute to sterility, and 2) by this behaviour the unpaired chromosomes are eliminated gradually from generation to generatiou so that the hybrid (triploid) resorts back to diploid with a few dominant characters of the tetraploid.*

We shall discuss in detail the first aspect, that is, the relation of univalents to sterility. The occurrence of univalents in frequencies as high as nine found in the hybrids, gives rise to a considerable proportion of gametes with different chromosome numbers and in turn to aneuploid progeny. If the univalents behave in the normal way, that is to say, they migrate at random to the poles in the A–I and homeotypically divide in A–II, then naturally one can expect gametes with varying numbers of chromosomes. Assuming that the E.M.C. behaves in the same way, then in the second generation the gametes give rise to aneuploid plants with a wide range of chromosome numbers. Chromosomal sterility may not be high unless other

TABLE 40. *Chromosomal segregation in F_2**

S. No.	Hybrids	F_2 segregation Number of chromosomes															Total number of plants
		22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	
1	Malta × Luik	2	1	—	—	1	1	1	1	1	1	2	4	3	2	5	25
2	Malta × Bern	1	4	4	4	4	4	2	2	—	—	—	—	—	—	—	25
3	Malta × Sacavem	—	—	—	1	—	1	2	—	1	—	1	5	6	5	3	25
4	Malta × Sintra-Algueiras	2	2	4	3	1	—	1	—	1	—	—	1	4	4	2	25
5	Malta × Lisbon	6	10	3	2	1	—	1	—	—	—	1	1	—	—	—	25

*) This has been determined from the root tips of the seedlings raised by sowing selfed F_1 seeds.

factors such as incompatibility of the chromosomes or the genes, are present in the gametic interplay. But in a situation like the one met in the hybrids investigated here, along with the formation of sterile pollen grains, the unpaired chromosomes are eliminated gradually. If we examine the chromosomal segregation in the F_2 progeny as indicated in Table 40, it is interesting to note that most of the segregants fall below the triploid number ($2n = 33$). In the second generation (8 percent in the case of Malta × Luik and Malta × Sintra Algueiras, 4 percent Malta × Bern, 24 percent in Malta × Lisbon) even the diploid level is reached. This could be possible only if the gametes carry at least eleven chromosomes each. Gametes with less than eleven chromosomes except in the hybrid Malta × Lisbon, may not function. Further, this same trend is noticed in the F_3 indicating that the proportion of plants with a diploid number increases. This kind of mechanism is possible only if the unpaired chromosomes are eliminated gradually and the plant succeeds in this because of the peculiar behaviour of the univalents.

What will happen to the micronuclei? The micronuclei generally consist of univalents only. Since they contain less than the absolute minimum required for the normal function of the gametes, they are infertile and inviable.

Moreover, the percentage of normal tetrads as shown in table 9 (p. 46), is not exactly correct because the absolute percentage must be higher. The reason is as follows. For example, each tetrad with one extra micronucleus in the normal course will produce three normal pollengrains plus two micronuclei, so that we see five pollengrains whether they may be fertile or not. So also, if we consider a tetrad with two extra micronuclei, the possibilities are that there can occur two normal pollengrains plus 4 micronuclei or 3 normal pollengrains + 3 micronuclei as the case may be. Such a proportion of the number of normal pollen grains against the number of micronuclei for a given number of univalents can be calculated. But it can not be statistically expressed as the number of possibilities for the formation of micronuclei are not the same as the number of probabilities. However, the estimation of the number of probabilities is possible if the number of chromosomes present in the various micronuclei can be determined.

What we estimate on the basis of normal tetrads against tetrads with micronuclei, is not always the absolute value for the expected percentage of pollen sterility. From the table 9, it is seen that the percentage of normal tetrads is 30.4 for Malta × Luik. Under the circumstances discussed above, it is possible that the absolute percentage of normal tetrads increases and consequently the percentage of fertile pollengrains. But the actual percentage of fertility estimated from the pollengrains is 7.5 as indicated in the last column in table 9. This indicates that a large amount of normal tetrads have become sterile pollengrains. This is perhaps due to chromosomal or genic disturbance which causes a deleterious effect on the formation of good pollen. Further, all good pollen need not be viable. But this point cannot be discussed as no investigations regarding the viability of the pollen are available. *Thus the sterility in the hybrids is partly due to the high irregularity in the behaviour of the unpaired chromosomes in meiosis and partly due to chromosomal or genic incompatibility.*

Apart from sterility, these unpaired chromosomes can cause disturbed genetic ratio's in the F_2 (HOLLINGSHEAD 1932), which will be discussed later.

When eight or nine univalents are found in the F_1 hybrids, that number is considerably reduced to a number from seven to four in

most of the F_2s investigated. Proportionately the percentage of mean fertility increases. Hence by providing such a mechanism the sterile hybrid plants after gradual elimination of their unpaired chromosomes restore back their fertility in the course of a few following generations.

Intraspecific hybrids of parents with the same chromosome numbers (F_1-hybrids in the group d).

When different so-called cryptic types from different geographical areas are intercrossed, the F_1-hybrids may show a ring of four or a more complex association in the meiosis revealing structural differences between the parent types (BLAKESLEE 1929; BERGNER, SATINA and BLAKESLEE 1933; BLAKESLEE, BERGNER and AVERY 1937, MÜNTZING 1938). ÅKERMAN and HAGBERG (1954) have found partial intraspecific sterility in oats which on cytological analysis has shown that more than half of the P.M.C.'s are irregular. Such meiotic irregularities show a specific degree of partial sterility. It has been demonstrated that this sterility is due to the death of certain definite classes of recombination gametes (MÜNTZING 1956). However, in the ecotypes studied here, the F_1 combinations amongst these types do not show any irregularity in the meiosis nor give any sterility, eventhough the presence of structural differences in the somatic complements of these types is evident. *This possibly suggests that these ecotypes are genetically well balanced, inspite of their structurally different chromosomes.*

Inheritance of characters investigated:

Chief characters such as height, branchiness, width and length of the leaf, colour of the petal, of the filament and of the seed coat have been investigated. Before discussing the mode of inheritance, it is worthwhile to mention that the parents involved in the crosses in groups a, b and c have different somatic numbers; in other words, the hybrids in group a are between the tetraploid and the diploid, in group b between the tetraploid and the 'nullisomic' and in group c between the 'nullisomic' and the diploid.

As we have pointed out earlier, the occurrence of unpaired chromosomes will cause, in addition to sterility, disturbed genetic ratios in the F_2 progeny (HOLLINGSHEAD 1932, MÜNTZING 1932). Hence a true

mendelian segregation can not be expected, as certain classes of recombination gametes are lethal.

We shall now discuss the inheritance in the interspecific crosses (groups a and b). From table 27 (p. 77), it is quite evident that perhaps the genes for height in Sacavem and Sintra-Algueiras are much less expressive than those of the other types in the 22 chromosome group. Besides, it is interesting to note that the height in the F_2s does not differ much, but within each F_2 there is a considerable deviation. In the F_1-hybrids in group c, the F_1s with regard to height are either intermediate or nearer to the taller parent. It is surprising to observe that the mean height of the F_2 is lower than of the F_1s. Like the other groups, the deviation within the F_2 is rather high.

Regarding the number of branches, no appreciable differences have been noticed.

In the case of the length of the leaf, it is seen that the short leaf growth of Malta seems to prevail in the F_1s and F_2s. Here again, in the hybrids of group d, the growth genes in Sacavem and Sintra-Algueiras seem to have less intensity than those in the other 22 types. Like the length of the leaf, for width, the factors for small width in Malta appear to manifest in the F_1s and F_2s, whereas in the other groups c and d, the hybrids are intermediate. As the area of the leaf is directly proportional to the length and width of the leaf, it is probable that the genes for the leaf size of Malta seem to express themselves in the hybrids and in the F_2s. From such a large variation in the size of the leaf and in the height of the plants, it is presumed that these characters are controlled by polymeric genes.

Now, considering the colour of the petal, it is rather difficult to state the exact mode of inheritance, as an array of different colours in the petal ranging from White to Red is observed in the F_2 progeny. Even based on the main colour groups, namely, White, Pink, Light Purple, Purple, Reddish Purple and Red, no exact mendelian ratios have been obtained. Two reasons can be assumed for these disturbed ratios namely (1) the difference in chromosome number in the parents and (2) the death of certain classes of recombination gametes. However, from the F_1-hybrids, the following general conclusions may be drawn, apart from the fact that these colours are due to the action of polymeric factors. The recessive nature of the white flower to the

coloured is a well known phenomenon in various plants (MIYAKE and IMAI 1927). So here also, White acts as a recessive to Light Purple and Red, whereas with Purple it interacts to produce the intermediate colour Pink. But MIYAKE and IMAI have reported that Purple is fully dominant over White and segregates as 3 Purples and one White in the F_2. Light Purple is found to be recessive to Red. The genes for the colour of the petal and for the colour of the filament are not found to be linked. The expression of these factors are independent as can be seen in the cross between Light Purple petal with Dark Purple filament and Red petal with White filaments, giving in the F_1 Red petal with Dark Purple filaments (Example cross no. 2 – Malta × Bern, in table 31, p. 81). When both parents have White filaments the F_1 also shows White filaments irrespective of the petal colour in the parents (Example cross no. 13 Luik × Bern in table 31). It is also seen that the colour of the filaments behaves in the same way as the colour of the petals in its dominance or recessiveness; but they seem to be independent in their manifestation.

It is interesting to note that the cross between Malta × Luik differs from the reciprocal (table 31) hybrid with regard to the flower colour in the F_1. Malta with Luik gives in the F_1 Red flowers, whereas in the reciprocal the Light Purple colour of the male parent (Malta) is seen. If it is purely of cytoplasmic influence, then the results must be otherwise. Perhaps, it is possible that the genes for Red colour are present in Luik which produces the red colour when introduced into the cytoplasm of Malta, whereas, in the reciprocal cross such a behaviour perhaps cannot take place. Moreover, in the other hybrid combinations (except with Lisbon) having Malta as female, they produce only Red flowers.

The colour of the seed coat namely White or Straw-coloured – both classified under the colourless group – coincides with the white colour at the base of the petal. If the base of the petal is Light to Dark Purple, then the colour of the seed coat is from Dark Grey to Black. Such a correlation between the colour at the base of the petal and colour of the seed coat has also been observed by LEAKE and PERSHAD (1920), while FRUWIRTH (1924) and PROCHASKA (1926) do not find any such positive correlation.

Besides the correlation found between the colour at the eye of the petal and the seed coat, the Black colour of the seed coat seems

to be dominant over Grey and Brown. As indicated in table 32 (p. 82), one of the parents (Malta) has Black colour for the seed coat, while the others have Grey or Brown colour. In all the F_1 combinations, the colour of the seed coat is Black, thereby indicating that the colour Black is dominant over other colours. From the F_2s, however, no interpretation of the exact nature of inheritance is possible due to the occurrence of disturbed ratios.

Now, coming to the diameter of the pollengrains, there seems to exist a difference on the species level; that is to say, that the pollengrains of Malta are larger in diameter than the other types. This might be due to the size of the nucleus which in turn contains more chromosomes than in the other species. Amongst the types having 22 chromosomes, excepting Luik, the other types produce pollengrains of nearly the same diameter. No precise explanation can be given to the exceptional behaviour found in Luik. The diameter of the pollengrains in Lisbon being 9.8 ± 0.93 is comparable to the other diploid types (except Luik) on the basis of the presence of the somatic number.

Before concluding this portion of the chapter, one point of interest is that the parental types do not set seed well when they are selfed. However, PHILP (1933) in his investigations in *Papaver Rhoeas*, has found that selfed flowers frequently set seed although selfincompatibility is common.

Male Sterility. (F_2s of the hybrids under groups a and b)

We shall now discuss the sterility observed in the F_2 progeny. We have seen the reason and the mechanism by which partial fertility is restored in the F_2s. As seen from table 37 (p. 85), the parents are highly fertile; the mean fertility ranges from 92.8 ± 1.86 to 80.3 ± 1.37. Leaving aside the hybrids in group d, the other F_1 hybrid combinations at both inter- and intraspecific level, show a low fertility mean ranging from 10.3 ± 5.09 to 0.8 ± 0.56. However, the mean fertility goes up in the F_2 progeny with a range from 20.5 ± 22.9 to 42.3 ± 26.7. If we examine the fig. 56, it can be observed that the F_2s investigated, show almost a similar trend in their frequency of plants in different fertile groups. As the fertility goes up, the number of plants in all the F_2s falls down gradually as indicated in tables 35 and 36 (p. 84).

Apart from this general trend, it is interesting to find that there seems to exist a certain correlation between the colour of the flower and the mean fertility level in the F_2s. The details have been discussed elsewhere (HRISHI, unpublished). If we suppose that various types of F_2s behave in the same way with regard to the difference in mean fertility for different colour groups, it is possible to apply the test of significance based on Wilcoxon's weighted sum test

$$\frac{\sum n_i . m_i}{{\sigma_i}^2} s_i$$

where i is for the i-th type of crossing, n_i for plants of one colour and m_i for a second colour. The results obtained from the test of significance are indicated in the following table.

TABLE 41. *Results of the test of significance*

Colour	Number of observations	Mean fertility %	Colour			
			Red	Pink	Reddish purple	Purple
Light purple	264	20.1	+ +	+ +	+ +	+ +
Red	304	29.1		0	+ +	+ +
Pink	31	40.2			0	+
Reddish purple	130	50.5				0
Purple	73	56.5				

0 means that the test is *not* significant on a level of 5%

\+ means that the test is significant on a level of 5% but it is not on a level of 1%

\+ + means that the test is significant even on a level of 1%.

Perhaps it is superfluous to observe that the high significance need not be based on the difference in mean fertility level, but it may perhaps be caused by the greater number of plants that occur in one particular colour group. In the case of colour Pink, not only the number of plants is very small, but also it does not give any decisive significance over other colour groups with regard to fertility. However, it is evident from this analysis, that there is a certain degree of correlation between the flower colour and its mean fertility.

The exact cause of this selective behaviour of the colours with

reference to the fertility can not definitely be inferred. *However, all available data seem to support the hypothesis that the genes for sterility are associated with genes for flowercolours; the expression of which is perhaps controlled by the maternal plasm.*

Can the type from Lisbon be considered a nullisomic?

Although monosomics have been observed fairly frequently in polyploid species, nullisomic plants have seldom been reported. CLAUSEN (1941a) has isolated at least 20 out of the 24 possible monosomic types in *Nicotiana Tabacum*, but so far he (1941b) has not obtained any nullisomics. In hexaploid *Avena sativa*, HUSKINS (1927) has recorded one nullisomic with 20 pairs of chromosomes and PHILP (1935, 1938) has isolated two more nullisomics. LOVE (1940) has evolved many nullisomic plants and even nullisomic lines in 50 strains (F_5 to F_7) selected for agronomic characters from hybrids of *Triticum vulgare* $\times$ *T. durum* and most of these nullisomics are to some extent fertile. Intraspecific polyploidy (called as such by TANDON and MZALIK, 1959) with two chromosomes less than the normal diploid type has been reported in *Convolvulus pluricaulis*. But no mention as to the viability of this type has been made.

SEARS (1944) has stated that "only in the higher polyploid, however, such as the allohexaploid *Triticum vulgare* (n = 21) common wheat, are nullisomics viable". Similar observation has been made by MÜNTZING (1958) who states that "in diploid species not only nullisomics but also monosomics are as a rule inviable, whereas trisomics are viable and less influenced by the presence of an extra supernumerary member of the chromosome complement". But the "nullisomic", that we are discussing here, stands exception to the statements of SEARS and MÜNTZING, as this happens to be a viable "nullisomic" of the diploid. This type has 20 chromosomes in its somatic complement; that is to say, two chromosomes less than the diploid level. Whether these two lacking chromosomes form a homologous pair or not, has to be considered. We shall go back to the table 3 (p. 24), where the length of the long arm and the total length of the chromosomes are indicated. In these groups 15, 31, 32, 34 and 35, the homologous chromosome is lacking, whereas, in group 2, one extra chromosome is present apart from the homologous pairs. We shall compare the length of these chromosomes under the

different groups.

Group 31 – $2.8 + 2.2 = 5.0\ \mu$

Group 34 – $2.7 + 0.6 = 3.3\ \mu$

This suggests that a deletion to the extent of about 1.6 μ might have occurred and that the portion of the chromosome is lost in the short arm of the chromosome in group 34. Or, otherwise, they form a homologous pair. Similarly, the chromosome in group 32 can be compared to the extra chromosome (third chromosome) in group 2. Their lengths being:

$2.2 + 2.2 = 4.4\ \mu$ in Group 32

$2.2 + 1.6 = 3.8\ \mu$ in Group 2

It is evident that a deletion perhaps, might have happened to the extent of 0.6 μ in one of the arms of the otherwise median chromosome in the group 2. If so, these two median chromosomes are similar in homology. Now, it remains to discuss about the single chromosome seen in the groups 15 and 35. The chromosome in the group 15, can be considered comparable with the homologous chromosomes of the same group in Luik; thereby indicating that in this 'nullisomic' perhaps one chromosome in the homologous set is lost. No comparable chromosome is seen for the chromosome in group 35, either in the karyotype of Lisbon or in the karyotypes of other diploid types of *somniferum* and in *setigerum*. Perhaps it is possible to find a comparable chromosome pair in some other karyotype if more karyotypes of other races of the diploid species, from geographical zones nearer to this 'nullisomic' are investigated. Hence, we see from this analysis of the karyotype, that this 'nullisomic' does not lack one homologous pair of the diploid but two chromosomes from two homologous sets; that is to say, this 'nullisomic' is 2n — 1 — 1 and not 2n — 2. Moreover, the absence of two chromosomes from the two homologous sets, perhaps balances the genic make up; or otherwise, this 'nullisomic' would have been sterile or partially sterile as reported in wheat (SEARS 1944).

In view of the fact that by chromosome number, this type could be classified under nullisomics (2n — 2), however, this type differs from other nullisomics (2n — 2) in the genome make up. In the former case, a homologous pair is lacking whereas here, two chromosomes from two homologous pairs are absent as pointed out earlier. *So, this type can be considered as "double monosomic" (2n – 1 – 1)*

This terminology is especially chosen to be on a par with the double trisomic, where the genome is represented as $2n + 1 + 1$.

Nullisomic wheat plants produce only nullisomic progeny when selfed (SEARS 1953). Monosomics, however, may give three kinds of offspring namely, disomic, monosomic and nullisomic normally in frequencies 2 : 1 : 1 respectively. The type Lisbon, being double monosomic has a normal meiosis and gives only double monosomic progeny on selfing as in the case of nullisomic wheat.

Further, for such a double monosomic, normally one can expect two unpaired chromosomes in synapsis, as opposed to the nullisomics where one homologous set is only lacking. Here, no such univalents are noticed. However, from that bivalent, which is formed by the end to end attachment of the two chromosomes (with one terminal chiasma) and disjoins precociously often even at the late diakinesis, inference may be drawn that these two chromosomes pair at one of their ends having very little homology. Otherwise, they will behave as unpaired chromosomes and cause disturbances in meiosis. Such irregularities in meiosis will tend to give infertile and inviable pollengrains. Absence of all these irregularities suggests that this double monosomic behaves just like a true diploid.

Now, we have to consider whether this type can be treated as a separate species? If the taxonomical definitions proposed by LÖVE (1950) "are really accepted and practised by all botanists, the so called 'intraspecific chromosome races' of the cytologists would never be accepted by taxonomists, as differences in chromosome number without exception, reveal a very strong barrier of sterility". The types with different chromosome numbers are never connected by 'a clinal variation' nor can they be classified as ecotypes; although they are always ecologically distinct. DOBZHANSKY (1951) has pointed out that the process of speciation, as distinct from the race formation, consists in the development of 'reproductive isolating mechanisms'. Due to the sterility barrier, as we have seen between the double monosomic (Lisbon) with the other diploid types (e.g. Luik, Bern, Sacavem and Sintra-Algueiras), such a type is not classifiable as subspecies or variety (LÖVE 1950). The only taxonomical group in which this type can be classified into is that of a separate species. If this is to be treated as a separate species according to LÖVE's hypothesis, then the question naturally arises is, under which genus

this type can be placed? If we see the basic numbers of the different genera under Papaveraceae, only the genus *Chelidonium* and the genus *Bocconia* have 5 and 10 as their basic numbers respectively. But, there is no justification to place this type under one of these genera, purely on the basis of chromosome number, as no morphologically distinguishing features are sufficient enough to separate this type from the section Mecones in the genus *Papaver*. Moreover, this type in its somatic complement possesses chromosomes which are comparable to the chromosomes of the other types in the diploid species *P. somniferum* L. and also of the allotetraploid species *P. setigerum* DC., both coming under the section Mecones. Hence, it is perhaps more accurate to consider this type for the present as a viable double monosomic of the diploid species *P. somniferum* L. *

Before concluding this aspect, it is interesting to mention the basic importance of the new lines of research work being carried out (SEARS 1953) with the isolation of viable monosomic and nullisomic lines to facilitate genic analysis. With the help of these materials, considerable progress has been made in locating genes on definite chromosomes (MÜNTZING 1956). If that be so, the double monosomic of the diploid *P. somniferum* L. can be utilized for further work for locating genes in certain chromosomes. In this connection, we may note that only this type exhibits a characteristic rosette which is not found in the diploid ecotypes studied here. It can be conjectured that perhaps the genes to produce this characteristic rosette might be present in the single chromosome in group 35. Besides, another distinguishing feature observed in meiosis, quite peculiar to this double monosomic, is that some of the bivalents are found to be connected with thin threadlike structures (fig. 24, p. 38), perhaps simulating "sticky chromosomes". It is presumed that the genes responsible for this character might be located in the chromosome in group 35. However, this assumption can be proved only by proper breeding experiments together with karyological analysis.

* According to the Director, Royal Botanic Gardens, Kew, P. 5901 (type from Lisbon) apparently is *Papaver somniferum* L. and indistinguishable from the bulk of the material of this species in the herbarium. White flowers are not unusual in the species.

Relationship between P. somniferum L. and P. setigerum DC.

Before concluding this chapter, it is of paramount importance to discuss the exact relationship of the cultivated species *P. somniferum* L. to the wild type *P. setigerum* DC. It has already been pointed out that *P. setigerum* DC. (Malta) is found to be an allotetraploid of *P. somniferum* L. If so, can the view held by the taxonomists beginning from DE CANDOLLE that *P. somniferum* L. has originated from this wild type, be justified? At this juncture, it is not superfluous to analyse critically the views of VESSELOVSKAYA (1933), KUZMINA (1935), YASUI (1940) and SUGIURA (1940).

VESSELOVSKAYA reports that "the crosses of *P. somniferum* and *P. setigerum* are readily effected and give rise to perfectly normal fertile hybrids with viable seeds". Based on the investigations reported here, it may be concluded that the statement of VESSELOVSKAYA is largely inaccurate, as the crossing though readily effected, gives rise to only highly sterile hybrids with a very few viable seeds. Further, KUZMINA has not agreed that *P. setigerum* has been the progenitor of *P. somniferum* because of the fact that *setigerum* possesses 44 chromosomes in comparison with 22 in *somniferum*. In view of the findings, the author, however, hesitates to recognize the view of KUZMINA. It has been mentioned earlier that *P. setigerum* DC. has been found to be an allotetraploid of *P. somniferum* L. whereas *P. setigerum* DC. perhaps, possesses three genomes namely genome A consisting of 11 chromosomes, genome B consisting of 3 chromosomes (which pair by autosyndesis) and genome C having 8 chromosomes (that behave as unpaired chromosomes in the interspecific cross). The genome A of *setigerum* is comparable to the genome of *somniferum*, which can also be designated as A. These two genomes have been found to pair, although they possess structurally different chromosomes. However, a valid explanation has to be sought for the presence of two different genomes namely B and C, besides the genome A. If we accept the hypothesis of SUGIURA (1940) that "*Papaver, Argemone, Meconopsis* and *Roemeria* are derived from both Corydaleae and Chelidonieae, the former having the basic number 4, and the latter 3", then, it is possible to put forth a working hypothesis that the genomes B and C of *setigerum* have been contributed perhaps by two species of these genera. We can not exactly name those two species unless we have a thorough investigation of

all the members under these genera. Also, it is possible that those species might be extinct in nature; such can be inferred from the findings of the archeologists that *setigerum* itself has been found to exist in the glacial period.

The view of SUGIURA that *P. glaucum* could be the ancestor of *P. setigerum* can not be accepted as her hypothesis is solely based on the chromosome number n = 11 given for *setigerum*, the nomenclature of this plant being very doubtful.

Finally, the hypothesis of YASUI (1940) that *P. somniferum* L. is an amphitriploid, whose probable origin has been already referred in chapter III p. 11, remains to be discussed. The chromosome constitution of this species is given as $((3 + 4) = 7 + 4) = 11$. Based on this chromosome constitution, she has denied the possibility that *setigerum* (n = 22) can be considered an ancestor of *somniferum*. We have seen that the interspecific hybrids between *P. setigerum* DC. and *P. somniferum* L. in later generations resort back to diploidy having the dominant characters of the tetraploid parent. From this, it may be inferred that *P. setigerum* DC. would have hybridized in nature with some other species closely resembling *P. somniferum* L. In a few generations later, by the process of elimination of unpaired chromosomes, a diploid type might have formed. This view is further supported by the fact that amongst the 22 chromosome types, varying kinds of morphologically distinguishable races are met with; one form nearly resembling *P. setigerum* DC. and the other form highly differentiated in the process of evolution, like the ecotype from Luik.

Chances of obtaining such forms from the hybridization between *P. setigerum* DC. and *P. glaucum* Boiss. et Hausskn. (2n = 14) are remote, as the species *glaucum* has morphologically distinguishable characters from the other two species in question, such as the shape of the leaves and the shape and form of the flower etc. The author cannot state whether the other two members in the section Mecones namely *P. gracile* Auch. and *P. Decaisnei* Hochst. et Steud. can be one of the other ancestors, as neither detailed karyological investigations nor even the chromosome numbers have been determined. But it looks probable from the shape of the capsules of all the species in the section Mecones as illustrated by FEDDE (1909), that there is certainly a high degree of resemblance amongst them. Hence, it is

presumed that a complete karyological investigation of the other three members of this section, may throw light on the problem of speciation of *P. somniferum* L. and its relationship with *P. setigerum* DC. and with the other co-species. *So far such investigations, that can supplement the data already presented here, are not carried out, we may only conclude for the moment that P. setigerum DC. is one of the allotetraploids of P. somniferum L. and that the latter species perhaps has evolved from species hybrids. This hypothesis is quite in accordance with the theory of evolution by species hybrids founded by Lotsy in 1916.*

SUMMARY

Cytogenetical investigations on *Papaver setigerum* DC. and *Papaver somniferum* L. and their interspecific cross, are reported. One ecotype of *P. setigerum* DC. from the island Malta and five ecotypes of *P. somniferum* L. from Luik (Belgium), Bern (Switzerland), Sacavem, Sintra-Algueiras and Lisbon (Portugal) have been taken for this study.

Along with the cytogenetical studies, the mode of inheritance of main morphological characters such as the height, branchiness, length and width of the leaf and colour of the petal, of the filament and of the seed coat, has been indicated. With regard to the size of the leaf, the small size of *P. setigerum* DC. is found to manifest in the F_1s and F_2s. As to the colour of the petal in the F_1s, the colour White is found to be recessive to Light Purple and Red, whereas with Purple, it interacts to give the intermediate coulour Pink. The difference in the appearance of colour in the cross and in the reciprocal, of Malta $\times$ Luik, is explained hypothetically that this may be due to the reaction between the maternal plasm and the genes for the colour. The colour in the filaments seems to behave just like the colour in the petal, although the genes for colour of the petal and filament are found to express independently of the other. The colours at the base of the petal and of the seed coat are found to be correlated.

However, interpretation of the exact mendelian inheritance of these characters is not possible due to the disturbed ratios in the F_2. Two reasons are assumed for the disturbed ratios namely (1) the difference in the chromosome number of the parents and (2) the death of certain classes of recombination gametes.

Male sterility in the F_1s and F_2s has been investigated. That there is a certain degree of correlation between the flower colour and its mean fertility in the F_2, is evident from this kind of selective behaviour of the colours with reference to the fertility; the exact cause of which cannot definitely be inferred.

Structural variations in chromosomes like deficiency, deletion or fragmentation in the karyotypes of the six parents studied, are evident. Based on the length and position of the centromere in each chromosome, the genomes of these types have been indicated. No more than two satellites have been observed in each karyotype.

The 'quadrivalents', 'sexivalents' or the 'octavalents' formed as the result of interlocking between bivalents, observed during meiosis, are not typical. It has been proposed to give the name pseudo-quadrivalent, pseudo-sexivalent or pseudo-octavalent, as the case may be, for these types of associations between bivalents which enter into an interlocking in the prophase and separate out as bivalents in the late diakinesis. Based on the assumption that these associations are perhaps genetically controlled by five polymeric genes, the genotypes of the parents and the F_1s with regard to this character, are indicated.

From the absence of multivalents formation, or unpaired chromosomes in meiosis in the parents, it has been concluded that there is some extent of pairing between the heteromorphous chromosomes at one of their ends.

That *P. setigerum* DC. is an allotetraploid of *P. somniferum* L. is evident from the fact that mainly allosyndesis occurs and to a very low degree autosyndesis within the genome of *P. setigerum* DC.

The univalents divide in the heterotypic spindle and segregate at random or lag behind as seen often in the second anaphase, to form micronuclei. Two consequences arise from this kind of peculiar behaviour of the unpaired chromosomes namely, (1) this type of behaviour and the number of univalents present directly contribute to sterility and (2) by this behaviour the unpaired chromosomes are eliminated gradually from generation to generation so that the hybrid (triploid) resorts back to the fertile diploid with a few dominant characters of the tetraploid.

The sterility in the hybrids is partly due to the high irregularity in the behaviour of the unpaired chromosomes in meiosis and partly

due to chromosomal or genic incompatibility. Apart from sterility, these univalents can cause disturbed genetic ratios in the F_2, as mentioned earlier.

From the study of the intraspecific crosses of the parents with the same chromosome numbers, it has been found that these ecotypes are genetically well balanced, notwithstanding their having structurally different chromosomes.

The reasons for considering the viable type from Lisbon with $2n = 20$, as a 'double monosomic' of the diploid species *P. somniferum* L. have been discussed at length.

The views of VESSELOVSKAYA, KUZMINA, YASUI and SUGIURA regarding the progenitor of *P. somniferum* L. have been examined in detail. It has been found that *P. setigerum* DC. possesses three genomes namely genome A consisting of 11 chromosomes (which pair with the A genome of *P. somniferum* L.), genome B consisting of 3 chromosomes (which pair by autosyndesis) and genome C having 8 chromosomes (that behave as unpaired chromosomes in the interspecific cross). That the genomes B and C have been contributed perhaps by two species under Corydaleae and Chelidonieae, the former having the basic number 4 and the latter 3, has been suggested on a hypothetical basis.

It has been concluded that *P. setigerum* DC. is one of the allotetraploids of *P. somniferum* L. and that the latter species perhaps has evolved from species hybrids.

SAMENVATTING

Een cytogenetisch onderzoek van *Papaver setigerum* DC. en *P. somniferum* L. en hun soortshybride. Van *P. setigerum* DC. werd een ecotype onderzocht, dat afkomstig was van het eiland Malta, van *P. somniferum* L. vijf ecotypen, afkomstig uit Luik (België), Bern (Zwitserland), Sacavem, Sintra-Algueiras en Lissabon (Portugal).

Naast deze cytogenetische studies werd de wijze van overerving van de voornaamste morphologische eigenschappen onderzocht, nl. de planthoogte, vertakking, lengte en breedte der blaren, kleur van het kroonblad, van de meeldraad en van de zaadhuid. Ten aanzien van de bladgrootte bleken de kleine afmetingen van *P. setigerum* DC. in de F_1 en F_2-generaties zich sterk te manifesteren. Voorzover de

kleur der kroonbladeren betreft, bleek wit recessief te zijn tegenover lichtpurper en rood, maar met purper het intermediaire type pink te geven. Het verschil in kleur tussen de reciproke kruisingen van Malta en Luik, kan wellicht toegeschreven worden aan verschil in reactie van het moederlijk plasma. De kleur der meeldraden gedraagt zich analoog aan die der kroonbladeren, hoewel ze in hun erfelijk gedrag onafhankelijk van elkaar zijn. Een correlatie werd gevonden tussen de kleur van de basis der kroonbladeren en die van de zaadhuid.

Een scherp mendelistische verklaring van het gedrag dezer genen kan echter niet gegeven worden, op grond van de verstoorde splitsingen in de F_2-generatie. Deze storing is toe te schrijven aan 1) het verschil in chromosomenaantal tussen de beide ouders, en 2) het letale karakter van bepaalde klassen van recombinatie-gameten.

Pollensteriliteit komt voor in de F_1- en F_2-generaties. Dat een zekere correlatiegraad schijnt te bestaan tussen de bloemkleur en de gemiddelde fertiliteit in de F_2, lijkt aannemelijk op grond van de selectieve rol, die deze kleuren spelen in verband met deze fertiliteit. Een verklaring van deze samenhang kan echter niet gegeven worden.

Het blijkt, dat in de verschillende karyotypen der zes oudertypen, structurele chromosoomvariaties voorkomen, zoals deficiency, deletion en fragmentatie. Op grond van de lengte der chromosoomarmen en de ligging van het centromeer in ieder chromosoom, kunnen de genomen van elk dezer typen worden vastgesteld. In alle karyotypen werden slechts twee satellieten waargenomen.

De 'quadrivalenten', 'sexivalenten' en 'octavalenten' die tengevolge van interlocking tussen bivalenten gedurende de meiose worden waargenomen, hebben geen blijvende betekenis. Er wordt voorgesteld, voor deze typen van associatie de termen pseudo-quadrivalent, pseudo-sexivalent, pseudo-octavalent te gebruiken; de bivalent-associaties leiden tot een interlocking in de prophase en worden in de late diakinese weer opgelost. De veronderstelling lijkt gewettigd, dat deze associaties op de werking van vijf polymere genen berusten.

Uit de afwezigheid van multivalente of ongepaarde chromosomen in de oudertypen schijnt te volgen, dat heteromorphe chromosomen aan een van hun uiteinden kunnen conjugeren.

De soort *P. setigerum* DC. mag beschouwd worden als een allotetraploide van *P. somniferum* op grond van het feit, dat hoofd-

zakelijk allosyndese voorkomt, en slechts in geringe mate autosyndese binnen het genoom van de soort *P. setigerum* DC.

De univalenten splijten in de heterotypische spoel en worden willekeurig gescheiden of blijven achter, zoals vaak in de tweede anaphase wordt waargenomen; er ontstaan dan micronuclei. Uit dit eigenaardig gedrag der ongepaarde chromosomen volgen twee resultaten: 1) dat het gedragstype en het aantal der univalente chromosomen leidt tot steriliteit en 2) dat daardoor de ongepaarde chromosomen geleidelijk van generatie tot generatie geëlimineerd worden, zodat de triploide hybride terugkeert tot een fertiele diploide, waarin enkele dominante kenmerken van de tetraploide ouder aanwezig zijn.

De steriliteit der hybriden is gedeeltelijk toe te schrijven aan het onregelmatig gedrag der ongepaarde chromosomen, gedeeltelijk ook aan chromosomale of genen-incompatibiliteit. Behalve deze steriliteit kunnen ook verstoorde genetische splitsingsverhoudingen in de F_2 van dit gedrag der univalenten het gevolg zijn.

Uit de studie der kruisingen binnen de soort van ouders met hetzelfde chromosomenaantal bleek, dat deze ecotypen genetisch uitstekend gekarakteriseerd zijn, ondanks het feit, dat ze structureel in chromosomenconfiguratie kunnen verschillen.

Uitvoerig wordt gesproken over de conclusie, dat het type van Lissabon met $2n = 20$ te beschouwen is als een 'double monosomic' van de diploide soort *P. somniferum* L. en niet als een 'nullisomic'.

Een discussie is gewijd aan de opvattingen van VESSELOVSKAJA, KUZMINA, YASUI en SUGIURA over de oorsprong van *P. somniferum* L. Het is gebleken, dat *P. setigerum* DC. drie verschillende genomen bevat, nl. genoom A, dat uit elf chromosomen bestaat (die met de elf van het genoom van *P. somniferum* paren), genoom B gevormd door drie chromosomen (die door autosyndese kunnen paren), en genoom C, dat acht chromosomen telt (die in de soortshybride zich als ongepaarde chromosomen gedragen). Het lijkt niet uitgesloten, dat beide genomen B en C afkomstig zijn van twee soorten, uit de Corydaleae en uit de Chelidonieae, daar de eerstgenoemde het basisgetal 4, de anderen het getal 3 tonen.

De conclusie volgt, dat *P. setigerum* DC. een allotetraploide van *P. somniferum* L. is en dat deze laatste soort wellicht op haar beurt als soortshybride is ontstaan.

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