MEIOTIC ABNORMALITIES AND SECONDARY ASSOCIATIONS IN TWO DIPLOID PROGENITORS OF CULTIVATED *BRASSICA*

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ABSTRACT:

Analysis of meiotic pairing and secondary associations were done in two elementary cultivars belonging to two diploid species *B. campestris* L. ssp. rapifera and *B. oleracea* L. convar. capitata cultivated in Egypt. The results showed the occurrence of chromosomal abnormalities such as univalents and quadrivalents in some cases of the two cultivars studied. Univalents were detected in few PMCs (7%) of the cultivar Turnip Baladi, while 93% of the analyzed PMCs were free from pairing failure. Quadrivalents were detected in high frequency of 38% of the examined cells of the cultivar Cabbage Baladi. Quadrivalents frequency were interpreted as being due to a heterozygous reciprocal translocation between two non-homologous chromosomes or the existence of segmental chromosome duplications within the diploid genome in this cultivar. Ten and nine bivalents were found in the *B. campestris* L. and *B. oleracea* L. genotypes, respectively in most of their metaphase I cells. Estimated average number of chiasmata/PMC was greater in *B. oleracea* L. (16.956) than in *B. campestris* L. (16). These results indicate more pairing intensity between *B. oleracea* L. chromosomes than between *B. campestris* L. chromosomes. Likewise, separation of chromosomes at anaphase I and II proceeded, with the exception of few cases, normally in all examined cells of the two *Brassica* species. The most frequent abnormalities were the existence of anaphase bridge with or without fragments and lagging chromosomes at anaphase I. Secondary associations were detected in the two studied cultivated *Brassica* species. At metaphase I, a variable number of bivalents are secondarily paired. Secondary pairing may be described as pairing at metaphase resulting from a generalized attraction between bivalents related phylogenetically. It is therefore characteristic of polyploidy, and in many cases can be used as a structural changes in the complement of chromosomes. Chromosomal structural changes and rearrangements may play an important role in the gradual process of evolution and morphological differentiation in the two species *B. campestris* L. and *B. oleracea* L.. Such a study may throw more light also on the basic number of the two elementary diploid *Brassica* species.

INTRODUCTION

During the study of cytological features of meiosis in many species, chromosomal abnormalities and secondary associations has drawn the attention of several authors **(Consolaro *et al.*, 1996; Khazanehdari & Jones, 1997; Souza *et al.*, 1997; Pires Bione *et al.*, 2000 and Bellucci *et al.*, 2003)**. In the genus *Brassica* (*Cruciferae*), it has been found that the very large number of types and great diversity of forms can be reduced, if classified on

cytological bases, into a limited number of elementary monogenomic and amphidiploid digenomic species **(Prakash & Hinata, 1980)**. It was established definitely that *Brassica* crops consist of three elementary diploid species, *B. campestris* (AA), *B. oleracea* (CC) and *B. nigra* (BB) having 20, 18 and 16 chromosomes, respectively. From these diploids, three tetraploid species had originated through interspecific crosses followed by amphidiploidization. These species are *B. napus* (AACC), 2n = 38; *B. juncea* (AABB), 2n = 36 and *B. carinata* (BBCC), 2n = 34. The three elementary *Brassica* species exhibit variable degrees of chromosome pairing in hybrids produced between them **(Prakash & Hinata, 1980)**. In oilseed rape haploids, homeologous chromosome pairing at metaphase I was found to be genetically based and controlled by a major gene **(Liu *et al.*, 2006)**. The diploid progenitor species of the genus *Brassica* show a continuous haploid number of chromosomes ranging from 7 to 12 **(Mizushima, 1980)** and are evidently of aneuploid nature originating from a common prototype with a basic chromosome number of x = 6 **(Röbbelen, 1960 and Venkateswarlu & Kamala, 1971)**. It was concluded that the diploid genomes AA, BB, and CC may themselves be polyploid derived from a common ancestor with x = 6 chromosomes. The diploid ancestors themselves have been proposed to be polyploid derivatives. In a cytological study of the meiotic behavior of the elementary diploid progenitors of the allotetraploid *B. napus*, namely *B. campestris* L. and *B. oleracea* L., univalents were detected in one genotype of diploid *B. campestris* L. ssp. rapifera, and quadrivalents were detected in one genotype of diploid *B. oleracea* L. convar. botrytis **(Attia, 1987)**. The existence of multivalent in some diploid genotypes of *B. oleracea* L. has also been observed by other workers **(Sampson, 1970 and Gustafsson *et al.*, 1976)**.

Secondary associations in some species of *Brassica* were studied **(Howard, 1939 and Hussein & Abobakr, 1976)**. Also, **Darlington (1965)** suggested that cytologists studying meiosis usually illustrated the nuclei that were free of secondary associations to avoid the suspicion of bad fixation, and in consequence its occurrence has been neglected. The interrelationships among the monogenomic species could be determined either by studying the chromosome pairing in their F_1 hybrids **(Attia & Röbbelen, 1986)** or by analyzing the mode of secondary pairing of bivalents during their meiotic division **(Hussein & Abobakr, 1976)**. Structural alterations in *Brassica* chromosomes have been deduced from studies of meiotic karyotypes of the diploid species which showed differences in some minute details of their chromosomes, even within the same species **(Mukherjee, 1974; Chiang *et al.*, 1979 and Allam *et al.*, 1985)**. Due to a possible important role of chromosomal structural changes and rearrangements in the gradual evolution process in the genus *Brassica*, mechanisms indicating such chromosomal alterations (translocation, inversion, etc.) deserve special attention in cytological investigations of *Brassica*.

In Egypt, a number of local and introduced commercial *Brassica* varieties are repeatedly grown but only little information about their cytology is available. The present paper deals with the meiotic behavior and special attention has been paid to the primary and secondary pairing in two species of *Brassica* (*campestris* L. and *oleracea* L.) cultivated in this country. Also, the present study on the meiotic behavior aims to detect types and frequencies of abnormalities in the chromosome pairing and their possible significance for

these varieties. Meiotic chromosomes were studied exclusively on temporary smears preparations.

MATERIALS AND METHODS

Materials

Two of the most common commercial varieties of *B. campestris* L. and *B. oleracea* L. cultivated in Egypt, i.e., Turnip Baladi (ssp. rapifera) and Cabbage Baladi (convar. capitata) were used in this work. Seeds were obtained from the Department of Horticulture, Faculty of Agriculture, Fayoum University, and used in this study. Seeds were cultured in pots and kept in the greenhouse until flowering.

Methods

For the meiotic analysis, plants of the two cultivated *Brassica* species were grown in the greenhouse. Twenty plants of each cultivar were used for the meiotic studies. Small flower buds in appropriate size were collected between 8 and 10 a.m., killed and fixed in a solution composed of 4 parts chloroform: 3 parts ethyl alcohol: 1 part glacial acetic acid. After fixation for few hours, the material was kept in a refrigerator at 5 °C until used. Temporary preparations were made using iron-acetocarmine squash technique for meiotic studies. Slides were prepared for microscopic examination by the standard acetocarmine squash method. Pollen mother cells (PMCs) at the right stage were analyzed by research microscope with phase contrast and half automatic camera. Analysis of chiasma frequency based on the number of ring and rod bivalents was made. The study was confined to configurations and intensity of chromosome pairing at diakinesis, metaphase I, anaphase I, and when possible, anaphase II stage has also been analyzed. Taking in consideration that the interpretation of pairing configurations was sometimes not easy, chromosomal abnormalities and secondary associations has also been studied.

RESULTS AND DISCUSSION

Chromosome number

The chromosome number is n = 10 and 2n = 20 in *B. campestris* L. while, it is n = 9 and 2n = 18 in *B. oleracea* L. **(Darlington, 1965 and Eissa Ahmed, 1992)**. The small size of the chromosomes precludes the possibility of any critical study of the prophase stages. Therefore, the observations have been made solely from diakinesis to anaphase II. In the present material, examinations of meiotic cells showed the occurrence of the normal chromosome number reported by other workers as 2n = 20 and 18 for *B. campestris* L. and *B. oleracea* L., respectively. The results showed that in meiosis, the two *Brassica* species were almost normal in chromosomal pairing, with 10 bivalents in *B. campestris* L. and 9 bivalents in *B. oleracea* L. in most of their metaphase I cells, 2454 and 1998 PMCs (Table 1). Both ring- and rod-shaped bivalents occurred at metaphase I stage. The two members of a bivalent thicken and shorten, and also come closer to one another in 40 individual plants in the two studied cultivars.

Table 1. Meiotic analysis and chiasma frequency at normal metaphase I of the two elementary diploid species of the cultivated *Brassica* species, *B. campestris* L. and *B. oleracea* L..

Diploid species	Plant No.	No. of cells	Bivalents		Total Chias. No.	Aver. Chias./Cell	Aver. Chias./Biv.
			Rod	Ring			
	1	154	739	801	2341	15.201	1.520
B. campestris L.	2	91	339	571	1481	16.275	1.627
(var. Turnip	3	107	598	472	1542	14.411	1.441
Baladi)	4	75	500	250	1000	13.333	1.333
	5	194	973	967	2907	14.985	1.498
	6	94	674	266	1206	12.830	1.283
	7	150	634	866	2366	15.773	1.577
	8	112	836	284	1404	12.536	1.254
	9	125	189	1061	2311	18.488	1.849
	10	125	145	1105	2355	18.840	1.884
	11	115	86	1064	2214	19.252	1.925
	12	121	152	1058	2268	18.744	1.874
	13	120	176	1024	2224	18.533	1.853
	14	110	344	756	1856	16.873	1.687
	15	115	538	612	1762	15.322	1.532
	16	96	444	516	1476	15.375	1.538
	17	180	972	828	2628	14.600	1.460
	18	80	400	400	1200	15.000	1.500
	19	161	773	837	2447	15.199	1.520
	20	129	542	748	2038	15.798	1.580
Total	**20**	**2454**	**10054**	**14486**	**39026**	**16.000**	**1.590**
	1	153	223	1154	2531	16.542	1.838
B. oleracea L. (var.	2	151	129	1230	2589	17.146	1.905
Cabbage Baladi)	3	112	175	833	1841	16.438	1.826
	4	253	386	1891	4168	16.474	1.830
	5	88	147	645	1437	16.330	1.814
	6	51	72	387	846	16.588	1.843
	7	191	377	1342	3061	16.026	1.781
	8	130	166	1004	2174	16.723	1.858
	9	150	15	1335	2685	17.900	1.989
	10	60	34	506	1046	17.433	1.937
	11	85	40	725	1490	17.530	1.948
	12	100	27	873	1773	17.730	1.970
	13	32	32	256	544	17.000	1.889
	14	70	50	580	1210	17.286	1.921
	15	62	41	517	1075	17.339	1.927
	16	50	34	416	866	17.320	1.924
	17	30	28	242	512	17.067	1.896
	18	80	15	705	1425	17.813	1.979
	19	120	24	1056	2136	17.800	1.978
	20	30	70	200	470	15.667	1.741
Total	**20**	**1998**	**2085**	**15897**	**33879**	**16.956**	**1.884**

***Meiotic abnormalities in B. campestris* L.**

Detection of univalents and quadrivalents at diakinesis and metaphase I of some cells of the studied *Brassica* species in the present work represent the two main meiotic abnormalities which could be discussed separately. The *B. campestris* L. genotype revealed normal pairing and formation of 10 bivalents in most of the metaphase I cells (Fig. 1a, b). Chiasma frequency estimated for each plant ranged between 12.536 and 19.252/PMC giving an average of 16 chiasmata/PMC and 1.59 chiasmata/bivalent for the 20 plants (Table 1). Among the studied 2639 PMCs of *B. campestris* L., Turnip Baladi (2n = 20) only 185 cells showed 2 univalents and 9 bivalents (Fig. 1d, e and f) giving an average of 15.912 chiasmata/PMC and 1.602 chiasmata/ bivalent (Table 2).

Table 2. Averages of the different pairing configurations and chiasmata at normal and total No. of examined metaphase I cells of the two elementary diploid species of the cultivated *Brassica*, Turnip and Cabbage Baladi.

Diploid species	Total No. of examined cells	No. cells with Biv. only	Aver. Chias.		No. cells with different Chrom. pairing	Different pairing configurations			Aver. Chias.	
			/cell	/Biv.		Univ.	Biv.	Quadriv.	/cell	/Biv.
B. campestris	2639	2454	16.00	1.590	185	7%	9.93	0	15.912	1.602
B. oleracea	3223	1998	16.956	1.884	1225	0	8.62	38%	15.809	1.919

Failure of some homologous chromosomes to pair during the meiotic division of diploid *Brassica* species is of non-frequent occurrence and consequently rarely mentioned in previous cytological studies. In the present investigation, univalents could be detected in only 7% PMCs. This finding supports strongly the rare occurrence of pairing failure and absence of univalents in most cultivated diploid varieties of *B. campestris* L.. Thus, agreeing with the findings of many workers, univalents could be detected in various subspecies of *B. campestris* L. **(Allam *et al.*, 1985; Gad & El-Nadi, 1986 and Attia, 1987)**. Owing to the low frequency of detected PMCs showing pairing failure, this meiotic irregularity is expected to be of negligible effect on the stability and fertility of the used *Brassica* genotype.

At anaphase I, in spite of the slight abnormalities observed in Turnip Baladi, most of the cells were almost normal and showed normal distribution of 10 chromosomes at each pole (Fig. 1g, h and i). Separation of chromosomes in all examined anaphase I and II cells was normal with the exception of 0.54% cells (Fig. 1 j). A low frequency of meiotic abnormalities was noted also by **Pires Bione *et al.*, (2000)** in soybean varieties. Irregular chromosome segregation, chromosome stickiness, cytoplasm connections between cells, cytomixis and irregular spindles were the main abnormalities observed. In our study abnormalities were mainly anaphase bridges without fragments and in few cases they were accompanied with fragments. The authors attributed the presence of these bridges to structural differences between the paired chromosomes, possibly inversions. Threads or bridges without fragments between the separating chromosomes at first anaphase were probably caused by delayed terminalisation of the chiasmata. This could be due to non-homologous segments at the terminal or subterminal part of the paired chromosomes. Unequal separation of chromosomes, false bridges, in addition

to lagging bivalents were also observed in few cells. Lagging chromosomes were observed at anaphase of both divisions along with misdivision in some cells. The disjunction of all the bivalents was not synchronous sometimes. A few chromosomes which did not show polar movement, were included in rare cases of the anaphase I groups.

***Meiotic abnormalities in B. oleracea* L.**

One genotype of *B. oleracea* L. was meiotically analyzed, it expressed normal pairing and formation of 9 bivalents in most of the metaphase I cells (Fig. 1l and Fig. 2a, b and c). Chiasma frequency estimated for each plant ranged between 15.667 and 17.9/PMC giving an average of 16.956 chiasmata/PMC and 1.884 chiasmata/bivalent for 20 examined plants (Table 1). These results indicate more pairing intensity between *B. oleracea* L. chromosomes than between *B. campestris* L. chromosomes. Out of the studied 3223 PMCs of *B. oleracea* L., Cabbage Baladi (2n = 18), 1225 cells showed quadrivalents in addition to the 7 bivalents giving an average of 15.809 chiasmata/PMC and 1.919 chiasmata/bivalent (Table 2).

The results showed that in more than 38% of PMCs, one quadrivalent in addition to the 7 bivalents was found in each PMC. (Fig. 2i, j, k and l and Fig. 3a, b and c). Similar results in various genotypes of *B. oleracea* L. were obtained by **Attia, (1987)**. He mentioned that quadrivalents could be detected in *B. oleracea* L. convar. botrytis (var. botrytis "cauliflower"). In the present study, the meiotic regularity and the formation of bivalents only has also been found in *B. oleracea* L., Cabbage Baladi in 62% of analyzed PMCs. This finding is in agreement with the findings of many workers. Quadrivalents are repeatedly detected in certain genotypes of *B. oleracea* L. and has been attributed either to the existence of segmental chromosome duplications within the diploid genome **(Sampson, 1970 and Gustafsson *et al.*, 1976)** or to the existence of reciprocal translocations **(Chiang & Grant, 1975 and Attia, 1987)**. Chromosomal structural changes and rearrangements may play an important role in the gradual process of evolution and morphological differentiation in the species *B. oleracea* L..

Regular distribution of 9 chromosomes to each pole was found in most of the anaphase I cells in *B. oleracea* L. (Fig. 2e, f and g). Separation of chromosomes at anaphase II proceeded-with the exception of rare cases-normally (Fig. 2h and Fig. 3k and l). The most frequent abnormality was the existence of anaphase bridge or bridges, mostly without fragment, and lagging chromosomes (Fig. 3j).

These two *Brassica* species differed in their meiotic behavior as far as formation of univalents and quadrivalents at metaphase I were concerned. Comparison between *B. campestris* L. and *B. oleracea* L. at normal metaphase I, Table (1) shows that *B. oleracea* L. had the highest average number of chiasmata/PMC (16.956 and 16.) and lowest chiasmata/ bivalent (1.590 and 1.884). Comparison between *B. campestris* L. and *B. oleracea* L. at all examined metaphase I cells, Table (2) shows that *B. oleracea* L. had the lowest average of chiasmata/PMC (15.809 and 15.912) and highest chiasmata/bivalent (1.919 and 1.602). Indicating less pairing intensity and the formation of more bivalents with only one chiasma.

Secondary (pairing) associations

In all the plants studied a variable number of bivalents are found to be secondarily paired. Secondary pairing may be described as a generalized attraction between chromosomes phylogenetically related. It appears to be due

to a residual attraction between chromosomes in which ancestral homology is still discernible. This is an indication of polyploidy. In examined cells without univalents and multivalents, secondary associations and connections between some bivalents were frequently visible at diakinesis and metaphase I in the two cultivated *Brassica* species in a part of the examined PMCs (Fig. 1k and Fig. 3d, e, f, g, h and i). Genetic similarity through duplication of some chromosomal segments in diploid species of *Brassica* used in the present study was considered to be the reason of observed secondary associations and connections between some bivalents at diakinesis and metaphase I stages. In this study, we noticed that associations of more than four chromosomes are observed. Sometimes, however, three bivalents have been found to be secondarily paired. In no case has more than one group of three secondarily paired bivalents been found in the same cell. Secondarily paired bivalents were always close to one another. **Catcheside (1937)** concluded that secondary associations in diploid *B. oleracea* L. were not due to bad fixation or to the possibility of mistaken observation, but were caused by real structural complexity. There are many indications that elementary diploid species are secondary balanced polyploidy originating from a common prototype with the basic chromosome number x = 6. However, in meiotic studies there was a predominance of univalents in haploids of *B. campestris*, *B. oleracea* and *B. nigra*. Associations of only two and rarely more chromosomes were sometimes observed **(Prakash, 1973 and Armstrong & Keller, 1981 and 1982)**. Nevertheless, such chromosomal homology and genetic similarity between phylogenetically similar chromosomes within the diploid genome may be enough to cause the repeatedly observed secondary associations in *Brassica* species **(Hussein & Abobakr, 1976 and Attia, 1987)**. This has been also observed in the present work. More data from further intensive studies are necessary to confirm the meiotic abnormalities in the elementary diploid species of *Brassica*.

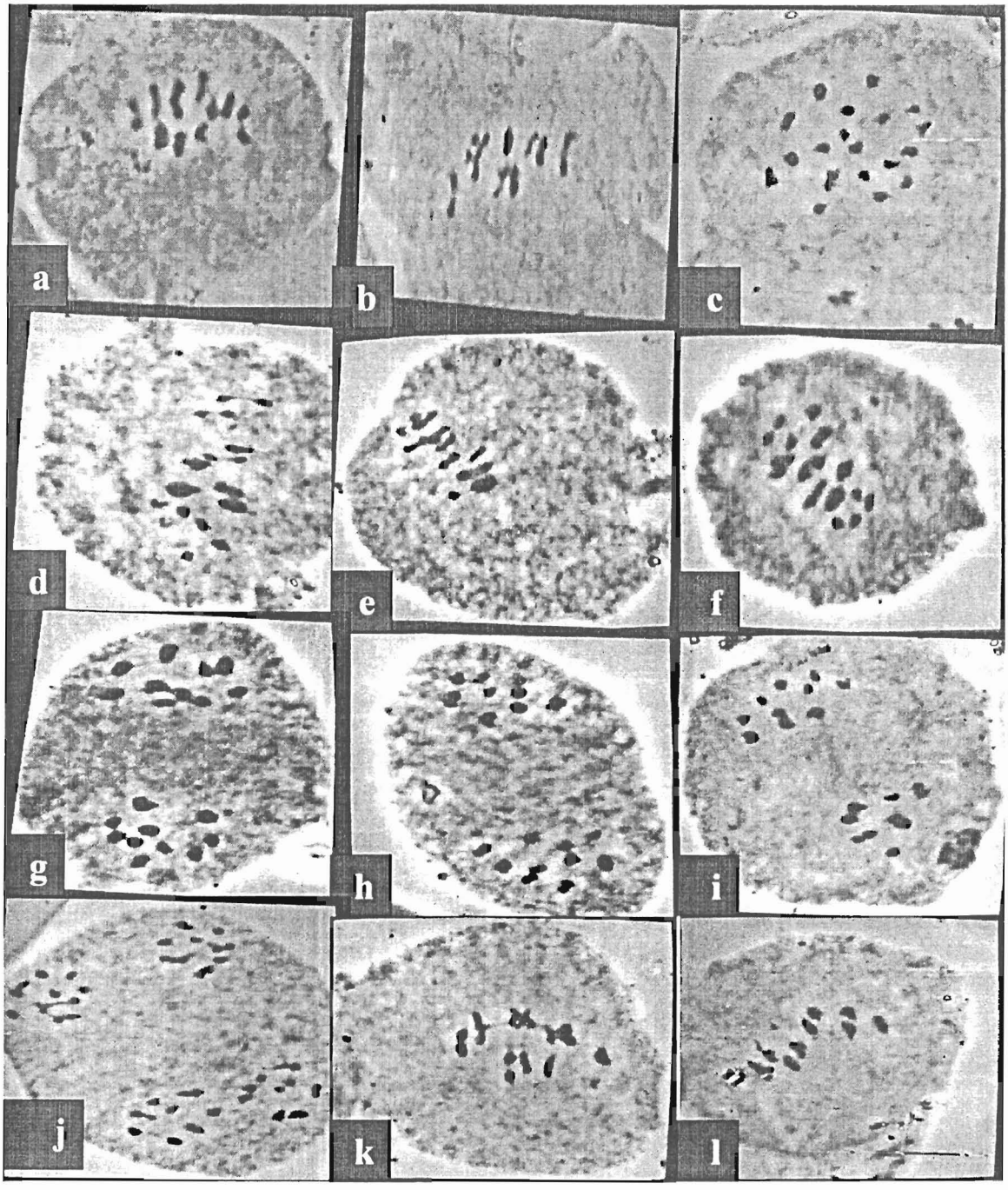

Fig. 1. *B. campestris* (a, b): MI cells showing normal pairing (10 II), (c): cell with 20 chromosomes, (d, e and f): MI cells showing 9 II+2I, (g, h and i): AI cells showing normal separation (10 chromosomes at each pole), (j): AII cell showing normal separation, (k): MI cell with two I and secondary associations, (l): MI cell of *B. oleracea* showing normal pairing (9 II).

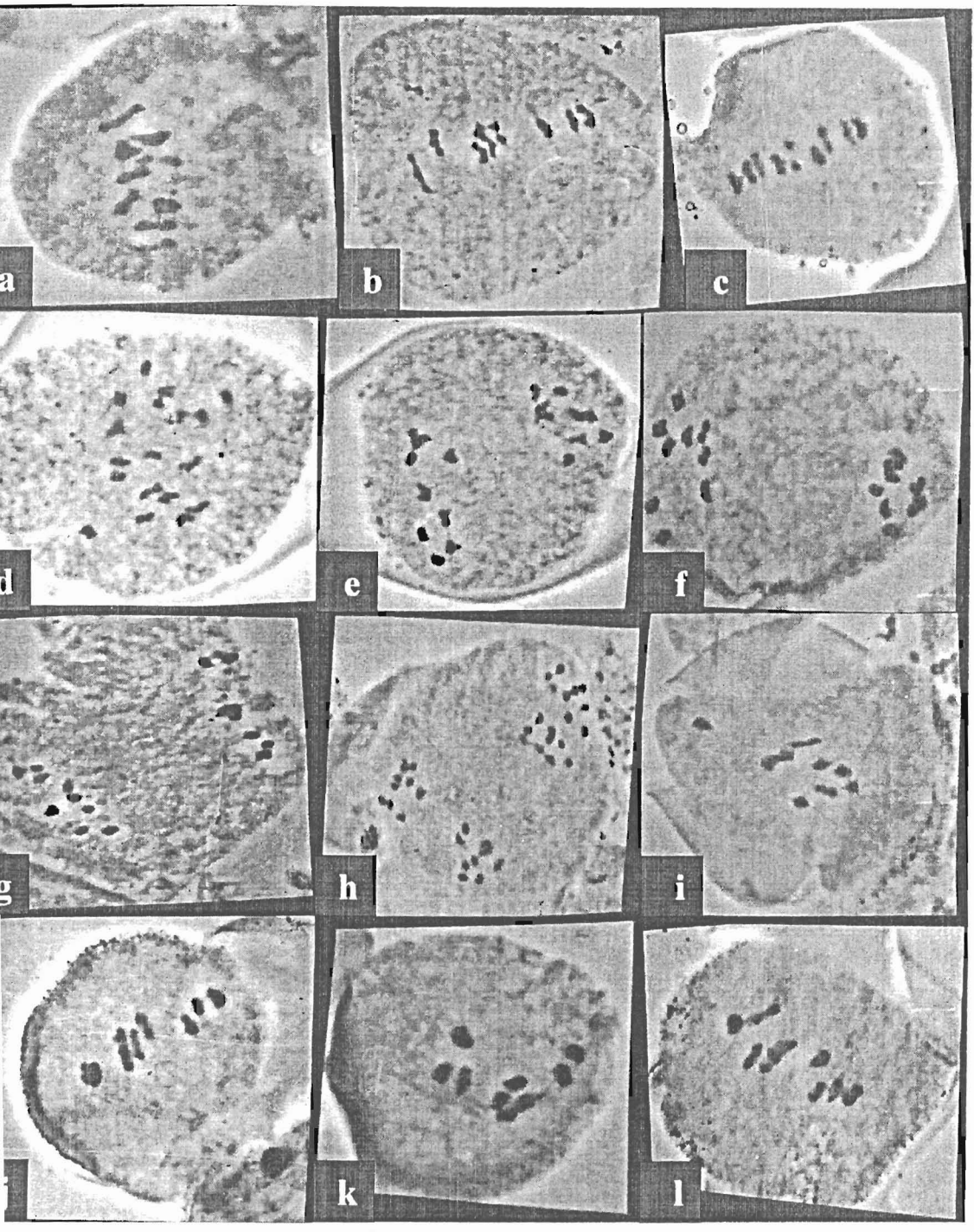

Fig. 2. *B. oleracea* (a, b and c): MI cells showing normal pairing (9 II), (d): cell with 18 chromosomes, (e, f and g): AI cells showing normal separation (9 chromosomes at each pole), (h): AII cell showing normal separation, (i, j, k and l): MI cells showing 1 IV+7 II.

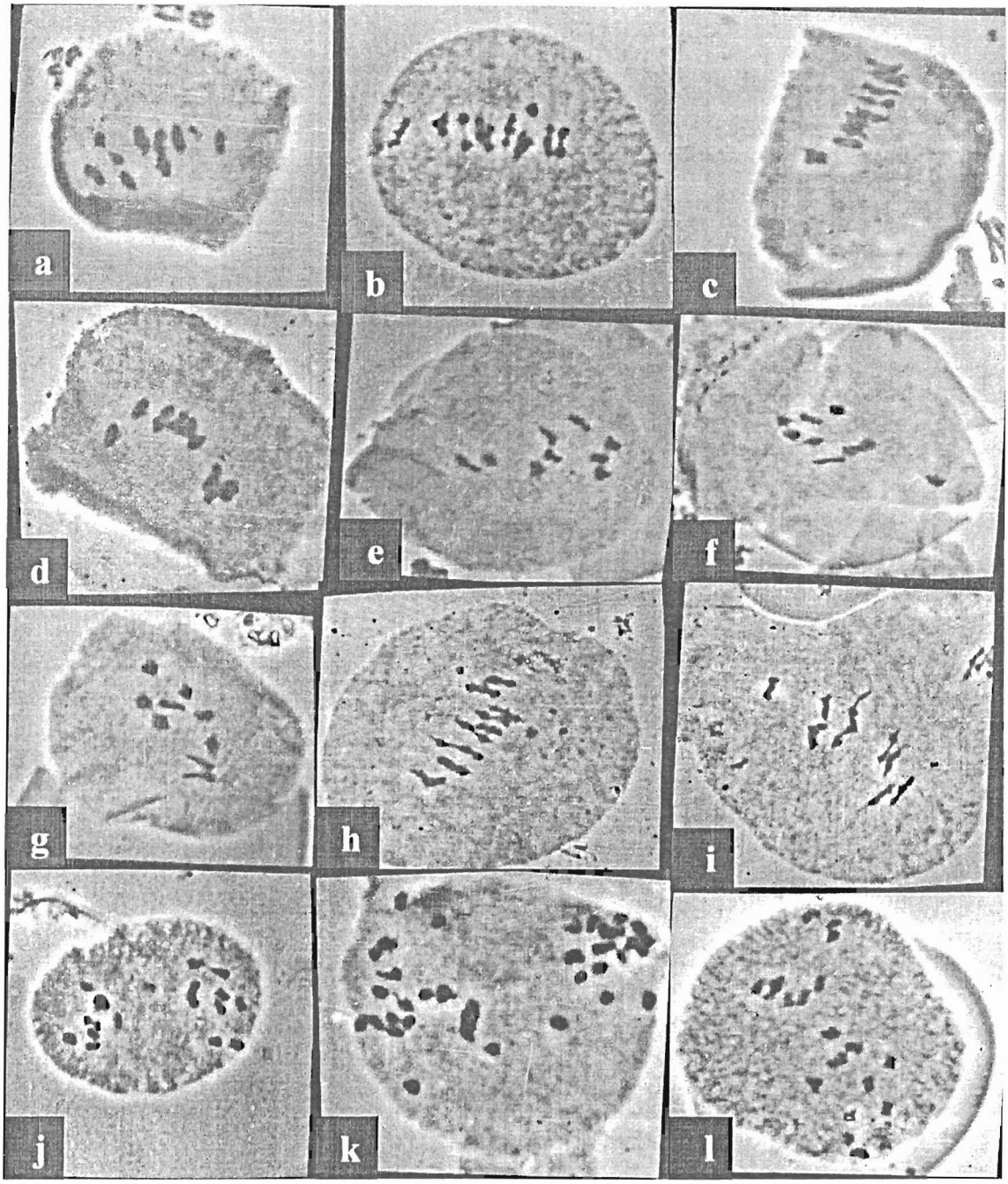

Fig. 3. *B. oleracea* (a and b): MI cells showing 1 IV+7 II, (c): MI cell showing 1 IV+7 II, and secondary associations, (d, e, f, g, h and i): MI cells showing secondary associations, (j): AI cell showing 1 lagging chromosomes, (k and l): AI cells showing lagging and unequal distribution of chromosomes.

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الشذوذات الميوزية و التزاوج الثانوى فى اثنين من أسلاف البراسيكا المنزرعة ثنائية المجموعة الكروموسومية

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تعتبر معظم الأنواع المنزرعة التابعة لجنس البراسيكا من الخضروات الهامة و يعتبر اللفت والكرنب من أهم محاصيل الخضر التى تتبع هذا الجنس - أجريت هذه الدراسة على صنفين هما اللفت و الكرنب التابعين لنوعين أساسيين كلاهما ثنائي المجموعة الكروموسومية وهما الكامبسترس والاوليراسيا حيث يعتبرا من الأسلاف المنزرعة التى نشأت منها الأنواع الرباعية الاخري - وتم دراسة الأنماط المختلفة للسلوك الشاذ فى تزاوج الكروموسومات والتزاوج الثانوى خلال الانقسام الميوزى. **ويمكن تلخيص النتائج المتحصل عليها فيما يلي:** حدوث بعض الشذوذات الكروموسومية مثل الوحدات أحادية الكروموسوم في الصنف التابع للنوع كامبسترس والوحدات رباعية الكروموسوم في الصنف التابع للنوع أوليراسيا فى بعض الحالات. تم تمييز الوحدات أحادية الكروموسوم والناتجة عن فشل كروموسومين نظيرين فى التزاوج معا فى 7% فقط من الخلايا الأمية لحبوب اللقاح التى تم فحصها فى اللفت التابع للنوع كامبسترس - بينما 93% من الخلايا كانت خالية تماما من وجود كروموسومات فردية غير متزاوجة. تم التعرف على الوحدات رباعية الكروموسوم وتمييزها بتكرار عالى (أكثر من 38%) من الخلايا وزادت نسبة الخلايا التى ظهرت بها هذه الوحدات فى الطور التشتتى فى الكرنب التابع للنوع أوليراسيا وتم تفسير تكوين مثل هذه الوحدات بأنه يرجع إلى حدوث انتقالات متبادلة بين بعض الكروموسومات غير النظيرة فى هذا الصنف أو إلى وجود أجزاء مكررة أو متماثلة من الكروموسومات داخل الجينوم الثنائى فية. لقد

أشارت النتائج إلى التشابه فى سلوك الكروموسومات خلال الانقسام الميوزى من حيث شدة التزاوج وتكوين الوحدات ثنائية الكروموسوم فى كلا الصنفين التابعين للنوعين محل الدراسة و كان السلوك الميوزى منتظما أيضا فى معظم الخلايا التى تم فحصها فى كلاهما و تم مشاهدة 10و 9 وحدات ثنائية فى النوعين كامبسترس وأوليراسيا على الترتيب فى كل خلية وذلك فى معظم خلايا الطور الاستوائى الأول التى تم فحصها وأن انفصال الكروموسومات خلال الطور الانفصالى الأول والثاني كان طبيعيا باستثناء بعض الحالات القليلة. معظم الشذوذات الكروموسومية كانت متمثلة فى وجود الجسر الانفصالى مصحوبا بشظية أو بدون شظية كروموسومية وكروموسومات متلكئة فى الانفصال خلال الطور الانفصالى الأول وعدم تساوى الكروموسومات المنفصلة فى كلا الصنفين. تم تقدير متوسط عدد الكيازمات لكل خلية ووجد أن متوسط عددها فى الأوليراسيا (16.956) بينما فى الكامبسترس (16) و تشير هذه النتائج إلى أن شدة التزاوج بين كروموسومات الأوليراسيا أعلى منها فى الكامبسترس. تم مشاهدة الاتحاد الثانوى بين الوحدات ثنائية الكروموسوم فى كلا النوعين و كان هناك تباين فى عدد الوحدات المشتركة فية خلال الطورين التشتتى و الاستوائى الأول فى كلا الصنفين التابعين للنوعين المعنيين بالدراسة ويمكن تفسير حدوثة بأنه ناتج عن تجاذب عام بين الوحدات الثنائية التى لها علاقة وراثية مكتسبة خلال التطور البيولوجي.