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MEIOTIC SPECTRUM IN CROWN DAISY

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Chrysanthemum coronarium Linn., member of tribe Anthemidae, a diploid (2n=18) has four head types, viz. creamish white radiate, creamish white ligulate, deep yellow radiate and deep yellow ligulate. Its meiotic analysis revealed tetramorphic pattern i.e., bivalent interlocking of various patterns and combinations (72%), translocation heterozygosity (15.5%), normal meiosis (12%) and telomere adhesions. Of these, 2+2 bivalent interlocking is the most predominant among the bivalent interlocking types and 1 translocation ring of 4 chromosomes + 7 ring bivalents is most common among translocation heterozygotes. But none of these anomalies impede or interfere with the male meiotic course which is normal. Pollen and seed fertility is high (> 95%) in all the four head types. Probably, there exists a preferential directed disjunction of translocated chromosomes that maintains high gametic fertility in this species. Some of the interlockings and telomere adhesions simulate translocation heterozygosity. Do these lead to chromosomal translocations or not is an open question.

Keywords : Tetramorphic meiosis; Bivalent interlocking; Translocation heterozygosity; Telomere adhesion.

Introduction

Compositae or Asteraceae is the largest family having about 1,000 genera and 20,000 species occuring almost in all possible habitats and comprise over 10% of the total number of flowering plants existant over this globe. They are economically important, having use as food, feed, decoration and are used in preparation of dyes, drugs and insecticides. Of the various ornamentals, *Chrysanthemum coronarium* Linn. (Crown daisy), a diploid (2n=18), popular winter ornamental, is cultivated for its cut flowers available during February to end of March when other ornamental flowers are not available. Its capituli vary in colour and form. The distinct ones are: (1) creamish white radiate, (2) creamish white ligulate, (3) deep yellow radiate, and (4) deep yellow ligulate (Fig.1). Whereas the deep yellow coloured head types have only yellow coloured florets, the creamish white head types have variably distributed yellow tinge at the base of the corolla. In the subsequent account of this paper, these are termed as white (creamish white and yellow (deep yellow) heads for brevity and simplicity. The meiotic pattern of these 4 head types were investigated and forms text of this paper.

Materials and Methods

The seeds of the four head types, obtained by artificially crossing the two plants of the same head type with each other, were sown in October. The young flower buds of each head type were fixed in freshly prepared mixture of glacial acetic acid and absolute alcohol (1:3) between 11.00 - 11.30 a.m. After 24 hours, they were washed with tap water and preserved in 70% alcohol. For slide preparation, young florets were squashed in 2% acetocarmine, washed

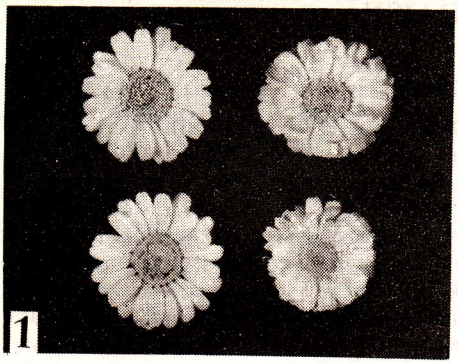


Fig. 1.4 Head types

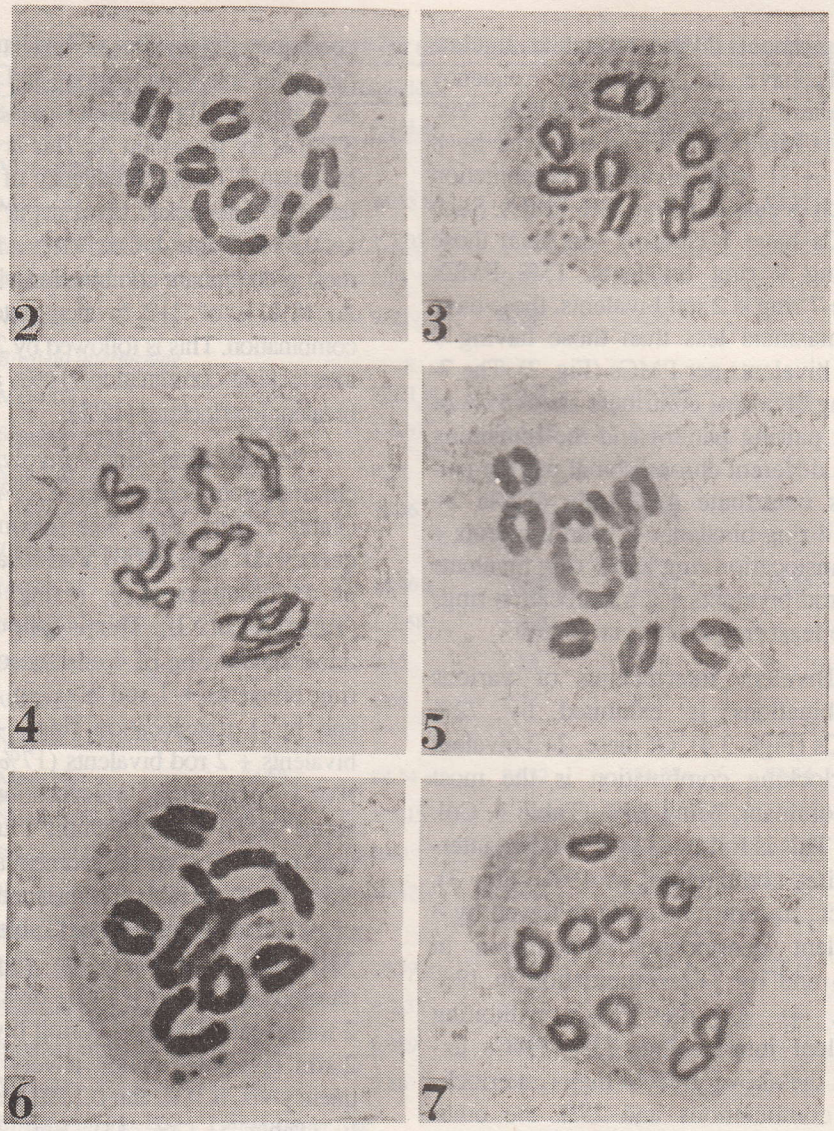
and tapped gently after coverslip placement and observed for the meiotic patterns. For male meiotic study, about 300 PMCs of each head type were studied. Finally 275 PMCs were chosen for data compilation, the extreme types and rare observations were eliminated. The data obtained were subjected to usual statistical analysis. For testing the significance of difference of the mean values, Duncan's multiple range test, as given by Gomez and Gomez[1] was followed. The level of significance for mean differences was evaluated at 5P level. When the mean values between rows are followed by sub-scripts of different alphabets, the values differ significantly from each other at 5P level. Wherever overlaps occurred, students paired t-test was used (Table 1) to decide the significance of difference.

Observations

Meiotic analysis revealed tetramorphic meiotic patterns viz., the presence of (a) normal meiosis, (b) bivalent interlocking, (c) translocation-heterozygo-sity, and (d) telomere adhesion in all the four head types. The PMCs exhibit either normal bivalency, or bivalent interlocking, or translocation heterozygo-sity or telomere adhesions or one or more of these in various proportions. Their mean, standard deviation and variance in each head type are given in Table 1 and depicted in Figs. 2-7.

A perusal of this table indicates that the bivalent interlocking exhibits the highest frequency, i.e. 72%. In this respect, it is followed by translocation heterozygosity in 15.5% PMCs and by the frequency of normal bivalency which is 12%. The mean differences among 4 head types in normal bivalency differ significantly from one another. Their respective variance also differ considerably. Despite these differences, the mean value differences among the 4 head types in translocation heterozygosity are statistically insignificant. Same is true for normal bivalency + bivalent interlocking values, but reverse occurs for normal bivalency + translocation ring as their mean value differences are significant. Bivalent interlocking + translocation ring exhibit significant mean differences in yellow radiate and yellow ligulate head types but the mean differences between the white radiate and white ligulate head types are statistically insignificant.

Among the various chromosomal pairing types and patterns, perfect bivalency exhibits the highest frequency



Figs. 2, 4-7 Diakinesis stage; 3 Diplotene stage; 2-9 bivalents (uncaccompanied by bivalent interlocking and translocation ring); 3 Bivalent interlocking (1 interlocking involving 2 bivalents); 4 Bivalent interlockings (1 interlocking involves 3 bivalents, another involves 2 bivalents); 5-6 Tranlocation rings of four chromosomes each; 7 Telomere adhesion (giving translocation ring appearance).

being about 24%, the white ligulate heads have the maximum frequency 29% and yellow ligulate the least, viz. 20% (Table 2). This is followed by 8 ring + 1 rod bivalents combination which occurs in about 18% PMCs. Such PMCs have 1 chiasma less than those having 9 ring bivalents. 15% PMCs have 7 ring + 2 rod bivalents, these have 2 chiasmata less than those having 9 ring bivalents per PMCs (Fig. 2). The 7-9 ring bivalents contribute about 57% of total pairing pattern and the remaining with different chromosomal pairing patterns contribute 43% only (Table 2). The 4 ring bivalents + 3 rod bivalents + 1 translocation ring and 3 ring bivalents + 2 rod bivalents + 2 translocation rings have least frequency, viz. 0.16%.

Bivalent interlocking of various combinations is exhibited by 72% PMCs (Figs. 3,4). Of these, 2+2 bivalent interlocking combination is the most predominant, being 25% (Table 3, Col. IX). This is followed by 2 bivalent interlocking combination in 19% (Fig. 3), which, in turn, is closely followed by 3 bivalent interlocking combination in 16% and by 3+2 combination in 12% (Fig. 4). Of the PMCs exhibiting bivalent interlocking, 73% PMCs exhibit the above given 4 major interlocking combinations and 27% the other bivalent interlocking combinations (Table 3, Col. IX). The least frequency is of 4+2+2 and of 6 interlocking combinations 0.74% and 0.77%, respectively.

As already indicated, the bivalent interlocking exhibits various combinations. These were grouped into 4 sets according to the number of bivalents taking part in the interlocking group and are given in Table 4. The highest frequency (i.e. 37%) is for the group A. This is followed by group B (28%). Frequency of group D having 6 interlocked bivalents is the least, i.e. 0.55% (Table 4, Col. VIII). Among the most predominant combination viz., group A, 18% is of 2+2 bivalent interlocking combination. This is followed by 2 bivalent interlocking combination (14%) and by 3 bivalent interlocking (12%).

Translocation rings involving four chromosomes occurs in 15.5% PMCs (Table 1; Figs. 5,6). The maximum frequency viz. 47%, is of 1 translocation ring of 4 chromosomes + 7 ring bivalents (Table 5, Col.XII). This is followed by 1 translocation ring of 4 chromosomes + 6 ring bivalents + 1 rod bivalent, i.e. 31% and by 1 translocation ring + 5 ring bivalents + 2 rod bivalents (17%). Of the PMCs exhibiting translocation rings, about 96.5% PMCs exhibit 1 translocation ring of 4 chromosomes and only 3.5% PMCs exhibit 2 translocation rings of 4 chromosomes each (Table 5, Col. XII). The 2 translocation rings of 4 chromosomes each + 5 ring bivalents and 2 translocation rings + 3 ring bivalents + 2 rod bivalents, exhibit a very low frequency viz. 0.38% and 0.16%, respectively (Table 5, Col. XI). Fig. 7 shows telomere adhesion which gives the appearance of a translocation ring. Its proportion and frequency are variable.

Discussion

(a) *Bivalent interlocking: Chrysanthemum coronarium* Linn. is a prolific

Table 1. Mean and variability parameters for chromosomal alignments in *C. coronarium*

Sr.No.	Chromosomal alignments and their variability	Yellow capitulum		White capitulum		General Mean
		Radiate	Ligulate	Radiate	Ligulate	
1.	***Normal Bivalency***					
	Mean (%)	11.08 a	14.33 b	12.41 a	11.04 b	12.21
	Standard Deviation	± 2.52	± 3.05	± 2.93	± 2.75	
	Standard error	0.15	0.18	0.17	0.16	
	Variance	6.35	9.30	8.58	7.56	
2.	***Bivalent interlocking***					
	Mean (%)	73.51 a	70.21 b	71.91 a	73.29 b	72.23
	Standard deviation	± 6.18	± 5.93	± 5.82	± 6.05	
	Standard error	0.37	0.35	0.35	0.36	
	Variance	38.19	35.16	33.87	36.60	
3.	***Translocation ring***					
	Mean (%)	15.41 a	15.46 a	15.68 a	15.67 a	15.55
	Standard deviation	± 2.25	± 2.58	± 3.07	± 3.12	
	Standard error	0.13	0.15	0.18	0.18	
	Variance	5.06	6.65	9.42	9.73	
4.	***Normal bivalency + bivalent interlocking***					
	Mean (%)	84.59 a	84.54 a	84.32 a	84.33 a	84.44
	Standard deviation	± 7.92	± 8.15	± 7.54	± 8.06	
	Standard Error	0.47	0.49	0.45	0.48	
	Variance	62.72	66.42	56.85	64.96	
5.	***Normal bivalency + translocation ring***					
	Mean (%)	26.49 a	29.79 b	28.09 a	26.71 b	27.77
	Standard deviation	± 2.16	± 2.35	± 2.25	± 2.13	
	Standard error	0.008	0.009	0.008	0.008	
	Variance	4.67	5.88	5.06	4.54	
6.	***Bivalent interlocking + Translocation ring***					
	Mean (%)	88.92 a	85.67 b	87.59 a	88.96 a	87.78
	Standard deviation	± 9.15	± 9.42	± 8.73	± 9.85	
	Standard error	0.55	0.56	0.52	0.59	
	Variance	83.72	88.73	76.21	97.02	

N=275

Mean values not followed by the same alphabet in radiate and ligulate flowers differ significantly from each other at 5 P level.

Table 2. Frequency of chromosomal pairing types and translocations at diakinesis in 4 head types of *C. coronarium*

Bivalent types and translocations *				Yellow capitulum			White capitulum			
R	r	I	T	Radiate (%)	Ligu-late(%)	Mean (%)	Radiate (%)	Ligu-late(%)	Mean (%)	General Mean
(I)	(II)	(III)	(IV)	(V)	(VI)	(VII)	(VIII)	(IX)	(X)	(XI)
9	0	nd	nd	22.35	20.0	21.18	22.85	29.28	26.07	23.62
8	1	nd	nd	18.69	20.0	19.35	14.28	20.0	17.14	18.24
7	2	nd	nd	13.41	16.77	15.09	20.71	10.71	15.71	15.4
6	3	nd	nd	9.75	7.09	8.42	5.0	6.42	5.71	7.07
5	4	nd	nd	2.43	1.93	2.18	2.14	2.85	2.49	2.34
4	5	nd	nd	1.21	1.93	1.57	0.71	0.71	0.71	1.14
7	nd	nd	1	8.12	7.74	7.93	7.84	5.71	6.78	7.35
6	1	nd	1	4.05	4.51	4.28	5.70	4.99	5.35	4.81
5	2	nd	1	2.43	1.93	2.18	2.13	4.27	3.2	2.69
5	nd	nd	2	0.81	nd	0,41	nd	0.71	0.36	0.38
4	3	nd	1	nd	0.64	0.32	nd	nd	nd	0.16
3	2	nd	2	nd	0.64	0.32	nd	nd	nd	0.16
8	nd	1	nd	2.03	1.29	1.66	2.85	5.71	4.28	2.97
7	1	1	nd	2.03	2.58	2.31	5.71	1.42	3.57	2.94
7	nd	2	nd	2.43	3.22	2.83	0.71	1.42	1.07	1.95
6	1-2	1-2	nd	3.65	2.58	3.12	7.13	2.13	4.63	3.87
6	nd	3	nd	1.62	2.58	2.1	nd	nd	nd	1.05
5-6	nd	3-4	nd	nd	0.64	0.32	nd	0.71	0.36	0.34
5	1-3	1-3	nd	2.43	1.93	2.18	0.71	0.71	0.71	1.45
4	0-1	4-5	nd	1.21	0.64	0.93	nd	0.71	0.71	0.18
3	3	3	nd	nd	nd	nd	1.42	nd	0.71	0.36
3	nd	6	nd	1.21	1.29	1.25	nd	nd	nd	0.63
2	nd	7	nd	nd	nd	nd	nd	1.42	0.71	0.36

N=275

*R=Ring bivalents; r=rod bivalents, I=Interstitial bivalents, T=Translocations; nd=not detected

Table 3. Bivalent interlocking combinations in *C. coronarium*

*BI	Yellow capitulum			White capitulum				
	Radiate (%)	Ligulate (%)	Mean (%)	Radiate (%)	Ligulate (%)	Mean (%)	General Mean (%)	Relative Mean (%)
I	II	III	IV	V	VI	VII	VIII	IX
2	17.36	11.17	14.27	11.02	16.53	13.78	14.02	19.41
2+2	19.52	19.68	19.6	16.90	16.42	16.66	18.13	25.10
2+2+2	5.38	5.93	5.66	3.18	5.49	4.34	4.99	6.91
3	11.78	10.53	11.16	13.88	10.70	12.29	11.72	16.23
3+2	7.93	8.08	8.01	9.76	9.68	9.72	8.86	12.27
3+2+2	3.65	3.61	3.63	2.41	2.59	2.5	3.07	4.24
3+3	2.92	4.66	3.79	4.73	3.90	4.32	4.05	5.61
4	1.21	2.14	1.68	4.08	2.66	3.37	2.52	3.49
4+2	2.13	1.79	1.93	4.62	1.88	3.25	2.61	3.60
4+2+2	0.26	0.72	0.49	0.31	0.85	0.58	0.54	0.74
4+3	0.81	1.56	1.19	0.73	1.54	1.14	1.16	1.60
6	0.56	0.34	0.45	0.29	1.05	0.67	0.56	0.77
Total							72.223	

N=275, *BI=Bivalent interlocking combinations.

flower producer and bears four head types viz., creamish white radiate, creamish white ligulate, deep yellow radiate and deep yellow ligulate. All of these heads produce enormous number of highly fertile seeds whose germinability is very high, i.e. over 93 ± 2%. Therefore, this species has high gametic and pollen fertility. Accordingly, a normal course of male meiosis is expected. But Paria and Pradhan[2], Gill and Gupta[3] Gupta and Gill[4,5] documented the existence of translocation heterozygosity in about 40% plants of *C. coronarium*. On the other hand, Aakriti[6] found normal meiosis and bivalent interlocking but no translocation rings in the creamish white radiate head type of this species. On the other hand,we detected (a) normal meiosis, (b) bivalent interlocking, (c)translocation heterozygosity, and (d) telomere adhesion in various proportions in all the four head types of this species. Thus, the meiosis in this species exhibits tetramorphism. Of the three anomalies detected presently, maximal frequency was of bivalent interlocking. The cause of this interlocking is not known so far. Either the residual homology or localized chiasmata or smaller nuclear space or all these could be the causative agents of bivalent interlocking. In all the four head types of *C. coronarium*, the bivalent interlocking initiates during zygotene or pachytene of first meiotic

Table 4. Patterns (grouped) of interlocking combinations in floral types

	IP	Radiate Flowers			Ligulate Flowers			
	(Grouped)	Yellow (%)	White (%)	Mean (%)	Yellow (%)	White (%)	Mean (%)	General Mean (%)
	(I)	(II)	(III)	(IV)	(V)	(VI)	(VII)	(VIII)
Group A	2	17.36	11.02	14.19	11.17	16.53	13.85	14.02
	2+2	19.52	16.90	18.21	19.68	16.42	18.05	18.13
	2+2+2	5.38	3.18	4.28	5.93	5.49	5.71	4.99
	Total	42.26	31.1	36.68	36.78	38.44	37.61	37.15
B	3	11.78	13.88	12.83	10.53	10.70	10.62	11.72
	3+2	7.93	9.76	8.85	8.08	9.68	9.39	9.12
	3+2+2	3.65	2.41	3.03	3.61	2.59	3.1	3.07
	3+3	2.92	4.73	3.83	4.66	3.90	4.28	4.05
	Total	26.28	30.78	28.53	26.88	26.87	27.39	27.96
C	4	1.21	4.08	2.65	2.14	2.66	2.4	2.52
	4+2	2.13	4.62	3.11	1.79	1.88	1.84	2.47
	4+2+2	0.26	0.31	0.29	0.72	0.85	0.79	0.54
	4+3	0.81	0.73	0.77	1.56	1.54	1.55	1.16
	Total	4.41	9.74	6.81	6.21	6.93	6.57	6.69
D	6	0.56	0.29	0.42	0.34	1.05	0.69	0.55

N=275; IP=Interlocking patterns

Table 5. Bivalent types and translocation in 4 capitulum types of *C. coronarium*

Bivalent types and translocations				Yellow capitulum			White capitulum				
R	r	I	T	Radiate (%)	Ligulate (%)	Mean (%)	Radiate (%)	Ligulate (%)	Mean (%)	General Mean (%)	Relative Mean (%)
(I)	(II)	(III)	(IV)	(V)	(VI)	(VII)	(VIII)	(IX)	(X)	(XI)	(XII)
7	nd	nd	1	8.12	7.74	7.93	7.84	5.71	6.78	7.35	47.26
6	1	nd	1	4.05	4.51	4.28	5.70	4.99	5.35	4.81	30.93
5	2	nd	1	2.43	1.93	2.18	2.13	4.27	3.2	2.69	17.29
5	nd	nd	2	0.81	nd	0.41	nd	0.71	0.36	0.38	2.44
4	3	nd	1	nd	0.64	0.32	nd	nd	nd	0.16	1.02
3	2	nd	2	nd	0.64	0.32	nd	nd	nd	0.16	1.02
Total										15.55	

N=275; nd=not detected; R=Ring bivalents; r=rod bivalents; I=Interstitial bivalents; T=Translocations.

prophase and invariably involves non-homologous chromoso-mes. But whether this interlocking is chromosome or bivalent specific or not is not known. Furthermore, in all the cases, the bivalent interlocking is clearly visible and predominant during diplotene- diakinesis and disappears during metaphase I. Thus, the interlocking does not interfere or impede meiotic course or microspore development in this plant.

In *C. coronarium*, the bivalent interlocking was first documented by Aakriti[6] in creamish white radiate head type. Of these interlockings, 15% were unclear and being difficult to differentiate from translocation rings, a safe term "ring interlocking" was adopted. Almost the same percentage viz. 15.5% was obtained for translocation in the present material. May be the "ring interlocking" of Aakriti[6] actually represented translocation rings in this material. Of the bivalent interlocking types detected presently in all the 4 head types, 2+2 bivalent interlocking is the most predominant and 6 or 8 bivalent (4+2+2) interlocking the least (Tables 3 and 4). On the other hand, among the interlocking types involving 4 or more bivalents, the predominance is of 4 or 4+2 types, others are low in frequency (Tables 3 and 4). But no uniformly regular or symmetrical or statistical mean value differences exist among the four head types in the major bivalent interlocking types and their combinations. Despite this, non-lack of pattern or specificity in predominance or recurrence of bivalent interlocking type, about 72% PMCs exhibit this interlocking. Since the bivalent interlocking is of a high frequency and of regular occurance, it certainly appears gene controlled and not a random event. In case it is, *C. coronarium* lacking interlocking should be detected and crossed with *C. coronarium* having bivalent interlockings; the F_1 and its subsequent generations should indicate gene control of this interesting cytological phenomenon.

(b) *Translocation heterozygosity*: About 15.5% PMCs exhibit translocation heterozygosity involving 2 pairs of non-homologous chromosomes, majority of which are of ring type. The chromosomal ring attains various patterns and probably disjuncts alternatively as the pollen fertility is high (>95%). Preferential directed disjunction known to occur in *C. carinatum*[7,8] may also be operative in *C. coronarium*. This could account for the high pollen and seed fertility in this species. Does preferential or specifically directed segregation of quadruple chromosomes give a compensating adaptive advantage in *C. coronarium*, as does sporadically occur in *Hordeum vulgare, Secale cerale, Datura stramonium, Triticum aestivum* and in many insects[9-13] and lead to alternate orientation and disjunction of chromosomes exceeding 95% occur in all the 4 head types of *C. coronarium* needs to be investigated. If it does occur, pollen fertility exceeding 95% is guaranteed in this species. Fertility to this extent does occur in this species. Hence, its occurrence is probable. Is this

special segregation genetically controlled or not is not known.

That directed type of disjunctional segregation restoring fertility and offering adaptive advantage can certainly occur in *C. coronarium* is evidenced by the fact that this does exist in *C. carinatum*[7,8] a closely allied, genetically close to *C. coronarium* and a freely inter-breeding species of this genus. In *C. carinatum*, Rana and Jain[8] observed that chromosomal rearrangements affecting two common pairs of chromosomes have been particularly selected in the evolution of various currently grown varieties of this species. Same can be and may be valid for *C. coronarium*. That disfunctional orientation is genotypically controlled is well known in higher plants[14]. Probably *C. coronarium* genome lodges a co-adapted "gene complex" or a "supergene group" inherited as a unit that maintains adaptatively useful translocation heterozygosity with specifically directed disfunctional ability that does not impair genetic fertility or functionality. This gene complex is present at least in *C. carinatum* in which Rana[7] induced interchanges and synthesized an interchange stock in which 12 of the 18 chromosomes were involved in rearrangements and formed a single multiple association. Even such genotypes were highly fertile, mainly due to pronounced tendency of the interchange multiples to show preferentially a particular type of orientation viz. alternate at MI. Thus, both *C. carinatum* as well as *C. coronarium* appear to have a remarkable inherent capacity to withstand chromosomal rearrangements and maintain a high degree of gametic and seed fertility.

(c) *Telomere adhesion*: Telomeres, the terminal ends of chromosomes, have a compound structure, a special cycle of division and exhibit a tendency for non-homologous association at first meiotic prophase[15-17]. This adhesion is more common in plants having large and long chromosomes than in those having small and short chromosomes[18]. Almost 80% of such connections are of heterochromatin[19]. The interchromosomal connections in *Lathyrus sylvestris* are composed of heterochro-matin and are sticky in consistency[20]. Aakriti[6] found a considerable proportion of PMCs exhibiting telomere adhesions that simulate translocation rings in *C. coronarium*. Telomere adhesions in varying frequency in 4 head types were also detected presently. Some of these adhesions simulate translocation rings as was the case with the creamish white radiate head type of *C. coronarium*, material investigated by Aakriti[6].

Whereas on the one hand telomeres of some chromosomes in some plant species exhibit tendency to adhere, on the other hand telomeres prevent chromosomes from fusing permanently. They also permit the stable replication of chromosome termini[21]. Both these functions are due to the specific structure and are replicated by a specialized process in which

telomeres primer specificity. and chromosome healing as well as conservation of the end- sequences are always maintained by the telomeres[22-24]. Telomere sequence specificity plus its high degree of conservation and telomere recombinations[25-28] are two unique but diametrically opposite features; telomeres exhibit and indicate genetic specificity and purpose of telomere adhesion rather than randomness or cytological artifacts. Do the telomeres of some *C. coronarium* chromosomes have sticky ends or do they have a tendency to undergo telomere-telomere recombinations is not known. Does the adhesion simply represent DNA primer mutation or primer disfunction so that the GC rich ends get synthesized repeatedly and cause telomeres to become sticky is also not known in *C. coronarium.*

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