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Cytogenetic Studies in *Trifolium* sp. Related to Berseem

III. The Relationships between the *T. scutatum*, *T. plebeium* and the *echinata* Group*

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Summary. In a cytogenetic study of five annual *Trifolium* spp. the genetical relationships between (1) *T. scutatum* Boiss. and (2) *T. plebeium* Boiss., and between them and (3) *T. carmeli* Boiss., (4) *T. echinatum* M. B. and (5) *T. latinum* Seb., were studied in intra- and interspecific F_1 and F_2 hybrids. Germination, seedlings development, pollen fertility and chromosome configurations during meiosis and seedset were recorded. All the *T. scutatum* × *T. plebeium* F_1 were green, but the hybrids between either *T. plebeium* or *T. scutatum* and *T. carmeli*, *T. echinatum* or *T. latinum* were mainly albinos. Those that were green had a very high rate of mortality and the survivors produced many albino seedlings. Pollen fertility was about 60% in *scutatum* × *plebeium* F_1s, and one of their eight bivalents was heteromorphic. Hybrids between either of these and *T. carmeli*, *T. echinatum* or *T. latinum* had 30—50% stainable pollen and had several multivalents, suggesting the existence of a system of chromosomal translocations in these species. Seed set was roughly correlated with pollen stainability. The nature of the isolation mechanisms operating between these species is discussed.

Introduction

A study of crossability among twelve annual, East Mediterranean *Trifolium* species revealed that they may be divided into five groups on the basis of cross compatibility. Seed set upon hybridization is good in "within group" species combinations, and poor or very poor when the crossed species belong to different groups (Putiyevsky and Katznelson, 1973). *T. carmeli* Boiss., however, belongs to two crossability groups. It produces ample seed when crossed with *T. echinatum* M. B. and *T. latinum* Seb. The biosystematic relationships between the three, morphologically very similar, taxa have been described elsewhere (Katznelson and Putiyevsky, 1974). *T. carmeli* also produces ample seed when crossed with the morphologically very dissimilar *T. scutatum* Boiss. and *T. plebeium* Boiss. The two latter species are, however, very similar to each other and morphologically intermediate plants are found in nature. Moreover, three other species, *T. alsadami* Post, *T. sannineum* Mout. and *T. farayense* Mout., which are very similar to *T. scutatum* and *T. plebeium*, have been described as endemic to Syria and Lebanon. This morphological continuity between *T. scutatum* and *T. plebeium* suggests that only biosystematic study would clarify their taxonomic position and rank. As well as describing the relationship between these two species, the present paper reports the results of a study of the isolation mechanisms operating beyond the crossability stage between these two species on one hand, and *T. carmeli*, *T. echinatum* and *T. latinum* on the other.

Materials and Methods

The origins of the lines used as parent plants as well as the two methods of obtaining hybrid seeds, i.e. manually (HH) and by the "natural hybridization programme" (NHP), have been presented by Katznelson (1971) and Putiyevsky and Katznelson (1973). Altogether, four populations of *T. plebeium* (abbreviated in the text and tables to *Tple*), one population of *T. scutatum* (*Tscu*), and three, four and two populations of *T. carmeli* (*Tcar*), *T. echinatum* (*Tech*) and *T. latinum*** (*Tlat*), respectively, were studied. The last three species are referred to in the text as group II species or the *echinata* group. In addition, two populations of *Tcar* and one of *Tscu* were used as pollen sources in NHP.

A total of 207 hybrid F_1 and 72 F_2 seeds were sown and all except 12 were interspecific combinations. Each seed was germinated separately in a petri dish, transferred to soil in 3 kg pots, and kept in a glasshouse.

The methods employed in the cytological and pollen fertility studies were described by Putiyevsky and Katznelson (1970). Seed set upon selfing, backcrossing (since the plants are annuals, the hybrids were crossed to plants from the same source as their parent plants), and open pollination (with wide variety of pollen sources) was carried out as described earlier (Katznelson and Putiyevsky, 1974) and was determined for all the F_1 and some F_2 plants.

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** There was no problem in identifying *Tscu*, *Tple*, *Tcar* and *Tech*, but the populations of *Tlat* used in this study differ from Sebastiani's description in having wider leaflets, so that their identification as *Tlat* may be erroneous. In this case they should be regarded as part of the *T. echinatum* complex, and perhaps form a new species.

Table 1. *Germination and development of F_1 and F_2 hybrid seed*

Species combination	Total number of seeds	Number of seedlings	Albinos	Green but dead before flowering	Reached flowering	
					number	% of germinating seeds
F_1-intra						
Tple* × Tple	12	12		4	8	67
F_1-inter						
Tscu × Tple	55	53		27	26	49
Tscu × Tcar	97	73	29	17	27	37
Tscu × Tech	25	16	13	2	1	6
Tscu × Tlat	12	8	4	1	3	37
Tple × Tcar	55	45	19	22	4	11
Tple × Tech	6	6	6		0	0
Tple × Tlat	5	5	2		3	60
F_2						
(Tple × Tscu) × BC**	50	50	4	6	40	80
(Tscu × Tcar) × Tcar	19	19	13	5	1	5
(Tech × Tscu) × Tech	1	1			1	100
(Tlat × Tple) × Tlat	1	1			1	100
(Tech × Tscu) Selfed	1	1			1	100

* Tple — *T. plebeium*
Tscu — *T. scutatum*
Tcar — *T. carmeli*
Tech — *T. echinatum*
Tlat — *T. latinum*

** Back crosses to both parental species.

Results

a) Germination and Development

All twelve *T. plebeium* intraspecific, and most *T. plebeium* × *T. scutatum* interspecific F_1 hybrid seed germinated, compared with about 75% germination in combinations of either *Tple* or *Tscu* with group II species (Table 1). These values are much higher than those obtained in intra and interspecific hybrids *within* group II (Katznelson and Putiyevsky, 1974).

However, many of the germinating seedlings were either white or cream-coloured and devoid of chlorophyll. Albino seedlings were not found in intraspecific *Tple* hybrids, or when they were crossed to *Tscu*, but only in hybrids between either of them and any of the group II species. They were progenies of all populations studied. The frequency of albinos averaged 48% and ranged in species pair-combinations between 40–100% of the seedlings. The highest occurrence of albinos was in combinations with *T. echinatum* (19 from 22 germinating seeds). All the albino seedlings died, and no green plant was obtained from *Tech* × *Tple*. Reciprocal differences in albino formation seem to occur; most of the albino seedlings occurred when *Tscu-Tple* were females — 71 albinos from 139 germinating seeds, as opposed to one albino from 19 in reciprocal combinations.

Further mortality occurred in most of the pair-combinations and *Tple* × *Tcar* F_1 seedlings died much more often than the other combinations ($P < 0.01$), leaving only four flowering plants from 45 germinating seeds. Many of these seedlings died of some disease that was never observed in the parent plants, even in those growing adjacent to infected F_1s.

b) Pollen Fertility and Cytology

All eight *Tple* intraspecific hybrids were completely fertile, while the majority of *Tple* × *Tscu* F_1 hybrids had 50–80% stainable pollen (Table 2 presents the frequency distributions of pollen stainability for the various cross combinations). A wide variation in pollen stainability, ranging from 10% to 80%, was found in F_1 hybrids between *Tple* — *Tscu* and group II species; the few hybrids with *T. latinum* as a parent were less fertile (30–35%) than those of either *T. carmeli* (58%) or the one remaining plant of *Tech* × *Tscu* (47%).

Cytological observations revealed the following results. Nine *Tple* × *Tscu* F_1 hybrids studied cytologically had 8 II, except for one cell with 2 I, 7 II. However, one of the bivalents was easily recognizable as heteromorphic, a feature not observed in the parents (Putiyevsky and Katznelson, 1970) or in intraspecific hybrids. This heteromorphic bivalent had one distinctly larger arm, which never formed a ring bivalent and was stained much darker than the normal bivalents. *Tple* × *Tscu* hybrids had a lower chiasmata frequency (11.7 per cell) than did either the parents (Putiyevsky and Katznelson, 1970) or the group II hybrids (Katznelson and Putiyevsky, 1974). In contrast, F_1 hybrids between either *Tple* or *Tscu* and the group II species reveal a complicated chromosomal pattern (Table 3).

Table 2. *Frequency distribution of pollen fertility of intra and interspecific clover hybrids*

Combination	Number of plants with pollen fertility (%)										Total number plants	Average pollen fertility %
	0–10	11–20	21–30	31–40	41–50	51–60	61–70	71–80	81–90	91–100		
F_1												
Intraspecific												
Tple × Tple										8	8	96.5
Interspecific												
Tscu × Tple					2	9	9	2	2	2	26	64.8
Tscu × Tcar		1			4	7	3	5	1		21	58.1
Tscu × Tech					1						1	42.0
Tscu × Tlat	1	1			1						3	23.0
Tple × Tcar			1		1		1	1*			4	53.2
Tple × Tlat		1				2					3	44.7
F_2												
(Tple × Tscu) × BC**					3	9	8	3	3	14	40	73.5
(Tscu × Tcar) × Tcar					1						1	48.0
(Tech × Tscu) × Tech				1							1	33.0
(Tlat × Tple) × Tlat									1		1	83.8
(Tech × Tscu) × (S)***				1							1	37.0

* A trisomic plant.
** Back crosses to both parental species.
*** Selfing.

Table 3. *Multivalent formation in interspecific F_1 and F_2 clover hybrids*

Plant number	Species ♀	Species ♂	No. of cells exam-ined	No. B chromos. per cell	valents	number of cells with															Average chiasma per cell	Pollen ferti-lity %
					I		2	4	1	3	5			2	1		1	2	1	1		
					II	8	7	6	6	5	4	6	5	4	4	4	5	2	3	4		
					III				1	1	1		2	2	1			2				
					IV							1			1	2		1	1			
					V												1		1			
					VII															1		
F_1																						
1075/1	Tscu	Tcar	30	—		16	14														11.4	40
981/13	Tscu	Tcar	20	—		18	2														11.7	72
981/24	Tscu	Tcar	30	—		30															10.0	51
275/1	Tple	Tcar	30	—		30															12.2	67
1199/2	Tple	Tcar	10	—		2	2	1	1			4									12.6	25
1068/1	Tcar	Tple	30	—		3	3		16	3		2	3								12.8	42
986/1	Tech	Tscu	30	—		8	1		11			4		3		1	2				12.8	47
1081/2	Tlat	Tple	12	2		5	6	1													12.0	57
1081/1	Tlat	Tple	21	2		4	3	1	11			2									12.6	58
1189/1	Tlat	Tple	19	—					4			4	2		3	1	2	1	1	1	12.1	19
1191/1*	Tlat	Tscu	22	—		1			2	2		2	1				5	1		1	11.8	10
1193/1	Tscu	Tlat	20	—		1	1		2	1	1	2	3	2			5			2	12.0	44
F_2																						
1187	1081/2	Tlat	18			16	2														13.0	83
169	981/24	Tcar	18			18															14.8	48
977	986/1	986/1	15			7	1	2	5												12.8	37

* In addition to that mentioned above, plant 1191/1 also had one cell each with the following multivalent formation: 3 II, 2 III, IV; 2I, 3 II, 2 V; 3 I, 2 II, IV, V; 2 I, 3 II, III, V; 3 I, II, 2 III, V; 4 II, III, V; I, 3 II, 3 III.

T. latinum differs from both *T. plebeium* and *T. scutatum* by three, or more, chromosomal translocations, as shown by the existence of PMC with septavalents, or pentavalents and either trivalents or a quadrivalent in the same cell. One cell (V + + 2 III + II + 3 I) indicates that at least four translocations are involved in this combination.

Tech seems to differ from *Tscu* by at least two translocations, although the appearance of cells with either V or 2 III, and one cell with 2 IV may indicate the existence of at least three translocations

Tcar differs from *Tple* by at least one, probably two, translocations, whereas no multivalents (but many cells with 2—4 univalents) have been observed in its hybrids with *Tscu*. A trisomic ($2n = 17$) *Tcar* × *Tple* F_1 had mostly 8 II + I, but 6 out of 26 cells had III + 7 II.

An interesting cytological feature found in this study is the appearance of two B-chromosomes in each of two full sibs, F_1 hybrids between *Tlat* and

Table 4. *Seed formation in F_1 and F_2 clover hybrids*

Combination	Number plants examined	Seed set upon									Seed weight in open pollination in grams	% of plant weight
		Selfing			backcross to ♀			backcross to ♂				
		1	2	3	1	2	3	1	2	3		
F_1												
Intraspecific												
Tple × Tple	8	1457	0	0	25	16	64	30	21	70	0.10	0.21
Interspecific												
Tple × Tscu	25	4542	98	2.1	396	129	45	322	145	45	7.04	1.30
Tple × Tcar	4	799	0	0	139	4	2.9	136	4	2.9	0.08	0.02
Tple × Tlat	3	895	0	0	71	5	7.0	96	0	0	0.02	0.01
Tscu × Tcar	20	4990	5	0.1	81	8	9.9	93	9	9.7	2.45	0.21
Tscu × Tlat	3	303	0	0	63	0	0	73	0	0	0	0
Tscu × Tech	2	706	1	0.1	32	2	6.2	— ** —		—	0.38	0.21
F_2												
Tple × Tscu BC***	40	5381	1	0.01	—	—	—	—	—	—	11.15	1.02
(Tscu × Tcar) × Tcar	1	144	0	0	—	—	—	—	—	—	0.13	1.09
(Tech × Tscu) × Tech	1	88	0	0	—	—	—	—	—	—	0.01	0.01
(Tlat × Tple) × Tlat	1	60	0	0	—	—	—	—	—	—	0	0
(Tech × Tscu) × (S)	1	180	0	0	—	—	—	—	—	—	0.01	0.04

* 1 — number of flowers pollinated.
2 — number of seed obtained.
3 — % of seed set.
** not done.
*** BC — backcrosses to both parents. (S) — Selfed.

Tple whose parents had the normal $2n = 16$ complement with no B chromosomes. Meiosis in these two F_1 hybrids was superficially much more regular than in the third plant of this combination, No. 1189/1, which had no B's. This phenomenon is further discussed elsewhere (Putiyevsky and Katznelson, in preparation).

c) Seed Set in F_1s

Altogether, 64 F_1 plants of the combinations concerned in this paper set seed, and the results are presented in Table 4.

i. *Selfing.* No seeds were obtained in 1457 selfed florets of intraspecific *T. plebeium*. This is in accordance with the previous observations that all the species involved are self-incompatible (Putiyevsky and Katznelson, 1970). On the other hand, 98 seeds (2.1% of the selfed florets) were obtained in the *Tple* × *Tscu* F_1s. Most of these seeds, however, were produced in three of 25 F_1 selfed hybrids, and most were shrunken.

Six more seeds were obtained in all plants of the other combinations studied here, five from one plant of *Tcar* × *Tscu*. The other 13 plants of that combination did not produce any seed.

ii. *Backcrosses.* Seed set upon backcrossing in the intraspecific hybrids was very high (67%), even higher than in the production of these hybrids (about 45%, Putiyevsky and Katznelson, 1973).

The *Tscu* × *Tple* hybrids produced about 45% seed on backcrossing, but seed set in hybrids between either of these species and group II plants was much lower, especially when *Tlat* was the other parent. This is in accordance with F_1 hybrid pollen fertility, and since the pollen used in the backcrosses was from fully fertile, non-hybrid parents, the results suggest that megaspore fertility is similar to pollen fertility.

iii. *Seedset upon open pollination.* Seed set closely resembled the results of backcrossing, except for *Tcar* × *Tscu*, where seed production in a few plants was higher than expected. Since these plants have also shown reciprocal differences in seed set upon backcrossing, they are probably intraspecific entities; this is further supported by their morphology and pollen fertility.

d) F_2-Plants

The most interesting, and as yet unexplained, feature found in F_2 hybrids of the combinations considered was the complete germination of the 71 F_2 seeds sown, compared with 50—80% germination in the parents and F_1 hybrids. The same phenomenon was seen also in F_2 hybrids between group II species (Katznelson and Putiyevsky, 1974).

Albino seedlings also appeared among F_2 plants (i.e. progenies of green F_1s, Table 1). There were two kinds of albinos:

a) The fifty F_2 seeds of *Tscu* × *Tple* that were sown were from twelve combinations, i.e. progenies of six F_1 plants backcrossed in both directions. The four albino seedlings, together with four green ones, were all from one plant, NYT (239 × 237) × 239. The backcross of the same F_1 plant to 237 resulted in green seedlings only.

b) Many albinos appeared in (*Tscu* × *Tcar*) × *Tcar* F_2s. Here the 19 F_1 seeds were derived from five different F_1s, and backcrossed to three *Tcar* sources.

All five plants produced albino progenies so that 69% of the seedlings in F_2 were albino compared with 43% in the F_1. In addition, only one of the remaining six green seedlings survived to flowering stage. The other five died of similar causes as the *Tscu* × *Tcar* F_1s described earlier. Thus, while 80% *Tscu* × *Tple* F_2s set seed, only 5% *Tscu* × *Tcar* reached that stage.

Pollen fertility of F_2 plants was, on average, somewhat better than that of their parents (Table 2). Many of the *Tple* × *Tscu* backcrosses to both parental species completely restored fertility. Other plants of this combination, and the other four F_2 hybrids from other combinations, varied in their pollen fertility.

Cytological observations in F_2 were carried out on four (*Tple* × *Tscu*) × *Tscu* F_2s, and three other combinations. The first four were similar to their parents in not forming any multivalents, but had occasional univalents. The heteromorphic bivalent was sometimes present; in their F_1 parents all cells had this bivalent.

Two of the other three F_2 plants analysed cytologically (Table 3), 169 and 1187, were similar to their parents, i. e. there was either normal meiosis in the former, or appearance of univalents in the latter. Incidentally, the latter did not have B chromosomes, which were present in its F_1 parent.

The third F_2 plant, F_2 977, is interesting; whereas its parent, No. 986, probably had three translocations, the F_2 showed one trivalent only. In spite of this "normalization" of meiosis, pollen fertility of this F_2 was lower than of the parent, i.e., it was much more cytologically complicated.

Seed set in F_2 (Table 4) upon open pollination was good in most of the *Tple* × *Tscu* F_2, and also in the one (*Tscu* × *Tcar*) × *Tcar* hybrid. The other F_2, however, produced only 0—3 seeds, even in 1187 whose pollen stainability was above 80%. No seeds, not even shrunken ones, were formed in 5800 selfed flowers in the F_2 plants in contrast to the many shrunken ones obtained in their *Tple* × *Tscu* F_1 parents.

Discussion

The outstanding finding in this study is probably the systematic appearance of albino seedlings in F_1 and F_2 interspecific hybrids. This serves as a powerful isolation mechanism between *Tscu* — *Tple* on one side, and *Tcar* — *Tlat* — *Tech* on the other. They may be regarded as Chl (Chlorophyll) groups I and II respectively. No albino seedlings have been found in *Tscu* × *Tple* F_1 hybrids, and the appearance of albinos in the F_2 derived from this combination was sporadic. The latter two species are partially isolated from each other by other devices, such as some pollen sterility and subnormal seed set in F_1 and F_2. This "mild" isolation is also evinced by some morphological intermediates which are found in the wild in the few locations in Northern Israel where these two species are sympatric. These populations, however, are exceptions to the majority of monospecific stands, either of *Tscu* or *Tple*. Geographical and ecological isolation may thus be more important than the decreased fertility and fecundity described earlier. This pattern also fits the distribution of the other closely related taxa, *T. alsadami*, *T. sannineum* and possibly also *T. farayense*, all described from Lebanon and Syria. According to Mouterde (1970), *T. alsadami* belongs in fact to *T. plebeium*, whereas *T. sannineum* and *T. farayense*, which he quite hesitantly describes as two "good" species, occupy different regions and habitats. These three endemic taxa, especially *T. alsadami* and *T. sannineum*, are intermediate between *Tple* and *Tscu* in various morphological traits. Considering the cytogenetical and morphological proximity of *Tple* and *Tscu*, one wonders if there is a place for intermediate species between them. All the taxa concerned may actually be four or five subspecies which are somewhat different morphologically, and are separated geographically and ecologically, with some chromosomal heterogeneity between the two extremes, *Tscu* and *Tple*. If this is so, the group may be easily regarded as one, somewhat heterogeneous species, *T. scutatum* Boiss. The answer to this question may be obtained only by a biosystematic study involving all the taxa involved in the *T. scutatum* complex.

The isolation between this complex and the group II species is much more decisive and clear cut. It is here that we find the albinism as an isolation mechanism. It is here also that hybrids frequently die because of disease that was seldom seen to attack their parental species. Moreover, the surviving F_1 plants had a very low seed set, partly due to the existence of major chromosomal translocations between their parents. Both albinism, disease susceptibility and low fecundity appeared in F_2 plants even more drastically than in the F_1 plants. Very few seeds were formed in the few F_2 and BC_1 plants that survived, out of hundreds of F_1 hybrid seeds that were obtained quite easily. Thus, the isolation mechanisms operating between the *T. scutatum* complex and group II start to operate mainly after F_1 germination, but then they affect almost every possible stage, at least up to that of F_3 seeds.

Several forms of chlorophyll-deficient plants have been found in *Trifolium* (see de Haan, 1933, for a review of early work). Williams (1939) found at least 17 genes, either "albina" or "xantha", in inbred lines of *T. pratense* L. Several albino mutants have been isolated in inbred lines of *T. alexandrinum* L., a species related to those dealt with in this paper, by Sawyer (1952). All of these were apparently genic, not strictly cytoplasmic, and recessive, i.e. they comprised up to 25% of the progenies. The albinos obtained in our case are of a different kind, for the following reasons: Firstly, plants that produced albinos when crossed with plants of the other chlorophyll group did not produce them when crossed with individuals of their own chlorophyll group (Katznelson and Putiyevsky, 1974, and this work); secondly, their predominance, up to 100% of the germinating seed in some cases, rules out the possibility that they are simple, Mendelian recessives.

The appearance of white spots, or even complete albinos in interspecific hybrids, has been mentioned earlier (de Haan, 1933). Correns (1928) related the phenomenon to the "bastard nucleus". Two such cases have been reported in *Trifolium*. The albino seedlings in a cross between *T. repens* and *T. uniflorum* reported by Pandey (1957) may be a regular albino mutant, but albinos obtained by Newton *et al.* (1970) in *T. pratense* × *T. diffusum* hybrids seem to be similar to our albinos. There were too many albinos to be considered as a chance segregation of a simple recessive gene.

The appearance of albinos in inter-chlorophyll group-hybrids may result from various causes, genetic, cytoplasmic-genic interaction and cytoplasmic, which may operate together.

A system built on genetic factors only may be explained by different intermediary products of chlorophyll biosynthesis, or by factors responsible for the formation of the chloroplast. As a result, the species concerned are not completely complementary to each other genetically. In this case one would not expect to have reciprocal differences, and the variation in the frequency of albinos will depend on the amount of heterozygosity in the two parental plants. All progenies of a dominant homozygote in all of the non-complementary loci will be green regardless of the genetic make-up of the other parent. But 75% albinos are expected if each of the two plants is heterozygous for only one gene in the non-complementary part of chlorophyll, or chloroplast, formation.

A system built on purely cytoplasmic factors would result in clear cut reciprocal differences in albino formation, and all seeds of a specific cross combination would be either normal or albinos, i.e. would not segregate.

The reciprocal differences, accompanied by segregation within full sib seeds, may indicate that at least some of the albino formation in the combinations reported here is produced through interaction between the cytoplasms of *Tple* — *Tscu*, and genes of *Tcar*, *Tech* or *Tlat*, but non-complementary cytoplasmic and genic factors may also have their effects. Further study, which is in progress, may elucidate the nature of this chlorophyll deficiency.

The genetical nature of disease susceptibility may be of the same type or types as that of chlorophyll deficiencies. Both susceptibility and albinism are known to be usually recessives to disease resistance, and to normal chlorophyll formation. Pathogen attack may be common to all seedlings; most of the intraspecific entities are immune, but in some specific cross combinations, this immunity is lost.

The cytological evidence, although incomplete, suggests that all five taxa treated in this paper belong to one system of major chromosomal translocations. The heteromorphic bivalent in *Tscu* × *Tple* F_1 is a chromosomal rearrangement. This is also shown by the fact that the hybrids of these two species with either *Tech*, *Tlat* or *Tcar* differ in the number of translocations. The presence of fewer translocations in *T. carmeli* hybrids than in *Tech* or *Tlat* further supports the view, published earlier on the basis of crossability data (Putiyevsky and Katznelson, 1973), that *T. carmeli* forms a link between *Tscu* — *Tple* from one side and the *T. echinatum* complex from the other.

These facts may have two taxonomic implications. *First*, it supports our conclusion that *T. carmeli* deserves specific rank, and is not a mere varietas of *T. echinatum*, as suggested by Zohary (1972a).

Second, it shows that the separation of these species into two subsections, as proposed by Zohary (1972b), does not fit the cytogenetic results given in this paper which show clearly that the *T. scutatum* complex is closely related to the *T. carmeli* — *T. echinatum* complex, in spite of the morphological dissimilarity.

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