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Genome relationships in *Thinopyrum junceum* (L.) Löve polyploid complex

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SUMMARY

The genomic relationships between *Thinopyrum bessarabicum* $2n=14$, *T. junceiforme* $2n=28$, *T. sartorii* $2n=28$ and *T. junceum* $2n=42$ were determined by computer-aided karyotype analysis. The results revealed that the genome of *T. bessarabicum* is similar to one of the two nearly identical genomes of *J. junceiforme* and the genome designations $J^{j_1}J^{j_1}$ and $J^{j_1}J^{j_1}J^{j_2}J^{j_2}$ are proposed for the two taxa respectively. The chromosome complement of *T. junceiforme* is found very similar to that of *T. sartorii* for which the genome designation $J^{j_1}J^{j_1}J^{j_3}J^{3}$ is advocated, while both taxa are characterized as segmental allotetraploids. *Thinopyrum junceum* is characterized as segmental allohexaploid with the genome designation $J^{j_1}J^{j_1}J^{j_{(2)}}J^{j_{(2)}}J^{j_{(3)}}J^{j_{(3)}}$. Furthermore, the examined taxa of *T. junceum* polyploid complex are considered as separate biological species and it is suggested that they have modified versions of the same basic genome.

Key-words: genome relationships, karyotype, segmental allopolyploids, *Thinopyrum.*

INTRODUCTION

The *Thinopyrum junceum* (L.) Löve polyploid complex includes perennial littoral taxa from diploid to octoploid, with rhizomatous and tufted patterns of vegetative growth and spikes with a fragile rachis (Moustakas *et al.* 1986; Moustakas 1989, 1991), The complex consists of the taxa: *Thinopyrum bessarabicum* (Savul. and Rayss) Löve $2n=14$ (J_1J_1: Heneen & Runemark 1972; Moustakas & Coucoli 1982; Moustakas *et al.* 1986; Pienaar *et al.* 1988; E^jE^j: Dvorak 1981b; E^bE^b: McGuire 1984; Forster & Miller 1989; *JJ*: Wang 1985; Jauhar 1988, 1990a,b; Wang & Hsiao 1989; $J^{j_1}J^{j_1}$: Moustakas 1988, 1991; Moustakas *et al.* 1988), *Thinopyrum junceiforme* (Löve and Löve) Löve $2n=28$ ($J_1J_1J_2J_2$: Ostergren 1940; Heneen 1962; Cauderon 1966; Moustakas *et al.* 1986; Jarvie & Barkworth 1990; $E_3E_3E_4\mathrm{E}_4$: Schulz-Schaeffer & Jura 1967; $E^aE^aE^bE^b$: Dvorak 1981b; $E^jE^jE^{ju}E^{ju}$: McGuire 1984; $J^{j_1}J^{j_1}J^{j_2}J^{j_2}$: Moustakas *et al.* 1988; JJJ^eJ^e: Wang 1989; Wang & Hsiao 1989; *JJJJ*; Zhang & Dvorak 1990), *Thinopyrum sartorii* (Boiss and Heldr.) Löve $2n=28$ ($J_1J_1J_3J_3$ Heneen 1977a; Moustakas *et al.* 1986; $J^{j_1}J^{j_1}J^{j_3}J^{j_3}$: Moustakas *et al.* 1988; JJJ^eJ^e: Wang 1989; *JJEE*: Jarvie & Barkworth 1990; *JJJJ*: Zhang & Dvorak 1990), *Thinopyrum distichum* (Thunb.) Löve $2n=28$ ($E^{d_1}E^{d_1}E^{d_2}E^{d_2}$: Pienaar 1983; $J^{d_1}J^{d_1}J^{d_2}J^{d_2}$: Pienaar *et al.*

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1988; $J_1J_1J_2J_2$: Jarvie & Barkworth 1990; $JJJJ$: Zhang & Dvorak 1990), *Thinopyrum junceum* (L.) Löve $2n=42$ ($J_1J_1J_2J_2E_3\dot{E}_3$: Cauderon 1958, 1966; Gupta & Fedak 1986; $E^aE^aE^bE^bE^cE^c$: Dvorak 1981b; $J_1J_1J_2J_2J_3J_3$: Moustakas *et al.* 1986; $J_1J_1J_2J_2EE$: Charpentier *et al.* 1986; $JJJJEE$: Jarvie & Barkworth 1990; $JJJJJJ$: Zhang & Dvorak 1990), and *Thinopyrum runemarkii* Löve $2n=56$ ($J_{(1)}J_{(1)}J_4J_4J_{(4)}J_{(4)}J_6J_6$: Heneen 1977b; Moustakas *et al.* 1986; $JJJJJJJJ$: Zhang & Dvorak 1990).

From the above mentioned different genomic designations that were proposed, it is evident that much needs to be done to clarify the genomic relationships in the *Thinopyrum junceum* polyploid complex. This is important because the taxa of the polyploid complex possess agronomically desirable traits such as the perennial habit, disease resistance, drought and salt tolerance that are of interest to wheat, rye and barley breeders (Dewey 1984). A better understanding of the genetic constitution and evolutionary relationships of the taxa of *T. junceum* polyploid complex are essential if we are to efficiently utilize this rich source of genetic variation (McIntyre 1988).

Although observing chromosome pairing at meiosis of interspecific hybrids has been recognized as the most reliable method for studying the phylogenetic relationships of the parental genomes (Kimber 1983), karyotype analysis has also been considered an important method for genome analysis (Chennaveeraiah 1960; Hsiao *et al.* 1986).

The purpose of the present investigation was initiated to determine the karyotype patterns of the taxa of *Thinopyrum junceum* (L.) Löve polyploid complex, and the relationships of these karyotype patterns to genome affinity. In the present study, all the taxa of the *T. junceum* polyploid complex were included with the exception of *T. runemarkii* and *T. distichum*, the latter one being native to S. Africa (Pienaar *et al.* 1988).

MATERIALS AND METHODS

The sources of the seed materials examined cytologically are as follows: *Thinopyrum bessarabicum*: Greece: Agelochori, near Thessaloniki, littoral zone; *Thinopyrum sartorii*: Greece: Naxos, in schistose littoral rocks; *Thinopyrum junceiforme*: French Atlantic coast, seeds were kindly made available by Dr Y. Cauderon, I.N.R.A. Versailles, France; *Thinopyrum junceum*: Greece: Agelochori near Thessaloniki, littoral zone.

Somatic cells were prepared from root tips of young seedlings. Root tips were pretreated with a saturated solution of 1-bromonaphthalene at room temperature for 4–5 h, fixed in glacial acetic acid and hydrolysed in 1 N HCl for 10 min at 60°C. They were then stained with leukobasic-fuchsin and the meristematic tip was squashed in a drop of 1% acetocarmine. Metaphase cells with a complete chromosome complement were photographed.

The photomicrographs of well-spread metaphase chromosomes were analysed with a microcomputer program which used a digitizer stylus for measurement of the chromosome arms. The microcomputer chromosome analysis system (Moustakas 1989, 1991) greatly facilitated the measurement of chromosome lengths and automatically calculated data such as length, relative length, arm ratio, the ordering of chromosomes by length, the combining of data for pairing homologous or pooling different spreads for comparisons. Statistical parameters generated by the analysis (Moustakas 1991) are not shown. All the information was stored for immediate or long-term retrieval, and for drawing of karyograms based on chromosome lengths and arm ratios.

The arm ratio was calculated as the length of the short arm divided by the length of the long arm. In practice, the precision of this system of computer-assisted chromosome analysis (Moustakas 1989, 1991) was limited by the ability to define the ends of the chromosomes and the position of the centromere. The microcomputer program was implemented on a Macintosh Plus equipped with a Hitachi DT 2871 N digitizer.

RESULTS

The results of the microcomputer analysis of karyotype data for *Thinopyrum bessarabicum* (based on chromosome analysis of 10 metaphase cells) revealed (see also Moustakas 1991) that the karyotype (Table 1, Fig. 1). consists of seven pairs of chromosomes as follows: two long chromosome pairs easily distinguished from each other by arm ratio (the first, No. 1, submetacentric, and the second, No. 2, a typically metacentric chromosome), one pair of medium and one pair of large satellites on the short arms of chromosomes 4 and 5 respectively (chromosome pair No. 4 acrocentric and chromosome pair No. 5 submetacentric), two small chromosome pairs (No. 6 and No. 7) though overlapping in size, can be clearly separated by arm ratio (No. 6 a metacentric one and No. 7 a submetacentric one) and finally of chromosome No. 3 which is distinguished by its intermediate size. The genome length of *T. bessarabicum* is 51·6 μm.

The results of karyotype analysis of the tetraploids *Thinopyrum junceiforme* and *Thinopyrum sartorii* (based on chromosome analysis of eight metaphase cells) revealed that their karyotypes have similar morphologies and genome size (Table 1, Fig. 1). It is clear that the seven largest chromosome pairs (Nos 1–7) in the two taxa show a striking similarity in arm ratio to the seven chromosome pairs of *T. bessarabicum.* The other seven chromosome pairs (Nos 8–14) in the two taxa were similar in chromosome length (except chromosomes 11 and 14) and arm ratio (except chromosomes 12 and 13). The chromosome pair No. 14 has a secondary constriction in *T. sartorii* but in *T. junceiforme* this is lacking. Two out of the three satellite chromosome pairs of *T. sartorii* were closely similar to the satellite chromosomes of *T. bessarabicum* and *T. junceiforme.* The one pair with small to medium satellites (chromosome 4 in all taxa) is recognized as acrocentric while the pair with large satellites (chromosome 5 in all taxa) is recognized as submetacentric. The other satellite chromosome pair of *T. sartorii* (No. 14) represents another type within the submetacentric centromere class. The genome length of *T. sartorii* is 1·2 μm larger than that of *T. junceiforme.*

The results of the microcomputer analysis of karyotype data for *Thinopyrum junceum* (based on chromosome analysis of eight metaphase cells) revealed (Table 1, Fig. 2) that the karyotype was composed of six metacentric chromosomes (chromosome 2, 6, 8, 10, 16 and 20), 12 submetacentric chromosomes (chromosomes 1, 3, 5, 7, 9, 11, 12, 13, 14, 15, 19 and 21) and three acrocentric chromosomes (chromosomes 4, 17 and 18). Three chromosome pairs were found to have secondary constrictions (chromosomes 4, 5 and 19). The satellite chromosome pairs 4 and 5 were nearly similar to the corresponding satellite chromosomes of *T. bessarabicum, T. sartorii* and *T. juinceiforme.* The third chromosome pair of *T. junceum* representing one of the smallest chromosome pairs of the complement, coincides in the submetacentric centromere class and resembles chromosome pair No. 14 of *T. sartorii.* The genome length of *T. junceum* is 132·8 μm.

DISCUSSION

On the basis of karyotype analysis and electrophoretic investigations of seed proteins, Moustakas & Coucoli (1982) and Moustakas *et al.* (1986) were of the opinion that the *J* genome of *T. bessarabicum* is identical to one of the two genomes of *T. junceiforme* and designated it J_1. Previously the two genomes of *T. junceiforme* were symbolized J_1 and J_2

Table 1. Mean absolute (μm) and relative (%) lengths of *Th. bessarabicum*, *Th. junceiforme*, *Th. sartorii* and *Th. junceum* chromosomes

Species	Chromosome character	Chromosomes																				
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
Thinopyrum bessarabicum[a]	Total A.L.	8·873	8·336	7·649	7·234	6·697	6·463	6·407														
	Total R.L.	17·206	16·165	14·833	14·028	12·986	12·533	12·425														
	Short arm A.L.	3·686	3·931	2·968	2·001 0·493*	2·514 1·025*	2·984	2·574														
	Short arm R.L.	7·148	7·623	5·755	3·880	4·874	5·786	4·991														
	Long arm A.L.	5·187	4·405	4·681	5·233	4·183	3·479	3·833														
	Long arm R.L.	10·058	8·542	9·078	10·148	8·112	6·747	7·434														
	Arm ratio	0·71	0·89	0·63	0·38	0·60	0·86	0·67														
	Centromere class	sm	m	sm	st	sm	m	sm														
Thinopyrum junceiforme[b]	Total A.L.	6·503	6·480	5·927	5·922	5·853	5·676	5·475	5·372	5·207	5·070	4·673	4·621	4·510	4·298							
	Total R.L.	8·604	8·572	7·841	7·834	7·743	7·509	7·243	7·107	6·889	6·708	6·182	6·114	5·967	5·686							
	Short arm A.L.	2·696	3·076	2·328	1·608 0·299*	2·276 0·990*	2·608	2·125	2·172	2·473	1·946	1·882	1·120	2·107	1·622							
	Short arm R.L.	3·567	4·069	3·080	2·127	3·011	3·450	2·811	2·873	3·272	2·575	2·490	1·482	2·788	2·199							
	Long arm A.L.	3·807	3·404	3·599	4·314	3·577	3·068	3·350	3·200	2·734	3·124	2·791	3·501	2·403	2·636							
	Long arm R.L.	5·037	4·503	4·761	5·707	4·732	4·059	4·432	4·234	3·617	4·133	3·692	4·632	3·179	3·487							
	Arm ratio	0·71	0·90	0·65	0·37	0·64	0·85	0·63	0·68	0·90	0·62	0·67	0·32	0·88	0·63							
	Centromere class	sm	m	sm	st	sm	m	sm	sm	m	sm	sm	st	m	sm							

Table 1. (*Cont'd*)

Species	Chromosome character	Chromosomes 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
Thinopyrum satorii[c]	Total A.L.	6·987	6·867	6·361	5·898	5·583	5·567	5·559	5·423	5·378	5·197	4·996	4·527	4·443	4·063							
	Total R.L.	9·092	8·936	8·277	7·675	7·264	7·244	7·234	7·057	6·998	6·762	6·501	5·891	5·782	5·287							
	Short arm A.L.	2·908	3·237	2·433	1·603 0·415*	2·076 0·897*	2·570	2·234	2·221	2·521	2·003	2·032	1·449	1·955	1·539 0·668*							
	Short arm R.L.	3·784	4·212	3·166	2·086	2·701	3·344	2·907	2·890	3·280	2·606	2·644	1·886	2·544	2·003							
	Long arm A.L.	4·079	3·630	3·928	4·295	3·507	2·997	3·325	3·202	2·857	3·194	2·964	3·078	2·488	2·524							
	Long arm R.L.	5·308	4·724	5·111	5·589	4·563	3·900	4·327	4·167	3·718	4·156	3·857	4·005	3·328	3·284							
	Arm ratio	0·71	0·89	0·62	0·37	0·59	0·86	0·67	0·69	0·88	0·63	0·69	0·47	0·79	0·61							
	Centromere class	sm	m	sm	st	sm	m	sm	sm	m	sm	sm	st	m	sm							
Thinopyrum junceum[d]	Total A.L.	8·579	8·362	7·440	7·253	6·914	6·822	6·764	6·626	6·599	6·542	6·265	6·087	5·897	5·758	5·718	5·506	5·471	5·253	5·082	5·034	4·834
	Total R.L.	6·460	6·297	5·603	5·461	5·207	5·137	5·093	4·989	4·969	4·926	4·717	4·584	4·440	4·335	4·306	4·145	4·120	3·956	3·826	3·790	3·640
	Short arm A.L.	3·528	3·880	2·860	1·942 0·443*	2·528 1·053*	3·167	2·792	3·139	2·608	2·999	2·429	2·377	2·274	2·354	2·234	2·557	1·340	1·567	1·771 0·778*	2·342	1·866
	Short arm R.L.	2·656	2·922	2·154	1·462	1·904	2·385	2·102	2·364	1·964	2·258	1·829	1·790	1·712	1·772	1·682	1·925	1·009	1·180	1·333	1·763	1·405
	Long arm A.L.	5·051	4·482	4·580	5·311	4·386	3·655	3·972	3·487	3·991	3·543	3·836	3·710	3·623	3·404	3·484	2·949	4·131	3·686	3·311	2·692	2·968
	Long arm R.L.	3·804	3·375	3·449	3·999	3·303	2·752	2·991	2·625	3·005	2·668	2·888	2·794	2·728	2·563	2·624	2·220	3·111	2·776	2·493	2·027	2·235
	Arm ratio	0·70	0·87	0·62	0·37	0·58	0·87	0·70	0·90	0·65	0·85	0·63	0·64	0·63	0·69	0·64	0·87	0·32	0·43	0·53	0·87	0·63
	Centromere class	sm	m	sm	st	sm	m	sm	m	sm	m	sm	sm	sm	sm	sm	m	st	st	sm	m	sm

*Length of satellite.
[a] Genome length 51·6 μm.
[b] Genome length 75·6 μm.
[c] Genome length 76·8 μm.
[d] Genome length 132·8 μm.
A.L. Absolute length.
R.L. Relative length.

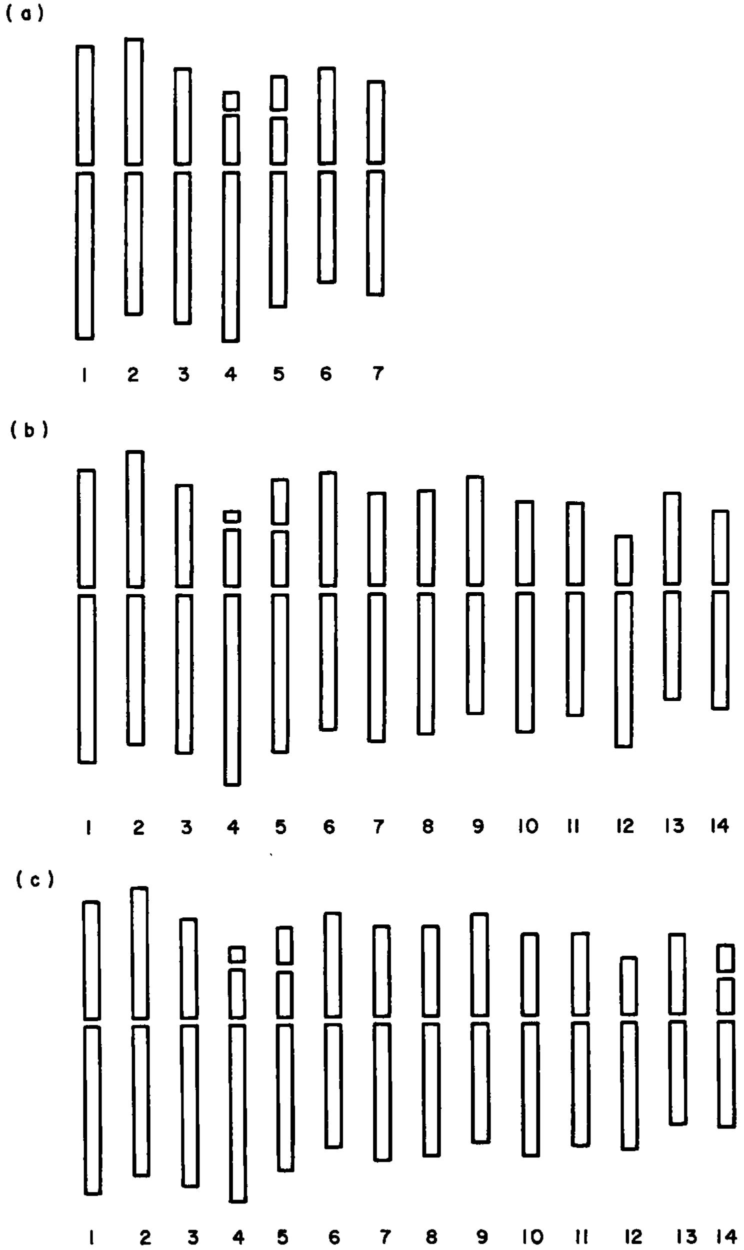

Fig. 1. Karyograms of (a) *Thinopyrum bessarabicum* $2n = 14$, (b) *Th. junceiforme* $2n = 28$ and (c) *Th. sartorii* $2n = 28$ based on computer-aided chromosome analysis of 8–10 metaphase cells.

by Östergren (1940) on the grounds of their autosyndetic pairing in a *T. junceiforme*/*Elytrigia repens* hybrid. The genome designation $J_1J_1J_2J_2$ was adopted also by Heneen (1962) for *T. junceiforme*. Pienaar *et al.* (1988) concluded that *T. junceiforme* is a near-autotetraploid or segmental allotetraploid with genome designation $J_1J_1J_2J_2$.

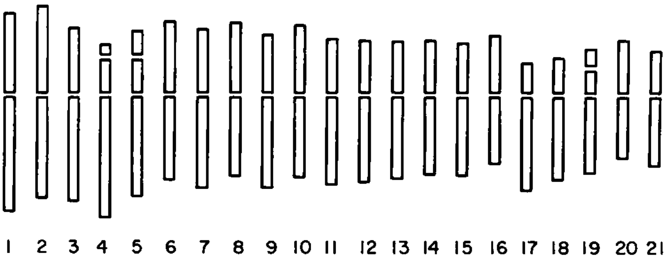

Fig. 2. Karyogram of *Th. junceum* $2n = 42$ based on computer-aided chromosome analysis of eight metaphase cells.

The chromosomes of *T. sartorii* and *T. junceiforme* are not distributed in groups of four, as seen in Fig. 1. This gives a clear impression that both taxa are segmental allotetraploids. Yet, from the results of our karyotype analysis, it can be concluded that the genome of diploid *T. bessarabicum* is similar to one of the two nearly identical genomes of *T. junceiforme* and we adopt the genome designations $J^{j_1}J^{j_1}$ and $J^{j_1}J^{j_1}J^{j_2}J^{j_2}$ for *T. bessarabicum* and *T. junceiforme* respectively. The latter species probably arose as an autotetraploid, but subsequently its two genomes underwent some differentiation (Cauderon 1958; Pienaar *et al.* 1988).

The chromosome complement of *T. sartorii* is very similar to that of *T. junceiforme*. However, the karyotypes of the two species differ from each other as regards the morphology of chromosome pairs 12, 13 and 14. In chromosome pair 12, the position of the centromere is more acrocentric in *T. junceiforme* than in *T. sartorii* as pointed out also by Heneen (1977a) while in chromosome pair 13, the position of the centromere is more metacentric in *T. junceiforme* than in *T. sartorii*. Yet, chromosome pair 14 is one of the three satellite chromosomes in *T. sartorii* whereas in *T. junceiforme* it lacks the secondary constriction. The genome designation $J_1J_1J_3J_3$ was proposed by Heneen (1977a) for *T. sartorii* and adopted by Moustakas *et al.* (1986). Later, Moustakas *et al.* (1988) proposed the genome designation $J^{j_1}J^{j_1}J^{j_3}J^{j_3}$ which is suggested also by the present investigation.

Sometimes in the metaphase cells of *T. junceum* all satellite chromosomes were not likely to be discernible in the same cell. This situation is within expectance as regards polyploidy and it was formerly reported by Östergren (1940) for *T. junceiforme*, by Heneen & Runemark (1962) and Heneen (1977a) for *T. sartorii* and by Heneen (1977b) for *T. runemarkii*.

The chromosome constitution of *T. junceum* according to our observations can be classified into the following three groups. A group of seven chromosome pairs representing the largest members of the complement whose chromosome morphology and arm ratio seem to represent the chromosome complement of *T. bessarabicum*. This chromosome set is likely to represent the basic J^{j_1} genome of *T. junceum* polyploid complex. Another set of seven chromosome pairs taken as a whole, and more precisely chromosome pairs Nos 8, 11, 13, 15, 17, 20 and 21 leads to the recognition of a striking similarity to the seven smallest chromosome pairs of *T. junceiforme*. This chromosome set is designated $J^{j_{(2)}}$ that is slightly differentiated from the genome designation J^{j_2} of the corresponding chromosome set of *T. junceiforme*. The group of the remaining seven chromosome pairs, i.e. chromosome pairs Nos 9, 10, 12, 14, 16, 18 and 19, corresponds slightly to the chromosome set given the genome designation J_3 by Heneen (1977a) for *T. sartorii* (J^{j_3} in the present investigation). Thus, it was designated $J^{j_{(3)}}$ genome. Both genomes $J^{j_{(2)}}$ and $J^{j_{(3)}}$ of

T. junceum are supposed to have been structurally differentiated from the basic J^{j_1} genome. Following the classification of polyploids proposed by Stebbins (1947) *T. junceum* can be characterized as segmental allohexaploid with the genome designation $J^{j_1}J^{j_1}J^{j_{(2)}}J^{j_{(2)}}J^{j_{(3)}}J^{j_{(3)}}$. This is in agreement with the suggestion of Gupta & Fedak (1986) that in the genome constitution of the hexaploid *T. junceum* three related genomes participate.

The evolutionary impact of structural rearrangements is well known, and this phenomenon has played a prominent part in speciation in addition to polyploidy in the genus *Thinopyrum* (Moustakas *et al.* 1986, 1988).

A problem as regards the taxonomic rank of the *Thinopyrum junceum* polyploid complex should also be discussed. As ploidy level differences taken as a powerful reproductive barrier that is likely to initiate genome divergence between such populations (Dvorak 1981a) and as no introgression was ever noticed in the areas where populations of diploid *T. bessarabicum* and hexaploid *T. junceum* meet (Moustakas 1989), we should consider the taxa of *T. junceum* polyploid complex as separate biological species.

In summary, we suggest that the examined species of *Thinopyrum junceum* polyploid complex have modified versions of the same basic genome, and agree with Dewey (1984), Wang (1985), Moustakas *et al.* (1986), Pienaar *et al.* (1988) that this genome be designated *J* after Östergren (1940).

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