Chromosoma (Berl.) 35, 206–216 (1971)

Chromosome Polymorphism in *Avena ventricosa* * **

TIBOR RAJHATHY
Research Branch, Canada Department of Agriculture, Ottawa, Ontario

Received June 22, 1971 / Accepted July 12, 1971

Abstract. The same karyotype which was described previously in *A. ventricosa* plants from Oran, Algeria was found in plants from Cyprus and in most of the plants from the Apsheron Peninsula, U.S.S.R. This karyotype, which consists of subterminal chromosomes, was designated C_v^1. In the karyotype of about one-third of the Apsheron plants a single pair of submedian chromosomes replaced a pair of long subterminals. This karyotype was designated C_v^2. The chromosomes formed 7^{II} at meiosis in both $C_v^1C_v^1$ and $C_v^1C_v^2$ hybrids regardless of geographic origin. A heteromorphic bivalent was apparent in PMCs in the $C_v^1C_v^2$ hybrids. A pericentric inversion was postulated as the origin of the submedian pair, the $C_v^2C_v^2$ karyotype being the inversion homozygote. The absence of duplication-deficiency gametes was inferred from the good fertility of the heterozygote. Members of the heteromorphic pair were transmitted in equal proportion and the segregates $C_v^1C_v^1$, $C_v^1C_v^2$ and $C_v^2C_v^2$ were equally fertile; thus the inversion did not handicap reproduction. The small contemporary colonies of *A. ventricosa*, with peripheral locations and vast distances between them, because of the full homology and interfertility, are considered remnants of a formerly large central population.

Introduction

Avena ventricosa, a wild diploid ($2n = 2x = 14$) oat species, has recently gained increased attention, following the suggestion that it is the putative donor of the C genome of the hexaploid species. The chromosomal evidence for this by Rajhathy (1966) and Ladizinsky and Zohary (1967) was later confirmed by biochemical results (Thomas and Jones, 1968; Murray *et al.*, 1970). Some of these biochemical results and a study of the ultrastructure of the chloroplasts (Steer *et al.*, 1970) indicated the presence of the *ventricosa* genome also in the recently discovered tetraploid species, *A. magna*. This further reflects on the importance of *A. ventricosa* in the evolution of the hexaploids, since cytogenetic results suggest that *A. magna* is one of their putative progenitors (Sadanaga *et al.*, 1968; Rajhathy and Sadasivaiah, 1969; Ladizinsky, 1969).

* Contribution No 282 from the Research Station, Central Experimental Farm, Ottawa, Ontario.

** This paper is dedicated to the memory of Dr. Barna Györffy, whose untimely death on August 5, 1970 ended a distinguished career that was an example of integrity and scholarship to a troubled generation of Hungarian geneticists.

Malzew (1930) combined *A. ventricosa* Balansa and *A. bruhnsiana* Gruner into one species *A. ventricosa* Balansa with two subspecies, ssp. *ventricosa* and ssp. *bruhnsiana*. He gave Oran, Algeria as the site for the former and the Apsheron peninsula in the Caspian Sea, U.S.S.R., for the latter subspecies. Malzew also noted that ssp. *ventricosa* was collected on Cyprus by Vavilov who considered it as an introduction to that island.

A. ventricosa was not available for experiments until the Canadian-Welsh expedition collected seeds of ssp. *ventricosa* around Oran in 1964 (Rajhathy, Zillinsky and Hayes, 1966). Since then, several samples of ssp. *bruhnsiana* were collected in the Apsheron region at my request by Russian botanists. Cyprus, the third site was explored by Drs. D. Zohary and G. Ladizinsky of the Hebrew University, Jerusalem in 1967, who kindly provided samples of seeds. Thus, material from all three sites was assembled for study.

The subject of this paper is the cytogenetics of *A. ventricosa* including plants from the three geographic populations and their hybrids. Chromosome polymorphism due to a pericentric inversion detected in the Apsheron population and the meiotic behaviour of the chromosomes in the inversion heterozygote is described and briefly discussed.

Materials and Methods

The material used in this study is listed in Table 1. Of the first 3 samples received in 1966 from the Apsheron region through the courtesy of Drs. F. Kh. Bakhteyev and T. N. Shevchuk (Leningrad, U.S.S.R.), two were identified as *A. ventricosa* (AVB II and III), while the third sample, omitted from this study, was found to be *A. pilosa*. All eight samples (AVB IV–XI) received in 1969 from Mr. S. H. Musajev (Baku, U.S.S.R.) were *A. ventricosa*.

The hybrids were produced in a growth cabinet by hand-pollinating emasculated florets. Some technical difficulty was encountered because of the small size of the anthers and the extreme toughness of the rachilla, which required the use of scissors in removing the secondary floret. F_1 and F_2 hybrids were grown also in a growth cabinet under a long day regime at a day temperature of 20° C and a night temperature of 15° C. Seed set was scored in the first panicle of each plant.

The cytological techniques employed were described previously (cf. Sadasivaiah and Rajhathy, 1968).

Results

Morphology and Classification

No single character was found by Malzew (1930) to separate ssp. *ventricosa* from ssp. *bruhnsiana*. The rank of subspecies had apparently been given to the Oran and Baku populations because of the geographical isolation and the larger size of the spikelets, glumes and basal

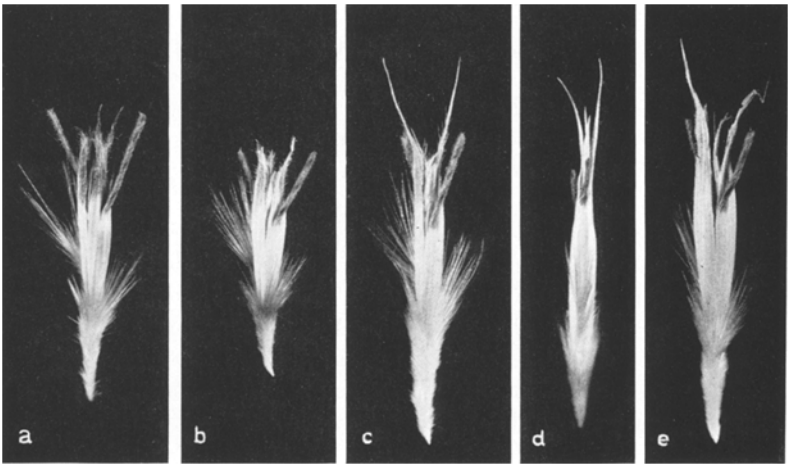

Fig. 1a–e. Spikelets of *A. ventricosa*. a Cyprus (AVC), b Oran (CW 50), c F_1 hybrid of CW 50×AVB II, d and e Apsheron region, AVB II and III, respectively

scar of the plants from the Apsheron region (Baku). When I grew them under uniform conditions in the growth cabinet the Baku plants had the largest and the Oran plants the smallest spikelets, while those of the Cyprus plants were intermediate (Fig. 1). The larger spikelet was dominant in the F_1 hybrids. I have found the shape and length of the lemma tips useful in separating plants from the Oran and Cyprus sites from those of the Apsheron region. The lemma tips of the plants from Oran and Cyprus were shorter, wide and blunt and densely covered by short hairs, while those of the plants from the Apsheron region were attenuated, narrow and pointed and the hairs were longer and more sparse (Fig. 1). The Apsheron-type lemma tips were dominant in the F_1 plants. The juvenile growth of the plants from Oran is more erect and the leaves are greyish-blue, whereas the juvenile growth of the plants from the two other sites is prostrate and the leaves are green. In the F_1 hybrids, the Apsheron-type lemma tips and the Oran type semierect growth and greyish-blue leaves were dominant.

Malzew (1930) classified *A. ventricosa* with *A. longiglumis* into the series *Stipitatae* and *A. clauda* and *A. pilosa* into the series *Inequaliglumes*. However, cytogenetic evidence clearly shows that, chromosomally, *A. clauda*, *A. pilosa* and *A. ventricosa* form a closely related group, while *A. longiglumis* belongs with the *Eubarbatae* diploids. All attempts to obtain hybrids between these two groups have failed thus far (Rajhathy and Thomas, 1967).

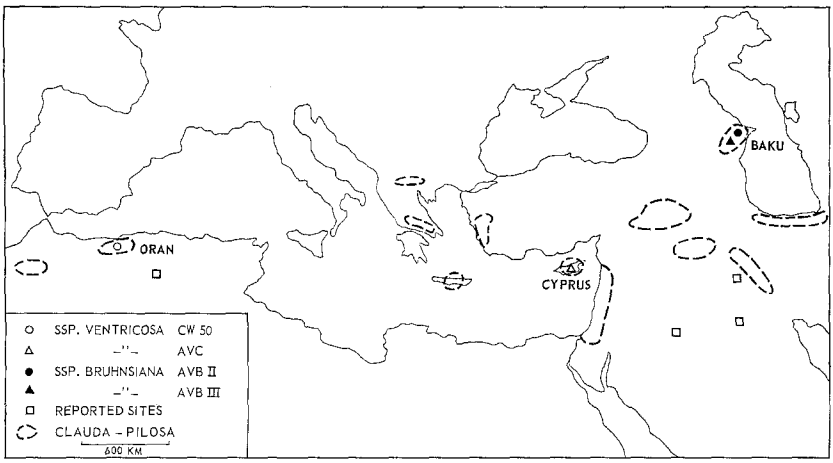

Fig. 2. Collection sites of the samples of *A. ventricosa* used in this study and sites of herbarium specimens and areas of *A. clauda* and *A. pilosa*

Geographical Distribution and Habitat

It has already been stated that *A. ventricosa* had been reported from and recently collected in Oran, Algeria, the Island of Cyprus and the Apsheron Peninsula (Baku) in the Caspian Sea. In addition to these locations, herbarium specimens were seen from Aflou, Algeria; Shargat and Nukhaib, Iraq; and Jabal-al-Annudah, Northern Saudi Arabia (pers. commun. from Dr. B. Baum). These sites, separated by vast distances, may be indicative of a once large and more or less contiguous population covering most of the contemporary distribution area of *Avena* (Fig. 2). The suggestion of Holden (1969) that "*A. ventricosa* may also turn out to be quite common once its primary habitat can be defined" is doubtful since the Canadian-Welsh expedition in 1964 located only a single and previously known site and none was located in 1970 by the Middle East expedition which collected some 2200 samples of other *Avena* species (Baum *et al.*, in preparation). It appears more likely that the existing small populations are peripheral remnants of a former central population.

A. ventricosa is a truly wild species forming small colonies in undisturbed habitats. It is a plant of barren, stony lands and deserts, covered with sparse herbaceous vegetation. Its slender spikelet with a narrow, pointed base, assisted by two long, twisted, geniculate awns is eminently adapted for dispersal by drilling itself into rocky crevices. *A. pilosa* or *A. clauda* or both are usual companions of *A. ventricosa* but

Table 1. *The origin of the samples of Avena ventricosa*

Subspecies	Code	Site of collection	Country	Collector
ventricosa	CW 50	3 km east of Oran	Algeria	Rajhathy, Zillinsky and Hayes (1964)
ventricosa	CW 51	3 km east of Oran	Algeria	Rajhathy, Zillinsky and Hayes (1964)
ventricosa	AVC I	2 km south of Nicosia	Cyprus	Zohary and Ladizinsky (1967)
ventricosa	AVC II	2 km south of Nicosia	Cyprus	Zohary and Ladizinsky (1967)
bruhnsiana	AVB II	Apsheron pen., Baku	U.S.S.R.	Mustafaev (1966)[a]
bruhnsiana	AVB III	Apsheron pen., Baku	U.S.S.R.	All-Union Institute, Leningrad, 1966[b]
bruhnsiana	AVB IV	Apsheron pen., Baku	U.S.S.R.	Musajev (1969)
bruhnsiana	AVB V	Apsheron pen., Artema distr.	U.S.S.R.	Musajev (1969)
bruhnsiana	AVB VI	Apsheron pen., Shveliani	U.S.S.R.	Musajev (1969)
bruhnsiana	AVB VII	Apsheron pen., Shveliani	U.S.S.R.	Musajev (1969)
bruhnsiana	AVB VIII	Apsheron pen., Artema Island	U.S.S.R.	Musajev (1969)
bruhnsiana	AVB IX	Apsheron pen., Artema Island	U.S.S.R.	Musajev (1969)
bruhnsiana	AVB X	Apsheron pen., Baku	U.S.S.R.	Musajev (1969)
bruhnsiana	AVB XI	Apsheron pen., Artema Island	U.S.S.R.	Musajev (1969)

[a] Received from Dr. F. Kh. Bakhteyev, Leningrad, U.S.S.R.
[b] Received from Dr. T. N. Shevchuk, Leningrad, U.S.S.R.

the former two are much more widely distributed and form rather large populations in some regions, particularly in Turkish and Iraqui Kurdistan.

Karyotypes

The karyotype of the Oran population (CW 50 and 51) was described previously (Rajhathy and Thomas, 1967). All the chromosomes are heterobrachial having subterminally located centromeres (Fig. 3a). There

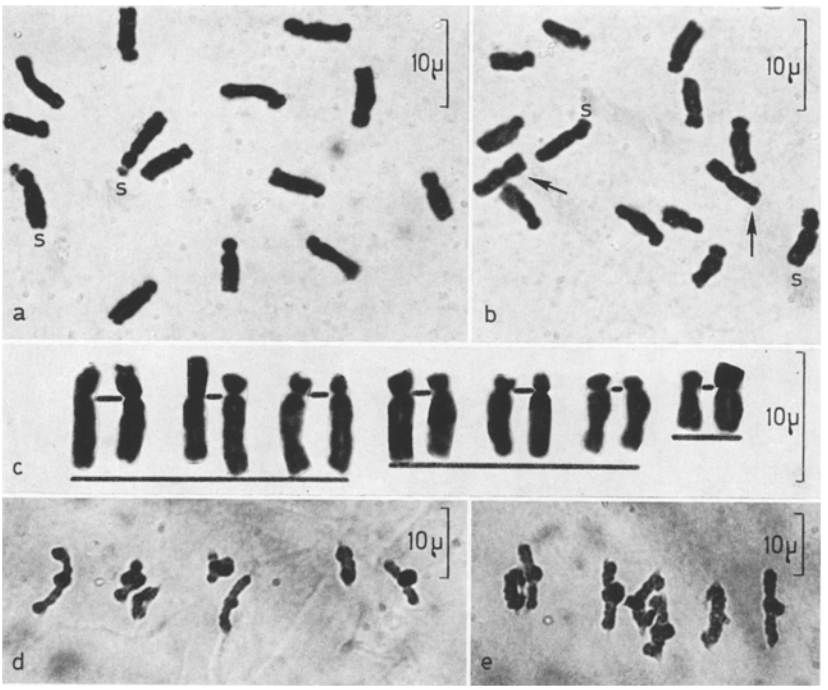

Fig. 3a–e. The chromosomes of *A. ventricosa*. a The C_v^1 karyotype (S denotes the SAT pair). b The C_v^2 karyotype (arrows point to the pair of submedians). c Karyotype prepared from the $C_v^1C_v^2$ hybrid, heteromorphic pair second from the left. d and e Metaphase plates from the $C_v^1C_v^2$ hybrid, note the heteromorphic rod first from the left in d, and the heteromorphic ring at the centre in e

is only a single pair of nucleolar chromosomes in the complement. By size, there are three pairs of long, three of shorter and one pair of short chromosomes.

No appreciable difference was found between the karyotype of the Oran population and that of the plants from Cyprus (AVC I and II). This karyotype, shared by the Oran and Cyprus populations is designated here as C_v^1.

Approximately two-thirds of the plants from the Apsheron population had the same karyotype C_v^1; one-third of the plants had essentially the same karyotype with one obvious difference. One of the long pairs of subterminals was replaced by a pair of submedians of similar length (Fig. 3b). This karyotype is designated here as C_v^2.

The karyotype prepared from the hybrids ($C_v^1 \times C_v^2$) did not reveal any appreciable difference between the parental chromosomes apart

from that between the members of the heteromorphic pair. It also clearly demonstrated that the submedian chromosome belongs to the group of the longest chromosomes but its actual subterminal homologue could not be identified (Fig. 3c). These results suggest a single pericentric inversion as the probable origin of the submedian pair, but the meiotic behaviour should be more revealing as to the mode of origin.

Chromosome Pairing

Parents. All the parental plants, irrespective of geographic origin and karyotype, had regular meiosis and the chromosomes formed 7 bivalents (Table 2). A high frequency of open bivalents and a slightly interstitial position of the incompletely terminalized chiasma in the long arm is characteristic for this species. Similar behaviour was noted in *A. pilosa* and *A. clauda* whose chromosomes are also subterminal. Chromosome distribution at AI and tetrad formation were regular.

Intrakaryotype Hybrids ($C_v^1 C_v^1$). Meiosis in hybrids derived from plants from different sites but of the same karyotype was regular and similar to that in the parental plants (Table 2).

Interkaryotype Hybrids ($C_v^1 C_v^2$). Meiosis in the interkaryotype hybrids was regular and similar to that in the parents and intrakaryotype hybrids. The chromosomes formed 7 bivalents. Neither pairing failure nor multivalent formation were observed (Table 2). However, a heteromorphic bivalent, formed apparently by the submedian chromosome and its subterminal homologue could be detected in most PMCs (Fig. 3d and e). The heteromorphic bivalent was usually a ring. This may have been due to the known effect of the inverted segment in promoting chiasma formation in the noninverted region. While no evidence was obtained for the absence of chiasmata in the inverted segment, this was inferred from the unimpaired seed set. Distribution at AI, second division and tetrad formation were regular. Because of the absence of a multivalent and the presence of a heteromorphic bivalent, a single pericentric inversion appears to be the most probable origin for the pair of submedium chromosomes in the C_v^2 karyotype.

Fertility. No appreciable difference was noted between the parental plants and the intra- or interkaryotype hybrids in the stainability of pollen and in seed set. Heterozygosity for this inversion presented no apparent handicap since the heterozygotes were as fertile as the homozygotes.

Transmission of the Heteromorphic Chromosomes

The number of basic homozygotes, heterozygotes and inversion homozygotes were scored in 72 F_2 plants. There was a good fit between the expected 1:2:1 ratio and the observed distribution of 19:36:17, indicat-

Table 2. *Chromosome pairing in parents and intra- and interkaryotype hybrids (50 PMCs per plant)*

Parents and hybrids	Karyotype	Bivalents		Chiasmata per cell	Seed set %
		Ring	Rod		
CW 50	$C_v^1C_v^1$	3.66	3.33	10.75 ± 0.21	97.8
CW 51	$C_v^1C_v^1$	3.87	3.12	10.80 ± 0.20	98.2
AVC I	$C_v^1C_v^1$	3.38	3.62	10.30 ± 0.20	94.6
AVB III	$C_v^1C_v^1$	3.88	3.12	10.90 ± 0.17	92.1
AVB II	$C_v^2C_v^2$	3.01	3.98	10.11 ± 0.23	93.8
Average		3.56	3.43	10.57 ± 0.20	95.3
CW 50 × CW 51	$C_v^1C_v^1$	3.55	3.44	10.51 ± 0.19	94.8
CW 50 × AVC I	$C_v^1C_v^1$	3.04	3.96	10.08 ± 0.21	97.9
CW 50 × AVB III	$C_v^1C_v^1$	3.11	3.89	10.22 ± 0.17	93.7
CW 50 × AVB II—1	$C_v^1C_v^2$	3.45	3.55	10.45 ± 0.22	90.2
—2	$C_v^1C_v^2$	3.58	3.42	10.64 ± 0.21	94.1
Average		3.34	3.65	10.18 ± 0.19	94.0

ing no preferential transmission for either chromosome of the heteromorphic pair.

Discussion

A full homology of the chromosomes of *A. ventricosa* plants irrespective of geographic origin and karyotype was clearly demonstrated by results presented in this paper. These results and the absence of reproductive isolation support Malzew (1930) for combining *A. ventricosa* Balansa and *A. bruhnsiana* Gruner into one species. The lemma tips and spikelet size were found to be good characters to separate plants from Oran, Cyprus and the Apsheron region.

The peripheral distribution of the contemporary colonies, the preservation of full homology of the chromosomes and interfertility of plants from distant sites constitute strong evidence that at one time they were members of the same population which may have been contiguous throughout the distribution area of *Avena*. That the Oran colony is a relict is suggested by its very small size, restricted to a cliff at the sea, while a number of species including *A. clauda* and *A. pilosa*, its closely related allies, form sizeable populations in and around the site (Rajhathy *et al.*, 1966; Rajhathy and Thomas, 1967).

The karyotype described by Rajhathy and Thomas (1967) for the Oran population and by Ladizinsky and Zohary (1967) for this and for the Apsheron population was confirmed and an identical one was found

in plants from Cyprus. This karyotype, which consists of subterminal chromosomes was designated C_v^1. A modified form of this karyotype, designated C_v^2, which contains a pair of submedians was found in approximately one-third of the Apsheron plants. Thus, the Apsheron population, Malzew's ssp. *bruhnsiana*, is karyotypically polymorphic.

The simplest hypothesis for this chromosome polymorphism is a single pericentric inversion which altered the arm ratio by changing the position of the centromere. The absence of a multiple configuration from the $C_v^1C_v^2$ heterozygote rules out an exchange origin. On the other hand, the presence of a heteromorphic bivalent, which fits the type described by White (1945) as "asymmetrical bivalent", indicates heterozygosity for a pericentric inversion. Pachytene is not amenable for analysis in *Avena*, therefore the presence of a loop could not be ascertained. The good pollen and seed fertility of the heterozygote suggests the absence of chiasmata from the inverted segment and the formation of duplication-deficiency gametes. This inversion apparently does not interfere with normal reproduction in the heterozygous condition. It may be concluded that the structural difference between karyotype C_v^1 and C_v^2 is due to a pericentric inversion, consequently the plants with these karyotypes are basic and inversion homozygotes.

The size of the total sample from the Apsheron region was too small to estimate the ratio of the basic and inversion homozygotes in the population. It is clear, however, that the C_v^1 karyotype is much more common than the C_v^2 karyotype with the pair of submedian chromosomes. This suggests that C_v^1 is the primary karyotype which is then the basic homozygote. This is also supported by the fact that all plants from Oran and Cyprus have the C_v^1 karyotype and that the whole closely related group of *A. clauda* and *A. pilosa* have exclusively subterminal chromosomes (Rajhathy and Thomas, 1967). This is apparently a case where a subterminal chromosome gave rise to a submedian one in spite of the belief that pericentric inversions are hindered in subterminals because of the small size of the short arm.

The absence of inversion heterozygotes from the Apsheron samples can readily be explained by small sample size and by the fact that the species is self-pollinating. A study, including many plants of the native population, may detect heterozygotes since they are not impaired by sterility but their frequency is halved with each generation of selfing. Heterozygotes must repeatedly arise *de novo* in mixed stands of basic and structural homozygotes, since a low amount of outcrossing does occur in *Avena*. There was no preferential transmission for either chromosome of the heteromorphic pair in the experiment. If heterozygotes are being eliminated from the natural population it is not because of irregular chromosome behaviour or reduced seed set.

Polymorphism for pericentric inversion is common in *Drosophila*, grasshoppers, bark weevils and rodents (cf. John and Lewis, 1968). It appears to be less widespread in plants in which interchanges and paracentric inversions are more common. Pericentric inversions have been found in corn (McClintock, 1931), in natural populations of *Paeonia* (Walters, 1952), in a variety of *Vicia faba* (Michaelis and Rieger, 1959) and in a plant trisomic for chromosome 6 in *Hordeum spontaneum* (Tsuchiya, 1969). The Apsheron population of *A. ventricosa* provided the first example of polymorphism for a pericentric inversion in oats.

A pericentric inversion is the simplest structural change which can alter the karyotype without upsetting meiosis. In species, such as oats, in which a terminal or near terminal chiasma is the rule, one is not likely to form in the inverted segment; consequently the heterozygote's fertility need not be reduced. Although a single pericentric inversion in one of the putative genome donors of the hexaploids is not sufficient for generalization, one is tempted to speculate on the potential role of this type of structural change in the evolution of *Avena*. In both hexaploid wheats and oats homoeologous pairing is genetically controlled and homoeology in wheat evolved by the accumulation of differential mutations without major structural changes of the chromosomes (cf. Riley and Law, 1965). Indeed, there is little morphological variation amongst wheat chromosomes. In contrast, the complement of hexaploid oats consists of morphologically very different chromosomes (Rajhathy, 1963). The simplest mechanism bringing about variation in the karyotype without reshuffling linkage groups, thus preserving the homoeologous groups, would be pericentric inversions. Karyotypic divergence through pericentric inversions together with differential mutations in the progenitors and a diploidizing mutation in the raw allohexaploid might have produced the primitive form of hexaploid oats.

References

Holden, J. H. W.: Field studies of some wild species of *Avena*. Econ. Bot. **23**, 339–345 (1969).

John, B., Lewis, K. R.: The chromosome complement. Protoplasmatologia, VI/A, p. 1–203. Wien: Springer 1968.

Ladizinsky, G.: New evidence on the origin of the hexaploid oats. Evolution (Lawrence, Kans.) **23**, 676–684 (1969).

— Zohary, D.: *Avena ventricosa*: possible diploid contributor to hexaploid oats. Science **155**, 1553–1554 (1967).

Malzew, A. I.: Wild and cultivated oats. Bull. appl. Bot., Genet. Plant Breed. (Leningrad), Suppl. **38** (1930).

McClintock, B.: Cytological observations on deficiencies involving known genes, translocation and inversions in *Zea mays*. Miss. Agr. Exp. Sta. Res. Bull. **163**, 1–30 (1931).

Michaelis, A., Rieger, R.: Strukturheterozygotie bei *Vicia faba*. Züchter **29**, 354–361 (1959).

Murray, B. E., Craig, I. L., Rajhathy, T.: Protein electrophoretic study of three amphiploids and eight species in *Avena*. Canad. J. Genet. Cytol. **12**, 651–665 (1970).

Rajhathy, T.: A standard karyotype for *Avena sativa*. Canad. J. Genet. Cytol. **5**, 127–132 (1963).

— Evidence and an hypothesis for the origin of the C genome of hexaploid *Avena*. Canad. J. Genet. Cytol. **8**, 774–779 (1966).

— Sadasivaiah, R. S.: The cytogenetic status of *Avena magna*. Canad. J. Genet. Cytol. **11**, 77–85 (1969).

— Thomas, H.: Chromosomal differentiation and speciation in diploid *Avena*. III. Wild Mediterranean populations. Canad. J. Genet. Cytol. **9**, 52–68 (1967).

— Zillinsky, F. J., Hayes, J. D.: A collection of wild oat species in the Mediterranean region. Ottawa Research Station Publ. pp. 1–25 (1965).

Riley, R., Law, C. N.: Genetic variation in chromosome pairing. Advanc. Genet. **13**, 57–107 (1965).

Sadanaga, K., Zillinsky, F. J., Murphy, H. C., Smith, R. T.: Chromosome associations in triploid, tetraploid and pentaploid hybrids of *Avena magna* ($2n = 28$). Crop Sci. **60**, 594–597 (1968).

Sadasivaiah, R. S., Rajhathy, T.: Genome relationships in tetraploid *Avena*. Canad. J. Genet. Cytol. **10**, 655–669 (1968).

Steer, M. W., Holden, J. H. W., Gunning, B. E. S.: *Avena* chloroplasts: species relationships and the occurrence of stomacentres. Canad. J. Genet. Cytol. **12**, 21–27 (1970).

Thomas, H., Jones, D. I. H.: Electrophoretic studies of proteins in *Avena* in relation to genome homology. Nature (Lond.) **220**, 825–826 (1968).

Tsuchiya, T.: Cytogenetics of a new type of barley with 16 chromosomes. Chromosoma (Berl.) **26**, 130–139 (1969).

Walters, J. L.: Heteromorphic chromosome pairs in *Paeonia californica*. Amer. J. Bot. **39**, 145–151 (1952).

White, M. J. D.: Animal cytology and evolution, 1st ed. Cambridge: Cambridge Univ. Press 1945.

Dr. Tibor Rajhathy
Central Experimental Farm
Ottawa, Ontario K1A OC6,
Canada