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SHORT COMMUNICATIONS

Cytogenetic Analysis of Diploid *Avena* L. Species Containing the As Genome

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Abstract—Cytogenetic examination showed that three diploid oat species containing the As genome are highly similar in karyotype structure and chromosome C-banding patterns. *Avena strigosa* is more similar to *A. wiestii*, while *A. hirtula* is to an extent separated from the two species, differing in the C-banding pattern of chromosome 6. The karyotypes of all three species harbor a small acrocentric chromosome, which is absent from diploid oat species containing other variants of the A genome. The results made it possible to assume genome specificity of the rearrangement resulting in this chromosome.

The genus *Avena* L. is one of the most ancient cereal genera and includes diploid, tetraploid, and hexaploid species with the basic chromosome number $x = 7$. Most oat species are wild, and only a few—*Avena strigosa* Schreb. ($2n = 2x = 14$), *A. abyssinica* Hochst. ($2n = 4x = 28$), *A. sativa* L., and *A. byzantina* C.K. ($2n = 6x = 42$) are cultivated now or were cultivated in the past. According to taxonomic data, the genus *Avena* consists of 26 species, including 12 diploid, 8 tetraploid, and 6 hexaploid [1]. Analysis of the karyotype structure in diploid oat species has revealed two main genomes, A and C [2, 3]. Species carrying the A genome have a symmetrical karyotype and a comparatively low content of heterochromatin (HC). In contrast, mostly asymmetrical, heterochromatic chromosomes are characteristic of species containing the C genome [4]. Fluorescence in situ hybridization has shown that the A and C genomes differ in relative arrangement of the 18S–5.8S–26S and 5S ribosomal DNA loci [5]. Sequencing of highly polymorphic regions of the internal transcribed spacers 1 and 2 (ITS1, ITS2) and the 5.8S rRNA genes has confirmed that the A and C genomes are phylogenetically separate [6].

The origin and genome composition of polyploid oat species have been studied by comparing the karyotype structure and chromosome banding patterns, analyzing the meiotic conjugation of chromosomes in hybrids, localizing the rRNA genes, and examining genome in situ hybridization patterns. The data accumulated so far make it possible to assume that only one tetraploid species, *A. macrostachya*, is an autopolyploid [6, 7], while the other species result from hybridization of different diploid ancestors. According to the genome composition, the allotetraploid species are divided into two main groups, AB (*A. abyssinica, A. vaviloviana*, and *A. barbata*) and AC (*A. maroccana, A. murphyi*, and *A. insularis*) [1, 6, 8–14]. The genome formula of the hexaploid *Avena* species is ACD [8, 14]. Note that none of the known diploid species has the B and D genomes, which are present in polyploid forms. This can be explained by considerable structural rearrangements affecting the original genomes during polyploidization so that their donors are difficult or even impossible to identify.

Studies of the karyotype structure, seed storage proteins (avenins), and RAPD markers have made it possible to classify diploid oat species with the A genome into subclusters, which combine phylogenetically related forms. The first subcluster (the As genome) includes cultivated *A. strigosa* and its close relatives *A. hirtula, A. wiestii*, and *A. atlantica.* The second subcluster includes several species with different variants of the A genome: Al (*A. longiglumis*), Ad (*A. damascena*), Ap (*A. prostrata*), and Ac (*A. canariensis*) [2, 14–19]. Crosses between the species containing the As genome (*A. strigosa, A. wiestii, A. hirtula*, and *A. atlantica*) yield fertile progenies, and up to seven bivalents are formed during meiosis in the hybrids [3, 14]. In the case of species with different variants of the A genome, the results of hybridization depend on the combination. Thus, *A. prostrata* (Ap) is well compatible with *A. longiglumis* (Al), *A. damascena* (Ad), and *A. canariensis* (Ac); *A. longiglumis* is crossable with *A. strigosa* and *A. damascena;* whereas *A. canariensis* × *A. damascena* hybrids are sterile, notwithstanding regular chromosome conjugation in meiosis [2, 8, 14–16, 20–22].

Analysis of chromosome conjugation in *A. strigosa* × *A. sativa* hybrids, similarity of chromosomes of these species with respect to C-banding patterns and distribution of rDNA loci, and data of genomic in situ hybridization make it possible to assume that *A. strigosa* is one of the direct ancestors of modern cultivated hexaploid oat [23–27]. The cytogenetics of *A. strigosa* has

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Oat accessions examined in this work and their origins

No.	Cat. no.	Species	Subspecies	Variety	Origin
1	k-5229	*A. strigosa*	*brevis*	*secunda, tephera*	Portugal
2	k-5244	*A. strigosa*	*strigosa*	*albida*	Portugal
3	k-3063	*A. strigosa*	*strigosa*	*typica*	Bryansk oblast, Russia
4	k-4481	*A. strigosa*	*brevis*	*candida*	United Kingdom
5	k-94	*A. wiestii*			Egypt
6	k-2032	*A. hirtula*			Sardinia, Italy

been studied only poorly. In view of this, the objective of this work was to compare the chromosome C-banding patterns for cultivated diploid *A. strigosa* and its close wild relatives, *A. wiestii* and *A. hirtula.*

We examined six accessions (table), which were obtained from the collection of the All-Russia Institute of Plant Industry (St. Petersburg, Russia).

Chromosome preparations were obtained and stained by a modification of a C-banding technique developed for wheat chromosomes [28]. The *A. strigosa* chromosomes were identified according to the published nomenclature [4], while the *A. wiestii* and *A. hirtula* chromosomes were classified by similarity to the *A. strigosa* chromosomes (in contrast to [4]).

According to taxonomic data, the diploid cultivated species *A. strigosa* Schreb. includes three subspecies: *strigosa, brevis*, and *nudibrevis.* The first subspecies combines ten varieties and four forms; the second subspecies, eight varieties and three forms; and the third one contains a single naked-seeded form, which was described as *A. nuda* in the Linnaean classification. *Avena wiestii* Steud. and *A. hirtula* Lagas. are exclusively wild [29].

Avena strigosa Schreb. The stems are erect or sometimes prostrate at the base and have nude nodes. Leaf sheaths are nude or rarely pubescent. The panicle is equilateral or semicompressed, unilateral, rarely compressed (flagged). Spiklets are of two or three (rarely one) flowers. Glumes have seven to nine veins, are slightly uneven, and are 15–25 mm in length. The inner palea is narrow-lanceolate; pubescent or nude; with two awnlike points at the apex and one geniculate awn, rounded at the bottom, on the lamina. The callus is absent, all flowers are inarticulate, the lowermost flower mostly has a peduncle. Grains are 6–7 mm in length, narrow or broad, and glumaceous or rarely nude. Paleae are mostly dark (gray or brown) and rarely white or yellow.

Avena strigosa is widespread in Western Europe, northwestern Russia, Belarus, and Estonia. In accordance with its Russian name (sand oat), *A. strigosa* prefers sandy light soils. The species occurs as a weed (ruderal or segetal) and as a cultivated form. Throughout its area, the species is represented by only a few forms, which belong to two or three varieties. The major diversity region is in northern Portugal and northwestern Spain (Galicia) and harbors forms with all variety-specific characters of the species and numerous endemic forms, which are absent from the other European countries. At present, a secondary diversity center of *A. strigosa* is in Brazil (Rio Grande do Sul). As weeds, various ecological groups of *A. strigosa* occur in Japan and South Korea. Few diploid naked-seeded forms (subsp. *nudibrevis*) are restricted to Wales (United Kingdom) [1].

Avena wiestii Steud. The stem is bent-geniculate or erect, thin, elastic, with nude nodes. Leaf sheaths and leaves are pubescent or nude. The panicle is equilateral or unilateral, with drooped spiklets. Spiklets are small, two-flowered, and awned. Glumes are slightly uneven and have seven to nine veins. The callus is short (approximately 2 mm in length) and blunt. The lower palea has two apical awns 3–6 mm in length and two lateral denticles. All flowers in a spiklet are articulate and easily fall during ripening. Grains are elongate, pubescent, and small. Paleae are mostly dark (gray or brown) or rarely yellow. *Avena wiestii* occurs in eastern Trans-Caucasia, Azerbaijan (the Apsheron Peninsula and Lenkoran: the Apsheron and Lenkoran lowlands and the Muganskaya and Sal'yanskaya lowlands of the Kura-Araksinskaya Plain), and on southern slopes of the Great Caucasian Ridge. Plants of this species grow on lowlands, dry grassy sites, seaside sands, limy slopes, and hills in association with steep and desert ephemeral plants. *Avena wiestii* is most abundant in Spain, forming isolated islands in steppes on sandy loess soils, on mountain slopes, at the bottom of falls, and on cliffs (rarely) and growing in open plant associations in the arid zone with an annual precipitation of 50–250 mm. The species grows at the margin of the southern Mediterranean region, in Algeria (Djelfa), Egypt, Syria, Jordan, Israel (Oorim, Misaf Haneger), Turkey, Iraq, Iran (Chalus, Ghazvin), northern Sahara, and on the Arabian Peninsula. In the Mediterranean region, *A. wiestii* is rather widespread on coastal dunes, dry stony or sandy hills, clay–sandy soils of deserts, and volcanic soils and grows in intact associations with *A. barbata* and *Stipa* species [1].

Avena hirtula Lagas. The stem is prostrate at the base and then erect, with nude nodes. Leaf sheaths and leaves are pubescent or nude. The panicle is multispiklet, drooped, equilateral, unilateral, or semicompressed. Spiklets are of two or three flowers and are

awned. Glumes are slightly uneven and have seven to nine veins, two apical awns, and a lateral barb. The callus is elongate, approximately 2 mm in length, and slightly blunt. The scar is elongate. The lower palea has two elongate apical awns, which appreciably exceed the glumes, and a single denticle. All flowers in a spiklet are articulate and easily fall during ripening. Grains are elongate, pubescent, and small. Paleae are mostly dark (gray or brown) and rarely white. *Avena hirtula* is most polymorphic and abundant in Spain and Portugal. Surprising diversity of the species was observed on Pyrenean spurs. Typical habitats of *A. hirtula* are small-stony and limy soils, sand dunes, pastures, disused trenches, and fields. Plants of the species grow rather rarely on fecund, well-cultivated soils. Twelve highly polymorphic *A. hirtula* populations were recently found in southern Spain. The species is scattered throughout the Mediterranean region, especially its Arabian and Nubian parts, and is often morphologically similar to *A. barbata*, being reliably distinguishable only by chromosome number. *Avena hirtula* plants occur in Crete, Sardinia, Sicily, Corsica, Algeria, Morocco (Atlas Mountains), Tunisia, and Turkey. In eastern Mediterranean region, *A. hirtula* occurs in Syria, Jordan, and Israel, where it grows most commonly on dry stony soils; slopes covered with maquis; on the verges of fields and roads, as a weed (ruderal) plant; and in the seaside region on sandy soils, forming intact associations with *A. barbata* and *A. longiglumis* [1].

Examination confirmed that our six accessions of *A. strigosa, A. wiestii,* and *A. hirtula* are diploid ($2n = 2x = 14$). The karyotypes of all accessions are structurally similar, each including two metacentric, two submetacentric, one subacrocentric, and two morphologically different satellite (SAT) chromosomes (Fig. 1). All species have low heterochromatin content: small and medium-sized C-bands were detected predominantly in pericentromeric and telomeric regions and rarely in interstitial regions of chromosomes. In addition, distinct heterochromatin blocks were detected in the regions of secondary constrictions on two chromosomes. In general, our accessions proved to be similar in karyotype structure and C-banding patterns to *A. strigosa* and *A. hirtula* lines described in the literature [4]. Unlike in published works, however, small C-bands were found in virtually all chromosomes of the three species, considerably simplifying their identification (for comparison, only telomeric and satellite C-bands have been reported for *A. strigosa* chromosomes [4]). Since there are no available data on homeology of individual chromosomes in oat and wheat, *A. strigosa* chromosomes were classified according to the cytological nomenclature [4], i.e., in order of decreasing size. The largest chromosome was designated 1 and the smallest one, 7. Chromosomes of the related species *A. wiestii* and *A. hirtula* were classified by similarity to chromosomes of the cultivated species (Fig. 2). According to this system, SAT chromosomes were designated 2 and 3.

To study the specific features of C-banding patterns of individual *A. strigosa* chromosomes and to estimate the intraspecific polymorphism, we examined four accessions belonging to two different subspecies and growing in different geographical regions (table). Although the accessions slightly differed in the presence and size of some telomeric and interstitial C-bands (Figs. 1a–1d), all chromosomes were easily identifiable and were characterized as follows.

Chromosome 1 is the largest chromosome of the set and is approximately metacentric. The short and long arms end with telomeric C-bands, which are usually larger in the long arm or similarly sized in some cases. A small marker C-band is present in the proximal region of the long arm of chromosome 1. In addition, an extremely weak C-band adjacent to the centromeric one is detectable in the short arm in some accessions.

Chromosome 2 is a large, approximately metacentric chromosome with a large satellite. Telomeric C-bands located in the long arm and at the end of the satellite vary in size. A distinct marker C-band is in the proximal region of the long arm. The largest heterochromatic block was detected in the vicinity of the satellite and varied in size among the accessions.

Chromosome 3 is submetacentric and has a small satellite in the short arm. The secondary constriction area contains a large heterochromatic block. The long arm contains a telomeric C-band, varying in staining intensity, and a series of two or three relatively small interstitial blocks.

Chromosome 4 is a relatively long submetacentric. The telomeric C-band of the short arm is appreciably larger than that of the long arm. The short arm contains two polymorphic interstitial C-bands, which divide the arm into three nearly equal parts. Weak polymorphic blocks are detectable in the subterminal and distal regions of the long arm.

Chromosome 5 is a small, nearly metacentric chromosome and contains intensely stained telomeric C-bands in both arms and a distinct interstitial C-band in the proximal one-fourth of the long arm. In some cases, an extremely weak additional C-band is detectable between the intercalary and the pericentromeric C-bands.

Chromosome 6 is a small submetacentric and has intensely stained telomeric C-bands in the short and long arms and a large marker C-band in the middle of the long arm. The C-banding pattern of chromosome 6 is relatively conserved, varying only in the presence of a weak subterminal C-band in the short arm.

Chromosome 7 is the smallest *A. strigosa* chromosome and is acrocentric. This chromosome contains small telomeric C-bands in both arms and a marker intercalary C-band in the distal one-third of the long arm. Small polymorphic C-bands are detectable in the subterminal and distal regions of the long arm. In general, the *A. strigosa* accessions only slightly differed in chromosome C-banding patterns.

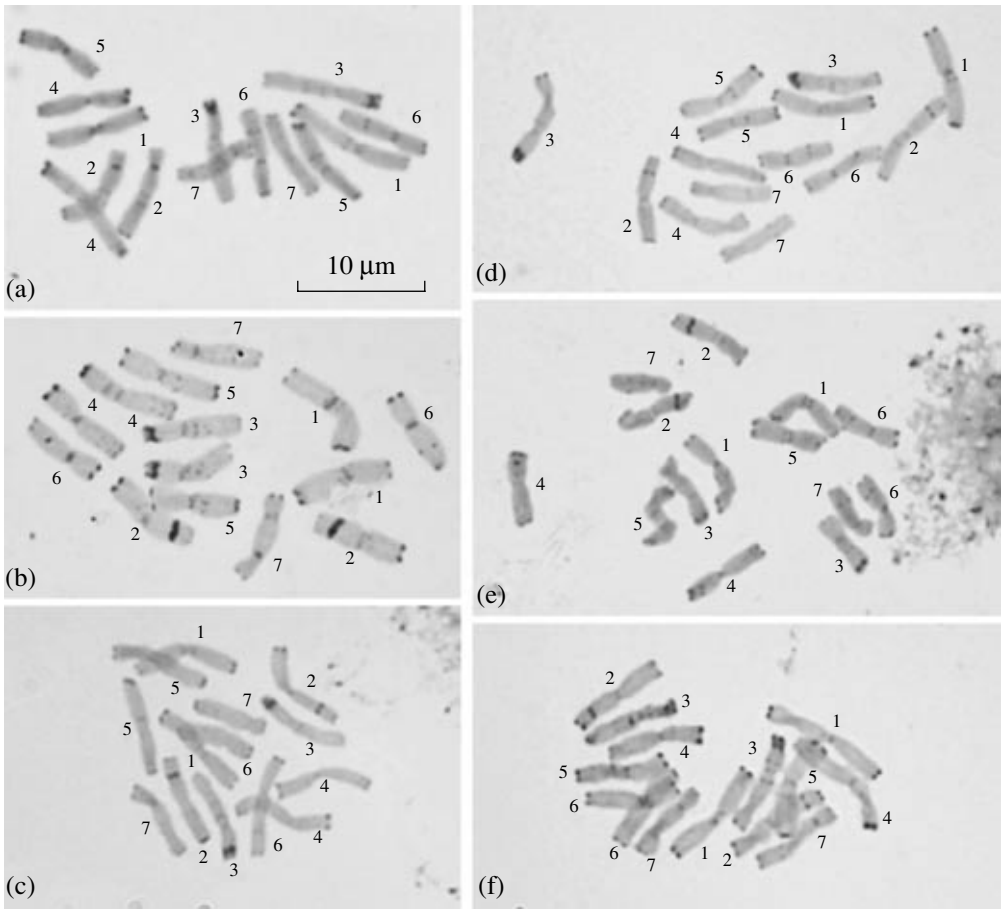

Fig. 1. Distribution of heterochromatin blocks on metaphase chromosomes of the diploid oat species (a–d) *A. strigosa* (a, k-4481; b, k-5229; c, k-3063; and d, k-5244), (e) *A. wiestii* (k-94), and (f) *A. hirtula* (k-2032). Chromosome numbers (1–7) are indicated.

The *A. wiestii* accession is similar to *A. strigosa* and *A. hispanica* [30]. Specifics of its karyotype include the absence of a telomeric C-band from the short arm of chromosome 1, the presence of an intensely stained intercalary C-band in the distal region of the short arm of chromosome 4, and a somewhat smaller size of chromosome 7. To establish whether these features are species-specific, it is necessary to examine several other accessions of *A. wiestii.*

Avena hirtula, the third species with the As genome, is similar to the two other species in the morphology and C-banding patterns of chromosomes 1, 2, 4, 5, and 7, although its chromosome 2 lacks the marker interstitial C-band of the long arm. Chromosome 3 differs from the corresponding chromosomes of *A. strigosa* and *A. wiestii* in having a distinct intercalary C-band in the proximal region of the short arm. In addition, its satellite is somewhat larger than in the other species. The most distinct difference was observed for the C-banding pattern of chromosome 6, which lacks the marker C-band in the middle of the long arm and has a small C-band adjacent to the pericentromeric one in the short arm. Since we examined only one *A. hirtula* accession, it is impossible to determine whether this modification of chromosome 6 is species-specific or characteristic of our accession.

It is of interest that *A. hirtula* chromosome 7 is virtually identical to the corresponding chromosomes of *A. strigosa* and *A. wiestii*, although this chromosome is presumably involved in species-specific translocation in *A. strigosa* [31]. Note, however, that *A. longiglumis* and *A. canariensis* (Al and Ac genomes, respectively) lacks a pair of acrocentric chromosomes similar to chromosome 7 of *A. strigosa* and three other species of this group examined in this work and in [30]. Consequently, our results suggest that the translocation is specific for the As genome rather species-specific than for *A. strigosa.*

Thus, cytogenetic examination of the three diploid oat species containing the As genome showed that *A. strigosa* and *A. wiestii* are similar, while *A. hirtula* is to an extent separated from the other two species in this group. Our findings contradict the published hypothesis that the chromosome 7 rearrangement is species-specific for *A. strigosa* [31], because all three species examined in this work (as well as *A. hispanica* described in [31]) are similar in the morphology and C-banding patterns of chromosome 7. This finding sug-

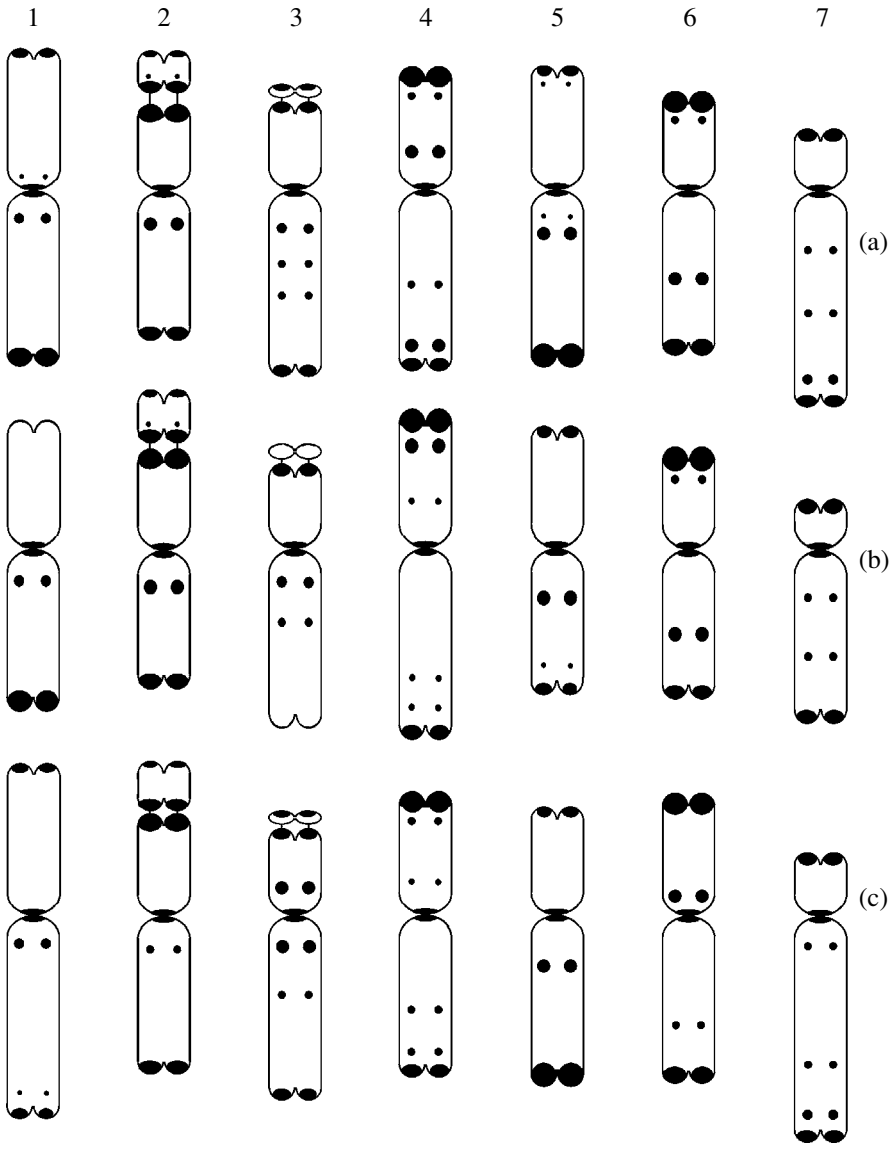

Fig. 2. Idiograms of C-banded chromosomes 1–7 of (a) *A. strigosa*, (b) *A. wiestii*, and (c) *A. hirtula.*

gests genome specificity of the rearrangement. To check this assumption, however, it is necessary to examine other accessions of *A. hirtula* and the diploid oat species containing the As, Ap, and Ad genomes.

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