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ORIGINAL ARTICLE

A new hexaploid wheat species *Triticum aminovii*

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Abstract

The hexaploid wheat (*Triticum aestivum* L., genome BBAADD, $2n = 6x = 42$) is one of the most important food crops. Enhancement and preservation its biodiversity is a key issue in the agrobiology of the twenty-first century. Related cultivated and wild species are the most practical source of this enhancement. The problem of genetic introgression is most successfully addressed by producing artificial amphidiploids and their subsequent use as "bridges" in breeding programs. Artificial amphidiploids are also a convenient model for solving genealogical issues of wheat. The karyotype formation and the genome stabilization of allopolyploid species are some of the most interesting points in evolutionary biology, because it is not enough to obtain between-species hybrids and to double their haploid genomes—it is required to restore their fertility. Intergeneric crosses undertaken within the tribe Triticeae Dumort led to quite a lot of fertile artificial amphidiploids possessing a wide variety of genome combinations, including the three elementary genomes of cultivated wheat. Among them are new forms (species) previously unknown in the nature. Following this study, we have added a new artificial hulled hexaploid amphidiploid, genome formula BBAASS, to the taxonomy of the genus *Triticum* under the name *Triticum aminovii* N.P. Gontsch. The karyotype of *T. aminovii* is provided, and its genome formula BBAASS has been validated by fluorescent in situ hybridization. The holotype of the new species is held in the I.M. Krasnoborov Herbarium (NS) of the Central Siberian Botanical Garden of the Siberian Branch of the Russian Academy of Sciences, voucher number NS0000947.

Keywords Wheat · Biodiversity · Artificial amphidiploids · *Triticum aminovii*

Introduction

Wheat (the genus *Triticum* L.) is one of the main food crops. The genus encompasses a number of amphidiploid species that arise from interspecific hybridization of the diploid wheat *Triticum urartu* Thum. ex. Gandil. and one (giving rise to tetraploid wheats) or two (giving rise to hexaploid wheats) diploid *Aegilops* L. species followed by chromosome doubling (Feldman and Levi 2023).

Enhancement of the biodiversity of principal cultivated plants, including wheats, is a key issue in the evolutionary biology of the twenty-first century. One of the solution is to create artificial (also known as synthetic or man-made) amphidiploids by crossing wheat-related wild species and then using them in breeding programs as bridge species to transfer valuable genetic material to cultivated polyploid wheats (Spetsov and Savov 1992; Plamenov and Spetsov 2011; Davoyan et al. 2012; Laikova et al. 2013; Stoyanov 2014; Das et al. 2016; Gadimaliyeva et al. 2018; Li et al. 2018; Morgounov et al. 2018; Kishii et al. 2019; Goncharov et al. 2020; Nyine et al. 2020; Adonina et al. 2021).

Wheat artificial amphidiploids have for decades been produced in large amounts in Japan, Mexico, Armenia, Bulgaria, Azerbaijan, the Russian Federation and in a number of other countries. Gene banks around the world hold considerable collections of artificial amphidiploids, see, for example, National BioResource Project, Japan (https://shigen.nig.ac.jp/wheat/komugi/strains/aboutNbrp.jsp), VIR (http://www.vir.nw.ru/), IPK (https://www.ipk-gatersleben.de/en/genebank/) and some other European gene banks (https://www.ecpgr.cgiar.org/resources/germplasm-databases).

Such amphidiploids occupy an important place in genetic and phylogenetic studies of the genus *Triticum* (Sears 1941; McFadden and Sears 1946; Dorofeev et al. 1979; Goncharov 2011; Feldman and Levi 2023; etc.) and the tribe Triticeae

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in general (Feldman and Sears 1981; Golovnina et al. 2007; Goncharov et al. 2007, 2009; and others). An appreciation of the evolutionary consequences of (allo)polyploidy is central to the understanding of crop domestication and agricultural improvement. Our attempt in using artificial amphidiploids allowed us to consider marker trait expression as a result of amphidiploidization (Goncharov et al. 2007, 2009; Goncharov 2011).

There have been many attempts to add artificial amphidiploids to the taxonomy of the genus *Triticum* (see review by Feldman and Levy 2023). V.F. Dorofeev et al. (1979) added *T. kihara* Dorof. et Migusch. N.N. Tsvelev (1983) made reference to four artificial amphidiploids, *T.* ×*fungicidum* Zhuk., *T.* ×*edwardii* Zhebrak, *T.* ×*sovieticum* Zhebrak and *T.* ×*borisovii* Zhebrak. J. Mac Key (2005) and K. Hammer et al. (2011) included the rye-wheat amphidiploids ×*Triticale* Tscherm.-Seys. ex Müntzing (syn. ×*Triticosecale* Wittm. and A. Camus). We have included all artificial amphidiploids of wheat in a separate section *Compositum* N.P. Gontsch. within the genus *Triticum* (Goncharov et al. 2009; Goncharov 2011; Pronozin et al. 2021; among others).

All possible combinations of elementary genomes A^b, A^u, B, G and D have already been used in the creation of artificial amphidiploids. The resulting forms have been included in the system of genus *Triticum* as part of the section *Compositum* (Goncharov 2005). Amphidiploids with the genome S are presented in various gene banks and institute collections. However, their genomic composition must first be checked. One of such fertile amphidiploids with genome BBAASS was obtained in the early 1980s by professor N.Kh. Aminov (the Genetic Resources Institute of the Azerbaijan National Academy of Sciences, Baku, Azerbaijan) from crossing the cultivated emmer *T. dicoccum* ($2n = 4x = 28$) to *Ae. speltoides* Tausch ($2n = 2x = 14$) followed by chromosome doubling in the hybrid (Aminov 1989).

The aims of our study are: (1) to define the karyotypes of these experimentally produced amphidiploids, (2) to understand whether their genomes are stable, (3) to determine the place for these amphidiploids in the genus *Triticum* taxonomy.

Materials and methods

Plant material and sampling

The plants used were (1) hexaploid amphidiploids (genome formula BBAASS ($2n = 6x = 42$)) resulting from hybridization between the cultivated emmer *T. dicoccum* ($2n = 4x = 28$) and *Ae. speltoides* ($2n = 2x = 14$) followed by chromosome doubling (Aminov 1989) (Fig. 1); (2) several hexaploid amphidiploids of unknown origin with a similar genome formula from an Australian Grain Genebank (Victoria, Australia), and (3) four amphidiploids of unknown origin, AUS21840 (*T. timopheevii* (Zhuk.) Zhuk. + *Ae. speltoides*, supposed genome GGA^tA^tSS), AUS21843 (*T. turgidum* L. + *Ae. speltoides*, supposed genome BBAASS), AUS21842 (*T. dicoccum* + *Ae. sharonensis* Eig, supposed genome $BBAAS^{sh}S^{sh}$) and AUS21844 (*T. durum* Desf. + *Ae. sharonensis*, supposed genome $BBAAS^{sh}S^{sh}$).

Plants were grown in a greenhouse at a standard temperature of 23–25 °C under a 16 h' daylight regimen. The nutrient solution consisting of water and a fertilizer was added, and phytosanitary protection measures were taken according to local practice.

Fertility was quantified by counting the number of grains per spikelets. Spike density was calculated as D = (number of spikelets minus one) × 10/spike length, cm, according to K.A. Flaksberger (1939).

Fluorescent in situ hybridization (FISH)

FISH was carried out with probes constructed of cloned repeated DNA sequences pSc119.2 (Bedbrook et al. 1980), Spelt1 (Salina et al. 1997, 1998) and Spelt52 (Salina et al. 2004) according to a previously published technique (Salina et al. 2006). The probes were labeled with biotin (biotin-16-dUTP, 11,093,070,910 Roche) or digoxygenin (digoxigenin-11-dUTP, DIUTP-RO Roche) using Nick Translation Mix (11,745,808,910 Roche). Detection of the biotinylated probes was carried out using fluorescein avidin (Fluorescein Avidin D, FITC, A-2001 Vector Laboratories). The hybridization signal was amplified using fluorescein anti-avidin (Fluorescein Anti-Avidin D, SP-2040 Vector Laboratories). Digoxigenin-labeled probes were detected using Antidigoxigenin–rhodamine Fab fragments (Antidigoxigenin–rhodamine Fab fragments, 11,207,750,910 Roche). The samples were embedded in fluorescence fading-inhibiting medium (Vectashield mounting medium, H-1000-10 Vector Laboratories) containing 0.5 mg/mL DAPI (4',6-diamidino-2-phenylindol, D8417 Sigma–Aldrich) for chromosome staining and analyzed using an Axio Imager M1 microscope (Zeiss, Germany). Images were captured using a ProgRes MF CCD camera (Jenoptik); the image acquisition software was Isis (MetaSystems).

Results

To resolve the karyotypes of the artificial amphidiploids we used FISH with probes constructed of various repeated sequences. The satellite DNA families Spelt1 and Spelt52 (Salina et al. 1997, 1998, 2004) are highly repetitive, tandemly organized sequences located in subtelomeric regions (Anamthawat-Jonsson and Heslop-Harrison 1993;

ГЕРБАРИЙ им И.М. КРАСНОБОРОВА (NS)
Центральный сибирский ботанический сад СО РАН
I.M. Krasnoborov Herbarium CSBG SB RAS

Triticum aminovii N.P. Gontsch.

Country: Азербайджан **Region:** Баку

Locality: Поля Института генетических ресурсов АН Азербайджана. Искусственный амфиплоид от скрещивания *T. dicoccum* × *Ae. speltoides*

Lat.: 40°24'46"N **Lon.:** 49°49'59" **Altitude:**

Biotope:

Reproduction: ИЦиГ СО РАН (г. Новосибирск).

Date: 12.12.2020 Гончаров Н.П.

Det.: Гончаров Н.П.

Fig. 1 The BBAASS amphidiploid

Salina et al. 1998, 2004). Spelt1 is species-specific for *Ae. speltoides*, while Spelt52 is present in *Ae. speltoides*, and *Ae. sharonensis*. Simultaneous hybridization with probes pSc119.2 and Spelt1 or pSc119.2 and Spelt52 allows us to learn whether the amphidiploid has the chromosomes of these species in its genome, and if it does, to identify them (Badaeva et al. 1996, 2024; Ruban and Badaeva 2018). By looking at the distribution of hybridization signals from pSc119.2, it is possible to identify the chromosomes of the B and G genomes of the tetraploid and hexaploid wheats as well as some chromosomes of the A^u genome (Jiang and Gill 1994; Schneider et al. 2003). Of note, sites of Spelt1 and Spelt52 repeats can be found on some chromosomes of polyploid wheats (Salina et al. 2006).

FISH with Spelt1 revealed *Ae. speltoides* chromosomes only in the amphidiploid *T. dicoccum* + *Ae. speltoides*, BBAASS (Table 1, Fig. 2e).

Table 1 Pedigree, genome formula and karyotypes of the amphidiploids studied

Amphidiploids	Pedigree	Genome formula		Karyotype specifics[a]
		Supposed	Actual	
Triticum aminovii	*T. dicoccum* + *Ae. speltoides*	BBAASS	BBAASS	2*n* = 42
AUS21840	*T. timopheevii* + *Ae. speltoides*	GGA^{t}A^{t}SS	GGA^{t}A^{t}A$^{?}$A$^{?}$	2*n* = 42
AUS21843	*T. turgidum* + *Ae. speltoides*	BBAASS	BBAAS^{sh}S^{sh}	2*n* = 42 N7B, T5S^{sh}
AUS21842	*T. dicoccum* + *Ae. sharonensis*	BBAAS^{sh}S^{sh}	BBAAS^{sh}S^{sh}	2*n* = 39–41 N2B, T5S^{sh}, M5B
AUS21844	*T. durum* + *Ae. sharonensis*	BBAAS^{sh}S^{sh}	BBAAS^{sh}S^{sh}	2*n* = 39–43 N7B

[a] N, nullisomic; M, monosomic; T, trisomic

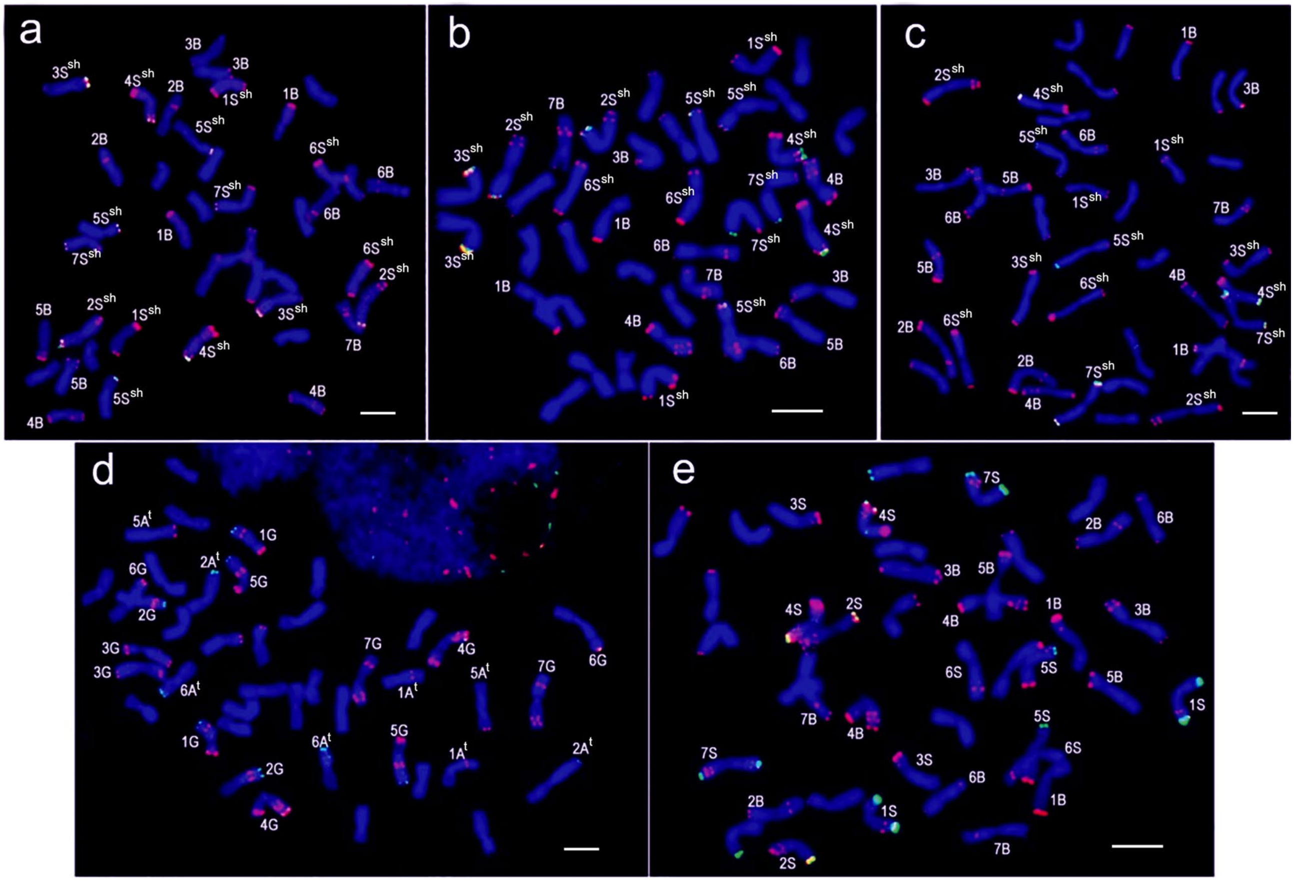

Fig. 2 Karyotypes of the amphidiploids: **a**—AUS21843; **b**—AUS21842; **c**—AUS21844; **d**—AUS21840; **e**—*T. aminovii*. **a**, **b**, **c**—FISH with the probes Spelt52 (green) and pSc119.2 (red); **d**, **e**—FISH with the probes Spelt1 (green) and pSc119.2 (red). Scale bars = 10 μm

Its karyotype was BBAASS. Neither AUS21840 (*T. timopheevii* + *Ae. speltoides*, genome GGA^{t}A^{t}SS) nor AUS21843 (*T. turgidum* + *Ae. speltoides*, genome BBAASS) had *Ae. speltoides* chromosomes. The profile of hybridization with the probes Spelt1 and pSc119.2 allowed us to conclude that AUS21840 possess some *T. timopheevii* chromosomes, some A-genome chromosomes of unknown origin (Fig. 1d) and none of the *Ae. speltoides* chromosomes. Simultaneous hybridization with the probes Spelt52 and pSc119.2 showed that AUS21843 (Fig. 2a) possesses chromosomes from *Ae. sharonensis* rather than from *Ae. speltoides*. Hybridization with the same probes confirmed the presence of *Ae. sharonensis* chromosomes in AUS21842 (*T. dicoccum* + *Ae. sharonensis*, BBAAS^{sh}S^{sh}) and AUS21844 (*T. durum* + *Ae. sharonensis*, BBAAS^{sh}S^{sh}) (Fig. 1 b, c). At the same time, AUS21842, AUS21843 and AUS21844, (genome formula BBAAS^{sh}S^{sh}) were found to have a number of chromosomal aberrations. In AUS21842 (Fig. 1b), chromosome number varies from 39 to 41 (Table 1); this accession has no chromosomes 2B, has three chromosomes $5S^{sh}$ and one chromosome 5B (one of its homologs is replaced by $5S^{sh}$). The metaphase plates of AUS21843 and AUS21844 have 39–43 chromosomes on them (Table 1), with one of the chromosome 7 homologs missing. Moreover, AUS21843 has three chromosomes $5S^{sh}$.

Thus, only the *T. aminovii* karyotype has the S genome of *Ae. speltoides* (Fig. 2e) and indeed, its consist of three elementary genomes, A, B and S. It has preserved its ploidy $2n=6x=42$ for 40 years of reproduction. Its fertility is high enough. It has an average of 1.5 grains per spikelet (Table 2).

T. aminovii has fragile rachis (Fig. 1), the trait probably inherited from *Ae. speltoides*. The shape of its spike makes this plant look like wheat rather than *Aegilops* (Fig. 1). Additionally, the number of fertile spikelets in it is closer to that in tetraploid wheats (Table 1) than to that in diploid ones. Ordinarily hexaploid wheats have three and more grains per spikelet (Dorofeev et al. 1979).

Discussion

Many crop species are relatively recent allopolyploids resulting from interspecific hybridization and polyploidy. The development of the karyotype in allopolyploid plants (amphidiploids) followed by genome stabilization is one of the most interesting points in evolutionary biology (Rodionov 2013).

It has been noted before that, it is not enough just to obtain between-species hybrids and to double their haploid genome; what is required, is to restore their fertility. In the tribe Triticeae, not all combinations of wheat/*Aegilops* genomes are fertile. It took some of them 19 generations before their genomes were stabilized (Tanaka 1980). Artificial amphidiploids often have a problem with the excessive genetic material and here genome stabilization comes to the rescue. In the genus *Triticum*, octoploids ($2n=8x=56$) and amphidiploids with higher levels of ploidy are cytologically unstable (Badaeva et al. 2024). The overwhelming majority of artificial amphidiploids have no habitats and cannot survive without human care. "Natural" species, which in botany are considered to be "good" species, and their domesticated (cultivated) counterparts have morphological differences; additionally, the formers have habitats, which the latters do not ones (Goncharov 2011; Yen and Yang 2020; Feldman and Levy 2023). All domesticated wheat species are cultivated by humans. Genetically stable artificial amphidiploids with different genomic composition deserve to take a certain place in the genus *Triticum* taxonomy. Natural amphidiploids of the genus *Aegilops* do not possess the elementary wheat genomes and plasmons (van Slageren 1994; Tsunewaki 2009), and we suggest to include the new artificial amphidiploid, genome formula BBAASS, in the genus *Triticum* under the name of *Triticum aminovii* N.P. Gontsch.

Table 2 Fertility of *Triticum aminovii*

Sample number[a]	Spikelets number per spike	Grains per spike	Grains per spikelet
1	11.08 ± 0.66	18.67 ± 1.26	1.70 ± 0.08
2	11.30 ± 0.55	18.00 ± 1.11	1.62 ± 0.06
3	11.91 ± 0.57	18.45 ± 1.27	1.55 ± 0.07
4	12.00 ± 0.35	17.78 ± 1.72	1.47 ± 0.12
average	11.55 ± 0.27	18.33 ± 0.61	1.58 ± 0.04

[a]-$n=10$ spikes per sample

Taxonomy

Triticum × *aminovii* N.P. Gontsch.—Aminov wheat nothosp. nova.

Type: amphidiploid from crossings *T. dicoccum* Schrank ex Schuebl. to *Ae. speltoides* Tausch. Reproduction by the Institute of Cytology and Genetics, SB RAS, 12 December 2020, Novosibirsk.

Holotype: the I.M. Krasnoborov Herbarium of the Central Siberian Botanical Garden, SB RAS, Novosibirsk. Voucher number NS0000947.—$2n=42$.—Genome BBAASS.

Diagnosis

Stems erect, sheath split, auricles stubby, ligules membrane-like. Inflorescence is an erect, lax, fusiform and fragile spike, peduncle glabrous, caryopsis ovate with a deep ventral crease. Leaves narrow, linear, coarse, with raised parallel veins, hirsute.

Etymology

Named in honor of Prof. Naib Kh. Aminov, cytogeneticist from the Genetic Resources Institute of the Azerbaijan National Academy of Sciences, Baku, Azerbaijan, who worked with intergeneric hybrids of *Triticeae* species.

This species should be the last entry in this genus, because all possible combinations of the genomes A, B (G) and D in others species have been used. Admittedly, the allohexaploid with two DD genomes, namely, DDAADD or AADDDD, makes an exception. However, it has not yet been obtained with the wheat (a likely maternal form possesses the AA genome of wheat) or *Aegilops* (a likely maternal form possesses the DD genome of goat grass) cytoplasm. It is likely that without the *Ph* gene, which is located in the B genome on 5B chromosome (Dvořák et al. 2006) and controls normal meiotic progression in polyploids (Riley and Chapman 1958), such hexaploid amphidiploids are not fertile and thus cannot be produced, while amphidiploids with an extra genome from *Ae. speltoides* are fertile and often serve as research objects (Navalikhina et al. 2021). *Ae. tauschii* do not show a *Ph1*-like activity (Chen and Dvorak 1984).

Conclusion

Following this study, we suggest to include the new artificial hulled hexaploid amphidiploid, genome formula BBAASS, in the genus *Triticum* under the name *Triticum aminovii* N.P. Gontsch. The karyotype of *T. aminovii* is provided, and its genome formula BBAASS has been validated by fluorescent in situ hybridization.

We believe that the only way to preserve artificial amphidiploids in gene banks is by finding them a place in the *Triticum* taxonomy (Goncharov 2011), because working and genetic collections in research and breeding institutions do not commonly have them last alive for long enough (Goncharov and Shumny 2008).

No matter what changes our taxonomy of *Triticum* (Goncharov 2011) may undergo in the future, the number of artificial amphidiploids (species) in it will remain the same, because all possible combinations of the elementary genomes A^b, A^u, B, G, S and D have been used and there is nothing more to add, and chances of finding a new wild wheat species out there are virtually nil. The taxonomy that we propose does not include amphidiploids with the einkorn cytoplasm (Tsunewaki 2009), as they are not fertile and a single such amphidiploids have been produced so far (Feldman and Levi 2023).

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Author contributions Nikolay P. Goncharov conceived and designed the experiments, planting and description of the species. Irina G. Adonina performed the cytogenetic experiments

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Declarations

Conflict of interest The authors have no conflicts of interest and agree with publication.

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