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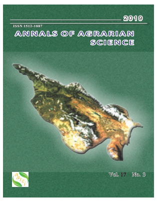

Aegilops tauschii, the D-genome donor of *Triticum* and the geographic origin of hexaploid wheat

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ABSTRACT

The place of origin of alloploid hexaploid wheat is directly connected with the distribution area of its parent species. One of them is wild plant *Aegilops tauschii,* the donor of D-genome. The distribution area of *Ae. tauschii* is stretched extensively from the western Transcaucasus (Georgia) to Central Asia, Pakistan and China. However, it is known that *Ae. tauschii* diverged into subsp. *tauschii* and subsp. *strangulata* at the very beginning of its existence as a species and each of its two subspecies - subsp. *tauschii* and subsp. *strangulata* - originated in the Caucasus. Studies of *Aegilops tauschii* provide evidence that common wheat (*T. aestivum*) was derived from single or limited number of accessions of *Ae. tauschii* and *Ae. tauschii* subsp. *strangulata* populations from its birthplace (the western Transcaucasus) were involved in the formation of common wheat, which originated in the Transcaucasus ca. 8000 BP. Natural diversity of wheat and archaeological excavations of the Neolithic sites of Georgia dated back to 8,000 BP provide evidence that the Transcaucasia is the most probable place of origin of common wheat, because: a) agriculture had been already developed and represented by all founder crops in Georgia; b) AABB-genome containing domesticated hulled and free-trashing tetraploid wheat species (*T. dicoccum, T. palaeocolchicum, T. carthlicum* and *T. durum*) had already existed in Georgia; c) hexaploid wheat species: *T. spelta, T. spaerococcum, T. compactum,* and *T. aestivum* were also present here. These three archaeological findings provide sufficient ground to propose that Ae. *tauschii* subsp. *strangulata* cross with a tetraploid wheat species could had happened here by 8000 BP.

Keywords: *Aegilops tauschii,* Subsp. *strangulata,* Hexaploid wheat, Hulled wheat, Free-threshing wheat, Western Transcaucasus.

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Introduction

Georgia is one of the most important centers of diversity of the cultivated wheat. Despite the small territory (ca 69,000 sq. km), Georgia is the only country in the world, where 15 species (*sensu strricto* classification) of wheat (*Triticum boeoticum* Boiss., *T. monococcum* L., *T. dicoccum* (Shrank) Schübl., *T. palaeocolchicum* Menabde, *T. timopheevii* (Zhuk.) Zhuk., *T. durum* Desf., *T. turgidum* L., *T. carthlicum* Nevski, *T. macha* Dekapr. & Menabde, *T. zhukovskyi* Menabde & Ericzjan, *T. turanicum* Jacubz., *T. polonicum* L., *T. spelta* L., *T. compactum* Host, *T. aestivum* L.) are present. Among them 5 species (*T. macha*, *T. palaeocolchicum*, *T. timopheevii, T. zhukovskyi, T. carthlicum*) are endemics to Georgia. Only one species – *T. carthlicum* (Georgian name 'dika') is naked and rest 4 endemics are ancient hulled wheat. Among 5 endemic species of Georgia, 4 ancient hulled wheats originated from province Lechkhumi. Lechkhumi is situated in a rather isolated valley between the mountains of the central part of west Georgia. Endemic Georgian wheat species are healthy food, quite precious for breeders, all characterized by high resistance to fungal diseases [1].

Georgia is the only country in the world where all 7 species of domesticated hulled wheat are present (4 endemic and 3 non endemic species): *T. palaeocolchicum, T. carthlicum, T. timopheevii, T. macha, T. monococcum, T. dicoccum, T. spelta*). At the same time, Georgia is the only country in the world where all the genomes (AA, AABB, AAGG, AAGGAA, AABBDD) of the wheat can be found (AAGGAA only in Georgia). Hexaploid AABBDD wheat originated about 8,000 years ago [2, 3] by hybridization of D genome donor diploid *Aegilops tauschii* with the already domesticated tetraploid AABB wheat [4-6]. As many as four species (*T. spelta, T. spaerococcum T. compactum* and *T. aestivum*) of domesticated hexaploids (AABBDD) wheat dating back to 8,000 BP were identified in archaeological excavations in Arukhlo, Shulaveri, Khramis Didi Gora of Lower Kartli region (south eastern Georgia) [7, 8].

Origin and geographic spread of Aegilops tauschii

Aegilops tauschii Coss. (- *Aegilops squarrosa* auct. non L.) is a diploid (2n = 14) cleistogamic (self-pollinating) species of the family Poaceae. Its modern natural distribution range is from the western Transcaucasus (west Georgia) and northeastern Turkey to Central Asia, China and Pakistan. While the putative primary region of *Ae. tauschii*'s origin is the Transcaucasus [the South Caucasus] [9]. From the Caucasus, *Ae. tauschii* dispersed eastward to China across northern Iran and Central Asia and southward to central Syria [10].

Ae. tauschii divided into subsp. *tauschi*i and subsp. *strangulata* at the very beginning of its existence as a species and each of its two subspecies - subsp. *tauschii* and *subsp. strangulat*a - originated in the Caucasus. The mutation Tf(s)225b (which appeared after the origin of Ae. *tauschii* but before its subdivision into the subspecies) was retained in both subspecies (Fig. 1). Another mutation Tc(s)380 (black dots) had existed even before the origin of Ae. *tauschii* and could be found only in some local populations of subsp. strangulata, which is represented only by two accessions t9(1)s and AE929 from the Caucasus: Dagestan and Georgia, respectively [11].

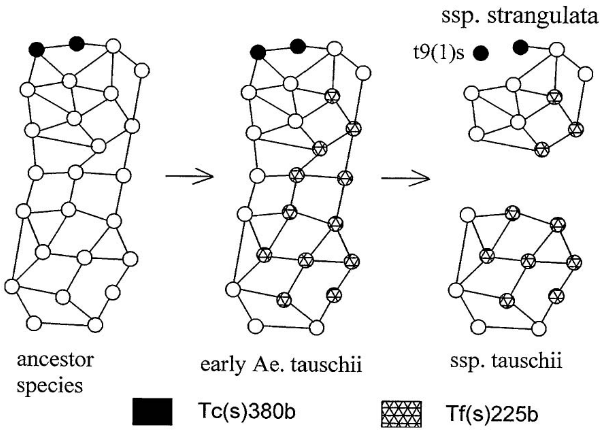

Fig. 1. *A presumed scheme of Ae. tauschii evolution. The circles present local populations in the field of gene combinations of Sewall Wright (credit of the illustration [11]).*

Subsp. *tauschii* was the first to start geographic expansion and relatively rapidly occupied a vast area from the Caucasus—eastward up to central Tien Shan and western Himalayas [11]. In contrast to subsp. *tauschii*, only some linages of subsp. *strangulata* managed to expand to the East. Therefore, the Caucasus is the only region where all the five subsp. *strangulata* lineages, Tc(s)21b, Tc(s)492b, Nf(d)237b, Tc(d)132b and Tf(s)225b were found [11**]**.

Primary habitats of Ae. *tauschii* are patches of dwarf-shrub steppe-like formations in hilly or mountainous regions. Subsp. *strangulata* "prefers" the habitats with relatively warm and moist winter, while subsp. *tauschii* occupies habitats with relatively continental climate [12].

Ae. tauschii likely dispersed from the temperate desert vegetation (TDV) zone at the Last Glacial Maximum (25,000–15,000 BP)[1] in the postglacial era and the southern habitats were established as the environment experienced change to humid conditions in the Holocene [13]. Because *Ae. tauschii* has a weedy growth habit, human disturbance may have contributed to population migrations after the beginnings of agriculture 10,000 years ago.

When 205 accessions of *Ae. taushii* from the whole area of its distribution were analyzed based on chloroplast DNA variation, four intraspecific linages were identified, which were characterized by different haplogroups: HG7, HG16, HG9 and H17. It was found that the accessions of the HG7 lineage were distributed across the entire range of natural

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[1] It should be noted that West Georgia, the Western Transcaucasus is an important glacial refugia, where many relict plants have been preserved, and this region is rich in endemic plant species

habitats and the eastward dispersal of *Ae. tauschii* was driven by the HG7 and HG16 lineages [3]. The HG9 lineage accessions were specific to western habitats, while the distribution area of five HG17 accessions was only found in Georgia [14].

It was found that flowering time of *Ae. tauschii* varied from the earliest (144 days) to the latest (190 days) in the temperate desert vegetation zone. The eastward dispersal was driven by the HG7 and HG16 lineages (Fig. 3). HG16 diverged from HG7 in the west and independently migrated to the east. The HG9 lineage was phenotypically uniform, with 26 out of 28 accessions (92.9%) having the intermediate-flowering phenotype. All five accessions of the HG17 lineage had the late-flowering phenotype. Among the intermediate and late-flowering phenotypes, accessions of the HG7 lineage were common [3].

Ae. tauschii evolved from late flowering to early flowering and the ancient, late flowering forms (colored in blue on Fig. 3) of both subsp. *taushii* (HG7) and subsp. *strangulata* (HG9, HG17) are found only in the Caucasus [3, 14]. In contrast to subsp. *tauschii*, geographic spread of subsp. *strangulata* was a complicated, multi-stage and slow process. At the beginning of subsp. *strangulata* evolutionary history its major phylogenetic lineage for a lengthy time span had existed as a small isolated population. Several forms of subsp. *strangulata*, better adapted to relatively moister and cooler habitats, had originated [11]**.**

In Fig. 3, HG9 (the D genome donor to hexaploid wheat) is represented by ancestral late flowering phenotypes (blue triangle) in Georgia and the South Caucasus. As it was mentioned above "geographic spread of subsp. *strangulata* was a compli-

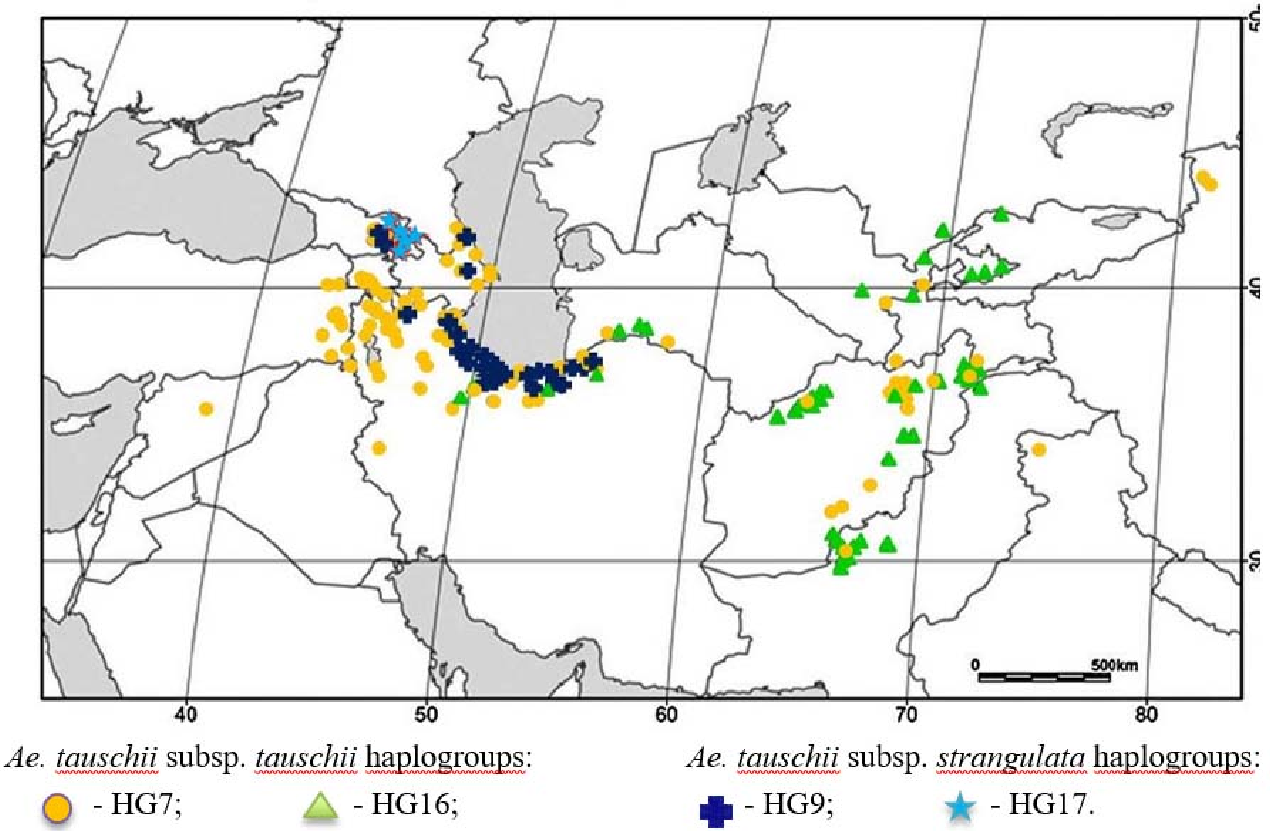

Fig. 2. *Geographical distribution of Ae. tauschii accessions. Adventive populations in the Shaanxi and Henan provinces of China are not shown. Circles, crosses, triangles, and stars indicate the HG7, HG9, HG16, and HG17 lineages, respectively (credit of the map [14]). Haplogroups HG7 and HG16 represent subsp. tauschii and while HG9 and H17 belong to subsp. strangulata.*

cated, multi-stage and slow process". i.e. in Georgia and the South Caucasus, the D genome donor subsp. *strangulata* should have existed at least 1000 years earlier before subsp. *strangulata* reached the Caspian region. Pre-Caspian Iran cannot be assumed as a place of hexaploid wheat origin because *Ae. tauschii* subsp. *strangulata* could not have been presented there earlier than 7000 BP [15].

Amplified fragment length polymorphism (AFLP) analysis was applied for a total of 122 accessions of *Ae. tauschii* to clarify the population structure of this widespread wild wheat species. Phylogenetic and principal component analyses revealed two major lineages in *Ae. tauschii*: L1 and L2. Among three major haplogroups (HG7, HG9 and HG16) previously identified in the *Ae. tauschii* population based on chloroplast variation, HG7 accessions were widely distributed to both L1 and L2, HG9 accessions were restricted to L2, and HG16 accessions belonged to L1, suggesting that HG9 and HG16 were formed from HG7 after divergence of the first two lineages of the nuclear genome [18].

Later, to identify the *Ae. tauschii* intraspecific lineage, the same 122 accessions were grouped into three intraspecific lineages: TauL1 (renamed from L1), TauL2 (renamed from L2), and TauL3 (renamed from HGL17). Geographically, the TauL1 accessions are widely spread across the species range, whereas the TauL2 and TauL3 accessions are restricted to the Transcaucasus/Middle East region and Georgia, respectively [6].

Within each TauL1 and TauL2 lineage, three sublineage groups were identified: TauL1a TauL1b and the intermediates (named TauL1x) and TauL2a, TauL2b and TauL2x (Fig.4). The chloroplast DNA haplotype evidence supported that TauL1a is ancestral to TauL1b, Similarly, TauL2a is ancestral to TauL2b. The TauL2a accessions tend to spread in the Transcaucasus, whereas TauL2b has its distribution center in the Caspian coastal region. Each TauL1a and TauL2a has the center of distribution in the Transcaucasus and represents ancestral sublineages of the species [19]. The Transcaucasus (especially Georgia) is the only region where all ancestral linages and sublineages of TauL1, TauL2 and TauL3 were found. According to Gogniashvili *et al.* [20] TauL3 and TauL1 are ancestral linages while TauL2 diverged from the Taul3.

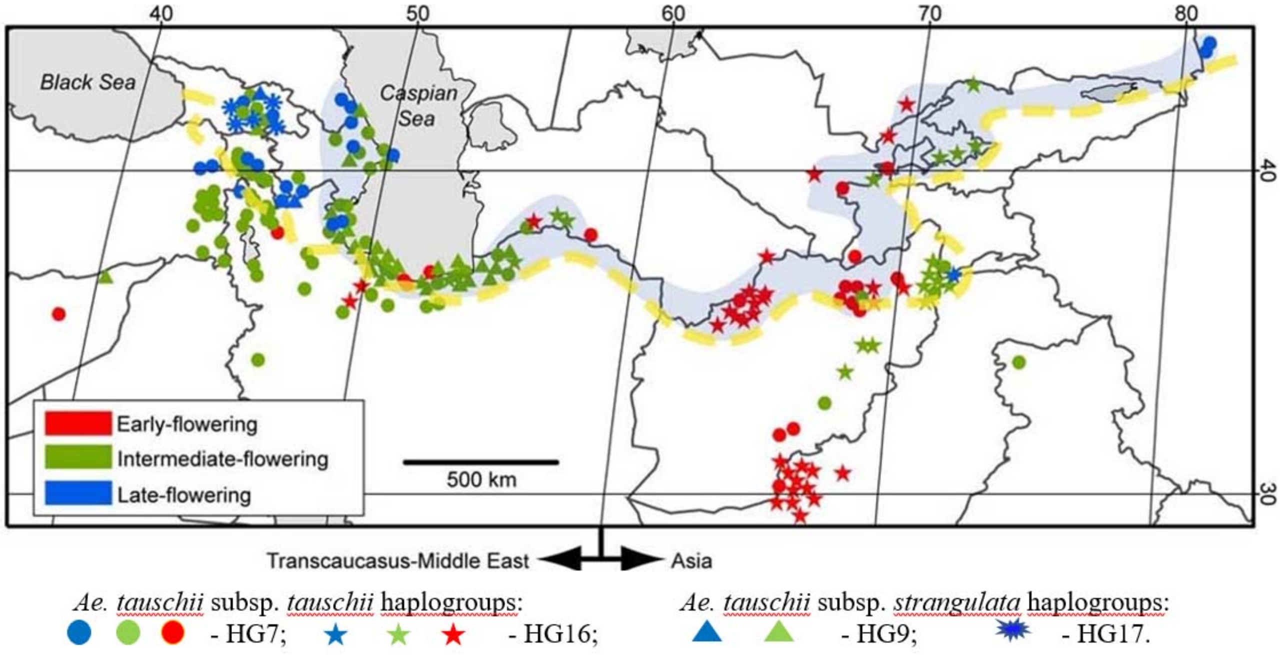

Fig. 3. *Geographic distribution of the 200 Ae. tauschii accessions. Circles, triangles, stars and asterisks denote, respectively, accessions of the HG7 lineage, HG9 lineage, HG16 lineage, and HG17 lineage. For each accession, flowering time phenotype is colored according to the key. The belt area where fairly undisturbed habitats exist is shaded [16, 17]. The dashed yellow line indicates the southern limit of the temperate desert vegetation zone at the Last Glacial Maximum. The species distribution was divided into two regions in the analyses: Transcaucasus-Middle East (longitude <60^0) and Asia (longitude >60^0) (credit of the map [3]).*

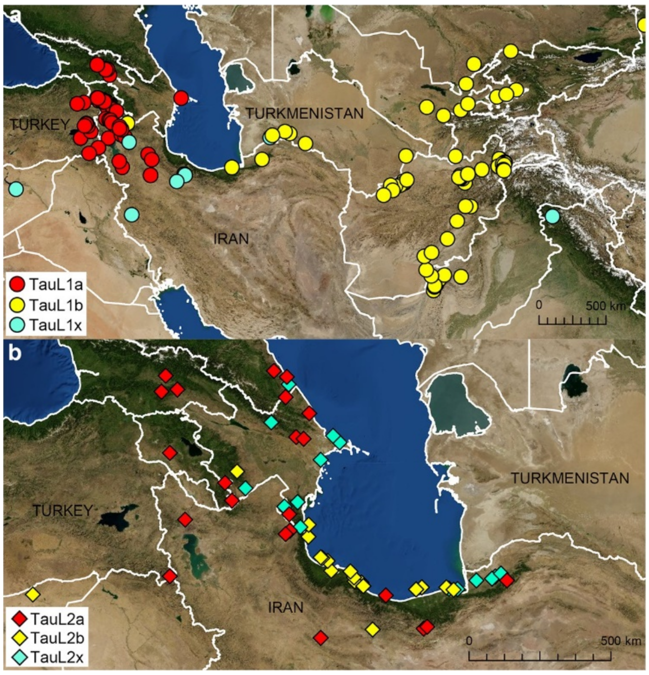

Fig. 4. *Geographic distributions of the TauL1 and TauL2 sublineages. a) The TauL1 sublineages. TauL1a, TauL1b, and TauL1x are colored red, yellow, and blue, respectively. The six accessions representing adventive populations in the Shaanxi and Henan provinces are not shown. b) The TauL2 sublineages. TauL2a. TauL2b, and TauL2x are colored red, yellow and blue, respectively (credit of the map [19]).*

TauL1 is associated with *Ae. tauschii* subsp. *tauschii*, while TauL2 and TauL3 are associated with *Ae. tauschii* subsp. *strangulata*. Subsp. *strangulata* linage TauL2 is considered to be the D-genome progenitor of hexaploid common wheat *Triticum aestivum*.

To identify the *Ae. tauschii* intraspecific lineage that is most closely related to the D genome of common wheat, Matsuoka *et al*. [6] conducted a population-level analyses using a

Diversity Arrays Technology (DArT) marker genotype dataset for 206 *Ae. tauschii* accessions that represented the entire species range and a diverse array of 188 common wheat accessions consisting of traditional and modern cultivars of the East and West and one synthetic wheat line W7984. Separation of the D genome of common wheat from *Ae. tauschii* was fully consistent with the results of restriction-fragment-length-polymorphism, microsatellite, and single-nucleotide-polymorphism studies [21-23].

Geographically, the TauL1 accessions are widely spread across the species range, whereas the TauL2 and TauL3 accessions are restricted to the Transcaucasus/Middle East region and Georgia, respectively. In contrast, almost all common wheat accessions formed a single isolated cluster that was more closely associated with TauL2 and TauL3 than TauL1 (Fig. 5). Two common wheat accessions were exceptionally closely associated with *Ae. tauschii*: the synthetic wheat line W7984 (placed near TauL2) and an Ethiopian landrace KU-9873 (placed near TauL3). The reason for the KU-9873 - *Ae. tauschii* association was not clear [6].

The PCA and Bayesian clustering, therefore, showed close genetic relationships of the TauL2

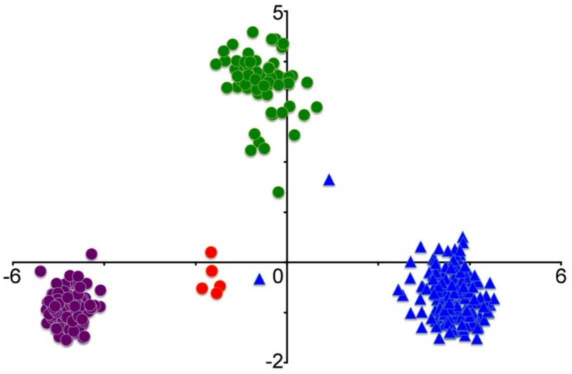

Fig. 5. *Graph of the first two axes from a PCA based on DArT marker variations. The first component (x) accounts for 41.8% and the second (y) for 8.5% of the total variance. Circles denote Ae. tauschii TauL1 (purple), TauL2 (green), and TauL3 (red), and triangles T. aestivum (credit of the chart [6]).*

and TauL3 accessions to the D genome of common wheat. Notwithstanding the observed close genetic relationship of TauL2 with the D genome of common wheat, whether the TauL2 accessions represented descendants of the *Ae. tauschii* populations that were involved in the 8,000-years-ago allopolyploid speciation of common wheat was not clear [6].

The birthplace of common wheat has been assumed to be Transcaucasia or the south coastal region of the Caspian Sea [21, 24 - 26]. Common wheat was derived from single or limited accessions of *Ae. tauschii*, and *Ae. tauschii* populations far from its birthplace were not involved in the formation of common wheat [14].

According to Nesbitt [27] the origin of bread wheat in the Near East remains as problematic as the origin of spelt in Europe. The hybridization between a tetraploid wheat and *Aegilops tauschii* could take place only once agriculture with tetraploid wheats reached the distribution zone of *Aegilops tauschii.* This extends from northern China westwards to west and southwest of the Caspian Sea, well northeast of the fertile crescent. As agriculture did not reach the Caspian Sea until after 6000 BC, the hybridization could not have occurred until then [27].

Archaeological evidence for wheat and other crops in Georgia (the south Caucasus)

The Neolithic revolution probably began in the 8th millennium B.C. [10,000 B.P.] in Georgia [28]. It is distinguished by a number of innovations in the archaeological records. Along with the diversity of tools and pottery production the remains of various domesticated plants (cereals, legumes, grape, etc.) including soft wheat, provide evidence of the high level of farming. Excavated wheat grains include transitional forms from wild to domesticated varieties.

Wheat, barley, oil-fiber crops were widely cultivated along with the vineyards and fruit gardens [29 - 31].

Fig. 5. *The Neolithic archaeological site of Arukhlo (8000 BP), Lower Kartli region of southeast Georgia*

According to McGovern *et al.* [32], the earliest evidence for grape wine in the Near East was from the early Neolithic village of Hajji Firuz Tepe in the northwestern Zagros Mountains of Iran, ca. 5,400–5,000 BC. Chemical analyses of ancient organic compounds absorbed into the pottery fabrics from sites [Gadachrili Gora and Shulaveris Gora] in Georgia in the South Caucasus region, dating to the early Neolithic period, provide the earliest biomolecular archaeological evidence for grape wine and viniculture from the Near East, at ca. 6,000–5,800 BC. The discovery of early sixth millennium BC grape wine in this region is crucial to the later history of wine in Europe and the rest of the world. Now that wine jars from as early as ca. 6,000 BC have been confirmed for Gadachrili Gora and Shulaveris Gora, preceding the Hajji Firuz jars by half a millennium [32]. Alcohol plays a central role in formation of human civilization. According to McGovern *et al.* [32] the very large-capacity jars, some of the earliest pottery made in the Near East, probably served as combination fermentation, aging, and serving vessels. They are the most numerous pottery type at many sites comprising the so-called "Shulaveri- Shomu Culture" of the Neolithic period. All these finds: the oldest grape wine, domesticated grape seeds (pips), large-capacity ceramic jars for storing wine in the early Neolithic sites of Shulaveri and Gadachrili Gora in 6,000 cal. BC shows high level of agricultural civilization in Georgia (the south Caucasus).

While not more than two species of domesticated wheat (*T. monococcum* and/or *T. dicoccum*) were identified in the majority of the Anatolian and Mesopotamian Neolithic sites contemporary with Arukhlo [28, 33]. Archeological findings from the Shulaveri – Shomu Culture suggest that a very high diversity of domesticated wheat was grown in Georgia in the early Neolithic period. Nine species of wheat including one wild (*T. baeoticum*) and eight domesticated (*T. monococcum, T. diccoccum, T. carthlicum, T. durum, T. spelta, T. spaerococcum, T. compactum,* and *T. aestivum*) were identified in archaeological excavations of Arukhlo (the end of the 7th to the beginning of the 6th millennium BC). It is the earliest appearance of the naked tetraploid (AABB) wheat (*T. carthlicum* & *T. durum*) is in the oldest layers in Arukhlo [7].

Out of 9 species of Arukhlo and Khramis Didi Gora 4 species: *T. spelta, T. spaerococcum T. compactum* and *T. aestivum,* are Hexaploids (AABBDD), three of them are free-trashing [7, 8]. As many as seven species of domesticated wheat dating back to 8,000 BP were identified in archaeological excavations in Shulaveri, Khramis Didi Gora of Lower Kartli (south eastern Georgia): *T. monococcum, T. dicoccum, T. durum, T. spelta, T. aestivum, T. compactum, T. spaerococcum* alongside with other 'founder' crops: barley (*Hordeum vulgare* and *H. distichum*), oat (*Avena sativa*), rye (*Secale cereale*), lentils (*Lens esculenta*), peas (*Pisum sativum*) and bitter vetch (*Vicia ervilia*) [7, 34, 8]. Wheat grains from Arukhlo, Khramis Didi Gora and Gadachrili Gora providing the earliest archaeological evidence of existence of hulled hexaploid *T. spelta*, as well as free-thrashing hexaploids *T. aestivum, T. compactum* and *T. spaerococcum*) in the Near East in 6,000 -5,800 cal. BC [7, 8, 35].

The South Caucasus was more diverse in terms of the wheat diversity than South Anatolia and Mesopotamia [36]. This became evident when the Shulaveri - Shomu complex was compared to its contemporary sites in northern Mesopotamia (the Halaf and Hassuna cultures) and Anatolia (Hacilar). The cereals cultivated in the South Caucasus are much more diverse than in Anatolia and Mesopotamia. The great variety of endemic wheat species in the Transcaucasus could have favored local domestication of cereals, even if these cereals were already cultivated in the Near East [36].

The origins of hulled and free-trashing hexaploid wheat in the South Caucasus

Allohexaploid common wheat (AABBDD genome) originated in the Middle East/ Transcaucasus region ca. 8,000 years ago and is derived from a natural hybrid cross between a cultivated form of *T. turgidum* (female parent) and the wild species *Ae. tauschii* (male parent) [6, 37, 38]

Archaeological work since the 1960s has confirmed van Zeist's dating of the earliest agricultural sites around the Caspian. Sites further to the south, in the Zagros mountains, such as Jarmo, Ali Kosh and Abdul Hosein have good evidence of farming (including emmer) by 6500--6400 uncal BC. In contrast, intensive surface survey around Haji Firuz Tepe and Yanik Tepe, both in Iranian Azerbaijan southwest of the Caspian Sea, failed to uncover any evidence of occupation earlier than 5500 uncal BC [27, 39].

Dvorak [5] noted that it is a widely believed hypothesis that *T. aestivum* originated by hybridization of domesticated tetraploid emmer (*T. turgidum* subsp. *dicoccon*) [38, 40, 41] with *Ae. tauschii* subsp.

strangulata. However, the belief that the tetraploid ancestor of *T. aestivum* was domesticated hulled emmer has been recently questioned [5] with a suggestion that the tetraploid ancestor of bread wheat was free-threshing.

T. carthlicum, a free-threshing tetraploid Karthlian[2] wheat, endemic to Georgia (erroneously named as Persian wheat)[3] is considered as a subspecies of *T. turgidum* by modern *sensu lato* classifications: *Triticum turgidum* subsp. *carthlicum*, common name in Georgian - 'Dika'. This wheat has been cultivated for at least 8000 years in Georgia according to the data of the Neolithic archeological excavations [7]. 'Dika' is mentioned in the fifth century historical documents in Georgia [31].

Karthlian wheat's spike morphology resembles more the morphology of common wheat (*T. aestivum*) rather than that of other subspecies of free-threshing tetraploid wheat [42]. Moreover, it was shown that the morphology of synthetic hexaploid wheat derived from crosses between *T. turgidum* subsp. *carthlicum* and *Aegilops tauschii* resembles that of common wheat and considered subsp. *carthlicum* as a candidate for the AB genome donor of common wheat [42, 43]. With many beneficial traits and easiness of gene transferring to common wheat *T. carthlicum* has been suggested as one of the most desirable donors for bread wheat improvement [44].

There are two polyploid lineages in the genus *Triticum* [45]:

a) *T. timopheevii* - *T. zhukovskyi* lineage with AAGGAA - genome and

b) *T. turgidum* – *T. aestivum* lineage with AABBDD - genome.

Both polyploid lineages of the genus T*riticum* found only in Georgia:

1. *T. timopheevii* - *T. zhukovskyi* lineage (with domesticated AAGG tetraploid, Georgian endemic - *T. timopheevii* and AAGGAA hexaploid Georgian endemic -*T. zhukovskyi*) originate and grow only in Georgia [46].

2. *T. turgidum* – *T. aestivum* lineage with AABBDD genome represented with two sub linages:

2a –AABBDD genome hulled hexaploid represented with

2a.1. AABBDD genome hulled hexaploid endemic "Makha" linage of diploid DD (*Ae. tauschii* subsp. *strangulata*), hulled tetraploid AABB endemic (*T. palaeocolchicum)* and hulled hexaploid AABBDD endemic *T. macha* represented only in Georgia.

2a.2. AABBDD genome hulled hexaploid 'Spelta' linage of diploid DD (*Ae. tauschii* subsp. *strangulata*), hulled tetraploid AABB *T. dicoccum* and hulled AABBDD *T. spelta*

2b - AABBDD genome naked (free-threshing) hexaploid

The presence of free-threshing polyploidy lineage of diploid DD (*Ae. tauschii* subsp. *strangulata*), naked tetraploid AABB (*T. carthlicum*), naked hexaploid AABBDD (*T. aestivum/T. compactum*) in recent Georgia and in archaeological excavations of the 8000 BP in Arukhlo, Shulaveri, Khramis Didi Gora, in the same time that common wheat originated ca. 8000 years ago.

Archaeological excavations of the Neolithic sites of Georgia dated back to 8,000 BP have confirmed that both hulled and naked (free-trashing) AABB genome domesticated tetraploid wheat (*T. dicoccum, T. palaeocolchicum, T. carthlicum, T. durum*) already existed in Georgia ca. 8,000 BP and subsp. *strangulata* could have crossed with them. This is confirmed with existence of hulled hexaploid (*T. macha, T. spelta*) and naked hexaploid wheat (*T. aestivum*, *T. compactum, T. sphaerococcum*) samples in the Neolithic archaeological sites of west Georgia (Dikha Gudzuba, Anaseuli) and east Georgia (Arukhlo, Khramis Didi Gora, Gadachrili Gora) 8,000 years ago [7, 35].

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[2] Karthli – a province in East Georgia

[3] Kartlian wheat *T. carthlicum* Nevski (common name in Georgian 'Dika' erroneously named by N. Vavilov in 1919 as *T. persicum* Vavilov [nomen provisorium]. In 1921 Zhukovskyi found it in Georgia and described as *T. persicum* Vavilov ex Zhuk. 1923. This name [*T. persicum*] is a later homonym of *Triticum persicum* (Boiss.) Aitch. & Hemsl. (*Aegilops persica* Boiss., 1846) and therefore is illegitimate (ICN Art. 53.1). Seed of this wheat was sent to Vavilov by a German private seed company under the name of Persian wheat ("Persischer Weizen"). However, the German company itself had received the seeds from Moscow, not from Iran (that time Georgia was part of the Russian Empire). According to the "International Code of Nomenclature for algae, fungi, and plants" the earliest legitimate name of this species is *Triticum carthlicum* Nevski (ICN Art. 11.4). This endemic species was widely cultivated in Georgia and is presented by 12 varieties in Georgia [47].

The great variety of endemic wheat species in the Transcaucasus could have favored local domestication of cereals, even if these cereals were already cultivated in the Near East [36].

Zhukovsky [48] mentioned that: "among 19 species of wheat in the world, 13 species represented in the Transcaucasus and the Transcaucasus (especially Georgia) is the birthplace of wheat". According to Dorofeev [49] "To the Transcaucasus - the primary center of origin of wheat belongs a leading historical role in it's domestication and dispersal. By the number of endemic species and varieties of the genus *Triticum*, this territory has no equal in the world".

As a conclusions Georgia is one of the most important centers for the diversity of cultivated wheat: 15 species of *Triticum*, out of 20 species in the world; 5 endemic wheat species (more than in any other country), all 7 cultivated hulled wheat species, as well as *Aegilops tauschii* with all 3 linages and all ancestral sub-linages represented only in Georgia. 9 species of wheat, among them 4 species AABBDD hexaploids (*T. spelta, T. aestivum, T. compactum, T. sphaerococcum*), together with all founder crops, discovered in the early Neolithic sites of Lower Kartli region (southeastern Georgia), reveals an importance of this region in wheat evolution and the origin of hexaploid wheat.

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