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Georgia, the South Caucasus as the homeland of the hexaploid wheat

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A B S T R A C T

The importance of the local wheats of the South Caucasus for the evolution of the hexaploid wheat is largely overlooked. The South Caucasus and, especially, Georgia is the only country where all suitable conditions (on a very small territory are created for the origin of hexaploid wheat: 1) high diversity of local flora of wild and cultivated plants; 2) ancient Neolithic farming society confirmed by numerous archeological findings, which included nine species of wheat in Arukhlo and eight domesticated wheat species in each of Shulaveri and Khramis Didi Gora (southeast Georgia) dated as 8000 BP; 3) highest diversity and endemism of ancient hulled wheats represented with all seven hulled species; 4) highest diversity and endemism of free-threshing wheats; 5) presence of all tetraploid wheats - potential donors of AABB-genome; 6) presence of the of D-genome donor - all linages of *Aegilops tauschii* subsp. *strangulata* including the ancient, late flowering forms; 7) the presence of the endemic *T. timopheevii* - *T. zhukovskyi* lineage (AAGG-AAGGAA genomes); 8) The representation of the *T. turgidum* – *Tr. aestivum* lineage (AABB-AABBDD) genomes with two sub-linages: i) endemic hulled *T. turgidum* subsp. *palaeocolchicum* – *T. aestivum* subsp. *macha* and *ii*) free-threshing *T. turgidum* subsp. *carthlicum* – *T. aestivum*.

Keywords: Wheat, Domestication, Bexaploid wheat, Hulled wheat, Free-threshing wheat, Endemic.

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Introduction

The diversity of wheat species in Georgia, the South Caucasus is exceptionally high and Georgia exceeds in that countries of the Fertile Crescent which are widely recognized as the center of wheat domestication. Sinskaia [1] remarks that Front Asia, which includes Asia Minor, Near East, West Iran and the South Caucasus, is the native place of 12 wheat endemic species, out of which eight originated from the South Caucasus. The remaining four species originated from Syria, Palestine, Turkey and Iran - only one species per each country, respectively. Furthermore, out of the eight endemic species of the South Caucasus, five originated from Georgia. Georgia occupies the first place with richness in wheat species and forms on the earth [1].

According to the *sensu stricto* classification, fifteen species of wheat are identified in Georgia: *Triticum boeoticum* Boiss., *T. monococcum* L., *T. dicoccum* Schrank, *T. palaeocolchicum* Menabde, *T. timopheevii* (Zhuk.) Zhuk., *T. zhukovskyi* Menabde & Ericzjan, *T. carthlicum* Nevski, *T. durum* Desf., *T. turgidum* L., *T. turanicum* Jacubz., *T. polonicum* L., *T. macha* Dekapr. & Menabde, *T. spelta* L., *T. compactum* Host and *T. aestivum* L. [2-11]. The wheat species of Georgia are reviewed in Table 1. Most of the species are characterized by high infraspecific variation and are presented by 188 varieties in total [12].

It was noted that the wheat diversity of Georgia includes ancient, initial, relict species, as well as evolutionary advanced species and their inter-relationship shows all directions and transitional stages in the wheat evolution [5, 6, 8]. Georgia is the only country in the world where all genomes and ploidy levels of wheat (AA, AABB, AAGG, AABBDD and AAGGAA) are represented. The five species of wheat, which are endemic to Georgia, include four hulled species (*T. palaeocolchicum, T. macha, T. timopheevii* and *T. zhukovskyi*) and one free-threshing (*T. carthlicum*). At the same time, Georgia is the only country in the world where all 7 species of ancient hulled wheat are represented, including: 4 endemic and 3 non-endemic species (*T. monococcum, T. dicoccum* and *T. spelta*).

According to Nesbitt & Samuel [13] Agriculture in the South Caucasus has always been characterized by great diversity in the range of crops. This must be due in part to isolation of regions within the highly mountainous landscape. The same diversity is found in ancient plant remains [14]. However, the problem of poorly published data and lack of cultural context is perhaps greater for these areas to the north of the Near East than anywhere else: "… a fascinating variety of hulled wheats is grown, but we have nothing more than lists of plant species. We know virtually nothing of how the hulled wheats were used nor how their cultivation changed through time and came to cease"[13].

The present publication is an attempt to underline importance of the Georgian endemic wheat species for understanding of the wheat evolution through consideration of the agricultural history and biodiversity of Georgia, as well as summarize major findings of archeologists and wheat scientists, which emphasize importance of the area of Georgia for wheat domestication.

Table. *The wheat species of Georgia classified according to Sensu stricto [11] and sensu lato [43] classifications*

Wheat taxonomy (Ploidy / Genome)	
Sensu stricto classification	Sensu lato classification
Traditional [11]	Genetic [43]
Diploid (2n=14), AA, Wild, Hulled	
T. boeoticum Boiss.	*T. monococcum* subsp. *aegilopoides* (Link) Thell.
Diploid (2n=14), AA Domesticated, Hulled	
T. monococcum L.	*T. monococcum* L. subsp. *monococcum*
Tetraploid (2n=28), AABB, Domesticated Hulled	
T. *dicoccum* Schrank ex Schübl.	*T. turgidum* subsp. *dicoccum* (Schrank ex Schübl.) Thell.
● *T. palaeocolchicum* Menabde (*T. karamyschevii* Nevski)*	● *T. turgidum* subsp. *georgicum* (Dekapr. & Menabde) Mackey ex Hanelt
Tetraploid (2n=28), AABB Domesticated, Free-threshing	
● *T. carthlicum* Nevski	● *T. turgidum* subsp. *carthlicum* (Nevski)) Á. & D. Löve
T. durum Desf.	*T. turgidum* subsp. *durum* (Desf.) Husn.
T. turgidum L.	*T. turgidum* L. subsp. *turgidum*
T. polonicum L.	*T. turgidum* subsp. *polonicum* (L.) Thell.
T. turanicum Jacubz.	*T. turgidum* subsp. *turanicum* (Jakubz.) Á. & D. Löve
Tetraploid (2n=28), AAGG Domesticated, Hulled	
● *T. timopheevii* (Zhuk.) Zhuk.	● *T. timopheevii* (Zhuk.) Zhuk. subsp. *timopheevii*
Hexaploid (2n=42), AAGGAA Domesticated, Hulled	
● *T. zhukovskyi* Menabde & Ericzjan	● *T. zhukovskyi* Menabde & Ericzjan
Hexaploid (2n=42), AABBDD Domesticated, Hulled	
●*T. macha* Dekapr. & Menabde	● *T. aestivum* L. subsp. *macha* (Dekapr. & Menabde) Mackey
T. spelta L.	*T. aestivum* L. subsp. *spelta* (L.) Thell.
Hexaploid (2n=42), AABBDD Domesticated, Free-threshing	
T. compactum Host	*T. aestivum* subsp. *compactum* (Host) Mackey
T. aestivum L.	*T. aestivum* L. subsp. *aestivum*

Higher Plant Diversity and Agrobiodiversity in Georgia

According to Vavilov [2] centers of plant domestication are characterized by 1) high diversity of plants in the local flora that are suitable for domestication and 2) existence of old farming civilization. Both applies to Georgia.

The Caucasus region is ranked among the 36 most important global biodiversity hotspots [15]. The importance of the western Caucasus, especially the Colchis region, should be emphasized as it was a refugium during the glaciation where, among others, Neogene relict species survived [16-20].

The Caucasus biodiversity hotspot covers an area of more than 500,000 km^2 between the Caspian Sea and the Black Sea. The vegetation of the Caucasus is remarkably diverse, ranging from alpine meadows and mountain conifer forests to arid shrub-lands and semi-deserts. Of about 6,300 species of vascular plants, ca. 1,600 are endemic to the region. Georgia is a small country with total area of 69,000 km^2. It covers only 14% of the Caucasus territory. However, its vascular flora includes 4,150 species, which is 65% of all vascular plants of the Caucasus species. It is characterized by high endemism: 900 species (21%) found in Georgia are local endemics.

More than 2 000 species of the Georgian flora have direct economic importance for food, timber, edible fruits and nuts, forage and fodder, medicine, colorants, industry and essential oil production. In addition, there are many farmer-selected varieties and wild relatives of cultivated plants. A variety of crops, such as cereals (wheat, barley, rye, sorghum, millet), legumes (faba bean, grass pea, chickpea, lentil, cowpea), also flax, onion, garlic, and various fruits (grape, apple, pear, quince, medlar, peach, apricot, plum, cherry, cornelian cherry etc.) have been cultivated here since ancient times [21].

Evidences of existence of ancient gricultural civilization in Georgia

The Neolithic revolution in the South Caucasus could have begun as early as the 8th millennium BC (10 000 BP). The earliest a ceramic (lacking pottery) Neolithic sites in Georgia are mainly found in West Georgia, on the Black Sea coast and in the Colchis lowland.

One of the sites describing the dawn of the farming society in Georgia is cave 'Kotias Klde', which is found in the Kvirila River basin in West Georgia [22, 23]. Archeologists identified four cultural layers beneath the cave ranging from the Upper Paleolithic to the Bronze Age. A series of radiocarbon dates indicates a time range of the 11th to 9th millennia BC (10,850–8,240 BC) for 'Layer B' (Mesolithic) and 8th millennium BC (7,690–7,300 BC) for 'Layer A2' (Early Neolithic) [24]. The end of the Mesolithic period in Georgia, according to the archaeological records, was characterized by a number of innovations: tool production by means of scrubbing and polishing hard rocks, or by means of a macrolithic technique (bilateral slicing), the new shapes of tools, and the advent of pottery production. Along with the diversity of tools, the remains of various domesticated plants such as cereals, legumes, oil-fiber crops, grape, etc. bear witness to the high level of farming in the Neolithic period [26, 27].

By and large, macrofossil remains of crops cultivated by the Neolithic people of Georgia were the same as those 'founder' crops of the Fertile Crescent and Levant [27-29]. These included einkorn, emmer, bread wheat, barley, oats, rye, millet, grapes and various legumes [25-27].

Purported finds of endemic wheat species (*Triticum carthlicum* and *T. macha*) at early agricultural sites in Georgia [30] might suggest that Neolithic settlements in this region were sited to take advantage of wild cereal stands [31]. There is an opinion that wild wheat with dehiscent spikelets could have been cultivated for over one millennium before the emergence of domestic varieties with indehiscent spikelets. The reason is that early farmers had to harvest wild wheats before the spikelets fell to avoid loss, so indehiscent mutants that paved a way for domestic wheat were not easy to identify. Furthermore, when crops failed, farmers would have had to gather from the wild. These two practices lowered the probability of the rare indehiscent mutant being selected and prolonged the domestication period [32].

In Georgia, relic tools used to collect ancient hulled wheat spikes with brittle (fragile) rachis have survived to present. This is a woody tool, known as 'Snakvi' (Fig.1-a) originally created for wheat, and a stone mortar for dehusking (peeling) of ears of hulled wheat: makha, zanduri & asli. The method of collecting these crops with brittle rachis is very original in Georgia: the ears were cut into baskets with wooden scissors – 'Shnakvi' and the straw was collected with sickles. This method of collecting makha and zanduri wheat was used in the province of Lechhumi until the 1970s and 1980s.

a. b. c. d.

Fig. "*Snakvi" - the oldest tool for harvesting ears (spike) of hulled wheat species of "makha" "zanduli" and "asli" and b. Stony mortar, for dehusking hulled wheat spikes and spikelets; c, d.* Pestles in a mortar, a heavy woody tool with a rounded end, used for crushing and grinding tools for dehusking hulled wheat: makha, zanduri & asli.

Georgia is the homeland of viticulture and viniculture. The oldest domesticated grape (*Vitis vinifera*) pips and fermented wine were found by archeological excavations of 8000 BP in Shulaveri and Khramis Didi Gora in Kvemo Kartli Region (south-east Georgia). Chemical analyses of ancient organic compounds absorbed into the pottery fabrics from sites in Georgia in the South Caucasus region, dating to the early Neolithic period (ca. 6,000–5,000 BC), 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 [33].

In the 7th millennium BC a Neolithic culture known as the 'Shulaveri – Shomu' Culture appeared [34] and it diffused widely in the 6th millennium BC in the over what is now East Georgia, but mainly in Kvemo (Lower) Kartli. The archeological study of two sites Khramis Didi Gora and Arukhlo provided rich data on the 'Shulaveri – Shomu' Culture. It is known to be characterized by permanent settlements, circular vaulted mud-brick houses and farm buildings, tools made of obsidian, stone, bone and horn, female figurines reflecting fertility beliefs or clay vessels decorated with relief and notched ornaments. Production of cattle, pigs, wheat and barley was widely spread [35, 36].

Carbonized wheat grains discovered at archeological sites of Arkhulo, Khramis Didi Gora and Shulaveri of the 'Shulaveri – Shomu' Culture are dated back to the 6th millennium BC. Based on the analysis of these findings, archeologists and paleobotanists concluded that:

a) In late 7th and beginning of the 6th millennia, crop production was rather developed in Arkhulo, Khramis Didi Gora, Shulaveri (southeast Georgia) and wheat was cultivated alongside with other crops such as barley (*Hordeum vulgare and H. distichum*), oat (*Avena sativa*), rye (*Secale cereale*) and millet (*Panicum sativum*) in Khramis Didi Gora [28]. Legumes such as lentils (*Lens esculenta*), peas (*Pisum sativum*) and beans (*Vicia*) were also present in the South Caucasus [37].
b) During the Neolithic period (at archeological sites of Arkhulo, Khramis Didi Gora, and Shulaveri of the 'Shulaveri – Shomu' Culture (dated back to the 6th millennium BC) local farmers cultivated a large diversity of wheat, which included eight domesticated species: *Triticum monococcum, T. diccoccum, T. turgidum, T. carthlicum T. durum,T. spelta, T. aestivum, T. compactum,*
c) The South Caucasus was more diverse in terms of the wheat diversity than South Anatolia and Mesopotamia. 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) [34]. Archeological investigations of the Anatolian and Mesopotamian Neolithic sites provided evidence of existence of one, two or maximum three species of domesticated wheat [38, 39, 35]. As well as the cereals cultivated in the South Caucasus are much more diverse than in Anatolia and Mesopotamia [34].
d) Domesticated species largely prevailed over

wild species in the South Caucasus. *Triticum baeoticum* was the only wild species presented in Arukhlo.

e) The earliest appearance of naked tetraploid wheat species of *T. carthlicum* and *T. durum* is associated with the oldest layers of Arukhlo (i.e. late 7th and beginning of the 6th millennia) [25].

f) In contrast to the South Anatolian and Mesopotamian sites, naked free-threshing wheats dominated over hulled species in the early Neolithic period in Arukhlo. The Neolithic archaeological monuments of Arkhulo, Khramis Didi Gora, Shulaveri (south east Georgia) and Chikhori (west Georgia) are characterized by dominance of free-threshing (naked) *T. aestivo-compactum* type wheat. Based on the analysis of archeological and paleo-botanical data, it was estimated that the share of the *T. aestivo-compactum* type plants naked wheat was about 50-75 % of the total population of wheat. The 2nd most abundant wheat species in the Lower Kartli Neolithic sites was found to be emmer wheat (*T. dicoccum*). Its share was between 25% and 31%. Production of emmer declined over time and became less common in Bronze (ca. 3000 BC) and Iron [25, 40, 41].

Based on the above-mentioned facts, we can argue that agriculture was well-developed and high diversity of wheat (both hulled and naked) was cultivated in Georgia in late 7th and beginning of the 6th millennia BC (8000 BP). So, we can suggest that wheat domestication could have started at least at the beginning of the 7th millennium BC (9000 BP) in Georgia.

The possible role of the endemics of Georgia in the origin of cultivated hexaploid wheat

There are two polyploid lineages in *Triticum* genus: a) *T. timopheevii - T. zhukovskyi* lineage with AAGGAA-genome and b) *T. turgidum – Tr. aestivum* lineage with AABBDD-genome.

The AAGGAA-genome lineage has limited distribution and both tetraploid (*T. timopheevii*) and hexaploid (*T. zhukovskyi*) members of the linage are endemic to West Georgia, the South Caucasus [42]. Together with diploid *T. monococcum* (AA) they grow in admixtures forming local landrace "Zanduri".

The *T. turgidum – Tr. aestivum* lineage has much wider distribution covering the whole West Asia. However, three species (*sensu stricto*) out of this linage were apparently domesticated in Georgia and are considered as local endemics: *T. paleocolchicum, T. carthlicum*, and *T. macha.* In this paper, we would like to draw the reader's attention to the latter two species, which are distinguished with exceptionally high intraspecific variability. They are presented by 12 and 14 varieties, respectively [12].

T. macha a hulled hexaploid (AABBDD) wheat species endemic to Georgia was described by Dekaprelevich and Menabde in 1932 from prov. Lechkhumi (west Georgia) with 14 [12][1] varieties. This species always grows in admixture with another endemic hulled but tetraploid AABB genome species *T. palaeocolchicum.*

T. carthlicum, a free-threshing tetraploid Karthlian[2] wheat (erroneously named as Persianwheat)[3] is considered as a subspecies of *T. turgidum* by modern *sensu lato* classifications: *Triticum turgidum* subsp. *carthlicum* (Neyski) Á. Löve & D. Löve (syn. *T. persicum* Vav.). This wheat has been cultivated for at least 8000 years in Georgia according to the data of the Neolithic archeological excavations [25]. Out of the eleven varieties identified within *T. carthlicum*, all eleven were found only in Georgia and only one out of the eleven extended its areal to adjacent Armenia [43]. According to Matsuoka [42] *T. carthlicum* is strikingly similar to *T. aestivum* in morphology.

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 [44]. Moreover, Kihara *et al*. [45] showed that the morphology of synthetic hexaploid wheat derived from crosses between subsp. *carthlicum* and *Aegilops tauschii* Coss., resembles that of common wheat and considered subsp. *carthlicum* as a candidate for the AB-genome donor of common wheat [44].

Wheat breeders noted that it was easy to transfer genes from Karthlian wheat to hexaploid bread wheat and it was suggested to be a very desirable donor because of many beneficial traits, such as good resistance to powdery mildew dust brand and stem rust, higher number of tillers and fertility, good

1. 14 varieties are described in the works of L. Dekaprelevich and Menabde, but only 12 are conserved in seed genebanks at present.
2. Karthli – a province in East Georgia.
3. Endemic to Georgia, never grown in Persia, erroneously named as Persian wheat by N. Vavilov.

fecundity, tolerance to low temperature and preharvest sprouting [46-55].

Despite the striking similarity of Karthlian and bread wheat, it was widely believed that allohexaploid common wheat (AABBDD genome) was derived from a natural hybrid cross between a cultivated form of hulled tetraploid *T. turgidum* (female parent) and the wild species *Ae. tauschii* (male parent) and that common wheat originated in the Middle East/South Caucasus ca. 8000 years ago. The nascent wheat of this hybridization was spelt, which had hulled and narrow grain, similar to emmer, from which free-threshing wheat evolved by mutations [56-59].

Accordingly, it was assumed that free-threshing tetraploid wheats were derived through hybridization between free-threshing hexaploid wheat and hulled tetraploid wheat. E.g. free-threshing Karthlian wheat was considered as a secondary species derived from an interspecific cross between hulled emmer and free-threshing common wheat [2, 42]. Kuckuck [60] found hexaploid wheat accessions showing the subsp. *carthlicum*-like morphology, and these accessions, called *T. aestivum* subsp. *carthlicoides* nom. nud., were distributed in the border region of Iran, Turkey and the South Caucasus. He proposed that subspecies c*arthlicum* originated from spontaneous hybridization between subsp. *carthlicoides* and cultivated emmer wheat *T. turgidum* subsp. *dicoccon* (Schrank) Thell [60].

However, this hypothesis contradicted with more recent archeological findings. Free-threshing hexaploid wheat seems to precede spelt in some archaeological records [13]. The oldest remnants of non-hulled grains identified as hexaploid wheat come from Anatolia and are dated to the middle of the 7th millennium BC [56, 61], whereas the oldest remnants of spelt came from the South Caucasus and Kurdistan and are dated to the fifth millennium [62, 63].

Dvorak *et al*. [64] proposed that a fee-threshing tetraploid wheat, not a hulled tetraploid was the A and B donor for the hexaploid wheat. The authors assumed that if the hypothesis of evolvement of free-threshing wheat from spelt through mutations was right and if free-threshing tetraploid wheats originated later through hybridization of free-threshing hexapliod and hulled tetraploid wheats, the resulting nascent free-threshing tetraploid should have D-genome germplasm fragments in its genome. The authors searched for D-genome germplasm in fourteen *T. turgidum* subsp. *carthlicum* accessions with 29 RFLP loci evenly distributed across the D genome failed to reveal any D-genome germplasm in the genome of *T. turgidum* subsp. *carthlicum* [64].

Assuming a free-threshing tetraploid wheat as the donor of A and B genome was more logical because the roundish shape of seeds, which is characteristic of free-threshing hexaploid wheat, is controlled to a large extent by genes in the A and B genomes. It was shown by the shape of seeds in tetraploid *T. turgidum* subsp. *carthlicum*, that it is virtually indistinguishable from those of bread wheat [64].

According to Dvorak *et al.* [64] the descent of hexaploid wheat from free-threshing tetraploid wheat was also more consistent with the origin and distribution of the Q gene. The Q allele is essential for the square-head spike morphology of hexaploid wheat and its free-threshing. If Q originated only once, it could have originated either at the tetraploid or at the hexaploid level [65]. If it originated at the hexaploid level (spelt being ancestral), free-threshing hexaploid wheat would have to precede free-threshing tetraploid wheat and Q would have to migrate from hexaploid wheat to tetraploid wheat to become fixed in all free-threshing tetraploid lineages. If mutation of q into Q took place at the tetraploid level, the nascent hexaploid would have Q, which would be immediately fixed in the hexaploid population. It was suggested before that most free-threshing wheat in archaeological sites in western Asia was tetraploid [29].

Originally, *Triticum spelta* was known only from Europe. It was described by Linne (1753) from Germany. Because *Ae. tauschii* does not grow anywhere in Europe, initially, spelt was not considered as an ancestral form of hexaploid wheat [66, 67]. Later, *T. spelta* was discovered in Iran [11, 68, 69] and other places in Asia [67]. Spelt was discovered also in the South Caucasus [10, 70]. However, Blatter *et al.* [71] showed that European and Asian spelt had different origins and that European spelt did not derive from the hulled progenitors of bread wheat.

Tzevelev (72:167) considered that the South Caucasian and Middle Asian *Triticum spelta* specimens, which had been determined as subsp. *kuckuchianum* Gökgöl described from Iran be similar to *T. macha* or *T. aestivum*. [10] suggested that “the presence of great variety of *T. spelta* forms found in the South Caucasus makes it possible to consider the Transcaucasia as the home land of the first hexaploid wheat prototype, which can be west Georgian endemic wheat makha (*T. macha*)“ [10]. Earlier the same author noted that from the South Caucasus the first hexaploid wheat of the *T. spelta* type penetrated to Iran and other regions of Inner Asia, as well as to Europe [70].

Distribution of D-genome donor Aegilops taushii in the South Caucasus

It is widely believed that *Aegilops tauschii* originated in the South Caucasus [73, 74] and from there it dispersed eastwards to western China across northern Iran and Central Asia and southwestward to central Syria [75]. Origin of *Ae. tauschii* (and each of its two subspecies: subsp. *tauschii* and subsp. *strangulata*) took place in the Caucasus [74]. *Aegilops tauschii* with all linages (TauL1, TauL2, TauL3) including the D-genome donor *Aegilops tauschii* subsp. *strangulata*, with both linages (TauL2, TauL3) represented only in Georgia [59]. Chloroplast DNA of TauL1 and TauL2 diverged from the TauL3 lineage [76). TauL3 accessions are restricted only to Georgia [77].

Conclusion

The South Caucasus and, especially, Georgia is the only country where all suitable conditions (on a very small territory) have been created for the homeland of hexaploid wheat:

1) Ancient farming society and archeological findings provide evidence of cultivation of 8 species of domesticated hulled and free-threshing wheat, among them 4 species of hexaploid species (*T. aestivum, T. compactum, T. spelta, T. sphaerococcum*) in the Neolithic settlements (6th millennium BC) of southeast Georgia (Arukhlo, Shulaveri and Khramis Didi Gora in Kvemo [lower] Karthli Region).
2) The presence of both polyploid lineages of the genus *Triticum* only in Georgia: a) *T. timopheevii - T. zhukovskyi* lineage with AAGGAA-genome and b) *T. turgidum – Tr. aestivum* lineage with AABBDD-genome.
    a. The presence of "Zanduri"-landrace, admixture of three species of diploid AA (*T. monococcum*), endemic tetraploid AAGG (*T. timopheevii*), endemic hexaploid AAGGAA (*T. zhukovskyi*) only in Georgia.
    b. The presence of "Makha "landrace, admixture of hulled tetraploid AABB (*T. palaeocolchicum*), and hulled hexaploid AABBDD (*T. macha/ T. spelta*) only in Georgia.
    c. The presence of free-threshing polyploid 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.
3) The highest diversity of ancient hulled wheat. All seven species of the ancient domesticated hulled wheat recognized in the world are found in Georgia.
4) The highest endemism of hulled tetraploid (*T. palaeocolchicum, T. timophevii*) and hexaploid wheat (*T. zhukovskyi; T. macha-spelta*).
5) The highest diversity of tetraploid AABB wheats including free-threshing tetraploids (*T. durum* (25 varieties) and *T. turgidum* (25 varieties).
6) The highest diversity and endemism of free-threshing tetraploid AABB *Triticum turgidum* subsp. *carthlicum* to Georgia, with the common name in Georgian "dika".
7) Origin of *Ae. tauschii* in the South Caucasus (Dudnikov, 2012); distribution of all linages of *Aegilops tauschii* subsp. *strangulata* including the ancestral sub-linages in Georgia [59] and the presence of ancient, late flowering forms of both subspecies (subsp. *tauschi* and subsp. *strangulata*) only in the South Caucasus [74].

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