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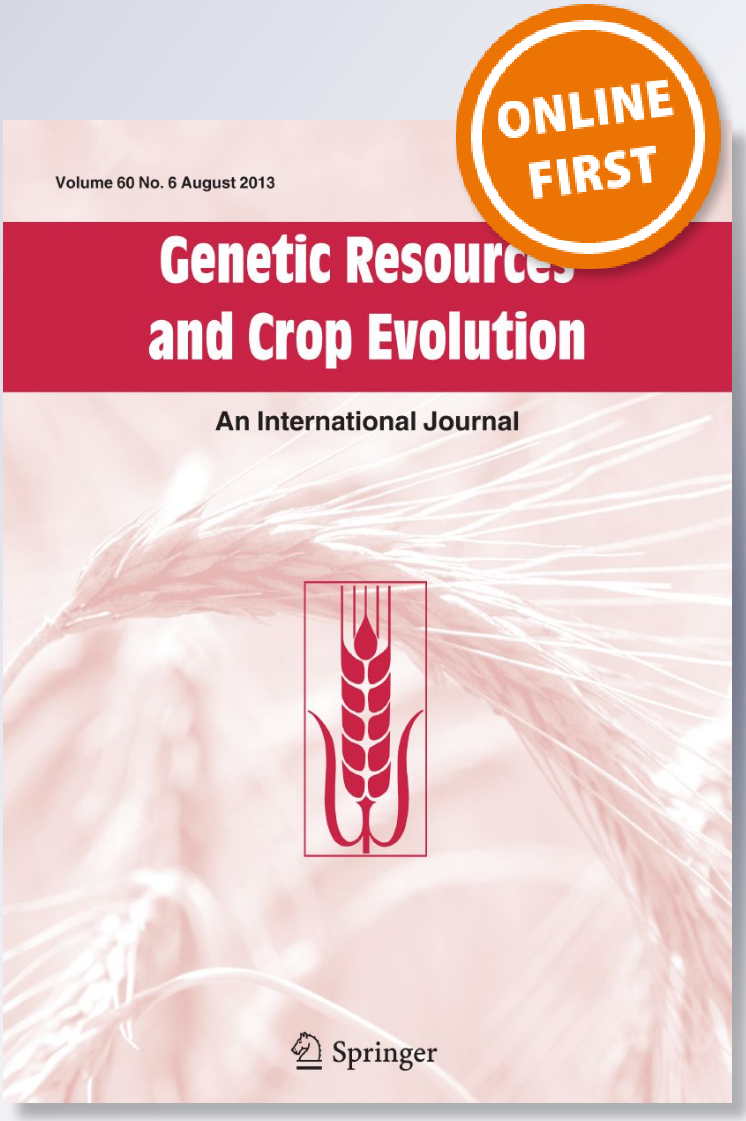

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RESEARCH ARTICLE

The 'Wheat Puzzle' and Kartvelians route to the Caucasus

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Abstract Wheat (*Triticum* L.) originated in the Fertile Crescent approximately 10 kya BP and has since spread worldwide. The 'Wheat Puzzle' was termed the observation that wild predecessors of five Georgian endemic wheat subspecies are found in Fertile crescent quite far from the South Caucasus. Kartvelian peoples are the ethno-linguistic group of speakers of Kartvelian languages (Georgian, Megrel, Laz, Svan). Kartvelian language is one of the seven language families of Eurasiatic superfamily, that may have arisen from a common ancestor over 15 kya BP (Pagel et al. in Proc Natl Acad Sci USA 110:8471–8476, 2013). One of the possibility to explain 'Wheat Puzzle' is that speakers of Protokartvelian language could be separated from Protoeurasiatic language speakers after migration from Africa to the Arabian peninsula and later moved to the northern part of Mesopotamia where wheat was domesticated. Kartvelian speakers could migrate further to South Caucasus together with domesticated wheat subspecies.

Keywords Wheat · Domestication · Kartvelians · Caucasus · Migration

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Introduction

South Caucasus (notably Georgia) and their earlier residents played an important role in wheat formation. 17 domesticated species and subspecies of *Triticum* are known (Table 1). Diploid-1; Tetraploid-9, from which Georgian endemic 3; Hexaploid-7, from which Georgian endemic 2. (https://en.wikipedia.org/wiki/Taxonomy_of_wheat).

Georgian endemic wheat species include one *Triticum* species and four subspecies (Menabde 1948; Menabde 1961; Hammer et al. 2011):

1. *Triticum turgidum* subsp. *palaeocolchicum* (Menabde) Á. Löve
2. *Triticum turgidum* subsp. *carthlicum* (Nevski) Á. Löve
3. *Triticum timopheevii* subsp. *zhukovskyi* (Menabde & Ericzjan) L. B. Cai
4. *Triticum zhukovskyi* Menabde & Ericzjan
5. *Triticum aestivum* subsp. *macha* (Dekapr. & Menabde) McKey

Some of these species bear an evolutionarily close affinity to wild wheat species or have retained some of their features (Menabde 1961). All these cultivated species and subspecies have been found in Western Georgia, except subsp. *carthlicum* which was predominantly distributed in Eastern Georgia. All these species and subspecies grew in the territory of Georgia until the middle of the last century.

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Table 1 Domesticated wheat species and subspecies

	Botanical name (http://www.theplantlist.org/tpl1.1/search?q=Triticum)	Genome
Diploid (2×)		
1	*Triticum monococcum* L.	A^m
Tetraploid (4×)		
2	*Triticum turgidum* subsp. *dicoccon* (Schrank) Thell.	BA^u
3	*Triticum ispahanicum* Heslot	BA^u
4	*Triticum turgidum* subsp. *palaeocolchicum* (Menabde) Á. Löve	BA^u
5	*Triticum turgidum* subsp. *durum* (Desf.) Husn.	BA^u
6	*Triticum turgidum* subsp. *turgidum*	BA^u
7	*Triticum turgidum* subsp. *polonicum* (L.) Thell.	BA^u
8	*Triticum turgidum* subsp. *turanicum* (Jakubz.) Á. Löve & D. Löve	BA^u
9	*Triticum turgidum* subsp. *carthlicum* (Nevski) Á. Löve	BA^u
10	*Triticum timopheevii* subsp. *zhukovskyi* (Menabde & Ericzjan) L. B. Cai	GA^m
Hexaploid (6×)		
11	*Triticum aestivum* subsp. *spelta* (L.) Thell.	BA^uD
12	*Triticum aestivum* subsp. *macha* (Dekapr. & Menabde) McKey	BA^uD
13	*Triticum aestivum* subsp. *vavilovii* (Jakubz.) Sears	BA^uD
14	*Triticum aestivum* subsp. *aestivum*	BA^uD
15	*Triticum aestivum* subsp. *compactum* (Host) Mackey	BA^uD
16	*Triticum sphaerococcum* Percival	BA^uD
17	*Triticum zhukovskyi* Menabde & Ericzjan	GA^mA^u

On the basis of genetic and morphological evidence, Georgian wheat (*T. turgidum* subsp. *palaeocolchicum)* is assumed to be a segregant from a hybrid cross between wild emmer wheat and *T. aestivum* subsp. *aestivum* (Dvorak and Luo 2001), whereas subsp. *carthlicum* may be a segregant from a hybrid cross between domesticated emmer wheat and *T. aestivum* (Kuckuck 1979).

The third subspecies of wheat detected in Western Georgia is hexaploid domesticated, hulled spelt wheat *T. aestivum* subsp. *macha* (Dekaprelevich and Menabde 1932). This subspecies is endemic to Georgia and is cultivated along with tetraploid West Georgian wheat *T. turgidum* subsp. *palaeocolchicum.*

Another line of *Triticum* species is the Timopheevi group, which contains the G genome. *T. timopheevii* wheat was discovered in Western Georgia, where it was termed Zanduri wheat. In the past, the Zanduri population was a set of diploid-*T. monococcum* var. *hornemannii* (2n = 14) (Gvatsa Zanduri), tetraploid *T. timopheevii* (2n = 28) (Chelta Zanduri) and hexaploid *T. zhukovskyi* (2n = 42). Hexaploid wheat *T. zhukovskyi* is the result of hybridization of *T. timopheevii* subsp. *zhukovskyi* with *T. monococcum* L. var. *hornemannii* (Menabde and Eritsian 1960).

Earlier we termed as the 'Zanduri Puzzle', the observation that the wild *T. timopheevii* subsp. *armeniacum* (Á. Löve) van Slageren was not found in Georgia, though cultivated *T. timopheevii* is detected only here (Gogniashvili et al. 2015). This statement is true also for both domesticated tetraploid wheats subsp. *paleocolchicum* and subsp. *carthlicum*. The wild emmer was not found in Georgia (and in South Caucasus), though cultivated tetraploid wheats were only detected there (Gogniashvili et al. 2018).

Mori et al. (2009) analyzed the molecular variation at 23 microsatellite loci in the chloroplast genome of Timopheevi wheats. None of the *T. araraticum* plastotypes collected in South Caucasus was closely related to the *T. timopheevii* plastotype. However, the plastotypes found in northern Syria and southern Turkey showed closer relationships with *T. timopheevii*. These results suggested that the domestication of *T. timopheevii* wheat might have occurred in regions including southern Turkey and northern Syria (Mori et al. 2009).

Wheat history

Wheat (*Triticum* L.) originated in the Fertile Crescent approximately 10 kya ago and has since spread worldwide. According to Tsunewaki et al. the wheat genus *Triticum* contains six species (Wang et al. 1997):

1. Diploid species: *Triticum monococcum* L. and *Triticum urartu* Thumanjan ex Gandilyan.
2. Tetraploid species: *T. turgidum* L. and *T. timopheevii*.
3. Hexaploid species: *T. aestivum* L. and *T. zhukovskyi*.

All *Triticum* species are native to the 'Fertile Crescent' of the Near East, which encompasses the eastern Mediterranean, southeastern Turkey, northern Iraq and western Iran, and its neighboring regions of the South Caucasus, and northern Iran (Matsuoka 2011).

There are four wild species, which grow in the Fertile Crescent of the Near East:

1. *Triticum monococcum* subsp. *aegilopoides* Asch. & Graebn.
2. *Triticum urartu* Thumanjan ex Gandilyan.
3. *Triticum turgidum* subsp. *dicoccoides* (Körn.) Thell.
4. *Triticum timopheevii* subsp. *armeniacum* (Á. Löve) van Slageren.

The diploid wheat *T. monococcum* L. (einkorn) is among the first crops domesticated by humans in the Fertile Crescent. The site of domestication of diploid wheat (einkorn) was identified (Heun et al. 1997). Wild populations from the Karacadag Mountain of southeastern Turkey were more similar to domesticated einkorn than other wild populations. The first step in the evolution of cultivated wheat was the formation of a tetraploid species *T. turgidum* subsp. *dicoccoides* (Körn.) Thell. (Schneider et al. 2008). The domesticated tetraploid wheat is very closely related to wild populations sampled in southeastern Turkey.

Wild emmer (*T. turgidum* L. subsp. *dicoccoides*) is found today in the western Fertile Crescent in Jordan, Syria, Israel, the central part of southeastern Turkey and mountain areas in eastern Iraq and western Iran. Ozkan and colleagues summarized issues concerning geography and domestication of wild emmer wheat based on published molecular and archaeobotanical data and on their own findings. The authors suggest that modern domestic tetraploid wheats derived from wild emmer lines from southeast Turkey (Ozkan et al. 2011; Allaby et al. 2017).

Northeast expansion of domesticated emmer cultivation resulted in sympatry with *Aegilops tauschii* Coss. (genome DD). Approximately 7 kya ago, the hexaploid bread wheat *T. aestivum* L. (BBA^{u}A^{u}DD) arose in the South Caucasus region by allopolyploidization of the cultivated Emmer wheat *Triticum dicoccum* Schrank with the Caucasian *Ae. tauschii* subsp. *strangulata* (Eig) Tzvelev (Dvorak et al. 1998; Dubcovsky and Dvorak 2007).

Kartvelian ethnolinguistic history

One of the central questions of wheat domestication is which people (s) participated in wheat domestication. Who lived in Fertile Crescent 10 kya ago in the area of wheat domestication?

The areas of wheat domestication:

T. monococcum-the Karacadag Mountain of southeastern Turkey (Heun et al. 1997).

T. turgidum-southeastern Turkey (Ozkan et al. 2011).

T. timopheevii-northern Syria and southern Turkey (Mori et al. 2009).

One of the possibility to explain 'Wheat Puzzle' is that Kartvelians lived (with other peoples) in the area of Fertile Crescent (possibly participated in wheat domestication) and brought some wheat species and subspecies further north to South Caucasus.

Using the expression of David Reich (Reich 2018)-Who are Kartvelians and how they got to the Caucasus?

A geographical study of mtDNA and Y chromosome revolutionized knowledge of the peopling of the world (Cann et al. 1987; Rosser et al. 2000; Underhill et al. 2000, 2001). Current consensus indicates that modern humans originated from an ancestral African population between ~ 100 and 200 kya (Reyes-Centeno et al. 2014). Anatomically modern humans left Africa about 70 kya ago and rapidly spread around the world (Oppenheimer 2012). Furthermore, on leaving Africa, modern humans may have immediately separated into two waves of dispersal. As proposed, one wave led ultimately to the founding of

Australasia and New Guinea and the other contributed to the ancestry of present-day mainland Eurasians (Nielsen et al. 2017). However, the exact routes of migration in the early diversification of people outside Africa remain a topic of research and controversy.

European populations are likely to be composed of three or more genetic components, some of which entered Europe at different times (Nielsen et al. 2017). The first anatomically modern humans lived in Europe as early as 43 kya ago. These early Paleolithic Europeans have probably made little genetic contribution to the European people of today (Nielsen et al. 2017).

Around 11 kya ago, after the Last Glacial Maximum had passed, a new way of life based on animal husbandry, agriculture, sedentarism and known as a Neolithic lifestyle started to emerge in several sub regions of the Fertile Crescent (Asouti and Fuller 2013; Nielsen et al. 2017). Analyses of ancient DNA showed that this population of farmers expanded from Central Anatolia into Europe; another wave of migration into Europe, which introduced the third European genetic component, occurred during the late Neolithic period and the early Bronze Age. Herders from the Pontic–Caspian steppe who belonged to the Yamnaya culture were involved in a migration to central Europe about 4,5 kyr ago (Nielsen et al. 2017).

Ancient DNA data provided evidence as regards the origins of the Yamnaya themselves. From seven thousand until five thousand years ago a steady influx is observed into the steppe of a population whose ancestors traced their origin to the south-as it bore a genetic affinity to ancient and present-day people of Armenia and Iran. A good guess is that the migration proceeded via the Caucasus isthmus between the Black and Caspian seas. Ancient DNA data have shown that the populations of the northern Caucasus had ancestry of this type (Reich 2018).

Kartvelian peoples are the ethno-linguistic group of speakers of Kartvelian languages. The question of the origin of language was one of the eighteenth century's major philosophical problems. And it is still one of the most controversial scientific topics thanks to the confluence of linguistics, psychology, biology, and paleoanthropology (Trabant 2001). Historically the Kartvelian peoples include Georgians, Zans (Megrels and Lazs) and Svans. According to Pagel et al., Kartvelian language is one of the seven language families of the Eurasiatic superfamily. Pagel et al. used a statistical model, which takes into account the frequency with which words are used in common everyday speech, to predict the existence of a set of highly conserved words among seven language families of Eurasia postulated to form a linguistic superfamily that evolved from a common ancestor around 15 kya ago (Pagel et al. 2013) (Fig. 1). The authors derived a dated phylogenetic tree of this proposed superfamily with a time-depth of ~ 14,45 kya BP, implying that some frequently used words have been retained in related forms since the end of the last ice age. These seven language families-Dravidian, Kartvelian, Uralic, Indo-European, Altaic, Chukchi-Kamchatkan and Inuit-Yupik are hypothesized to form an ancient Eurasiatic superfamily that may have arisen from a common ancestor over 15 kya BP, and whose languages are now spoken over all of Eurasia.

One possibility is that speakers of Protoeurasiatic language lived 15 kya ago in the southern part of the Arabian peninsula. Shortly thereafter Protodravidians migrated to India via the coastal route. Protokartvelian language speakers may also have originated in this area and then moved to the northern part of Mesopotamia (Fig. 2a). Presumably, they lived in this area for a long period of time, because according to our

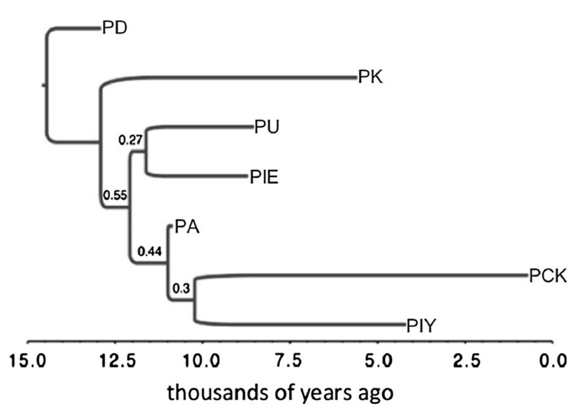

Fig. 1 Consensus phylogenetic tree of Eurasiatic superfamily rooted tree with estimated dates of origin of families and of superfamily (Pagel et al. 2013). *P* proto followed by initials of language family: *PD* proto-Dravidian, *PK* proto-Kartvelian, *PU* proto-Uralic, *PIE* proto–Indo-European, *PA* proto-Altaic, *PCK* proto–Chukchi-Kamchatkan, *PIY* proto–Inuit-Yupik. Consensus tree rooted using proto-Dravidian as the outgroup. The age at the root is 14.45 ± 1.75 kya (95% CI = 11.72–18.38 kya) or a slightly older 15.61 ± 2.29 kya (95% CI = 11.72–20.40 kya) if the tree is rooted with Proto-Kartvelian (PNAS granted permission for use of this figure)

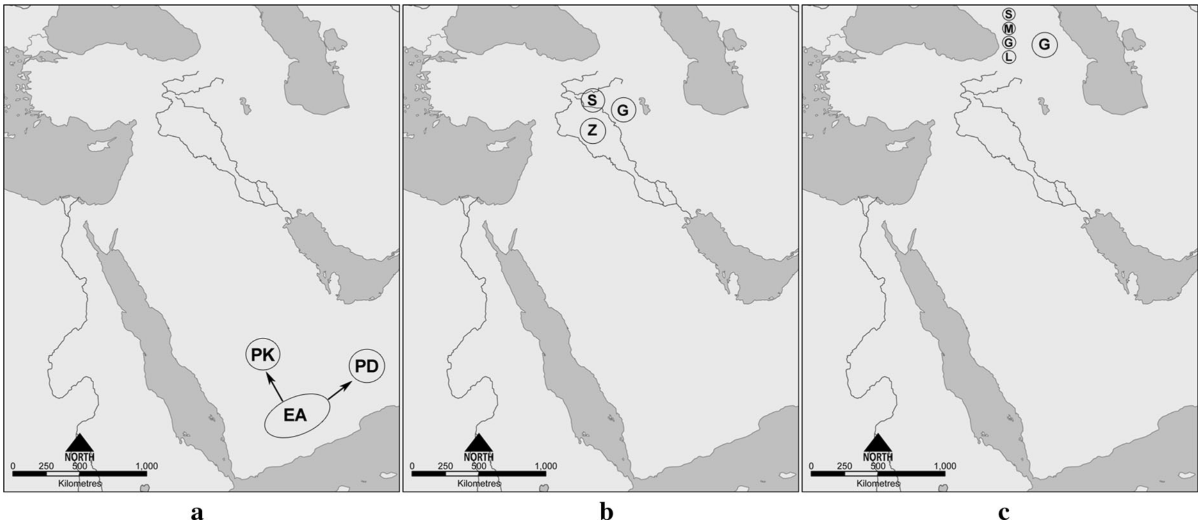

Fig. 2 **a** Separation of Protodravidian and Protokartvelian speakers from Eurasiatic Language Superfamily (∼ 12–15 kya BP); **b** Kartvelians location during wheat domestication period (∼ 12–10 kya BP); **c** Modern location of Kartvelians. *G* Georgians, *M* Megrels; *L* Lazs; *Z* Zans (Megrels + Lazs), *PK* Protokartvelians, *PD* Protodravidians

hypothesis Protokartvelian speakers took part in wheat domestication. The fixation of domestication traits needs thousands of years (Gaut et al. 2018). The time of the movement of the Protokartvelians from Mesopotamia to the Caucuses is not known, though according to Gamkrelidze and Ivanov (2010) Proto-Kartvelian prior to its breakup must be placed, on the evidence of archaic lexical and toponymic data, in the mountainous regions of the western and central part of the Little Caucasus (the Transcaucasian foothills) (Fig. 2b).

It is proposed that the split of the Proto-Kartvelian language into Svan and Proto-Karto-Zan the absolute time of separate development can be fixed for these languages at approximately 2600 and 4200 years BP, respectively (Klimov 1998). According to Gamkrelidze and Ivanov the first wave of Kartvelian migrations to the west and northwest, in the direction of the Colchidian plains, must have begun with one of the western dialects in the fifth millennium BP and led to the formation of Svan, which spread to the western Transcaucasus. Cattle-breeding vocabulary is common to Svan and other Kartvelian languages while agricultural terms are rarely shared. The further movement from Fertile Crescent of Kartvelian speakers from south to north can be represented as follows: Svans, Megrels, Lazs-north and Georgians (Kartvels)-north-east (Fig. 2c).

Proto-Kartvelians and bread wheat

The archaeobotanical data of wheat remains in the Caucasus is very scarce. Zohary et al. summarized the information on wheat archaeobotanical remains retrieved from Neolithic and Bronze Age sites in Caucasus (Zohary et al. 2012):

1. Chokh, Dagestan. Neolithic (end of eighth millennium BP to the seventh millennium BP).: einkorn wheat; emmer wheat; free-threshing wheat.
2. Arukhlo 1 and Arukhlo 2, Bolnisi district, Georgia. Neolithic (8000–7150 BP) mostly imprints: einkorn wheat; emmer wheat; free-threshing wheat; spelt wheat.
3. Imiris-Gora, Marneuli district, Georgia. Eneolithic (7400–7000 BP). Imprints: emmer wheat; free-threshing wheat; spelt wheat (?).
4. Aratashen and Aknashen, Ararat Valley, Armenia. Neolithic (7950–7150 BP). Numerous charred remains and imprints: einkorn wheat (rare); emmer wheat (few); free-threshing wheat (frequent).

Klimov (1998) and Starostin and Bronnikov (1998) cite three wheat names in the Kartvelian languages:

1. dika (subsp. *carthlicum*): Proto-Kartvelian dik; Georg, *dika*- 'spring wheat'; Laz *(m)dika*-'wheat, corn'. In Megrelian it seems to be lost.
2. ipkli (*T. astivum* L.): Proto-Kartvelian ipkL; Georg, *ipkl*— 'wheat'; Megr. *irk;* Svan *itk*; the word is well attested in Old Georgian, where it had also a meaning 'bread, grain'. It does not exist in Laz.
3. maxa (subsp. *macha*): Georg, *maxa*- 'sort of wheat'; Laz *moxa*-. Svan *maxar.* There are no traces of it in Megrelian.

Conclusion

Finding ancient and still alive *T. aestivum* varieties is a very important task. According to some authors genetic evidence suggests that Caspian Iran was the geographic place of bread wheat origin (Wang et al. 2013; Jorgensen et al. 2017). But was Caspian Iran single geographic place of bread wheat formation? It was previously noted that Georgian wheat (*T. turgidum* subsp. *palaeocolchicum)* is assumed to be a segregant from a hybrid cross between wild emmer wheat and *T. aestivum* subsp. *aestivum*, whereas subsp. *carthlicum* may be a segregant from a hybrid cross between domesticated emmer wheat and *T. aestivum*. All this may mean that in Western Georgia, before the formation of these subspecies can be supposed growing of *T. aestivum* subsp. *aestivum.*

The consolidated list of the Georgian wheat taxa includes 48 varieties of bread wheat (Mosulishvili et al. 2017). According to Matsuoka one accession ancient and still alive *T. aestivum* varieties may be subsp. *carthlicoides* (Matsuoka, personal communication). Hexaploid wheat *T. aestivum* subsp. *carthlicoides* was found by Kuckuck (1979) near the border of Turkey and Western Georgia. This hexaploid wheat acces-sion showed the subsp. *carthlicum*-like morphology. Subsp. *carthlicum* was proposed to have originated from spontaneous hybridization between subsp. *carthlicoides* and cultivated emmer wheat, *T. turgidum* subsp. *dicoccon* (Schrank) Thell. (Kuckuck 1979; Takumi and Morimoto 2015). Kuckuck proposed the hypothesis that the 6 $\times$ subsp. *carthlicoides* should be considered as the original and elder genotype from which genes for the particular morphology of the ear were transferred together with the *Q*-factor to *T. carthlicum* (Kuckuck 1979).

It was mentioned above that approximately 7 kya ago, the hexaploid bread wheat *T. aestivum* L. arose in the South Caucasus region by allopolyploidization of the cultivated Emmer wheat with the Caucasian *Ae. tauschii* subsp. *strangulata*. This means that the ancestors of Kartvelians for this period have already lived in South Caucasus. They have brought tetraploid wheats (together with other peoples possibly Proto-Indo-Europeans) from Mesopotamia and with their help created hexaploid bread wheat.

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