

Toward the theory of origin and distribution history of *Triticum spelta* L.

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An analytical review of scientific references on various theories of eco-geographical and genetic origin of spelt wheat (*Triticum spelta* L.) is given. The analysis found that now scientists have no consensus in this regard. However, the hypothesis of polyphyletic origin of this wheat species is the most probable. According to it, the Asian spelt first appeared on the Caspian coast of Iran and became the ancestor of soft wheat. The European spelt is the result of hybridization of soft and tetraploid wheat. This spelt division into Asian and European subspecies was confirmed by C-differential staining of chromosomes, as well as by the technology of artificial neural networks.

Keywords: wheat species, spelt wheat, theories of origin, eco-geographical distribution.

Introduction

Spelt wheat (*Triticum spelta* L.) is one of the oldest species of *Triticum* genus which crops have dominated in the fields for a long time. Using aged spelt all modern high-yielding wheat varieties with high yield potential were selected tolerant to pathogens of diseases and extreme weather conditions. However, since the nineteenth century, after the selection of a number of varieties of huskless winter wheat, there was a sharp reduction in spelt sowing. In the middle of the twentieth century it remained only on small areas in the mountainous regions of Europe and Asia.

Today, the interest in spelt growing returns both in Ukraine and around the world. So far, in Ukraine this type of wheat has not been grown commercially. Unfortunately, there are not many scientific publications on spelt and they are one-sided. Spelt wheat is a little studied species. It is known that this is a high-protein crop undemanding to growing conditions, able to withstand even mountain soils depleted on nutrients. Also, a significant advantage of this wheat type is that it does not shatter standing after sufficient mineral nutrition and therefore does not require the use of retardants and has a high resistance against excessive moisture during the tillering period in the presence of a significant amount of precipitation. Therefore, there is a clear interest of researchers and producers of agricultural products to this crop. Thus, due to the noticed features, it is grown in organic farming in most countries of Western Europe and the United States. In particular, in Germany, Belgium, Switzerland, France and Spain, now it is grown on an area of more than 100 thousand hectares.

In the international bread production the problem of hard wheat due to its lack in the world markets is well known. This is also true for Ukraine. The problem of quality wheat, as well as the issues of factors under which it is formed, is also of interest to plant selection breeders who create new varieties, agronomists who grow it and bread inspectors who determine wheat quality. Also, this problem concerns millers who process grain into flour, bakers who bake bread from this flour and chemists studying the chemical composition and properties of wheat grain components. Therefore, determining peculiarities of the origin of such valuable wheat species in the production has the important practical and theoretical value.

Material and methods

During studies general scientific methods were used, in particular, such as: hypothesis, observation, analysis, synthesis, induction and deduction, abstraction and generalization. The material was own observations and references on the chosen direction of studies.

Results and discussion

It is believed that hexaploid wheat has a common origin from the ancient wheat (*T. spelta* L., *T. macha* Dek. et Men.) as a result of the accumulation of spontaneous mutations (Kuckuck, 1964). A number of scientists distinguished hulled wheat *T. spelta* as the oldest hexaploid which formed all other species including soft wheat (Morris, Sirs, 1970; Zohary, 1999; Luo et al., 2007). However, according to others (Sinskaya, 1968), probably parent hexaploid species is only *T. macha* Dekapr. et Menabde. It is known that when crossing some species of macha and Iranian spelt you can get a species similar to soft wheat by ease threshing and flexibility of wheat ear. A number of scientists confirm proximity of *T. macha* and European spelt (Kuckuck, 1964; Zhukovskiy, 1971). Thus, V. L. Menabde (1948) believed that *T. macha* is an offshoot of *T. spelta* (*asturicum* and *bavaricum*). Similar components, as well as separate blocks of components in samples of *T. macha* *T. spelta* are defined by means of gliadin electrophoresis (Yakobashvili, 1989).

The results of archaeological studies indicate the existence of spelt about V century BC in Iraq which corresponds to the Neolithic time (Kislev, 1984). At the same time, soft wheat grain was found in archaeological excavations in the Middle East about VII century BC. Wild forms of spelt grow on a high plateau of East Central Iran (Kuckuck, 1964); also it was grown in Azerbaijan, Armenia and Nagorno Karabakh and Nakhichevan (Dorofeev, 1969). Other archaeological evidence indicates the spelt emergence in Central Europe in the early Bronze Age (Nesbitt, 2001), while naked grain soft wheat was found in Europe at the beginning of the Neolithic time. So, naked grain soft wheat appeared in Europe before spelt wheat. According to archaeological, historical and linguistic data, spelt distribution was limited to the territory of Central Europe (Nesbitt, Samuel, 1996).

According to K. A. Flaksberher (1935), in contrast, one of proofs of non Asian origin of spelt is the lack of a special word for this wheat species in the ancient peoples of Asia. According to the results of research generalization, he pointed out that the word which means emmer wheat that is *T. spelta* L. is absent in ancient languages of Asia. Also, there is no corresponding word in Sanskrit as there is no such word in modern Indian dialects. In general, in languages of the Asian nations, Chinese, Iranian, Arab, Afghan dialects, etc., there is no word that would mean spelt. In Hebrew words "kusemeth" and "kusemin" meant Emmer (*T. dicoccum* Schrank.), not spelt (*T. spelta* L.). In his opinion, such linguistic data indicated that the ancient Asian nations, most of all, did not know spelt. However, if there are some or occasional mentions, they belong to recently or accidentally imported spelt for experiments or based on erroneous definitions. Obviously, the same error in spelt defining happened with Olivier and Andre Michaux who pointed to *T. spelta* cultivation in Iran. F. Alefeld even identified his last discovery as a special var. *Michauxi*. Obviously, Olivier wheat ears and A. Michaux discovery were actually *T. vulgare* of *speltiforme*, not *T. spelta* L.

Also, there is no Russian word that means *T. spelta*. In Russian references, this type of wheat is commonly called as *T. dicoccum* – "emmer wheat".

In African dialects there is no word "spelt" too. In archaeological excavations of Egypt, spelt was not found while there are many guidelines and findings of *T. dicoccum* wheat ears. Even in bricks of Dashur pyramids such Abyssinian plants as *Eragrostis abyssinica* Link. were found currently not cultivated in Egypt. Thus, according to K. A. Flaksberher (1935), if *T. spelta* had been in ancient Egypt, it would have been found.

In Australia and America, in general, all varieties of wheat were imported for the last historical period; therefore, they are not of significant interest.

Thus, K. A. Flaksberher (1935) concludes that *T. spelta* has the European origin.

There were no ancient Greek words that meant spelt, according to recent studies, at least words "όλυ α", "ξέα" i "ξεία" do not refer to *T. spelta* L., they refer to *T. dicoccum* Schrank. (Schulz, 1913). Now, in Modern Greek language there is no word that means *T. spelta*, judging from it in Greece it is not grown. In Bulgaria, spelt (Kuckuck, 1964) is also not grown. In general, obviously, in the Balkan Peninsula, *T. spelta* has not previously grown and is not cultivated today.

Obviously, the ancient Romans also did not know spelt. The ancient Latin word for this plant is unknown, and the words of the ancient Latin authors Horace, Columella, Pliny and others "ador", "adoreum", "far", "arinca" and others mean *T. dicoccum* Schrank. or relate to other wheat species. For the first time the word, "spelt" appears in Quintus Rhemnius Fannius Palaemon, the Roman grammarian who lived in the first century AD (Zhukovskiy, 1971). Some authors (Körnicker, Werner, 1885; Caballero, Martin, Alvarez, 2008) refer the first mention about spelt to 301 AD, namely the edict of Diocletian in which these plants are mentioned: "Speltae mundaе scandulae sive speltae".

Today, *T. spelta* is not grown in the Apennines. No archaeological finds relating to the Stone and Bronze ages that would indicate growing *T. spelta* in the Apennines up to the Alps were found. So, spelt does not belong to the indigenous vegetation of the Apennine Peninsula.

It is believed (Kuckuck, 1964) that this crop was brought to Spain (province of Asturias) by Romans, as evidenced by archaic methods of its cultivation. It is claimed that the first direct mention about this crop is in Albelden chronicle (883) in which among food products in Spain rye from Asturias was mentioned. The origin of the Spanish word for spelt – "scandula" is not completely cleared but apparently, it is of Latin origin. It should be noted that in the edict of Diocletian this word is used in the sense of *T. spelta*. It is necessary to say that there is no Basque word for *T. spelta*. In general, there they did not have this variety of wheat, while the oldest word was *T. dicoccum*. On the whole, peoples of Transcaucasia, including the Basques, do not grow spelt. In these data on Italy and Spain there is a mismatch because in Spain *T. spelta* was brought by the Romans who did not cultivate and know it till BC.

As for France, among the oldest archaeological finds *T. spelta* was not found. The references contain only a series of guidelines for its cultivation but during last centuries. Obviously, spelt was not widespread and cultivated. In a letter to K. A. Flaksberher (1935), L. Bretigniere says that *T. spelta* in France is not common and he does not see it. In Dodonaeus'a (1618), there are the old French names for *T. spelta* – "espeaultre" and "espeautre" which undoubtedly are intermediate between the Latin "spelta"

and the modern French "épeautre".

De Candolle simply indicates the origin of the modern French word "épeautre" from the word "spelta". Thus, there are no data to consider *T. spelta* as a plant of the French or Spanish origin, according to K. A. Flaksberher (1935).

In the first half of the twentieth century (Hospodarenko et al., 2016) spelt crop covered approximately the area of Palatinate and Alsace provinces to the west of the Rhine in the Vosges. To the east of the Rhine they are the whole province Baden, all Württemberg, Hohenzollern and to the north of Thuringia. In Bavaria, they are the western part of Donau Kyeis to the river Lech and in the upper reaches the east of the river Lech. In Austria, it is the most western part of Tyrol, namely Vorarlberg. In Switzerland, it is mainly in the cantons of Zurich and Berne that is a part of Switzerland to the north of the Berner Alpen range and Todi-Kette. Only unbearded varieties were grown everywhere. Interestingly, in 1818 Schübler indicated that only unbearded varieties were grown in Württemberg. As other authors and preserved specimens in herbaria show that sometimes bearded varieties were grown so Schübler's indication shows that the displacement of bearded varieties by unbearded varieties began in the early seventeenth century. This shows that the area of *T. spelta* cultivation in Central Europe covered mountain regions of northwestern Alps, with the Vosges, Schwarzwald entering the Swabia Jura and Tyurinhervald. This area is continuous, and beyond, there are only a few small localities, for example, Eyfels (Belgium), in southern Bavaria and some other places. Historical and ethnographic composition of the population in the indicated area is an old German Alamanni living area. Fischer called spelt as "Allemanischer Brotfrucht". In this area *T. spelta* had from 0.1 to 40% or more crop area. According to Engelbrecht data, it had more than 40% of the average of southern half of Württemberg. The people of Alsace have known spelt for 800 years. It is interesting to note that in Württemberg the national soup is prepared with so-called "grime Kerner" or "Grunkern" that means unripe green grains of *T. spelta*, as observed in the ancient literature. In this region *T. spelta* is called in the old German (Althochdeutsch): Spelza, Spelze, Spelzo, Spelzu, Spelta, Spedta, Spigil, Spalteehorn Dinchil, Dincil, Thincil; in the middle German (Mittelhochdeutsch): Speelz, Spelte, Spelcz, Spaltehorn, Dinchil, Dinchel, Dinkel, Tinkl, Tinckel, Vese, Vesen, Vess, Wessn, Körn. Now, in Germany, *T. spelta* is called Spelz and Dinkel and husked grain is called Vesen. Local old German words for spelt also show an old age of this type of wheat. According to K. A. Flaksberher (1935), lack of local ancient unborrowed names in other languages indicates that the ancient Germans first began to grow spelt. However, the ancient Romans knew *T. spelta* and the word "spelta" appears only in the first century AD. Therefore, there is the most likely assumption. When in the middle of the first century BC the Romans conquered Germany, Spain and almost all Central and Western Europe, they learned the local German plant and latinized this word "spelta", brought bread into Spain, where it is preserved to this day. Later, during the return to the Roman Empire conquerors brought both the plant and the Latinized word "spelta".

These data indicate that spelt first became known for ancient Germans. The absence of any findings and mentions of its existence in the Stone Age, when in Switzerland and Germany club and soft wheat were grown (*T. vulgare* Host i *T. compactum* Host), as well as *T. dicoccum* i *T. monococcum*, indicates the occurrence of *T. spelta* in Bronze Age (later than Stone Age). At the same time, the lack of archaeological finds of *T. spelta* in Asia (club and soft wheat came from it) shows that it could not be taken from Asia into the Aleman country and it could not be taken from other European countries (Hospodarenko et al., 2016).

Thus, according to K. A. Flaksberher (1935), *T. spelta* is a plant of Northern Alpine recent origin. He agrees with De Candolle and believes that *T. spelta* derived from *T. vulgare* and not vice versa, in Bronze Age of the prehistoric era.

Subsequent studies in the middle of XX century, when the expedition of N. Kuckuck discovered spelt crops in Iran (Zohary, Hopf, 1988), demonstrated the falsity of conclusions of K. A. Flaksberher. Thus, isolated spelt crops or spelt impurities in soft wheat plantings were found in other parts of Central Asia and of Transcaucasia (Azerbaijan, Tajikistan, Turkmenistan) (Dorofeev, 1969; Zohary, Hopf, 1988). At the same time, the local population of the valley of the Isfara river (Tajikistan) that has been growing spelt for a long time, calls it "гапдүми обджүвози" that means wheat thrashed in water peeling mills, while there is a name "hapdumi hallohovi" for soft wheat that means wheat thrashed by running bulls (Dorofeev, 1987).

According to researchers, the origin of *T. spelta* from *T. vulgare* is confirmed by experiments of Vilmorin (Candolle, 1855), the lack of it in Asia during Stone Age when there was soft wheat and by special lodging of *T. spelta* wheat ears that are different than ears of wild species of wheat and barley. This kind of lodging ears does not allow analogy to *T. dicoccum*, *T. monococcum* and *Hordeum spontaneum*. Thus, the argument is disposed that older varieties are those that have brashy ears. It should be noted that *T. vulgare* has the speltoid ability as evidenced by the presence of many forms of soft wheat in Asia with speltoid chaff (*speltiforme* Vav.). In addition, in N. Nillson-Ehle in Sweden there were forms (mutants) with speltoid chaff that had been absent previously.

It is also necessary to point out that in primary areas of soft, club, durum and English wheat (Central Asia and Abyssinia) there is a great diversity of these species. At the same time, there are a few species of *T. spelta* (according to Körnicke, only 12 known varieties) of which only 4-5 are grown, the others are rare or only grown in botanical gardens. In this regard, it is possible to draw an analogy with *T. persicum* Vav., endemic variety to Transcaucasia, which has only nine varieties, as well as with *T. timopheevi* Zhuk. from Transcaucasia that has only two varieties (*var. typicum* Zhuk. and *var. viticulosum* Zhuk.) and with *T. sphaerococcum* Perciv. with only six known varieties. Comparison with *T. persicum* is of particular interest also in the sense that, as this species and *T. spelta* have black-eared bearded forms, while *T. persicum* does not have black-eared beardless forms and they are rare for *T. spelta*. However, red-eared and white-eared forms are beardless (bearded forms are rare for *T. spelta*). It is possible to say that unlike primary centers (for *T. vulgare* and *T. durum*) secondary centers have rather weak polymorphism. *T. macha* seems to contradict it as it has a great polymorphism by generic features but, obviously, it is a hybrid origin.

However, P. M. Zukowski does not agree with the opinion of J. Persival that *T. spelta* has a parallel origin with *T. vulgare*, *T. compactum* and *T. sphaerococcum* by crossing *T. dicoccoides* (including *T. dicoccum* and *T. durum*) × *Aegilops cylindrica* and *Aegilops ovata*. In his opinion (Zhukovskiy, 1971), *T. Spelta* formed from *T. vulgare* Host at a relatively late prehistoric period (probably later Stone Age) in the north-western Alps, Schwarzwald and the Swabian Jura, the country of ancient Alamanni and Swabians.

Further archaeological findings show (Andrews, 1964) that from Neolithic times club wheat (*T. sphaerococcum* Perciv. and *T. compactum* Host.), emmer (*T. dicocum* Schrank.), eincorn (*T. monococum* L.), easily threshed tetraploid wheat species were long-time varieties in Europe. From the late Neolithic period club wheat is the dominant crop in this area. Thus, European spelt appeared later club wheat. In Spain, *T. monococum* L. and *T. dicocum* Schrank. were presented in the Neolithic period but not as main crops, while spelt was only in Iron Age in northern Spain (Caballero, Martin, Alvarez, 2007). Now, spelt and emmer are not widespread in Astoria (northern Spain) (Pena-Chocarro, Zapata-Pena, 1998). Thus, lack of archaeological remains of spelt on the way from Asia to Europe suggests that the European spelt could have an independent origin from the Asian spelt.

M. I. Vavilov (1935) first suggested the Near Eastern origin of spelt. J. Percival (1921), E. Tschermak (1926) and other researchers recorded facts of spelt separation after interspecific hybridization that persuaded M. I. Vavilov (1926) on the secondary hybrid origin of European spelt.

According to N. Helbaek (1965), hexaploid wheat *T. aestivum* L. existed in the Near East during V-VII millennia BC. Here, in this period or even earlier there was the first hexaploid *T. spelta* L. Secondary spelt was found in Iran, initially by P.M. Zhukovsky and then H. Kuckuck. It was formed in the mountains from soft wheat – *rigidum* group due to mutation or hybridization of *T. aestivum* × *T. ispahanicum*.

Summarizing the analysis of the scientific research on the spelt origin it can be concluded that this issue has not been clarified yet. Now there is an increased interest of both domestic and foreign scientists to solve this issue. A number of scientists (Kuckuck, Schiemann, 1957; Zohary, Hopf, 1988) agree with the hypothesis of the Asian origin calling the Asian spelt as an ancestress of soft wheat.

Supporters of the hypothesis of the European origin of spelt believe that it could have another origin (McFadden, Sears, 1946; Luo et al., 2007) and was the product of hybridization of tetraploid wheat (*T. dicocum*, AABB) and *Ae. tauschii* (*syn. Ae. squarossa*, DD). There is a hypothesis (Bertsch, 1950) of the origin of the European spelt as a result of hybridization of *T. compactum* Host. (AABBDD) and *T. dicocum* Schrank. (AABB) in the early Bronze Age. Thus, among the grown offspring fully fertile types of spelt were obtained by crossing *T. compactum* Host × *T. dicocum* Schrank (MacKey, et al., 1966; Ohtsuka, 1998). V. F. Dorofeev (1969) analyzing interspecific hybrids of wheat also concluded about secondary polyphyletic origin of Asian and European spelt. The geographical localization of genes of restoring fertility, hybrid necrosis and chlorosis shows the polyphyletic origin of spelt. Thus, the Spanish spelt has gene *Ch2*, spelt of Central Europe has gene *Ne1* and spelt of Iran and Azerbaijan has genes *Ne1* and *Ch2*. The results of the comparative analysis of genes of hybrid necrosis and chlorosis found (Tsunewaki, 1971) that spelt of the European origin and other hard threshed wheat varieties, like *T. macha*, originate from different pentaploid hybrids between tetraploid variety *T. dicocum* and hexaploid variety *T. aestivum*.

Based on the analysis of genes of high molecular glutenin of European and Asian spelt, soft and hard wheat (Blatter, Jacomet, Schlumbaum, 2004), a different geographic distribution of β -alleles *Glu-B1-1* and *Glu-A1-2* was found. This confirms the independent origin of European and Asian spelt. The results were confirmed in several studies (Jaaska, 1978; Luo et al., 2007). Blatter with others (Blatter, Jacomet, Schlumbaum, 2004) analyzed all six subunits of high molecular glutenin of ancient spelt and soft wheat. Alleles *Glu-B1-1*, *Glu-A1-2* and *Glu-B1-2b* of ancient spelt and saved local Swiss spelt differed from alleles of glutenin coding loci of chromosomes of ancient and modern soft wheat. Moreover, speltoid allele *Glu-B1-1* is closely coupled with the so-called β -sub cluster which was mostly identified in tetraploid wheat species (Brown, 1999). At the same time, alleles of glutenin coding loci of D-genome of spelt and soft wheat are not different (Blatter, Jacomet, Schlumbaum, 2004). Thus, the obtained results confirm the hypothesis that the European spelt was formed by introgression of tetraploid wheat into hexaploid easily threshed soft wheat. Data on glutenin coding loci of ancient spelt indicate that β -alleles *Glu-B1-1* and *Glu-A1-2* existed at least 300 years ago. It was found spelt specific alleles of γ -gliadin of β -genome differ from alleles of tetraploid wheat (Von Buren, 2001) and β -allele *Glu-B1-V* of tetraploid wheat differs from β -allele *Glu-B1-VI* of European spelt by two mutations. It is possible to say that the European spelt received β -alleles of HMW-glutenin from the parental tetraploid wheat. Studying the composition of glutenin subunits (HMW-GS and LMW-GS) of the European spelt of related tetraploid and hexaploid species of the genus *Triticum* confirms the hypothesis of secondary origin of the European spelt (Yan, et al., 2003). Regarding the low molecular glutenin subunits, the LMW-glutenin variability of spelt is higher than of other types (Caballero, Martin, Alvarez, 2007). Variability of C-zone of LMW-glutenin of spelt is slightly higher in comparison with *T. tauschii* (Gianibelli, Wrigley, MacRitchie, 2002) and significantly higher in comparison with durum wheat (Nieto-Taladriz, et al., 1997). Variability of C-zone of LMW-glutenin of diploid species is higher compared with spelt (Lee, et al., 1999; Gianibelli, Wrigley, MacRitchie, 2002).

Unlike the European spelt, division of glutenin coding alleles between the Asian spelt and soft wheat can be if the Asian spelt originates from husked ancestors of soft wheat. It is known that the subunit composition of HMW and LMW glutenin of the Iranian spelt is more similarly to soft wheat. Some European spelt species have components of gliadin and alleles of necrosis genes that differ from the Iranian spelt (Campbell, 1997). Data were obtained on the similarity of the structure of karyotypes and distribution of heterochromatic areas of spelt and soft wheat (Salamini, 2002) indicating their genetic proximity. C-banding results show that *T. spelta* occupies an intermediate position between tetraploid and other types of hexaploid wheat.

Thus, the hypothesis of polyphyletic origin of spelt is the most probable (Fig.). It provides that the Asian spelt first appeared on the Caspian coast of Iran and became the ancestor of soft wheat. The European spelt is the product of hybridization of soft and tetraploid wheat (Von Buren, 2001; Salamini, 2002).

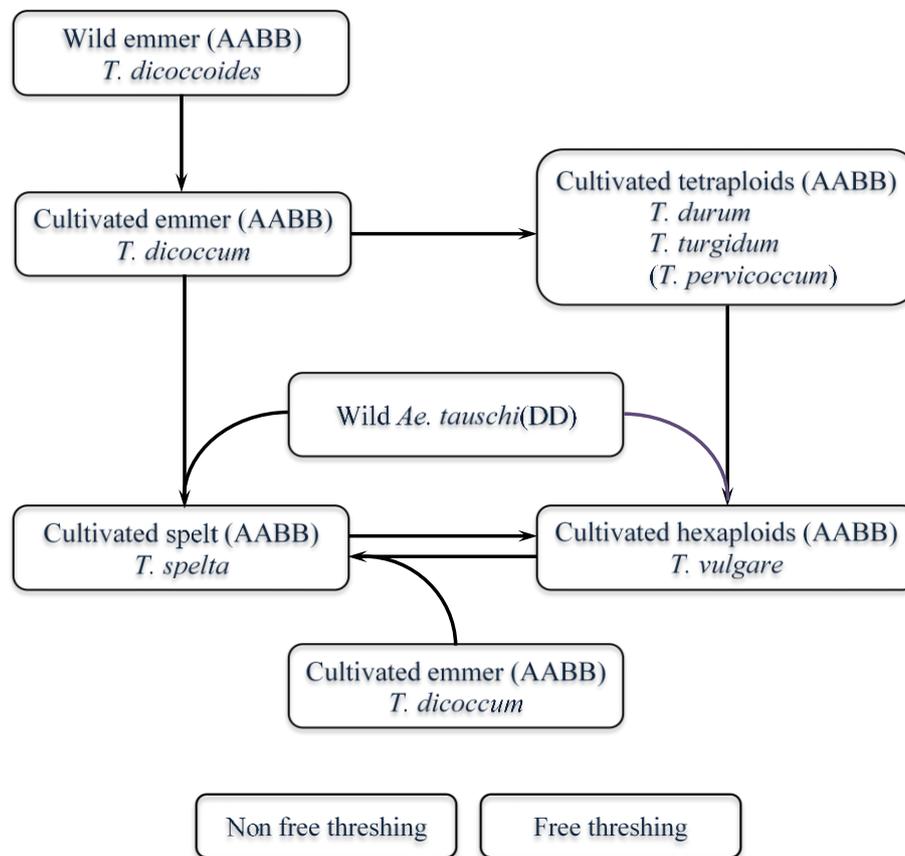


Figure 1. The model of the evolution of polyploid wheat species as a result of domestication:

Subsequently, the spelt division into Asian and European subspecies was confirmed by C-differential staining of chromosomes, as well as by the technology of artificial neural networks (Dedkova, 2008). Also, division of the European spelt into two groups (Spanish and European) including samples from Western, Central and Eastern Europe is confirmed.

Conclusions

The most probable is the polyphyletic hypothesis of the origin of spelt wheat. According to it, the Asian spelt first appeared on the Caspian coast of Iran and became the founder of soft wheat and the European spelt is a result of hybridization of soft and tetraploid wheat. Such spelt division into the Asian and European subspecies was confirmed by results of C differential staining of chromosomes, as well as by artificial neural network technology.

References

- Andrews, A. C. (1964). The genetic origin of spelt and related wheats. *Ziichter*, 34, 17–22.
- Bertsch, K. (1950). Vom Ursprung der hexaploiden Weizen. *Ziichter*, V. 20, pp. 24–27 (in German).
- Blatter, R. H. E. Jacomet, S., Schlumbaum, A. (2004). About the origin of European spelt (*Triticum spelta* L.): allelic differentiation of the HMW Glutenin Bl-1 and Al-2 subunit genes. *Theor. Appl. Genet.*, 108, 360–367.
- Brown, T. A. (1999). How ancient DNA may help in understanding the origin and spread of agriculture. *Proc. R. Soc. Lond. B. Biol. Sci.*, 354, 89–98.
- Caballero, L., Martin, L. M., Alvarez, J. B. (2007). Agrobiodiversity of hulled wheats in Asturias (North of Spain). *Gen. Resour. and Crop Evol.*, 54, 267–277.
- Caballero, L., Martin, LM, Alvarez, J.B. (2008) Genetic diversity in Spanish populations of *Triticum spelta* L. (escanda): example of an endangered genetic resource. *Genet Resour Crop Evol.*, 55, 675–682.
- Campbell, K.G. (1997). Spelt: agronomy, genetics, and breeding. *Plant Breeding Rev.*, 15, 187–213.
- Candolle, A. de. (1855). *Géographie botanique raisonnée ou exposition des faits principaux et des lois concernant la distribution géographique des plantes de l'époque actuelle*. Paris: V. Masson; Genève: J. Kessman (in French).
- Dedkova, O.S. (2008). Comparative phylogenetic investigation of polyploid wheat *Triticum dicoccum* (Schrank) Schuebl., *T. spelta* L., *T. aestivum* L. using cytogenetic markers. Moscow (in Russian).
- Dorofeev, V. F. et al. (1987). *Wheat world*. Leningrad (in Russian).
- Dorofeev, V.F. (1969). Problems of modern phylogeny and systematics of wheat. *Herald of agricultural science*, 3, 25–35 (in Russian).
- Flyaksberger, K. A. (1935). *Wheat is the genus Triticum L. "Cultural flora of the USSR"*. Cereals. Wheat. Moscow-Leningrad.
- Gianibelli, M.C., Wrigley, C.W., MacRitchie, F. (2002). Polymorphisms of low Mr glutenin subunits in *Triticum tauschii*. *J. Cereal. Sci.*, 35, 277–286.

- Helbaek, H. (1965). Archeological evidence for genetical changes in wheat and barley. *Plant Introd. Rev. Austr. CSIRO*, No2.
- Hospodarenko, G. et al. (2016). Spelled wheat. Kiev (in Ukrainian).
- Jaaska, V. (1978). NADP-dependent aromatic alcohol dehydrogenase in polyploid wheats and their diploid relatives. On the origin and phylogeny of polyploid wheats. *Theoretical and Applied Genetics*, 53(5), 209–217.
- Kislev, M. (1984). Emergence of wheat agriculture. *Palaeorient*, 10(2), 61–70.
- Körnicker, Fr., Werner, H. (1885). *Handbuch des Getreidebaues*. Berlin–Bonn: Sort. Und Anb. (in German).
- Kuckuck, H. (1964). Experimental investigation on the origin of wheat. *Z. Pflanzenzucht*, 51(2), 97–140.
- Kuckuck, H. Schiemann, E. (1957). Über das Vorkommen von Spelz und Emmer (*Triticum spelta* and *T. dicoccum* (Schubl.) im Iran. *Z. Pflanzenzucht*, 38, 383–396 (in German).
- Lee, Y.K., et al. (1999). The low-molecular-weight glutenin subunit proteins of primitive wheats. I. Variation in A-genome species. *Theor. Appl. Genet.*, 98, 119–125.
- Luo, M.C., Yang, Z.L., You, F.M., Kawahara, T., Waines, J.G., Dvorak, J. (2007). The structure of wild and domesticated emmer wheat populations, gene flow between them, and the site of emmer domestication. *Theoretical and Applied Genetics*, 114(6), 947–959 .
- MacKey, J. et al. (1966). Species relationships in *Triticum*. *Proceedings of the 2nd International Wheat Genetics Symposium*, 19–24 August 1966. Lund (Sweden): Berlingska Boktryckeriet.
- McFadden, E. S. Sears, E. R. (1946). The origin of *Triticum spelta* and its free-threshing hexaploid relatives. *Journal of Heredity*, 37(3), 81–89.
- Menabde, V.L. (1948). *Wheat of Georgia*. Tbilisi (in Russian).
- Morris, E.R., Sims, E.R. (1970). *Cytogenetics of wheat and related forms*. Wheat and its improvement. Moscow (in Russian).
- Nesbitt, M. (2001). Wheat evolution: integrating archaeological and biological evidence. *Wheat Taxonomy: the legacy of J. Percival*, 37–60.
- Nesbitt, M., Samuel, D. (1996). From staple crop to extinction? The archaeology and history of hulled wheats. In: *Hulled wheats. Promoting the conservation and use of underutilized and neglected crops*. Proc. 1st Int. Workshop Hulled Wheats, Int. Plant Genet. Resources Institute, Rome, Italy.
- Nieto-Taladriz, M.T. et al. (1997). Variation and classification of B low-molecular-weight glutenin subunit alleles in durum wheat. *Theor. Appl. Genet.*, 95, 1155–1160.
- Ohtsuka, I. (1998). Origin of the central European spelt wheat. In: *Proc. 9th Int. Wheat Genet. Symposium*, University Extension Press, Canada.
- Pena-Chocarro, L., Zapata-Pena, L. (1998). Hulled wheats in Spain: history of minor cereals. In: Jaradat A.A. (ed.), *Triticeae III*. Science Publisher Inc., Bombay, India.
- Percival, J. (1921). *The wheat plant*, A monograph. London, Duckworth & Co.
- Salamini, F. (2002). Genetics and geography of wild cereal domestication in the Near East. *Nature Reviews Genetics*, 3, 429–441 .
- Schulz, A. (1913). *Die Geschichte der kultivierten Getreide*. Verlag Louis Neberts, Halle (in German).
- Sinskaya, E.N. (1968). Historical review of the VIR works on taxonomy. *Proceedings of Applied Botany, Genetics and Breeding*, 39(2), 3–38 (in Russian).
- Tschermak, E., Bleier, H. (1926). Über fruchtbare Aegilops-Weizenbastarde (Beispiele für die Entstehung neuer Arten durch Bastardierung). *Berichte der Deutsch. Botan. Gessellschaft*, 44(2), 110–132 (in German).
- Tsunewaki, K. (1971). Distribution of necrosis genes in wheat. V. *Triticum macha*, *T. spelta* and *T. vavilovii*. *Jpn. J. Genet.*, 46, 93–101.
- Vavilov, N. I. (1926). Centers of origin of cultivated plants. *Proceedings on Applied Botany, Genetics and Selection*, 16(2), 248 (in Russian).
- Vavilov, N. I. (1935). *Scientific foundations of wheat selection*. Moscow-Leningrad (in Russian).
- Von Buren, M. (2001). Polymorphisms in two homeologous gammagliadin genes and the evolution of cultivated wheat. *Genet. Res. Crop. Evol.*, 48, 205–220.
- Yakobashvili, Z.A. (1989). Establishment of phylogenetic connections between species of wheat by means of analysis of polymorphism and inheritance of reserve proteins. Moscow. (in Russian).
- Yan, Y. et al. (2003). HMW and LMW glutenin alleles among putative tetraploid and hexaploid European spelt wheat (*Triticum spelta* L.) progenitors. *Theor. Appl. Genet.*, 107, 1321–1330.
- Zhukovskiy, P. M. (1971). *Cultivated plants and their relatives*. Leningrad (in Russian).
- Zohary, D. (1999). Monophyletic vs. polyphyletic origin of the crops on which agriculture was founded in the Near East. *Genetic Resources and Plant Evolution*, 46(2), 133–142.
- Zohary, D., Hopf, M. (1988). *Domestication of plants in the Old World. The origin and spread of cultivated plants in west Asia, Europe, and Nile valley*. Oxford: Clarendon Press.

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