Chapter 2
Domestication and Evolution of Ancient Wheats

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2.1 Introduction

Wheat is one of the most prominent crop plants, discovered approximately 10,000 years ago, and has great importance as a major food source in human diets worldwide. In the Paleolithic era, humans used to hunt wild animals and gather the leaves, fruits, seeds, and roots of wild plants to feed. The climate conditions became milder and favored plant diversity in the natural environment. This factor might have enriched and diversified the plant food resources for human food and led to an increase in population size that brought about the requirement for an increase in food resources, because the collection of only wild plant food resources was not enough to supply the increased populations' needs. Therefore, in the late Paleolithic and early Neolithic eras, humans started to collect the seeds of wild emmer wheat for food, and some were left for the next year's planting. After the plants ripened, they were harvested, or they were harvested before maturation, as wild emmer wheat has a brittle rachis, which ensures independent seed dispersal and self-burying of the seeds into the soil, thus giving rise to the first form of primitive agriculture. This was the huge revolution in human lifestyle, which arose in the Levantine region and then spread to the Fertile Crescent, Europe, and Africa; it was thought that the transition from a hunter-gatherer lifestyle to a sedentary lifestyle started with agriculture.

Charred wheat grains, reaps made with silex attached to animal horns, stones used for grinding (millstone-like) processes, and cereal storage wells were found in archaeological remains in Diyarbakır Çay Önü (7000 BC), Konya Çatal Höyük (6800–5700 BC), and Burdur Hacılar (6750–6500 BC) in Anatolia (Kunter, 2011)

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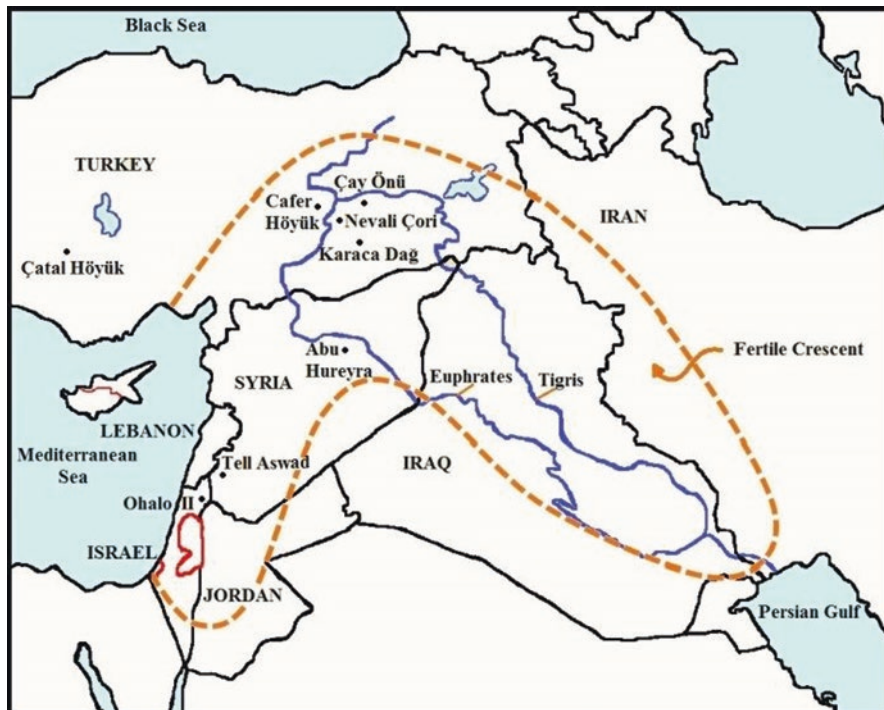
Fig. 2.1 The map is representing the domestication geography of wheat and excavated archaeological sites, where wheat grains were found, in the Fertile Crescent (orange dashed region) represented on the Near East

(Fig. 2.1). These findings suggested that people were harvesting and grinding cereal grains and stored them as food resources. Most probably, they cooked the ground cereal flours as food or bread-like food in ash.

According to the archaeological remains, in 4000 BC, people cooked bread in bakeries in Babylon. It was thought that the ancient Egyptians used the first leavened dough to make bread. There is even a legend about a bread made with leavened dough. Once upon a time (around 2600 BC) in ancient Egypt, slaves were charged with the task of making bread, and 1 day, the slaves had fallen asleep and the fire went out; the dough was left in a warm environment, and it fermented and became sourdough. When the sourdough was cooked, they noticed that the bread was softer, more delicious, and more easily digested than flatbread. After that, they started to cook bread leavened by fermentation. Therefore, it is thought that fermented bread spread out from Egypt and Israel (Kapucu, 2015). The ancient Greeks learnt how to make leavened bread from Egyptians and Jews. In 312 BC, there were 254 bakeries controlled by governments in Rome, and there were bread standards (e.g., bread weight and price). Turks knew how to cook flatbread (pitta), a thin leaflike bread, sac bread, and a thin pitta-like (lavaş) bread, from non-fermented dough; these breads had a long life and kept fresh when the people had a nomadic lifestyle.

Bread wheat is used to produce many products, such as cookies and bread, while durum wheat is used to make items such as macaroni, couscous, bulgur, and homemade macaroni. In the beginning, wheat was ground between stones and emulsified with water and then cooked on heated stones or in ash.

2.2 Evolution of Wheat

There are many theories, proposed by different research groups, about the origin of wheat. Solms-Laubach (1899) thought that the cultivation of all wheats started in Central Asia and then migrated westward, while Much (1908) proposed that many cereals, especially wheat and barley, were cultivated in Europe and domesticated there (Feldman & Millet, 2001). Körnicke saw a spike segment of two-grained wheat with brittle rachis found by Kotschy in Rashayya on the north slope of Mt. Hermon in 1855, in the National Museum, Vienna, in 1873. Körnicke claimed that the two-grained wild progenitor of wheat originated in this area. Then, he made expeditions to find it in this area, but he did not succeed. Aaronsohn made an expedition to this area in 1904, but he could not find this wheat too. Aaronsohn made a second expedition in 1906, and he found a single plant at Rosh Pinna in Eastern Galilee, Israel. After that, Aaronsohn saw this wild wheat on Mt. Hermon and other sites in Israel, Jordan, Lebanon, and Syria (Aaronsohn, 1910). After this great discovery, it was assumed that the two-grained wild wheat (*Triticum dicoccoides*) was the progenitor of most cultivated wheats, and this enabled a search for the origin and evolution of wheat by cytogenetic methods (cited in Feldman & Millet, 2001).

Wheat belongs to the subfamily Pooideae, which diverged 20 million years ago (MYA) from the family Poaceae (grasses), which evolved 50–70 MYA (Peng et al., 2011). The tribe Triticeae started to diverge from its progenitor approximately 35 MYA and the *Triticum* genus diverged from its progenitor about 11 MYA. *Triticum* and *Aegilops* taxa evolved from a common ancestor, with seven basic chromosome numbers, about 3 MYA (Gustafson et al., 2009).

When an organism has more than a diploid complement of chromosomes, the situation is called polyploidy, which is the basic driving evolutionary force in the evolution of wheat and many crop plants (Stebbins, 1950, 1971). There are two types of polyploidy; hybridization between two species with different genome formulae, called allopolyploidy, a good example for the wheat speciation based on which. The other type of polyploidy is whole-genome duplication, in which the existing organism may have at least three copies of the same (or a near identical) genome. The new organism existing as a result of either type of polyploidization will have multivalent pairs or, in autopolyploidy, random bivalent pairs between homologous chromosomes (Renny-Byfield & Wendel, 2014). Polyploidy contributes to polyploid plant species being able to adapt to diverse environmental conditions by buffering the effect of their genomes and may provide phenotypic divergence (Soltis et al., 2009).

In the *Triticum* genus, there are two wild diploid species with genome A, *Triticum monococcum* ssp. *aegilopoides* ($2n = 2x = 14$, *AA*) and *Triticum urartu* ($2n = 2x = 14$, A^uA^u) (Fig. 2.2), which diverged from its progenitor about 2.6 MYA (Fig. 2.2). All these diploid wheats, except for *Triticum monococcum* ssp. *monococcum* ($2n = 2x = 14$, A^mA^m) (Fig. 2.3), with non-brittle rachis (*br*), which arose as a result of a mutation in the brittle rachis (*Br*) gene of *Triticum monococcum* ssp. *aegilopoides*, are wild type. In the *Aegilops* genus, there are six diploid wild wheats, also called sytopsis: *Aegilops tauschii* ($2n = 2x = 14$, *DD*), *Aegilops bicornis* ($2n = 2x = 14$, S^bS^b), *Aegilops searsii* ($2n = 2x = 14$, S^sS^s), *Aegilops longissima* ($2n = 2x = 14$, S^lS^l),
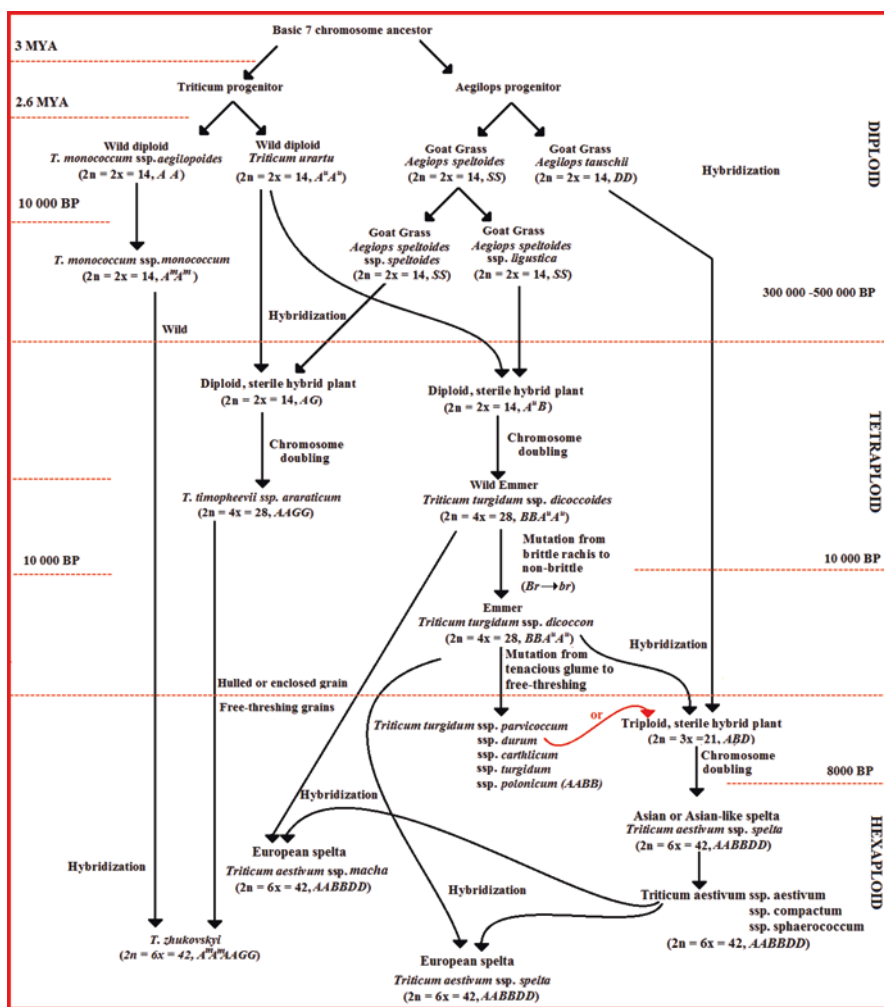

Fig. 2.2 Evolutionary lineage of wheat. (The figure is modified from Faris (2014) and Peng et al. (2011))

Fig. 2.3 *Triticum monococcum* spike morphology. (Photo taken by Ö. Özbek in 2017)

Fig. 2.4 Wild emmer wheat (*Triticum dicoccoides*) in the natural growing field at Golan Height in Israel. (Photo taken by Ö. Özbek in 2005)

Aegilops sharonensis ($2n = 2x = 14$, S^hS^h), and *Aegilops speltoides* ($2n = 2x = 14$, *BB/GG*), which diverged about 2.6 MYA (Feldman & Millet, 2001; Faris, 2014; Peng et al., 2011).

The first tetraploid wild wheats *Triticum araraticum* ($2n = 4x = 28$, A^uA^uGG) and *Triticum turgidum* ssp. *dicoccoides* ($2n = 4x = 28$, BBA^uA^u) (Figs. 2.4 and 2.5) existed about 300,000–500,000 years before the present (BP), formed by the

Fig. 2.5 Wild wheat (*Triticum dicoccoides*) in its natural field in Israel. (Photo taken by Ö. Özbek in 2005)

hybridization of *Triticum urartu* ($2n = 2x = 14$, $A^u A^u$) with *Ae. speltoides* ssp. *speltoides* ($2n = 2x = 14$, GG), and with *Aegilops speltoides* ssp. *ligustica* ($2n = 2x = 14$, SS) (Fig. 2.2), respectively. The resultant hybrids were most probably sterile owing to the incomplete meiosis of non-homologous chromosome pairs of different genomes (*A* and S/*B* genome pairs, *A* and *G* genome pairs). After a chromosome doubling process by autopolyploidization, new species of fertile wild emmer wheat (*Triticum dicoccoides*, $2n = 4x = 28$, $BBA^u A^u$) and *Triticum araraticum* ($2n = 4x = 28$, $A^u A^u GG$) were formed (Feldman & Millet, 2001; Faris, 2014; Peng et al., 2011).

A mutation event in the genes controlling tenacious glume in *T. dicoccum* led to the evolution of naked tetraploid wheat ($2n = 4x = 28$, $AABB$), ssp. *parvicoccum*, ssp. *durum*, and ssp. *carthlicum* around 7500–8000 BC.

A spontaneous hybridization occurred between emmer wheat (*Triticum turgidum* ssp. *dicoccon*, $2n = 4x = 28$, $BBA^u A^u$) and *Aegilops tauschii* ($2n = 2x = 14$, DD), when it arrived at the growing area of *Ae. tauschii* after having spread from the Fertile Crescent to different regions of the world. This hybridization event produced a new form of wheat, hexaploid wheat (*Triticum aestivum* ssp. *spelta*, $2n = 6x = 42$, $AABBDD$) (Fig. 2.6), considered to be Asian spelt wheat, about 8000 BP. *Triticum monococcum* ssp. *monococcum* contributed the A^m genome of *Triticum zhukovskyi* ($2n = 6x = 42$, $A^m A^m AAGG$), another hexaploid wheat form, the *A* and *G* genomes of which, contributed by the wild progenitors of *Triticum timophevii* ($2n = 4x = 28$,

Fig. 2.6 Bread wheat field and its spike morphology. (Photos taken by Ö. Özbek in 2017)

AAGG), resulted from hybridization between *T. urartu* and *Ae. speltoides* ssp. *speltoides* (Faris, 2014; Feldman & Millet, 2001; Charme, 2011).

2.3   Domestication of Wheat

Archaeological researches at archaeological remains have produced fruitful results that shed light on the domestication of several crop plants and early forms of agriculture in the Fertile Crescent, and this has helped us to date the domestication time of these species. Thus, researchers have suggested different scenarios about when and where the domestication of these crop plants took place and how and when the first forms of agriculture started. Many of these scenarios share the idea that the domestication of eight crop plant species [wheats: diploid einkorn wheat (*Triticum monococcum*), tetraploid emmer wheat (*Triticum dicoccon*), and barley (*Hordeum vulgare*); two pulses: lentil (*Lens culinaris*) and pea (*Pisum sativum*); and flax (*Linum usitatissimum*), bitter vetch (*Vicia ervilia*), and chickpea (*Cicer arietinum*) (Lev-Yadun et al., 2000; Terence et al., 2008; Weiss & Zohary, 2011)] took place in the Fertile Crescent. However, agriculture developed independently in several regions of the world at around the same time. Other than the Fertile Crescent region, the regions are Mesoamerica, where maize was first grown, rice was first grown in the Yangtze region of Southeast Asia, and potato, peanut, and manioc were first grown in South America (Terence et al., 2008; Harlan, 1998; Feldman & Kislev, 2007).

2.4   Genetics of Domestication in Wheat

The domestication of wheat was accelerated by evolution. Domestication is the process of cultivation toward the plant's adaptation to a new anthropized environment following anatomical, morphological, and genetic changes, which also modified yield and yield components (Brown, 2010; Nesbitt, 2002; Peng et al., 2011). Cereals, particularly wheat, were among the first crop plants to have been domesticated in the Middle East and then spread out to the world. The genetic changes in the transition from wild to domesticated forms include three major genes—brittle rachis (*Br*), tenacious glume (*Tg*), and non-free-threshing character (*q*)—found in wild forms (Faris, 2014).

The domestication process caused a domestication syndrome, which can be defined as the genetic modifications in some genes in wild forms to a human-dependent state owing to human needs (Peleg et al., 2005). The factors driving the domestication syndrome are important not only from an evolutionary perspective, but also they have important economic and social conclusions. Therefore, much attention should be paid to the analysis of the traits related to the domestication syndrome.

2.4.1   *Brittle Rachis (Br)*

The evolutionary significance of brittle rachis (*Br*) is its adaptive value, because that is responsible for the free shattering of seeds, not dependent on humans for seed dispersal and self-sowing into the soil (Zohary & Hopf, 2000) in the wild form, whereas loss of seeds was seen before this mutation. In Triticeae, the spikelets can disarticulate or shatter at maturity owing to brittle rachis, and this enabled seed dispersion and self-planting (Nesbitt, 2002; Zohary & Hopf, 2000) independently in wild forms such as wild emmer wheat [*Triticum turgidum* ssp. *dicoccoides* (Körn. Ex Asch. and Graebner) Thell., $2n = 4x = 28$, *BBAuAu*], but in cultivated emmer wheat (*Triticum turgidum* ssp. *dicoccon*, $2n = 4x = 28$, *BBAuAu*), the seeds stay intact, with non-brittle rachis—dependent on humans for seed dispersion, which is the major distinguishing feature between them—until the plants are harvested. The genes *brittle rachis* 2 (*Br-A2*) and *brittle rachis* 3 (*Br-A3*) controlling rachis fragility were characterized as dominant and were located on the short arms of chromosomes 3A and 3B, respectively, in wheat (Cao et al., 1997; Chen et al., 1998; Watanabe & Ikebata, 2000; Watanabe et al., 2002; Salamini et al., 2002; Watanabe, 2005; Li & Gill, 2006; Nalam et al., 2006; Gill et al., 2007; Peng et al., 2011).

A mutation in the *Br* locus led to a recessive non-brittle locus *br* in cultivated forms that occurred independently in both diploid and tetraploid wild wheats (Gill et al., 2007). The mutation existed in wild einkorn wheat *Triticum monococcum* ssp. *aegilopoides*, giving rise to domesticated *Triticum monococcum* ssp. *monococcum* (Fig. 2.3), while the same mutation event took place in tetraploid wild emmer wheat

(*Triticum turgidum* ssp. *dicoccoides*) and *Triticum timophevii* ssp. *araraticum* (*AAGG*); the *br* locus resulted in domesticated tetraploid emmer wheat (*Triticum turgidum* ssp. *dicoccon*) (Fig. 2.7) and *Triticum timophevii* ssp. *timophevii* (*AAGG*), respectively. In both cases, the species are very similar to each other in phenotype, but the latter one has a tough rachis (Faris, 2014). Today all wild wheat forms, both diploid and tetraploid, have a brittle rachis, while domesticated forms have a tough (non-brittle) rachis (Gill et al., 2007).

Disarticulation due to brittle rachis resulted in two basic types of disarticulation in wheats. When the whole spike is broken at the base and the whole spike is dispersed, this is called spike-type disarticulation, controlled by the *Br1* gene, as observed in *Ae. speltoides* var. *speltoides* (Chen et al., 1998). The second type of disarticulation is the spikelet type, which is subdivided into two other disarticulation types depending on the breakage point of the spikelets. In wedge-type (W-type) disarticulation, the spikelet is broken at a point between the upper side of the junction of the rachis and spikelet base attached to a rachis fragment, and it is controlled by *Br1³ᴬ* (3AS), *Br1³ᴮ* (3BS), and *Br1³ᴰ* (3DS) genes (Li & Gill, 2006), as observed in species possessing *A*, *B*, *G*, *S*, and *T* genomes (Faris, 2014; Kimber & Feldman, 1987; Li & Gill, 2006), while non-allelic recessive genes or complementary recessive genes on 5A and 7A control W-type disarticulation in *T. monococcum* (Fig. 2.8) (Sharma & Waynes, 1980). Peng et al. (2003, 2004) reported a gene (*Br42A*) (2AL) related to rachis brittleness in *T. turgidum* ssp. *dicoccum* (Fig. 2.9).
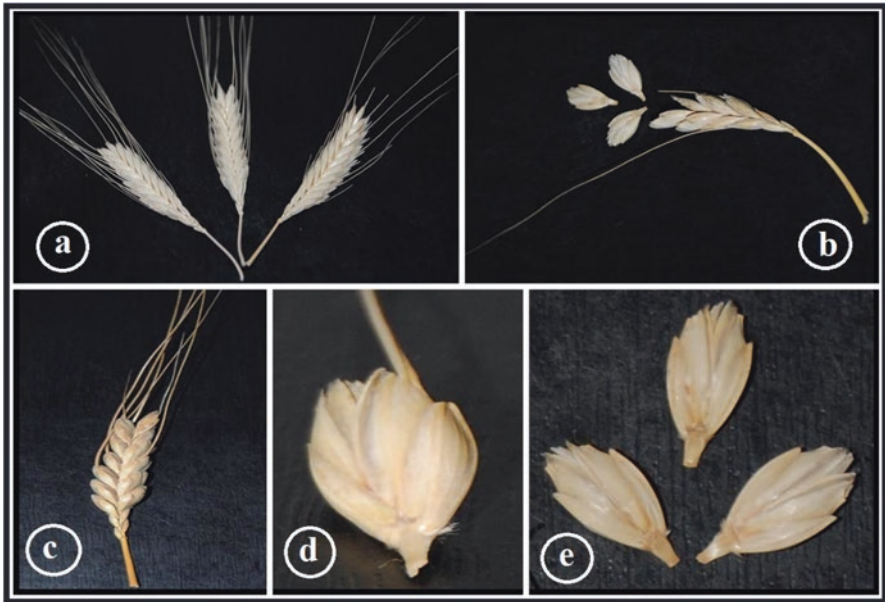
Fig. 2.7 *Triticum dicoccon* spike morphology (**a**, **b**, and **c**) and wedge-type spikelet (**d** and **e**). (Photo taken by Ö. Özbek in 2017)

Fig. 2.8 Wedge-type disarticulation of *T. monococcum* spikelet. (Photo taken by Ö. Özbek in 2017)
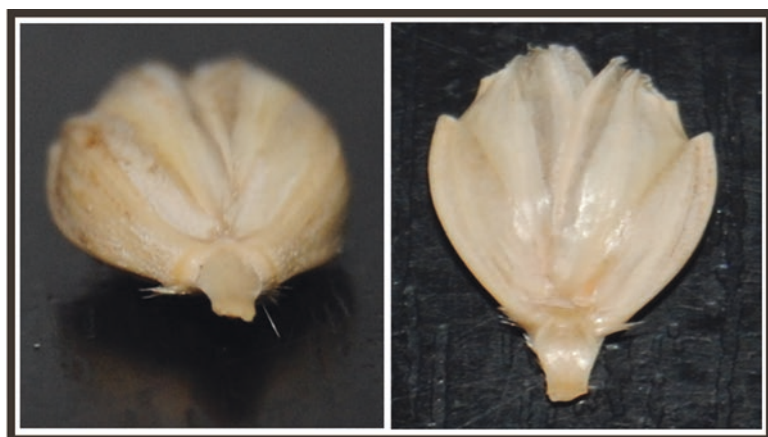
Fig. 2.9 Wedge-type disarticulation in *T. dicoccum* spikelet. (Photos taken by Ö. Özbek in 2017)

In barrel-type (B-type) disarticulation, the spikelet is detached from the rachis junction point, having a flat-like scar at its base, and it is controlled by the $Br2^{3D}$ (3DL) gene, as observed in species containing the D genome, such as *Ae. tauschii* (Faris, 2014; Gill et al., 2007; Li & Gill, 2006).

2.4.2 Tenacious Glume (Tg)

There needs to be a mechanism or a structure to protect wheat seeds from harsh environmental conditions to ensure their survival until self-planting occurs during the period of natural seed dispersal. That structure is called a tenacious glume; it is tough and tightly encases the seed, and it is not threshed from the seed in wild wheats; it occurs in what is called hulled wheats, such as ssp. *aegilopoides* and ssp. *dicoccoides* and some domesticated forms, ssp. *monococcum* (Fig. 2.10) and ssp. *dicoccum* (Fig. 2.11). The characteristics of tenacious glume were defined for the first time by Kerber and Dyck (1969); the structure is controlled by an incompletely dominant gene, $Tg1^{2D}$, and it was mapped and validated on chromosome 2DS by Jantasuriyarat et al. (2004) in *T. aestivum* ssp. *aestivum*. Simonetti et al. (1999) reported another gene, $Tg2^{2B}$, mapped on chromosome 2BS in *T. turgidum* ssp. *parvicoccum*, a subspecies which is not known for certain—possibly it might have been extinct and it might have been *parvicoccum* or *durum* or may be another tetraploid subspecies (Faris, 2014). On the other hand, a domesticated einkorn wheat, *T.*

Fig. 2.10 *T. monococcum* spike and hulled grains. (Photos taken by Ö. Özbek in 2017)

Fig. 2.11 *Triticum dicoccum* spike and hulled grains. (Photo taken by Ö. Özbek in 2017)

sinskajae, has a free-threshing soft glume (*sog*) trait controlled by a single recessive gene located on *2A^m^* (Faris, 2014; Sood, 2009; Taenzler et al., 2002).

The genes *Tg1^{2D}* and *Tg2^{2B}* controlling tenacity possibly might be homeologous, or another possibility is that *Tg2^{2B}* and *Sog* on *2A^m^* are homeologous genes (Faris, 2014). Free-threshing or naked grain has a shorter dormancy period, enhancing the possibility of germination and growth under favorable conditions. Domestication started 10,000 years ago and resulted in fully domesticated wheat, *Triticum turgidum*, and *Triticum aestivum*, through rachis and free-threshing naked seed. It is not clear whether early farmers through the collection of wheat plants, which had naked seeds that were then resown, by the farmers drove domestication.

2.4.3 Free Threshing (Q Factor)

Following the domestication process, polyploid wheat species existed, having non-brittle rachis and a free-threshing nature. These transitions gave rise to the development of the two most common modern wheats, bread wheat (*Triticum aestivum*, $2n = 6x = 42$ *AABBDD*) and durum wheat (*Triticum turgidum*, $2n = 4x = 28$ *AABB*). The free-threshing nature in the phenotype of wheat controlled by two genes was gained through changes from tenacious and tightly enveloped glume to softened and easily separable hulls (Faris, 2014). The latter change was driven by mutations that

occurred in the genes; *Tg* controls the tenacious glume character and is mapped on chromosome 2B of the *BB* genome, and *q* controls non-free threshing and is mapped on the long arm of chromosome 5A of the *AA* genome. After mutations, the alleles *tg* and *Q* control free threshing; they are partially recessive and partially dominant, respectively (Peng et al., 2011).

The genotype of a free-threshing tetraploid (*AABB*) genome should be *tgtg-$^{2B}QQ^{5A}$*. On the other hand, a second mutation could have occurred in the *DD* genome of bread wheat, contributed by *Ae. tauschii*. If this has not occurred, the *Tg* locus gained from *Ae. tauschii* prohibits free threshing in bread wheat (*AABBDD*), which has the *tgtg^{2B}tgtg^{2D}QQ^{5A}* genotype (Sang, 2009). *Tg* is epistatic to (Gill et al., 2007) or has a dominant effect over the *Q* allele under hulled or non-free-threshing conditions, while the plants with *br* and *tg* alleles, but lack of *Q*, also have a non-free-threshing character. In addition to this latter character, these plants have a semi-brittle rachis, a speltoid spike, and a tenacious glume and are taller; they flower earlier and display differences in yield compared with plants that have the *Q^{5A}* allele (Faris, 2014). These consequences infer the pleiotropic effects of *Q^{5A}* on other traits: squarehead spike, rachis fragility, glume toughness, glume shape, and plant vigor, which are important in wheat domestication and in agronomy (Faris, 2014; Muramatsu, 1963; Simons et al., 2006). According to previous studies, it was confirmed that homoeologous *q* loci appeared on chromosomes 5B and 5D (Simons et al., 2006; Zhang et al., 2011). The high conservation of Q/q gene sequences also described all ploidy levels in the *A*, *B*, *S*, and *D* genomes. It was thought that duplication of the *q* gene in a diploid ancestor genome of diploid wheats occurred before they separated, about 5.8 MYA.

In the evolution of diploid wheat, one copy of the gene was conserved in *A* genome progenitor, while the other copy was lost in *B*, *S*, and *D* genomes. The *q^{5D}* allele in *Ae. tauschii* and hexaploid wheat is still present and helps to suppress the speltoid syndrome, but to a lesser degree compared with *Q^{5D}*. During allopolyploidy formation, the *q^{5B}* allele changed to a pseudogene, but it is still involved in the regulation of domestication-related traits; finally, *q^{5S}* is present in *Ae. speltoides*, also still functional and with the whole sequence conserved. Consequently, the mutant *Q^{5A}* allele is the major effective allele in the domestication of wheat, with the contributions of *q5B* and *q^{5D}* (Faris, 2014). Peleg et al. (2005) reported qualitative trait loci related to glume toughness on chromosomes 4A, 4B, and 7B, in addition to the major tough glume genes *Tg* and *sog* on chromosome 2 and the *Q* gene on chromosome 5AL in emmer wheat.

2.5 Domestication Geography of Hulled Wheats

The origin of domestication of plants and the origin of agriculture may not be the same. But agriculture helped the spread of domesticated wheats westward around the Mediterranean; across North Africa and southern Europe; northward across the Balkans to western Europe, the British Isles, Scandinavia, and Russia; and from the

Ethiopian Plateau to India (Harlan, 1966). Archaeological remains have contributed to our understanding of the domestication origins or geography of crop plants; here we concentrate on hulled wheats (einkorn and emmer wheat) particularly. Many investigations have been done on botanical remains in Anatolia, which is part of the domestication area considered as a cradle of agriculture. It is thought that this domestication process took place about 10,000 BP in the Fertile Crescent. The first domesticated wheat variety was the einkorn wheat, *Triticum monococcum* ssp. *monococcum*, which has a diploid *AA* genome derived from the wild einkorn wheat *Triticum boeoticum*; both were found together, considered as a mark of domestication, at an archaeological site that was characterized as being about 10,500 calibrated years before the present (cal BP) (Gopher et al., 2002; Zohary & Hopf, 2000). Although *Triticum monococcum* ssp. *monococcum* became abundant at about 9500 cal BP (Nesbitt & Samuel, 1995) and then spread to Cyprus, Greece, and the Balkans in 8000 cal BP (Van Zeist, 1981; Renfrew, 1979a, b, cited in Salamini et al., 2002), later spreading to the countries of the former Yugoslavia, Bulgaria, and Hungary, its cultivation started to decrease in the Bronze Age (Salamini et al., 2002), and today, it is regarded as a relic crop and cultivated in a very limited area in the world, including a few provinces in Turkey, Italy, and the former Yugoslavia, primarily as animal fodder. Recently in Turkey, popular interest in organic farming and its healthy end products has led to the reinstatement of the farming of domesticated einkorn wheat (Morgounov et al., 2016).

Earlier studies indicated that *Triticum monococcum* ssp. *boeoticum* and *Triticum monococcum* ssp. *urartu* displayed differences in both morphology (Dorofeev et al., 1979; Gandilian, 1972) and biochemical and molecular markers (Dvořák et al., 1988; Jaaska, 1974; Johnson, 1975). Valkoun et al. (1998) reported that two wild diploid wheats (*Triticum monococcum* ssp. *boeoticum* and *Triticum monococcum* ssp. *urartu*) differed in their geographical distribution, with ssp. *urartu* existing in the area extending from Transcaucasia through eastern Anatolia and the Fertile Crescent to Jordan and Hauran and the Jebel Al Arab region of southern Syria, including the Syrio-Palestinian region (Johnson, 1975), while ssp. *boeoticum* existed mainly in southern Turkey, where it was most probably domesticated (Heun et al., 1997) extending as well across Turkey from Transcaucasia to Greece (Johnson & Dhaliwal, 1976). The ssp. *urartu*, an *A* genome donor of tetraploid and hexaploid wheats, exhibits a distribution similar to that of *Triticum turgidum* ssp. *dicoccoides*. Heun et al. (1997) used amplified fragment length polymorphism (AFLP) fragment analysis to investigate the site of einkorn domestication. They concluded that Karacadağ *Triticum monococcum* ssp. *boeoticum* lines could have been the progenitor species of cultivated einkorn domesticated about 10,000 years ago in the Karacadağ mountain region. Thus, Karacadağ mountain is most probably the site of einkorn domestication, a finding that was also supported by findings from early settlements near Karacadağ mountain, covering Cafer Höyük (De Moulins, 2000), Çay Önü (Van Zeist & de Roller, 1991/1992), Nevali Çori (Pasternak, 1998), and Abu Hureyra (De Moulins, 2000; Hillman, 2000; Salamini et al., 2002) (Fig. 2.11).

Then genetic diversity was investigated using 151 AFLP loci and 18 haplotype loci in *Triticum monococcum* (einkorn) germplasm by Kilian et al. (2007). The

natural genetic differentiation was determined among the wild einkorn wheats, and the wild einkorn (*Triticum monococcum* ssp. *boeoticum*) underwent genetic differentiation prior to domestication. The larger nucleotide diversity was observed within *Triticum monococcum* ssp. *monococcum* than within *Triticum monococcum* ssp. *boeoticum*, and *T. urartu* was genetically diverged than others. *Triticum monococcum* ssp. *aegilopoides* was not found in the Karacadağ mountain and Kartal–Karadağ region (Kilian et al., 2007). Einkorn wheat replaced with tetraploid and hexaploid wheats in the last 5000 years and neglected by modern breeders, cultivated until the early Bronze Age (Bar-Yosef, 1998). *Triticum turgidum* ssp. *dicoccoides* emerged by the hybridization of two wild diploid wheats, *Triticum urartu* ($2n = 2x = 14$ *AA*), considered as the paternal *A* genome donor, and *Aegilops speltoides* ($2n = 2x = 14$ *SS/BB*), considered as the maternal parent *B* genome donor, around Mount Hermon and the Jordan River in the Fertile Crescent about 360,000 years ago (Dvořák & Akhunov, 2005; Feldman & Kislev, 2007; Özkan et al., 2011). This inference was made owing to the great morphological, phenological, biochemical, and molecular variation observed in wild emmer populations from southeastern Turkey, northern Iraq, southwestern Iran, Israel, and Jordan (Nevo & Beiles, 1989; Ozbek et al., 2007a, b; Özkan et al., 2002).

The geographical distribution of wild emmer has been described in other research (Harlan & Zohary, 1966; Johnson, 1975; Özkan et al., 2005, 2011; Valkoun et al., 1998; Zohary & Hopf, 2000). Its major distribution area is placed in the Fertile Crescent, including the central southeastern part of Turkey, the eastern part of the mountainous area of Iraq, western Iran, and the Jordan Valley (Harlan & Zohary, 1966; Zohary, 1973), where the habitat was characterized by Nevo et al. (2002). The population structure and distribution in Israel was described as an archipelago in which populations were isolated or semi-isolated, showing an island model (Nevo & Beiles, 1989; Ozbek et al., 2007a). This characteristic might be associated with the soil type; where wild emmer wheat grows, the area is not covered continuously by the same type of soil. Wild wheats grow on basalt bedrock or decalcified alluvial soils, and much of the area is unsuitable for wild wheats and rye, owing to the presence of Eocene and Paleocene chalk limestone (Willcox, 2005). The distribution of wild emmer wheat is scarce throughout Iraq and Iran, and the density of another tetraploid wheat, *Triticum araraticum* Jakubz. ($2n = 4x = 28$, *AAGG*), displays dominance (Johnson, 1975) in those areas. In southeastern Turkey, a dense wild emmer wheat population grows on the slopes of the Karacadağ mountain (Şanlı Urfa and Diyarbakır provinces) and the Kartal–Karadağ mountain range region (Harlan & Zohary, 1966; Özkan et al., 2011). Wild emmer wheat is distributed mainly in primary habitats from Karacadağ mountains to Israel, ranging in altitude from 100 to 150 m below sea level up to 1600–1800 m above sea level (Aaronsohn, 1909; Nevo et al., 2002; Schweinfurth, 1908), and occasionally, it is distributed in secondary habitats, as in Turkey (Özkan et al., 2005, 2011).

Grains of wild emmer wheat were found for the first time at Ohalo II, a permanent site of Epipaleolithic settlement 19,000 BP (Fig. 2.2); this find showed that hunter-gatherer humans collected and used wild emmer wheat seeds (Feldman & Kislev, 2007). When the gene responsible for brittle rachis (*Br*), also called the domestication

gene, had undergone mutation in wild tetraploids, the cultivated tetraploid forms, *Triticum araraticum* (2*n* = 4*x* = 28, *AAGG*) and emmer wheat (*Triticum turgidum* ssp. *dicoccon*, 2*n* = 4*x* = 28, *BBA^uA^u*) were formed. The only difference between wild emmer wheat and cultivated emmer wheat is non-brittle rachis (*br*).

Nevali Çori (NÇ) is a prehistoric settlement dated from the early pre-Pottery Neolithic B era to the early Bronze Age (Fig. 2.2) (Hauptmann, 1984, 1987, 1988, 1997). Pasternak (1998) reported some botanical remains, including 26,792 items determined as wheat, from NÇ. Although there were some difficulties about the identification of one-seeded and two-seeded grains as *T. boeoticum* or *T. dicoccoides* in his findings, he revealed that 4 of 30 larger types of grains were obviously two seeded. These four types could have been identified as *T. dicoccum* and the others as *T. monococcum*, while 23 terminal spikelets of 500 complete spikelet forks were an indication of the existence of tetraploid wheat. Domesticated emmer wheat, *T. dicoccum* (2*n* = 4*x* = 28 *BBAA*), is a hulled wheat type, while *T. parvicoccum* (2*n* = 4*x* = 28 *BBAA*), the naked form, assumed to be an extinct tetraploid form (Faris, 2014), had small grain (Kislev, 1980); both have a *BBAA* genome formula, as is common for tetraploid wheats. Although domesticated emmer wheat was the most important cereal for cultivation in the Fertile Crescent, einkorn wheat was cultivated until the early Bronze Age (Bar-Yosef, 1998), and today, only traditional farmers are growing einkorn wheat on a limited scale in Ethiopia, Iran, Italy, Transcaucasia, Turkey, and the Balkans. Einkorn wheat was found at early Neolithic sites (such as Tell Aswad, ~10,800 BP; Van Zeist & Bakker-heeres, 1982; Özkan et al., 2005). In the Fertile Crescent, emmer wheat (*Triticum turgidum* ssp. *dicoccon* [Schrank] Thell.) was the first domesticated tetraploid wheat, and its subspecies were identified as follows: (1) ssp. *maroccanum* Flaksb. (Moroccan emmer); (2) ssp. *abyssinicum* Vav. (Ethiopian emmer); (3) ssp. *europaeum* Vav. = ssp. *dicoccon* (European emmer); and (4) ssp. *asiaticum* Vav. (Eastern emmer) (Gökgöl, 1955; Dorofeev et al., 1979; Szabó & Hammer, 1996; Teklu et al., 2007; cited in Özkan et al., 2011). Previous studies (Heun et al., 1997; Lev-Yadun et al., 2000) had described a small core area in southeastern Turkey where several cereal crops and some other crop plant progenitors were distributed, and the origin of domestication of cereal crops was reported to have existed in that area.

Özkan et al. (2002) investigated the core area to determine whether it was the place where additional founder crops of the Fertile Crescent also originated; they used 204 AFLP loci in 43 domesticated lines and 99 wild emmer (Turkey, 22; Israel, 37; Jordan, 8; Lebanon, 13; Syria, 18; and Iran, 1) populations of tetraploid wheats from their primary habitats. These researchers found that 15 of 19 Karacadağ lines were closely related to domesticated emmer wheat; as well, a line from a secondary habitat from İzmir was also closely related to cultivated emmer. Overall, the results indicated that there were two genetically distinct different wild emmer taxa: the central-eastern one, which includes Turkey and Iran, and the western one, which includes Israel, Jordan, Lebanon, and Syria. The results were consistent with previous studies (Abbo et al., 2002; Gopher et al., 2002; Heun et al., 1997; Lev-Yadun et al., 2000), suggesting that a small core area located in southeastern Turkey near the Tigris and Euphrates Rivers was the place of origin of tetraploid wheat

domestication. This place also covers the area for the domestication of the wild progenitors of other founder crops of pea, chickpea, lentils, and einkorn.

Özkan et al. (2005) investigated the domestication geography of tetraploid wheats using the same method (AFLP) as in their previous study (Özkan et al., 2002), but using a new set of wild emmer lines; 69 accessions from the collections of Mori et al. (2003), 7 lines from Dr. B. Gill, and 12 lines from Dr. A. Karagöz. *Triticum dicoccoides* was domesticated in the same core area previously described by Özkan et al. (2002), which was confirmed, and the domestication origin was considered as monophyletic. However, Salamini et al. (2004) suggested that the domestication origin of tetraploid wheats might have been possibly diphyletic, with two major phylogenetic tree topologies taking place by *T. durum* (free threshing) and *T. dicoccum* (hulled) lines. According to AFLP markers, two genetically very different taxa of *T. dicoccoides*—one with its primary habitat in Israel, Jordan, Lebanon, and Syria, named the western colony, and the other in Turkey, Iran, and Iraq, named the central-eastern colony (Sachs, 1953; Harlan & Zohary, 1966; Rao & Smith, 1968; cited in Özkan et al., 2005).

Cultivated emmer wheat, a domesticated form of hulled wheat, arose in the Fertile Crescent, and advances in knowledge and agricultural technology led to its spreading west, east, north, and south, giving rise to agriculture in the area. Examples of these sites are ca. 9000–7600 cal BP, Dhali Agridhi, Cyprus (Stewart, 1974); ca 9000–8050 cal BP, Franchthi Cave (Hansen, 1992); ca. 8650–8200 cal BP, Sesklo, Greece (Hopf, 1962; Kroll, 1981); and ca. 8650–8400 cal BP, Knossos, Crete (Sarpaki, 2009). Cultivated emmer wheat continued to spread around 4500 BP, and it arrived in the Balkan countries. Emmer wheat findings in Egypt date to ca. 7500–6650 cal BP in Fayum and 1325 BC in Tutankhamun's tomb (Caton-Thompson & Gardner, 1934; Täckholm, 1976; Germer, 1989; Hepper, 1990; Wetterstrom, 1993; De Vartavan, 2010). Toward the east, the botanical remains found at Neolithic sites in Caucasia and Transcaucasia were considered to be from ca. 7950–7150 cal BP at Aratashen and Aknashen, Armenia, and emmer wheat was one of the main crop elements (Wasylikowa et al., 1991; Hovsepyan & Willcox, 2008; cited in Zohary et al., 2012).

2.6 Conclusion

The wild wheat was first found in the Fertile Crescent region, the cradle of agriculture, and then evolution and domestication of wheat followed. The hybridization events by allopolyploidization between the species belong to genus *Triticum* and *Aegilops* taxa, evolved from a common ancestor about 3 MYA, giving rise to the wild tetraploid wheats and hexaploid spelt wheat species. The mutations existed in three major genes, which are brittle rachis (*Br*), tenacious glume (*Tg*), and non-free-threshing character (*q*) found in wild forms that led to the development of wheats with non-brittle rachis or with both non-brittle rachis and free-threshing modern wheats. Today, modern wheat varieties are distributed throughout the world, and it became a staple food and consumed as primary food and calorie source in the world.

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