Chi Yen · Junliang Yang

Biosystematics of Triticeae

Volume I. Triticum-Aegilops complex

Translated by
Zhongwei Yuan, Shunzong Ning,
Lianquan Zhang, Ming Hao and
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A Brief Introduction to *Biosystematics of Triticeae*

Biosystematics of Triticeae written by Prof. Chi Yen and Prof. Junliang Yang in Sichuan Agricultural University includes a series of five volumes. These volumes present the most valuable results of comprehensive studies on the tribe Triticeae (Poaceae), with a wide range of disciplines from traditional taxonomy and cytogenetics to molecular phylogeny. As I remember, to compile the five volumes is a great project that has lasted for nearly 20 years, only for data summarizing and book writing by Prof. Yen and Prof. Yang who have devoted their entire life to Triticeae. As a previous master student of the two professors, I am honored to brief the five volumes, although my introduction may only catch a small fraction of the essence in these great Triticeae books.

According to Prof. Yen and Prof. Yang, the traditional taxonomy and classification systems of plant species are essentially based on morphological characterization. Due to the dominant/recessive features of a gene that determines the phenotypes of a plant under certain environmental conditions, only those phenotypes controlled by the "visible" (dominant) genes can be observed and used in morphological characterization. The other proportion of "nonvisible" (recessive) genes may only be detected by other means, such as cytogenetic and molecular analyses. Therefore, traditional methods may not be able to resolve the true relationships of Triticeae. Many such examples are included in the books. Two well-documented species in the genus *Eremopyrum* (*Er. bonaepartis* and *Er. sinaicum*) show very similar morphological characters, but the former is a tetraploid (FsFsFF), and the latter is a diploid (FsFs) with different genomes. Without the assistance of a cytological method, classification between the two taxa is difficult. Similarly, the two perennial genera, *Elymus* (HHStSt) and *Campeiostachys* (HHStStYY), have different genomic combinations and phylogenetic origins, but to identify the two genera based only on morphology characters is extremely difficult. Furthermore, as mentioned earlier, phenotypes of a plant are usually the results of genotype-environment interaction. Plants with the same genetic background may show completely different phenotypes (morphological characters) in different environments. This conclusion can well be illustrated by some *Leymus* species that contain the same genomes (NsNsXmXm) but show considerable morphological divergence in different environments. Also, taxonomists classified *Leymus duthiei* and *L. arenarius* into different genera based only on morphological characters, but such a morphological-based treatment is misleading.

Consequently, traditional classification system of plant species needs improvement, combining research results from cytogenetic and molecular studies into classification, which is commonly referred to as biosystematics. Prof. Yen and Prof. Yang attempted to make a thorough revision for the tribe Triticeae in their books, including the worldwide research results and current achievements in the related fields for the last hundred years. Such a revision could truly reflex the biosystematic relationships of the tribe. Prof. Yen and Prof. Yang tried to absorb the available knowledge to formulate the natural classification and biosystematics of Triticeae for the first time. Such a classification system can reflect the direction of modern biosystematics.

Triticeae is an important tribe in the grass family (Poaceae). It includes the major cereal crops, such as wheat, barley, rye, and triticale—an artificially created crop—in addition to many valuable forage crops found in different genera, such as *Agropyron*, *Psathyrostachys*, *Elymus*, and *Leymus*. The knowledge of appropriate Triticeae taxonomy and biosystematics will serve as important theoretical bases for introducing alien germplasm harbored in Triticeae species for genetic breeding of wheat, barley, rye, and forage grass. Because of the economic values of many Triticeae species, a great amount of research efforts has been made to the Triticeae around the world. In return, a great success has been made in utilizing Triticeae than in other groups of plant species. Prof. Yen and Prof. Yang particularly mentioned Dr. Hitoshi Kihara who established the genome theory first in 1931 based on his wok of cytogenetics—the famous research on the important genera, *Triticum* and *Aegilops*, including their taxonomy, which significantly influenced the current biosystematics of Triticeae. However, there are still a lot of questions concerning the generic delimitation in this tribe (e.g., *Roegneria*) which remains to be addressed. Even for the relatively well-resolved genera, there are still some contradictory taxonomic treatments at the species level. The resolution of all these problems requires more detailed analyses at the specific and genetic levels.

Prof. Yen and Prof. Yang have compiled most available results from a great number of studies and literatures in the closely related fields. Their objectives are to review and rearrange the research data of Triticeae published over hundreds of years applying a modern scientific approach. They attempted to remain the truth and remove the false for deriving a more natural biosystematics of Triticeae. They wished that these books would serve as a useful reference for Triticeae scientists such as taxonomists, breeders, and geneticists. The set of books includes five volumes that are arranged for the convenience of compilation and utilization. Genera that are closely related or small with only a few species are arranged together in a volume. Genera and species with limited published research data are also included in the volumes for audience as references. All together, these volumes have included 30 genera, 2 subgenera, 464 species, 9 subspecies, and 186 varieties in Triticeae known and published to date.

Prof. Yen and Prof. Yang wish that these volumes can serve as highly qualified, valuable, and convenient handbooks for audience who are interested in Triticeae. Therefore, some important data or materials are listed in appendices as easy-accessing references. These volumes also include many illustrations, in addition to description, to help audience understand morphological features of the concerned taxa, which makes explanation more precise and obvious. With the fast development and progress in scientific research, some contents in these volumes may become out of date or even be disproved, but information presented in these volumes will surely provide a historical review of research in Triticeae. Prof. Yen and Prof. Yang have expressed their sincere wishes to receive comments and suggestions from audience concerning the information presented in these books.

Contents in each volume of the *Biosystematics of Triticeae* will be briefly introduced as follows:

Volume 1 introduces the historical classification of two genera, *Triticum* and *Aegilops*, two of the economically most important groups in the tribe. The main focus of the volume is on the taxonomy and generic relationships of the two genera. However, research data concerning the origin of common wheat as a crop are also presented and discussed.

Volume 2 introduces the following genera: *Secale*, *Triticosecale*, *Pseudosecale*, *Eremopyrum*, *Henrardia*, *Taeniatherum*, *Heteranthera*, *Crithopsis*, and *Hordeum*. Except for *Pseudosecale*, *Eremopyrum*, and *Hordeum*, species in other genera contain only one unique genome. The scientific name of *Pseudosecale* is revised from *Haynaldia* Durand following the "International Code of Nomenclature (ICN)." *Secale cereale* is a cereal crop domesticated by human comparatively recently but cultivated worldwide, particularly in regions with alpine climate and acid or desert land with poor soils, owing to its unique characteristics and wide adaptation. It is also planted in northeast Europe as raw materials for a special type of "Vodka," in addition to a particular type of bread widely found in the markets of Germany, Russia, and Poland. This crop is also used as popular forages. *Triticosecale*, widely referred to as "triticale"—a common but not a legal Latin name—is the first artificially synthesized cereal crop species. After nearly one century of studies and genetic improvement, it is cultivated as a cultivar at a considerable scale. According to the "International Code of Nomenclature for Cultivated Plants (ICNCP)," it should be appropriately treated as a species in a new genus with proper description.

Secale, *Pseudosecale*, and *Eremopyrum* are closely related genera based on their morphological classification. C. Linné classified *Pseudosecale villosum* and *Eremopyrum orientale* into *Secale*. However, these genera do not share a close relationship based on genetic and biosystematic studies, although species in these genera may have a parallel evolution status. These genera were therefore listed together in this volume, only for the convenience of their comparison and identification. A few small annual genera, such as *Henrardia*, *Taeniatherum*, *Heteranthelium*, and *Crithopsis*, may also have a parallel evolution status. These genera are the ephemerals evolved under the Mediterranean ecological conditions characterized by the special climate with warm and dry summers but warm and humid autumns, winters, and springs.

Hordeum is a large genus including both annual and perennial species. It comprises of four independent groups associated with four genomes (I, Xa, Xu, H genomes). Conventionally, species are treated in *Hordeum* because of their morphological similarities. *Hordeum* can be divided into four genera in the light of experimental biosystematics of its genomic constitution. However in this volume, *Hordeum* remains as a genus following the conventional classification but is divided into four groups based on their genome constitutions. Undoubtedly, H is the key genome of many species in the genus. *Hordeum vulgare* has a long history (~10,000 y) of cultivation. A great number of varieties have been produced under human selection. Different groups of varietal taxa are treated as cultivar groups or concultivar in this volume.

Volume 3 and the following volumes introduce all perennial genera and species. Volume 3 has two chapters. Chapter 1 includes *Kengyilia* and *Douglasdeweya* that are newly established genera. *Kengyilia*, separated from *Roegneria*, includes 8 newly described species and 2 varieties, as well as 17 new combinations. *Douglasdeweya* only includes two species. Based on cytological studies, *Kengyilia* contains the PStY genomes and *Douglasdeweya* the PSt genomes. Chapter 2 introduces three genera, *Agropyron*, *Austrolopyrum*, and *Anthosachne* that have unique biosystematic relationships. *Agropyron* contains the P genome that is the donor of other P-genome genera. *Austrolopyrum* contains the W genome that is the donor of other W-genome genera. *Anthosachne* contains the StWY genome. *Anthosachne* has genetic relationships with other genera such as *Australopyrm* (W genome), *Kengvilia* (PStY genome), *Douglasdeweya* (PSt genome) presented in this volume, *Pseudoroegneria* (St genome) and *Roegneria* (StY genome) in Volume 4, and *Elymus* (StH genome) and *Trichopyrum* (ESt genome) in Volume 5.

Volume 4 introduces the perennial genera, *Stenostachys*, *Psathyrostachys*, *Leymus*, *Pseudoroegneria*, and *Roegneria*, with different number of taxa. *Stenostachys* is a small genus endemic to New Zealand, containing the HW genome. *Psathyrostachys* contains the Ns genome. *Leymus* is a large genus, containing the NsXm genomes, with Ns genome donated by *Psathyrostachys*, but the donor of Xm genome is still unknown. Some researchers considered the Xm genome as a variant of the Ns genome because the two genomes share a large similarity. *Pseudoroegneria* contains an St genome—an important donor of *Roegneria*, *Elymus*, *Trichopyrum*, *Kengvilia*, *Douglasdeweya*, and *Anthosachne*. The donor of a Y genome present in *Roegneria*, *Kengvilia*, and *Campeiostachys* has not been found. Some researchers consider the Y genome being evolved from the St genome due to their close relationship, similar to the situation in wheat where the B genome is derived from the B^{SP} genome of *Aegilops speltoides*.

Volume 5 introduces nine unique genera: *Campeiostachys*, *Elymus*, *Pascopyrum*, *Lophopyrum*, *Trichopyrum*, *Hordelymus*, *Festucopsis*, *Peridictyon*, and

Psammopyrum. *Campeiostachys* was established by a Russian taxonomist, Василий Петрович Дробов, in 1941, with the type species *Campeiostachys schrenkiana*. Considering its HStY genomes, the taxonomic treatment of this genus should be natural. *Elymus* is an old genus established by Carl Linné in 1753, with the type species *Elymus sibiricus* (StH genomes). It is a the largest genus in Triticeae, possibly including 83 species, 20 varieties, and a number of taxa referred to as a "form" that may not be a natural taxonomic grade. *Elymus* has a wide distribution, including in South and North America, Eurasia, and Africa. The morphological characters of *Elymus* species vary remarkably due to significant differences in their habitats. Therefore, this is a polymorphic genus, similar to *Leymus*. Previously, taxonomists split *Elymus* into several genera, such as *Elymus*, *Sitanion*, and *Elytrigia*, based merely on morphological variation. They also treated species with a single spikelet per rachis as *Agropyron* or *Roegneria*, although all these species contain StH genomes and should be included into the same genus *Elymus*.

Pascopyrum includes one wild grass species (StHNsXm genomes) that is one of the important constructive species of the grassland in the northwest parts of North America. It was derived from hybridization between allotetraploids of *Elymus* and *Leymus* based on genomic analysis. *Lophopyrum* and *Thinopyrum* are two genera published in 1982, which contain different genomes, namely, an E genome and a J genome, respectively. However, studies showed that the E and J genomes are very close. Thus, they should be merged into one genus, *Lophopyrum*, and treated as subgenus. The allopolyploid *Trichopyrum* was treated as a genus from . *Trichophorum* of *Elytrigia*. Species in the genus contains ESt genomes, obviously evolved from natural hybridization between a *Lophopyrum* species (E genome) and a *Pseudoroegneria* species (St genome).

Many taxonomists consider *Elytrigia* as an independent genus, but it consists of many taxa with different genomes. This volume treats *Elytrigia* species into other genera based on their genomes. For example, the type species, *Elytrigia repens* ($HHSt^1St^1St^2St^2$ genomes), is included in *Elymus*. Other species are included into different genera according to their genomic constitutions. Obviously, *Elytrigia* is an artificial genus established by taxonomists only based on morphological characters, which does not naturally reflect the true relationships of these species.

Hordelymus is a monotypic understory genus found in central to northern Europe. Its habitats and morphological characters are very similar to those of understory *Leymus*, but *Hordelymus* does not have a close biosystematic relationship with *Leymus*. Á. Löve used to believe that this genus was derived from the hybridization of *Taeniantherum* and understory *Hordeum*, possibly containing HT genomes. In 1994, R. von Bothmer et al. suggested a distant relationship of *Hordelymus* with either of the two genera based on studies of hybridization and C-banding patterns of karyotypes. Actually, *Hordelymus* contains the XoXr genomes having completely different origin.

Festucopsis (C. E. Hubbard) Melderis is a diploid genus with a unique genome, which Á. Löve named as an L genome. *Peridictyon* is a monotypic genus that was separated from *Festucopsis* by Seberg et al. based on its Xp genome. The two genera are mainly distributed on Balkan Peninsula in southeast Europe, although *Festucopsis* can expand westwards to the north part of Morocco in North Africa. *Psammopyrum* is an allopolyploid genus distributed in western and southern Europe. It is a perennial grass occurring in the coastal sand beach and brackish swamp. This genus includes only an allopolyploid species (EL genomes) derived from the natural hybridization between *Lophopyrum* and *Festucopsis* species.

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2013, 3

Bao-Rong Lu

Preface to the Second Edition[1]

Scientific research has been developing continuously. With historical progress and the development of science and technology, a scientific book will inevitably present some outdated contents or even wrong views or conclusions. The limitation of the author's knowledge will also produce some errors or inappropriate narratives. The authors hope that the readers can correct them.

The first volume of *Biosystematics of Triticeae* was published 13 years ago. Since that time, some great breakthroughs have been achieved in wheat scientific research around the world. For instance, Professor Wuyun Yang in Sichuan Academy of Agricultural Sciences developed the commercial variety Chuanmai 42 in 2003 by using synthetic hexaploid wheat obtained from CIMMYT scientists. This is the first documented release of a wheat variety derived from synthetic hexaploid wheat. Due to the outstanding economic traits including high yield, the varieties have been used in wheat production in a large scale in Southwest China. Synthetic hexaploid wheat is artificially created by crossing of *Triticum turgidum* with wild *Triticum tauschii* (*Aegilops tauschii*). Compared to modern varieties that have been improved over hundreds of years, synthetic hexaploid wheat has a bad genetic background harboring many unfavorable genes. Its success utilization in modern breeding provides new viewpoints and ways for rational and effective utilization of wild resources. The related works should be added to the reprint manuscript.

There are still many mistakes and shortcomings in the first edition of other volumes. Although there are errata, it is better to reprint and rearrange them.

Chengdu, Sichuan, China — Chi Yen
Ya'an, Sichuan, China — Junliang Yang

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[1] The reprint manuscript was completed in Davis, California, USA, in June 2012.

Preface to the First Edition[1]

Modern Systematics of Triticeae is based on cytogenetics, molecular biology, and other related disciplines to explore the phylogenetic relationships of Triticeae and their natural classification.

Triticeae is an important tribe in the grass family (Poaceae). It includes the major cereal crops, such as wheat, barley, rye, and triticale—an artificially-created crop, in addition to many valuable forage plants found in different genera such as *Agropyron*, *Psathyrostachys*, *Elymus*, and *Leymus*.

The knowledge of Triticeae taxonomy and biosystematics serves as an essential theoretical base for introducing alien germplasm in Triticeae species for genetic improvement of wheat, barley, rye, and forage grass.

Because of the highly economic values of many Triticeac species, a great amount of research efforts has been made to the Triticeae around the world. In return, a great outcomes has been achieved in Triticeae. Dr. Hitoshi Kihara established the genome theory in 1931 on basis of his great works on genera *Triticum* and *Aegilops.* Genome theory laid on a foundation for the current cytogenetics and biosystematics. Up to now, however, there are still a lot of biosystematics questions remaining to be addressed in Triticeae, such as the generic treatment on *Roegneria*. Even for well-investigated genera, there are still some contradictory taxonomic treatments at the species level. For instance, where did the B genome of *Triticum* come from? For a long time, there have been very different opinions. Recent studies on molecular genetics, especially whole DNA in situ hybridization and DNA sequence analysis, have basically reached a conclusion that B was divergent from S genome. However, the nomenclature of B and S genome has not been unified for the time being.

Authors have compiled results from a great number studies and literatures in the closely related fields. The objectives are to provide reference for beginners engaged in this research, as well as for breeders. The set of books includes five volumes that are arranged for the convenience of compilation and utilization. Genera that are

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[1] Chi Yen initiated the manuscript works in the West Lake in midsummer 1983.
Revised in August 1998 in Brookings, South Dakota, USA

closely related or small with only a few species are arranged together in a volume. Genera with limited research data are left to be written when the time is ripe.

Authors wish that the set of books can serve as highly qualified, valuable, and convenient handbooks for audience. Therefore, some important data or materials are listed in appendices as easy-accessing references. The books also include many illustrations, in addition to description, to help audience understand morphological features of the concerned taxa, which makes explanation more precise and obvious.

With the fast development and progress in scientific research, some contents in these volumes may become out of date or even some views or conclusions be proved to be wrong, which need to be revised in the future. Due to the limitation of the author's knowledge, there may also be some errors or inappropriate narratives. we hope readers can correct them.

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Chi Yen
Junliang Yang

About the Book

When we do scientific research, our first problem is the object of the study. For instance, for a wheat material investigated, we ask the following questions: What kind of wheat are we studying? What is its phylogenetic relationship with other wheat materials and other cereal plants? These are, of course, the first two questions that need to be answered clearly. These are the questions of taxonomy, which are also an issue of biological systematics.

Scientific taxonomy has been established since the sixteenth century. The scientific classification of wheat and its related species in *Aegilops* was established after the genera *Triticum* L. (using *T. aestivum* L. as the lectotype) and *Aegilops* L. (using *Aegilops ovata* L. as the lectotype) were published in Linné's book *Genera Plantarum* in 1737. Wheat is an ancient crop with tens of thousands years of cultivation history. However, its genera and species relationship with other related species have been basically clarified with the development of bioscience, especially in cytogenetic and molecular genetics. It also thanks experimental methods to illustrate how cultivated wheat originated.

The following is a brief introduction to the research achievements on the classification of wheat and *Aegilops* and the origin of wheat according to the historical development of taxonomy.

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Chapter 1
Classical Morphological Taxonomy

Before nineteenth century, biological science was restricted by the level of development and technical conditions. The classical taxonomy based on comparative morphology was the leading discipline of the development of biological science. The research method is based on the comparative morphological study of herbarium, with reference to geographical distribution and other collecting records to identify similarities and differences, thus to classify and identify species. Although using this shallow method can also reflect natural system relations to some extent, it is impossible to clarify complex problems between species by this strategy, which inevitably brings many wrong results.

Before Linné, according to the characteristics of hulled and naked grain, botanist called the cultivated hulled spelt wheat as *Zea* (not the present-day *Zea* genus containing corn), and called the naked grain wheat as *Triticum*. In 1753, *Zea* was canceled by Carl von Linné in his book *Species Plantarum*, while spelt wheat and *Agropyron* were classified into *Triticum*. In the version 1 of *Species Plantarum*, the cultivated wheat was classified into five species, i.e., *Triticum aestivum* L., *T. hybernum* L. (winterness wheat), *T. turgidum* L., *T. spelta* L., and *T. monococcum* L. *T. polonicum* L. was added in version 2 published in 1763. The species *T. compositum*, L. fils. was added in *Supplement of Species Plantarum* in 1781 by his son.

In the research on wheat-related species, two goat grasses were recorded by Scheuchzer J. in his book *Agrostographia* in 1719. They were later named as *Aegilops ovata* L. by Linné and *Ae. triaristata* Willd. by Willdenow K. L. In 1728, another goat grass, which was named as *Ae. squarrosa* L. later by Linné, was recorded by Buxbaum in his book *Plantarum minus coginitarum* (Cent. I: p31). The two pioneers' records preceded the binomial nomenclature established by Linné, so they were informal nomenclature.

In 1753, Linné published five goat grass species in his *Species Plantarum*, i.e., *Ae. ovata* L., *Ae. caudata* L., *Ae. squarrosa* L., *Ae. triuncialis* L., and *Ae. incurva* L. In its second edition in 1763, *Ae. incurva* L. was combined into the genus *Lepturus*, so only four remained. Meanwhile, the specimen of *Ae. squarrosa* L. includes three different taxonomic groups mixed together, all called *Ae. squarrosa*

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L. Until 1837, Tausch I. F. made them separately, one retained the name *Ae. squarrosa* L. (specimen No. LINN 1218–9) and the other two groups were identified as two new species.

In 1769, Schreber J. C. D. combined *Ae. triuncialis* L. and *Ae. squarrosa* L. as a same species and *Ae. triuncialis* L. and *Ae. triaristata* Willd. as a same species in his book *Beschreibung der Graser*. Nowadays, it seems that his former opinion is correct, but the latter one is inappropriate.

In 1772, Scopoli J. A. combined *Ae. ovata* L. into the genus *Phleum* and renamed as *Phleum aegilops* Scopoli in his book *Flora Carniolica* (Volume 1, p55). However, the plants of *Ae. triaristata* Willd. were also mixed within this taxonomic group together.

In 1775, Swedish scholar, born in Finland, Forsskål Petter (or Petrus, or Pehr) published the new species *Triticum bicorne* Forssk. in *Flora Aegyptiaco Arabica*. This was the first discovery of species in the Sitopsis group.

In 1778, Lamarck J. B. M. followed the view of many cultivated scientists that winterness and springness could not be used as a standard to distinguish species. He combined *T. aestivum* L., *T. hybernum* L., and *T. turgidum* L. into one species named as *T. sativum* Lam. (cultivated wheat) that was published in *Flore Francaise* (Volume 3, p625). It now appears that Lamarck's combination of *T. aestivum* L. and *T. hybernum* L. was right, but it was obviously wrong to merge *T. turgidum* L. together. In page 632, he renamed *Ae. triuncialis* L. as *Ae. elongate* Lam.

In 1786, Lamarck classified *Triticum* as five species in *Encyclopedie Methodique* (Volume 2), i.e., *T. sativum* Lam. (including Linné's *T. aestivum* L, *T. hybernum* L., and *T. turgidum* L), *T. compositum* L. fils., *T. polonicum* L., *T. spelta* L., and *T. monococcum* L. In that book, *Ae. squarrosa* L., depicted in Figure 839, included other plants that were renamed as *Ae. juvenalis* (Thellung) Eig later as Eig A.

In 1787, French botanist Villars, Dominique divided *Triticum* into seven species in the second volume of *Histoire des Plantes de Dauphine, Grenoble, Lyon et Paris,* including *T. vulgare* (=*T. aestivum* L.), *T. touzelle* (=*T. hybernum* L.), *T. turgidum* L., *T. maximum* (close to *T. polonicum* L.), *T. compositum* L. fils., *T. spelta* L., and *T. monococcum* L. In the same year, Roth A. W. renamed Linné's *Ae. ovata* L. as *Ae. geniculata* Roth in *Botanische Abhandlungen und Beobachtungen* (p45~46). However, it named another species, later called *Ae. triaristata* Willd., as *Ae. ovata* Roth.

In 1788, Austrian scholar Winterl, Jacob Joseph recorded the new species *Ae. nova* Winterl in *Index Horti Botaniei Universitatis Hungaricae Quae Pestiniest*. However, this species was later renamed as *Ae. cylindrica* Host. According to the annotation of Mary A. Chase index, there are many species named as "nova" throughout the article, even more than one in a same genus, for instance three for *Silene* and two for *Heleborus*. This indicates that "nova" was not used as a species name, but only to indicate that it was a new species. Therefore, in 1802, *Ae. cylindrica* Host named by Host N. T. was a valid species name.

In 1789, Franz von Paula von Schrank thought that *Triticum* has only two species in *Baier Flora* (Volume 1, p387), i.e., *T. cereal* including varieties *aestivum* and *hybernum* and *T. spelta*. He named the cultivated emmer wheat in Wurtemberg as

T. dicoccon. However, he was not sure whether it was an independent species. He said if it was not an independent species, it should be classified into *T. spelta*.

In 1791, Cavanilles, Antoni Jos drew and described *Ae. squarrosa* L. in *Icones et Descriptiones Plantarum quae aut Sponte in Hispania Crescunt aut in Hortis Hosppitantur* (p62, table 90, figure 2). However, this species was later named as *Ae. ventricosa* Tausch. Early botanists often confused *Ae. triuncialis* L, *Ae. squarrosa* L., *Ae. caudata* L, *Ae. cylindrica* Host, and *Ae. ventricosa* Tausch with each other.

In 1798, French botanist Desfontaines, René Louiche in *Flora Atlantica* (Volume 1) treated durum wheat as an independent species, i.e., *T. durum* Desf., that is still used today.

In 1802, Nicolaus Thomas Host identified *Ae. cylindrica* Host as an independent new species in *Icones et Descriptiones Graminum Austriacorum Vienna* (Volume 2, p5~6, fig 7).

In 1805, Nicolaus Thomas Host classified *Triticum* as seven species in the third volume of *Icones et Descriptiones Graminum Austriacorum Vienna*, including *T. vulgare* (= *T. aestivum* L. + *T. hybernum* L.), *T. compositum* L. fils., *T. turgidum* L., *T. zea* (= *T. spelta* L.), *T. spelta* (= *T. amyleum* Ser.), *T. polonicum* L., and *T. monococcum* L. In 1809, four species were added in volume 4, including *T. hordeiforme* (= a type of durum wheat), *T. villosum* (a durum wheat with hair glume and white spike), *T. compactum*, and *T. atratum* (= a type of *T. turgidum* with brown dark or black hair glume). In 1805, in his book *Synopsis Plantarum*, he still followed Lamarck's *T. sativum*. In his subsequent book *Icones et Descriptiones Graminum Austriacorum Vienna*, the emmer wheat were divided out. Meanwhile, *T. aestivum* and *T. hybernum*, which were wrongly divided into two species by Linné, were correctly combined as one species.

In 1806, Sibthorp J. and Smith J. published the new species *Ae. comosa* Sibth. et Smith in *Flora Graeca* (Volume 1, p71–75, tables 93–95). Meanwhile, they described *Ae. ovata* L., *Ae. cylindrica* Host, and *Ae. comosa* Sibth. et Smith with drawing pictures.

In 1809, Italian botanist Bayle-Barelle, Giuseppe, a professor at the Paris University, divided *Triticum* as two groups in his book *Monografia Agronomica dei Cereali Milan*. He described 11 species as well as 3 supplemental species. The 14 species were *T. compositum* L. fils., *T. turgidum* L., *T. polonicum* L., *T. cerulescens* Bayle-Barelle (= a variety of durum wheat), *T. tomentosum* Bayle-Barelle (= emmer wheat with hair glume), *T. candidissimum* Aduini (= durum wheat with red grain and hairless glume), *T. creticum silvestre* Baninio ex Bayle-Barelle (= *T. sylvestre creticum* C. Bauhin, with compact spikes without awn), *T. farrum* Bayle-Barelle (a kind of hulled spelta wheat), *T. monococcum* L., *T. spelta* L., *T. bicorne* Forsskl., *T. fumonia* Beguillet, *T. blate* de caure Spagnuoli, and *T. sativum* Pers. (= *T. hybernum* L.). The last species was divided into four varieties, i.e., *T. sativum* var. *mutica alba* Bayle-Barelle, *T. sativum* var. *mutica alba tomentosa* Bayle-Barelle (*T. angilicum* Arduini), *T. sativum* var. *ruffa aristata* Bayle-Barelle, and *T. sativum* var. *ruffa mutica* Bayle-Barelle.

In 1816, Spanish botanist Lagasca y Segura Mariano described 16 *Triticum* species in his book *Genera et Species Plantarum, Madrid.* The four species are hulled type, including *T. monococcum* L., *T. cienfuegos* Lag., *T. bauhini* Lag., and *T. spelta* L. Ten are naked grain type, including *T. hybernum* L., *T. aestivum* L., *T. linneanum* Lag., *T. turgidum* L., *T. fastuosum* Lag., *T. gaertnerianum* Lag., *T. platystachyum* Lag., *T. cochleare* Lag., *T. cevallos* Lag., and *T. durum* Desf. The remaining two *T. polonicum* L. and *T. spinulosum* Lag. have two-lobed long glume.

In 1817, Johann Jakob Roemer and Julius Hermann Schultes thought *Triticum* had 21 species in *Caeoli a Linné Systema Vegetabilium Secundum Classes, Ordines, Genera, Species, cum Charcteribus, Differtiis et Synonymiis* (Volume 2). They mainly followed the specific name of Lagasca and Host. Only *T. siculum* Roemer et Schultes was newly named. However, this species was actually durum wheat.

In 1818, 16 species were described in Gustav Schübler's book *Characteristica et Descriptiones Cerealium*. He divided *Triticum* as two groups according to the character of the naked and hulled grain. Group I was for naked grain, including *T. mutica* Schübler (= awnless common wheat, a. *aestivum* Schübler; b. *hybernum* Schübler), *T. aristatum* Schübler (= awned common wheat, a. *aestivum* Schübler; b. *hybernum* Schübler), *T. sibiricum* Schübler (a precocious spring wheat from Siberia, it was actually *T. aestivum* L.), *T. velutinum* Schübler (= common wheat), *T. compactum* Host (a. *aristatum* Schübler; b. *muticum* Schübler), *T. turgidum* L., *T. hordeiforme* Host (= durum wheat), *T. durum* Lag (An Arabian winter durum wheat), *T. siculum* Schmidt (a durum wheat produced in Sicily), *T. compositum* L., and *T. polonicum* L. Group II was for hulled wheat, including *T. spelta* L. [a. *mutica* Schübler et Mertens, (a)*alba* Schübler and(b)*rubra* Schübler; b. *aristata* Schübler; c. *velutina* Schübler; d. *aestiva* Schübler], *T. monococcum* L., *T. dicoccum* Schrank (a. *album* Schübler; b. *rufum* Schübler), *T. atratum* Host, and *T. tricoccum* Schübler (= *turgidum*).

In 1818, Spanish botanist Clemente y Rubio, Simon de Rojas thought *Triticum* had 20 species in *Herrera's Agriculture General, Madrid*. Among them, he continued to use *T. monococcum* L., *T. spelta* L., *T. hybernum* L., *T. aestivum* L., *T. turgidum* L., *T. polonicum* L., and *T. durum* Desf. In addition, some specific names that had been published 2 years ago by Lagasca were republished in his own name. These species included *T. Cienfuegos*, *T. bauhinia*, *T. linneanum*, *T. gaertnerianum*, *T. platystachyun*, *T. cochleare*, *T. cevallos*, *T. fastuosum,* etc. Five of the twenty species were newly named by him, i.e., *T. hornemanni* Clemente, *T. forskalei* Clemente, *T. arias* Clemente, *T. koeleri* Clemente, and *T. horstianum* Clemente.

In the same year, Seringe N. C. thought that it is necessary to revise the classification strictly according to the morphological differences. He divided *Triticum* into only eight species in his two books *Melanges Botaniques* and *Monographie des Cereale de la Suisse, Berne et Leipzig*. Section I—Framenta included *T. vulgare* Vill., *T. turgidum* L., *T. durum* Desf., and *T. polonicum* L.; section II—Speltae included *T. spelta* L., *T. amyleum* Ser., *T. monococcum* L., and *T. venulosum* Ser that might be an emmer wheat from India and Ethiopia, close to *T. monococcum* L., but with large and obviously interconnected veins.

In 1820, Presl, Jan Svatopluk named the new species *Ae. echinata* Presl in his book *Cyperaceae et Gramineae Siculae* (p47). However, it was actually *Ae. triuncialis* L.

In 1824, Metzger, Johann continued to use Seringe's classification in his book *Europaeische Cerealien, Heidelberg*. However, he canceled *T. venulosum* Ser that had problems in classification.

At the same year, Delile, Alire Reffeneau recorded *Triticum bicorne* Forsskål in *Description de l′ Égypte* (Volume 19, p182–184, table 5 and figure 1).

In 1825, French scholar Francois Vincent Raspail recorded *Ae. ovata* L., *Ae. triuncialis* L., and *Ae. squarrosa* L. in *Annales des Sciences Naturelles Botanique Vegetale* (ser 1, 5: 435). Similar to Linné's classification, *Ae. squarrosa* L. was also mixed with *Ae. ventricosa* Tausch.

In 1827, German botanist Johann Friedrich Link continued to use Seringe's classification in *Hortus Regius Botanicus Berolinensis, Descriptus* (volume 1). However, he added the species *T. compactum*.

In 1833, Link obtained specimens of wild einkorn wheat from the Balkans and Asia Minor. He published it as a new genus and new species *Crithodium aegilopoides* Link in *Linneaea* 9: 132 (1834).

In 1834, Bertolini, Antonio published *Ae. neglecta* Requien ex Bertolini based on the previous works of French botanist Esprit Requien, and the hybrid *Ae. triticoides* Requien ex Bertolini between *Triticum* and *Aegilops* in *Flora Italica* (Volume 1, p787–788).

In 1834, Reichenbach H.G. took *Ae. cylindrica* Host as the synonym of *Ae. caudata* L. in *Agrostographia Germanica*. In other words, He had mixed *Ae. cylindrica* Host with *Ae. Caudata* L. He also made the same treatment in *Deutschlands Flora* (1847, Bd II: 23, table VIII).

In 1837, Ignaz Friedrich Tausch carefully compared the specimens of Linné for *Ae. squarrosa* L. He found three different groups from the specimens. One of them still keeps Linné's specific name, i.e., *Ae. squarrosa* L. (specimen LINN 1218.9). He definitely thought that the other two were not *Ae. squarrosa* L. The one with spikelets protruded laterally, obviously different from the Linné's specimen LINN 1218.9, was named as *Ae. ventricosa* Tausch. He treated the third group as a new species, namely *Ae. speltoides* Tausch. His research also proved it was correct that *Ae. triuncialis* L and *Ae. triaristata* Willd. were divided into two species. These findings were published in *Flora*, 20: 107–109.

In 1841–1842, Seringe published his monograph *Descriplions et Figueres des Cereales Europeenes, Paris-Lyon*. He made a big change in the classification. He reclassified previously identified eight species into three genera. Genus *Triticum* included *T. vulgare* Willd. (= *T. aestivum* L. + *T. hybernum* L. + *T. compactum* Host), *T. turgidum* L., *T. durum* Desf., and *T. polonicum* L. Genus *Spelta* included *S. vulgare* Seringe (= *T. spelta* L.) and *S. amylea* Seringe (= *T. dicoccon* Schübler). Genus *Nivierria* included *N. monococcum* Seringe and *N. venulosa* Seringe.

In 1842–1852, Italian botanist Visiani, Roberto de, born in Dalmatia, Yugoslavia, published two new species in *Flora Dalmatica* (1842, vol 1, p90, table 1 and figure 2; 1852, vol 3, p344–345), namely *Ae. biuncialis* Vis and *Ae. uniaristata* Vis.

In 1844, Swiss botanist Pierre Edmond Boissier published two new species in *Diagonses Plantarum Orientalium Novarum* (ser I, 5: 73–74), namely *Ae. aucheri* Boiss. and *Ae. mutica* Boiss.

In 1844–1846, French botanist Hippolyte-Francois Comte de Jaubert and Ḗdouard Spach published their study on goat grass genus in *Illustrationes Plantarum Orientalium* (Vol 3, 1844–1846, p16, table 200; Vol 4, 1850–1853, p10–23, tables 309–316). They combined *Triticum bicorne* Forsskål into the goat grass genus and changed its name as *Ae. bicornis* (Forsskål) Jaubert et Spach. They recorded *Ae. squarrosa* L., *Ae. cylindrica* Host, *Ae. caudata* L., *Ae. ventricosa* Tausch, *Ae. comosa* Sibth et Smith, and *Ae. speltoides* Tausch and published the new species *Ae. macrura* Jaubert et Spach, *Ae. loliacea* Jaubert et Spach, and *Ae. tripsacoides* Jaubert et Spach. However, *Ae. macrura* Jaubert et Spach was exactly *Ae. speltoides* Tausch; *Ae. loliacea* Jaubert et Spach was later named as a subspecies of *Ae. mutica* Boiss. by Жуковский П. М., i.e., *Ae. mutica* Boiss. ssp. *loliacea* (Jaub. et Spach) Zhuk.; *Ae. platyathera* Jaubert et Spach was exactly *Ae. crassa* Boiss.; while *Ae. tripsacoides* Jaubert et Spach was exactly *Ae. mutica* Boiss.

In 1846, Italian scholar Savignone in *Atti Ott Riun Sci Ital, Genova* (p138) published the new species *Agropyrum tournefortii* Savig., which was a taxonomic group of *Ae. speltoides* Tausch identified by Tausch in 1837. In page 601–602 of this book, he published *Agropyrum ligusticum* Savig. In 1864, this species was changed as *Aegilops ligustica* (Savig.) Cosson by Cosson.

In the same year, Boissier published three new species in *Diagnoses plantarum orientalium Novarum* (ser I, 7:129), namely *Ae. kotschyi* Boiss., *Ae. persica* Boiss., and *Ae. crassa* Boiss.

In 1847, Antonio Bertoloni changed *Agropyrum ligusticum* Savig. as *T. ligusticum* (Savig.) Bertol. in *Flora Italica* (vol VI, p622).

In 1848, Italian scholar Filippe Parlatore recorded *Ae. ovata* L., *Ae. triuncialis* L., *Ae. triaristata* Willd., *Ae. cylindrica* Host, *Ae. ventricosa* Tausch, *Ae. triticoides* Requ., and *Triticum ligusticum* Bert. in *Flora Italiana* (Vol 1, p507–516). He published the new combination of *T. aucheri* (Boiss.) Parl. and the new species of *Ae. fragilis* Parl. The new species was actually *Ae. ventricosa* Tausch.

In 1849, French botanist Ernest Saint-Charles Cosson published *Ae. tauschii* Cosson in *Notes sur quelques plantes DE France critiques, rares ou nouvelles, fase* (II, p69). He carefully re-identified the specimens respectively collected from Iberia (Buxbaum, J. C. loc. Cit., adjacent to the Caucasus, present Georgia) and Taurra (Tausch, I. F. loc. Cit.). The two specimens were confused as *Ae. squarrosa* L. by von Schreber J. C. D. (1769) and Tausch I. F. (1837). Again, James Edward Smith and John Sibthorp confused them as *Ae. caudata* L. in 1806 (*Flora Graeca*, I: 76). The specimens from Taurra were then identified as *Ae. cylindrica* Host var. *taurica* Roemer et Schultes by Johann Jakob Roemer and Josef August Schultes in 1817 (*Caroli a Linne systema vegetabilium secundum classes, ordines, geners, species, Cum characteribus, differtiis et synonymiis* (II: 77). Cosson found that the two specimens were neither *Ae. squarrosa* L. or *Ae. caudata* L., nor *Ae. cylindrica* Host. Of course, it could not be the varieties *Ae. cylindrica* var. *taurica*. He hence named the two specimens as a new species called *Ae. tauschii* Cosson.

In 1850, French wheat breeder de Vilmorin L. L. thought that *T. venulosum* Ser. should not become an independent species in the book *Essai d'um catalogue methodique et synonymique des froments* (Paris), according to his observations on specimen and cultivation experiments. He thought that *Triticum* only contained seven species, i.e., *T. sativum*, *T. turgidum*, *T. durum*, *T. polonicum*, *T. spelta*, *T. amyleum*, and *T. monococum*.

In 1850–1853, Jaubert and Spach published their *Aegilops* classification system in *Illustrationes plantarum orientalium* (Vol 4, p10–23). They divided this genus into six subgenera and eleven species. The subgenus *Sitopsis* Jaub. et Spach included *Ae. bicornis* (Forsk.) Jaub. et Spach and *Ae. speltoides* Tausch; subgenus *Cylindropyrum* Jaub. et Spach included *Ae. squarrosa* L., *Ae. cylindrica* Host, and *Ae. caudata* L.; subgenus *Gastropyrum* Jaub. et Spach included *Ae. platyathera* Jaub. et Spach (= *Ae. crassa* Boiss. var. *macrathera* Boiss.) and *Ae. ventricosa* Tausch; subgenus *Comopyrum* Jaub. et Spach contained the species *Ae. comosa* Sibth. et Smith; subgenus *Uropyrum* Jaub. et Spach contained *Ae. macrura* Jaub. et Spach; subgenus *Amblyopyrum* Jaub. et Spach included *Ae. loliacea* Jaub. et Spach and *Ae. tripsacoides* Jaub. et Spach. *Ae. macrura* is the only one species in subgenus *Uropyrum*. This species was a variant of *Ae. speltoides* Tausch. Therefore, this subgenus doesn't actually exist. *Ae. loliacea* and *Ae. tripsacoides* were also two variants of *Ae. mutica* Boiss.

In 1853, August Heinrich Rudolph Grisebach recorded *Ae. squarrosa* L. and published a new variety β *meyeri* Griseb. in *Gramineae ex Ledebour Flora Rossica* (Vol. IV). The specific name of this new variety should be *Ae. tauschii* Cosson, rather than the misused *Ae. squarrosa* L.

In 1853–1854, French botanist Dominique Alexandre Godron in *Florula Juvenalis*, Ed. I (1853), Ed. II (1854), recorded *Ae. ventricosa* Tausch, *Ae. cylindrica* Host, *Ae. tauschii* Cosson, changed *Ae. speltoides* as *Ae. agropyroides* Godron, changed a variety of *Ae. ovata* L. as *Ae. echinus* Godron, and published the new species of *Triticum emerginatum* Godron.

In 1855, the German botanist Ernest Gottlieb Steudel recorded 32 species of *Aegilops* in *Synopsis plantarum graminearum* (p354–356), namely *Ae. ovata* L., *Ae. lorenti* Hochst (= *Ae. biuncialis* Vis.), *Ae. triaristata* Willd., *Ae. neglecta* Requien (= *Ae. triaristata* Willd.), *Ae. triuncialis* L., *Ae. echinata* Presl (= *Ae. triuncialis* L.), *Ae. triticoides* Requien, *Ae. intermedia* Steud. (= *Ae. biuncialis* Vis.), *Ae. uniaristata* Steud. (= *Ae. uniaristata* Vis.), *Ae. hordeiformis* Steud. (= *Triticum monococcum* L.), *Ae. kotschyi* Boiss., *Ae. singularis* Steud. (= *Ae. tauschii* Cosson), *Ae. squarrosa* L., *Ae. caudata* L. (this species should be *Ae. cylindrica* Host), *Ae. macrura* Jaub. et Spach (= *Ae. speltoides* Tausch), *Ae. cylindrica* Host (this species should be *Ae. caudata* L.), *Ae. tauschii* Cosson, *Ae. bicornis* (Forsskål) Jaub. et Spach, *Ae. speltoides* Tausch (it refers to *Ae. speltoides* var. *ligustica*), *Ae. crithodium* Steud. (= *Triticum monococcum* L.), *Ae. ventricosa* Tausch, *Ae. mutica* Boiss., *Ae. crassa* Boiss., *Ae. aucheri* Boiss. (= *Ae. spetoides* var. *aucheri*), *Ae. pltyathera* Jaub. et Spach (= *Ae. crassa* var. *macrathera* Boiss.), *Ae. agropyroides* Godr. (= *Ae. speltoides* Tausch), *Ae. tripsacoides* Jaub. et Spach (= *Ae. mutica* Boiss.), *Ae. loliacea* Jaub. et Spach (= *Ae. mutica* Boiss.), *Ae. comosa* Sibth. et Smith, *Ae. cannata* Steud. (= *Ae. comosa* Sibth. et Smith), *Ae. echinus* Godr. (= *Ae. ovata* L.), and *Ae. fluviatilis* Blanq. (it should belong to the genus *Rottboellia*). It seemed that none of the new species established by him was valid.

In 1855, Jean Charles Marie Grenier and Dominque Alexandre Godron placed *Aegilops* into *Triticum* as a group, namely Section *Aegilops*, in *Flora DE France* (vol 3, p601–603). In his treatment, *T. ovatum* Godr. et Gren. replaced *Ae. ovata* L., *T. triaristatum* Godr. et Gren. replaced *Ae. triaristata* Willd., *T. triunciale* Godr. et Gren. replaced *Ae. triuncialis* L., and *T. caudatum* Godr. et Gren. replaced *Ae. caudata* L.

In 1857, Godron D. A. changed *T. speltoides* Godr. as *Ae. speltoides* Tausch in *Florula Massil advent*, Mem. soc Emul. Doubs [3. Ser. II: 34 (48)].

In 1860, Johan Martin Christian Lange published the new variety *Ae. ovata* L. var. *latiaristata* Lange in his article "Pugillus plantarum imprimis hispanicarum" (Nat. For. Kjob. 2 Aart, II: 56).

In 1864, *Ae. triaristata* Willd. was considered as a variety of *Ae. ovata* L., i.e., *Ae. ovata* L. var. *vulgare* Lange (= *Ae. ovata* L.) and *Ae. ovata* L. var. *triaristata* Lange (= *Ae. triaristata* Willd.) by Ernest Saint-Charles Cosson in his article "Appendix Florae Juvenalis altera" (Bull. Soc. Bot. France, 11: 163).

In 1866, German botanist Friedrich Georg Christoph Alefeld in his book *Landwirtschaftliche Flora, Berlin*, treated polish wheat as new genus, named *Deina*, with the specific name *D. polonica*. All of the other wheat was merged into one species—*T. vulgare*. He used the trinomial nomenclature to name nine subspecies, namely *T. vulgare durum*, *T. vulgare turgidum*, *T. vulgare compositum*, *T. vulgare compactum*, *T. vulgare muticum*, *T. vulgare aristatum*, *T. vulgare dicoccum*, *T. vulgare monococcum*, and *T. vulgare spelta*.

In 1868, French botanist Jordan, Alexis Claude Thomas, and Jules Pierre Fourreau published 11 new species of goats grass genus in "*Breviarium plantarum novarum*" (fasc. II: 128~132), namely *Ae. nigrescens* Jord. et Fourr., *Ae. divaricata* Jord. et Fourr., *Ae. sicula* Jord. et Fourr., *Ae. procera* Jord. et Fourr., *Ae. virescens* Jord. et Fourr., *Ae. erratica* Jord. et Fourr., *Ae. vagans* Jord. et Fourr., *Ae. parvula* Jord. et Fourr., *Ae. erigens* Jord. et Fourr., *Ae. pubiglumis* Jord. et Fourr., and *Ae. microstachys* Jord. et Fourr. The *Ae. vagans* Jord. et Fourr. was actually *Ae. ovata* L. var. *geniculata*.

In 1869, Vincenzo Barone de Cesati, Giovanni Passerini and Giuseppe Gibelli combined *Aegilops* into *Triticum* in *Comp. Florae Ital* (IV: 86). *T. ventricosum* (Tausch) Cesati, Pass. et Gib. replaced *Ae. ventricosa* Tausch and *T. cylindricum* (Host) Cesati, Pass. et Gib. replaced *Ae. cylindrica* Host.

In 1869, Duval-Jouve J. C. in his article "Sur quelques *Aegilops* DE France" (*Bull Soc. Bot. France*, 16: 384) published *Ae. macrochaeta* Shuttlew. et Huet ex Duval. This taxonomic group actually was *Ae. biuncialis* Vis.

In 1874, Auguste Nicolas Pomel in *Nouveaux Materiaux pour la Flore Atlantique* (p388–389) published new species *Ae. subulata* Pomel and *Ae. brachyathera* Pomel. In fact, the former was *Ae. ventricosa* Tausch, while the latter was *Ae. ovata* L.

In 1880, Eduard August von Regel in the article "Descriptiones plantarum novarum et minus cognitarum" (*Acta horti Petropolitani*, Tom VII, fasc. VIII) published *Ae. squarrosa* L. var. *pubescens* Regel. This variety was actually *Ae. crassa* Boiss.

In 1881, Greek scholar Theodor von Heldreich in *Herb. norm. plant. exsicc. flor. Hellen* (p898, p986) published species *Ae. heldreichii* Holzm. in honour of Holzman.

In 1882, Alphonse Louis Pierre Pyramus de Candolle, a Swiss botanist, followed the classification opinion of Vilmorin, a wheat breeder. He also discussed the origin of wheat and other cultivated crops based on plant morphological taxonomy and plant geography and referring to paleontology and archaeology and history and dialect. He thought that studying origins and original places of cultivated plants was of great importance to investigate wild species. Probably due to limitation of historical conditions, he did not see the important role of experimental biology emerging at that time, such as physiology and genetics, in studying the origin of species. He wrongly asserted that experimental biology was not important in studying the origin of plants. On the other hand, based on a large amount of data, he concluded that western Asia, especially in Mesopotamia, might be the origin place of wheat. This conclusion was basically correct.

In 1884, French scholar Jules Aime Battandier and Louis Charles Trabut documented two varieties named by Hackel, i.e., *Ae. triaristata* var. *trispiculata* Hackel and *Ae. triaristata* var. *robusta* Hackel, in *Flore d'Alger (Monocotyledones)* (p167 and p208 in supplements). Both of them should be a variety of *Ae. ovata* L.. Later, Eig A. named var. *robusta* Hackel as *Ae. ovata* ssp. *atlantica* Eig.

In 1884, Swiss scholar Edmond Boissier recorded nine species in *Flora Orientalis* (Vol 5, p673–679), i.e., *Ae. ovata* L., *Ae. triuncialis* L., *Ae. caudata* L., *Ae. comosa* Sibth. et Smith, *Ae. squarrosa* L., *Ae. crassa* Boiss., *Ae. bicornis* (Forssk.) Jaub. et Spach, *Ae. aucheri* Boiss., and *Ae. mutica* Boiss. Among them, the varieties of *Ae. ovata* L. var. *lorenti* (Hochst.) Boiss. included *Ae. triaristata* Willd. and *Ae. ovata* ssp. *controcta* Eig. His *Ae. triuncialis* L. var. *brachyathera* Boiss. was exactly the taxonomic group of *Ae. variabilis* later named by Eig A., including var. *kotschyi* (Boiss.) Boiss. Due to the limitation of his research technology at that time, it was impossible for him not to make some mistakes only by morphological comparison. He confounded the classification of *Ae. caudata* L. and *Ae. comosa* Sibth. Et Smith. He named two varieties under *Ae. caudata* L., i.e., var. *polyathera* Boiss. and var. *heldreichi* Boiss. Under *Ae. comosa* Sibth. et Smith, he named the variety var. *subventricosa* Boiss. This variety was essentially the same as his *Ae. caudata* L. var. *heldreichii* Boiss. although it was appropriate to take it as a variety of *Ae. comosa*. He also confounded *Ae. squarrosa* L. and *Ae. tauschii* Cosson. His *Ae. squarrosa* L. var. *meyer* Griseb. should be a variety of *Ae. tauschii* Cosson. His *Ae. bicornis* (Forssk.) Jaub. et Spach included *Ae. sharonensis* Eig and *Ae. speltoides* Tausch var. *ligustica* (Savign) Fiori.

In 1885, Kornicke F. thought that *Triticum* only had three species in the book *Die Arten und Varietaten des Getreides* (vol 1), namely *T. vulgare* Vill., *T. polonicum* L., and *T. monococcum* L. He divided *T. vulgare* into two sections (naked grain and hulled), including six subspecies. Naked grain subspecies included *vulgare*, *compactum*, *turgidum*, and *durum*. Hulled subspecies included *spelta* and *dicoccum*.

In 1886, British James Edward Tiery Aitchison and William Botting Hemsley placed *Ae. crassa* Boiss. and *Ae. persica* Boiss. into *Triticum*, and changed their names as *T. crassum* (Boiss.) Aitchison et Hemsley and *T. persicum* (Boiss.) Aitchison et Hemsley.

In 1887, Eduard Hackel merged *Aegilops* into *Triticum* that was divided into two sections in *Die naturlichen Pflanzenfamien* edited by Engler A. and Prantl K. (Vol 2).

Section I was for *Aegilops* (goat grass section, round glume without obvious *keel-like protuberance*). In this group, he documented *T. triunciale* Gren. et Godron (p80–81, fig 93).

Section II was for Sitopyros (cereal section, glume having prominent keel-like protuberance).

T. monococcum;
T. sativum.
Group I. Brittle rachis, hulled glume
1. Sparsely arranged spikelets, four-rowed, with blunt keel-like protuberance.
   (a) *T. sativum spelta*.
2. Sparsely arranged spikelets, flat, with sharp keel-like protuberance.
   (b) *T. sativum dicoccum*.

Group class II. Tough rachis, naked grain
  (c) *T. sativum tenax*;
    vulgare (*T. vulgare* Vill.);
    compactum (*T. compactum* Host);
    turgidum (*T. turgidum* L.);
    durum (*T. durum* Desf.).

In 1887, German scholar Carl Sigismund Kuntze published the variety *T. ovatum* Godr. et Gren. var. *bispiculatum* Kuntze in the article "Plantae orientali-rossicae" (*Acta Horti Petroplitani*, 20: 255–256). However, this taxonomic group should be a variety of *Ae. biuncialis* Vis.

In 1889, French scholar Abbe Michel Gandoger published the new species of *Ae. Croatica* Gdgr. in *Flora Croatica Exsiccata* (No. 6046). This taxonomic group was actually *Ae. triuncialis* L.

In 1890, Austrian botanist Karl Richter also placed *Aegilops* into *Triticum* in *Plantae Europaeae* (Vol 1, p127–129). He recorded a total of 15 species, including *T. ovatum* Raspil, *T. macrochaetum* Richt., *T. biunciale* Richt., *T. triaristatum* Godr. et Gren., *T. triunciale* Raspail, *T. caudatum* Godr. et Gren., *T. cylindricum* Ces, Pass. et Gib., *T. uniaristatum* Richt., *T. ventricosum* Ces, Pass. et Gib., *T. fragile* Richt., *T. comosum* Richt., *T. heldreichii* Richt., *T. ligusticum* Bertol., *T. aucheri* Parl., and *T. speltoides* Godr.

In 1896, van der Post C. G. published the new variety *Ae. ovata* L. var. *quinquearistata* Post in *Flora of Syria, Palestine, and Sinai* (p899). This taxonomic group was later named as the new species *Ae. umbellulata* Zhuk by Жуковский П. М. Later studies from Japanese scholar Kihara found that it was an important diploid basic species of wheat-*Aegilops* flora. In this book, van der Post documented eight species of *Aegilops*, i.e., *Ae. ovata* L., *Ae. triuncialis* L., *Ae. caudata* L, *Ae. comosa* Sibth. et Smith, *Ae. squarrosa* L., *Ae. crassa* Boiss., *Ae. bicornis* Forsk. [= *Ae. bicornis* (Forssk.) Jaub. et Spach], and *Ae. aucheri* Boiss., as well as varieties previously published by other scholars. In addition, he published the new variety *Ae. bicornis* var. *mutica* Post. Later Eig put it into *Ae. sharonensis* and became *Ae. sharonensis* Eig var. *mutica* (Post) Eig. Meanwhile, he published two forms, namely *Ae. ovata* L. f. *cabylica* Post and *Ae. ovata* L. f. *submutica* Post. In the records on *Ae. bicornis* Forsk., he included *Ae. speltoides* Tausch var. *ligustica* (Savign.) Fiori and later named *Ae. sharonensis* Eig.

In 1897, Russian scholar Ivan Fedorovich Schmalhausen (alternate name, Johanne Theodor Schmal' gauzen) combined *Ae. tauschii* Cosson into *Triticum*, renamed it as *T. tauschii* (Cosson) Schmalh. in *Fl. Centr. et S. Russia* (2: 662).

In 1898, German scholar Joseph Friedrich Nicolaus Bornmueller in the article "Ein Beitrag zur Kenntn. d. Fl. v. Syrien u. palestina" (Verh. d. k. u. k. Zool. Bot. Verh., Wien, S.109) published the new variety *Ae. triuncialis* var. *leptostachya* Bornm. In fact, the taxonomic group was *Ae. kotschyi* Boiss.

In 1896–1899, Pierre Tranquille Husnot in his book *Gramnees Spontanees et Cultuvees de France, Belgique, iles Britanniques et Suisse* (p87–89, Table 30) documented *Ae. ovata* L., *Ae. macrochaeta* schutt. et Huet. (= *Ae. biuncialis* Vis.), *Ae. triaristata* Willd., *Ae. triuncialis* L., and *Ae. caudata* L. and three intergeneric hybrids between wheat and goat grass, i.e., *Ae. grenieri* (Richt.) Husnot, *Ae. triticoides* Regu, and *Ae. lorentii* Husnot. Among them, *Ae. grenieri* was newly published, while *Ae. lorentii* was published in 1845 in *Flora* (28: 25).

In 1901, German scholar Paul Friedrich August Ascherson and Karl Otto Robert Peter Paul Graebner in *Synopsis der Mitteleuropaischen Flora Bd.* II followed the Hackel's *Triticum* classification system, where *Aegilops* was also incorporated into *Triticum*. He recorded the six species of *T. triunciale* Godr. et Gren., *T. uniaristatum* Richt., *T. ventricosum* Ces., Pass. et Gib., *T. speltoides* Godr., *T. ovatum* Ascher. et Graeb. (= *T. ovatum* Godr. et Gren.), and *T. caudatum* Godr. et Gren. (including *Ae. cylindrica* Host). *T. ovatum* Ascher. et Graeb. contained three subspecies, ssp. *euovatum* Ascher. et Graeb. (= *Ae. ovata* L.), ssp. *triaristatum* (Willd.) Ascher. et Graeb. (= *Ae. triaristata* Willd.), and ssp. *biunciale* (Vis.) Ascher. et Graeb. (= *Ae. biuncialis* Vis.). *T. caudatum* Godr. et Gren. also included three subspecies, ssp. *eucaudatum* Ascher. et Graeb., ssp. *heldreichii* Ascher. et Graeb. (= *Ae. heldreichii* Holzm.), and ssp. *polyathera* Ascher. et Graeb., based on *Ae. caudata* var. *polyathera* Boiss.

In 1902, Ascherson published the paper titled "*Ae. speltoides* Jaub. et Spach u. ihr Vorkommen in Europa" (*Magyar. Bot. Lap.*, I, 6: 12). *Ae. speltoides* Tausch was treated as a variety of *Triticum bicornie* Forssk., i.e., *T. bicorne* Forssk. var. *muticum* Ascher.

In 1904, Austria scholar Eug. von Halacsy in *Conspectus Florae Graecae* (III: 430–430) published the variety *Ae. comosa* var. *pluriaristata* Halacsy. This variety was actually *Ae. comosa* var. *polyathera* Haussk once named by Haussknocht H. C.

In 1907, Swiss botanist Albert Thullung in his article "*Triticum* (*Aegilops*) *juvenale* n. sp." (*Fedde Repert*, 3: 281–282) published the new species *T. juvenale* Thull. In 1929, this species was combined as *Ae. juvenalis* (Thull.) Eig by Eig A.

In 1907, Eduard Hackel in *Annals of Scottish Nat. Hist. Quart. Mag.* (p101–103) published a new species of *Triticum* called *T. peregrium* Hackel. It was treated as *Ae. variabilis* later by Eig A. Meanwhile, he put the *Ae. mutica* Boiss. into *Triticum*, renamed as *T. muticum* (Boiss.) Hackel.

In 1912, Muschler R. in *A Manual Flora of Egypt* (vol 1, p154–157) recorded four goat grass species, i.e., *Ae. ovata* L., *Ae. triuncialis* L., *Ae. bicornis* (Forssk.) Jaub. et Spach, and—the new species—*Ae. longissima* Schw. et Muschler. His *Ae. ovata* var. *triaristata* Cess. et Dur. included *Ae. triaristata* Willd. and *Ae. kotschyi* Boiss.; his *Ae. triuncialis* var. *brachyathera* Boiss. included *Ae. variabilis* Eig ssp. *cylindrostachys* Eig et Feinbrun.

In 1914, German scholar Joseph Friedrich Nicolaus Bornmuller in the article "Zur Flora des Libanon und Antilibanon" (*Beih. z. Bot. Zentrabl., Bd.* XXXI *Abt.*, II, 275–276) treated *Ae. triuncialis* L. var. *brachyathera* Boiss. as an independent species, named as *Ae. brachyathera* (Boiss.) Bornm.

It can be said that the classification of wheat and *Aegilops* before 1830s was mainly the identification of species. Wheat was a very old cultivated plant. In the Old Stone Age, the ancient people began to collect and eat wheat. In the Neolithic Age, human beings began to understand the rule of plant growth. In the attempt of crop cultivation, wheat had become one of the earliest cultivated crops in Western Asia (about 7000 BC~4000 BC). Wheat was also the most widely distributed crop, almost all over the world's agricultural areas. A great number of varieties had been produced under the long-term selection of human and nature. The research on plant taxonomy had been flourishing since eighteenth century, but the method of research was very shallow at the early stage. It was only based on the morphological analysis of the external morphology of the specimen, and with the tendency for naming purpose, which made the classification of *Triticum* very confused. More than 500 species names had been published (see Appendix). Many of them were the same species but with different names. Due to strong artificial classifications, many species were divided and emerged frequently among related genera, leading to a great inconsistency. *Aegilops* are wild plants. Sometimes, the difference between species populations is not obvious compared to wheat, but its distribution region was much larger than that of wild wheat. Under natural selection, *Aegilops* formed more than 10 to more than 20 species and some varieties, depending on different standards of botanists. Except for a new species (*Ae. searsii* Feldman et Kislev, Wheat Information Service, 45/46: 39–40) was found in 1978, other known species had been discovered before 1920s. Therefore, *Aegilops* classification had essential condition to be summarized comprehensively. Some scholars such as the former Soviet Union Жуковский П. М. and German A. von Eig had made great efforts on this work.

Chapter 2
Systematical Survey of the Genus *Aegilops*

In 1928, the Soviet botanist П. М. Жуковский published his works "A critical systematical survey of the species of the genus *Aegilops*" in *Тридыпо Прикладной Бот Ген и Сел* (18: 417–609). In this work, he acknowledged 20 species, two of which were newly published. He divided this genus into nine sections. The system was as follows:

1. sect. *Polyoides* Zhuk.
- (1) *Ae. ovata* L.
  - ssp. *gibberosa* Zhuk.
  - ssp. *unbonata* Zhuk.
    - var. *vernicosa* Zhuk.
    - var. *puberulla* Zhuk.
  - ssp. *globulosa* Zhuk.
  - ssp. *planiuscula* Zhuk.
- (2) *Ae. triaristata* Willd.
  - ssp. *recta* Zhuk.
  - ssp. *contorta* Zhuk.
  - ssp. *intermixta* Zhuk.
    - var. *ochreata* Zhuk.
    - var. *hirtula* Zhuk.
- (3) *Ae. biuncialis* Vis.
    - var. *vulgare* Zhuk.
    - var. *velutina* Zhuk.
- (4) *Ae. umbellulata* Zhuk.

2. sect. Sarculosa Zhuk.
- (5) *Ae. columnaris* Zhuk.
- (6) *Ae. triuncialis* L.
  - ssp. *typica* Zhuk.
  - ssp. *kotschyi* Boiss.
  - ssp. *brachyathera* Boiss.

C. Yen, J. Yang, *Biosystematics of Triticeae*,
https://doi.org/10.1007/978-981-13-9931-2_2

- ssp. *caput medusae* Zhuk.
- ssp. *fascicularis* Zhuk.
  - var. *prima* Zhuk.
  - var. *secunda* Zhuk.
  - var. *muricata* Zhuk.
  - var. *hirta* Zhuk.

ssp *persica* (Boiss.) Zhuk.

3. sect. *Cylindropyrum* (Jaub et Spach) **Zhuk.**

- (7) Ae. *cylindrica* Host
  - ssp. *aristata* Zhuk.

4. sect. *Comopyrum* (Jaub. et Spach) **Zhuk.**

- (8) *Ae. caudata* L.
  - ssp. *polyathera* Boiss.
  - ssp. *dichasians* Zhuk.
- (9) *Ae. comosa* Sibth. et Smith

ssp *pluriaristata* Halacsy

- (10) *Ae. heldreichii* Holzm.
- (11) *Ae. uniaristata* Vis.

5. sect. *Gastropyrum* (Jaub. et Spach) **Zhuk.**

- (12) *Ae. ventricosa* Tausch
  - ssp. *comosa* Cosson et Dur.
  - ssp. *truncata* Cosson et Dur.
  - ssp. *fragilis* (Parl.) Fiori

6. sect. *Sitopsis* (Jaub. et Spach) **Zhuk.**

- (13) *Ae. speltoides* Tausch
  - ssp. *ligustica* Fiori
    - var. *scandens* Zhuk.
    - var. *muricata* Zhuk.
- (14) *Ae. aucheri* Boiss.
  - ssp. *virgata* Zhuk.
    - var. *vellea* Zhuk.
    - var. *striata* Zhuk.
  - ssp. *polyathera* Boiss.
- (15) *Ae. bicornis* (Forssk.) Jaub. et Spach
- (16) *Ae. longissima* Schw. et Musch.
  - ssp. *aristata* Zhuk.
    - var. *polycarpa* Zhuk.
  - ssp. *suprahians* Zhuk.
    - var. *solaris* Zhuk.

7. sect. *Amblyopyrum* (Jaub et Spach) **Zhuk.**

- (17) *Ae. mutica* Boiss.
  - ssp. *loliacea* (Jaub. et Spach) Zhuk.
  - ssp. *tripsacoides* (Jaub. et Spach) Zhuk.

8. sect. *Vertebrata* Zhuk.

- (18) *Ae. squarrosa* L. (Here referring to *Ae. tauschii* Cosson)
  - ssp. *meyeri* Griseb.
  - ssp. *salinum* Zhuk.
  - ssp. *typica* Zhuk.

9. sect. *Polyloides* Zhuk.

- (19) *Ae. crassa* Boiss.
  - ssp. *macrathera* Boiss.
  - ssp. *vavilovi* Zhuk.
  - ssp. *trivialis* Zhuk.
- (20) *Ae. turcomanica* Roshev. [= *Ae. juvenalis* (Thull.) Eig]

In 1929, German scholar A. Eig published his work “Monographisch—Kritische Uebersicht der Gattung *Aegilops*” in *Repertorium specierum novrum regni vegetabilis, Beihefte* (55: 1–228). He divided *Aegilops* into 6 sections (sectionen), including 22 species. He added cytological data on chromosome counts in this book. The classification system is shown in Table 2.1.

Table 2.1 The cytological analysis of *Aegilops.* (Eig 1929)

Sections	Species	Chromosome number	
		n	2n
Anathera	*Ae. mutica* Boiss. …………………………………......		14
Platystachyum	*Ae. bicornis* (Forssk.) Jaub. et Sp. ………….…..	7	14
	Ae. sharonensis Eig ……………………………..….		14
	Ae. longissima Schweinf et Musch ……………..		14
	Ae. ligustica Coss. ………………………………....	7	14
	Ae. spltoides Tuasch ……………………………..…	7	14
Pachystachys	*Ae. squarrosa* L. ……………………………….…..	7	14
	Ae. crassa Boiss. …………………………………...	14, 21	28, 42
	Ae. juvenalis (Thell.) Eig ……………………..…	ca. 21	
	Ae. venticosa Tausch ……………………………....	14	
Monoleptathera	*Ae. cylindrica* Host ………………………………....	14	
Macrathera	*Ae. caudata* L. ……………………………………..….		14
	Ae. comosa Sibth. et Sm. ………………………….		14
	Ae. uniaristata Vis. …………………………………..		14
Pleionathera	*Ae. variabilis* Eig ……………………………...….	14	28
	Ae. kotschyi Boiss. ……………………………….…..		28
	Ae. triuncialis L. ……………………………………....	14	28
	Ae. columnaris Zhuk. ……………………………….	14	28
	Ae. biuncialis Vis. ……………………………….…...	14	28
	Ae. triaristata Willd. ……………………………..…..	14, 21	28, 42
	Ae. umbellulata Zhuk. ……………………………..	7	14
	Ae. ovata L. ……………………………………….….	14	28

He set up two subgenus under *Aegilops*, i.e., *Eu-Aegilops* Eig and *Amblyopyrum* Jaub. et Spach. The section *Anathera* Eig belongs to the latter, the remaining five sections all belong to subgenus *Eu-Aegilops* Eig.

Subgenus *Amblyopyrum* Jaub. et Sp.
1. sect. Anathera Eig
  Ae. mutica Boiss.
      var. *typica* Eig
      var. *loliacea* (Jaub. et Sp.) Eig (= f. *glabra* Haussk.)
Subgenus *Eu-Aegilops* Eig
2. sect. *Platystachys* Eig
  I. subsect. *Emarginata* Eig
    Ae. bicornis (Forsk.) Jaub. et Sp.
      var. *typica*
      var. *mutica* (Aschers) Eig
    Ae. sharonensis Eig
      var. *typica* (= var. *major* Eig)
      var. *mutica* (Post) Eig
    Ae. longissima Schweinf. et Musch.
  II. Subsect. Truncata Eig
    Ae. ligustica Coss.
    Ae. speltoides Tausch
      var. *typica*
      var. *polyathera* Eig (= *Ae. aucheri* Boiss. var. *polyathera* Boiss.)
3. sect. *Pachystachys* Eig
  I. subsect. *Oligomorpha* Eig
    Ae. squarrosa L. (actually being *Ae. tauschii* Cosson)
    ssp. *eusguarrosa* Eig
      var. *typica*
      var. *meyeri* Griseb.
      var. *anathera* Eig
    ssp. *stranthera* Eig
  II. subsect. *Polymorpha* Eig
    Ae. crassa Boiss.
      var. *typica*
      var. *palaestina* Eig
      var. *glumiaristata* Eig
      var. *macrathera* Boiss.
    Ae. juvenalis (Thullung) Eig
  III. subsect. *Occidentalis* Eig
    Ae. ventricosa Tausch
      var. *vulgaris* Eig
      var. *comosa* Coss. et Dur.
      var. *truncata* Coss. et Dur.
4. sect. *Monoleptathera* Eig

- *Ae. cylindrica* Host
  - var. *typica*
  - var. *pauciaristata* Eig

5. sect. *Macrathera* Eig

- *Ae. caudata* L
  - var. *typica* (non Fiori.)
  - var. *polyathera* Boiss.
- *Ae. comosa* Sibth. et Sm.
- subsp. *eu-comosa* Eig
  - var. *typica* (= var. *major* Haussk.)
  - var. *thessalica* Eig
  - var. *ambigna* Eig
- subsp. *heldreichii* (Holzm.) Eig
  - var. *achaica* Eig
  - var. *subventricosa* Boiss
  - var. *biarstata* Eig
- *Ae. uniaristata* Visiani

6. sect. *Pleionathera* Eig

- I. subsect. *Adhaerens* Eig
  - *Ae. variabilis* Eig
  - subsp. *eu-variabilis* Eig et Feinbrun
    - var. *typica*
    - var. *multiaristata* Eig et Feinbrun
    - var. *mutica* Eig et Feinbrun
    - var. *planispicula* Eig et Feinbrun
    - var. *latiuscula* Eig et Feinbrun
    - var. *intermedia* Eig et Feinbrun
    - var. *peregrina* (Hackel) Eig
  - subsp. *cylindiostachys* Eig et Feinbrun
    - var. *aristata* Eig et Feinbrun
    - var. *brachyathera* Eig et Feinbrun
    - var. *elongata* Eig et Feinbrun
  - *Ae. kotschyi* Boiss.
    - var. *typica*
    - var. *leptostachys* (Bornm.) Eig
    - var. *palaestina* Eig
    - var. *caucasica* Eig
    - var. *hirta* Eig
- II. subsect. *Libera* Eig
  - *Ae. triuncialis* L.
  - subsp. *eu-triuncialis* Eig
    - var. *typica*
    - var. *constantinopolitana* Eig
  - subsp. *orientalis* Eig

    - var. *assyriaca* Eig
    - var. *persica* (Boiss. pro sp. Eig l. c.)
    - var. *anathera* Haussk. et Bornm
- *Ae. columnaris* Zhuk.
- *Ae. biuncialis* Visiani
    - var. *typica*
    - var. *macrochaeta* (Shuttl. et Huet) Eig
    - var. *archipelagica* Eig
- *Ae. triaristata* Willd.
- subsp. *typica* Eig
    - var. *vulgaris* Eig
    - var. *quadriaristata* Eig
    - var. trojana Eig
- *Ae. umbellulata* Zhuk.
- *Ae. ovata* L.
    - var. *vulgare* Eig
    - var. *hirsuta* Eig
    - var. *africana* Eig
    - var. *eventricosa* Eig
    - var. *latiaristata* Lange
    - var. *brachyathera* (Pomel) Eig
    - var. *echinus* (Godron) Eig

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Chapter 3
Discovery of Wild *Triticum* Species

As mentioned above, as early as in 1833, Link found a wild plant similar to *T. monococcum* in the Balkans and Asia Minor. He named it as *Crithodium aegilopoides* Link. In 1854, Balansa found the same wild wheat in Mt. Sipylus, Syria, Iraq, and Iran in Asia Minor. They were merged into *Triticum* and changed to *T. aegilopoides* (Link) Bal. E. Boissier (1853) named the specimen collected from Boeotia Plain as *T. boeoticum* Boiss. In fact, they were the same species. *T. aegilopoides* (Link) Bal. was also the same name as *T. aegilopoides* Forssk. that was earlier published by Forsskål P. According to plant nomenclature rules, *T. aegilopoides* (Link) Bal. should be abandoned and *T. boeoticum* Boiss. should be the valid name of the wild wheat. In 1855, Kotschy discovered the wild barley *Hordeum spontaneum* in Mount Hermon, Palestine. Kärnicke found that partial spikes in the specimen belonged to another wild wheat species that was named as *T. dicoccoides* Körn in 1873. It also attracted the attention of agronomists because it was similar to the cultivated species *T. dicoccon* Schrank. Aaronsohn made a special investigation in 1904. At first, he did not find the wild wheat near Mt. Hermon. However, in 1906, he rediscovered the plant at 1900 m above sea level in Hermon and the Jordan Valley. In 1910, Cook discovered that this species was sporadically distributed in rock crevices on the slopes of Mount Anti-Lebanon in the limestone savanna eco-environment. Later, it was also discovered in Syria, Armenia, the Transcaucasus, and Western Iran. Compared to *T. dicoccoides,* the distribution of *T. boeoticum* was wider, including the Balkans, Asia Minor, Crimea, the Transcaucasus, Palestine, Syria, Iraq, and most parts of Iran, where the eco-geographic types vary somewhat. Reuter divided it into two species according to spikelets with one or two long awns. He designated the species with two long awns as *T. thaoudar* Reuter. However, Schiemann (1932) considered that it could only belong to a taxon class of subspecies.

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Chapter 4
Reihe System of Genus Triticum

From the end of the nineteenth century to the beginning of the twentieth century, many problems in wheat taxonomy were gradually clarified. August Albert Heinrich Schulz (1913) made a great contribution to the natural system relation of *Triticum*. His research had made clear that *Triticum* includes three natural groups (reihe), i.e., Einkorn-reihe, Emmer-reihe, and Dinkel-reihe. Referring to the classification opinion of A. de Candolle's based on structural morphological and adaptive traits, he classified the species of *Triticum* into the system in Table 4.1.

Schulz's results were supported by a series of cross-fertility tests (Tschermak 1915; Sax 1921). Вавилов (1913, 1914) analyzed the susceptibility of wheat to powdery mildew and three kinds of rust and found that the results of these experiments coincided with Schulz's reihe division. The serological studies of Zade (1914) also supported the classification system. The old taxonomic problem on natural relationship between the species of Triticum, which had been conducted for more than 100 years, was thoroughly resolved until the research results of cytological investigation were published. Observation of root-tip somatic cells by Sakamura (1918, 1920) showed that chromosome number of *T. monococcum* was 14; *T. dicoccum*, *T. durum*, *T. turgidum*, and *T. polonicum* was 28; and *T. vulgare*, *T. compactum*, and *T. spelta* was 42. Kihara (1919, 1921) observed the pollen mother cells and found that the haploid chromosome numbers of three reihes were 7, 14, and 21, respectively. Sax (1918, 1921) and many other studies since then had consistently demonstrated that Schulz's reihe division has correctly reflected the relationship of the natural systems.

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Table 4.1 Schulz's classification system. (Schulz 1913)

		Cultivation type		
			Naked grain type	
	Wild type (hull)	Hulled type	Normal type	Abnormal type
Einkorn	*T. aegilopoides*	*T. monococcum*		
Emmer	*T. dicoccoides*	*T. dicoccum*	*T. durum*	*T. polonicum*
			T. *turgidum*	
Dinkel		*T. spelta*	*T. compactum*	
			T. vulgare	
			T. capitatum	

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Chapter 5
Triticum Taxon of British School and Soviet School in the Twentieth Century

In the early twentieth century, the British botanist Percival J. and the Soviet botanist Н. И. Вавилов organized worldwide surveys and collections of wheat and conducted cultivation experiments, genetic, breeding, and taxonomic studies. Percival's viewpoints of classification system were published in *The wheat plant, a monograph*. He ignored the scientific achievements including cytology at that time, also including his own observation and study, and subjectively classified *Triticum* into two species and eleven cultivation races. Percival (1921) said that "To these groups I have applied the term 'race' rather than the term 'species', although they might with equal justice be designated 'cultivated species', for the methods used in their grouping and delimitation are same as those adopted in the case of wild species." He only admitted 2 wild wheat species, but combined the emmer with dinkel wheat and put 11 cultivated wheat under 2 species as cultivated races, namely:

Species I. *T. aegilopoides* Bal.
    Cultivated group 1. *T. monococcum* L.
Species II. *T. dicoccoides* Korn.
    Cultivated group 2. *T. dicoccum* Schudler.
        3. *T. orientale* Percival
        4. *T. durum* Desf.
        5. *T. polonicum* L.
        6. *T. turgidum* L.
        7. *T. pyramidale* Percival.
        8. *T. vulgare* Vill.
        9. *T. compactum* Host
        10. *T. spherococcum* Percival
        11. *T. spelta* L.

From the perspective of the natural relationship between taxa, Percival's classification system was retrograde compared to Schulz's. He confused the relationship of tetraploid and hexaploid populations. He put 11 taxa, which were generally regarded

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as species, under the species as cultivation races. This treatment represented the viewpoints of many geneticists and breeders engaging in genetic and cross-breeding experiments. This is because numerous experiments indicated that hybridization between these cultivation races is usually easy and the hybrids are partial fertile and produce continuous types of intermediate variation. It seems that his classification treatment had a progressive significance.

The Soviet school correctly inherited the principles of the reihe classification system of Schulz. However, there were several different forms in dealing with the taxonomic position of rehei, reflecting their concept differences on groups and species. For example, Фляксбергер initially designated the reihe as three conspecies, i.e., *T. monococcum* L., *T. eudicoccoides* Flaksb., and *T. speltoides* Flaksb. The Soviet school quickly absorbed the achievements of cytological research. In 1935, Фляксбергер changed conspecies as congretio based on chromosomal ploidy and named them as *diploides* Flaksb., *tetraploides* Flaksb., and *hexaploides* Flaksb. Вавилов (1935, 1964) even divided species directly according to the number of chromosomes, ignoring the taxon ranks of reihe, conspecies, and congretio. Usually, the so-called wheat species were treated as the species level of natural classification, so the number of species was larger compared to Percival's classification. Species was further divided into subspecies varietas and forma. However, classification below the rank of varietas adopted the ways of Körnicke that is usually artificial. In 1935, Фляксбергер and Вавилов separately published their own classification systems. However, they were highly similar, as shown below.

Фляксбергер's classification system (1935)

Congretio I. *diploides* Flaksb.
    Species 1. *T. spontaneum* Flaksb.
        including *T. aegilopoides* Bal. and *T. thaouder* Reut.
    2. *T. monococcum* L.
Congretio II. *tetraploides* Flaksb.
    3. *T. dicoccoides* Korn.
    4. *T. timopheevi* Zhuk.
    5. *T. dicoccum* (Schrank) Schubl.
    6. *T. durum* Desf. (including *T. orientale* Perc. and *T. pyramidale* Perc.)
    7. *T. abyssinicum* Vav. (separating from *T. durum*)
    8. *T. turgidum* L.
    9. *T. polonicum* L.
    10. *T. persicum* Vav.
Congretio III. *hexaploides* Flaksb.
    11. *T. vulgare* (Vill.) Host
    12. *T. compactum* Host
    13. *T. sphaerococcum* Perc.
    14. *T. spelta* L.
    15. *T. macha* Dek.et Men.

Вавилов's classification system (1935)

I. Chromosome number n = 21
  1. *T. vulgare* Vill.
  1a. *T. vulgare compositum* Tum. (*T. vavilovianum* Jakubz.)
  2. *T. compactum* Host
  3. *T. sphaerococcum* Perc.
  4. *T. spelta* L.
  5. *T. macha* Dek. et Men.
II. Chromosome number n = 14
II a. *T. durum* Desf. in sensu lato
  6. subsp. *abyssinicum* Vav.
  7. subsp. *expansum* Vav.
  8. *T. orientale* Perc.
II b. *T. turgidum* L. in sensu lato
  9. subsp. *abyssinicum* Vav.
  10. subsp. *mediterraneum* Flaksb.
II c. *T. polonicum* L in sensu lato
  11. subsp. *abyssinicum* Steud.
  12. subsp. *mediterraneum* Vav.
II d. *T. dicoccum* Schubl.
  13. subsp. *abyssinicum* Stoletova
  14. subsp. *Europaeum* (Perc.) Vav.
  15. subsp. *asiaticum* Stoletova
  16. *T. persicum* Vav.
  17. *T. dicoccoides* Korn.
  18. *T. timopheevi* Zhuk.
III. Chromosome number n = 7
  19. *T. monococcum* L.
  20. *T. aegilopoides* Bal. sensu lato

In 1964, in his posthumous book, Вавилов amended the classification system, but the classification principle nearly remained unchanged. It was introduced as follows for reference.

Wheat species with 14 chromosomes

Wild wheat species
I. *T. boeoticum* Boiss. in s.l.
a) subsp. *aegilopoides* Balan.
  Distribution area: Anatolia, Balkan, former Soviet Union, Turkey, Armenia, Nakhichevan, the southern seaside of Crimea.
b) subsp. *thaouder* Reut.
  Distribution area: Anatolia.
c) subsp. *urartu* Tum.
  Distribution area: south Armenia.

Cultivated wheat species

II. *T. monococcum* L.
  Distribution area: Anatolia, Yugoslavia, Bulgaria, Spain, Italy, Bavaria, North Caucasus mountains, Nagorno-karabakh, Crimea.

Wheat species with 28 chromosomes

Wild wheat species

III. *T. dicoccoides* Koern. in s.l.
  a) subsp. *armeniacum* Jakubz.
    Distribution area: former Soviet Union, Turkey, Armenia, Nakhichevan.
  b) subsp. *horanum* Vav.
    Distribution area: south Syria mountains.
  c) subsp. *palestinicum* Jakubz.
    Distribution area: north Palestine.

Cultivated wheat species

IV. *T. timopheevi* Zhuk.
  Distribution area: west Georgia, mixed growth in Kabarda-kabakal areas.

V. *T. dicoccum* (Schubl.) Schrank in s.l.
  a) subsp. *georgicum* Dek.et Men.
    Distribution area: west Georgia
  b) subsp. *asiaticum* Stoletova
    Distribution area: north Iran, Anatolia, and Nagorta-karabakh.
  c) subsp. *maroccanum* Flaksb.
    Distribution area: Morocco mountains.
  d) subsp. *abyssinicum* Vav.
    Distribution area: Ethiopia, Eritrea Eritrea, Yemen, northwest India.
  e) subsp. *Europaeum* (Perc.) Vav.
    Distribution area: south Spain mountains.
  f) subsp. *volgense* Nevski.
    Distribution area: north Volga and Bulgaria.

VI. *T. durum* Desf.
  a) subsp. *abyssinicum* Vav. (*acutidenticum* Flaksb.)
    Distribution area: Ethiopia, Eritrean mountains, Yemen.
  b) subsp. *expansum* Vav.
    Distribution area: Mediterranean coast, Dagestan, Azerbaijan, European grassland, Syria, America, Canada, and Argentina.
  c) subsp. *horanicum* Vav.
    Distribution area: common type in plateau mountain area of Syria, Palestine, Jordan, Egypt, and some areas of Asia Minor.
  d) subsp. *orientale* Perc.
    Distribution area: common in the eastern Mediterranean, oasis areas in Iranian, and Dagestani.
  e) subsp. *sinicum* Vav.

VII. *T. polonicum* L.
  a) subsp. *Abyssinicum* (Steud.) Vav.

Distribution area: Ethiopia and Eritrea mountains.

- b) subsp. *mediteraneum* Vav.
  - Distribution area: Mediterranean and former Soviet Union south.

VIII. *T. turgidum* L. s.l.

- a) subsp. *abyssinicum* Vav. (subsp. *turgidoides* Flaksb.)
  - Distribution area: Ethiopia and Eritrea mountain areas.
- b) subsp. *mediterraneum* Vav.
  - Distribution area: South Europe, western Iran, and Asia Minor.
- c) subsp. *sinicum* Vav.
  - Distribution area: eastern China.

IX. *T. persicum* Vav.

- Distribution area: plateau areas of Armenia, Georgia, and Dastan.

Wheat species with 42 chromosomes

X. *T. macha* Dek. et Men.

- Distribution area: western Georgia.

XI. *T. spelta* L.

- Distribution area: western Europe Mountains.

XII. *T. vavilovianum* Jakubz.

- Distribution area: Turkey, Armenia.

XIII. *T. compactum* Host

- a) subsp. *armeno-turkestanicum* Vav.
  - Distribution area: Armenia, central Asia and Afghanistan, some areas of Syria.
- b) subsp. *eurasiticum* Vav.
  - Distribution area: upland meadow in Western Europe, Western Tianshan, and Yakutia.
- c) subsp. *sinicum* Vav.

XIV. *T. sphaerococcum* Perc.

XV. *T. vulgare* Host

- a) subsp. *irano-turkestanicum* Vav. (irano-asiaticum Flaksb.)
  - Distribution area: central Asia, Nakhichevan, Iran, Afghanistan, China.
- b) subsp. *indicum* Vav.
  - Distribution area: India, Kashmir, Baluch.
- c) subsp. *sinicum* Vav.
  - Distribution area: east China and Mongolia.
- d) subsp. *eurasiaticum* Vav.
  - Distribution area: Europe, Asia, north and south America, Oceania, north and south Africa.
- e) subsp. *abyssinicum* Vav.
  - Distribution area: Ethiopia and Eritrea.

It was clearly right to classify natural groups according to chromosome number. However, they didn't face up to the data on genetics analysis, and the classification of species had obvious anthropogenic nature and was very complicated.

Soviet school also did great works on the investigation and identification of species. In 1928, Жуковскии published an important wheat species found in the mountains of Georgia, named *T. timopheevi* Zhuk. In 1932, Дикаприлевич and Менабде published a hulled cultivated wheat found in west Georgia, named *T. macha* Dek. et Men. That is a hexaploid wheat. In 1933, Якубцинер published a cultivated hexaploid species with elongate rachilla, found in Armenia, named *T. vavilovii* Jakubz. In 1937, Туманян found a wild diploid wheat in Armenia. It has two awns and its spikelets had no hairs, different from *T. boeoticum* Boiss. It was named as *T. urartu* Tum. Менабде (1940) published *T. paleocolchium* Men. found in west Georgia. Невскй (1934) revised *T. persicum* Vav. published by Вавилов (1919) as *T. arthicum* Nevski., as *T. persicum* (Boiss.) Aitch. et Hemal had already been named in 1838. Якубцинер (1947) revised *T. orientale* Perc. published by Percival (1921) as *T.turanicum* Jakubz., as M. Bieberstein had named another species using this name in 1808 (*Flora Tauo-Caucasica,* Vol. I: 86). At the same time, he changed *T. durum* Desf. subsp. *abyssinicum* identified in 1931 by Vav. Вавилов as a species, named as *T. aethiopicum* Jakubz., because Steudel had already used this name to name a Polish wheat in Ethiopia in 1855. In 1958, Менабде and Ерзяи found a kind of wheat in *T. timopheevi* Zhuk. distribution area. Despite of resembling *T. timopheevi* Zhuk., it is a hexaploid, named as *T. zhukovskyi* Men. et Er.

Якубциер published a classification system in 1958 to represent the views of the Soviet school in more recent years. They had made some revisions on scientific name at the species level by following Schulz's classification system. Якубцинер's classification system is provided in Table 5.1. Until now, this system is still used by many works of different countries.

Table 5.1 Якубциер's classification system (1958)

Congretio	Species	Distribution areas	Habits
Diploidea	Wild species		
2n = 14	*T. boeoticum* Boiss.	Armenia, Nakhichevan, Georgia, Crimea, the Near East, Asia Minor, Balkan Peninsula	Winterness, springiness (rare)
	T. urartu Tum.	Armenia	Winterness
	Cultivated (hulled)		
	T. monococcum L.	Transcaucasia, Ciscaucasia, Asia Minor, Balkan Peninsula, Morocco, Spain	Springness, winterness
Tetraploidea	Wild		
2n = 28	*T. araraticum* Jakubz.	Armenia, Azerbaijan, Nakhichevan, Iran	Winterness
	T. dicoccoides (Korn.) Schwein.	Asia Minor, the Near East	Springness
	Cultivated hulled		

(continued)

Table 5.1 (continued)

Congretio	Species	Distribution areas	Habits
	T. timopheevi Zhuk.	Georgia	Springiness (winter sowing)
	T. paleocolchium Men.	Georgia	Winterness
	T. dicoccum Schubl.	Transcaucasia, Dagestan, Volga, Karma, Mediterranean countries, Iran, Balkan Peninsula, west Europe, Asia Minor, India, America	Springness, winterness
	Cultivated naked grain		
	T. durum Desf.	Ciscaucasia, Volga, Ukraine, west Siberia, Transcaucasia, Dagestan, mediterranean countries, Asia Minor, the Near East, China, America, Canada	Springness, halfwinterness
	T. turgidum L.	Transcaucasia, Kazakhstan, Asia Minor, mediterranean countries, China, west Europe, Balkan Peninsula	Springness, winterness, halfwinterness
	T. turanicum Jakubz.	Republics of Central Asia, Dagestan, Asia Minor, Syria, Iran, Iraq, west China	Springness
	T. polonicum L.	Mediterranean countries, west China, Siberia, Kazakhstan	Springness, winterness, halfwinterness
	T. carthlicum Nevski.	Transcaucasia, Dagestan, Turkey	Springness
	T. aethiopicum Jakubz.	Ethiopia, Eritrea, Yemen	Springness
Hexaploidea	Cultivated hulled		
2n = 42	*T. zhukovskyi* Men.et Er.	Georgia	Springness
	T. macha Dek.et Men.	Georgia	Winterness
	T. spelta L.	Iran, south Germany, Spain	Winterness, springness
	Cultivated naked grain		
	T. aestivum L.	All over the world	Springness, winterness, half winterness
	T. compactum Host	Transcaucasia, Kazakhstan, Asia Minor, Afghan, Chile	Springness, winterness, halfwinterness
	T. vailovii Jakubz.	Armenia	Winterness
	T. sphaerococcum Perc.	Pakistan, India	Springness

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Chapter 6

Cytogenetic Relationship of *Triticum* and *Aegilops* Species

As mentioned above, some scientists such as Sakamun, Kihara, and Sax had found that *Triticum* plants have three types of chromosome numbers, i.e., 14, 28, and 42 chromosomes in the somatic cells of root tips and 7, 14, and 21 in the gamete cells. They are a ploidy relationship. Similar ploidy distribution was also observed in *Aegilops* species, as shown in Table 6.1.

Based on the list in Table 6.1, it is clear that the chromosome numbers of *Triticum* and *Aegilops* species are all multiples of seven. This means that seven is the cardinal number of chromosome sets, usually represented by x. For instance, *T. boeotium* is a diploid with 2x = 14, *T. dicoccum* is a tetraploid with 4x = 28, while *T. aestivum* is a hexaploid with 6x = 42. In other words, diploid, tetraploid, and hexaploid has two, four, and six sets of chromosomes, respectively. Their gametes generated by meiosis only contain a half of the chromosome sets, i.e., one for *T. boeoticum*, two for *T. dicoccum*, and three for *T. aestivum* (Fig. 6.1). A chromosome set is also called a nuclear genome that is a term corresponding to plasmon. Hexaploid has three sets of paired chromosomes, three times as many as in diploid wheat.

Kihara (1919) observed pollen mother cells of wheat interspecific hybrids and found that the F1 hybrids of *T. durum* × *T. aestivum* were pentaploid with 35 chromosomes. It is the expected chromosome number of hybrids between tetraploid and hexaploid wheat. Among them, there were 14 paired chromosomes (bivalent) and 7 unpaired chromosomes (univalent).

Sax (1922) observed 21 chromosomes in pollen mother cells of F_1 hybrids of *T. monococcum* × *T. turgidum.* They formed seven bivalents and seven univalents. Sax also observed the chromosome pairing of the reciprocal F_1 hybrids of *T. durum* × *T. aestivum* and found same results as those obtained by Kihara (1919). Later, similar experiments were done by others such as Kihara (1924), Watkins (1924), and Thompson (1926). Based on these studies, it was concluded that the same sets of chromosomes can pair and the paired chromosomes usually had similar morphology, called homologous chromosomes. The paired chromosomes can normally move to the opposite poles during the anaphase of cell division and evenly distribute in the daughter cells. However, Kihara and Nishiyama (1928) also found trivalents

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Table 6.1 Chromosome number of *Triticum* and *Aegilops* species

Genus	Species	Chromosome no. gametes	References
Triticum	*T. boeoticum* L.	7	Kihara (1924), de Mol (1924), Stolze (1925), Percival (1926) et al.
	T. monococcum L.	7	Sakamura (1918), Kihara (1919), Sax (1921), Percival (1926) et al.
	T. dicoccoides Korn.	14	Kihara (1924), Stolze (1925), Percival (1926) et al.
	T. dicoccon Schrank	14	Kihara (1919), Николаеьа (1920), Percival (1926) et al.
	T. durum DesL	14	Sakamura (1918), Kihara (1919), Sax (1918, 1921), Николаеьа (1920), Percival (1926) et al.
	T. turgidum L.	14	Sakamura (1918), Kihara (1919, 1924), Sax (1921, 1922), Николаеьа (1920), Percival (1926) et al.
	T. polonicum L.	14	Sakamura (1918), Kihara (1919, 1924), Sax (1921, 1922), Николаеьа (1920, 1923), Percival (1926) et al.
	T. carthlicum Nevski	14	Николаеьа (1920, 1923)
	T. turanicum Jakubz.	14	Николаеьа (1923), Percival (1926) et al.
	T. timopheevi Zhuk.	14	
	T. araraticum Jakubz.	14	Светозароева (1939)
	T. aestivum L.	21	Sakamura (1918), Kihara (1919, 1924), Sax (1921, 1922), Percival (1926) et al.
	T. spelta L.	21	Sakamura (1918), Kihara (1919, 1924), Sax (1921), Percival (1926) et al.
	T. compactum host	21	Sakamura (1918), Kihara (1919, 1924), Sax (1921), Percival (1926) et al.
	T. sphaerococcum Perc.	21	Percival (1926)
	T. macha Dek. et Men.	21	Ерицян (1932)
Aegilops	*Ae. umbellulata* Zhuk.	7	Schiemann (1928)
	Ae. ovata L.	14	Percival (1923), Kihara (1924), Sax and Sax (1924), Aase and Pewers (1926), Bleier (1926, 1930), Tschermak and Bleier (1926), Kagawa (1927), Schiemann (1928) et al.
	Ae. biuncialis Vis.	14	Schiemann (1928), Longley and Sando (1930) et al.
	Ae. triaristata Willd.	14	Schiemann (1928), Longley and Sando (1930) et al.

(continued)

Table 6.1 (continued)

Genus	Species	Chromosome no. gametes	References
	Ae. recta (Zhuk.) Chennev.	21	Schiemann (1928)
	Ae. caudata L.	7	Bleier (1928a, b), Schiemann (1928), Сорокина (1928) et al.
	Ae. comosa Sibth. Et Sm.	7	Schiemann (1928), Сорокина (1928) et al.
	Ae. heldreichii Holzm.	7	Schiemann (1928)
	Ae. uniaristata Vis	7	Schiemann (1928)
	Ae. aucheri Boiss.	7	Schiemann (1928), Сорокина (1928)
	Ae. speltoides Tausch		Percival (1926), Kagawa (1926, 1927), Schiemann (1928), Сорокина (1928), Jinkins (1929) et al.
	Ae. longissimi Schw.	7	Сорокина (1928)
	Ae. bicornis Forsk.	7	Сорокина (1928)
	Ae. sharonensis Eig	7	
	Ae. crassa Boiss.	14	Emme (1924), Percival (1926), Kihara (1937a) et al.
		21	Percival (1926), Сорокина (1928), Longley and Sando (1930) et al.
	Ae. juvenalis (Thell.) Eig	21	Сорокина (1928)
	Ae. triuncialis L.	14	Emme (1924), Aase and Pewers (1926), Percival (1923), Kagawa (1928), Schiemann (1928), Сорокина (1928) et al.
	Ae. variabilis Eig (*Ae. kotschyi* Boiss.)	14	Сорокина (1928)
	Ae. columnaris Zhuk.	14	
	Ae. ventricosa Tausch	14	Percival (1923, 1926), Emme (1924), Kihara (1924), Bleier (1928a, b), Schiemann (1928), Сорокина (1928) et al.
	Ae. cylindrica host	14	Emme (1924), Sax and Sax (1924), Aase and Pewers (1926), Gaines and Aase (1926), Bleier (1928a, b), Schiemann (1928), Сорокина (1928), Kagawa (1928) et al.
	Ae. tauschii Cosson	7	Percival (1926), Сорокина (1928) et al.
	Ae. mutica Boiss.	7	

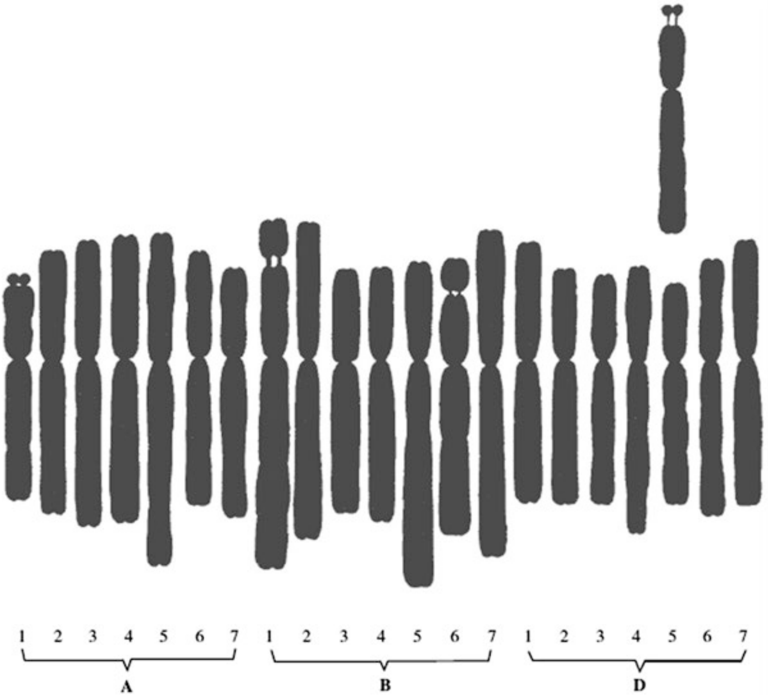

Fig. 6.1 The three chromosome sets (A, B, D) of wheat. The satellites on chromosomes 1A and 5D are usually smaller in hexaploid *T. aestivum* L. than in diploid species *T. boeotium* and *Ae. tauschii* Cosson

formed by three chromosomes and quadrivalents formed by four chromosomes in some F_1 hybrids such as *T. monococcum* × *T. turgidum* (Fig. 6.2a–e) *and T. spelta* × *T. boeoticum* (Fig. 6.2f–j). They observed 5 types of pairing configurations in *T. spelta* × *T. boeoticum*, including 7 bivalents and 14 univalents; 2 trivalents, 4 bivalents, and 14 univalent; 1 quadrivalent, 5 bivalents, and 14 univalents; 1 trivalent, 7 bivalents, and 11 univalents; 10 bivalents and 8 univalents. These results indicated that one of the three sets of chromosomes in *T. spelta* can normally pair with *T. boeoticum*. Although the remaining two sets of chromosomes showed a low level of pairing, they are different from the set of *T. boeoticum*. A quite of experiments indicated that there are two same sets of chromosomes between *T. dicoccum* and *T. aestivum* (Table 6.2). Based on the analysis on triploid hybrids between *T. monococcum* and *T. dicoccum*, a set of chromosomes is the same. According to extensive studies on chromosomal pairing of interspecific hybrids, Kihara (1930) established the genome theory. Three sets of chromosomes of *Triticum* were respectively named A, B, D genome. Although genome D was once called C (Hector 1936), genome C had been firstly used to name the set of chromosomes of *Aegilops caudata*. Now it has been uniformly called D genome. The genome of Einkorn wheat is AA, emmer wheat is AABB, and common wheat is AABBDD.

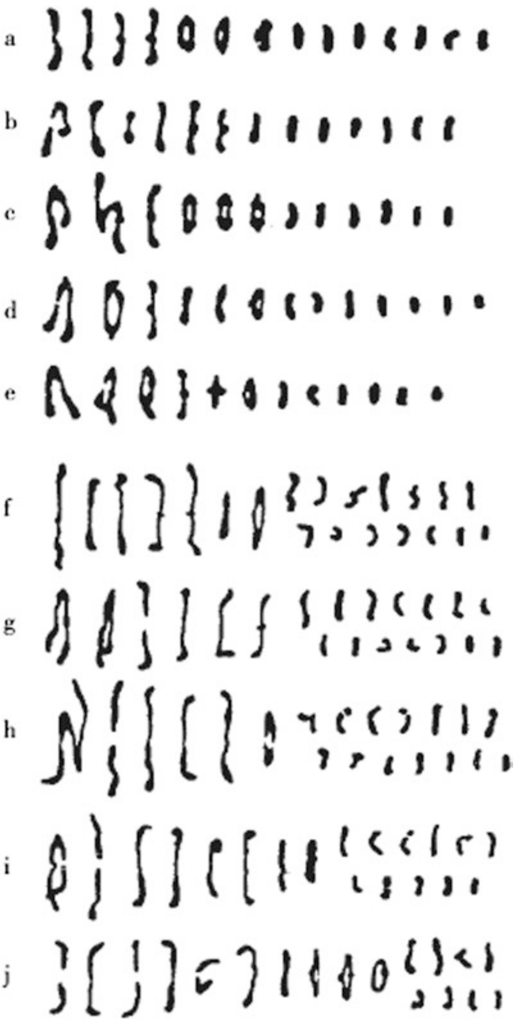

Fig. 6.2 Chromosome pairing of F_1 hybrid between *Triticum* species. (**a–e**) *T. monococcum* var. *boeoticum* × *T. turgidum* concv. Emmer wheat; (**f–j**) *T. aestivum* concv. *Spelta* × *T. monococcum* var. *boeoticum.* (**a**) 7 II + 7 I; (**b**) 1 III + 6 II + 6 I; (**c**) 1 IV + 1 III + 4 II + 6 I; (**d**) 2 III + 4 II + 7 I; (**e**) 3 III + 3 II + 6 I; (**f**) 7 II + 14 I; (**g**) 2 III + 4 II +14 I; (**h**) 1 IV + 5 II + 14 I; (**i**) 1 III + 7 II + 11 I; (**j**) 10 II + 8 I (Kihara and Nishiyama 1928)

T. timopheevi found in Georgia by П. М. Жуковский (1928a, b) was special, as it was difficult to cross with other tetraploid wheat and the resulting hybrids had low fertility. In 1934, Lilienfeld and Kihara published the research results on chromosomal behaviors in its hybrids. They believed that it has 14 A-genome chromosomes that can normally pair with A-genome chromosomes of other tetraploid species. However, the remaining 14 chromosomes had low pairing level with B-genome chromosome of other tetraploid (Fig. 6.3). They hence named this set 1 chromosomes specific for *T. timopheevi* as G genome. They classified wheat containing the G genome into a separating group. Their classification system on basis of genome constitutions was shown in Table 6.3.

Table 6.2 Meiotic chromosome pairing of F_1 hybrids between emmer and dinkel wheat. (According to Kihara et al. 1954)

Hybrid combination	No. of chromosomes	Bivalent		References
		Range	The highest number	
T. durum × *T. aestivum*	35	12~14	14	Kihara (1919, 1924), Kihara and Nishiyama (1928), Sax (1921), Stevenson (1930), Aase (1930), Horton (1936)
T. aestivum × *T. durum*	35	11~14	14	Sax (1922), Kattermann (1931), Bakap (1933), Вакар (1932)
T. turgidum × *T. aestivum*	35		14	Вакар (1932)
T. poLonicum × *T. spelta*	35		14	Kihara (1919, 1924)
T. spelta × *T. poLonicum*	35		14	Вакар (1932)
T. poLonicum × *T. compactum*	35		14	Kihara (1924)
T. carthlicum × *T. aestivum*	35	13~14	14	Вакар (1932)
T. aestivum × *T. dicoccum*	35	13~14	14	Hollinshead (1932)
T. compactum × *T. durum*	35		14	
T. sphaerococcum × *T. turgidum*	35		14	Вакар (1932)
T. sphaerococcum × *T. durum*	35		14	Вакар (1932)
T. spelta × *T. carthlicum*	35		14	Вакар (1932)

According to the results of genome analysis on hybrids, the relationship between wheat and its relative plants became clear. A compilation of studies based on Kihara et al. was shown in Table 6.4.

Based on Table 6.4, it is clear that *Aegilops tauschii*, *Ae. cylindrica*, *Ae. ventricosa*, *Ae. vavilovii*, and *Ae. juvenalis* have very close relationships with *Triticum*, as they share the same D genome. Experimental results have also showed that *Triticum*, *Aegilops*, *Secale*, *Haynaldia*, *Elymus*, *Kengyilia*, *Roegneria*, *Leymus*, *Hordeum*, and other genera in tribe Triticeae can produce hybrids with each other. However, the hybrids are usually sterile or low fertile. These genera have more distant relationship and contain homoeologous chromosomes.

Based on the results of plant morphology and genome analysis, Kihara (1944) concluded that *Ae. tauschii* was a species which shared the D genome with hexaploid wheat. In the same year, Mcfadden and Sears achieved the same conclusion, and announced that they artificially synthesized *Triticum spelta* by crossing *T.*

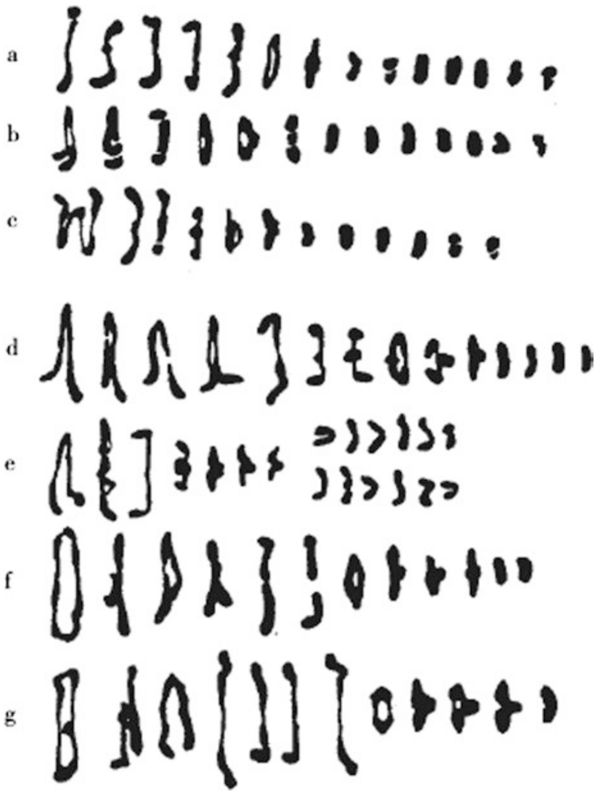

Fig. 6.3 Chromosome pairing of F_1 hybrids between *T. timopheevi* and other species. (a–c) *T. monococcum* var. *boeoticum* × *T. timopheevi;* (d–g) *T. timopheevi* × *T. turgidum.*
(**a**) 7 II + 7 I; (**b**) 2 III + 4 II + 7 I; (**c**) 1 V + 5 II + 6 I; (**d**) 4 III + 6 II + 4 I; (**e**) 2 III + 5 II + 12 I; (**f**) 1 V + 3 III + 6 II + 2 I; (**g**) 2 IV + 1 III + 8 II + 1 I (Lilienfeld and Kihara 1934)

Table 6.3 Genome analysis and wheat classification (Lilienfeld and Kihara 1934)

Einkorn	Emmer	*T. timopheevi*	Dinkel
AA	AABB	AAGG	AABBDD
T. aegilopoides Bal.	*T. dicoccoides* Korn.	*T. timopheevi* Zhuk.	*T. speta* L.
T. monococcum L.	*T. dicoccum* Schubl.		*T. vulgare* Vill.
	T. durum Desf.		*T. compactum* Host
	T. turgidum L.		*T. sphaerococcum* Perc.
	T. pyramidale Perc.		*T. macha* Dek. et Men.
	T. orientate Perc.		*T. persicum* Vav.

dicoccoides with *Ae. tauschii*. Two years later (1946), a detailed report on this work was published. As early as in 1930, a cross combination between *T. dicoccoides* and *Ae. tauschii* was made by Mecfadden, and F_1 hybrids were obtained in 1931. The F_1 hybrids were very similar to *T. spelta*, but completely sterile. After the method of

Table 6.4 The genome of wheat and its related plants. (Modification according to Kihara et al. 1954)

Genus	Species	n	Haplome	References
Triticum	*T. monococcum* L.	7	**A**	Aase (1930)
	T. turgidum L.	14	**AB**	
	T. timopheevi Zhuk.	14	**AG**	Lilienfeld and Kihara (1934)
	T. aestivum L.	21	**ABD**	Kihara (1924–1944)
	T. zhukovskyi men. Et Er.	21	**AAG**	Upadhya and Swaminathan (1963)
Aegilops	*Polyoides*			
	Ae. umbellulata Zhuk.	7	**(C^{u})**	Kihara (1937a, b)
			U	Kimber and Sears (1983)
	Ae. ovata L.	14	**(C^{u}M^{o})**	
			UM	Kimber and Sears (1983)
	Ae. triaristata Willd.	14	**(C^{u}M^{t})**	Lindschau and Oehler (1936)
			UM	Kimber and Sears (1983)
	Ae. recta (Zhuk.) Chenn.	21	**(CM^{l}Mt^{2})**	Kihara (1937a, b)
			UMUn	Kimber and Sears (1983)
	Ae. columnaris Zhuk.	14	**(C^{u}M^{c})**	Kihara (1937a, b)
			UM	Kimber and Sears (1983)
	Ae. biunciais Vis.	14	**(C^{u}M^{b})**	
			UM	Kimber and Sears (1983)
	Ae. variabilis Eig	14	**(C^{u}S^{v})**	Kihara (1937a, b)
			US^{1}	Kimber and Sears (1983)
	Ae. kotschyi Bois.	14	**(C^{u}S^{v})**	
			US	Kimber and Sears (1983)
	Ae. triunciaLis L.	14	**(C^{u}C)**	Kihara (1949)
			UC	Kimber and Sears (1983)
	Cylindropyrum			
	Ae. caudata L.	7	**C**	Kihara and Lilienfeld (1935)
	Ae. cylindrica Host.	14	**CD**	Kihara (1937a–1949)
	Comopyrum			
	Ae. Comosa Sibth. et Sm.	7	**M**	Kihara (1949)
	Ae. heldreichii Holzm.	7	**M**	Percival (1932)
	Ae. uniaristata Vis.	7	**(M^{u})**	Kihara (1949)
			Un	Kimber and Sears (1983)
	Amblyoprum			
	Ae. mutica Boiss.	7	**M^{t}**	Kihara and Lilienfeld (1935)
	Vertebrata			

(continued)

Table 6.4 (continued)

Genus	Species	n	Haplome	References
	Ae. tauschii Cosson.	7	**D**	Kihara and Lilienfeld (1935)
	Ae. crassa Boiss.	14	**(DM^{cr})**	Kihara (1949)
			DM	Kimber and Sears (1983)
		21	**(DDM^{cr})**	Kihara (1949)
			DDM	Kimber and Sears (1983)
	Ae. ventricosa Tausch.	14	**(DM^{v})**	Percival (1930)
			DUn	Kimber and Sears (1983)
	Ae. vavilovii (Zhuk.) Chenn.	21	**(DM^{cr}S^{1})**	
			DMS	Kimber and Sears (1983)
	Ae. juvencdis (Thell.) Eig	21	**(DC^{u}Mj)**	
			DMU	Kimber and Sears (1983)
	Sitopsis			
	Ae. speltodes Tausch	7	**S**	Kihara and Lilienfeld (1935)
	Ae. aucheri Boiss.	7	**S**	Kihara and Lilienfeld (1932)
	Ae. longissma Schw. et Musc.	7	**S^{1}**	Kihara (1949)
	Ae. sharonensis Eig	7	**S^{s}**	Kihara (1949)
	Ae. bicornis (Forssk.) Jaub. et Spach	7	**S^{b}**	Kihara (1949)

chromosome doubling induced by colchicine was published by Blakeslee and Avery (1937) and Nebel and Ruttle (1937, 1938), Macfadden and Sears repeated the crossing of *T. dicoccoides* with *Ae. tauschii*. The F$_1$ hybrids were treated with colchicine to double their chromosomes and produced allohexaploid that had 42 chromosomes with high seed-setting rate. The plant morphology of artificially synthetic hexaploid was similar as *T. spelta*. The artificial hexaploid was highly crossable with natural *T. spelta* and *T. aestivum*, and the hybrid progenies exhibited normal fertility. These experiments not only proved that the D genome of *T. aestivum* was donated by *Ae. tauschii.*, but also demonstrated that *T. aestivum* originated from the cross between emmer wheat and *Ae. tauschii* (Fig. 6.4).

Kihara and Lilienfeld (1949) re-synthesized *T. spelta* without colchicine treatment on *T. dicoccoides*-*Ae. tauschii* hybrids. They obtained a few F$_2$ seeds by selfing of F$_1$ hybrids with 21 chromosomes. Out of the analyzed three F$_2$ plants containing 42 chromosomes, one exhibited normal chromosome pairing and produced progenies with 42 chromosomes. Plant morphology of new hexaploid wheat was also similar with *T. spelta*. The synthetic hexaploid was generated by spontaneous chromosome doubling. Today, spontaneous chromosome doubling has been frequently observed in haploid plants or hybrids. This phenomenon can be caused by the union

Fig. 6.4 The artificial synthetic hexaploid wheat (middle). Spike morphology of artificial hexaploid wheat is very like that of Yunnan hulled wheat that is a common wheat native to Yunnan province, China. The artificial wheat is highly resistant to preharvest sprouting inheriting from *Ae. tauschii* accession collecting in Henan province, China (right). Its female parent was *T. turgidum* cv. Jianyangailanmai (left)

of unreduced male and female gametes. Formation of unreduced gametes can result from a failure of one meiotic division, but it can be either the first or the second division. The experiment of Kihara and Lilienfeld confirmed that *T. aestivum* originated from natural hybridization of emmer wheat and *Ae. tauschii* followed natural chromosome doubling. Further studies by Kihara et al. (1950) again supported this conclusion (Fig. 6.5). *Ae. tauschii* has a wide distribution east from Henan province, China, west to the Karim Peninsula at the Black Sea, including the middle reaches of the Yellow River and Xinjiang province, Central Asia, Afghanistan, northern Pakistan, Iran, Azerbaijan, Armenia, the Outer Caucasus, the north Caucasus, etc. It has overlapping distribution area with wild emmer and cultivated emmer wheat. In particular, *Ae. tauschii* grown in field of the cultivated emmer wheat as weeds and their natural hybridization was easy. In recent years, molecular genetic analysis showed that D genome of *T. aestivum* was derived from *Ae. tauschii* var. *strangulata*, genetically highly close to the accessions distributing in northern Iran (Fig. 6.6).

On the origin of the B genome of *Triticum*, the exact donor species has not been found so far. This is contrast to the clear conclusion that D and A genomes of *Triticum* were contributed by *Ae. tauschii* and *T. monococcum* ssp. *urartu*, respectively. Some researchers such as Sears (1948) speculated that the B genome in wheat has underwent many changes during the long evolutionary history after the origin of tetraploid wheat. The high divergence of B genome between wheat and its ancestor diploid species results in the difficulty to find the exact donor species.

Fig. 6.5 Synthetic hexaploid wheat between *T. persicum* and *Ae. squarrosa.* (**a**) *T. persicum straminecum*; (**b**) *Ae. squarrosa* No. 2; (**c**) F_1; (**d**) F_2 (amphiploid); (**e**) *T. vulgare* (Kihara et al. 1954)

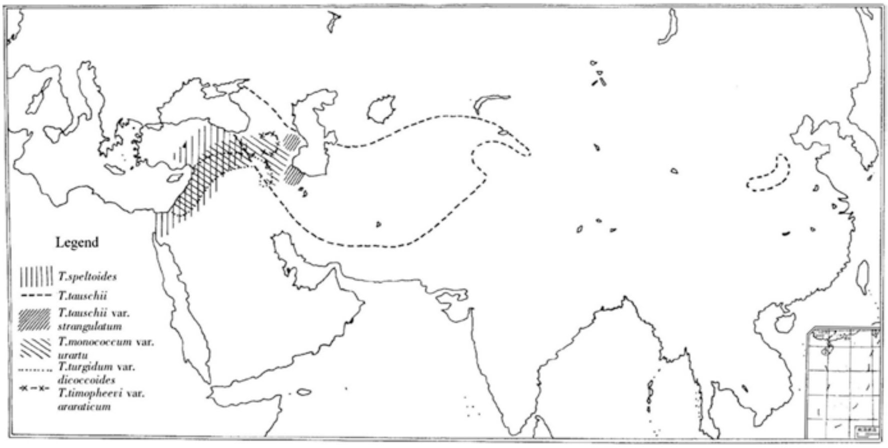

Fig. 6.6 Geographical distribution of wild species of wheat

In 1956, Sarkar and Stebbins studied the phylogenetic relationship of B genome by morphological comparative analysis. They compared spike morphology of einkorn wheat, emmer wheat, *Aegilops speltoides* var. *ligustica* and var. *aucheri*, *Ae. bicornis*, *Ae. sharonensis*, and *Ae. longissma*. They used Anderson's "inductive correlation method" (1949) to analyze the obtained data and suggested that if emmer wheat was an allopolyploid derived from the hybridization of einkorn wheat with another species, the unknown species should have some characteristics, including long and narrow rachis internode, spikelet containing more than three florets, glume having unobtrusive ridge with more than six veins and its tip having only one tooth with thicker edge, lemma having long awn and lemma shoulder having obvious teeth or blunt flat, palea without dividing when matures, and large and thick grains with a groin. *Ae. speltoides* var. *ligustica* have all these characteristics. Based on the morphological analysis, it was suggested that hybridization between einkorn wheat and *Ae. speltoides*-like diploid species generated two or more allotetraploids. The following chromosome rearrangements and gene mutation resulted in that S genome of *Ae. speltoides* was evolved as B genome of emmer wheat. In more recent years, molecular genetic analysis agreed that B genome of wheat came from *Ae. speltoides*. In other words, B genome is S genome. Although A. Löve (1984) had changed S into B, this correction was not widely followed. S genome and B genome are still kept in the recommendation report of the Genome Nomenclature Committee at the second International Triticeae Symposium in 1994. As for G genome, from the data of molecular genetic analysis, it is basically the same as the S genome. Dvorak et al. changed G as S genome.

In earlier reports, Peto (1936) and Вакар (1935) thought that B genome came from *Agropyron*. McFadden and Sears (1946) suggested B genome might have come from the diploid species *Ag. triticeum*. Later, Sears (1956a, b) proposed B genome came from *Ae. bicornis*, as the hybrid plant morphology of *T. monococcum* × *Ae. bicornis* was very similar with *T. dicoccum*. Riley et al. (1958) re-investigated the origin of B genome using the genome analysis method. They focused on the species in the Sitopsis group of *Aegilops*. They crossed *Ae. speltoides*, *Ae. bicornis*, *Ae. sharonensis*, and *Ae. longissima* with *Triticum monococcum*, *T. georgicum*, *T. dicoccoides*, *T. durum*, *T. turgidum*, and *T. timopheevi*. The results are shown in Table 6.5.

Based on Table 6.5, the hybrids of emmer wheat with *Ae. speltoides* showed a high level of chromosome pairing compared to those with *Ae. bicornis*, *Ae. sharonensis*, and *Ae. longissima*. This indicated that S genome of *Ae. speltoides* was highly similar to the B genome of wheat. The relationship between G genome of *T. timopheevi* and S genome of *Ae. speltoides* was also very close, based on the chromosome pairing data (Table 6.5). B and G genomes might be differentiated from a same species. However, S and A genome paring rate also exhibited a middle level of chromosome pairing (3.57 ± 0.17) in hybrids of *Ae. speltoides* with *T. monococcum*. Meanwhile, multivalents were formed in hybrids of *Ae. speltoides* with emmer wheat. Therefore, S and A genomes seemed partially homologous, although the high number of univalents (7.25 ± 0.35) in *Ae. speltoides* × *T. monococcum* indicated obvious differentiation between the two genomes.

Table 6.5 Chromosome pairing of hybrids between *Triticum* and *Aegilops*. (Riley et al. 1958)

Hybrid combination	No. of observed cells	No. of univalents	No. of bivalents	No. of trivalents	No. of quadrivalents
Ae. speltoides × *T. monococcum*	75	7.25 ± 0.35	3.57 ± 0.17	–	–
Ae. speltoides × *T. dicoccoides*	35	5.94 ± 0.36	5.21 ± 0.26	1.59	0.06
Ae. speltoides × *T. dicoccum*	50	6.70 ± 0.28	6.22 ± 0.18	0.62	–
Ae. speltoides × *T. georgicum*	30	8.00 ± 0.53	4.96 ± 0.28	1.00	0.08
Ae. speltoides × *T. durum*	50	5.90 ± 0.25	5.96 ± 0.20	1.06	–
Ae. speltoides × *T. turgidum*	50	7.92 ± 0.36	5.94 ± 0.18	0.40	–
Ae. speltoides × *T. timopheevi*	30	7.60 ± 0.41	6.28 ± 0.19	0.28	–
T. dicoccoides × *Ae. Bicornis*	40	17.37 ± 0.36	1.17 ± 0.18	0.02	–
T. turgidum × *Ae. sharonensis*	40	16.48 ± 0.31	2.22 ± 0.15	0.02	–
Ae. longissima × *T. dicoccum*	40	17.43 ± 0.47	1.60 ± 0.17	0.01	–

Sears and Okamoto (1958) observed homoeologus chromosome pairing between subgenomes in the plants nullisomic for chromosome V, indicating the existence of a gene on chromosome V that inhibited homoeologus chromosome pairing. Okamoto (1957) confirmed that chromosome V belonged to B genome. Chromosome V is 5B according to the chromosome nomenclature of Sears. This gene was later located on the long arm of 5B, namely 5BL. The discovery of this gene could be used to explain the above-observed phenomenon that there had a middle level pairing between S and A genomes in *Ae. speltoides* × *T. monococcum* and the existence of multivalents in hybrid progeny of *Ae. speltoides* and emmer wheat (Table 6.5). Probably, *Ae. speltoides* had a genetic system that reduced the inhibiting role of the gene on wheat 5BL and thus caused homoeologus chromosome pairing. Although the high possibility of B genome evolved from S genome of *Ae. speltoides*, during the long time of evolution, the current B genome might have some modifications due to gene mutation, chromosomal structural variation, and partial chromosome substitution caused by interspecific hybridization.

Okamoto (1957) confirmed the Larson' hypothesis (1952) that B genome contained two pairs of satellite chromosome, absent in A and D genomes. Two pairs of similar satellite chromosomes were only observed in *Ae. speltoides* (Pathak 1940). In terms of chromosomal morphology, S genome of *Ae. speltoides* was also similar to B genome of *Triticum*. Rees and Davies (1963) found that DNA content of *Ae. speltoides* adding *T. monococcum* (AA) was equal to DNA value of *T. durum*

(AABB). The DNA sum of *Ae. speltoides*, *T. monococcum*, and *Ae. tauschii* (DD) was equal to that in AABBDD (*T. aestivum*). The DNA content is higher and lower in *Ae. bicornis* and *Ag. triticeum* than *Ae. speltoides*. This experiment was agreed that B genome was probably derived from *Ae. speltoides*. From the phytogeography, *Ae. speltoides* and *T. urartu* have common distribution regions in eastern Turkey, Syria, Palestine, and Jordan, thus providing the chance for their natural hybridization. It is consistent that *T. dicoccoides* is also distributed in these areas.

On the other hand, some scientists found obvious differences between B genome of wheat and S genome of *Ae. speltoides.* For instance, Hadlaczky and Belea (1975) observed a pair of chromosomes with four heterochromatin dots out of two pairs of satellite chromosomes (1B and 6B) in B genome by using C-banding techniques (Fig. 6.7). The four dots were absent in *Ae. speltoides,* indicating morphological differences between B and S chromosomes. However, they also thought that significant variation occurring in the process of *Ae. speltoides* evolution is a possible reason of the chromosome differences. Shands and Kimber (1973) and Kimber (1974) thought that *Ae. speltoides* and *T. timopheevi* had a common genome. In other words, S and G genome was highly similar. They suggested that *Ae. speltoides* was G genome donor of the *T. timopheevi*, but not the B genome donor of the *T. turgidum*. According to more recent studies, the genetic relationship between G and B genome was very close. Based on its genetic relationship with B genome of other tetraploid wheat, Костов thought G as just a modification of B genome and suggested using AAB^GB^G to represent the genome of *T. timopheevi* to differentiate it from AABB in other tetraploid wheat. However, Sachs (1953) analyzed in detail chromosome pairing in meiosis of F_1 hybrids of *T. timopheevi* with *T. durum, T. dicoccum, T. turanicum, T. turgidum,* and *T. dicoccoides*. He thought that there was no need to divide them into two distinct genomes. He thought that the appearance of univalents and the production of reduced fertility in hybrid between *T. timopheevi* and other tetraploid wheat were due to a small scale of chromosome structure variation of *T. timopheevi*.

Wagenaar (1961) observed a range variation of number of univalents among 79 hybrid combinations of *T. timopheevi* with other tetraploid wheat. The hybrids between tetraploid wheat with AABB genome having normal meiosis and good seed setting also observed a few univalents. He hence thought *T. timopheevi* had genome AABB. The abnormal meiosis of its hybrids might relate to genes affecting chromosomes pairing. Different genotypes in different cross combinations could result in varied number of univalents. Wagenaar (1966) argued that the G genome of wild varieties *araraticum* of *T. timopheevi* was evolved from *T. dicoccoides*. However, G was closer to S genome of its donor species *Ae. speltoides* than B of *T. dicoccoides*. Therefore, a higher possibility is that *araraticum* originated from the hybrid of *T. monococcum* and *Ae. speltoides*. Compared with S genome, less variation existed in G than B genome. Compared to emmer wheat, *T. timopheevi* has low morphological variation and a narrow distribution region area in northwest Iran and northern part of Iraq where locates on the edge of distribution areas of wild emmer wheat. These observations suggested that the origin of *T. timopheevi* was later than emmer wheat.

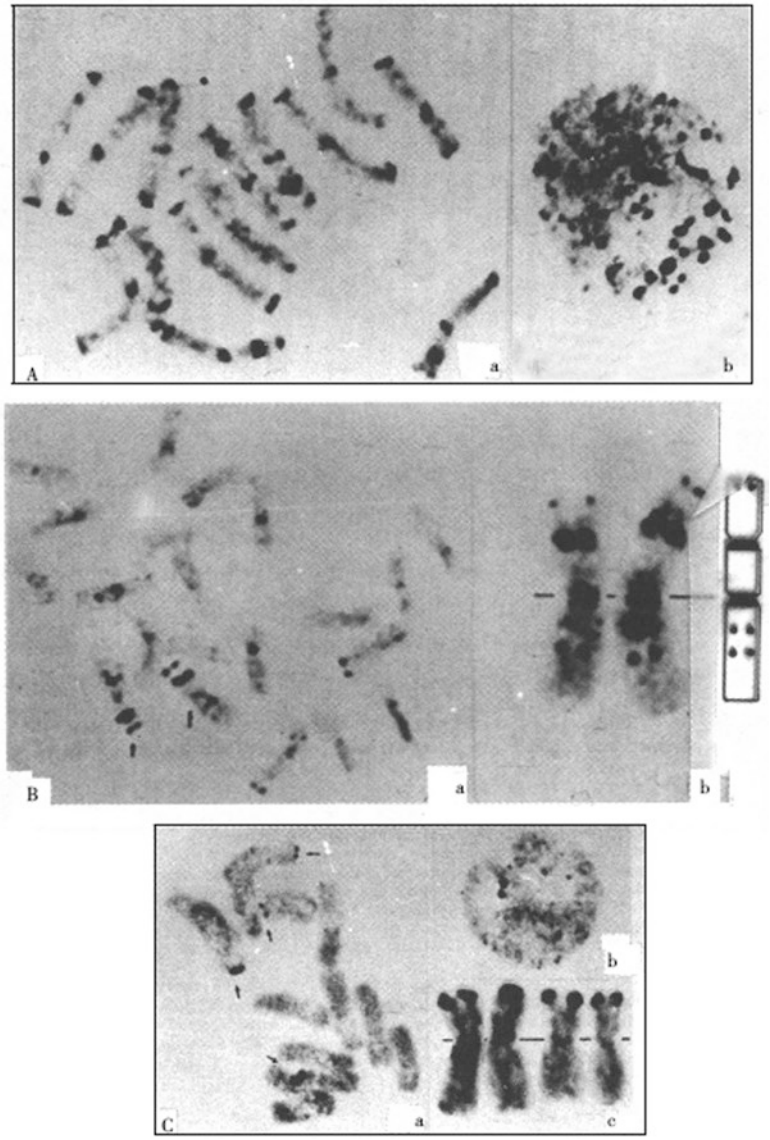

Fig. 6.7 C-banding of *T. monococcum*, *T. turgidum*, and *Ae. speltoides. F*our heterochromatic dots on the long arm of B-genome chromosomes (B), absent in *T. monococcum* (A) and *Ae. speltoides* (C). (From Hadlaczky and Belea 1975)

In the 1970s, Johnson and Dhaliwal proposed a new view on the origin of polyploid wheat (Dhaliwal and Johnson 1976; Johnson and Dhaliwal 1976, 1978). They thought that B genome was derived from *T. urartu*. Tetraploid wheat originated from the *T. boeoticum* × *T. urartu* hybrids, followed by chromosome doubling. Their suggestion was based on morphological similarity in several traits between artificial amphiploid of *T. boeoticum* × *T. urartu* and wild emmer wheat. Meanwhile, the diploid *T. boeoticum* and *T. urartu* are sympatric with one another throughout the geographic range of wild emmer wheat. Meanwhile, they indicated that *T. urartu* genome paired with A and not with B in its F1 hybrids with emmer wheat, in the presence of the *Ph* gene on chromosome 5B. Similarly, in crosses with emmer wheat, S of *Ae. speltoides* paired with A and not with B, indicating that S was quite different from B. Since B genome of emmer wheat was different from those in the extant diploid-related species, if not the donor species of B genome had become extinct, the genome of emmer wheat had changed dramatically compared to its donor species. In the context, it was impossible to determine if the donor species of B genome were *T. urartu* or *Ae. speltoides* by using chromosome pairing method. Instead, morphological comparative method was adopted. They thought the anther morphology and pollen length of emmer wheat is a middle type between *T. boeoticum* and *T. urartu*. For instance, the pollen length 2.8 mm for *T. dicoccoides* and 3.0 mm for *T. araraticum* was situated between 3.6 mm for *T. boeoticum* and 2.2 mm for *T. urartu*. For anther dehiscence mode, *T. dicoccoides* was similar to *T. boeoticum*, while *T. araraticum* was similar to *T. urartu*. For the morphology of the anther tip, however, *T. dicoccoides* was not similar to both *T. boeoticum* and *T. urartu*. Meanwhile, anther characteristics including anther length of the amphiploids between *T. boeoticum* and three diploid species of *Aegilops*'s Sitopsis group (including *Ae. longissima* var. *sharonensis*) were different from that of emmer wheat.

Compared to *Triticum*-*Sitopsis* amphiploids, the *T. boeoticum*-*T. urartu* amphiploids exhibited some traits similar to those of wild emmer wheat, including rachilla edge having fluff, short rachis node, glumes having double ridges, glumes having broad triangular teeth shoulder, size, and shape of spikelets, spikelets with the third awn differing in length (in *Triticum*-*Sitopsis* amphiploids, only *Triticum*-*Ae. speltoides* var. *ligustica* have the third awn but with poor development), and anther length (*Ae. speltoides*-*T. monococcum* amphiploids, 5.05 ± 0.6 mm; *T. dicoccoides*, 3.43 ± 0.05 mm; *T. araraticum*, 3.33 ± 0.05 mm; *T. boeoticum*-*T. urartu* amphiploids, 3.30 ± 0.04 mm).

The distribution of *T. urartu* was not limited to Armenia; its distribution range from the Caucasus to the eastern Anatolia, throughout the Fertile Crescent, as well as Syria-Palestinian (Johnson 1975; Johnson and Dhaliwal 1976). This species is sympatric with *T. boeoticum* (The *T. boeoticum* considered by Johnson and Dhaliwal should include *T. monococcum* var. *boeoticum* and var. *thaoudar*, the later had a large distribution area in the Fertile Crescent). However, there was reproductive isolation when *T. urartu* was used as female parent in hybridization. As a result, they thought that *T. boeoticum* should be the female parent when emmer wheat originated.

It seemed that Johnson and Dhaliwal's arguments based on morphological comparison were still inadequate. Some important morphological traits did not support their arguments. For instance, the caryopsis of *T. boeoticum* and *T. urartu* and their amphiploids were vertical flat on both sides, but not in tetraploid and hexaploid wheat. The caryopsis morphology of tetraploid wheat was the intermediate form between *T. urartu* with vertical flat on both sides and *Ae. speltoides* with transverse flat on up and down edges; the palea of *T. boeoticum* and *T. urartu* dehisced when matured, which was not observed in tetraploid wheat. It seems that the inductive correlation analysis of morphological features of Sarkar and Stebbins (1956) is more comprehensive than the morphological analysis of Johnson and Dhaliwal. As aforesaid, evidences from cytology and molecular biology experiments supported that *Sitopsis* in *Aegilops* (including *Ae. Speltoides*) was the donor species of B genome. Feldman (1977) using common wheat "Chinese spring" as test material to inspect chromosome pairing of hybrids with *Ae. longissima* and *Ae. searsii* observed that the chromosome pairing level between S and B genomes was significantly higher than S-A and S-D pairing. This experiment provided a strong evidence that S was closely related to B genome. In the report of Johnson and Dhaliwal (1978), there was a high level of chromosome pairing between *T. urartu* and *T. monococcum* var. *boeoticum*, usually showing six ring bivalents and one rod bivalent in metaphase I of meiosis. This indicated that the two species carry a same genome (A). Chapman et al. (1976) clearly demonstrated that the genome of *T. urartu* was A rather than B.

Dvorak (1983) compared chromosome 4A and 4B using Giemsa C-banding and observed their pairing. He thought that 4A was actually 4B, while 4B should belong to A genome. From C-banding patterns, 4A of *T. aestivum* and *T. timopheevi* resembled a pair of *Ae. speltoides* chromosomes, but different from the corresponding chromosomes of *Ae. sharonense*. Chromosome 4A was similar to B-genome chromosomes that contain heavy heterochromatins. When *Ph* gene was present, it was not paired with any chromosome of einkorn wheat *T. monococcum* and *T. urartu*. Similar situation also existed in *T. timopheevi*.

Chen and Gill (1983) using Giemsa N-banding technique (heterochromatin banding) observed the somatic chromosomes of *T. dicoccoides* (AABB), *T. araraticum* (AAGG), and the possible donor species of B and G genome: *Ae. speltoides*, *Ae. longissima*, *Ae. bicornis*, *Ae. sharonensis*, and *Ae. searsii*. They also observed extensive heterochromatins distributed in G and B genomes. Out of their possible donor species, the N-banding patterns of *Ae. speltoides* and *Ae. longissima* were more similar to B and G genome (Fig. 6.8). It is interesting that a pair of chromosomes in *T. araraticum*, *Ae. speltoides*, and *Ae. longissima* was also similar to 4A of *T. dicoccoides*. This experiment suggested that *Ae. speltoides* and *Ae. longissima* are the potential donor species of B and G genome as well as chromosome 4A of tetraploid wheat. Chromosome 4A in tetraploid wheat showed the heavy heterochromatins nearby centromere regions. However, none of the chromosomes of *T. boeoticum* and *T. urartu* had the 4A pattern of tetraploid wheat. Therefore, so-called 4A was actually 4B or 4G, and 4B and 4G was actually 4A. The 4A ditelosome and 4S in the hybrids of ditelosomic lines with *Ae. speltoides* could be paired into V type in metaphase I of meiosis. This also evidenced that 4A assigned in the past was

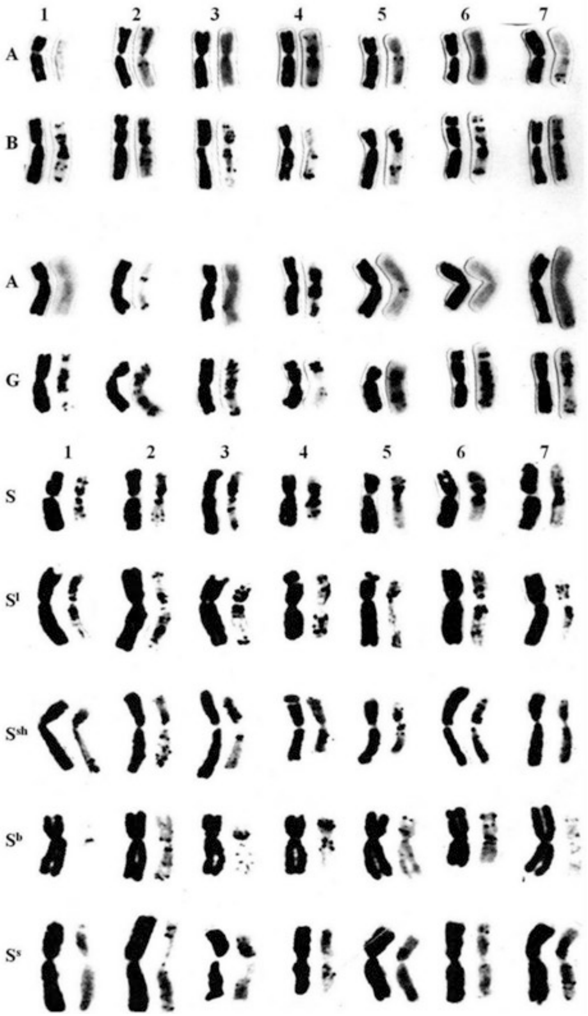

Fig. 6.8 Karyotype (left) and N-banding (right) patterns. A and B genome of *T. dicoccoides*; A and G genome of *T. araraticum; Ae. speltoides* (S) accession TAI772; *Ae. longissimi* (S^l) accession TAI924; *Ae. sharonensis* (S^{sh}); *Ae. bicornis* (S^b), and *Ae. searsii* (S^s). (From Prof. Peidu Chen)

highly homologous to 4S, and *Ae. speltoides* is the potential donor species of B and G genomes.

Using Giemsa staining of chromosomes, Noda observed eight pairs of chromosomes with strong but similar banding signals among wild emmer, cultivated emmer wheat, durum wheat, and Persian wheat. Their banding patterns were similar to those in chromosomes 4A and 1B-7B of common wheat Chinese Spring. *T. timopheevi* groups, including *T. timopheevi* and *T. araraticum* lines, also exhibited strong banding in eight pairs of chromosomes. However, there were obvious differences among *T. timopheevi* lines and between *T. timopheevi* and emmer wheat. He believed that B and G genome underwent extensive changes in chromosomal structure during the differentiation of tetraploid wheat. Based on Noda's observation and works from Chen and Gill (1983), B and G might be formed by multiple changes of S genome of *Ae. speltoides*. Kawahara and Tanaka investigated genome exchanges occurring in B and G by analyzing the hybrids of tetraploid with diploid wheat. They observed 6 and 15 different chromosome types in *T. dicoccoides* and *T. araraticum*, respectively. However, the exchange involving in A genome is little. They thought that due to frequent exchange, B and G genome in tetraploid wheat no longer resembled S genome in their ancestors.

Above evidences provided such a reliable prospect that multiple hybridizations naturally occurred between the sympatric *Ae. speltoides* and *T. monococcum* ssp. *urartu* and following chromosome doubling of hybrids generated allotetraploid plants. In such a group of ancient tetraploids, further multiple hybridizations with closely related plants containing various genomes caused chromosome structural variations. Significant changes of S genome derived from *Ae speltoides* evolved into B genome. The wild *T. turgidum* var. *dicoccoides* was firstly formed. In the long history of artificial cultivation, hybridization, and mutation under the action of selection, rich types of cultivated *T. turgidum* were gradually generated.

In a more recent history, a new tetraploid species was similarly formed by crossing *Ae. speltoides* with *T. monococcum* ssp. *urartu*. That was the wild variety *araraticum* of *T. timopheevi*. After the artificial cultivation and breeding, *T. timopheevi* cultivar was developed. The research of Upadhya and Swaminathan (1963) had shown that *T. zhukovskyi* might be originated from the hybrid between *T. timopheevi* and *T. monococcum*. According to the chromosome morphology, two in three pairs of satellite chromosome in *T. zhukovskyi* was exactly consistent with that of *T. timopheevi* and the other pair was similar to that of *T. monococcum* var. *hornemanni*. They also had very similar arm ratio (Table 6.6 and Fig. 6.9).

T. zhukovskyi exhibited normal seed-setting. However, according to chromosome pairing behavior, this species itself had multivalent and univalent during meiosis (quatrivalent: 0~4, average 1.35; trivalent: 0~2, average 0.35; bivalent: 11~21, average 16.89; univalent: 0~6, average 1.42). The existence of multivalents suggested that it had the nature of autopolyploid in a certain degree.

In terms of morphology, *T. zhukovskyi* and *T. monococcum* had similar incision glume shoulders, different from the square shoulder of *Ae. tauschii*.

T. zhukovskyi × *T. spelta* hybrids exhibited 0~2 quatrivalents (average 0.33), 0~4 trivalents (average 1.39), 6~16 bivalents (average 10.70), and 9~24 univalents (average 15.12). This pairing configuration reinforces the view that *T. timopheevi* is a parent of *T. zhukovskyi*.

Among the hybrids with *T. timopheevi*, the overall morphology of *T. timopheevi* × *T. monococcum* amphiploid was most similar to *T. zhukovskyi* (Bell et al. 1955; Watanabe et al. 1956). *T. timopheevi* × *T. monococcum* amphiploid (2IV + 17II) also exhibited a similar chromosome pairing to *T. zhukovskyi* (1.5IV + 17II + 2I) (Watanabe et al., 1955, 1956).

Table 6.6 Data of satellite chromosomes (According to Upadhya and Swaminathan 1963)

Species	2n	Chromosome total length (µm) Average ± S.E.	Satellite chromosome			Satellite chromosome			Satellite chromosome		
			Length (µm)	Satellite length (µm)	Arm ratio	Length (µm)	Satellitelength (µm)	Arm ratio	Length (µm)	Satellite length (µm)	Arm ratio
T. zhukovskyi	42	461.52 ± 12.68	10.42	0.48	0.58	7.82	1.80	0.80	7.61	1.40	0.62
T. spelta	42	452.77 ± 16.42	9.21	0.58	0.50	10.65	2.30	0.61	9.79	1.15	0.36
T. timopheevi	28	329.47 ± 12.79	–	–	–	9.67	2.13	0.73	8.79	1.42	0.57
T. momococcum var. *hornemanni*	14	146.43 ± 6.44	10.36	0.31	0.53	–	–	–	–	–	–
Ae. tauschii	14	146.85 ± 2.79	9.33	0.52	0.43	–	–	–	–	–	–

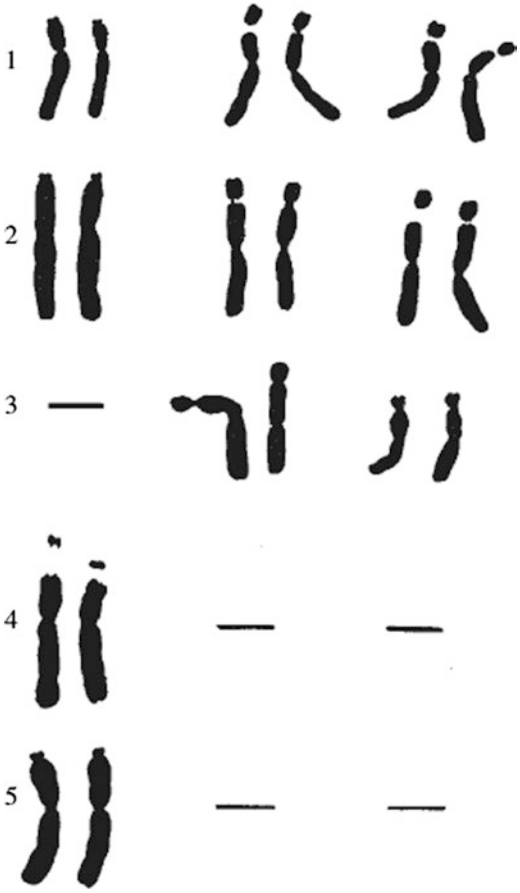

Fig. 6.9 Comparison of satellite chromosomes of wheat and related species. 1. *T. aestivum* 2. *T. zhokovskyi* 3. *T. timopheevi* 4. *T. tauschii* 5. *T. monococcum*. (Redrawn based on Upadhya and Swaminathan 1963)

If *T. monococcum* was another parent of *T. zhukovskyi*, the chromosome composition of *T. zhukovskyi* × *T. spelta* F_1 hybrids should be AAABGD. This is consistent with meiotic observation because of the existence of trivalent and a high frequency of univalent (15.12 I) in F_1 hybrids (Upadhya and Swaminathan 1963; in this paper, the authors thought that G was B and the genome of *T. zhukovskyi* is AAABBD, consistent with Wegenaar's view. We will discuss about this point later. Here we temporarily used AAABGD instead AAABBD to just differentiate B from G).

The geographical distribution of *T. zhukovskyi* was sympatric with *T. timopheevi* and *T. monococcum*. Therefore, *T. zhukovskyi* was likely to be a hybrid of *T. timopheevi* and *T. monococcum*, followed by spontaneous chromosomes doubling.

The systematic origin of *Triticum* and its closely related plants has become relatively clear compared to other plant systems. The nomenclature of genomes has been unified and consistently used by scholars after some modifications. For instance, genome D was once named C, which was confused with C of *Ae. caudata*. However, there are different nomenclatures for B, G, and S genomes. The existence of such a problem was very natural. Its solution depends on further in-depth research. Just as the identification and nomenclature of a species are sometimes revised accompanying the updates of new knowledge.

Based on current research results, the boundary between A and D genome in Triticeae is very clear. Although there were obvious differences between B and G, they basically belong to a same type. They also had similar relationship with S genome. With the development of molecular cytogenetics in recent years, genomic in situ hybridization (GISH) using total genomic DNA provides a tool to identify genome constitution of a species. GISH analysis showed that the genome of *Ae. speltoides* could be hybridized with all the B-genome chromosomes of wheat (Mukai et al. 1993; Mukai 1995). These experiments demonstrated that B and S genomes had a high genetic identity. They should be the same genome. Their differences are only a reflect of genome subtypes. On the other hand, they were very active in the process of genome evolution, representing a typical mode of species divergence. In order to show the systematic and hierarchical relationship, some modifications on genome names were made. Since B genome was named first, it was suggested that SS of *Sitopsis* group in *Aegilops* was modified as BB and SS of *Ae. speltoides* was amended as $B^{sp}B^{sp}$ on basis of the advice of Áskell Löve (1984). Since GG of *T. timopheevi* is proved to be SS, it was changed here to $B^{sp}B^{sp}$. Similarly, S^bS^b of *Ae. Bicornis* was amended as B^bB^b, S^IS^I of *Ae. longissima* as B^IB^I, S^sS^s of *Ae.searsii* as B^sB^s.

On the origin and classification system of wheat, the Soviet Синская in 1955 published a retrogressive view mainly based on the old morphological taxonomy. Although she cited some experimental data on interspecific hybridization, she took the Lisenko's leap theory of species formation as the theoretical basis. She ignored numerous experimental evidences of modern cytogenetics and artificial synthesis of wheat species, and denied the role of distant hybridization in the species formation of *Triticum*. In her supposition, all *Triticum* species except einkorn wheat originated from the hypothetical *T. protomacha* that originated from the hypothetical "extinct *Protoelytrigia*." Wild einkorn wheat evolved from *Protoelytrigia* without the change of chromosome number. *T. protomacha*, the ancestor of other wheat, had a "jumping in the number of chromosomes" and produced 2n = 28 or 2n = 42. *Triticum* species originated from different species; thus, they were not related to each other. She made the classification system of wheat as following:

Triticum L.
Group I (section I) — Monococca Schiemann
  1. *T. aegilopides* Bal.
  2. *T. urartu* Thum.
  3. *T. monococcum* L.
Group II (section II)—Dicoccoides Sinsk.
  Subgroups I (subsection I)—Eudicoccoides Sinsk.
    1. *T. dicoccoides* Korn.
  Subgroups II (subsection II)—Transcaucasica Sinsk.
    1. *T. araraticum* Jacubz; *T. chaldicum* Men.
    2. *T. timopheevi* Zhuk.

Group III (section III)—Eutriticea Sinsk.
- Subgroup I (subsection I)—Prototriticea Sinsk.
  1. *T. macha* Men.
  2. *T. paleocolchicum* Men.
  3. *T. antiquorum* Heer.
  4. *T. aethiopicum* Jacubz.
- Subgroup II (subsection II)—Vulgaria Sinsk.
  1. *T. vulgare* Vill; *T. compactum* Host.
  2. *T. spelta* L.
  3. *T. sphaerococcum* Perc.

  Subgroup III (subsection III)—Duriuscula Sinsk.
  1. *T. durum* Desf. Emend., including *T. turgidum* L.
  2. *T. dicoccum* Schubl
  3. *T. persicum* Vav.; *T. carthlicum* Nevski

Синская's viewpoint about the origin and classification of wheat not only had no exact facts as evidences, but also could not be supported by the test and analysis of modern experimental biology. Here it has been just mentioned incidentally to demonstrate that such an arbitrary and unsubstantiated view was published in 1950s.

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Chapter 7
Development of *Triticum* Taxonomy

Over the past 20 years, the development of cytology, genetics, and crossbreeding has accumulated abundant objective data and documents for wheat, one of the most important crops in the world. New knowledge is helpful for understanding phylogeny of wheat. Correspondingly, some questions challenged the old concept of wheat taxonomy. For instance, the generally accepted six species including commercial cultivars in dinkel reihe can easily hybridize each other and their hybrids usually had normal chromosome pairing and high fertility. The morphological difference used as a key trait of species classification can be caused by a single gene. Such as for the spike shape of *T. aestivum* and *T. spelta*, there is only the gene difference between *Q* and *q*. The difference between *T. compactum* and other species is only caused by the gene *c*, while the difference between *T. sphaerococcum* and *T. aestivum* is due to the gene *S* (Ellerton 1939). Therefore, many scholars disagreed the treatment of six "species." They thought that *T. aestivum*, *T. spelta*, *T. compactum*, *T. macha*, *T.* vavilovii, and *T. sphaerococcum* belong to a same species. Thellung (1918), Mackey (1954), and Sears (1956a, b) regard them as subspecies of *T. aestivum*, as following:

Triticum aestivum L. emend. Thell.

subsp. *spelta* (L.) Thell.
subsp. *macha* (Dek. et Men.) MacKey
subsp. *vavilovii* (Tuman) Sears
subsp. *vulgare* (Vill.) MacKey
subsp. *compactum* (Host) MacKey
subsp. *sphaerococcum* (Perc.) MacKey

Bowden (1959) published a taxonomic system on *Triticum*. He combined some *Aegilops* species that closely related to wheat into this genus. Allotetraploid wheat originated from hybridization was considered a same species, including three varietas, two forma, and eight cultivar groups. He did not consider allohexaploid common wheat as a species, as he accepted the old taxonomic concept that one species

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must have a stable geographical distribution in wild status. Although common wheat is cultivated all over the world, with the widest geographical distribution and the largest population in plant kingdom, Bowden think common wheat has no wild distribution. Allotetraploid *T. turgidum,* also originated from hybridization, was considered as a species since it has the wild var. *dicoccoides*. He treated hexaploid wheat *T. aestivum*, *T. spelta*, *T. compactum*, *T. sphaerococcum*, *T. macha*, and *T. vavilovii* as cultivar groups, which was considered as an interspecific hybrid of *Triticum* × *aestivum* L. emend. Bowden's taxonomic system is summarized as follows:

Bowden's taxonomic system (1959)
I. Diploid species (2n=14)
  1. *T. monococcum* L. (including *T. boeoticum* Boiss., *T. thaoudar* Reut.)
  2. *T. bicorne* Forsk. Syn. *Aegilops bicornis* (Forssk.) Jaub. et Spach.
  3. *T. speltoides* (Tausch) Gren. Ex Richter (=*Aegilops speltoides* Tausch)
    f. *ligusticum* (Savign.) Bowden comb. Nov. (=*Agropyrum ligusticum* Savign.)
  4. *T. comosum* (Sibth. et Sm.) Richter (=*Aegilops comosa* Sibth. et Sm.)
  5. *T. uniaristatum* (Vis.) Richter (=*Aegilops uniaristata* Vis.)
  6. *T. longissimum* (Schwerinf. et Muschl. in Muschl) Bowden, comb. nov. (=*Aegilops longissima* Schw. et Musch.)
  7. *T. umbellulatum* (Zhuk.) Bowden comb. nov. (=*Aegilops umbellulatum* Zhuk.)
  8. *T. tripsacoides* (Jaub. et Spach) Bowden, comb. nov. (=*Aegilops tripsacoides* Jaub. et Spach.)
    a. f. *tripsacoides*
    b. f. *loliaceum* (Jaub. et Spach) Bowden, comb. nov. (=*Aegilops loiacea* Jaub. et Spach.)
  9. *T. dichasians* (Zhuk.) Bowden, comb. nov.
(=*Aegilops caudata* L. subsp. *dichasans* Zhuk.)
  10. *T. aegilops* P. Beauv. ex R. et S. (=*Aegilops squarrosa* L.∗)
∗ In 1812, Ambrois Marie Francois
Joseph Palisot de Beauvois mistaken it as Linné's *Ae. squarrosa* L., and
hence combined it into *Triticum*, named *T. aegilops*. In fact, the plant was
not *Ae. squarrosa* L. and it's a different species that has the correct name
of *Ae. tauschii* Cosson.
II. Allopolyploid (Hybridization origin)
II a. Allotetraploid species(2n=28)
  11. *T. turgidum* L. emend.
  (1) Cultivar group
    a. *turgidum*
    b. *polonicum*
    c. *dicoccoum*
    d. *durum*
    e. *carthlicum*
    f. *palaeocolchicum*
    g. *turanicum*

h. *aethiopicum*
(2) var. *dicoccoides* (Korn. in litt. in Schwinf.) Bowden, comb. nov.
(3) var. *timopheevi*
a. f. *timopheevi*
b. f. *zhukovskyi* (Men. et Er.) Bowden, comb. nov.
(4) var. *tumanianii* (Jakubz.) Bowden, comb. nov. (=*T. dicoccoides* Korn. subsp. *armeniacum* Jakubz. var. *tumanianii*)
II b. Allohexaploid (2n=42)
12. *Triticum*×∗*aestivum* L. Emend.
∗ ×: Here is a common sign of taxonomy for hybrid plants, not a sign of crossbreeding.
Cultivar group
a. *aestivum*
b. *spelta*
c. *compactum*
d. *sphaerococcum*
e. *macha*
f. *vavilovii*
II c. Allopolyploid (2n=28 or 42)
13. *T. ovatum* (L.) Raspail (=*Aegilops ovata* L.)
14. *T. triaristatum* (Willd.) Godr. et Gren. (=*Aegilops triaristata* Willd.)
15. *T. kotschyi* (Boiss.) Bowden, comb. nov. (=*Aegilops kotschyii* Boiss.)
16. *T. triunciale* (L.) Raspail (=*Aegilops triuncialis* L.)
17. *T. cylindricum* Ces., Pass. et Gib. (=*Aegilops cylindrica* Host)
18. *T. macrochaetum* (Schuttl. et Huet, ex Duval-Jouve) Richter Syn. A. *biuncialis* Vis. (non T. *biunciale* Vill.)
19. *T. crassum* (Boiss.) Aitch. et Hemsl. (=*Aegilops crassa* Boiss.)
20. *T. turcomanicum* (Rosh.) Bowden, comb. nov. (=*Aegilops turcomanica* Rosh.)
21. *T. juvenale* Thellung in Fedde
Syn. *Aegilops juvenalis* (Thellung in Fedde) Eig in Fedde
22. *T. ventricosum* Ces., Pass. et Gib.
Syn. *Aegilops ventricosa* Tausch., *Ae. squarrosa* sensu Cosson, *Ae. squarrosa* sensu Willd., *Ae. fragilis* Parlat., *T. fragile* (Parlat.) Ces., Pass. et Gib., non. *T. fragile* Roth.

Bowden believed that this classification is in line with the natural system relationship. However, the division of the genus is inherently subjective. Because in natural units only individuals are absolute in higher plants and animals, and species are consisted of individuals that are linked by sexual reproduction. Individuals within a species share a common gene pool and harbor a similar genetic structure. They form a unique and objective natural unit. Except for individuals and species, there are no exact boundaries between genera or higher taxon class. The classification in genus or higher class is relative and there are intermediate types. Hence, the subjectivity of division must exist. We think that the treatment on genus is adequate as long as it can basically reflect natural system relationship. The main purpose of systematic taxonomy is to identify species—the natural unit that exists objectively, and to reveal systematic and evolutionary relationships between species. In order to use species and to improve species on basis on systematic knowledge, that is for breeding services, the purpose of genus division is achieved as long as it can reflect the systematic relationship.

Morris and Sears (1967) followed Bowden's taxonomic system with some modifications according to recent works. They believed that:

1. *T. timopheevi* group is not only genetically isolated from other tetraploid wheat, but also the geographical distribution of its wild species is much north than *T. dicoccoides*. Therefore, *T. timopheevii* was treated as a species, including var. *timopheevii* and var. *zhukovskyi* (Men. et Er.) Morris et Sears. Meanwhile, they canceled var. *tumanianii*. They thought this varietas is *T. araraticum*, and *T. araraticum* is a wild type of *T. timopheevii* var. *timopheevii*.
2. They canceled the *T. turcomanicum*, as the hexaploid plant collected in the past is actually the species *T. juvenale*.
3. They added a species, namely *T. columnare* (Zhuk.) Morris et Sears comb. nov.
4. In the cultivar-group level, Bowden, following Якуыцинер, thought that *turanicum*, *ethiopicum*, and *poleocochicum* were independent groups of *T. turgidum*. Morris and Sears canceled them, as they thought that these cultivar groups belonged to *durum* or *dicoccum*. In addition, they canceled *T. macha* and classified it into *T. spelta*.

Bowden, Morris, and Sears represent the classification school of modern wheat taxonomy, that is incorporating *Aegilops* species into the *Triticum* established a big *Triticum* genus. Their treatment, in fact, is the following of Hackel's insights, but more focusing the utilization of cytogenetics research achievement.

The contrary opinion is the separation of *Aegilops* and *Triticum*. MacKey (1966, 1968) thought *Triticum* had only five species, as shown in Table 7.1. He thought that *T. timopheevi* was a young polyploid species. The hexaploid wheat *T. zhukovskyi* which was derived from *T. timopheevi* should be also an independent species.

In recent years, a new advance in the evolution study of *Triticum* is the elucidating of nuclear-cytoplasmic relationship. Studies on interspecific hybridization had accumulated much data on the relationship between nuclei and cytoplasm. Kihara (1966, 1968) noted the significance of nuclear-cytoplasmic relationship in systematics. The genetic materials in a cell can be divided into two parts, inside nucleus locating on chromosomes and outside nucleus existing in organelles of cytoplasm such as chloroplast and mitochondria. They have different genetic transmission and action systems, but they need cooperate to form a complete genetic system. In interspecific hybrids, different nuclear-cytoplasmic combinations exhibited distinct responses, as summarized in Table 7.2.

As mentioned before, the two most obvious pairs of satellite chromosomes in tetraploid and hexaploid wheat are 1B and 6B from B genome. The pair of satellites from A-genome chromosomes of *T. monococcum* ssp. *urartu* and D genome of *Ae.*

Table 7.1 Taxonomic system of *Triticum* (L.) Dumort (MacKey 1966)

Einkorn-reihe (2n=14)	Emmer-reihe (2n=28)	Dinkel-reihe (2n=42)
Monococca F_1	Dicoccoides F_1	Speltoidea F_1
T. monococcum L.	*T. timopheevi* Zhuk.	*T. zhukovskyi* Men. et Er.
subsp. *boeoticum* (Boiss.) MK.	subsp. *araraticum* (Jakubz.) MK.	*T. aestivum* (L.) Thell.
subsp. *monococcum* MK.	subsp. *timopheevi*	subsp. *spelta* (L.) Thell.
	T. turgidum (L.) Thell.	subsp. *vavilovii* (Tum.) Sears
	subsp. *dicoccoides* (Korn.) Thell.	subsp. *macha* (Dek.et Men.)
	subsp. *dicoccum* (Schrank) Thell.	subsp. *vulgare* (Vill)MK.
	subsp. *palaeocolchicum* (Men.) MK.	subsp. *compactum* (Host) MK.
	subsp. *turgidum* (L.) MK.	subsp. *sphaerococcum* (Perc.) MK.
	subsp. *durum* (Desf.) MK.	
	subsp. *turanicum* (Jakubz.) MK.	
	subsp. *polonicum* (L.) MK.	
	subsp. *carthlicum* (Nevski) MK.	

Table 7.2 Responses to nuclear-cytoplasmic combinations (According to Kihara 1968)

Phenotype	Cytoplasm	Nucleus
1) Male sterile	*Ae. caudata*	*T. aestivume* *
2) Hybrid vigour	*Ae. caudata*	Salmon (*T. aestivum*)
3) Hybrid weakness (lethal)	*Ae. longissima*	*Ae. aucheri*
4) Haploid and bi-embryo	*Ae. caudata*	Salmon (*T. aestivum*)
5) Pistillody	*Ae. caudata*	Emmer wheat except *T. durum melanopus*
	T. aestivum	*Secale cereal*
6) Delayed heading	*Ae. ovata*	Emmer wheat
7) Inembryonate grain	*Ae. caudata*	*T. aestivum*
8) Variegated leaf	*T. monococcum var. boeoticum*	*T. turgidum nigrobarbatum*
9) Female sterile	*Ae. caudata*	*T. durum reichenbachii*

For the sake of clear text and uniform scientific name, minor modifications have been made on the Kihara's original table. **T. aestivume* = *T. aestivum erythrospermum*

tauschii are hidden or become faint in tetraploid and hexaploid wheat (Morrison 1953). Satellite chromosomes are important for plants since they contain secondary constructs corresponding to nucleolar organizers that is the site of ribosome biogenesis. Ribosomes are the macromolecular machines that are responsible for mRNA translation into proteins. The dominance of nucleolar organizers of chromosomes

1B and 6B suggested that tetraploid and hexaploid wheat is compatible with the nucleolus of B genome. Kihara (1959) found that a satellite chromosome of *Ae. caudata* restored the fertility of wheat with the cytoplasm of *Ae. caudata*, which suggested the importance of nucleoli compatible with the cytoplasmic donor on normal plant development. Suemoto (1968) conducted an experimental test on the cytoplasmic origin of tetraploid wheat. He used *T. monococcum* var. *boeoticum* and *Ae. speltoides* as the female parent to supply the cytoplasm to their hybrids with *T. turgidum* and *T. timopheevi*. It was clearly indicated that *T. turgidum* with the cytoplasm of *T. monococcum* could only form small and dried anthers with sterile pollen, but its pistils were normal. This indicated that the cytoplasm of *T. monococcum* caused male-sterile but female-fertile. However, *T. turgidum* with the cytoplasm of *Ae. speltoides* developed normal stamens with fertile pollen and normal pistils (Figs. 7.1 and 7.2). This suggested that the male sterility was caused by the incompatibility between B genome and cytoplasm of *T. monococcum*, rather than the interaction between A and B genomes. After continuous backcrossing with normal emmer wheat as male, the pollen of *T. turgidum* with the cytoplasm of *T. boeoticum* was still sterile, but the seed-setting rate was significantly increased. This increasing is obviously caused by the recovery of normal meiosis behavior, not by cytoplasm. Therefore, it was concluded that the cytoplasm of *T. turgidum* is derived from *Ae. speltoides* or related species, but not from *T. monococcum*; the cytoplasm of *T. aestivum* is derived from *T. turgidum*, original from *Ae. speltoides*. On the other hand, it was difficult to determine the source of cytoplasm of *T. timopheevi*, although it is closer to the cytoplasm of *Ae. speltoides* than *T. monococcum*. A later experiment of Suemoto (1973) showed that cytoplasm of *Ae. speltoides* is very similar to that of *T. timopheevi*. *Ae. speltoides* can be considered as the donor species of the *T. timopheevi* nuclear and cytoplasmic genome.

In summary, in the originating process of *T. turgidum*, *Ae. speltoides* is the female parent and *T. monococcum* ssp. *urartu* is the male parent. *Ae. speltoides* is the donor of B genome and cytoplasm. For *T. aestivum*, *T. turgidum* is the female parent and *Ae. tauschii* is the male parent. *T. turgidum* is donor of A and B genomes and cytoplasm.

Ohtsuka (1983) tested the effects of *Ae. tauschii* cytoplasm in the *tetraploid wheat* nuclear background (Tables 7.3, 7.4 and 7.5). An emmer wheat with *Ae. tauschii* cytoplasm and chromosome 1D [abbrev. as (*sq*)AABB + 1D] as female was crossed with 100 tetraploid wheat strains to observe nuclear-cytoplasmic compatibility. Chromosome 1D in (*sq*)AABB + 1D is responsible for viability and pollen fertility in *Ae. tauschii* cytoplasm. Based on the responses, he divided tetraploid wheat strains into three categories, namely AB, AG, and AB′. The AB-type strains, such as from *T. turgidum*, *T. durum*, *T. dicoccum*, and Palestine *T. dicoccoides*, exhibited lethality against *Ae. tauschii* cytoplasm. Their nuclei were incompatible with *Ae. tauschii* cytoplasm. *T. timopheevi* and *T. araraticum* (AG type) with *Ae. tauschii* cytoplasm can be developed into normal plants, indicating full compatibility with *Ae. tauschii* cytoplasm. However, *T. persicum*, *T. pyramidale*, *T. palaeocolchicum*, and a few *T. dicoccoides* from Mesopotamian (AB′ type) differed from AB

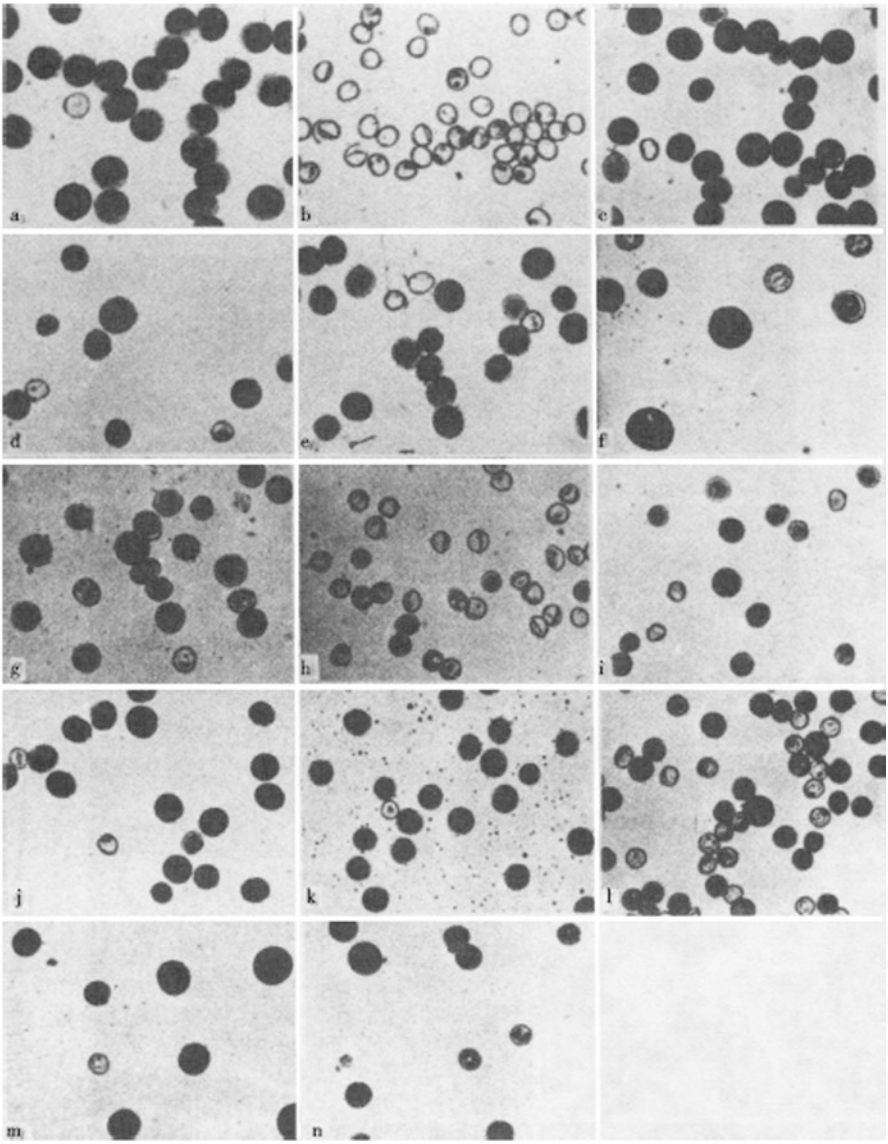


Fig. 7.1 Pollen grain. (**a**) Control, *T. turgidum*; (**b**) cultivar No. 267-1-4, *T. boeoticum* × *T. turgidum*; (**c**) 255-1-6, *Ae. speltoides* × T. *turgidum*; (**d**) 250-3-1, *T. monococcum* vulgare × *T. turgidum*; (**e**) 243-1-2, (S^bS^bAA × *T. dicoccum*) × *T. turgidum*; (**f**) 244-2-1, *Ae. longissima* × *T. turgidum*; (**g**) 247-1-1, *Ae. sharonensis* × *T. turgidum*; (**h**) 280-1-1, (*T. boeoticum* × *T. turgidum*) × *T. vulgare*; (**i**) 262-1-1, (*Ae. speltoides* × *T. turgidum*) × *T. vulgare*; (**j**) 272-1-1, (*T. boeoticum* × *T. turgidum*) × *T. dicoccoides kotschvanum*; (**k**) control, *T. timopheevi*; (**l**) 306-4-3, *T. boeoticum* × *T. timopheevi*; (**m**) 303-1-2, *Ae. speltoides* × *T. timopheevi*; (**n**) 290-1-9, (*T. boeoticum* × *T. turgidum*) × *T. timopheevi*. (According to Hinako Suemoto 1968)

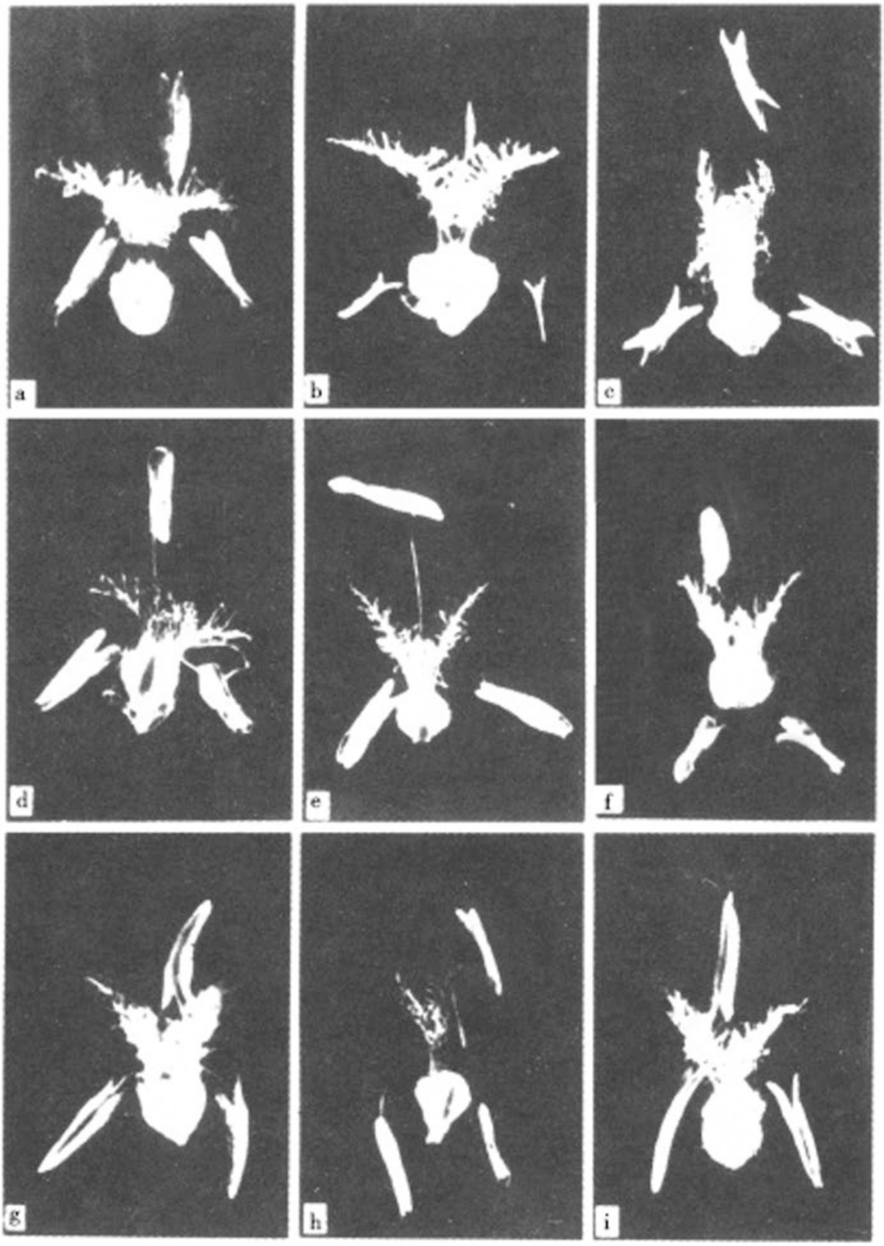


Fig. 7.2 Floral organ. (**a**) Control, *T. turgidum*; (**b**) cultivar no. 26714, *T. boeoticum* × *T. turgidum*; (**c**) 255-1-6, *Ae. speltoides* × *T. turgidum*; (**d**) control, *T. timopheevi*; (**e**) 306-1-4, *T. boeoticum* × *T. timopheevi*; (**f**) and (**g**) 303-1-2, 303-2-2, *Ae. speltoides* × *T. timopheevi*; (**h**) and i. 288-1-4, 290-1-9 (*T. boeoticum* × *T. turgidum*) × *T. timopheevi*. (According to Hinako Suemoto 1968)

Table 7.3 Seed and seedling development of F_1 hybrids between (*sq*) AABB + 1D and tetraploid wheat species (male). (According to Ohtsuka 1983)

Male parent	Seed morphology			Seedling growth			
	No. of florets pollinated	No. of normal seeds	No. of abnormal seeds∗	No. of normal plant	No. of dwarfing plant∗∗	No. of death after sprouting	No. of agensis
Emmer wheat (**AABB** genome)							
T. durum var. *reichenbachii*	294	24	208	20	0	0	4
T. turgidum var. *nigro-barbatum*	206	41	130	33	0	3	5
T. polonicum var. *vestitum*	270	99	118	99	0	0	0
T. dicoccum var. *liguliforme*	248	41	66	40	0	0	1
T. Dicoccoides var. spontaneo-nigrum	432	27	258	21	0	0	6
T. persicum var. *stramineum (= carthlicum)*	74	73∗∗∗	0	6	35	18	14
T. pyramidale var. *recognitum*	92	66∗∗∗	0	9	47	6	4
T. palaeocolchicum var. *schwamilicum (= georgicum)*	172	102∗∗∗	0	20	14	25	43
Triticum timopheevii (**AAGG** genome)							
T. timopheevi var. *typicum*	60	40	0	38	0	1	1
T. araraticum var. *thmaniani*	254	179	0	159	0	6	14

Note: ∗grains failed to germinate. ∗∗Dwarf plants stop growing in winter, and some showed chloroplast mosaics. ∗∗∗Shrunken but germinated grains were included

and AG types, as they formed dwarfing plants with mosaic leaves under *Ae. tauschii* cytoplasm. The different responses of tetraploid wheat to *Ae. tauschii* cytoplasm reflected their phylogenetic differentiation (Tables 7.3, 7.4 and 7.5).

Responses of hexaploid wheat *T. aestivum* to *Ae. tauschii* cytoplasm was related with tetraploid wheat types. *T. macha* and its derived some club wheat lines belong to AB′ type, while common wheat belongs to AB type (Table 7.6).

Ohtsuka's experiment indicated that Egyptian cultivar group of tetraploid wheat was AB′ type. It was a secondary tetraploid wheat, derived from hybridization between hexaploid club wheat (AB′ type) and durum wheat. Persian wheat, including AB′ and AB types, was also secondary wheat formed by hybridization between *T. palaeocolchicum* emmer and common wheat (Fig. 7.3).

Table 7.4 Seed and seedling development of F_1 hybrids between (*sq*)AABB + 1D and different tetraploid wheat types. (According to Ohtsuka 1983)

	Seeds		Seeding development		
	Viable		Dystrophia (lethal)	Normal plant	Dwarfing plant (Mosaic leaf)
Male parent	Normal	Shrink			
AB type	(sq) **AABB+1D**	—	(sq) **AABB**	(sq) **AABB+1D** (2n = 29)	—
AG type	(sq) **AABB+1D**	—	—	(sq) **AABG+1D**	—
	(sq) **AABG**			(sq) **AABG** (2n = 29 and 28)	
AB′ type	(sq) **AABB'+1D**	(sq) **AABB'**	…	(sq) **AABB'+1D** (2n = 29)	(sq) **AABB'** (2n = 28)

Table 7.5 Classification of tetraploid wheat based on the responses to *Ae. squarrosa* cytoplasm (According to Ohtsuka 1983)

AB type		AB′ type	AG type
Wild	Syria-Palestine	Mesopotamia∗	Mesopotamia∗
	T. dicoccoides (**AABB**); 4 strains	*T. araraticum* (**AAGG**); 1 strain—	*T. araraticum* (**AAGG**); 18 strains
	Mesopotamia∗	Mesopotamia∗	Transcaucasia
	T. dicoccoides (**AABB**); 5 strains——	*T. dicoccoides* (**AABB**); 3 strains—	*T. araraticum* (**AAGG**); 6 strains
Cultivated hulled	*T. dicoccum* (**AABB**); 17 strains	*T. palaeocolchicum* (= *georgicum*) (**AABB**); 4 strains	*T. timopheevi* (**AAGG**); 9 strains
Cultivated naked	*T. persicum* (= *carthlicum*) (**AABB**); 1 strain——	*T. persicum* (= *carthlicum*) (**AABB**); 9 strains	
	T. orientale (= *turanicum*) (**AABB**); 1 strain———	*T. orientale* (= *turanicum*) (**AABB**); 2 strain	
	T. durum (**AABB**); 12 strains	*T. pyramidale* (**AABB**); 4 strains	
	T. turgidum (**AABB**); 3 strains		
	T. aethiopicum (**AABB**); 2 strains		
	T. polonicum (**AABB**); 2 strains		
	T. isphahanicum (**AABB**); 1 strain		

∗Wild species were collected from the northern Mesopotamian highlands by Tanaka masatake et al. from the Highland Plant Survey Team of Kyoto University

Table 7.6 Responses of seed and seedling of hybrids between hexaploid and tetraploid wheat in *Ae. tauschii* cytoplasm. (According to Ohtsuka 1983)

Cross combinations	Seed setting rate (%)	Seeds		Seedling development			
		No. of normal seed	No. of agenesis seed (%)	No. of normal plants	Inlay mosaic* (%)	No. of death plants	No. of nongerminated plants
T. spelta var. *duhamelianum*							
(*T. spelta* × **AB** type $4x^1$) × **AB** type $4x^1$	56.9	141	0	132	0	6	3
[(sq) *T. spelta* × **AB** type $4x^1$] × **AB** type $4x^1$	38.6	219	111 (33.6%)	131	0	4	0
(*T. spelta* × **AB′** type $4x^2$) × **AB** type $4x^1$	41.4	264	0	—	—	—	—
[(sq) *T. spelta* × **AB′**type $4x^2$] × **AB** type $4x^1$	35.8	236	51 (17.8%)	—	—	—	—
T. macha var. *sub-letschumicum*							
(*T. macha* × **AB** type 4x) × **AB** type $4x^1$	52.0	579	0	226	0	11	0
(sq)*T. macha* × **AB** type $4x^1$	43.7	459	114 (19.9%)	133	31 (31.0%)	40	35
(*T. macha* × **AB′** type $4x^2$) × **AB** type $4x^1$	50.3	474	0	—	—	—	—
[(sq)*T. macha* × **AB′** type $4x^2$] × **AB** type $4x^1$	45.7	649	0	—	—	—	—
T. aestivum (=*vulgare*)							
var. *erythrospermum* (T.v.e.)							
(T. v. e. × **AB** type4) x^1 × **AB** type $4x^1$	35.7	137	0	—	—	—	—
[(sq) T. v. e. × **AB** type $4x^1$] × **AB** type $4x^1$	24.0	152	82 (35.0%)	—	—	—	—
(T. v. e. × **AB′** type $4x^3$) × **AB** type $4x^1$	21.5	101	1	—	—	—	—

(continued)

Table 7.6 (continued)

Cross combinations	Seed setting rate (%)	Seeds		Seedling development			
		No. of normal seed	No. of agenesis seed (%)	No. of normal plants	Inlay mosaic* (%)	No. of death plants	No. of nongerminated plants
[(sq) T. v. e. × **AB′** type 4x[3]] × **AB** type 4x[1]	32.2	274	42 (13.3%)	—	—	—	—
cv. Selkirk							
(Selkirk × **AB** type 4x[4]) × **AB** type 4x[4]	49.3	354	1	329	0	19	6
[(sq) Selkirk × **AB** type 4x[4]] × **AB** type 4x[4]	36.8	494	286 (36.7%)	294	0	28	7
(Selkirk × AB′ type 4x[5]) × **AB** type 4x[4]	36.3	434	0	—	—	—	—
[(sq) Selkirk × **AB′** type 4x[5]] × **AB** type 4x[4]	32.0	304	54 (15.1%)	—	—	—	—
cv. Chinese Spring							
(sq) **AABB+1D** line[6] × Tetra-Chinese Spring[7]	38.9	11	45 (80.4%)	—	—	—	—
cv. Prelude							
(sq) **AABB** + 1**D** line[6] × Tetra-Prelue[8]	48.1	19	80 (80.8%)	—	—	—	—
T. compactum var. *humboldti*							
(*T. compact* × **AB** type 4x[1]) × **AB** type 4x[1]	61.7	293	3	172	0	4	9
[(sq) *T. compact* × **AB** type 4x[1]] × **AB** type 4x[1]	35.8	236	69 (22.6%)	145	11 (6.5%)	12	1

Note: 1. *T. turgidum* var. *nigro-barbatum*; 2. *T. palaeocolchicum* (=*georgicum*) var. *Schwamilicum*; 3. *T. persicum* (=*carthlicum*) var. *Stramineum*; 4. *T. durum* var. *reichenbachii* and *T. turgidum* var. *nigro-barbatum*; 5. *T. persicum* (=*carthlicum* var. *fuliginosum*); 6. (*squarrosa*) *T. durum* var. *reichenbachii* + 1D; 7. tetraploid (AABB) derived from *T. aestivum* cv. Chinese spring by Dr. Furuta (unpublished); 8. tetraploid (AABB) derived from the of *T. aestivum* cv. Prelude by Dr. P. J. Kaltsikes et. al. (1969)

∗Seedlings with mosaic leaves at low temperatures

On the other hand, Okamoto (1957) crossed *T. aestivum* (AABBDD) with the amphiploid of *T. monococcum* var. *boeoticum* × *Ae. tauschii* (AADD). The F_1 (AABDD) hybrids were expected to have 14 bivalents and 7 univalents in meta-

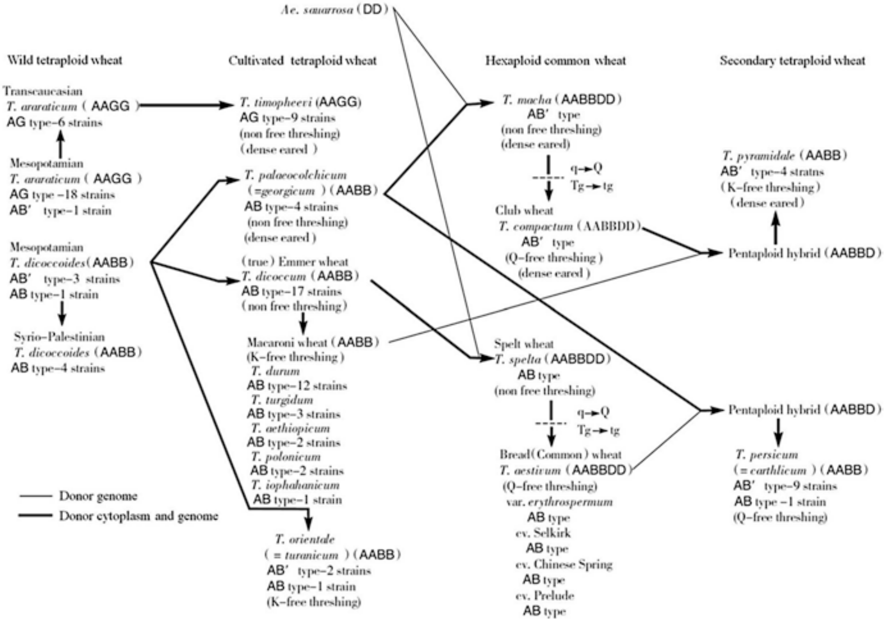


Fig. 7.3 Evolution pathways of polyploid wheat based on different responses of wheat genome to cytoplasm of *Ae. squarrosa*. (According to Ohtsuka 1983)

phase I of meiosis. However, only an average of 6 bivalents were observed although the highest was up to 13 bivalents among cells. When he crossed *T. aestivum* containing monosomic 5B, the hybrids lacking 5B showed an average of 12 bivalents, the highest cell having 15 bivalents. Sears and Okamoto (1958) observed 3-7 bivalents (5-6 on average) in the hybrids with genome AABD. When the hybrids were missing 5B, up to 14 bivalents were observed in a cell, with an average of 10 bivalents. Trivalents were also observed. It is obvious that chromosome paring were also involved in B and D genomes besides A genome between einkorn and common wheat. This phenomenon is caused by that chromosome 5B has a gene that inhibits pairing between homoeologus chromosomes and thus ensure the diploid-like behavior of meiotic chromosomes in polyploid wheat (Riley 1958). The diploidizing gene, known as *Ph1* gene, is located on the long arm of chromosome 5B (5BL) (Riley and Law 1965; Riley 1966). However, 5BS, 5D, and 5A may play an inhibiting role on *Ph1*, as increasing the doses of 5BS, 5D, and 5A will increase the pairing level between homoeologous chromosomes (Riley 1968). In addition, homoeologous chromosomes 3A, 3B, and 3D are responsible for the maintenance of regular bivalent formation, and the deficiency of any of these pairs leads to partial asynapsis. Mello-Sampaye (1968) observed that 3D also have a gene system inhibiting homoeologous chromosome pairing. However, its role is much weaker than *Ph1*.

Ph1 is a key gene for ensuring meiotic diploidization of polyploid species, which is also vital for genetic stability of newly formed allopolyploids. *Ae. speltoides* are not only the donors of cytoplasm, nucleolus, and A and B genomes, but also the main contributor of meiotic diploidization in polyploid wheat. Therefore, *Ae. speltoides* has played a key role in origination of polyploid wheat species.

According to the data accumulated from the interspecific hybridization, there was an evolution phenomenon centered with a genome (Zohary and Feldman 1962). In *Triticum-Aegilops* complex, *T. monococcum* (A), *Ae. umbellulata* (U), and *Ae. tauschii* (D) are self-pollinating plants. However, these annual species often crossed with diploid plants containing genome B (=S), C, or M genomes to form new tetraploid or hexaploid species. Diploid species containing genome S such as *Ae. speltoides* and M like *Ae. mutica* carried genes for meiotic diploidization and exhibited cross-pollination characteristics (Zohary and Imber 1963; Riley and Law 1965; Riley 1966; Upadhya 1966). The self-pollination trait of *Ae. caudata* containing genome C may be formed recently (MacKey 1968). Interspecific hybridization between self-pollinated and cross-pollinated plants can produce self-pollinated allotetraploid that has a diploid-like meiotic behavior. Because of the evolution phenomenon, *Triticum-Aegilops* complex naturally developed into three distinct genome-centered taxa. MacKey (1968) published a new taxonomic system based on these findings, as shown in Table 7.7.

Lilienfeld and Kihara (1934) classed *T. timopheevi* as the quaternary line. Their treatment reflect that *T. timopheevi* has a different evolutionary path from other tetraploid wheat species. MacKey (1968) classified *T. turgidum* and *T. timopheevi* into Dicoccoidea group according to chromosome ploidy, while classified *T. zhukovskyi* and *T. aestivum* into Speltoidea group. His treatment could not fully reflect the phylogenetic relationship of polyploid wheat species. However, the treatment on artificially synthetic species was appropriate (Table 7.7). In addition, he changed *T. monococcum* L. as *Crithodium aegilopoides* Link. This could avoid to highlight the A genome and to neglect the prominent role of B genome in the construction of *Triticum*. His treatment could also show the hybrid origin property of *Triticum* although the cytoplasmic supplier was not shown. However, his treatment as new genera increased the complexity of classification, which was inconsistent with the long-term habits, especially the customary view to einkorn wheat in agriculture. It was not necessary to establish new genera in evolutionary study and practical application. However, MacKey (1966) appropriately classified *Triticum* into six species, matching the results of cytological and genetic studies that demonstrated six natural units in these genera.

MacKey classified some conventional species as subspecies. However, there are often problems for subspecies classification. For instance, Xifu 1 is a common wheat variety in Sichuan province, China. If *T. aestivum* (L.) subsp. *vavilovi* (Tum.) Sears was a subspecies, should Xifu 1 be regarded as a subspecies since it has also elongated rachilla? Similarly, should branched common wheat be a subspecies under *T. aestivum* as well? Their significance and status in genetics and breeding

Table 7.7 MacKey's taxonomic system (1968)

Genus-species	2n	Chromosome sets	Pairs of satellite chromosomes	Reaction to gene *Ph1*
Aegilops L.				
Polyoides (Zhuk) Kihara				
Ae. umbellulata Zhuk.	14	$\mathbf{C}^{\mathrm{u}}$	2	Recessive
Ae. ovata L.	28	$\mathbf{C}^{\mathrm{u}}\mathbf{M}$	2	
Ae. triaristata Willd.	28	$\mathbf{C}^{\mathrm{u}}\mathbf{M}^{\mathrm{t}}$	1	
Ae. recta (Zhuk.) Chenn.	42	$\mathbf{C}^{\mathrm{u}}\mathbf{M}^{\mathrm{t}}\mathbf{M}^{\mathrm{t2}}$	2	
Ae. columnaris Zhuk.	28	$\mathbf{C}^{\mathrm{u}}\mathbf{M}^{\mathrm{c}}$	3	
Ae. biuncialis (Vill.) Vis.	28	$\mathbf{C}^{\mathrm{u}}\mathbf{M}^{\mathrm{b}}$	3	
Ae. variabilis Eig	28	$\mathbf{C}^{\mathrm{u}}\mathbf{S}^{\mathrm{v}}$	3	
Ae. triuncialis L.	28	$\mathbf{C}^{\mathrm{u}}\mathbf{C}$	3	
Cylindropyrum (Jaub. et Spach) Kihara				
Ae. caudata L.	14	**C**	2	Recessive
Ae. cylindrica Host	28	**CD**	1~3	
Vertebrata (Zhuk.) Kihara				
Ae. tauschii Cosson	14	**D**	1	Recessive
Ae. crassa Boiss. 4X	28	$\mathbf{D}\mathbf{M}^{\mathrm{cr}}$	2	
Ae. crassa Boiss. 6X	42	$\mathbf{D}\mathbf{D}^{2}\mathbf{M}^{\mathrm{cr}}$	3	
Ae. vavilovii (Zhuk.) Chenn. *	42	$\mathbf{D}\mathbf{M}^{\mathrm{cr}}\mathbf{S}^{1}$	3	
Ae. ventricosa Tausch.	28	$\mathbf{D}\mathbf{M}^{\mathrm{v}}$	1	
Ae. juvenalis (Thell.) Eig	42	$\mathbf{D}\mathbf{C}^{\mathrm{u}}\mathbf{M}^{\mathrm{j}}$	2	
Amblyopyrum (Zhuk.) Kihara				
Ae. mutica Boiss.	14	$\mathbf{M}^{\mathrm{t}}$	2	Dominant
Comopyrum (Jaub. et Spach) Sen. -Korch.				
Ae. comosa Sibth. et Sm.	14	**M**	2	Recessive
Ae. uniaristata Vis.	14	$\mathbf{M}^{\mathrm{u}}$	1	
Sitopsis Jaub.et Spach				
Ae. speltoides Tausch	14	**S (=B)**	2	Dominant
Ae. bicornis (Forsk.) Jaub. et Spach	14	$\mathbf{S}^{\mathrm{b}}$	2	Recessive
Ae. longissima Schweinf. et Muschl. *	14	$\mathbf{S}^{\mathrm{c}}$	2	
Crithodium Link				

(continued)

Table 7.7 (continued)

Genus-species	2n	Chromosome sets	Pairs of satellite chromosomes	Reaction to gene *Ph1*
Cr. aegilopoides Link	14	**A**	1	Recessive
Triticum L. emend MacKey (nov emend.)				
Dicoccoidea Flaksb.				
Tr. timopheevi Zhuk.	28	**AB (=AG)**	2	
Tr. turgidum (L.) Thell.	28	**AB**	2	
Speltoidea Flaksb.				
Tr. zhukovskyi Men. et Er.	42	**AAB (=AAG)**	2	
Tr. aestivum (L.) Thell.	42	**ABD**	2	
Triticale (Tscherm.) MacKey comb. nov.				
Tr. turgidosecale MacKey sp. nov.	42	**ABR**		
Tr. aestivosecale MacKey sp. nov.	56	**ABDR**		
Trititrigia MacKey sect. nov.				
Tr. turgidomedium MacKey, sp. nov.	42	**ABX**		
Tr. aestivomedium MacKey, sp. nov.	56	**ABDX**		

∗The genome symbols used in MacKey's taxonomic system were different from those used by Kihara. The genome of *Ae. longissima* in the book *A Study of Wheat* by Kihara et al. (1954) was S^l. Here MacKey used S^c to represent the genome of *Ae. longissima* and S^l to represent the S genome of *Ae. vavilovii*

were same and their position in taxonomy was also same. Therefore, it was meaningless to regard them as different subspecies either in theoretical study or breeding application. In fact, they should be synonym and should be abandoned. In agriculture, such groups that were described as "species" or "subspecies" should be varieties, or clutivar groups, or ecotypes, which were formed under natural selection.

Chen et al. (1975) analyzed chloroplast proteins and showed the protein patterns in *T. turgidum*, *T. timopheevi,* and *T. aestivum* were identical with those in *Ae. speltoides*, but different from *T. monococcum*, *T. urartu*, and *Ae. tauschii* (Fig. 7.4). This suggested that chloroplast genome of polyploid wheat was derived from *Ae. speltoides* or its closely diploid species. In other words, *Ae. speltoides* or its closely diploid species were the female parent of polyploid wheat.

Johnson and Dhaliwal (1976, 1978) and Dhaliwal (1977) observed hybrids between *T. monococcum* var. *boeoticum* and *thaoudar*. When *boeoticum* as female parent, obtaining hybrid seeds is relatively easy and F_1 plants grew normally, but F_1 plants were sterile although 1.8-28.4% of pollen could be dyed with I_2-KI. The F_1 plant exhibited normal chromosome pairing often with six ring bivalents and one rod bivalent, indicating no obvious variations on chromosomes structure that interfered with chromosome pairing. If *urartu* was used as the female parent, the cross

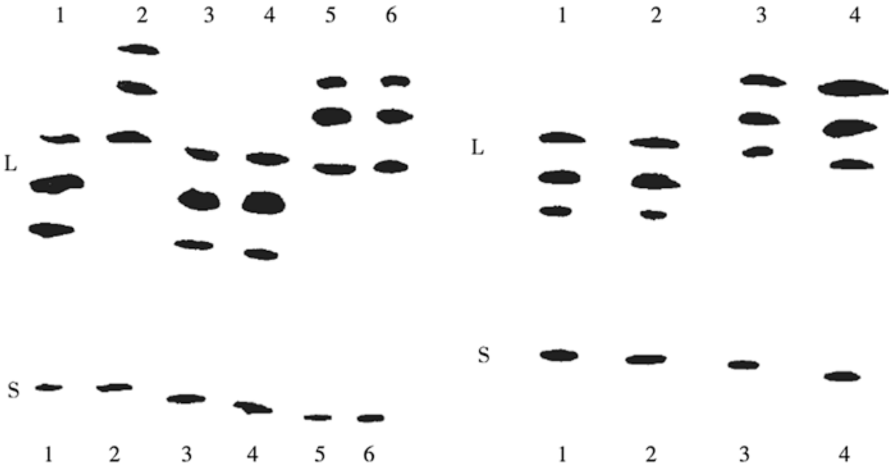


Fig. 7.4 Polypeptide patterns of chloroplast proteins from wheat and related species. Left: 1. *T. tauschii*; 2. *T. speltoides*; 3. *T. monococcum* ssp. *urartu*; 4. *T. monococcum* concv. einkorn; 5. *T. turgidum* concv. emmer; 6. *T. aestivum*. Right: 1. *T. monococcum* var. *boeoticum*; 2. *T. monococcum* var. *boeoticum* × *T. turgidum* var. *dicoccoides*; 3. *T. turgidum* var. *dicoccoides* × *T. monococcum* var. *boeoticum*; 4. *T. turgidum* var. *dicoccoides*. *L.* large subunits; S. small subunits. (According to Chen et al. 1975)

was unsuccessful due to failure of embryo development. Under artificial rescues of immature embryo, F1 plants were obtained; 10.8% of pollen grains in F_1 plants could be stained with I_2-KI, but F_1 plants were not still completely sterile. Using *urartu* as female parent and cultivated einkorn wheat as male parent, hybrid plants could grow normally. According to leaf villi and anther length, the character of cultivated einkorn was situated between *boeoticum* and *urartu*. Johnson and Dhaliwal (1976) suggested that cultivated einkorn probably originated from hybridization between *boeoticum* and *urartu*. Dhaliwal (1977) further believed that cultivated einkorn was derived from *boeoticum* but introgressed the genetic material of *T. urartu*. The authors suggested A^m as the genome symbols of *T. monococcum* and its *var. boeoticum* and *var. thaoudar*, while A for *T. urartu*, emmer wheat and common wheat.

There was reproductive isolation between *T. monococcum* and *urartu* although they have common distribution areas under natural conditions. They established their own independent development groups in system evolution. In terms of population evolution, it was appropriate to regard them as the independent species, just like the relationship between *T. timoppeevi* and *T. turgidum*. MacKey (1975) treated *T. urartu* as an independent species. Here we introduced the taxonomy system of MacKey (1975) as shown in Table 7.8.

When *T. timopheevi* was crossed with *T. turgidum* and *T. aesticum,* hybrids will produce cytoplasmic male sterility (Wilson and Ross 1962; Maan and Lucken 1968), indicating the cytoplasm differentiation between *T. timopheevi* and *T. turgidum* and *T. aestivum*. Compared to *T. turgidum* and *T. aestivum,* the cytoplasm of

Table 7.8 Intrageneric taxonomy of *Triticum* (L.) SUM. (MacKey 1975)

Monococca Flaksb	
2n = 14	
T. monococcum (L.) MK	
ssp. *boeoticum* (Boiss) MK	
var. *aegilopoides* (Bal. ex Korn.) MK	
var. *thaoudar* (Reut.) Perc.	
ssp. *monococcum*	
T. urartu Tum.	
Dicoccoidea Flaksb. 2n=28	conv. *turanicum* (Jakubz.) MK.
T. timopheevi (Zhuk.) MK.	conv. *polonicum* (L.) MK.
ssp. *araraticum* (Jakubz.) MK.	ssp. *carthlicum* (Nevski) MK.
ssp. *timopheevii* (Zhuk.) MK.	Speltoidea Flaksb. 2n=42
T. turgidum (L.) Thell.	*T. zhukovskyi* Men. et Er.
ssp. *dicoccoides* (Korn.) Thell.	*T. aestivum* (L.) Thell.
ssp. *dicoccum* (Schrank) Thell.	ssp. *spelta* (L.) Thell.
ssp. *paleocolchicum* (Men) MK.	ssp. *macha* (Dek. etmen.) MK.
ssp. *turgidum* (L.) MK.	ssp. *vulgare* (Vill.) MK.
conv. *turgidum* (L.) MK.	ssp. *compactum* (Host) MK.
conv. *durum* (Desf.) MK.	ssp. *sphaerococcum* (Perc.)

T. timopheevi was more similar to that of *Ae. speltoides* (Suemoto 1968, 1973), suggesting that the cytoplasm of *T. timopheevi* was directly derived from *Ae. speltoides*. In recent years, data from molecular genetics supported that G genome was actually S (Dvorak 1998). Where did the cytoplasm of *T. turgidum* come from? There were two different ways. One is that it originated from an extinct diploid species in *Sitopsis* that is genetically close to *Ae. speltoides* (Konzak 1977). The other is that the cytoplasm of primitive *T. turgidum* wheat was similar to *T. timopheevi* var. *araraticum*. After origination of *T. turgidum* by hybridization between *Ae. speltoides* and *T. urartu*, B^{SP} genome have evolved into B genome due to continuous natural hybridization and gene mutation. Correspondingly, the cytoplasm of *T. turgidum* var. *dicoccoides* has also changed obviously compared to the primitive *T. turgidum*. In *T. turgidum*, the nucleolar organizer is mainly on chromosomes 1B and 6B, which is probably a result of mutual adapting evolution between nucleus and cytoplasm genomes. *T. turgidum* var. *dicoccoides* is the ancestor species of *T. turgidum*. It has evolved new types of cytoplasm harmonious to its nucleus genome. Under natural selection, harmonious nucleus-cytoplasm relationship was favor to maintain. Compared to its diploid ancestor, the cytoplasm of *T. turgidum* var. *dicoccoides* might have changed largely. The origin relationship of nucleus and cytoplasm in *Triticum* species is shown in Fig. 7.5.

In 1976, Feldman published his new opinion on wheat evolution in the book "Crop Evolution" edited by Simmonds, later quoted by Croston and Williams (1981) (Table 7.9).

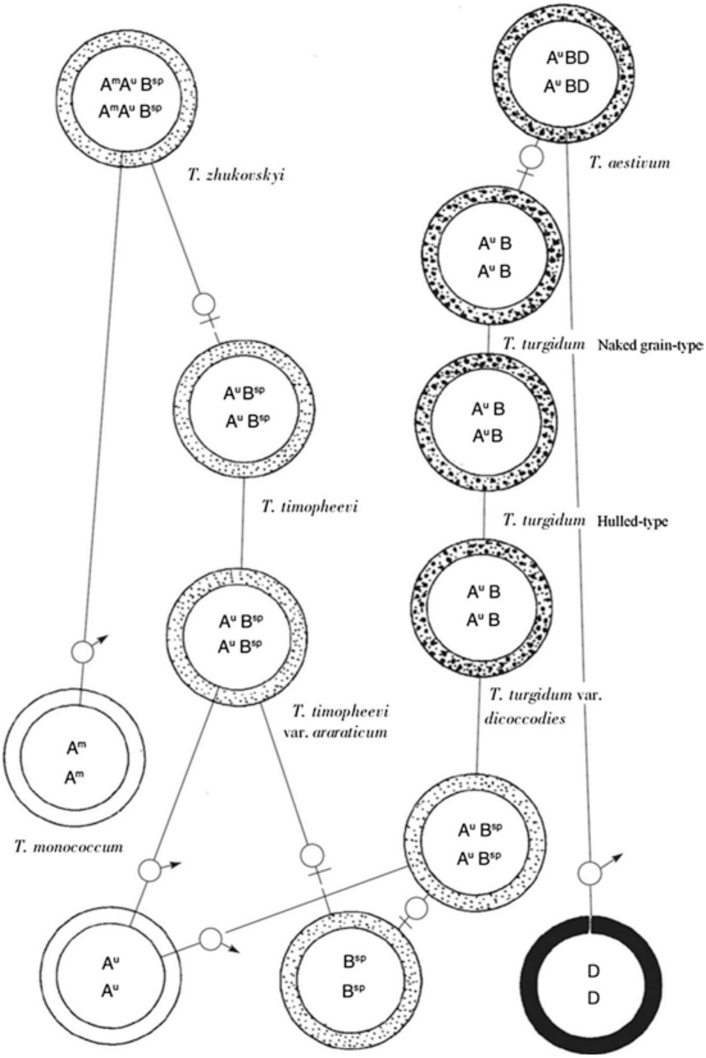
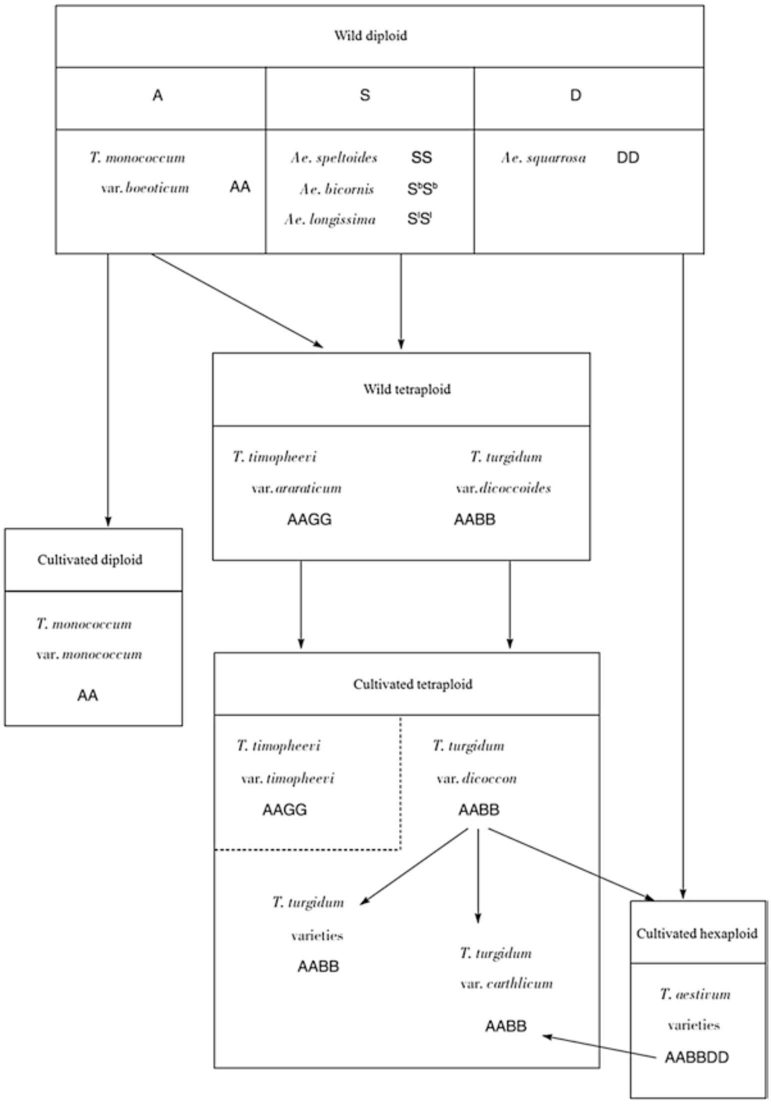


Fig. 7.5 Evolutionary relationship of nucleus and cytoplasm in *Triticum* species

In 1979, Soviet В. Ф. Дорофеев and З. Ф. Мигущова published an article on taxonomy system of *Triticum* species (Table 7.10). They divided *Triticum* into two subgenera, *Triticum* and *Boeoticum*. In cytology, A genome in the former was A^u and the latter was A^b (=A^m). In other words, A^u and A^b genome was used as the criterion of the two subgenera. However, it was inappropriate to put cultivated einkorn in the subgenus *Boeoticum* although its genome is A^b. As mentioned earlier, cultivated einkorn might be derived from hybridization between *boeoticum* and *urartu*.

Table 7.9 Evolutionary relationship of wheat species. (Feldman 1976; Croston and Williams 1981)



Dhaliwal (1977) believed that it contained the genetic material introgressed from *urartu*. In addition, the A genome of *T. timopheevi* was A^u from *T. urartu*, not A^b. It was also inappropriate for putting *T. zhukovskyi* in hulled tetraploid wheat population, which ignored its genome composition of A^{b}A^{b}A^{u}A^{u}GG. Based on chromosome karyotypes, they designated *T. kiharae* as a species. However, it seems an artificially synthetic material that did not yet have a definite distribution region.

Table 7.10 Taxonomy system of *Triticum* L. species. (According to Дорофеев and Мцгущова 1979)

Types	2n	*Triticm* subgenus			*Boeoticum* subgenus		
		Group	Chromosome composition	Species	Group	Chromosome composition	Species
Einkorn	14	Urartu Dorof et A. Filat	$\mathbf{A^u}$	*T. urartu*. Thum. ex Gandil.	Moncoccon Dum.	$\mathbf{A^b}$	*T. boeoticum* Boiss.
	14		$\mathbf{A^u}$	–		$\mathbf{A^b}$	*T. monococcum* L.
	14		$\mathbf{A^u}$	–		$\mathbf{A^b}$	*T. sinskajae* A. Filat.et Kurk.
Emmer	28	Dicoccoides Flaksb.	$\mathbf{A^uB}$	*T. dicoccoides* (Koern. ex Aschers. et Graebn.) Schweinf.	Timopheevii A. A. Filat. et Dorof.	$\mathbf{A^bG}$	*T. araraticum* Jakubz.
	28		$\mathbf{A^uB}$	*T. dicoccum* (Schrank) Schuebl.		$\mathbf{A^bG}$	*T. timopheevi* (Zhuk.) Zhuk.
	28		$\mathbf{A^uB}$	*T. ispahanicum* Heslot		$\mathbf{A^bG}$	–
	28		$\mathbf{A^uB}$	*T. kuramyschevii* Nevski		$\mathbf{A^bG}$	–
	42		$\mathbf{A^uB}$	–		$\mathbf{A^bG}$	*T. zhukovskyi* Menabde et Ericzjan
Naked-grain teraploid	28		$\mathbf{A^uB}$	*T. durum* Desf.		$\mathbf{A^bG}$	–
	28		$\mathbf{A^uB}$	*T. turgidum* L.		$\mathbf{A^bG}$	–
	28		$\mathbf{A^uB}$	*T. jakubzineri* Udacz.		$\mathbf{A^bG}$	–
				Et Schachm.			
	28		$\mathbf{A^uB}$	*T. turanticum* Jakubz.		$\mathbf{A^bG}$	–
	28		$\mathbf{A^uB}$	*T. aethiopicum* Jakubz.		$\mathbf{A^bG}$	–
	28		$\mathbf{A^uB}$	*T. polonicum* L.		$\mathbf{A^bG}$	–
	28		$\mathbf{A^uB}$	*T. persicum* Vav. (=*T. carthlicum* Evski)		$\mathbf{A^bG}$	*T. militinae* Zhuk. et Migusch.

(continued)

Table 7.10 (continued)

Types	2n	*Triticm* subgenus			*Boeoticum* subgenus		
		Group	Chromosome composition	Species	Group	Chromosome composition	Species
Spelta wheat	42	Triticum	$\mathbf{A^{u}BD}$	*T. spelta* L.	Kiharae Dorof	$\mathbf{A^{b}GD}$	*T. kiharae* Dorof. et Migusch.
	42		$\mathbf{A^{u}BD}$	*T. macha* Dekapr. et Menabde		$\mathbf{A^{b}GD}$	–
	42		$\mathbf{A^{u}BD}$	*T. vavilivii* Jakubz.		$\mathbf{A^{b}GD}$	–
Naked-grain hexaploid	42		$\mathbf{A^{u}BD}$	*T. aestivum* L.		$\mathbf{A^{b}GD}$	–
	42		$\mathbf{A^{u}BD}$	*T. compactum* Host		$\mathbf{A^{b}GD}$	–
	42		$\mathbf{A^{u}BD}$	*T. sphaerococcum* Perciv.		$\mathbf{A^{b}GD}$	–
	42		$\mathbf{A^{u}BD}$	*T. petropavlovskyi* Udacz. et Migusch.		$\mathbf{A^{b}GD}$	–

Similar synthetic materials have many. This treatment on the synthetic material could lead that "for one thing mentioned, ten thousand may have been left out." We suggest that there was no need to list the synthetic species.

Due to further development of cytogenetics research, by the 1980s, a considerable amount of data on genome analysis of Triticeae has been accumulated, making the natural relationship of genera and species clearer. Áskell Löve (1982) proposed that genomic constitution was used as the standard of generic classification of wheatgrasses. He defined species containing a genome or a genome combination as a genus. In "Conspectus of the Triticeae" published in 1984, he divided the *Triticum* L. into three genera:

1. *Crithodium* Link (1852), Linnaea 9: 132.
  - *C. monococcum* (L.) Á. Löve, 1984. Feddes Repert. 95: 490.
    - ssp. *monococcum* (L.) Á. Löve, 1984. Feddes Repert. 95: 490. **A**
    - ssp. *aegilopoides* (Link) Á. Löve, 1984. Feddes Repert. 95: 490. **A**
  - C. *urartu* (Thumanian) Á. Löve, 1984. Feddes Repert. 95: 491. **A**
  - C. *jerevani* (Thumanian) Á. Löve, 1984. Feddes Repert. 95: 491. **AA**
2. *Gigachilon* Seidl (1836), in Berchtold and Seidl, Oekon. -techn. Fl. Bohmens 1: 425.
  - sect. Gigachilon
  - *G. polonicum* (L.) Seidl, 1836. in Berchtold and Seidl, Oekon. -techn. Fl. Bohmens 1: 425. **AB**
    - ssp. *polonicum* (L.) Á. Löve, 1984. Feddes Repert. 95: 496.
    - ssp. *carthlicum* (Nevski) Á. Löve, 1984. Feddes Repert.95: 496.
    - ssp. *dicoccoides* (Korn. ex Schweinf.) Á. Löve, 1984. Feddes Repert. 95: 496.
    - ssp. *dicoccon* (Schrank) Á. Löve, 1984. Feddes Repert. 95: 497.
    - ssp. *durum* (Desf.) Á. Löve, 1984. Feddes Repert. 95: 497.
    - ssp. *palaeocolchicum* (Á. Löve and D. Löve) Á. Löve, 1984. Feddes Repert. 95: 497.
    - ssp. *turanicum* (Jakubz.) Á. Löve, 1984. Feddes Repert. 95: 497.
    - ssp. *turgidum* (L.) Á. Löve, 1984. Feddes Repert. 95: 497.
  - *G. aethiopicum* (Jakubz.) Á. Löve, 1984. Feddes Repert. 95: 497. **AB**

sect. Kiharae (Dorofeev and Migusch.) Á. Löve, 1984. Feddes Repert. 95: 497.
G. timopheevii (Zhuk.) Á. Löve, 1984. Feddes Repert. 95: 497. **AB**
ssp. *timopheevii*
ssp. *armeniacum* (Jakubz.) Á. Löve, 1984. Feddes Repert. 95: 497.
G. zhukovskyi (Menabde and Ericzjan) Á. Löve, Feddes Repert. 95: 498. **AAB**
3. *Triticum* L., 1753. Sp. Pl.: 85, p.p.
T. *aestivum* L., 1753. Sp. Pl.: 85. **ABD**
ssp. *aestivum* (L.) Bowden, 1959. Canad. J. Bot. 37: 674.
ssp. *compatum* (Host) Thell., 1918. Naturw. Wochenschr. 17: 471.
ssp. *hadropyrum* (Flaksb.) Tzvelev, 1973. Nov. Sist. Vyssch. Rast. 10: 43.
ssp. *macha* (Dekapr. and Menabde) MacKey, 1954. Svensk Bot. Tidskr. 48: 586.
ssp. *splta* (L.) Thell., 1918. Naturw. Wochenschr. 17: 471.
ssp. *sphaerococcum* (Perc.) MacKey, 1954. Svensk Bot. Tidskr. 48: 580.
ssp. *vavilovii* (Jakubz.) Á. Löve, 1984. Feddes Repert. 95: 499.

He divided *Aegilops* into 13 genera:

1. *Sitopsis* (Jaub. and Spach) Á. Löve (1982), Biol. Zentralbl. 101: 206.
S. *speltoides* (Tausch) Á. Löve, comb. nov. **B**
S. *bicornis* (Forssk.) Á. Löve, 1984. Feddes Repert. 95: 491. **B**
S. *longissima* (Schweidf. and Muschl.) Á. Löve, comb. nov. **B**
S. *searsii* (Feldman and Kislev) Á. Löve, 1984. Feddes Repert. 95: 492. **B**
S. *sharonensis* (Eig) Á. Löve, 1984. Feddes. Repert. 95: 492. **B**
2. *Orrhopygium* Á. Löve (1982), Biol. Zentralbl. 101: 206.
O. caudatum (L.) Á. Löve (1982), Biol. Zentralbl. 101: 206. **C**
3. *Patropyrum* Á. Löve (1982), Biol. Zentralbl. 101: 206.
P. tauschii (Cosson) Á. Löve, 1982. Biol. Zentralbl. 101: 206. **D**

   - ssp. *tauschii* (Cosson) Á. Löve. 1984. Feddes Repert. 95: 493.
   - ssp. *strangulatum* (Eig) Á. Löve, 1984. Feddes Repert. 95: 493.
   - ssp. *salinum* (Zhuk.) Á. Löve, 1984. Feddes Repert. 95: 493.

4. *Comopyrum* (Jaub. and Spach) Á. Löve (1982). Biol. Zentralbl.101: 207.
   - *Co. comosum* (Sibth. and Smith) Á. Löve, 1982. Biol. Zentralbl. 101: 207. **M**
   - ssp. *comosum* (Sibth. et Smith) Á. Löve, 1984. Feddes Repert. 95: 493.
   - ssp. *heldreichii* (Holzm.) Á. Löve, 1984. Feddes Repert. 95: 494.
5. *Amblyopyrum* (Jaub. and Spach) Eig (1929), Agric. Ree. (Tel-Aviv) 2: 199.
   - *Am. muticum* (Boiss.) Eig, 1929. Agric. Ree. (Tel-Aviv) 2: 199. **Z**
   - ssp. *muticum* (Boiss.) Á. Löve, 1984. Feddes Repert. 95: 494.
   - ssp. *loliaceum* (Jaub. and Spach) Á. Löve, 1984. Feddes Repert. 95: 494.
6. *Chennapyrum* Á. Löve (1982), Biol. Zentralbl. 101: 207.
   - *Ch. uniaristatum* (Vis.) Á. Löve, 1982. Biol. Zentralbl. 101: 207. **L**
7. *Kiharapyrum* Á. Löve (1982), Biol. Zentralbl. 101: 207.
   - *K. umbellulatum* (Zhuk.) Á. Löve, 1982. Biol. Zentralbl. 101: 207. **U**
   - ssp. *umbellulatum* (Zhuk.) Á. Löve, 1984. Feddes Repert. 95: 495.
   - ssp. *transcaucasicum* (Dorof. and Migusch.) Á. Löve, 1984. Feddes Repert. 95: 495.
8. *Aegilemma* Á. Löve, 1982, Biol. Zentralbl. 101: 207.
   - *Ae. kotschyi* (Boiss.) Á. Löve, 1982, Biol. Zentralbl. 101: 207. **BU**
   - *Ae. peregrina* (Hackel) Á. Löve, 1984. Feddes Repert. 95: 499. **BU**
   - ssp. *peregrina* (Hackel) Á. Löve, 1984. Feddes Repert. 95: 499.
   - ssp. *cylindrostachys* (Eig and Feinbrunn) Á. Löve, 1984. Feddes Repert. 95: 499.
9. *Cylindropyrum* (Jaub. and Spach) Á. Löve (1982), Biol. Zentralbl. 101: 207.
   - *C. cylindricum* (Host) Á. Löve, 1982. Biol. Zentralbl. 101: 207. **CD**

ssp. *cylindricum* (Host) Á. Löve, 1984. Feddes Repert. 95: 500.
ssp. *pauciaristatum* (Eig) Á. Löve, 1984. Feddes Repert. 95: 500.
10. *Aegilopodes* Á. Löve, 1982. Biol. Zentralbl. 101: 207
Ae. triuncialis (L.) Á. Löve, 1982. Biol. Zentralbl. 101: 207. **CU**
ssp. *triuncialis* (L.) Á. Löve, 1984. Feddes Repert. 95: 501.
ssp. *persica* (Boiss.) Á. Löve, 1984. Feddes Repert. 95: 501.
11. *Gastropyrum* (Jaub. and Spach) Á. Löve (1982). Biol. Zentralbl. 101: 208.
Ga. ventricosum (Tausch) Á. Löve, 1982. Biol. Zentralbl. 101: 208. **DM**
Ga. crassum (Boiss.) Á. Löve, 1984. Feddes Repert. 95: 501. **DM**
Ga. glumiaristatum (Eig) Á. Löve and McGuire, 1984. Feddes Repert. 95: 502. **DDM**
Ga. vavilovii (Zhuk.) Á. Löve, 1984. Feddes Repert. 95: 502. **DMM**
12. *Aegilonarum* Á. Löve (1982), Biol. Zentralbl. 101: 208.
Ae. juvenile (Thell.) Á. Löve, 1982. Biol. Zentralbl. 101: 208. **DUM**
13. *Aegilops* L. (1753), Sp. Pl.: 1050.
Ae. ovata L. 1753 Sp. Pl. 1050, emend. Roth. 1793, in Usteri, Ann. d. Bot. 4: 41. **UM**
Ae. geniculata Roth, 1787, Bot. Abhandl. Beobacht.: 45. **UM**
ssp. *geniculata* (Roth) Á. Löve, 1984. Feddes Repert. 95: 503.
ssp. *globulosa* (Zhuk.) Á. Löve, 1984. Feddes Repert. 95: 503.
Ae. lorentii Hochst., 1845, Flora 28: 25. **UM**
ssp. *lorentii* (Hochst.) Á. Löve, 1984. Feddes Repert. 95: 503.
ssp. *archipelagica* (Eig) Á. Löve, 1984. Feddes Repert. 95: 504.
ssp. *pontica* (Degen) Á. Löve, 1984. Feddes Repert. 95: 504.
Ae. columnaris Zhuk., 1928, Tr. Prikl. Bot. Genet. Sel. 18: 448. **UM**
Ae. recta (Zhuk.) Chennaveeraiah, 1960. Acta Horti. Gotob. 23: 165. **UMM**

According to Löve's classification, *Aegilops* was divided into 13 genera, of which 9 were monotypic genus. The division was too extreme, losing the value of genus classification. His taxonomy system was not accepted widely by other scholars. However, Á. Löve had denominated all the known Triticeae genomes at that time in his system. In a report on the nomenclature of Triticeae genome symbol in the 2nd International Triticeae Symposium, his system was cited to compare the similarities and differences between old and newly suggested genome symbols. Löve's conspectus objectively reflected new achievements of cytogenetics studies. He hoped that the various taxa could be systematically arranged according to natural system so as to conform to objective reality. Löve was the pioneer. However, there were some limitations at that time, for instance some genomes such as Y were not found or recognized. Genomic constitution of some species had not yet been identified. For instance, genome J and E in Löve's system were actually variants (J = E^b, E = E^e).

The genetic and evolutionary distances between species or genera may vary. For example, Yen and Kimber (1990) used variable loge (x/y) to determine the genetic distances between populations with S genome. The genetic distances were different based on the measured data were as follows:

Ae. searsii—*Ae. speltoides* = 1.964
Ae. searsii—*Ae. bicornis* = 1. 919
Ae. searsii—*Ae. longissima* = 2. 070
Ae. bicornis—*Ae. speltoides* = 1. 614
Ae. bicornis—*Ae. longissima* = 2. 031
Ae. bicornis—*Ae. sharonensis* = 2. 111
Ae. speltoides—*Ae. sharonensis* = 1. 361
Ae. speltoides—*Ae. longissima* = 2. 966
Ae. longissima—*Ae. sharonensis* = 1. 355

This work reflected the differences between species with genomes modified from the common S genome, such as S^l and S^s. The genetic distances between species with different genomes or genomic combinations might be greater, such as between *T. turgidum* and *T. timopheevi*, *T. turgidum* and *T. aestivum*. Despite the existence of variations, genetic distance did not prevent the determining of genomes or their subtypes. However, there was also no definite boundary for classification of genera and higher class due to the existence of numerous intermediate types. Therefore, the artificiality at a certain degree was inevitable for the classification of genus. Clustering species as a genus is the need of taxonomic application. For the purpose of application, it is also important to respect traditional using habits. Löve's classification system contained many monotypic genus that made the classification much complex. This may be the main reason why his system on *Triticum* was not widely accepted. We considered that treatment of genus need to properly reflect natural clustering and to also take care of traditional habits in order to conveniently apply.

In 1985, the book "Flora of Turkey and the East Aegean Islands," edited by Davis P. H. of the University of Edinburgh in Scotland, argued that *Aegilops* and *Triticum* were still divided into two genera. Davis recorded 15 species for *Aegilops*, including:

1. *Ae. speltoides*
2. *Ae. markgrafii*
3. *Ae. cylindrica*
4. *Ae. tauschii*
5. *Ae. crassa*
6. *Ae. comosa*
7. *Ae. uniaristata*
8. *Ae. umbellulata*
9. *Ae. peregrina*
10. *Ae. kotschyi*
11. *Ae. triuncialis*
12. *Ae. bicornis*
13. *Ae. columnaris*
14. *Ae. neglecta*
15. *Ae. geniculata*

Ae. markgrafii (Greuter) Hammer was used to replace *Ae. caudata* L. and *Ae. caudata* L. was used as synonym. *Ae. triaristata* Willd. was also replaced by *Ae. neglecta* Req. ex Bertol, and *Ae. ovata* L. and *Ae. ovata* sensu Willd. was replaced by *Ae. geniculata* Roth.

In the same book, *Triticum*, written by Kit Tan, Tan recognized 10 species, 2 subspecies, and 2 varieties, namely:

1. *T. boeoticum* Boiss.

   subsp. *boeoticum*
   subsp. *thaoudar* (Reuter ex Hausskn.) Schiemann

2. *T. monococcum* L.
3. *T. timopheevi* (Zhuk.) Zhuk.

   var. *araraticum* (Jukubz.) Yen
   var. *timopheevi*.

4. *T. dicoccoides* (Koern.) Koern.
5. *T. dicoccon* Schrank
6. *T. durum* Desf.
7. *T. turgidum* L.
8. *T. polonicum* L.
9. *T. carthlicum* Nevski
10. *T. aestivum* L.

T. boeoticum and *T. monococcum* were classified as two different species and *T. turgidum*, *T. dicoccon*, *T. durum*, *T. polonicum*, *T. carthlicum*, *T. dicoccoides* as different species. However, *arraticum* was treated as a variant of *T. timopheevi*. These treatments ignored achievements of modern genetic studies.

In 1994, "Wild wheats: a monograph of *Aegilops* L. and *Amblyopyrum* (Jaub. & Spach) Eig (Poaceae)" written by van Slageren M. W. was jointly published by the Wagenizen Agricultural University of the Netherlands and the Syrian International Centre for Agricultural Research in the Dry Areas. In this book, the author gave a detailed description of the literature before Linné. Although the title was "Wild wheat," it was a monograph emphasizing on *Aegilops* and *Amblyopyrum*. For *Triticum*, he described species as follows:

I. sect. *Monococcon* Dumort., Observ. Gramin. Belg. 94 (1824).

1. *T. monococcum* L.
    a. ssp. *monococcum*—cultivation type
    b. ssp. *aegilopoides* (Link) Thell.—wild type
2. *T. urartu* Tumanian ex Gandilyan, Bot. Zhurn. 57: 176 (1972).

II. sect. *Dicoccoide* Flaksb., Ann. State Inst. Exp. Agric. 6 (2): 39 (1928).

3. *T. turgidum* L. Sp. Pl. (ed. 1) 1: 86 (1753).
    a. ssp. *turgidum*
    b. ssp. *carthlicum* (Nevski) L. ve and D. Löve
    c. ssp. *dicoccon* (Schrank) Thell.
    d. ssp. *durum* (Desf.) Husn.
    e. ssp. *paleocolchicum* (Menabde) Á. Löve and D. Löve
    f. ssp. *polonicum* (L.) Thell.
    g. ssp. *turanicum* (Jakubz.) Á. Löve and D. Löve
    h. ssp. *dicoccoides* (Korn. ex Asc. and Graebn.) Thell.
4. *T. timopheevi* (Zhuk.) Zhuk.
    a. ssp. *timopheevii*—cultivation type
    b. ssp. *armeniacum* (Jakubz) van Slageren—wild type

III. sect. *Triticum*.

5. *T. aesticum* L.
    a. ssp. *aestivum*—bread wheat
    b. ssp. *compactum* (Host) MacKey
    c. ssp. *macha* (Dekapr. and Menabde) MacKey
    d. ssp. *spelta* (L.) Thell.
    e. ssp. *sphaerococcum* (Percival) MacKey
6. *T. zhukovskyi* Menabde and Ericz.

van Slageren's treatment on *Triticum* was mainly based on the old system of Swedish scholar MacKey (1954). As aforesaid, MacKey had updated the system since 1954. For example, MacKey no longer regards *turgidum*, *durum*, *turanicum*, and *polonicum* as subspecies, but as cultivar group (conv.).

This book advocated the separation of *Aegilops*, *Amblyopyrum*, and *Triticum*. We thought that the division and combination of genera were irrelevant, as long as they were consistent with natural clustering. *Amblyopyrum* was far away from *Aegilops* and *Triticum*. It was reasonable to separate *Amblyopyrum* from *Aegilops* and *Triticum*.

Van Slageren did a lot of detailed textual research on the two genera of *Aegilops* and *Amblyopyrum*, which was of great reference value. However, the author followed Greuter's treatment of *Ae. ovata* L. as a synonym of *Ae. geniculata* Roth. The reason was that Greuter designated Roth's specimen of *Ae. geniculata* Roth, published in 1787, as the "lectotype specimen (LT)" of this taxonomic group. He hence reversed previously published *Ae. ovata* L. as a synonym for *Ae. geniculata* Roth, while the synonym *Ae. geniculata* Roth of the original *Ae. ovata* L. was inverted as the scientific name. Meanwhile, van Slageren thought that *Ae. squarrosa* L. could not be used as the scientific name of D-genome diploid species because in 1966 Bowden designated specimen LINN1218. 9 as a lectotype specimen of *Ae. squarrosa* L., which was a variant of *Ae. triuncialis*. He hence used *Ae. tauschii* Cosson as the scientific name of this taxonomic group. However, we thought the reason why *Ae. tauschii* Cosson was the correct scientific name was mainly because Cosson first identified, described, officially named, and published this taxonomic group in 1849.

In addition, this book did not revise the boundaries of taxonomic group on the basis of new experimental evidences. For instance, *Ae. geniculata* Roth and *Ae. biuncialis* Vis., *Ae. columnaris* Zhuk. and *Ae. neglecta* Req. ex Bertol (*Ae. triaristata* Willd.) were still treated as independent species.

Table 7.11 gives a brief overview of his classification system.

Dvorak made an excellent summary report on the genome analysis of *Triticum*-*Aegilops* in the 9th International Conference on Wheat Genetics, held in Saskatoon, Canada, in August 1998. He had collected data on genome analysis, nucleotide sequence analysis of cytoplasmic organelles, and repeat nucleotide sequence analysis (RNS) of cell nucleus and integrated into a comparison table. This table clearly demonstrated the genetic relationship between *Triticum* and *Aegilops* species (Table 7.12).

Table 7.11 *Aegilops* and *Amblyopyrum* taxonomic groups (including lecto and neo types). [Minor modifications were made according to van Slageren (1994)]

Classification group	Mode
Aegilops L. genus	Type species *Ae. triuncialis* L.
	Hammer (1980) designed; Jarvis supported to use it instead of *Ae. ovata* L. in a special meeting on type species
Aegilops's group	
1. sect. *Aegilops*	Type species *Ae. triuncialis* L.
2. sect. *Comopyrum* (Jaub. and Spach) Zhuk.	Type species *Ae. comosa* Sm. in Sibth. and Sm.
3. sect. *Cylindropyrum* (Jaub. and Spach) Zhuk.	Type species *Ae. cylindrica* Host
4. sect. *Sitopsis* (Jaub. and Spach) Zhuk.	Specify type species *Ae. speltoides* Tausch
	Designed by Hammer (1980)
5. sect. *Vertebrata* Zhuk. emend Kihara	Type species *Ae. tauschii* Coss.
Aegilops' species	
1. *Ae. bicornis* (Forssk.) Jaub. and Spach	[Egypt] Forsskal s. n. (holotype **C**)
var. *bicornis*	
var. *anathera* Eig	[Libya] Ruhmer s. n. (401?)
	(lectotype: **PR**; isolectotype: **BR, FI, JE, MPU-Maire, P**)
2. *Ae. biuncialis* Vis.	Type: R. de Visiani (1842)
	Flora dalmatica 1, original table 1, original figure 2, Gandilyan designed (1980)
3. *Ae. caudata* L.	[Greece] de Tournefort 4940 (neotype:
	P-TRF, isoneotype: **LE**)
	Scholz and Slageren (1994) designed
4. *Ae. columnaris* Zhuk.	[Turkey] Zhukovsky s. n.
	(lectotype: **WIR**635)
5. *Ae. comosa* Sm. in Sibth. and Sm.	[Greece] Sibthorp s. n. (holotype: **OXF**)
var. *comosa*	
var. *subvantricosa* Boiss.	[Greece] von Heldreich 606
	(lectotype: **G-BOIS**; iso-
	lectotype: **A, C, G, FI, JE, K,**
	L, LE, LY, LY-Gandger,
	LY-Jordan, MPU, P, PL, W)
6. *Ae. crassa* Boiss.	[Iran] Kotschy 248 (holotype: **G-BOIS**;
	isotype: **BM, C, FI, G, K, L,**
	LE, MO, OXF, P. PI, PRC, TUB)
7. *Ae. cylindrica* Host	[Hungary] Kitaibel 226 (lectotype: **BP;**
	isolectotype: **B-W** 18878-1)
8. *Ae. geniculata* Roth	[Germany] Roth s. n. (holotype: **B-W;**

(continued)

Table 7.11 (continued)

Classification group	Mode
	isotype: **BM, LE, TUB**)
9. *Ae. juvenalis* (Thell.) Eig	[France] Touchy s. n. (holotype: **MPU**)
10. *Ae. kotschyi* Boiss.	[Iran] Kotschy 366a (lectotype: **G-BOIS**; isolectotype:
	BM, C, E, FI, G, K, LE, OXF, P. PI, PRC, TUB)
11. *Ae. longissima* Schweinf. and Muschl.	[Egypt] Schweinfurth s. n. (lectotype: **B;**
	isolectotype: **CAIM, MPU, US**)
12. *Ae. neglecta* Req. ex Bertol.	[France] Requien s. n. (holotype:
	BOLO-Bertoloni; isotype: **MPU**
	-Duval-Jouve)
13. *Ae. peregrina* (Hack. in J. Fraser) Maire	[United Kingdom, Scotland] Fraser s. n.
and Weiller	(lectotype: **E**; isolectotype: **K, RNG**)
var. *peregrina*	
var. *brachyathera* (Boiss.) Eig	[Lebanon] Blanche 805 (lectotype: G-BOIS)
14. *Ae. searsii* Feldman and Kislev ex Hammer	[Palestine] Feldman, Kislev and
	Kushnir s. n. (holotype: **HU**; isotype: **K**)
15. *Ae. sharonensis* Eig	[Palestine] Eig s. n. (holotype:
	HU; isotype: **MPU**)
16. *Ae. speltoides* Tausch	[Turkey] Bornmiller 1735 (neotype: **B;**
	isoneotype: **BM, FI, G,**
	JE, K, L, LD, LY-Jordan, LY-Gando-
	ger, NY, OXF, P, SO, W, Z)
var. *speltoides*	
var. *ligustica* (Savign.) Fiori	[Italy] Savignone s. n. (neotype: **FI;**
	isoneotype: LY-Gandoger)
17. *Ae. tauschii* Cosson	Lectotype: J. Ch. Buxbaum, Plan-
	tarum minus cognitarum Centuria
	1: table 50, figure 1 (1728) in original book
18. *Ae. triuncialis* L.	[Spain] Loefling 701 (holotype:
	LINN 1218. 8) Bowden (1959) allocate
var. *triuncialis*	
var. *persica* (Boiss.) Eig	[Iran] Kotschy 365 (holotype: **G-BOIS;**
	isotype: **BM, C, E, FI, G, JE, K, LE, MO,**
	MPU, OXF, P, PI, PRC, TUB)
19. *Ae. umbellulata* Zhuk.	[Turkey] Zhukovsky s. n. (lectotype:
	WIR 1439) Zhkovsky allocated using the
	WIR sample, did not print
20. *Ae. uniaristata* Vis.	[Croadia, Dalmatia] de Visiani
	s. n. (holotype: **PAD**; isotype: **W**)

(continued)

Table 7.11 (continued)

Classification group	Mode
21. *Ae. vavilovii* (Zhuk.) Chennav.	[Syria] Vavilov 29028 (lectotype: **WIR** 747)
22. *Ae. ventricosa* Tausch	[Spain] Boissier s. n. (neotype: **G**;
	isoneotype: **A, BR, C, E, F, G, JE,**
	K, LE, MPU, NY, P, PI, TUB, W)
Amblyopyrum (Jaub. and Spach) Eig	Type species *Am. muticum* (Boiss.) Eig
1. *Am. muticum* (Boiss.) Eig	[Turkey] Aucher-Eloy 2977
var. *muticum*	(holotype: **G**; isotype: [hairiness specimen]
	BM, FI, G-BOIS, K, MPU, OXF, P)
var. *loliaceum* (Jaub.	[Turkey] Aucher-Eloy 2977
and Spach) Eig	(holotype: **P**; isotype: [hairless specimen]
	BM, G, G-BOIS, MPU, OXF)

Table 7.12 *Triticum-Aegilops* species and their genomes

	Chromosomes pairing analysis		Organelle genome	RNS
Species	(1)	(2)	(3)	(4)
T. monococcum	**A**	**A**	**A**	**A**^{m}
T. urartu	–	–	–	**A**
Ae. speltoides	**S**	**S**	**S, G, G**^{2}	**S**
Ae. searsii	–	**S**^{s}	**S**^{v}	**S**^{s}
Ae. bicornis	**S**^{b}	**S**^{b}	**S**^{b}	**S**^{b}
Ae. sharonensis	**S**^{1}	**S**^{1}	**S**^{1}	**S**^{1}
Ae. longissima	**S**^{1}	**S**^{1}	**S**^{12}	**S**^{1}
Ae. uniaristata	**M**^{u}	**N**	**N**	**N**
Ae. comosa	**M**	**M**	**M**	**M**
Ae. heldreichii	**M**	**M**	**M**^{h}	**M**
Ae. caudata	**C**	**C**	**C**	**C**
Ae. umbellulata	**C**^{u}	**U**	**U**	**U**
Ae. mutica	**M**^{t}	**T**	**T, T**^{2}	**T**
Ae. tauschii	**D**	**D**	**D**	**D**
T. turgidum	**AB**	**AB**	**B** (like **S**)	**AB** (like **S**)
T. aesticum	**ABD**	**ABD**	**B**	**ABD**
T. timopheevi	**AG**	**AG**	**G**	**AS**
T. zhukovskyi	–	–	**G**	**ASA**^{m}
Ae. cylindrica	**DC**	**DC**	**D**	**DC**
Ae. ventricosa	**DM**^{cr}	**DN**	**D**	**DN**
Ae. crassa	**DM**^{cr}	**DM***	**D**^{2}	**DN**
Ae. crassa				
var. *glumiarista*	**DD**^{2}**M**^{cr}	**DDM**	**D**^{2}	**D**^{c}**X**^{c}**D**
Ae. vavilovii	**DM**^{cr}**S**^{p}	**DMS**	**D**^{2}	**D**^{c}**X**^{c}**S**^{s}
Ae. juvenalis	**DC**^{u}**M**^{j}	**DMU**	**D**^{2}	**D**^{c}**X**^{c}**U**

(continued)

Table 7.12 (continued)

	Chromosomes pairing analysis		Organelle genome	RNS
Species	(1)	(2)	(3)	(4)
Ae. triuncialis	$\mathbf{C^{u}C}$	**UC**	$\mathbf{U, C^{2}}$	**UC**
Ae. columnaris	$\mathbf{C^{u}M^{c}}$	**UM**	**U**	$\mathbf{UX^{t}}$
Ae. triaristasta	$\mathbf{C^{u}M^{t}}$	**UM**	**U**	$\mathbf{UX^{t}}$
Ae. recta	$\mathbf{C^{u}M^{t}M^{t}}$	**UMN**	**U**	$\mathbf{UX^{t}N}$
Ae. ovata	$\mathbf{C^{u}M^{o}}$	**UM**	$\mathbf{M^{o}}$	$\mathbf{UM^{o}}$
Ae. biuncialis	$\mathbf{C^{u}M^{b}}$	**UM**	**U**	$\mathbf{UM^{o}}$
Ae. kotschyi	$\mathbf{C^{u}S^{v}}$	**US**	$\mathbf{S^{v}}$	$\mathbf{US^{1}}$
Ae. variabilis	$\mathbf{C^{u}S^{v}}$	**US**	$\mathbf{S^{v}}$	$\mathbf{US^{1}}$

(1) Kihara (1963, 1970)
(2) Kimber (1994), Kimber and Feldman (1987)
(3) Ogihara and Tsunewaki (1988)
(4) Dubcovsky and Dvorak (1995), Dvorak et al. (1993), Dvorak et al. (1988), Dvorak and Zhang (1990), Zhang and Dvorak (1992), Zhang et al. (1992)

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Chapter 8
Taxonomy of the Genus *Triticum*

Stepping into the twenty-first century, researches on *Triticum* and its relative genera have passed three centuries. Many scientists from all over the world have been preoccupied with the classification and evolution, especially with the help of new genetic techniques in the twentieth century. The resulting great achievements offer the premise of the scientific management of germplasm and necessary theoretical knowledge for breeding utilization. Meanwhile, the following questions can be clarified, answered, or affirmed.

1. One is the definition of genus, species, subspecies, varietas, forma, concultivar (cultivar group), and cultivar. For different groups of organisms, the definition of taxon grade could be various, despite a similarity at a certain degree. For example, bacteria, viruses, and higher plants have different definition of these grades. Objectively, their patterns of evolution are much different. Many scientists have expressed their respective views on these taxonomic units. We do not comment on them one by one. In this book, we talk about our opinions on the principle of classification only.

    (1) Individuals and species: As mentioned before, only the concept of individual is absolute in biological world. Species of higher plants are consisted of specific individuals linked by reproductive reproduction, which have a common gene pool. There is a certain degree of reproductive segregation between different species, either failing to cross freely or to obtain normal offspring after hybridization. For cytological characteristics, a species has a specific genome or its subtypes (for example, A, D, B^{sp}, B^{1}, B^{s},… in *Triticum*) or genomic constitution (for example, BA, BAD, $B^{sp}AA^{m}$,…).

    (2) Subspecies: Subspecies is a much irregular classification noun, especially in the *triticeae*. Different authors might have much different concepts. Confusion even appeared in a same article by the same author. For instance, *carthlicum*, *turgidum*, *durum*, *turanicum*, and *polonicum* genetically have a similar position each other. However, in Table 7.8, MacKey had classified that *carthlicum* was classified as a subspecies of *T. turgidum*, while *turgidum*,

C. Yen, J. Yang, *Biosystematics of Triticeae*,
https://doi.org/10.1007/978-981-13-9931-2_8

durum, *turanicum*, and *polonicum* was considered as cultivar groups (conv.) of *T. turgidum*. In the same way, *spelta*, *macha*, *vulgare*, *compactum*, and *sphaerococcum* were classified as the subspecies of *T. aestivum*, although their morphological differences used as a key trait of species classification can be caused by a single or a few genes. The taxon groups below a species such as subspecies and varietas contain same genome constitution. They have no essentially different genetics and should be treated equally in breeding applications. They are subjectively created and have no practical meaning. In this book, on the basis of actual situation of *Triticum-Aegilops* complex, we discard these tedious taxon classes.

(3) Genus: A genus is a cluster group of similar species. Usually, there are no clear boundaries on genetics and evolution, and often have intermediate groups between genera. Although it also reflects natural clustering relations, the division between genera is inevitably subjective.

(4) Varietas, concultivar, cultivar, and forma: As mentioned above on subspecies, these classification levels are also a cluster of individuals at the same level in the concept of genetics, having similar genetic structures. Because of the existence of intermediate groups, sometimes their division is obviously man made. On the other hand, they suffered differential natural selections due to different ecological and geographical conditions. Meanwhile, artificial selections might be also different due to various cultivation conditions and economic purposes. Some specific groups were formed due to strong selection that eliminated intermediate types or unfavorable individuals. Because of their distinctive morphological characteristics as well as economic importance for human, their division is important. Hence, we have defined them in this book as:

   a. A varietas is a group of individuals having similar genetic structure formed by natural selection. Hybrids between some varietas are abnormal in reproduction and growth such as hybrid lethal. However, we still take them as the varietas class as they have a same genomic constitution.
   b. A forma is a group of individuals with unique characteristics despite only having a slight difference compared to others. Forma was also formed by natural selection. This class is not involved in this book.
   c. A cultivar is a group of individuals with highly consistent genotypes, formed by artificial selection. Cultivars are important production goods in agriculture production and should be recorded in the variety approval and registration. This class is also not involved in this book.
   d. A concultivar is a group of similar cultivars. It is an artificial classification group equivalent to the varietas class. This taxon has significance in germplasm management and breeding application. The book will reflect this class.

2. The classification on genus is highly subjective, as mentioned above. A reasonable classification need to comply International Code of Botanical Nomenclature

(ICNB), match natural cluster of species, respect traditional habits, and be convenient for application. As for the two generic names of *Triticum* and *Aegilops*, they conform to ICBN and thus are legal (Yen et al. 1997). In order to avoid confusion in application on germplasm management and scientific research, we suggest to integrate them into *Triticum*. The integrated genus containing more than 20 species is not too big. This system has been used more than 100 years, adopted by many scholars nowadays. Of course, it also is reasonable to keep the two separate genera. If *Triticum* and *Aegilops* are still used, group Sitopsis in *Aegilops* should be combined into *Triticum* according to natural clustering relationship as discussed above. We would like to adopt the integrated genus *Triticum*.

3. In *Triticum-Aegilops* complex, B (= S), D, and U are pivotal genomes that formed three major clustering groups. It seems appropriate to divide the three groups into genera *Triticum*, *Vertebrata*, and *Aegilops*. Their morphological boundaries are also distinct: *Triticum* has the characters of glumes with keel, lemma with a single awn, internodes of the rachis not embed with spikelets, and wedge or barrel type of disarticulation at maturity; *Vertebrata* has glumes without keel, lemma with a single awn, internodes of the rachis embed with spikelets (cylindrical shape), and barrel type of disarticulation at maturity; *Aegilops* has multiple-awn or multiple-teeth glume or lemma, rare single awn, and spikes umbrella likely fallen off at maturity. In this way, *Sitopsis* in *Aegilops* is grouped into *Triticum*, *Vertebrata* Zhuk is elevated to the genus *Vertebrata* that also includes the species of the *Cylindropyrum* group established by Kihara. The remaining species in *Aegilops* remain in the *Aegilops* genus. However, it is difficult to widely accept *Vertebrata* as a genus by scholars. Therefore, it is suggested that *Vertebrata* remains in the *Aegilops* subgenus (or genus), and closely related *Sitopsis* is group into the *Sitopyros* subgenus (or *Triticum*). This treatment accords with traditional habits at a high degree and appropriately reflects natural clustering relationship of species. *Ae mutica* Boiss, formerly a member of genus *Aegilops*, contains the genome T. Experiments have shown that it is not directly related to any species in *Aegilops-Triticum* complex. As early as 1929, Eig in his book on *Aegilops* followed the opinions of Jaubert and Spach that *Amblyopyrum* was treated as a subgenus. Meanwhile, he integrated five other subgenera of Jaubert and Spach as the subgenus, called *Eu-Aegilops* Eig. This work has actually separated *Amblyopyrum* from other *Aegilops* species, i.e., *Amblyopyrum* was no longer included in *Aegilops*. In the same year, he published *Amblyopyrum* as an independent genus. This is also a conclusion that has been demonstrated by van Slageren (1994) using 10 pages (p72~82). We agree that *Amblyopyrum* is an independent genus.

Some scholars prefer that *Aegilops* was group into *Triticum*. Here we treat the Hackel's sections as two subgenera, namely *Sitopyros* (Hackel) Yen et J. L. Yang and *Aegilops* (Hackel) Yen et J. L. Yang. Section Sitopsis Tausch (Gren.) of *Aegilops* is placed into subgenus *Sitopyros*. As early as the 1960s, Indian scholar Chennaveeraiah (1960a, b, 1962) also had demonstrated this opinion on the basis of

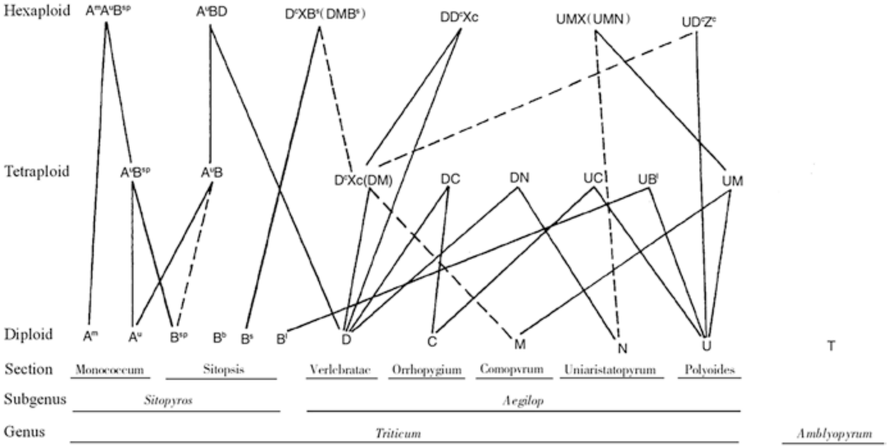

Fig. 8.1 Biosystematics relationship of *Triticum-Aegilops* complex and its related species
This diagram is drawn according to the analysis of repeat nucleotide sequences (RNS). Genomes in parentheses indicated inconsistent results between RNS cytological analysis. *T. triunciale* (UC) has two types of cytoplasm, probably derived from the reciprocal cross between *T. caudatum* (C) and *T. umbellulatum* (U).

cytological data. Except that *Amblyopyrum* was an independent genus according to Eig (1929), Löve (1982), and van Slageren (1994), all species in *Aegilops* are integrated into *Triticum*.

In conclusion, phylogenetic relationships of species in *Aegilops-Triticum* complex are shown in Fig. 8.1. Correspondingly, we describe the system classification of *Triticum* L. emend. as follows.

1. A Key to Species, Varietas, Concultivar of *Triticum* and *Amblyopyrum*

1. Spike broad, ovoid, elliptic, spindle, tapered, rectangular, linear, or cylindrical; 2–15 spikelets per spike, if 15–20 or more spikelets per spike, spikelets more closely aligned in two rows; internodes of the rachis less in length than or nearly equal to spikelet, seldom longer than spikelet; glume scaphoid, glume, and lemma often with awn, or awnless with sharp teeth at apex; spikelet umbrella-like abscission, the barrel or wedge type of disarticulation ………………genus *Triticum*
2. Spike with flatted two sides; usually 10–25 or more spikelets per spike, seldom 8 spikelets per spike, arranged in two rows, often inclined upward, not parallel to the rachis; glume often with ridge, generally awnless, except for individual concultivar, lemma of middle and lower spikelet usually with long awns or beak-like pointed-teeth, lemma of first floret of top spikelet usually with awn; rachis tough or with wedge type of disarticulation, seldom barrel type of disarticulation…………subgenus *Sitopyros*

3. Glume with ridges; spike significantly flat, oval, fusiform or rectangular ……………………………………sect. *Monococcum*

4. Glume with dual-ridges from base to top, two teeth at the apex of dual ridges, or a weaker inner ridge with a blunt shoulder at the apex.

5. Spikelet more closely aligned in two rows, spike without terminal central spikelet, spikelets with 2–4 florets, only basal one or two florets with seed, glume with well-developed dual ridges, forming a two-toothed tip, palea at maturity longitudinally divided into two, caryopsis with flatted two sides, upper and lower apex sharp, less apical hairs. 2n = 14.

6. Only 1 floret of spikelet with seed, only with 1 short or long awn.

7. Spikelet with 1 long awn, hulled.

8. Leaves with rare and less short hairs; culm wall thin; two ridges of internodes of rachis nearly hairless. A^m genome……………………*T. monococcum* concv. monococcum

8. Main vein of leaves with a row of long hair; culm wall thick and often solid; two ridges of internodes of rachis with tufts of hairs. A^m genome……………………*T. monococcum* var. *boeoticum*

7. Spikelet with a short awn, naked. A^m genome……………………*T. monococcum* concv. *sinskajae*

6. Two basal florets of spikelet with seed, with two long awns.

9. Main vein of leaves with long hairs, anthers long and big, 3–4 mm long, with crack holes at both ends, not helically twisted at dryness. A^m genome………………*T. monococcum* var. *Thaoudar*

9. Main vein of leaves without hair, anthers thin and small, 1.5–2 mm long, with longitudinal split fully, helically twisted at dryness. A genome………………*T. urartu*

5. Spikelet usually not closely aligned in two rows, spike with apical spikelet, apical spikelet and lateral spikelets arrangement at 90 degrees on the dorsal and ventral surface, some groups arrangement close, the inner ridge of glume with dual ridges usually weak development, usually with a single ridge and single tooth appearance; palea usually with strong long own, seldom awnless, palea with double ridges, no cracking; caryopsis without flatted two sides, the cross section of caryopsis round or nearly semicircular, upper and lower ends bluntly round.

10. Hulled.

11. Rachis nodes with the wedge type of disarticulation easily.

12. Spike rectangular, glumes ridges, and awns well developed, less hair. Tetraploid, 2n = 28, BA genome……………………*T. turgidum* var. *dicoccoides*

12. Spike rectangular or linear, both sides flatted, glumes ridges and awns
weakly developed, largely long hairs, tetraploid, 2n = 28, $B^{sp}A$ genome………………*T. timopheevi* var. *araraticum*

11. Rachis nodes tough.
13. Veins of leaves without long hairs, glume and lemma hairless usually, tetraploid, 2n = 28, BA genome…………………*T. turgidum* concv. dicoccon
13. Veins of leaves with long hairs.
14. Grains with no flatted both sides. Tetraploid, 2n = 28, $B^{sp}A$ genome……………………………………………………*T. timopheevi*
14. Grains with flatted both sides. Hexaploid, 2n = 42, $B^{sp}AA^{m}$ genome……………………………………………………*T. zhukovskyi*

10. Naked.
15. Glumes with a well-developed ridge, navicular, shorter than lemma. 2n = 28, BA genome.
16. Grains silty…………………………………*T. turgidum* concv. turgidum
16. Grains flinty…………………………………*T. turgidum* concv. durum

15. Ridges of glumes weakly developed, shorter or longer than lemma. 2n = 28, BA genome.
17. Glumes shorter than lemma, just with no conspicuous ridge at the upper portion, with short awn at the apex……………*T. turgidum* concv. arthlicum
17. Glumes longer than lemma, papery, no ridge, leaf-like; lemma with long awn or without awn……………………………*T. turgidum* concv. polonicum

4. Glume with ridge at the upper portion, ridge or no conspicuous ridge at the lower portion. The second ridge usually undeveloped, just a beak-like bulge or a formed short awn at glumes ends. Hexaploid, 2n = 42, BAD genome.
18. Glumes tip without short awn.
19. Hulled.
20. Rachis nodes disarticulation at maturity
21. The barrel type of disarticulation……………*T. aestivum* concv. spelta
21. The wedge type of disarticulation………*T. aestivum* concv. tibetanum
20. Rachis nodes disarticulation by powerful pressure at maturity.
22. Rachilla not elongated.
23. Glumes and lemma short round, with awn or curved short beak……………………………*T. aestivum* concv. yunnanense
23. Glumes and lemma long navicular, with short and thin awn……………………………………*T. aestivum* concv. macha
22. Rachilla elongated……………………*T. aestivum* concv. vavilovii

19. Naked.
24. Winter, many tillers at seedling stage, prostrate; leaves thin and small, long vernalization period, required 0–5°C low temperature at 30–60 days…………………………………………*T. aestivum* concv. hybernum

24. Spring, less tillers at seedling stage, erect or inclined growth; leaves broad and big, short vernalization period, required above 5°C at 0–30 days.

25. Spikelets arrangement not much close on rachis, less than 3 spikelets per centimeter.

26. Rachis node with only 1 spikelet…………*T. aestivum* concv. aestivum

26. Rachis node with multiple spikelets or branch.

27. Rachis node with 3 parallel spikelets ……………………………….*T. aestivum* concv. tripletum

27. Rachis node with branch………*T. aestivum* concv. ramulostachye

25. Spikelets arrangement much close on rachis, more than 3 spikelets per centimeter.

28. Spikelets arrangement long, pectinate, almost vertical to rachis; glumes and lemma navicular; grain insufficiently spherical……………………*T. aestivum* concv. compactum

28. Spikelets arrangement much close on rachis, not vertical to rachis, inclined upward, glumes and lemma round; grain small and spherical……………………………*T. aestivum* concv. sphaerococcum

18. Glumes tip with short awn. Glumes long and big, papery, leaf-like, as long as or longer than the lemma………………………………………………*T. aestivum* concv. petropavlovskyi

3. Glumes without ridge; spike not conspicuously flatted, linear, the wedge type of disarticulation ………………………………………………………sect. *Sitopsis*

29. The upper portion of the glumes truncate forming a hypertrophic margin, seldom with a thin tooth.

30. Lemmas of lateral spikelet without awn, with short beak, the lemma of apical spikelet with long awn. $2n = 14$, B^{sp} genome…………*T. speltoides* var. *aucherii*

30. Lemmas of lateral spikelet and apical spikelet with awns. $2n = 14$, B^{sp} genome…………………………………………………*T. speltoides* var. *ligusticum*

29. The upper portion of the glumes with two teeth, not forming hypertrophic margins.

31. Spikes thin and short, mostly less than 12 spikelets per spike; spikelets usually with just 3 florets.

32. Lemmas of lateral spikelet without awn, lemmas of apical spikelet with strongly long awn, awn length equal to or longer than the spike length, the base of two sides with a thin branch awn. $2n = 14$, B^{s} genome ……………………………………………………….*T. searsii*

32. Lateral and apical spikelet with two awns, awn of apical spikelet not particularly strong. $2n = 14$, B^{b} genome ……………………………………………………….*T. bicorne*

31. Spike thick and long, mostly more than 15 spikelets per spike; spikelets usually with 3–5 florets.
    33. Lateral spikelet without awn, apical spikelet with strongly long awn. 2n = 14, B^l genome...*T. longissimum*
    33. Lateral and apical spikelet with awn, awn of apical spikelet not particularly strong. 2n = 14, B^l genome......*T. longissimum* var. *sharonense*

2. Spike with no flatted two sides; usually with 10 or less spikelets, seldom up to 13 spikelets, Spikelet usually mutually embedding with the corresponding rachis internodes, spikelet arrangement with one or two rows, upward parallel to rachis; glumes without ridge, awn of glumes often stronger than lemma awn; In the event of no awn, often forming a hypertrophic everted upper edge or wide teeth; lemmas usually with awn, rachis with umbrella-like abscission or barrel type of disarticulation...subgenus *Aegilops*

34. Spikes with the barrel type of disarticulation......................................sect. *Vertebrata*
    35. Spikes long cylindrical.
    36. Glumes and lemma with densely tufts of short hairs. 2n = 42, $D^cX^cB^s$ genome.........*T. crassum*
    36. Glumes and lemma without densely tufts of short hairs.
        37. Glumes hairless, the upper edge truncate, no tooth, hypertrophy eversion.
            38. Spike not particularly swollen and forming a cylindrical shape by embedding with rachis. 2n = 14, D genome...*T. tauschii* var. *typicum*
            38. Spike particularly swollen, so whole spike moniliform. 2n = 14, D genome ....*T. tauschii* var. *strangulatum*
        37. Glumes growth sparsely or with very short spiny hairs, Upper portion with short awn, beak, and teeth, not particularly hypertrophic.
            39. Middle spikelet of spike not particularly swollen, with barrel-shaped form.
                40. Awn of lemma from upper spikelet especially long, broadly flat and leaf-like. 2n = 28, D^cX^c genome..*T. plathyatherum*
                40. Glumes and lemma from laterally spikelet at middle and upper portion of spike with a short awn, glumes and lemmas of apical spikelet with long hairs, slender and narrow, not leaf like. 2n = 28, DC genome..*T. cylindricum*
            39. Middle spikelets of spike particularly swollen, with nearly spherical form. 2n = 28, DN genome..*T. ventricosum*

34. Spike long and lanceolate.

41. Spike slightness, spike with 5–10 spikelets; glumes with 2–3 small teeth, the silvery-white fine hairs; lemmas of lateral spikelet with short beak and two teeth, lemma of apical spikelet with a long awn. 2n = 42, $D^cX^cS^s$ genome………………………………………………………*T. syriacum*
41. Spike stubby, spike with 4–7 spikelets, glumes with two teeth and one beak or with 1–2 awns, sparsely short prickly hairs, lemma with a beak or a short awn, awn of glume often longer than awn of lemma. 2n = 42, DcXcU genome……………………………………………………………*T. juvenale*
35. Spike umbrella-like abscission.
42. Spike slender, cylindrical.
43. Spike with 4–8 spikelets; glumes of lateral spikelet with a short awn and a tooth, glumes tip of apical spikelet tapering gradually toward the apex forming a strongly caudate and long awn without tooth-like bulge at base. 2n = 14, C genome………………sect. *Orrhopygium. T. dichasians*
43. Spike with 3–5 spikelets; glumes of lateral spikelet with two teeth; lemma with a short beak; glumes of apical spikelet with three long awns, lemma with a long awn usually. 2n = 14, M genome……………………sect. *Comopyrum*
44. Spikelet not swollen……………………………*T. comosum*
44. Middle and lower parts of spikelet swollen……*T. comosum* var. *heldreichii*
42. Spike stubby, lanceolate, oval, or spire.
45. Glumes of lateral spikelet with one awn and a blunt tooth, lemma with two short lobes, glumes of apical spikelet with a long awn or a basal cracked tooth forming short awn. 2n = 14, U genome ………………………sect. *Uniaristatopyrum. T. uniaristatum*

45. Glumes of lateral and apical spikelet with multiple awns………………………………………………………sect. *Polyoides*
46. Spikelets at the upper part of the spike thin and small abruptly forming spire or not thin and small forming ovate shape.
47. Spike ovate, spike usually with three developed spikelet concentrating at the top, seldom 2–4 spikelets. 0–2 vestigial basal spikelets.
48. Glumes with 4–7 awns, lemma with 2–4 awns. 2n = 28, UM^o genome……………………………………*T. ovatum* var. *vulgare*
48. Glumes with 2–3 awns, lemma with 3 awns. 2n = 28, MU^o genome…………………………………*T. ovatum* var. *biunciale*
47. Spike spire shaped.
49. Glumes of developed spikelets with 4 awns or more.
48. Developed spikelet usually 5, vestigial basal spikelets 2–4 seldom 3 or 6 spikelets; glumes with 4–5 awns, lemma with 2–3 short awns, spike and awn more slender. 2n = 14, U genome……………………………………*T. umbellulatum*
49. Glumes of developed spikelets with less than 4 awns.

50. Glumes of laterally developed spikelets usually with unequal width 2 awns, upper thin spikelets often shorter in length than their corresponding rachis internodes. 2n = 28, UX^t genome……………*T. triaristatum* var. *columnare*

50. Glumes of laterally developed spikelets with 3 awns usually.

51. Upper thin spikelets equal in length to the corresponding rachis internodes length. 2n = 28, UX^t genome………………………………*T. triaristatum*

51. Upper thin spikelets shorter in length than the corresponding rachis internodes length. 2n = 42, UX^tN genome………………………………………*T. rectum*

46. Spikes lanceolate gradually from middle to both ends.

52. Middle veins of the first glume of spikelets with equal width, nearly parallel, caryopsis hulled.

53. Spikes narrow, developed spikelets usually 4, seldom 2 or 6; vestigial basal spikelets usually 3, seldom 2 or 4; glumes with 3 awns, nearly equal size, middle awn slightly shorter. 2n = 28, US^1 genome………………*T. peregrinum* var. *kotschyi*

53. Spikes broad, developed spikelets usually 3–5, seldom 2 or 7 spikelets; vestigial basal spikelets usually 3, seldom 2; glumes with 2–3 teeth or short awns with unequal length and width. 2n = 28, US^1 genome………………*T. peregrinum* var. *variabile*

52. Middle veins of the first glume of spikelets with unequal width, glumes of lateral spikelets with 2–3 awns, the middle awn slightly shorter; glumes of apical spikelet with 3 awns, longer than lateral spikelets, middle awn the longest, caryopsis naked. 2n = 28, UC genome………………………*T. triunciale*

1. Spikes slender and linear, spikelets usually 15–20, a few more than 20, arrangement very sparsely as nearly to one row, rachis internodes significantly longer than spikelets; glumes inverted trapezoid, glumes and lemma without awn, mostly at apex with blunt bulge; spikelet with the wedge type of disarticulation. 2n = 14, T genome

…………………………………………………genus *Amblyopyrum*

54. Leaves, glumes, and lemmas with hairs………………………*Am. muticum*

54. Leaves, glumes, and lemmas without hair……… *Am. muticum* var. *loliaccum*

***Triticum* L. emend., according to Linné, 1754. Gen. P1., ed. 5, 37; 1753, Sp. P1., ed. 1, 85**

Triticum L. Lectotype species: *T. aestivum* L. (Hitchcook, Prop. Brit. Bot. 121, Aug. 1929).

Subgenus *Sitopyros* (Hackel) **Yen et J. L. Yang, stat. nov. according to *Triticum* sect. Sitopyros Hackel, 1887. in Engler et Prantl, Die naturllichen Pflanzenfamilien II, 80.**

Sect. Monococcum Dumort., 1823. Observ. Gram. Fl. Belg.: 94.
1. *Triticum monococcum* L., 1753. Sp. Pl., ed. 1. 86.

Synonyms: *T. pubescens* M. Bieb., 1800. Beschr. Lander Casp. Meere: 81;
T. hornemennii Clemente, in Herrera 1818. Agric. gener., 1: 3;
Crithodium aegilopoides Link, 1834. Linneaea, 9, 132;
Nivieria monococcum Seringe, 1841. Cer. Eur. 73;
Ae. crithodium Steud., 1855. Syn. Gram.: 355;
T. vulgare bidens Alef., 1866. Landw. F: 334;
T. monococcum β lasiorrachis Boiss. 1884. Fl. Orient. 5: 673;
Cr. monococcum (L.) Á. Löve, 1984. Feddes Repert. 95: 490.

Morphological characteristics: coleoptiles with two veins. Prostrate at seedling stage, erect or semierect. Leaves narrow, leaves of erect type often broad, cultivars with less short hair on leaves; The leaves of wild varietas often with fine hairs, and longitudinally prominent veins often with a row of long hairs. Culms slender and erect, cultivars often with hollow culms and thin walls, nodes with downward curved hairs; Wild varietas often with solid culms type, hollow culms type with thicker walls, and nodes with downward curved white hairs. Spikelets slender and flat, spikelets arrangement of cultivars often more closely than wild varietas, rachis flat and broken off easily, hairless or margin with densely short hairs; wild varietas often with long hairs, seldom short hairs or hairless. Apical spikelet undeveloped, no seed. Spikelets at both sides with 3 or 2 florets, generally the lowest floret with 1 seed, and the upper florets with no seed, seldom spikelet setting 2 seeds. Glume leathery, elongated, prominent, and straight keel connecting with sawtooth tip longitudinally through the glume; lateral veins straight up to the second teeth of glume tip. Lemma longer than glume, glume tip with curved awn or straight awn with rough serrations; upper florets of spikelet often with short awn or without awn, seldom with long awn. palea intact, longitudinally splitting at maturity. Anthers 3.0–3.9 mm long. Caryopsis small, sharp at both ends, flat in both sides, shallow ventral groove, flinty, often less apical hairs, amber yellow, pink, red or green.

Cytological characteristics: 2n = 14, A^m genome, one pair of chromosomes containing small satellites.

Concv. (cultivar group):

(1) ***Triticum monococcum* L. concv. *monococcum*** (Fig. 8.2)

Biennial or annual, winterness or springness. In the Neolithic age, it was widely cultivated in Western Europe and Asia Minor. It is now distributed in the Transcaucasia, the north Caucasus, the Balkans, Asia Minor, Morocco, Spain, and so on. Because of good tolerance to cold, heat, and drought, it is also cultivated as forage grass in barren mountainous areas sporadically.

(2)***Triticum monococcum* L. concv. Sinskajae** (in 1975, named as T. sinskajae A. Filat. et Kurk.; Fig. 8.3)

It is a naked grain type found in Russia.

Fig. 8.2 *T. monococcum* L. concv. einkorn 1. Adult plant; 2. caryopsis; 3. spikelet; 4. lemma; 5. the second and third florets; 6. lodicule, stamens, feathery stigma, and cracking palea; 7. palea

Triticum monococcum* L. var. *boeoticum (Boiss.) **Kneuck., 1903. in Allg. Bot. Zeitschr. 9: 34** (Fig. 8.4). E. Boissier originally described it as "æoticum." Many subsequent scholars wrote it as "boeoticum" based on its geographical name of the collection—Boeotia.

Synonyms: *Crithodium aegilopoides* Link 1834. Linneaea, IX: 132;
T. boeoticum Boiss., 1853. Diagn. Cer. I. fasc. 13: 65;
T. aegilopoides (Link) Bal. ex Koern., 1885. Handb, d. Getreideb. I: 109 (not Forsskal, 1775; and Mazzuoato, 1807);
T. spontaneum subsp. *aegilopoides* Flaksb. 1935.
Културная Флора СССР, Т. I. (Пшеница) 33, in clavi: 339.

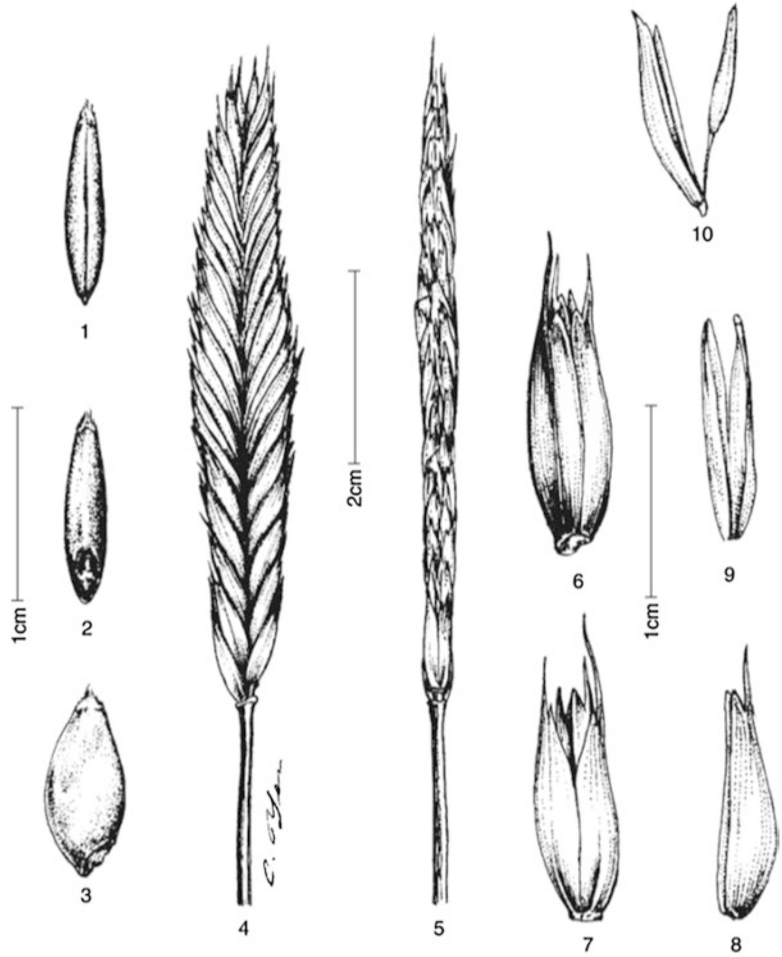

Fig. 8.3 *T. monococcum* L. concv. sinskajae (A. Filat. et Kurk) Yen et J.L. Yang
1. Caryopsis, ventral view; 2. caryopsis, dorsal view; 3. caryopsis, side view; 4. spike, front view; 5. spike, side view; 6. spikelet with glume, ventral view; 7. spikelet with glume, dorsal view; 8. lemma; 9. palea; 10. the second and third florets

Annual or biennial, usually winterness, seldom springness; only lemma of the first floret with well-developed long awns; usually only the first floret seed-setting. The wild varietas is distributed in the Caucasus, Crimea peninsula, Asia Minor, Syria, northern Iraq, northwestern Iran, Lebanon, southeastern Bulgaria, central and Northern Greece, southern Yugoslavia, and southern Albania. The distribution is concentrated in the eastern coast of Caspian Sea in the Caucasus and Crimea. It grows on red calcareous soil and alluvial soil in savanna and summer-dry shrubs of Mediterranean. It was first discovered in Nauplia-Corinth regions of Greece in 1833. Link published it under the name *Crithodium aegilopides* in 1834.

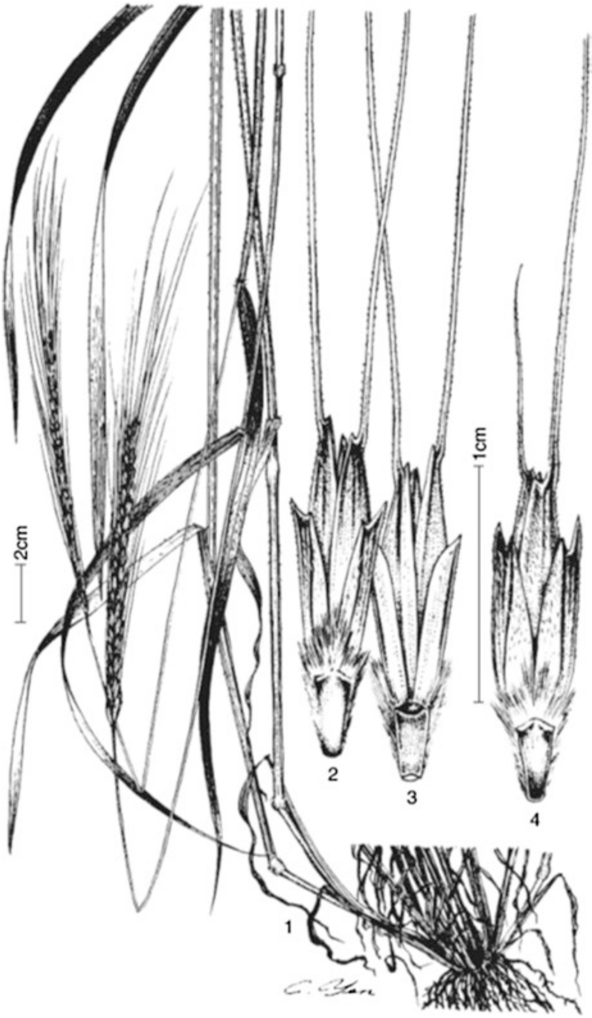

Fig. 8.4 *T. monococcum* L. var. *boeoticum* (Boiss.) Yen et J. L. Yang and *T. monococcum* L. var. *thaoudar* (Reut.) Flaksb
1. Adult plant; 2. var. *thaoudar* spikelet, dorsal view; 3.var. *thaoudar* spikelet, ventral view; 4. var. *boeoticum* spikelete, dorsal view

Triticum monococcum **L. var.** ***thaoudar*** (Reut.) **Flaksb., 1913. Bull. Angew. Bot. St. Petersb. 6: 673.** (Fig. 8.4)

Synonyms: *T. thaoudar* Reut. 1860. in Bourgeau, Pl. Exs. ex Boiss. 1884, Fl. Orient, 5: 673;
T. spontaneum subsp. thaoudar Flaksb. 1935. Културная Флора СССР, Т. I. (Пшеница) 33, in clavi: 339;

Synonyms: *T. thaoudar* Reut. 1860. in Bourgeau, Pl. Exs. ex Boiss. 1884, Fl. Orient, 5: 673;
T. baeoticum subsp. *thaoudar* (Reuter) Schiemann, 1948. Weizen. Rogen. Oersta, Syst. Gesch. Verw. 28.

Annual or biennial, usually winter, varietas spring; lemma of the first and second floret with well-developed long awns; usually the first and second floret seed-setting. This wild varietas is distributed in the Caucasus, Asia Minor, northern Iraq, Crimea peninsula, Syria, northwestern Iran, Palestine, northwestern Jordan and Lebanon, etc. In Europe, it is found only in southern Bulgaria. It is more common in Asia Minor, northwest Iran, and Syria and less common in the Caucasus and Crimea, which is different from the concentrated distribution of var. boeoticum. It grows on red calcareous soil and alluvial soil, in open grasslands with sparse trees or short shrubs.

2. ***T. urartu* Tum. ex Gandilyan, 1972. Бот. Журн.т. 57. (2): 173 ~ 181. according to *T. uraratu* Tum. 1938. Тр. Арм. Филиала АН СССР, сер. Биолог., II: 210 ~ 215 (Described by Russian only)** (Fig. 8.5)

Synonyms: *Crithodium urartu* (Thumanian) Á.Löve, 1984. Feddes Repert. 95: 491;
T. baeoticum subsp. *urartu* (Tum.) Vav., 1964. Пшеница: 17.

Morphological characteristics: Annual or biennial, plant height about 90 cm, coleoptile purple, scatteredly prostrate at seedling stage, culms glabrous. Leaves linear to lanceolate shape, 0.7–1.0 cm wide, 15 cm long; leaf sheath with very short hairs, breaking off latterly; auricles white; spike elongated, narrow, 7 ~ 9 cm long, 0.6 ~ 0.7 cm wide, above rachis nodes breaking off (wedge type) at maturity; internode of rachis nodes flat, margin with densely long hairs; glume with two ridges and two teeth, one long and the other short, glume surface rough with tumor bulge usually; the first and second florets generally fertile, lemma of the first and second florets with long awns; anthers small, 2 ~ 2.7 mm long. Both ends of seeds sharp, both sides flat, shallow ventral groove, flinty, reddish yellow.

Morphology of *T. urartu* very similar to *T. monococcum* var. *thaoudar*. However, leaves and leaf sheaths of T. urartu have no long hair or nearly glabrous. Its anther is small and longitudinally split during pollination, different from the porous dehiscence at both ends of *thaoudar*. Dried anthers of *T. urartu* helically twist, while var. *thaoudar* does not twist. When *T. urartu* as male parent is crossed with wild varietas of *T. monococcum*, F1 hybrids show nearly normal chromosome pairing but are sterile. When *T. urartu* is used as female parent, it is difficult to obtain hybrids due to the poor development of immature embryo after pollination. In the other words, *T. urartu* and varietas *beoticum* and *thaoudar* of *T. monococcum* have reproductive isolation, and thus *T. urartu* is an independent species.

Cytological characteristics: 2n = 14. A genome with one pair of satellite (5A).

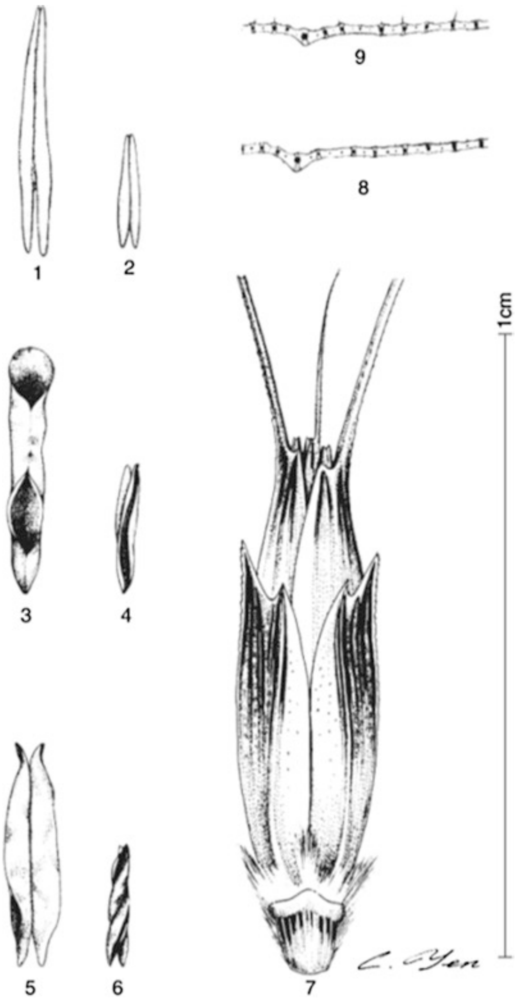

Fig. 8.5 Morphology comparison of *T. urartu* Tum. ex Gandilyan and *T. monococcum* var. *thaoudar* 1. Anther of *T. monococcum* var. *Thaoudar*; 2. shorter and smaller anther of *T. urartu*; 3. porous dehiscence of anther of *T. monococcum* var. *thaoudar*; 4. fully splitting of *T. urartu* anthers; 5. without twisting of dried anther of *T. monococcum* var. *thaoudar*; 6. helically twisting of dried anthers of *T. urartu*; 7. dorsal view of *T. urartu* spikelet (the wedge type of disarticulation) with awns for two lemma; 8. the transverse section of *T. urartu* leaf, showing without hairs on the veins; 9. the transverse section of *T. monococcum* var. *thaoudar* leaf, showing hairs on the veins

Distribution area: Armenia, Israel, Syria, Palestine, northwestern Iran, southeastern Turkey, the mountain area of Fertile Crescent. It grows on red calcareous soil, alluvial soil, open grasslands of sparse trees, summer drought shrubs of Mediterranean, and the edge of farmland and roadside.

3. ***Triticum turgidum* L., 1753. Sp. P1. 86. sensu lato** (Fig. 8.6)

Synonyms: *T. polonicum* L., 1762. Sp. Pl. Ed. 2: 127;
T. levissimum Haller., 1768. Strip. ind. Helv. 209, No. 1423;
T. dicoccon Schrank, 1789. Baiet. Fl. 1: 389;
T. glaucum Moench, 1794. Method.: 174;
T. durum Desf., 1789. Fl. Atlant. 1: 114;

Fig. 8.6 *T. turgidum* L.cv. Ailanmai

T. farrum Bayle-Berelle, 1809. Mon. de. Agron, Cereali: 50, t. 4, f. 1. 2;
T. atratum Host, 1809. Gram. Austr. 4: 5, 8;
T. atratum Schubl., Char. et Descr., 1818. Cerealium in Hort Tubing.: 32;
T. dicoccum Schubl., Char. et Descr., 1818. Cerealium in Hort Tubing.: 29;
T. amyleum Seringe, 1819. Melanges botaniques: 124;
T. atratum Roem. et Schult., 1819. Syst. Vegetab. 2, 766, No. 15;
T. zea Wagini., 1819. Anb. d. Getred: 33;
T. spelta amylea Seringe, 1841. Cer. Eur., 76 (114);
T. alatum Peterm., 1844. Flora, 27: 234;

T. abyssinicum Steud., 1855. Syn. Pl. Gram.: 342;
Gigachilon polonicum Seidl., Bercht. et Seidl., 1863. Oek. tech. Flora Bohmens 1: 425;
T. vulgare durum Alef., 1866. Landw. Fl.: 324;
T. vulgare dicoccum Alef., 1866. Landw. Fl.: 331;
Deina polonica Alef., 1866. Landw. Fl.: 336;
T. sativum dicoccum Hack., 1887. Nat. Pfl. Ed. 2, 2: 81;
T. tenax B. II., durum, Asch. et Graeb., 1901. Syn. 2: 692;
T. dicoccoides (Koern.) Koern., in litt. ex Schweinf., 1908. in Ber. D. Deutsch. Bot. Ges. 309;
T. hormonis Cook, 1913. Bureau of Pl. Ind (USA) Bull. No.274: 13, 52;
T. persicum Vavilov, 1919. in Ann. Acad. Petrovsk. 1 ~ 4;
T. orientale Perc., 1921. The Wheat Plant: 155, 204;
T. pyramidale Perc. 1921. The Wheat Plant: 156, 262;
T. carthlicum Nevski, 1934. in Komarov, Fl. URSS, 2: 685;
T. abyssinicum (Vav.) Jakubz. 1939. Key to the true cereal crops, 4th, ed. 92;
T. turanicum Jakubz., 1947. Селек.и Семен. 14 (5): 40;
T. aethiopicum Jakubz., 1947. Селен.н Семен. 14 (5): 46;
T. ispahanicum Heslot, 1958. Copmpetes Rend Sanoes 247: 2479.

Morphological characteristics: Coleoptiles usually with 2 veins, Indian-Ethiopian cultivars with 4–6 veins; mostly erect at seedling stage, wild varietas *dicoccoides* and some varieties of cultivar groups is prostrate at seedling stage; leaves with hairs or hairless; culms hollow, wall thick, scare solid culms; spikes elliptical, spindle, oblong, branched, various shapes depending on cultivars or varietas; except for concv. *polonicum* with long leaf-like glumes, others with glumes having conspicuously keeled protrusion, usually straight through the glumes from base to sharp teeth tip; Lemma usually with long awn, sometimes with short awn or awnless; caryopsis large, slender, or round, mostly having hard grains with good flour quality, some cultivars of concv. *turgidum* having soft grains with weak gluten.

Cytological characteristics: 2n = 28. Genome BA, two pairs of chromosomes (1B, 6B) with big satellites.

concv. (cultivar group):

(1) ***Triticum turgidum* L. concv. dicoccon** (Fig. 8.7). In 1789 it was named as *T. dicoccon* Schrank.

Winter, semi-winter, or spring habits; coleoptiles with 2 veins or 4–6 veins; spike flat, two sides of rachis often bristly, easily broken or tough; spikelet with 3–4 florets, usually setting two seeds; glume thick, tough, long, narrow, outer side flat; lemma with triangular awn or awnless, palea ovoid to lanceolate, tip narrow showing dichotomy splitting; grains slender, sharp at both ends, ventral parts flat or

Fig. 8.7 *T. turgidum* L. concv. *dicoccon* and *T. turgidum* L. var. *dicoccoides*
1. concv. *dicoccon* spike; 2. concv. *dicoccon* spikelet, dorsal view; 3. concv. *dicoccon* spikelet, ventral view; 4. concv. *dicoccon* caryopsis, ventral view, dorsal view, and side view; 5. var. *dicoccoides* spike; 6. var. *dicoccoides* spikelet, dorsal view showing wedge type of disarticulation; 7. var. *dicoccoides* spikelet, ventral view; 8. var. *dicoccoides* caryopsis, dorsal view, ventral view, and side view (left to right)

slightly concave, with narrowly ventral groove, flinty, not easily separated from the lemma—hulled.

It was widely cultivated from Denmark, Germany, Czech, Switzerland, to Egypt in the Neolithic age. In the Greek-Rome times, it was gradually replaced by durum wheat and common wheat. At present, it is only sporadically cultivated in Yugoslavia, the Caucasus, Iran, Pakistan, India, etc. in arid mountain areas. It is cultivated in the United States as pasture. Despite low economic value in wheat production, it is resistant to barren, heat, drought, and cold.

(2) ***Triticum turgidum* L. concv. durum wheat** (Fig. 8.8). In 1789, it was named as *T. durum* Desf.

Spring, semi-spring, rarely winter habits; hairless or nearly hairless for seedling leaf; spike slightly flat or four prism; rachis usually tough without broken, rachis nearby basal spikelet covered with bristles; glumes narrow and long, lateral outside surface flat, conspicuously keeled protrusion straight through the glumes from base to sharp tip, hairless or hairs, usually awnless; lemma thin, abaxially rounded, and the lemmas of basal florets with long and smooth awns, while the upper florets usually with short awns; caryopsis slender, hard, two tips pointed or slightly pointed usually with conspicuously back ridges, caryopsis section often triangular, white, amber, red, seldom purple; flour quality excellent, gluten content high. It has high economic value in production for its excellent wheat gluten quality and is used as macaroni. It has a big cultivation area only after common wheat. In the past, the yield per unit area was lower for durum varieties than common wheat. In recent years, high-yielding old cultivars with short culm and lodging resistant have been bred. It is mainly cultivated in the Mediterranean coastal countries and the former Soviet Union. It is also planted in other regions such as China, Iran, Iraq, Pakistan, India, Canada, the United States, Mexico, Argentina, Uruguay, and Chile.

(3) ***Triticum turgidum* L. concv. *turgidum*** (Figs. 8.6 and 8.8)

Spring, semi-winter, or winter habits; erect or prostrate at seedling stage; leaves short and narrow, often with soft hairs, blue-green color, especially at heading showing dark blue-green color, traditionally called "blue wheat" in China (“lanmai” in Chinese); spike often four-prism shaped, elliptical, spindle shaped, oblong, or branched; rachis tough and hard to be broken, the margins with densely white hairs; spikelet often with 5–7 florets, setting 3–5 seeds; glume leathery, wide, and short, length usually only about a half of lemma, the outer side bulges, with 5–7 veins, conspicuously keeled protrusion, tips with multiple teeth, prominent lateral veins; Lemma thin, break off easily, often oval, with 9–15 thin veins, awn thick and long, seldom awnless, awn usually triangular; caryopsis large, wide, and short, dorsal bulge; “Blue wheat” is characterized by soft grain with low gluten content that is favorable to making biscuits and cakes. Although yield is usually high, it is sporadically planted since its quality is not suitable for making main food such as bread, steamed bread, and noodles. In China, cultivars such as Ai-lanmai, Yuwei-lanmai, and branched lanmai from Sichuan province and fushoumai from Henan province are “Blue wheat.” However, in common wheat, we classify cultivars with branched spikes as an independent cultivar group because of its special value in breeding. Cultivar group itself is an artificial classification. We suggest that the classification of cultivar group should depend on the economic importance.

(4) ***Triticum turgidum* L. concv. polonicum** (Fig. 8.9). In 1762, it was named as *T. polonicum* L.

Spring habits; yellow-green color at seedling stage, hairless; spike characterized by long and large leaf-like glume; lemma with long awn or awnless; caryopsis slen-

Fig. 8.8 *T. turgidum* L. concv. turgidum and concv. durum
1. *T. turgidum* L. concv. turgidum cv. Henanfushoumai; 2, 3. *T. turgidum* L. concv. durum

der and flinty. Its yield is often lower than that of durum wheat. It has only sporadical cultivation in some countries.

(5) ***Triticum turgidum* L. concv. carthlicum** (Fig. 8.10). In 1934, it was named as *T. carthlicum* Nevski.

Spring habits; both glume and lemma having long awns as the notable feature. It is a secondary tetraploid that was formed by hybridization between tetraploid and hexaploid wheat.

Triticum turgidum* L. var. *dicoccoides (Koern. ex Schweinf.) **Bowden, 1959. Canadian J. Bot. 37: 657 ~ 684** (Fig. 8.7).

Fig. 8.9 *T. turgidum* L. concv. polonicum
1. Awnless variety: Ruoqianggumai; 2. Xinjiang polonicum; 3. lemma; 4. lodicule, stamens, feathery stigma and palea; 5. spikelet with long leaf-like glume; 6. the second, third, and fourth florets

Synonyms: *T. dicoccoides* Koern. ex Schweinf., 1908. Ber. Deutsch. Bot. Ges. 26a: 310;
T. hernonis Cook, 1913. U. S. Dept. Agric. Bull. 274: 13;
T. turgidum ssp. *dicoccoides* (Koern.) Thell., 1918. Naturw. wochenschr. 17: 470;
Gigachilon polonicum ssp. *dicoccoides* (Koern. ex Schweinf.) Á. Löve, 1984. Feddes Repert. 95: 496.

Morphological characteristics: Annual or biennial, winterness. Coleoptiles often with 4 veins, prostrate at seedling stage, leaves narrow with hair or tiny pubescence; culm solid or hollow with thick wall, nodes with downward curly hairs; spike flat, rachis breaking off at above attachment position of spikelet at maturity; rachis flat and smooth, two sides of margins with densely white, yellow or black-brown and

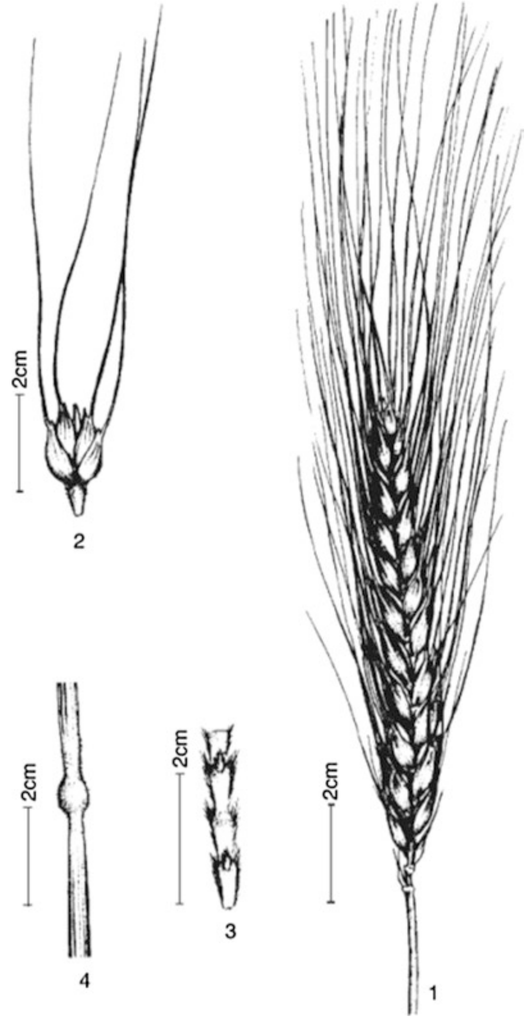

Fig. 8.10 *T. turgidum* L. concv. *carthicum*
1. Spike; 2. spikelet, dorsal view showing glume with long awn; 3. rachis with bristles; 4. culm nodes with pubescence

long bristle; apical spikelet often undeveloped, lateral spikelets often with 3 florets, producing 1–2 seeds usually; glume leathery, narrow, hairless or with silky hairs, with thin teethed keel, straight to glume apex, glume apex blunt or acuate, prominent lateral veins extending to the second tooth of glume apex; lemma slightly shorter or longer than glume, lemma apex slightly splitting with coarse awn. The palea tip splitting but not completely cracked at maturity. Caryopsis narrow and long, both ends sharp, both sides flat, caryopsis section nearly triangular, top hair long, white usually.

It is distributed in Israel, Palestine, Jordan, Lebanon, Syria along the eastern coast of the Mediterranean, Southeast Turkey, northeast Iraq, and northwest Iran. It grows on red calcareous soil and basalt soils in Mediterranean open savanna land and summer drought shrub environments.

4. *T. timopheevi* Zhuk., 1928. ТР. прикл′Бот. Геи.и Сел. 19, 2: 64.

Synonyms: *T. dicoccoides* subsp. armeniacum Jakubz., 1932. Тр. прикл Бот. Геи. и Сел. сер 5 (1): 164, 195;
T. armeniacum (Jakubz.) Makushina, 1938. in Compt. Rend. (Doklady) Acad. Sc. URSS, n. s. 21: 345;
T. araraticum Jakubz., 1947. Селек. и Семеи. 5: 46;
T. chaldicum Menabde, 1948. Pschen. Gruz.: 196.

Morphological characteristics: Annual or biennial, winter or spring habits; prostrate or semi-prostrate at seedling stage; leaf sheaths and leaves with densely white long hairs; spike wide and flat, spikelet compact (cultivar) or narrow-flat, spikelets sparse (wild varietas), rachis with short or long hairs; glume leathery and shorter, with a single conspicuously keeled bulge; lemma thin with small and short awns; palea often conspicuously longer than lemma, longitudinally splits at maturity; caryopsis sharp at both ends, medium size, and hulled. Spikelet usually producing 2 seeds.

Cytological characteristic: $2n = 28$, $B^{sp}A$ genome, two pairs of chromosomes with conspicuous satellites, with karyotype similar to that of *T. turgidum* (AB genome).

***T. timopheevi* Zhuk. concv. timopheevi** (Fig. 8.11)

Morphological characteristics: Annual or biennial, springness. Spike wide and flat, spikelet compact. It is famous for high resistance to rust, smut, and powdery mildew. The economic value is small in wheat production, only cultivated in a small area in the western mountains of Georgia. At present, it is widely used as materials for resistant breeding in many countries. Its cytoplasm is used for breeding male-sterility materials under other wheat backgrounds to research heterosis utilization in hybrid wheat.

T. timopheevi* Zhuk. var. *araraticum (Jakubz.) **Yen, 1983. Acta Phytotax. Sinica 21 (3): 294.** (Fig. 8.12)

Synonyms: *T. araraticum* Jakubz., 1947. Селек. и. Семеи. 5: 46.

Morphological characteristics: Annual or biennial, winterness. Spike narrow and flat, rachis internodes long, spikelets sparse. Two sides of rachis margins with long hairs. Other traits similar to cultivated *T. timopheevi*.

Distribution: Armenia, Azerbaijan, Nakhichevan, northwestern Iran, northern Iraq, and eastern Turkey. It grows on red calcareous soil, basalt soil, limestone crevices, and alluvial soil in the evergreen and hardwood oak forest gaps, shrubs, limestone slopes, the edge of farmland, and roadsides.

5. *T. zhukovskyi* Menabde et Ericzjan, 1958. Comm. Georgian Br. Acad. Sci. USSR. NO.16; 1960. Soobsch. AN Gruz. SSSR 25: 732. (Fig. 8.13)

Synonyms: *Gigachilon zhukovskyi* (Men. et Eric.) Á Löve, 1984. Feddes Repert. 95: 498.

Fig. 8.11 *T. timopheevi* Zhuk
1. Adult plant; 2. caryopsis; 3. spikelet; 4. lodicule, stamens, feathery stigma, and palea; 5. spike

Morphological characteristics: Semi-springness, semierect. Pale green at seedlings stage, leaf sheaths and leaves with long white hairs. Spike narrow and long, slightly flat, larger than that of *T. timopheevi*. Glume apex with two teeth, conspicuously keeled. Spike characteristics, growth habits and disease resistance very similar to those in *T. timopheevi*.

Cytological characteristics: $2n = 42$. $B^{sp}AA^{m}$ chromosome, four pairs of chromosomes with satellites, two pairs of satellites very obvious.

Distribution: It was found in western Georgia of the former Soviet Union, but the cultivated area is very small. It was formed by natural hybridization between *T. timopheevi* and *T. monococcum*. The economic value of direct utilization is low.

6. ***T. aestivum* L. 1753. Sp. Pl., ed. I. i, 85** (Figs. 8.14, 8.15, 8.16, 8.17 and 8.18)

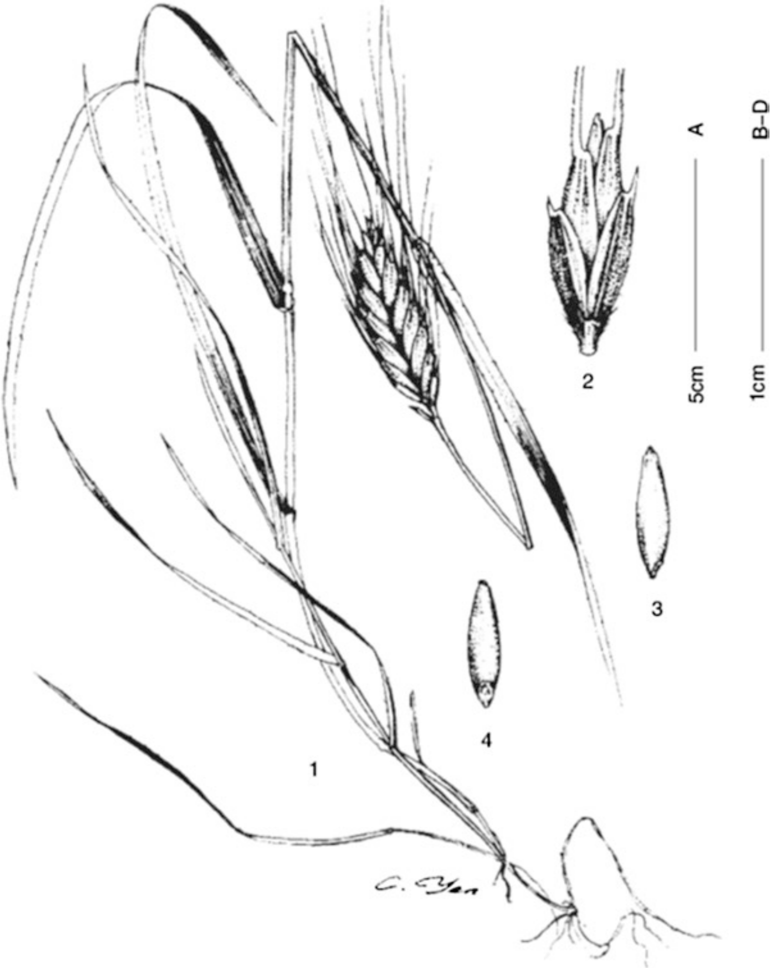

Fig. 8.12 *T. timopheevi* var. Araraticum (Jakubz.)Yen
1. Adult plant; 2. spikelet; 3. caryopsis, lateral view; 4. caryopsis, dorsal view

Synonyms: *T. hybernum* L., 1753. Sp. Pl., ed. I: 86;
T. spelta L., 1753. Sp. Pl. ed. I: 86;
T. sativum Lam., 1786. Ency. Meth. 2: 554;
T. vulgare Vill., 1787. Hist. Pl. Dauph. 2: 153;
T. vulgare Host, 1805. Icon. et Descr. Gram. Austr. 3: 18;
T. zea Host, 1805. Icon. et Descr. Gram. Austr. 3: 20, t. 29;
T. compactum Host, 1809. Icon. et Descr. Gram. Austr. 4: 4, t. 7;
T. sphaerococcum Perc., 1921. The Wheat Plant, a monograph: 321;
T. macha Dek. et Men., 1932. Тр. прикл Бот. Геи. и Сел. сер,
5 (1), 14: 38;

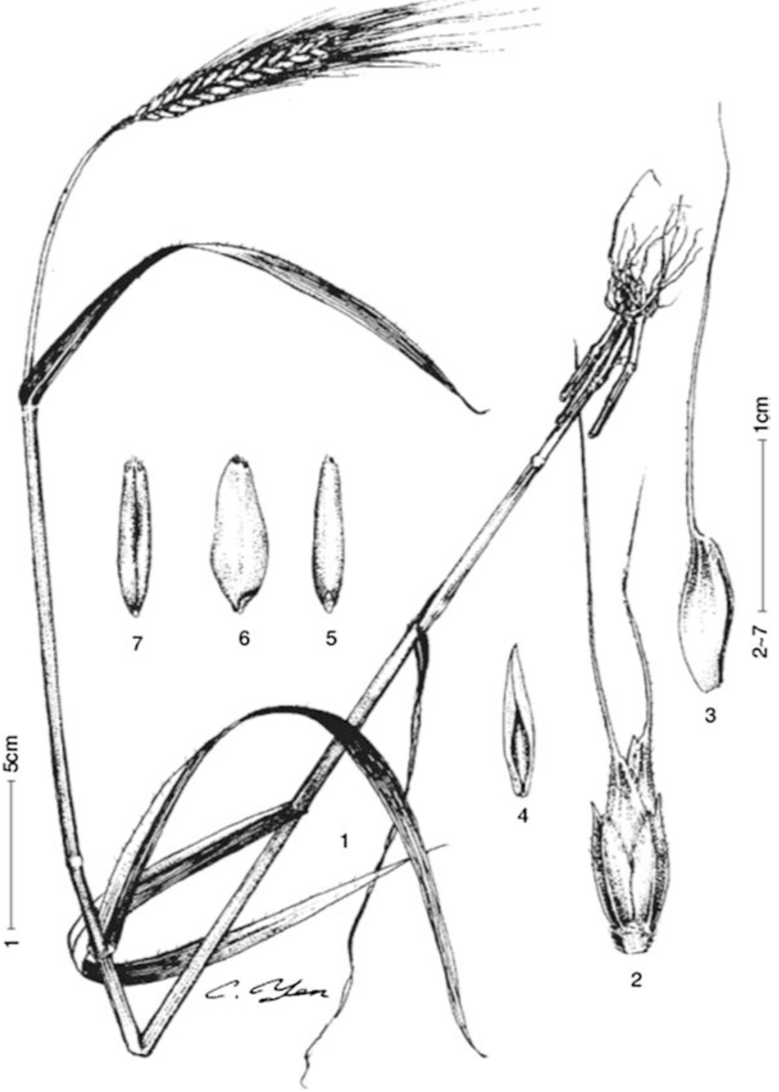

Fig. 8.13 *T. zhukovskyi* Menabde et Ericzjan
1. Adult plant; 2. spikelet; 3. lemma; 4. palea; 5. caryopsis, dorsal view; 6. caryopsis, lateral view; 7. caryopsis, ventral view

T. vavilovi (Tum.) Jakubz. 1933 Соц. Растениев, No 7, 222; 1933. Природа, No 11, 72;
T. amplissifolium Zhuk 1949. ДАН СССР, Т. 69: 261;
T. petropavlovskyi Udacz. et Migusch., 1870. Вестнцкк цс/х Науки, 9.

Fig. 8.14 *T. aestivum* L. concv. aestivum
1. Adult plant; 2. spikelet, dorsal view; 3. lemma, lodicule, stamens, feathery stigma and palea; 4. caryopsis, dorsal view and lateral view

Morphological characteristics: Annual or biennial, winterness, semi-winterness, or springness. Prostrate or erect at seedling stage. Young leaves with hairless or long hairs at longitudinally dorsal ridge, two sides with short hairs usually. Internodes of culms with hollow, with thin wall, solid, or thick wall seldom. Spike rectangular, oval, spindle shaped, rod shaped, conical, branched, etc. depending on cultivars. Spikelet arrangement sparse or dense, spikelets with 5–14 florets, producing 2–6 seeds usually or 7–11 seeds seldom. Glumes loose, broad, side convex-round, with ridge, ridge only in the upper part of glume usually, and the lower part more round and flat without ridge usually, a few cultivars with ridge direct to the lower part, glume apex forming teeth shape. Lemma thin, abaxially rounded without ridge, 7–11 veins, long awn, short awn, or no awn, hair or hairless. Palea and caryopsis separated easily or hulled. Seed shortly round, flinty, or silty.

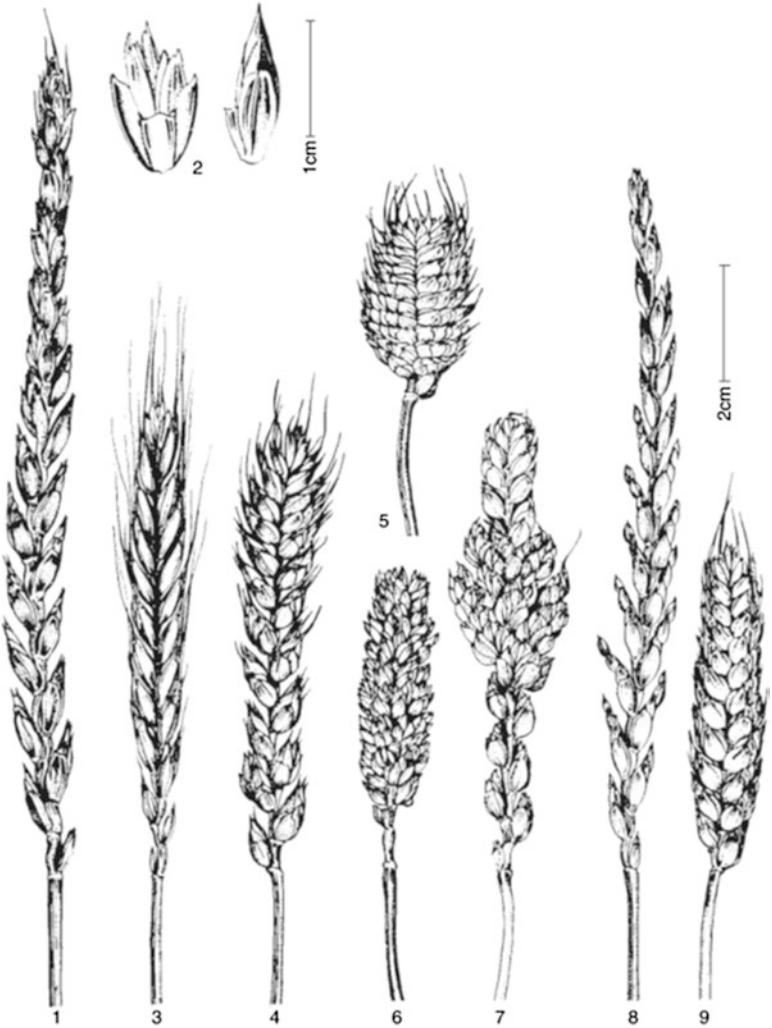

Fig. 8.15 *T. aestivum* L. con cultivar groups
1. *T. aestivum* L. concv. spelta; 2. spelta spikelet ventral and lateral view, rachilla with the barrel type of disarticulation (left); 3. concv. macha; 4. concv. aestivum; 5. concv. compactum; 6. concv. triplet; 7. concv. ramulostachye cv. branch spike No. 1; 8. concv. vavilovi; 9. concv. shaerococcum

Cytological characteristics: 2n = 42, genome AABBDD, containing four pairs of chromosomes with satellites, only two pairs of B chromosome (1B, 6B) obvious usually, A and D chromosomes invisible in some cultivars.

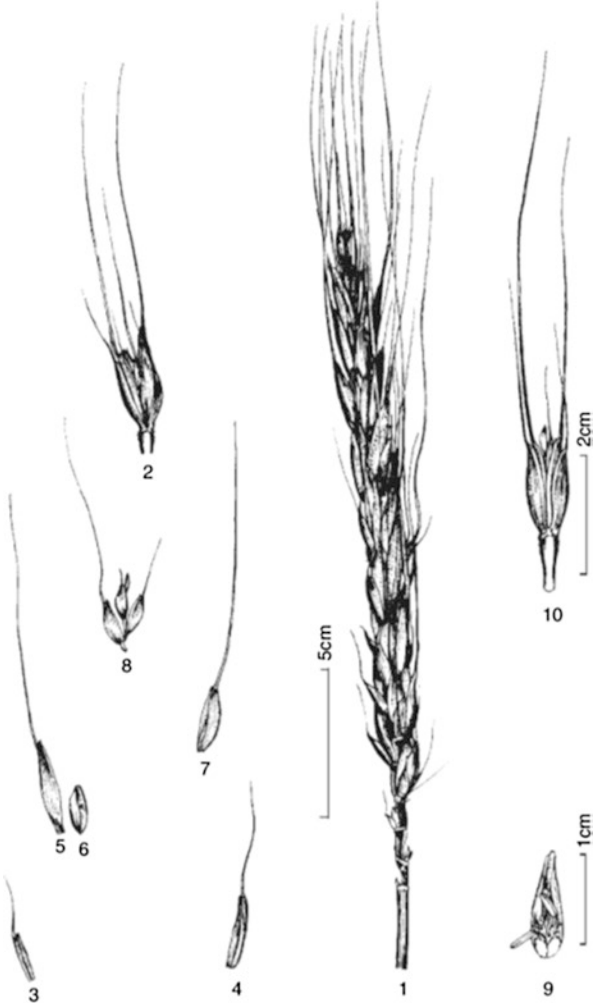

Fig. 8.16 *T. aestivum* L. concv. petropavlovskyi
1. Spike; 2. spikelets; 3. the first glume with awn; 4. the second glume with awn; 5. lemma of the first floret; 6. palea; 7. the second floret; 8. the third, fourth, fifth, and sixth florets; 9. lodicule, stamen, stigma, and feathery stigma and palea; 10. spikelet with the wedge type of disarticulation

Concv. (cultivar groups):

(1) ***T. aestivum*** **L. concv. hybernum**

Winterness, long vernalization period, about 30–60 days under 0–5 °C. Prostrate at seedling stage, tillers many, leaves thin and small. Spike slightly smaller, spikelet number less than 18 per spike often. In China, it is the major type cultivated in northern winter wheat areas. In 1753, it was named as *T. hybernum* L.

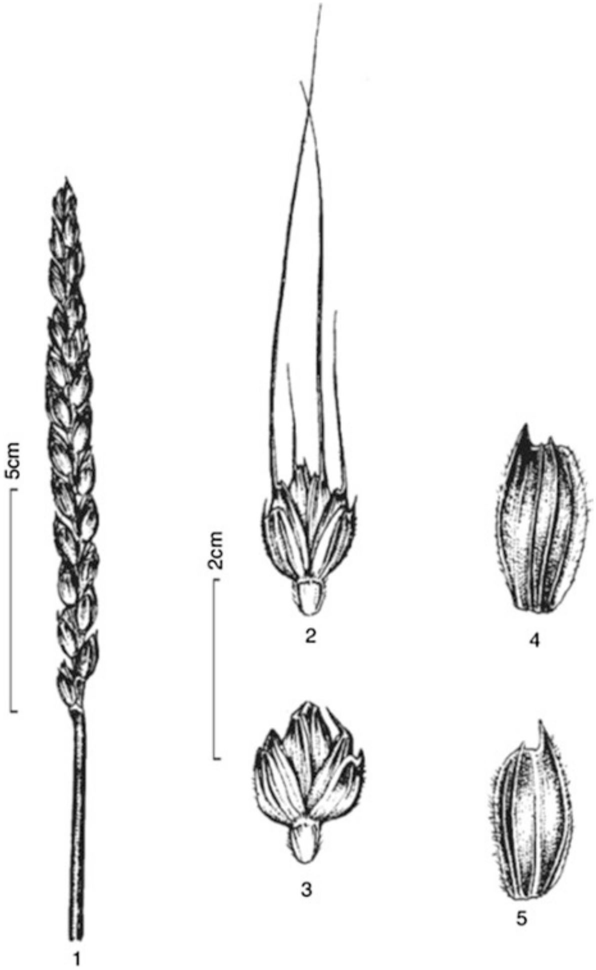

Fig. 8.17 *Treiticum aestivum* L. concv. yunnanense
1. Spike with awnless; 2. spikelet with awn, rachis with the wedge type of disarticulation; 3. spikelet with awnless, rachis with the wedge type of disarticulation; 4. the second glume with double ridges; 5. the first glume with double ridges

(2) *T. aestivum* L. concv. aestivum (Fig. 8.15-4)

Springness, short vernalization period, within 30 days under about 5 °C, some varieties with weak springness without vernalization requirement. Tillers less, erect, or inclined clusters (usually for semi-springness cultivars) at seedling stage. The leaves large and broad usually. Spike long and large, usually 18–25 spikelets, up to 35 in some cultivars. It is the major type cultivated in northern spring wheat areas (sensitive to day length response) and southern spring wheat areas with autumn sowing (weak response to day length).

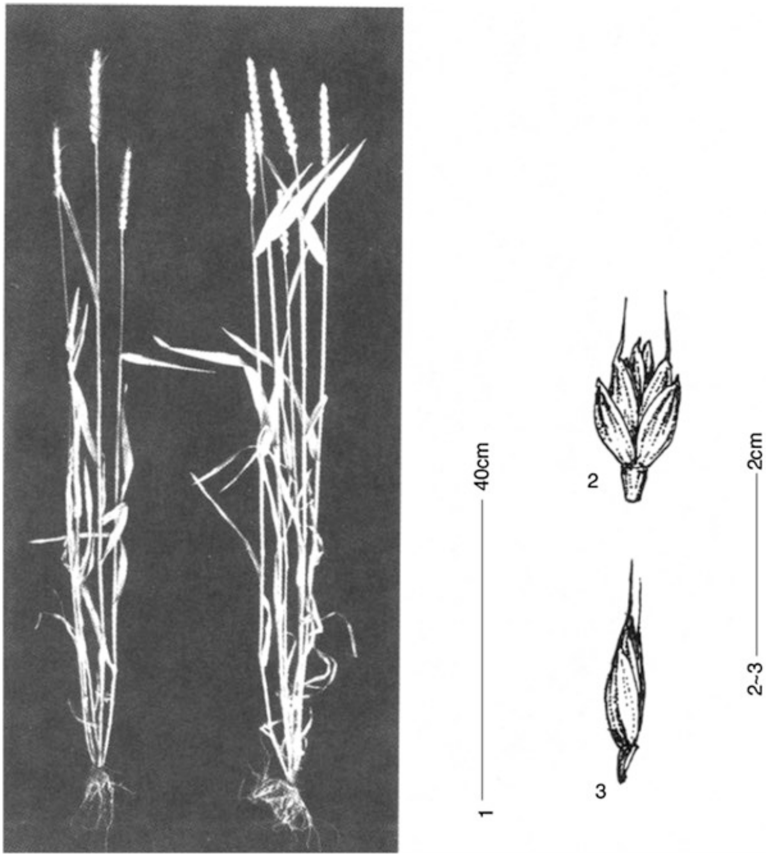

Fig. 8.18 *T. aestivum* L. concv. Tibetanum
1. Plant; 2. spikelet internode with the wedge type of disarticulation; 3. spikelet lateral view

(3) ***T. aestivum* L. concv. compactum** (Fig. 8.15-5)

Spikelet compact, average of more than 3–4 spikelets per centimeter on rachis. Spike short usually, oval, or oblong. It is a large group of ancient cultivars, widely cultivated throughout Europe in the Neolithic Age, common in the Eurasian landraces, seldom in Africa. As mentioned above, the compact-spike trait is controlled by the single gene C. In 1809, it was named as *T. compactum* Host.

(4) ***T. aestivum* L. concv. ramulostachye** (Fig. 8.15-7)

Branching spikes, a special genotype in common wheat, probably controlled by 3–4 branch genes br1, br2, br3, and br4, among which br4 gene can also increase spikelet number (Huang and Yen 1988). From the perspective of developmental genetics and morphology view, branching spikes or multiple spikelets are due to the long duration of the second developmental morphology stage. As a germplasm resource, this gene system has potential value for increasing spikelets, thus increasing grain number per spike and yield. However, its utilization in high-yield breeding is not successful at the current stage (Yen 1999). The landrace “Henanfushoumai” from Henan, China belongs to this group.

(5) ***T. aestivum*** **L. concv. macha** (Fig.. 8.15-3)

Culms hollow with thin wall, spike rachis with bristles, hulled, glume thick and tough with a conspicuous ridge from base to apex, spikelet setting 2 seeds. In 1932, it was named as *T. macha* Dekaprel et Nenabde.

(6) ***T. aestivum*** **L. concv. petropavlovskyi** (Fig. 8.16)

Highly similar to tetraploid *polonicum*. Springness. Glume long, leaf-like, with awns usually. Lemma with long awn or awnless. It is mainly distributed in Xinjiang, also found in Tibet. In the early 1950s, a number of materials were collected and identified as *polonicum* by China–the Soviet Union joint investigation. After cytological identification, it was identified as hexaploid wheat, containing genome AABBDD. In 1970, it was published in the Soviet Union as *T. petropavlovskyi* Udacz. et Migusch.

(7) ***T. aestivum*** **L. concv. spelta** (Fig. 8.15-1, 2)

Caryopsis hulled, spike with the barrel type of disarticulation. There are two distinct classes in the cultivar group. One is distributed in central and Western Asia, with primitive chromosome structure relative to its ancestor tetraploid (genome AABB) and diploid (genome DD) species. The other is distributed in European, cultivated before concv. compactum, which is a secondary hexaploid class with changed chromosome structure. The two characteristics, the barrel type of disarticulation and hulled, are controlled by the gene Q. It was once named as *T. spelta* L.

(8) ***T. aestivum*** **L. concv. vavilovii** (Fig. 8.15-8)

Hulled wheat with elongated rachilla internodes, founded in Armenia. Other traits are similar to concv. spelta. In 1933, it was named as *T. vavilovii* (Tum.) Jakubz. ex Zhukovsky.

(9) ***T. aestivum*** **L. concv. sphaerococcum** (Fig. 8.15-9)

Springness, dwarf, spikelets arranging compact, grain small and spherical, leaves short and upright. It is similar to *T. compactum* var. *globiforme*, prehistoric compact spike wheat. In 1921, it was named *T. sphaerococcum* Perc. by J. Percival.

(10) ***T. aestivum*** **L. concv. yunnanense** (Fig. 8.17)

Distributed in northwestern Yunnan in China. Round glumes, multiple florets, hulled caryopsis, tough rachis nodes usually. Under very dry conditions, spikelets show wedge type of disarticulation under a slight pressure. It was identified as a new subspecies by Jin Shanbao in the 1950s, named *T. aestivum* subsp. *yunnanense* King.

(11) ***T. aestivum*** **L. concv. tibetanum** (Fig. 8.18)

A weedy type with brittle spikelet, round glumes, multiple florets, hulled caryopsis, the wedge type of disarticulation. It grows mixed with other common wheat landraces. It was named as *T. aestivum* subsp. *tibetanum* Shao. by Shao Qiquan (1980).

(12) ***T. aestivum*** **L. concv. tripletum** (Fig. 8.15-6)

It is featured by each rachis with three spikelets. It is a special type, mixed with local common wheat landraces in Tibet. It is an example connecting *Hordeinae* with *Triticinae* in spike morphology.

T. aestivum is a cultivated species originated from the natural hybridization between *Triticum turgidum* and *T. tauschii*. No wild type has been found for this species. It may have originated from the common distribution regions of *T. turgidum* and *T. tauschii* var. *strangulata* in the southwestern coast of the Caspian Sea.

Sect Sitopsis (Jaub. et Spach) **Chennaveeraiah, 1960, Acta Horti. Gotob. 23:163**.

7. ***T. speltoides*** (Tausch) **Gren., 1857. in Mem. Soc. Enul. Daubs.** III**, 2: 434** (Fig. 8.19)

Synonyms: *Ae. speltoides* Tausch, 1837. Flora 20: 108–109;
Ae. aucheri Boiss., 1844, Diagn. Pl. Or., N. S. 1, 5: 74;
Agropyron ligusticum Savign., 1846. Atti Ott. Riun. Sci. Ital., Genova: 601–602;
Ae. ligustica (Ssvign.) Cosson, 1864. Bull. Soc. Bot. Fr. 11: 164;
Ae. macrura Jaub. et Spach, 1850. Illu. Pl. Or. 4: 21;
Sitopsis speltopides (Tausch) Á. Löve, 1984. Feddes Repert. 95: 491.

Annual or biennial. Plants 40–70 cm tall. Leaves linear, often with hairs, widthwise, and drooping growth. Spike linear, 6–18 (mostly 7–11) cm long, with 6–15 spikelets, rachis nodes curved slightly, often with the wedge type of disarticulation above vestigial spikelets. Spikelet with 4–6 florets, 8 florets seldom, upper 1–3 florets sterile. Glumes truncate, 1/3 shorter than lemma, oblique shoulder blunt. Apical lemma with long awn, lateral lemma with awn or awnless. Caryopsis hulled, laterally flat.

Cytological characteristics: 2n = 14, genome B^{sp} (= S), containing two pairs of satellite chromosomes.

var. aucheri (Boiss.), **Aschers., 1902. Magyer Bot. Lapok. 1: 11.**

Synonyms: *Ae. aucheri* Boiss. 1844. Diagn. Pl. Or., N. S. 1, 5: 74;
Ae. aucheri var. *polyathera* Boiss. 1884. Fl. Orient. 5: 67;
T. speltoides var. *polyathera* (Boiss) Aschere., 1902. Magyar Bot. Iapok 2: 11.

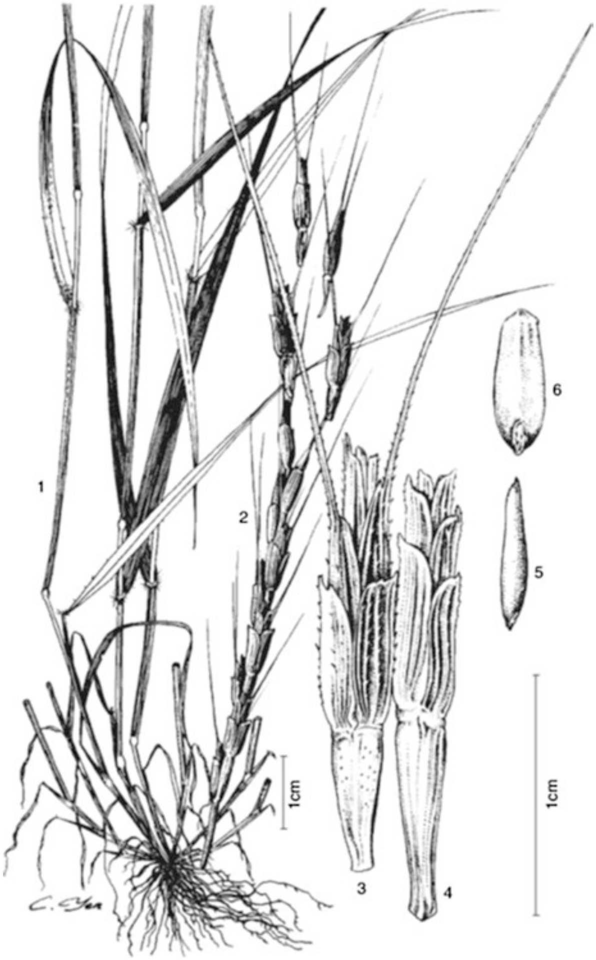

Fig. 8.19 *T. speltoides* (Tausch) Gren
1. Adult plant; 2. spikelets with the wedge type of disarticulation; 3. lateral spikelet with awn and the wedge type of disarticulation from *T. speltoides* var. *ligusticum*; 4. lateral spikelet with awnless and the wedge type of disarticulation from *T. speltoides* var. *aucheri*; 5. caryopsis lateral view; 6. caryopsis dorsal view

Morphological characteristics: Leaves with hairs or hairless. Spike relatively long (6–18 cm), lateral spikelet lemma without awn.

Distribution: The coastal plains of Israel, Jordan, Lebanon, Syria, northern Iraq, western Iran, southeastern and Western Turkey, the Anatolia Plateau, Greece, and southern Bulgaria. It grows on red calcareous soil, alluvial soil, open grasslands of sparse oaks, open land of summer drought shrub of Mediterranean.

var. ligusticum (Savign.) **Aschere., 1902. Magyar Bot. Lapok. 1: 12.**

Synonyms: *Agropyron ligusticum* Savign., 1846. Atti Ott. Riun. Sci. Ital., Genova: 601–602;
Ae. ligustica (Savign.) Cosson, 1864. Bull. Soc. Bot. Fr. 11: 164;
Ae. speltoides var. *ligustica* (Savign.) Fiori, 1907. Fl. Anal. Ital. 4, Appenl. 32.

Morphological characteristics: Leaves with hairs. Spike shorter (6–12 cm), lateral spikelet lemma with long awn.

Distribution: The coastal plains of Israel, Jordan, Lebanon, Syria, northern Iraq, western Iran, southeastern and Western Turkey, the Anatolia Plateau, Greece, and southern Bulgaria. It grows on red calcareous soil, alluvial soil, open grasslands of sparse oaks, open land of summer drought shrub of Mediterranean.

8. ***Triticum bicorne*** **Forsskal, 1775, Deser. Pl. Fl. Aegypt Arab. 1: 26.** (Fig. 8.20).

Synonyms: *Cr. aegyptiacum* Trin. ex Steud., 1840. Mon. ed, II, 1: 440;
Ae. bicornis (Forsskal) Jaub. et Spach, 1850. Illu. Pl. Orient. 4: 10;
Sitopsis bicornis (Forskal) Á. Löve, 1982. Biol. Zentralbl. 101: 206.

Morphological characteristics: Annual or biennial, plants 15–45 cm tall, tufted, tillers prostrate, culm knee bent upwardly after elongation, lower rachis nodes long, leaf position low. Spike linear, compact, spike 4–8 cm long, rachis internodes slightly bent, disarticulation above the spikelet, with the wedge type of disarticulation. Spikelets elliptic or oblong, longer than the adjacent rachis nodes, 3 florets, upper 1–2 sterile. Because of lower two florets well developed, the 3rd floret vestigial, the tip of the spikelet forming a bicorn shape, hence it is named as bicorne. Spikelets become smaller from the middle to the upper and lower ends. Glumes leathery, apex with two separated teeth. Navicular lemma with awn, lower lemma with short awn or awnless, upper lemma with long awn. Caryopsis hulled.

Cytological characteristics: $2n = 14$. Genome B^b ($= S^b$).

Distribution: Libya, Lower Egypt and Sinai Peninsula, southern Israel, southern Jordan, and northeastern Cyprus. It grows on sandy soil, open grasslands of short shrub, grassland, and desert steppe.

9. ***T. longissimum*** (Schweinf. et Muschl.) **Bowden, 1959. Can. J. Bot. 37: 666.** (Fig. 8.20)

Synonyms: *Ae. longissima* Schweinf. et Muschl., 1912. A Manual Fl. Egypt 1: 156;
Sitopsis longissima (Schweinf. et Muschl.) Á. Löve, 1984. Feddes Repert. 95: 492.

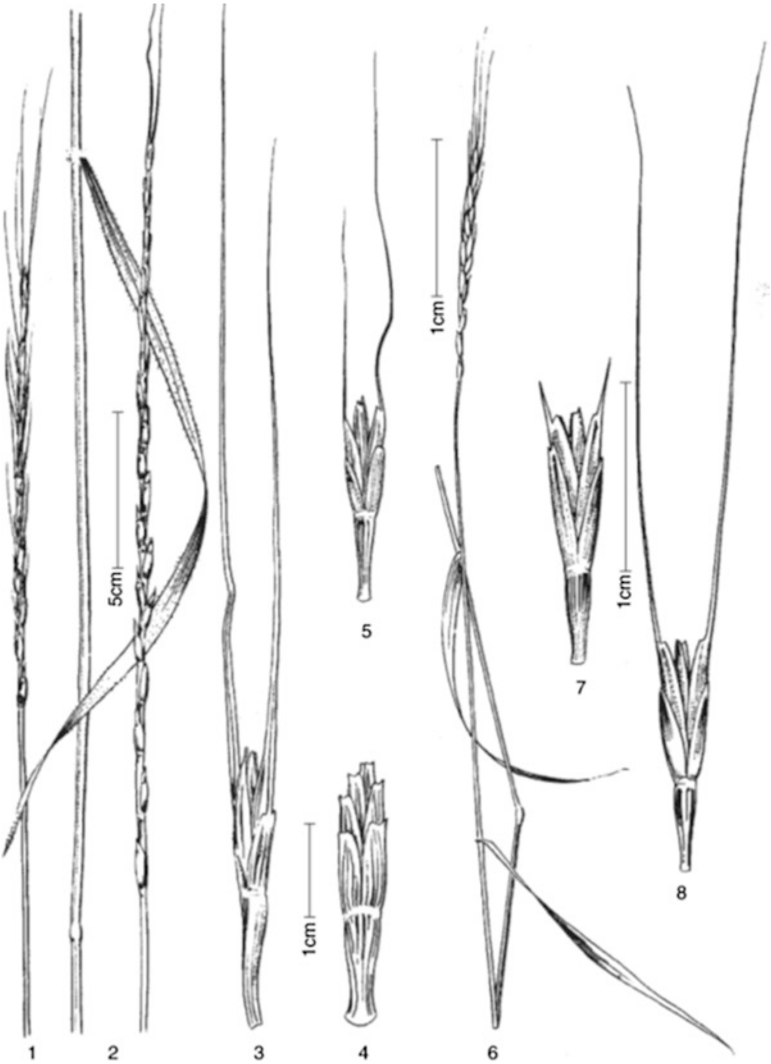

Fig. 8.20 *T. longissimum* (Schweinf. et Muschl.) Bowden, *T. longissimum* (Schweinf. Et Muschl.) Bowden var. *sharonense* (Eig) Yen et J. L. Yang, and *T. bicorne* Forskal
1. Awned spike of *T. longissimum* var. *sharonense*; 2. apically awned spike of *T. longissimum*; 3. apical spikelet of *T. longissimum*; 4. lateral spikelet of *T. longissimum*; 5. lateral spikelet of *T. longissimum* var. *sharonense*; 6. *T. bicorne*; 7. lateral spikelet of *T. bicorne*; 8. apical spikelet of *T. bicorne*

Morphological characteristics: Annual or biennial. Plants 40–110 cm tall. Prostrate at seedling stage, stem knee bent upwardly after elongation. Leaves linear. Spike long cylindrical, 8–15 spikelets, length of spikelet often shorter than rachis nodes (particularly the lower portion), spikelets closely attached to rachis internodes and gradually thinner and smaller from the middle and lower part to the top, spike tapering toward the apex, spike 10–20 cm long, spikelets with the wedge type of disarticulation at maturity except the basal portion at maturity. Spikelet with 3–5 florets. Glumes leathery, rough, usually with two teeth at apex, separated by membranous margins, upper spikelets with 3 teeth. Palea navicular, lateral spikelets awnless, apical palea formed long awn wide at lower part, both sides of base portion with denticulation. Caryopsis hulled.

Cytological characteristics: $2n = 14$. Genome B^l ($= S^l$).

Distribution: Lower Egypt and Sinai Peninsula, Israel, Jordan, coastal plain of southern Lebanon, Syria. It mainly grows in the sandy soil, grassland, or desert steppe.

var. *sharonense* (Fig) Y**en et J. L. Yang, stat. nov., according to *Ae. sharonensis* Eig, 1928. Notizbl. Bot. Mus. Dahlem 10: 489.** (Fig. 8.20)

Synonyms: *Ae. longissima* ssp. *artistata* Zhuk., 1928. Tr. Prikl. Bot. Genet. Sel. 18, 1: 543;
Ae. longissima ssp. *sharonensis* (Eig) Chennave eraian, 1962. Proc Summer School of Botany, Dajeeling: 46;
T. sharonense (Eig) Morris et Sears, 1967. in Quisenberry, Agron. Monogr. 13, Amer. Soc. Agron. (Madison, WI), ed. 1: 19;
Sitopsis sharonensis (Eig) Á Löve, 1984. Feddes Repert. 95: 492.

Morphological characteristics: Annual or biennial. Plants 40 ~ 100 cm tall. Prostrate at seedling stage, stem knee bent upwardly after elongation. Spike broad-linear, spike 7–13 cm long, bow-shaped rachis internodes forming curved rachis. Spikelets oblong oval, 14–22 spikelets per spike, spikelets gradually thinner and smaller from the middle to the both ends of the spike, spikelets with the wedge type of disarticulation. Spikelet with 3–5 florets, upper 1–3 florets sterile. Glumes leathery, glumes tip with two teeth, the inner teeth sometimes developed into a short awn. Navicular lemma, the apex with awn 4–6 cm long, wide and short teeth on both sides of the basal awn of lemma, lemma awn gradually longer from basal to apical spikelet, length of lemma awn of apical spikelet often longer than lemma. Caryopsis hulled.

Distribution: Israel and the coastal plains of Lebanon. It mainly grows in well-drained sandy soils and open shrub grassland.

10. ***T. searsii*** (Feldman et Kislev) **Kimber et Sears, 1978. in Heyne, Agron Monogr. 13, Amer Soc Agron.** (Madison, WI) **ed. 2: 154.** (Fig. 8.21)

Synonyms: *Ae. searsii* Feldman et Kislev, 1978. Israel J. Bot. 26: 191;
Ae. searsii Feldman et Kislev ex Hammer, 1980. in Feddes Repert. 91 (4): 191 (Index Kewensis XVII. note: revised author attribution unnecessary);

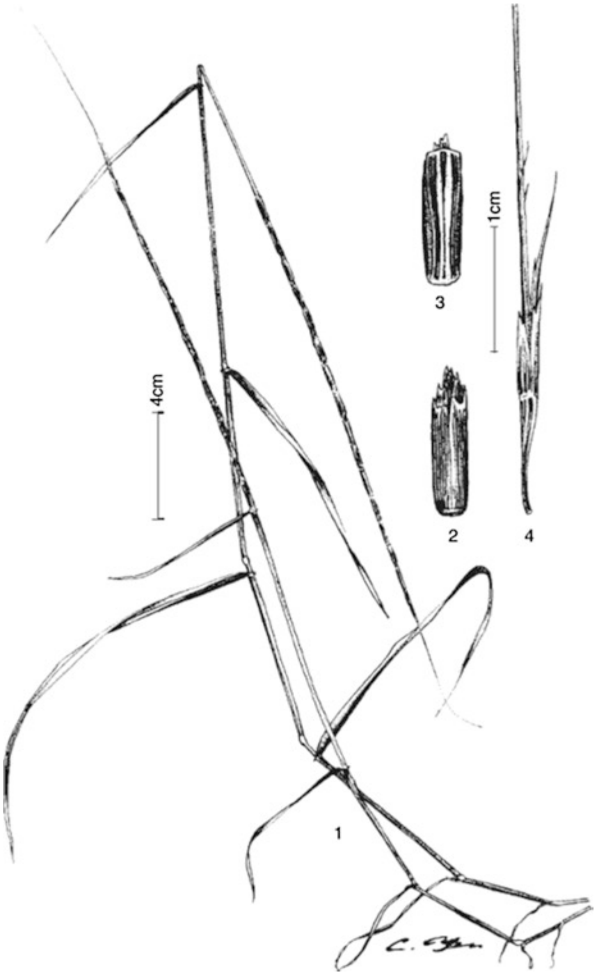

Fig. 8.21 *T. searsii* (Feldman et Kislev) Kimber et Sears
1. Adult plant; 2. lateral spikelet with the barrel type of disarticulation, dorsal view; 3. lateral spikelet with the barrel type of disarticulation, ventral view; 4. apical spikelet

Sitopsis searsii (Feldman et Kislev) Á. Löve, 1984.
Feddes Repert. 95: 492.

Morphological characteristics: Annual or biennial. Plants 20~50 cm tall. Prostrate at seedling stage, stem knee bent upwardly after elongation. Spike linear, 5–11 cm long, spike tapering toward the apex, 8–12 spikelets. Spikelet with 3 florets, upper florets sterile. Glume shorter than lemma, two teeth of apex separated by membranous margin. Lemma awnless, but one floret of apical spikelet with short awn and another floret with extremely long awn, equal or longer than spike length, the base of long awn accompanied with short and thin awns at both sides. Caryopsis naked at maturity.

Cytological characteristics: 2n = 14, Genome B^s (= S^s).

Distribution: Israel, Jordan, southeastern Lebanon, southwestern Syria. It grows in red calcareous soil and basalt soil, distributed in desert steppes, desert shrubs, and short shrubs.

Subgenus Aegilops (Hackel) **Yen et J. L. Yang, comb. et stat. nov. according to *Triticum* sect. *Aegilops* Hackel, 1887, in Engler et Prantl, Die naturlichen Pflanzenfamilien** II**: 80.**

Sect. *Vertebratae* Zhuk., 1928. Tr. Prikl. Bot. Genet. Sel. 18, 1: 464.

11. ***T. tauschii*** (Cosson) **Schmalh., 1897. Fl. Mittl. Sud. Rast. 2: 662.** (Figs. 8.22 and 8.23)

Synonyms: *Ae. tauschii* Cosson, 1849. Not. Pl. Rar. Nouv. 2: 667;
Ae. squarrosa auct. non L. 1753;
T. aegilops P. Beauv., 1812. Eas. Agrost 103, 146,180;
Patropyrum tauschii (cosson) Á. Löve, 1982. Biol. Zentralbl. 101: 206.

Morphological characteristics: Annual or biennial, springness or winterness. Culm slender, tillers many, without branch (lower branches seldom), erecting, plants 20–120 cm tall. Leaves linear, 10–20 cm long. Spike cylindrical, upper part of spike slightly thin, without sterile spikelets at lower part of spike usually, spikelets embedding into rachis internodes and equal to the length of rachis internodes (*var. typicum*); or the length of rachis internodes longer than that of the spikelet (*var. strangulatum*). Spikes with the barrel type of disarticulation at maturity, 5–13 spikelets per spike, 3–5 florets, upper 1–3 florets sterile. Glumes leathery, subquadrate shape, with equidistantly parallel veins, glume apex truncated, margin hypertrophy and slightly everted, awnless, with a small tooth, or toothless. Lower part of lemma membranous, naked upper part leathery, the apical margin thick, the upper part of the lemma with a ridge, ridge extending into an awn, the two sides with two-toothed bulge, or flatly truncated, the lower lemma with awn short, the upper spikelet lemma with awn long. Caryopsis flat, hulled.

Cytological characteristics: 2n = 14. Genome DD, one pair of chromosomes (5D) with satellites.

Distribution: Caucasus and Transcaucasia, Crimea, Turkey, northeastern Syria, Caspian Sea coast, Central Asia, Western Tianshan Mountains, Afghanistan, Pakistan, Kashmir, and Xinjing and the middle reaches of the Yellow River in China. It grows on calcareous soil, marl, loess, and alluvial sandy soil. It is distributed in degraded summer dry grassland of Mediterranean, shrub grassland, grassland, dry valley, farmland edge, roadside, or in the wheat field as weed in the middle reaches of the Yellow River, altitude 150 ~ 1400 m.

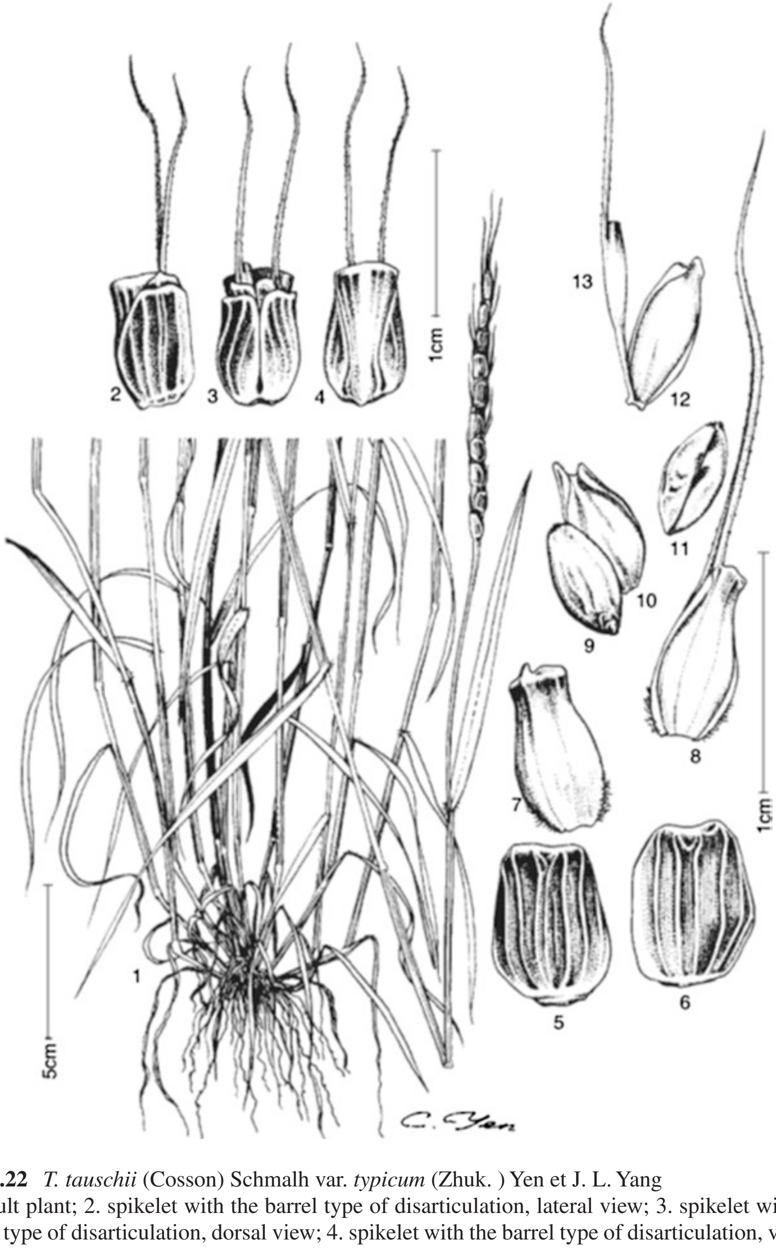

Fig. 8.22 *T. tauschii* (Cosson) Schmalh var. *typicum* (Zhuk.) Yen et J. L. Yang
1. Adult plant; 2. spikelet with the barrel type of disarticulation, lateral view; 3. spikelet with the barrel type of disarticulation, dorsal view; 4. spikelet with the barrel type of disarticulation, ventral view; 5. the first glume; 6. the second glume; 7. lemma of the first floret; 8. lemma of the second floret; 9. caryopsis, dorsal view; 10. palea; 11. caryopsis, ventral view; 12. the third floret; 13. the fourth floret

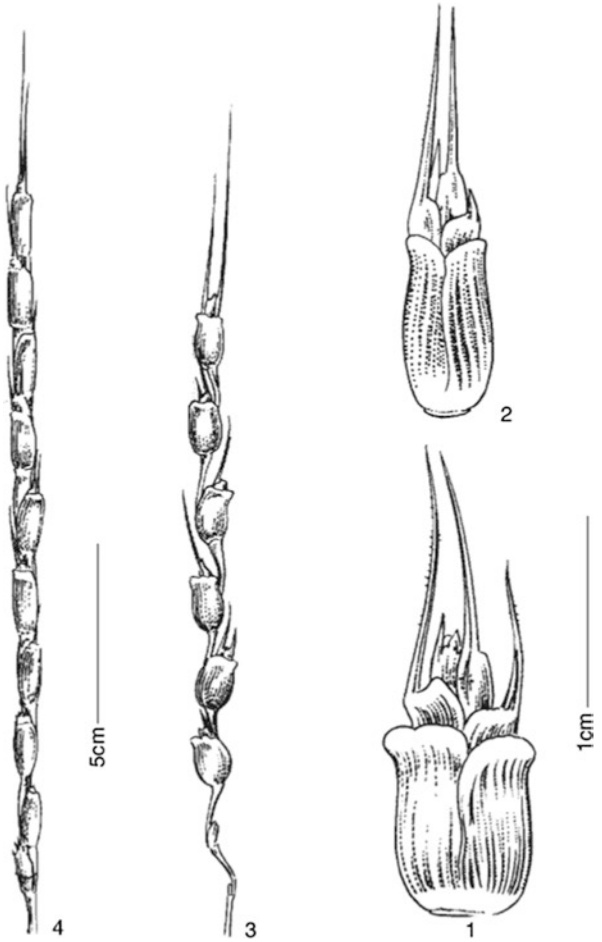

Fig. 8.23 *T. tauschii* (Cosson) Schmalh. var. *typicum* (Zhuk.) Yen et J. L. Yang and *T. tauschii* (Cosson) Schmslh. var. *strangulatum* (Eig) Kimber et Feldman
1. Spikelet of *T. tauschii* var. *strangulatum*; 2. spikelet of *T. tauschii* var. *typicum*; 3. spike of *T. tauschii* var. *strangulatum*, swollen spikelets; 4. spikelet embedded into rachis nodes, showing cylindrical shape for *T. tauschii* var. *typicum*

var. *typicum* (Zhuk.) **Yen et J. L. Yang comb. nov.** according to ***Ae. squarrosa* ssp. *typica* Zhuk., 1928. Tr. Prikl. Bot. Genet. Sel. 18: 549.**

Synonyms: *Ae. squarrosa* var. *meyeri* Griseb., 1853. in Ledeb. F. L. Ross. 4: 326;
Ae. squarrosa var. *eusquarrosa* Kimber et Feldman, 1987.
Wild Wheat: 66.

Morphological characteristics: Cylindrical spikes due to mutually embedding between spikelets and rachis internodes, and glume-tip without prominent valgus.

var. strangulatum (Eig) **Kimber et Feldman, 1987. Wild Wheat: 66.**

Synonym: *Ae. squarrosa* var. *strangulata* Eig, 1928. Bull. Soc. Bot. Geneve 2, 19: 328.

Morphological characteristics: Rachis internodes longer than nearly spherical spikelets, causing spikes monilifrom, glume-tip with prominent valgus.

Distribution: Caucasus, northwestern Iran. It grows on calcareous soil, marl, loess, and alluvial sandy soil. It is distributed in shrub grassland, grassland, dry valley, farmland edge, roadside, or in the wheat field as weed, altitude 150–1400 m.

12. ***T. plathyatherum*** (Jaub. et Spach) **Yen et J. L. Yang, comb. nov. according to *Ae. plathyathera* Juab. et Spach, 1850.** III. **Pl. Orient. 4: 17.** (Fig. 8.24)

Synonyms: *Ae. crassa* Boiss., 1846. Diagn. Pl. Orient. N. S. 1, 7: 129;
Gastropyrum crassum (Boiss.) Á. Löve, 1984. Feddes Repert. 95: 501.

Morphological characteristics: Annual or biennial. Tillers dense, culms 20–30 cm tall. Leaves linear, spike cylindrical, tapering toward the apex, stout, leaves 4–8 cm long. Length of rachis internodes as long as or slightly longer than spikelets length, the spikelets and rachis internodes mutually embedding, spikelet with the barrel type of disarticulation at maturity. 11–15 spikelets per spike, barrel type, spikelet with 3–5 florets, upper 1–3 florets sterile. Glume leathery, rectangle, densely covered with short hairs, mostly parallel veinlet, apex flatly truncated, often with two shallow teeth, seldom 1 or 3–4 teeth, seldom developed into a short awn. Naked upper part of lemma leathery, lower part of lemma covered by glumes membranous, ridge extending into an tooth or awn, awn with a tooth at the two sides, the upper lemma with broad leaf-like and long awn. Palea membranous. Caryopsis hulled.

Cytological characteristics: $2n = 28$. Genome D^cX^c.

Distribution: Transcaucasia, Turkestan, Pamir-Arai, Afghanistan, Iran, Iraq (Kurdistan and Mesopotamia), northeastern Syria, southeastern Turkey. It grows on calcareous soil, marl, loess, and alluvial sandy soil, rocky hillsides, and gravel terraces. It is distributed in degraded summer dry grassland of Mediterranean, Chinese juniper, shrub grassland, grassland, dry valley, farmland edge, roadside, altitude 200–900 m.

13. ***T. crassum*** (Boiss.) **Aitch. et Hemsl., 1888. Trans. Linn. Soc. London 11, 3: 127** (Fig. 8.25)

Synonyms: *Ae. crassa* Boiss., 1846. Diagn. Pl. Or. N. S. 1, 7: 129 ~130;
Gastropyrum glumiaristatum Á. Löve et mcguire, 1984,
Feddes Repert, 95: 502.

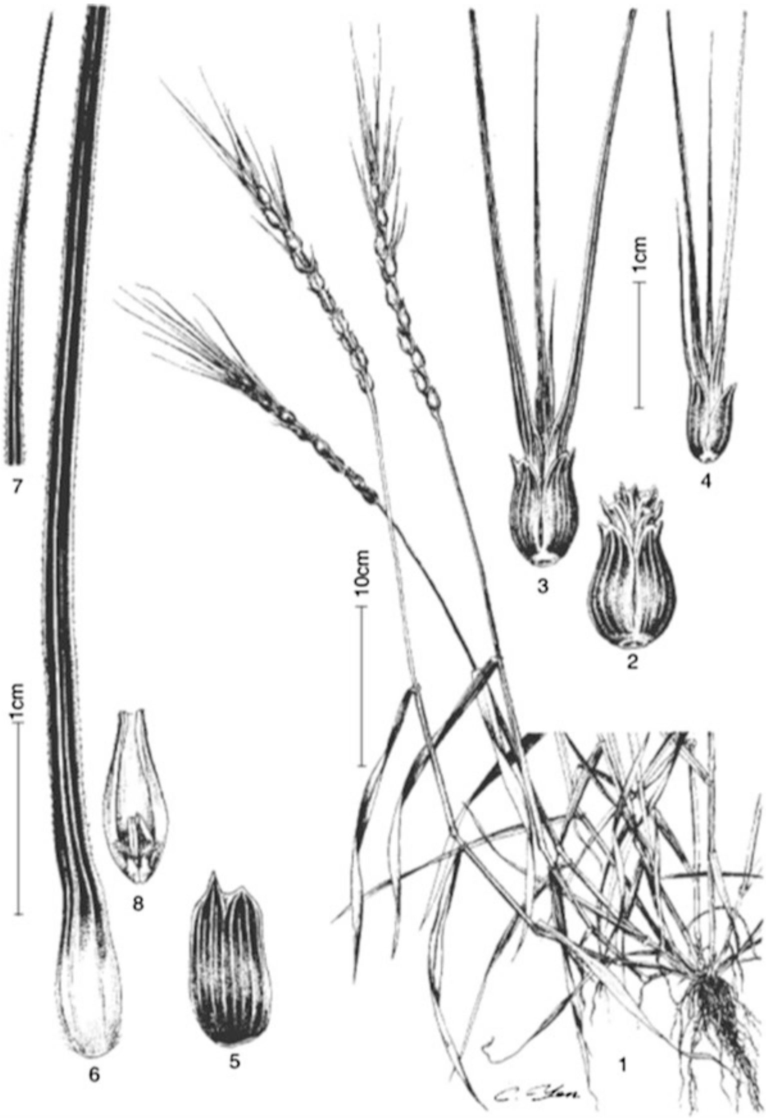

Fig. 8.24 *T. plathyatherum* (Jaub. et Spach) Yen et J. L. Yang
1. Adult plant; 2. awnless spikelet at lower spike with the barrel type of disarticulation, dorsal view; 3. spikelet with long awn at upper spike, dorsal view; 4. apical spikelet with long awn, the second glume also having long awn; 5. glumes with two teeth; 6. lemma, showing the lower part of leaf-like long awn; 7. the upper part of leaf-like long awn; 8. lodicule, stamens, feathery stigma, and palea

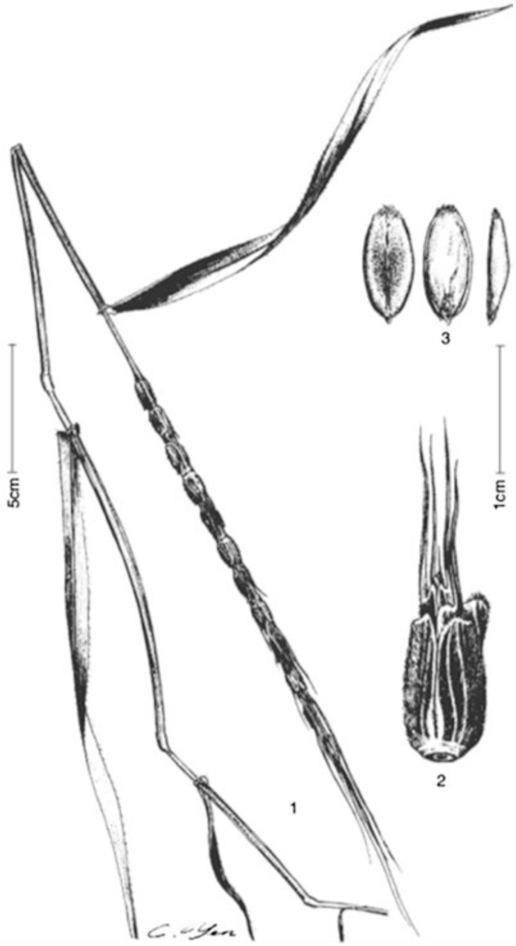

Fig. 8.25 *T. crassum* Aitch. et Hemsl
1. Adult plant; 2. spikelet with the barrel type of disarticulation, dorsal view; 3. caryopsis ventral view, dorsal view, and lateral view (left to right)

Morphological characteristics: Annual or biennial. Morphology very similar with *T. plathyatherum*, awn of apical spikelet long, narrow, thin, and not broad leaf-like shape.

Cytological characteristics: $2n = 42$. Genome: DD^cX^c.

Distribution: Transcaucasia, Turkestan, Pamir-Arai, Afghanistan, Iran, Iraq (Kurdistan and Mesopotamia), northeastern Syria, southeastern Turkey. It grows on calcareous soil, marl, loess, and alluvial sandy soil, rocky hillsides, and gravel terraces. It is distributed in degraded summer dry grassland of Mediterranean, Chinese juniper, shrub grassland, grassland, dry valley, farmland edge, roadside, altitude 200–900 m.

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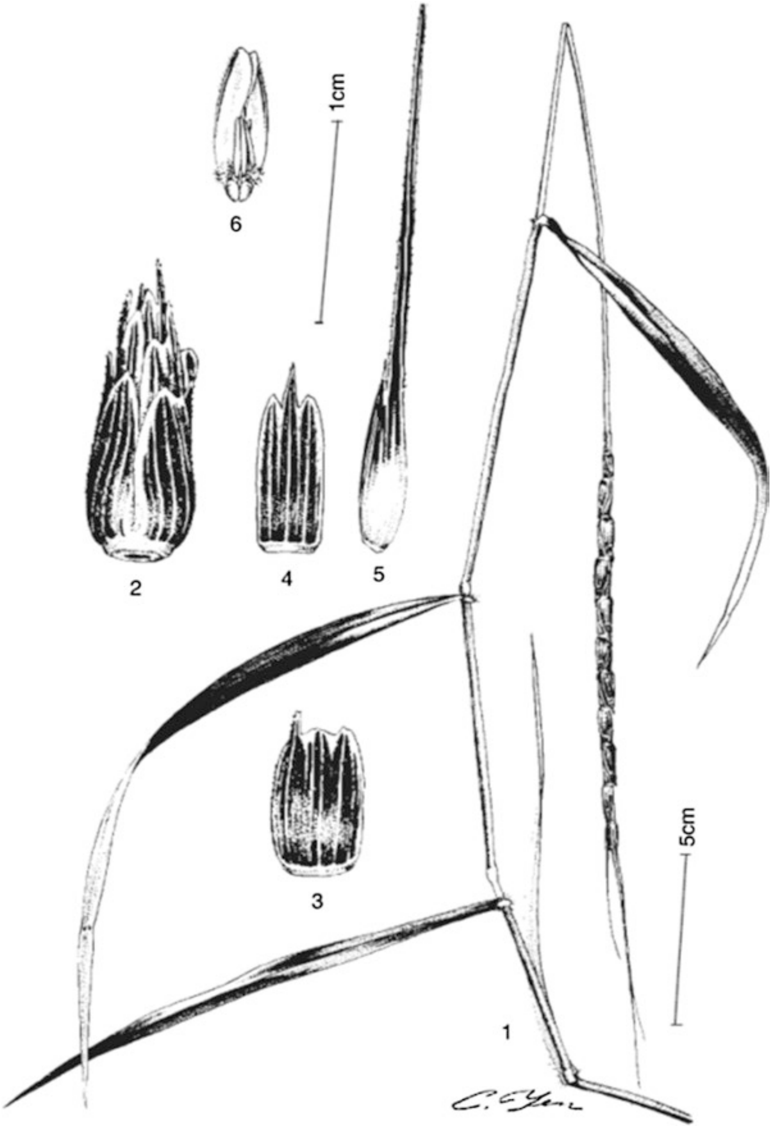

Fig. 8.26 *T. syriacum* Bowden
1. Adult plant; 2. lateral spikelet with the barrel type of disarticulation, dorsal view; 3. glume of the lateral spikelet; 4. glume of the apical spikelet; 5. long awn lemma of the apical spikelet; 6. ldicule, stamens, feathery stigma, and palea

14. ***T. syriacum*** **Bowden, 1966. Canad. J. Genet. Cytol. 8: 135.** (Fig. 8.26)

Synonyms: *Ae. crassa* Boiss. 1846. Diagn. Pl. Orient. N. S. 1, 7: 129;

Ae. crassa Boiss. var. *palaestina* Eig, 1928. Bull. Soc. Bot. Geneve II. 19: 326;
Ae. crassa Boiss. ssp. *vavilovii* Zhuk. 1928. Tr. prikl. Bot. Genet. Sel. 18: 554;
Ae. vavilovii (Zhuk.) Chennaveeraiah, 1960. Acta Horti Gotob. 23: 167;
Gastropyrum vavilovii (Zhuk.) Á. Löve, 1984. Feddes Repert. 95: 502.

Morphological characteristics: Annual or biennial. Tillers many, culms 20–30 cm tall. Leaves linear. Spike length 10–15cm, 5–10 spikelets, 0–3 vestigial basal spikelets. Length of rachis internodes as long as or slightly longer than length of adjacent spikelets, spikelets and rachis internodes mutually embedding with smooth cylindrical spike, spikelet with the barrel type of disarticulation at maturity. Spikelet cylindrical, two glumes slightly overlapped, containing 3–4 florets, basal two florets fertile. Glumes leathery, covered with shortly silvery white hairs, apex flat truncated, sometimes with 2 short-broad teeth bulge. Lemma leathery, longer than glume 1/4–1/3, with 2–3 teeth apex, one tooth of the central lemma of lateral spikelet developing into short awn, and lemma tip of apical spikelet forming a wide-stout long awn, up to 5–8 cm long, and two sides with 2 small teeth. Palea membranous, with 2 ridges. Caryopsis hulled.

Cytological characteristics: 2n = 42. $D^cX^cS^s$ genome.

Distribution area: Egypt (Sinai), southeastern Israel, Lebanon, Jordan, Syria. It grows on calcareous soil, calcic soil, alluvial sandy soil, rocky hillsides and gravel terraces. It is distributed in the Mediterranean summer drought grassland, also located in the Sinai seaside sandy soil plains, eastern Syria and Jordan semi-desert, altitude 50–1100 m.

15. ***T. ventricosum*** (Tausch) **Cess., Pass. et Gib., 1869. Fl. Ital. 4: 86.** (Fig. 8.27)

Synonyms: *Ae. squarrosa* L., 1753. Sp. Pl. 1051;
Ae. ventricosa Tausch, 1837. Flora 20: 108;
Ae. fragilis Parlat., 1869. Fl. Ital. 1, 4: 87;
Ae. subulata Pomel, 1874. Nouv. mat. Fl. Atl.: 388;
Gastropyrum ventricosum (Tausch) Á. Löve, 1982. Biol. Zentralbl. 101: 208.

Morphological characteristics: Annual or biennial. Many tillers, culms stout, plants 20–30 cm tall. Leaves linear, usually hairless, seldom hair. Spike slender, spike 4–6 cm long, well-developed spike up to 12 cm, 5–10 spikelets, rachis internodes longer than spikelet length, the lower part of internodes embedding in spikelet, middle of the spikelet swollen bottle-shape, causing whole spike moniliform, gradually tapering toward the apex, usually spikelet with the barrel type of disarticulation at maturity, sometimes the whole spike umbrella-like abscission at the base node. The bottle-shaped spikelet with 4–5 florets, the upper 1–3 florets sterile,

Fig. 8.27 *T. ventricosum* (Tausch) Cess, Pass. et Gib
1. Adult plant; 2. spikelet with the barrel type of disarticulation, dorsal view; 3. lemma; 4. caryopsis; 5. palea

the upper part of two glumes overlapped, the middle and lower parts of glumes swollen and bulge outside forming ovoid-shape. Glumes leathery, with mostly parallel veinlets, except densely short spiny veins, glumes smooth and glabrous, upper parts of glume with inconspicuous ridge, ridge extending into a short spiny awn inclined extension outward, both sides of awn forming two dentate bulges. Lower parts of lemma covered by glumes membranous, upper parts of lemma outside glumes leathery, the upper parts with inconspicuous ridge extending into a long awn, the transverse section of the awn triangular, awn length of the upper spikelet

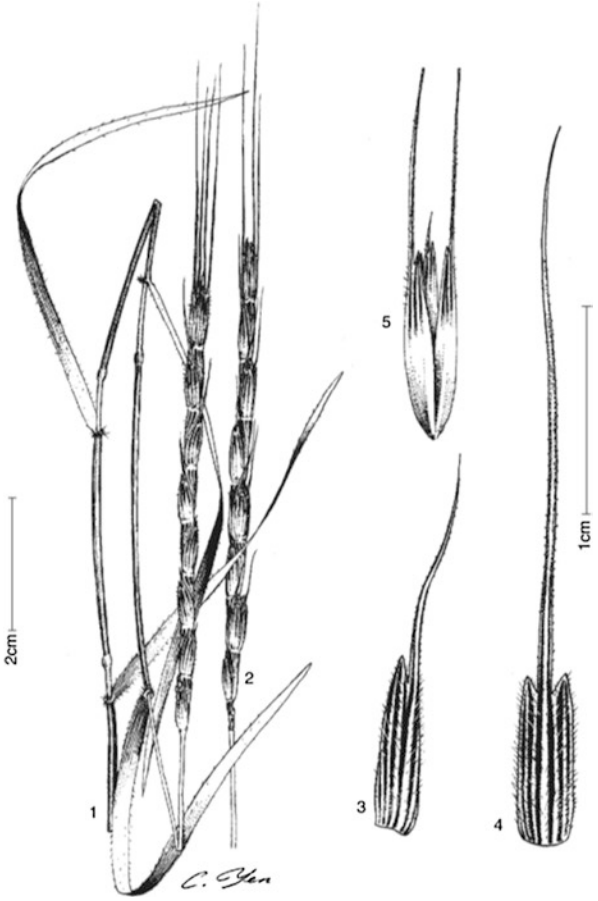

Fig. 8.28 *T. cylindricum* (Host) Cessati, Passer et Gibelli
1. Adult plant; 2. spike; 3. glume of lateral spikelet; 4. glume of the apical spikelet; 5. the first, second, and third florets, showing lemma

longer than that of the lower spikelet, two sides of the awn with two teeth, and the inner tooth sometimes undeveloped. Palea membranous. Caryopsis hulled.

Cytological characteristics: 2n = 28. DN genome.

Distribution: Portugal, Spain, southern France, Italy, Egypt Alexandria area, Libya, Tunisia, Algeria, Morocco. It grows in red calcareous soil, black calcareous soil, and light sandy soil. It is distributed in hard-leaved forest gap and forest edge of Mediterranean, summer dry grassland, shrub grassland, farmland edge, and roadside.

16. ***T. cylindricum*** (Host) **Cesati, Passer. et Gibelli 1869. Comp. Fl. Ital. 1, 4: 86** (Fig. 8.28)

Synonym: *Ae. cylindrica* Host, 1802. Gram. Austr. 2: 6;
Ae. caudata auct. non L.;
Cylindropyrum cylindricum (Host) Á. Löve, 1982.
Biol. Zemtralbl. 101: 207.

Morphological characteristics: Annual or biennial. Prostrate tillers, culms knee bent upwardly after elongation, plants 20–40 cm tall. Leaves linear, hairless or hair. Spike long cylindrical, 8–10 spikelets, gradually small and tapering toward the apex, generally vestigial basal 1–2 spikelets, spike length as long as length of adjacent rachis internode, spikelet with the barrel type of disarticulation or whole spike umbrella-like abscission at maturity. Spikelets cylindrical, glume with numerous parallel veinlet, veins with short bristles, glume apex with an awn and a tooth, glume awn length of the upper spikelet longer than that of the lower spikelet. Upper parts of lemma leathery, apical awn side with one or two teeth, lemma awn length longer than glume awn, and central apex of palea from apical spikelets forming long awn broad at the base, two sides with a small tooth. Palea membranous, double ridges. caryopsis hulled.

Cytological characteristics: 2n = 28. Genome CD.

Distribution: Southern France, Italy, Yugoslavia, Hungary, Romania, Bulgaria, Albania, Greece, Southern Ukraine, Crimea, Caucasus, Transcaucasia, Iran, northern Iraq, Turkey, Syria, Afghanistan, Turkmenistan, southwestern Kazakhstan; it has been introduced as weedy distributed in the field in the UK, Sweden, northwestern Russia, and the Midwest of USA; it has native natural communities in southern Europe, the Middle East, and Central Asia. It grows in in oak savanna steppe, shrub steppe, shrub gap, farmland edge, and roadside, and adapt to a variety of soil.

17. ***T. juvenale* Thell.**, 1907. Feddes Repert. 3: 281 (Figs. 8.29 and 8.30)

Synonyms: *Ae. turcomanica* Roshev., 1928. Tr Prikl. Bot. Genet. Sel.
18: 413, tab. 1;
Ae. juvenalis (Thell.) Eig, 1929. Feddes Repert. Beil. 55: 93;
Aegilonarum juvenale (Thell.) Á. Löve. 1982, Biol. Zentralbl.
101: 208.

Morphological characteristics: Annual or biennial. Prostrate tillers at seedling stage, stem knee bent upward after elongation, plants 20–40 cm tall, leaves linear. Spike lanceolate, 4–8 cm long, containing 6–9 spikelets (usually 7 spikelets), vestigial basal 1–2 spikelets usually, developed spikelets larger at lower parts of spike and smaller at upper parts of spike forming acuminate shape, lower spikelet length longer than that of the adjacent rachis internode, upper spikelet length equal to or slightly shorter than that of the adjacent rachis internode, spike umbrella-like abscission at maturity. Spikelets lanceolate. Glumes oval, leathery, hairy, apex flat trun-

Fig. 8.29 *T. juvenale* Thell
1. Adult leaves, culm, spike; 2. spikelet dorsal view (upper) and ventral view (lower); 3. lemma of the first floret; 4. lodicule, stamen, feathery stigma, and palea of the first floret; 5. the second, third, fourth, and fifth florets

cated, with 1–4 (usually 3) short awns or teeth, apical spikelet glume with 3 awns, or 1 awn and 2 teeth, or 3 teeth. Lemma awn longer than that of glume about 1/3, leathery, parts outside the glume with hairs, usually glume apex with 1 awn 2 side tooth, or 3 teeth seldom, lemma awn stronger than glume awn. Palea membranous, double ridges. caryopsis hulled.

Cytological characteristics: 2n = 42. Genome: D^cX^cU.

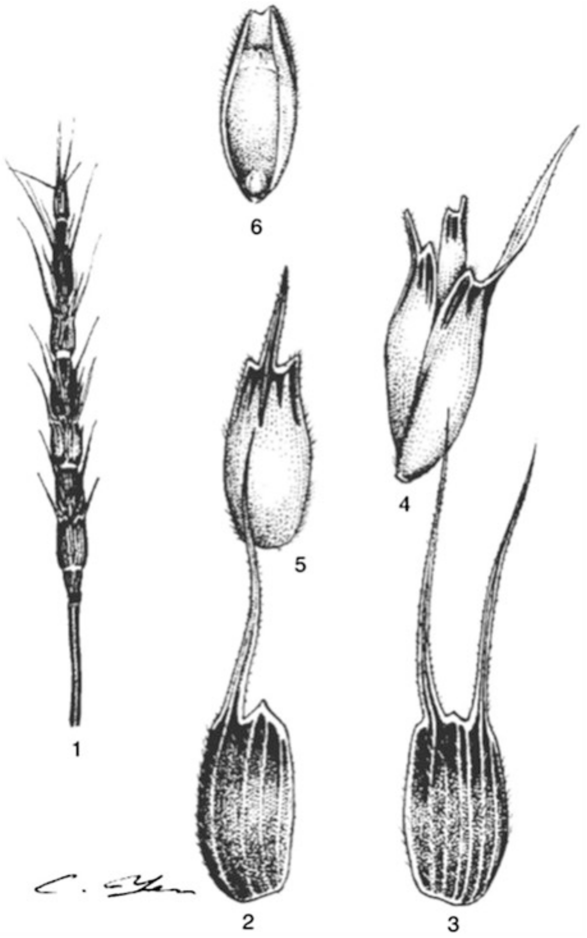

Fig. 8.30 *T. Juvenale* Thell. f. *aristatum* Yen et J. L. Yang
1. Spike; 2. the first glume; 3. the second glume; 4. the second, third, and fourth floret; 5. lemma of the first floret; 6. caryopsis and palea

Distribution area: Turkmenistan, Iran, Mesopotamia, northeastern Syria. It grows in gray calcareous soil, alluvial soil, and gravel slit. It is distributed on the edge of grassland and agricultural land. It also grows as weeds in central Asia and southern France. Type specimen was collected from Port Juvenal in southern France, hence its name.

sect. Orrhopygium (Á. Löve) **Yen et J. L. Yang, Comb. et Stat. Nov.** ***Orrhopygium*** **Á. Löve, 1982. Biol. Zentralbl. 101: 206**

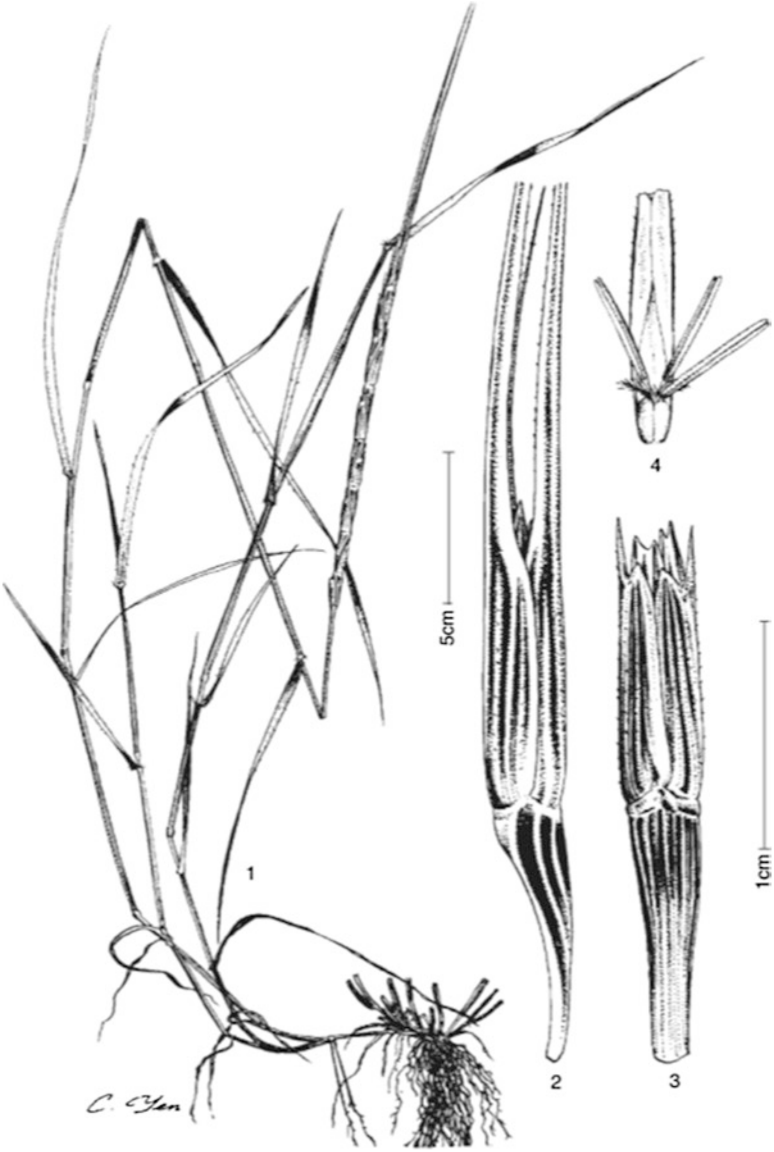

Fig. 8.31 *T. caudatum* (L.) Pers
1. Adult plant; 2. apical spikelet; 3. lateral spikelet, dorsal view; 4. lodicule, stamens, feathery stigma, and palea

18. ***T. caudatum*** (L.) **Godros et Gren., 1856. in Gren. et Godron, Fl. Fr. 3: 603** (Fig. 8.31)

Synonyms: *Ae. caudata* L. 1753. Sp. Pl.: 1051;
Ae. cylindrica Smith, 1806. Fl. Graec. Prodr. 1: 72, non Host, 1802;
T. dichasians (Zhuk.) Bowden, 1959. Can. J. Bot. 37: 667;
T. markgrafii Greuter, 1967. Boissiera 13: 172;
Ae. dichasians (Zhuk.) Humphries, 1970. Bot. J. Linn. Soc. 78: 236;
Ae. markgrafii (Greuter) Hammer, 1980. Feddes Repert. 91: 232;
Orrhopyrum caudatum (L.) Á. Löve. 1982. Biol. Zentralbl. 101: 206.

Morphological characteristics: Annual or biennial. Culms erect, plant 20–40 cm tall. Leaves linear, hairy. Spike thin cylindrical, upper parts of two glumes mutually overlapped, spike 6–8 cm long, with 4–8 spikelets, usually two vestigial basal spikelets, spike umbrella-like abscission at maturity. Spike cylindrical, nearly equal to the length of adjacent rachis internodes, 3–4 florets, upper 1–2 florets sterile. Glume rough, tip with a sharp tooth and a thin awn, apical spikelet glume tapering gradually forming long tail awn broad at base. Lemma covered by glume membranous, and a small part outside glume leathery, lemma tip with 2–3 teeth, the sharp teeth of the apical spikelet developing into small short awn. Palea membranous with two ridges. Caryopsis hulled.

Cytological characteristics: 2n = 14. Genome C.

Distribution: Southern Yugoslavia, southern Bulgaria, Greece, Turkey, Cyprus, Lebanon, Syria, northern Iraq, Iran, and Afghanistan. It grows in red calcareous soil, gray calcareous steppe, and other kinds of soil. It is distributed in oak forest land and forest edge, summer dry grassland, shrub grassland, cultivated land edge and roadside.

sect. Comopyrum (Jaub. et Spach) **Zhuk., 1928. Tr. Prikl. Bot. Genet. Sel. 18,1: 465.**

19. ***T. comosum*** (Sibth. et Smith) **Richter. 1890, Fl. Eur. 1: 128.** (Fig. 8.32)

Synonyms: *Ae. comosa* Sibth. et Smith, 1808. Fl. Greca Prodr.1: 72;
Comopyrum comosum (Sibth. et Smith) Á. Löve, 1982.
Biol. Zentralbl. 101: 207.

Morphological characteristics: Annual or biennial. Culms slender, plant 15–30 cm tall. Leaves narrow linear, leaf sheaths and leaves hairy. Spike slender cylindrical, lanceolate, or ovate-oblong, spike 2–7 cm long, with 4–5 spikelets, undeveloped basal 1 (2 seldom) spikelet vestigial, rachis internodes usually longer than adjacent spikelet length, spike umbrella-like abscission at maturity. The laterally fertile spikelet elongated bottle-shaped, with 3–4 florets, apical 1–2 florets sterile. Glumes rough or hairy, glume apex with 2 teeth, outside the tooth broad, the inner tooth slender or forming short awn, glume apex of apical spikelet with 3–9 long awns, 1 awn seldom, a broad and large central awn, lateral awns narrow, each awns dispersed open to the outside. Parts of lemma covered by glume membranous,

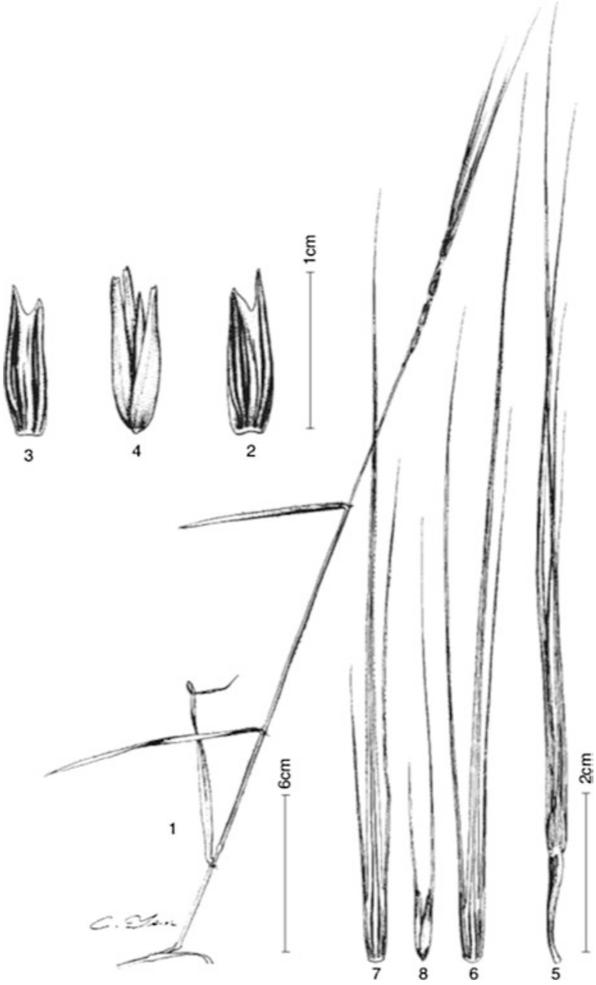

Fig. 8.32 *T. comosum* (Sibth. et Smith) K. Richter
1. Adult plant; 2. the first glume of laterally fertile spikelet; 3. the second glume of laterally fertile spikelet; 4. the first, second, and third floret; 5. apical spikelet; 6. the first glume of apical spikelet; 7. the second glume of apical spikelet; 8. the first and second florets of apical spikelet

exposed parts of lemma leathery, seldom with awn. Palea membranous, double ridges. Caryopsis hulled.

Cytological characteristics: 2n = 14. Genome M.

Distribution: The Aegean Islands of Greece, western Turkey. It grows in red calcareous soil. It is distributed in the Mediterranean evergreen oak forest edge and open space, summer dry grassland, shrub grassland, pasture and farmland edge, and roadside.

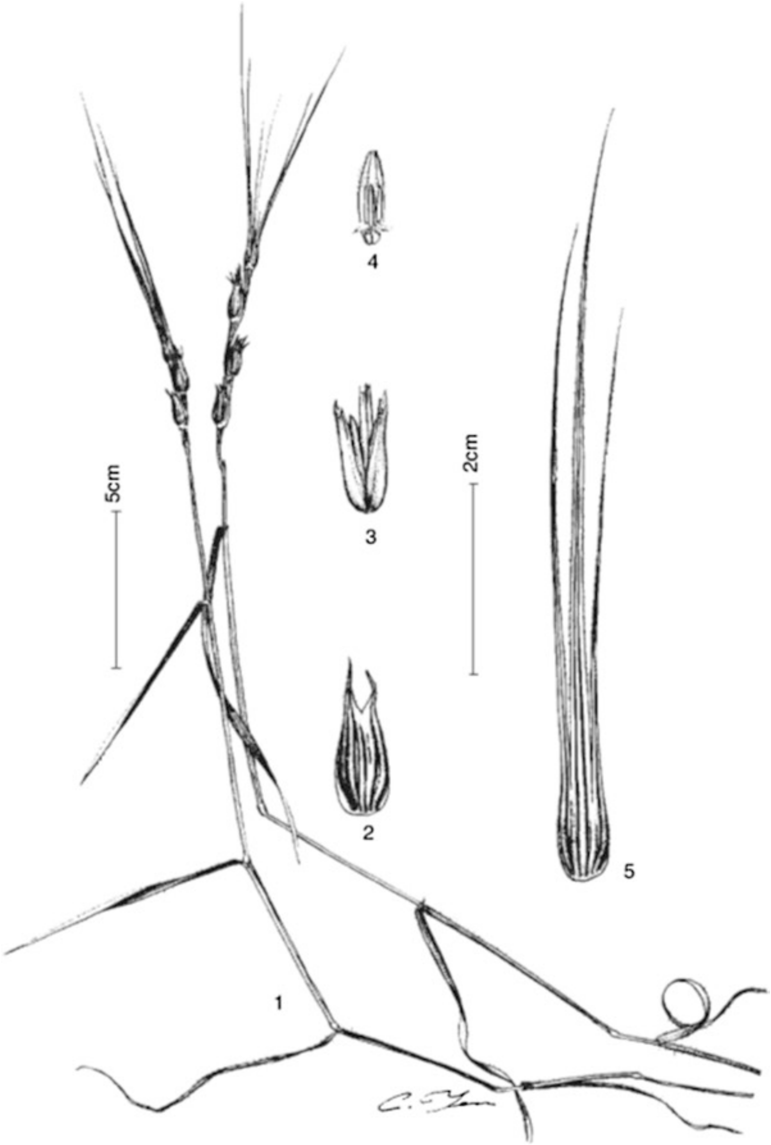

Fig. 8.33 *T. comosum* (Sibth. et Smith) K. Richter var. *heldreichii*
1. Adult plant; 2. glume of lateral spikelet; 3. the first, second, third, and fourth floret of lateral spikelet; 4. lodicule, stamens, feathery stigma, and palea; 5. glume of apical spikelet

var. heldreichii (Holzm ex Nyman) **Yen et J. L. Yang comb. Nov. According to A*e. heldreichii* Holzm ex Nyman, 1889. Consp. Fl. Eur. Suppl. 342.** (Fig. 8.33)

sect. Uniaristaopyrum Chennaveeraiah, 1960. Acta Horti Gotob. 23: 161.

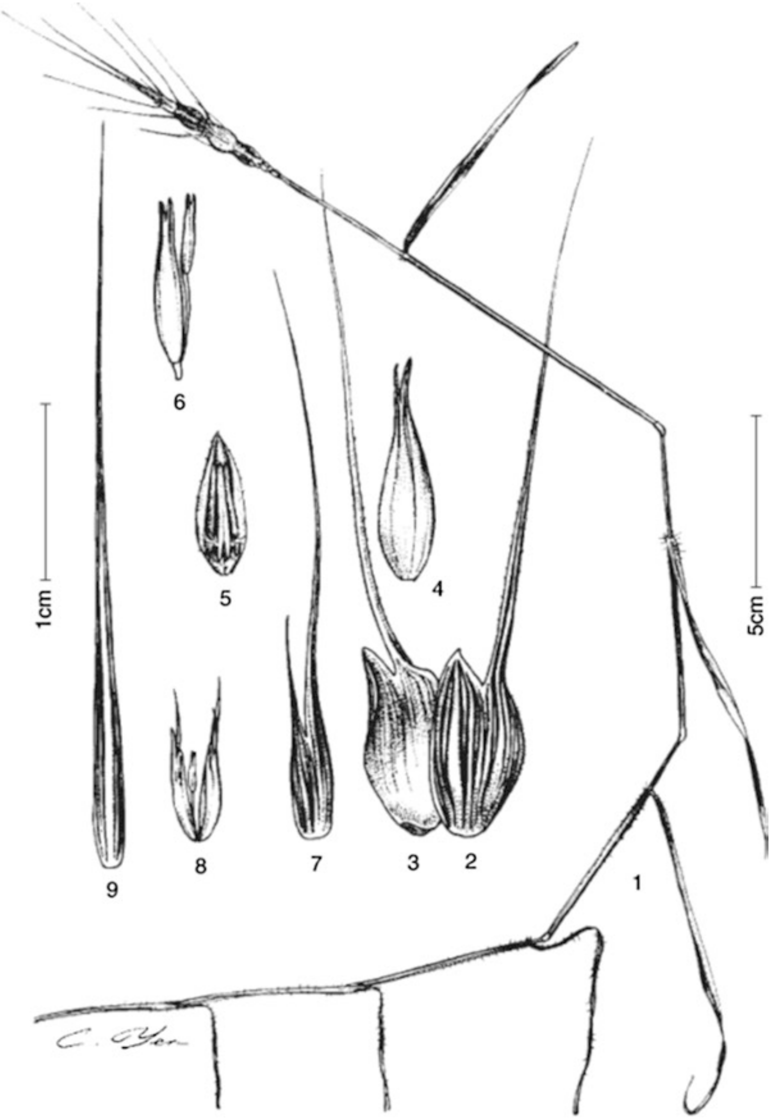

Fig. 8.34 *T. uniaristatum* (Vis.) K. Richter
1. Adult plant; 2. the first glume of fertile lateral spikelet; 3. the second glume of fertile lateral spikelet; 4. lemma of fertile lateral spikelet; 5. lodicule, stamens, feathery stigma, and palea; 6. the second and third florets; 7. the first glume of apical spikelet; 8. florets of apical spikelet; 9. the second glume of apical spikelet

20. ***T. uniaristatum*** (Vis.) **K. Richter, 1890. Fl. Eur. 1: 128.** (Fig. 8.34)

Synonyms: *Ae. uniaristata* Vis., 1852. Fl. Dalm. 3: 345;
Ae. notarisii Clementi, 1855. Sert. Or. : 99;

T. variabile Markgraf, 1932. Feddes Repert. Beih. 33: 225,
non *Ae. variabilis* Eig, 929;
Chennapyrum uniaristatum (Vis.) Á. Löve, 1982. Biol.
Zentralbl. 101: 207.

Morphological characteristics: Annual or biennial. Prostrate tillers, stem knee bent upward after elongation, culms 10–30 cm tall. Leaves linear, with hairs usually. Upper parts of leaf sheath with hairs usually. Spikes short and small, generally with 5–7 spikelets, basal spikelets 2–4 undeveloped, apical spikelet sterile usually, only 2–3 spikelets of middle parts producing seeds, small both ends of spike, lanceolate or broadly lanceolate, spike 1.5–3, 5 cm long, spike umbrella-like abscission at maturity. Laterally fertile spikelets ovoid, longer than adjacent rachis internodes, not adherent to each other. Glumes leathery, mostly parallel veins with densely short bristle, glume tip with a long awn (broad at base) and a triangular wide-short tooth. Glume tip of apical spikelet forming a broad-flat long awn, base of awn with a small tooth sometimes. Awn central vein conspicuously straight extending to the lower parts of glume, but not ridged. Lemma tip of the lateral fertile spikelets of the middle spike forming two small teeth, sometimes extending into small short awns, lemma of apical spikelet with a small short awn and 1–2 teeth. Palea membranous, double ridges. Caryopsis hulled.

Cytological characteristics: 2n = 14. Genome: N.

Distribution: Yugoslavia, Albania, Greece, northwestern Turkey. It grows in red calcareous soil. It is distributed in the Mediterranean evergreen oak forest edge and open space, summer dry grassland, shrub grassland, pasture and farmland edge, and roadside.

Sect. Polyoides Zhuk., 1928. Tr. Prikl. Bot. Genet. Sel. 18,1: 465.

21. ***T. umbellulatum*** (Zhuk.) **Bowden, 1959. Canad. J. Bot. 37: 666.** (Fig. 8.35)

Synonyms: *Ae. umbellulata* Zhuk., 1928. Tr. Prikl. Bot. Genet. Sel. 18, 1: 483;
Ae. ovata L. var. anatolica Eig, 1928. Bull. Soc. Bot.
Geneve ser. 2,19;
Kiharapyrum umbellulatum (Zhuk.) Á. Löve, 1982. Biol.
Zentralbl. 101: 207.

Morphological characteristics: Annual or biennial. Plants 10–30 cm tall. Leaves linear, 2–5 cm long, with dense or sparse hairs. Spike lanceolate or oval, 2.5–4 cm long, usually coarse and hairless, basal spikelets sterile. Developed spikelets 4–5, 3 or 6 seldom, upper 1–3 spikelets slight and sterile, umbrella-like fallen off at maturity; mid-fertile spikelets oval, usually with 4 florets, upper 2 florets sterile. Glume leathery, the middle part of glume of the fertile spikelet swollen and protruded outward, the upper parts of glume flat, with 4–5 slender awns, 3 or 6 awns seldom, the middle parts of glume of the sterile upper spikelet not swollen, and the upper parts

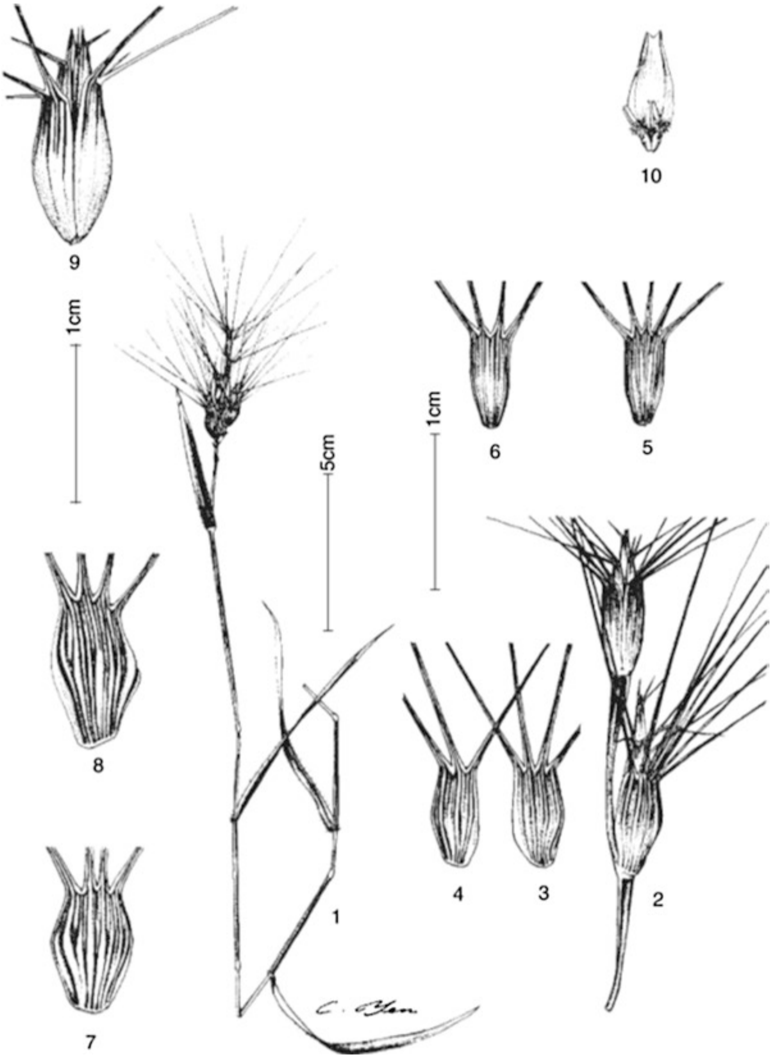

Fig. 8.35 *T. umbellulatum* (Zhuk.) Bowden
1. Adult plant; 2. sterile apical spikelet; 3–6. the glumes of sterile apical spikelets; 7. the first glume of fertile lateral spikelet; 8. the second glume of fertile lateral spikelet; 9. the first, second, third, and fourth floret of fertile lateral spikelet; 10. lodicule, stamens, feathery stigma, and palea

with 3–5 awns. Lower parts of lemma membranous, upper parts of lemma outside the glume leathery, with thin and short 1–3 glume-like awns. All the awns of glume and lemma dispersed flat outward with umbrella shape. Palea membranous, two ridges. Caryopsis naked.

Cytological characteristics: 2n = 14. Genome U.

Distribution: Greece, Turkey, Syria, northern Iraq, western and northern Iran, Transcaucasia, and Caucasus. It grows on red calcareous soil, gray calcareous grassland, basalt, and alluvial soil. It is distributed in the Mediterranean evergreen oak forest land and edge, summer dry grassland, shrub grassland, grassland, pasture and farmland edge, and roadside.

22. ***T. ovatum*** (L.) **Raspail, 1825. Ann. Sci. Nat. Ser. 1, 5: 435.**

Synonyms: *Ae. ovata* L., 1753. Sp. Pl. 1050;
Ae. geniculata Roth, 1787. Bot. Abhandl. Beobacht.: 45;
Ae. neglecta Requien ex Bertol., 1834. Fl. Ital. 1: 787;
Ae. brachyathera Pomel, 1844. Nouv. Mat. Fl. Atl.: 474;
Ae. lorentii Hochst., 1845. Flora. 28: 25;
Ae. vagans Jord. et Fourr., 1868. Brev. Pl. Nov. 2: 130;
Ae. macrochaeta Shuttlew. et Huet, 1869. Bull. Soc. Bot. Fr. 16: 384;
T. macrochaetum (Shuttlew. et Huet) K. Richter, 1890. Pl. Eur. 1: 128;
T. lorentii (Hochst.) Zeven, 1973. Taxon 22: 328.

var. vulgare (Cosson et Dur.) **Briq., 1910. Prodr. Fl. Corse 1: 190.** (Fig. 8.36)

Synonyms: *Ae. ovata* ssp. *euovata* var. *genuina* Griseb., 1844. Spicil. Fl. rum. Bithy. 2: 425;
Ae. ovata var. *vulgare* Coss. et Dur., 1864. Bull. Soc. Bot. France 11: 163;
T. ovatum ssp. *eu-ovatum* Aschers. et Graebn., 1901. Syn. Mitterleur Fl. 6: 705;
Ae. ovata ssp. *euovata* var. *vulgare* Eig, 1929. Repert. Sp. Nov. Feddes Beih. 55: 144, pl. 15a;
Ae. ovata ssp. *euovata* var. *africana* Eig, 1929. Repert. Sp. Nov. Feddes Beih. 55: 144;
Ae. ovata ssp. *euovata* var. *eventricosa* Eig, 1929. Repert. Sp. Nov. Feddes Beih. 55: 144, pl. 15a;
Ae. ovata ssp. *euovata* var. *hirsuta* Eig, 1929. Repert. Sp. Nov. Feddes Beih. 55: 144.

Morphological characteristics: Annual or biennial. Culms 10 ~ 20 cm tall. Leaves linear or long lanceolate, 2–5 cm long, hairy or hairless. Spike oval or oblong, 1–3 cm long, vestigial basal spikelets 0–1, 2 rarely, developed spikelets 2–4, 3 usually, apical spikelet sterile. Length of lateral spikelets longer than that of the adjacent rachis internodes, and umbrella-like abscission at maturity. Spikelets ovate, abruptly tapering, usually with 5 florets, upper 3 florets sterile. Glume leathery, upper apex with 2–5 awns, 4 awns usually, awn 2~3.5 cm long, glume awns of upper spikelets glume awns many. Lemma with 2–3 awns, 5–7 veins. Palea membranous, two ridges. Caryopsis naked.

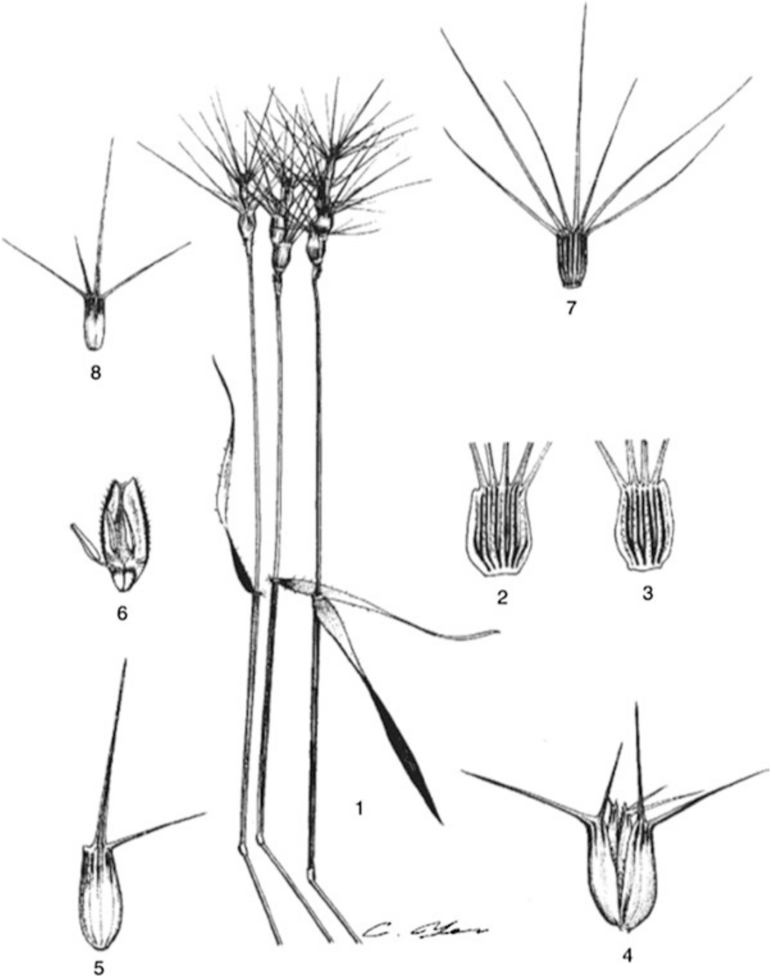

Fig. 8.36 *T. ovatum* (L.) Raspail var. *vulgare* (Cosson et Dur.) Briq
1. Leaf, stem, spike of adult plant; 2, 3. glume of fertile lateral spikelet; 4. the first, second, third, and fourth floret of fertile lateral spikelet; 5. lemma of the first floret of fertile lateral spikelet; 6. lodicule, stamens, feathery stigma, and palea of the first floret of fertile lateral spikelet; 7. glume of sterile upper spikelet; 8. lemma of sterile upper spikelet

Cytological characteristics: $2n = 28$; Genome: UM^{o}.

Distribution: Portugal, Spain, southern France, Italy, Yugoslavia, Bulgaria, Albania, Greece, Crimea, southern Ukraine, Caucasus, Transcaucasia, Turkey, northern Iraq, western Iran, Syria, Lebanon, Cyprus, Israel, Jordan, Egypt, Libya, Tunisia, Algeria, Morocco, and the Sahara oasis. It grows on red calcareous soil, basalt, black calcareous soil, calcareous sand, alluvial soil. It is distributed in the Mediterranean evergreen oak forest land and edge, summer dry grassland, shrub grassland, abandoned lands, gravel land, farmland edge, and roadside. Dense growth usually.

var. biunciale (Vis.) **Yen et J. L. Yang. comb. nov. according to *Ae. biuncialis* Visiani, 1842. Fl. Dalm. ed. 1: 90, Fig. 2, sine descr.; 1852. Fl. Dalm. ed. 3: 344, descr.** (Fig. 8.37)

Synonyms: *Ae. lorentii* Hochst., 1842. Flora 28: 25;
Ae. macrochaeta Shuttlew. et Huet, 1869. Bull. Soc. Bot. Fr. 16: 384;
T. macrochaetum (Shuttlew. et Huet) K. Richter, 1890. Pl. Eur. 1: 128;
Ae. ovata var. *biuncialis* (Vis.) Halac., 1904. Consp. Fl. Graec. 3: 431;
T. lorentii (Hochst.) Zeven, 1973. Taxon 22: 328.

Morphological characteristics: Annual or biennial. Culms 15–30 cm tall. Leaves narrowly linear, hairless or sparsely fine hairs, 2–5 cm long. Spike narrow lanceolate, 2–3 cm long, usually upper two spikelets developed, vestigial basal spikelet 1, 2 seldom, rachis internodes often shorter than adjacent spikelets, not adherent to spikelet, umbrella-like abscission at maturity. Spikelets ovate-oblong, with 4 florets, upper 2 florets sterile. Glume leathery, veins numerous, parallel, covered with short hairs, glumes of lateral spikelets with 2–3 awns, central awn shorter, glumes of apical spikelet with 3 longer awns, glume awns broad and flat, extension inclined upward. Lemma mostly membranous, exposed portion outside glume leathery, lemma awn shorter than glume awn, less than 3 awns. Palea membranous, two ridges. Caryopsis naked.

Cytological characteristics: 2n = 28. Genome UM^o.

Distribution: Portugal, Spain, southern France, Italy, Yugoslavia, Romania, Bulgaria, Albania, Greece, Crimea, southern Ukraine, Caucasus, Transcaucasia, Turkey, northern Iraq, western Iran, Syria, Lebanon, Cyprus, Israel, Jordan, Libya, Tunisia, Algeria, and Morocco. It grows on red calcareous soil, basalt, black calcareous soil. It is distributed in the Mediterranean evergreen oak forest land and edge, summer dry grassland, shrub grassland, stony slopes, abandoned lands, erosion land, farmland edge, and roadside.

23. ***T. triaristatum*** (Willd.) **Gren. et Godr., 1855. Fl. Franc. 3: 602.** (Fig. 8.38)

Synonyms: *Ae. ovata* var. *triaristata* (Willd.) Grisebach, 1844. Spicil. Fl. rume l. bithyn. 2: 425;
T. triaristatum Willd., 1806. Sp. Pl. 4: 493;
T. ovatum ssp. triaristatum (Willd.) Ascherson et Graebner, 1902. Syn. Mitteleur. Fl. 2: 705.

Morphological characteristics: Annual or biennial. Tillers less, culms 25–35 cm long, erect or inclined. Leaves linear, hairy, margins of leaves with fine hairs. Spike lanceolate, spikelets compact, 2.3–3.5 cm long; usually basal spikelet 3 undevel-

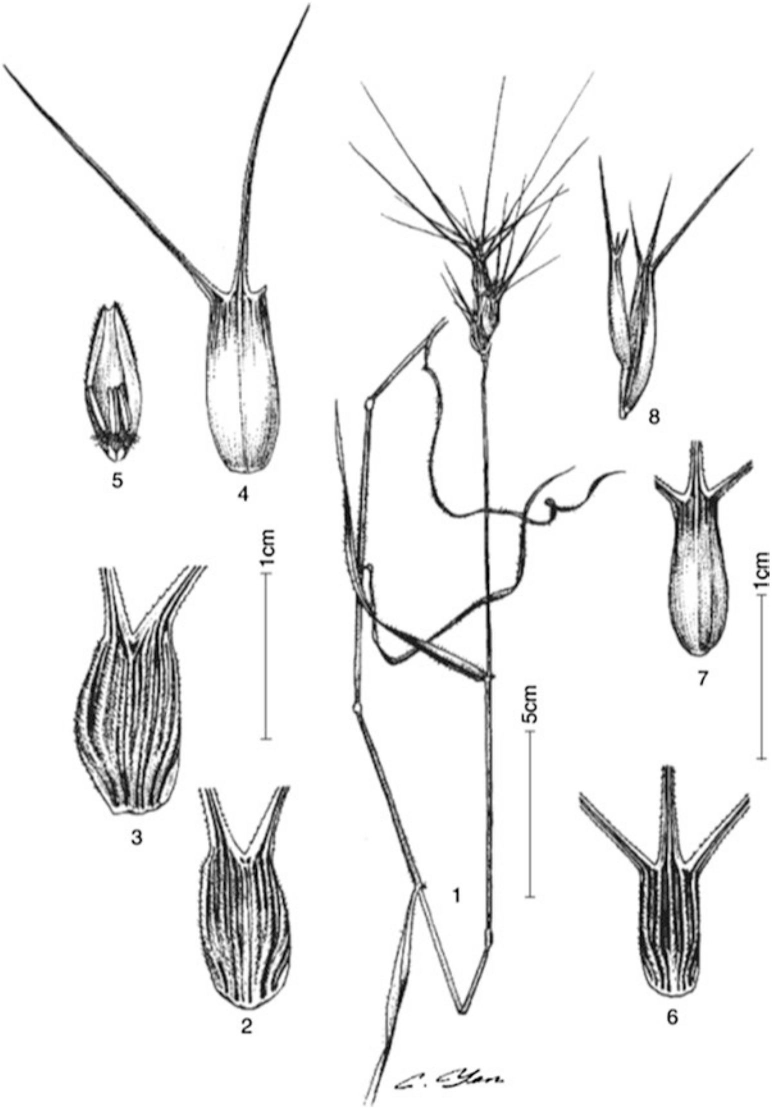

Fig. 8.37 *T. ovatum* (L.) Raspail var. *biunciale* (Vis.) Yen et J. L. Yang
1. Adult plant; 2. the first glume of fertile lateral spikelet; 3. the second glume of fertile lateral spikelet; 4. lemma of fertile lateral spikelet; 5. lodicule, stamens, feathery stigma, and palea; 6. glume of upper spikelet with 3 awns; 7. lemma of upper spikelet with 3 awns; 8. sterile floret

oped; middle and upper spikelets 3–6 developed, usually 4; upper 1–4 small spikelets sterility; umbrella-like abscission at maturity. Fertile spikelets with broad, leathery, and hairy glumes; glumes with parallel veins; apical spikelets with 3 awns, awn 3.5–4.5 cm long; Lemma of fertile spikelets with 2–4 awns, usually 2; lemma

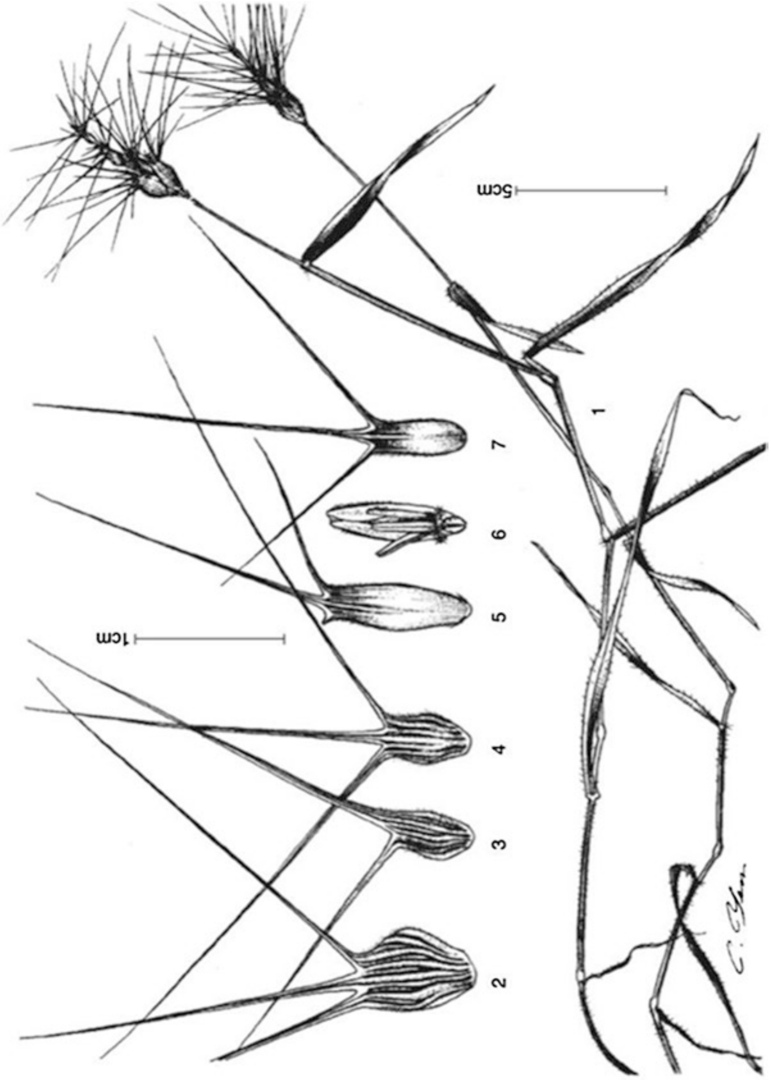

Fig. 8.38 *T. triaristatum* (Willd.) Gren. et Godr. var. *typicum* Yen et J. L. Yang
1. Adult plant; 2. the first glume of fertile lateral spikelet; 3, 4. glume of upper sterile spikelet; 5. lemma of fertile lateral spikelet; 6. lodicule, stamens, feathery stigma, and palea of fertile lateral spikelet; 7. lemma with 3 awns from upper sterile spikelets

of upper sterile spikelets without awn usually. Palea membranous, two ridges. Caryopsis naked.

Cytological characteristics: 2n = 28. Genome UX^t.

Distribution: Portugal, Spain, southern France, Italy, Yugoslavia, Bulgaria, Albania, Greece, Crimea, Caucasus, Transcaucasia, Turkey, northern Iraq, western Iran, Syria, Lebanon, Libya, Tunisia, Algeria, and Morocco. It grows on red calcareous soil, basalt, black calcareous soil, alluvial soil. It is distributed in the Mediterranean evergreen oak forest land and edge, summer dry grassland, shrub grassland, stony slopes, abandoned lands, erosion land, farmland edge, and roadside; altitude 0–1300 m.

var. *columnare* (Zhuk.) **Yen et J. L. Yang, comb. et stat. nov. According to *Ae. columnaris* Zhuk. 1928. Tr. Prikl. Bot. Genet. Sel. 18: 448.** (Fig. 8.39)

Synonym: *T. columnare* (Zhuk.) Morris et Sears, 1967. in Quisenb. et Reitz, Wheat and wheat improvement: 19.

Morphological characteristics: Annual or biennial. Multiple tillers, culms 20–30 cm tall. Leaves narrow linear, usually hairy. Spike 3–7 cm long, usually 3–5 cm, undeveloped basal spikelets 2–4 (usually 3); well-developed middle spikelets 2–3 with ovate-oblong shape, adjacent rachis internodes shorter than or equal to the length of spikelets; upper 3 spikelets small, sterile usually, adjacent rachis internodes longer than the length of spikelets, so the upper parts of spike abruptly tapering toward the apex forming column shape. The middle fertile spikelet with 4–5 florets, and the upper 2–3 florets sterile; the upper spikelet usually with 3 sterile florets, or only one basal floret producing one small caryopsis; umbrella-like abscission at maturity. The middle fertile spikelet glume elliptic, leathery, with 2 long awns, one conspicuously wider than the other; the upper spikelet glume with 3 long awns having similar width and length. Glumes usually with parallel veinlets, coarse. Lemma with 1–2 awns, conspicuously shorter than glume awns; the most part of lemma covered by glumes membranous, exposed portions leathery. Palea membranous, two ridges. Caryopsis naked.

Cytological characteristics: $2n = 28$. Genome: UX^t.

Distribution: Turkey, Syria, eastern Lebanon, northern Iraq, Iran, Caucasus. It grows in red calcareous soil, gray calcareous steppe, and basalt soil. It is distributed in open ground of oak forest, summer dry grassland, short shrub grassland, abandoned land, farmland edge, and roadside.

24. ***T. rectum*** (Zhuk.) **Bowden, 1966. Canad. J. Genet. Cytol. 8: 135.** (Fig. 8.40)

Synonyms: *Ae. triaristata* Willd. Ssp. *recta* Zhuk., 1928. Tr. Prikl. Bot. Genet. Sel. 18: 478;
Ae. recta (Zhuk.) Chennaveeraiah, 1960. Acta Horti Gotob. 23: 165;
Ae. neglecta ssp. recta (Zhuk.) Hammer, 1980. Feddes Repert. 91: 240.

Morphological characteristics: Annual or biennial. Tillers less, culms 20–30 cm tall, erect or inclined. Leaves linear, dense or sparse short hairs, leaves margins with

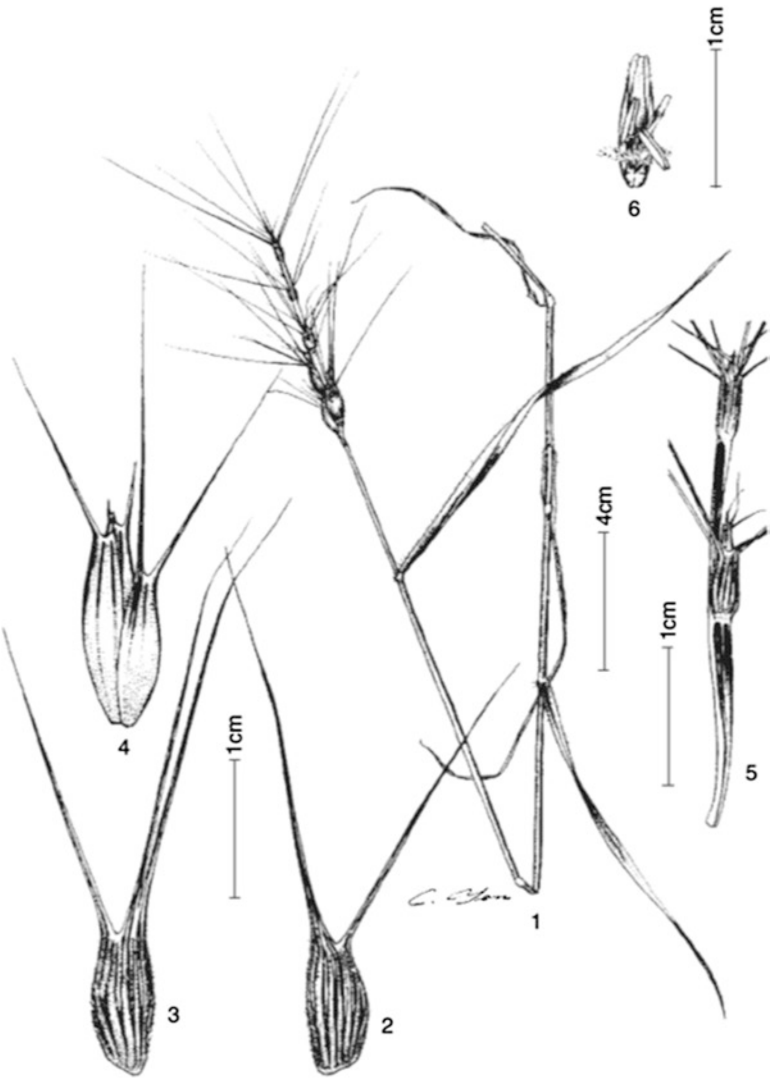

Fig. 8.39 *T. triaristatum* (Willd.) Gren. et Godr. var. *columnare* (Zhuk.) Yen et J. L. Yang
1. Adult plant; 2. the first glume of fertile lateral spikelet; 3. the second glume of fertile lateral spikelet; 4. floret of fertile lateral spikelet; 5. upper sterile spikelet; 6. lodicule, stamens, feathery stigma, and palea of fertile lateral spikelet

fine hairs. Spike lanceolate, 2–3.5 cm long, vestigial basal spikelets 3, seldom 2, developed spikelets 3–6, usually 4; the lowermost two spikelets well developed, larger than the upper spikelets, ovate-oblong shape, and spikelets longer than the adjacent rachis internodes; upper spikelets poorly developed, spikelets shorter than the adjacent rachis internodes, upper parts of spike slender gradually. Spikelets usu-

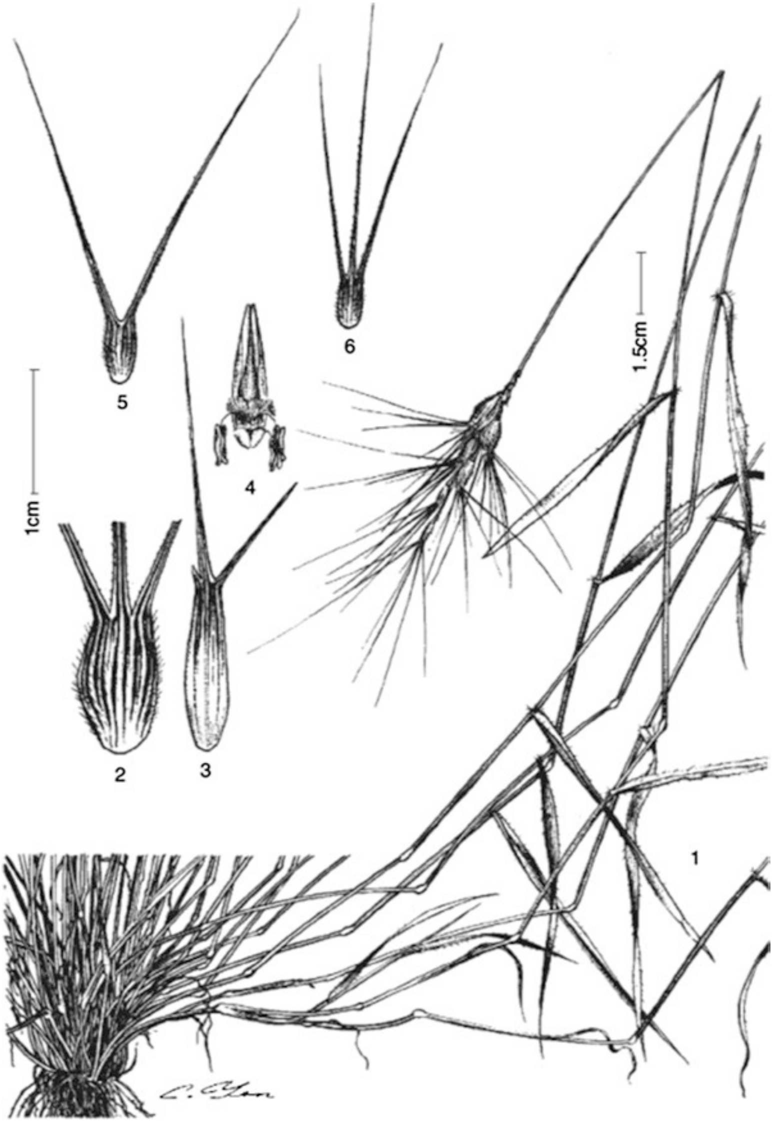

Fig. 8.40 *T. rectum* (Zhuk.) Bowden
1. Adult plant; 2. glume of fertile lateral spikelet; 3. lemma of the first floret of fertile lateral spikelets; 4. lodicule, stamens, feathery stigma, and palea of the first floret of fertile lateral spikelet; 5,6. glume of sterile upper spikelets

ally fertile, umbrella-like abscission at maturity. Glume leathery, parallel veins with short hairs, glume with 3 long awns usually, sometimes lower spikelets with only 2 awns. Lemma longer than glume; the lemma of lower spikelets usually with 2 awns, but up to 4 awns; the lemma of upper spikelet hairless usually, lemma awn shorter than glume awn. Palea membranous, two ridges. Caryopsis naked.

Morphology characteristics of *T. rectum* are very similar to *T. ovatum* var. *triaristatum* and var. *columnare*; hence they are often confused.

Cytological characteristics: 2n = 42. Genome: UX^{t}N.

Distribution: Portugal, Spain, southern France, Italy, Yugoslavia, Greece, and western Turkey. It grows in red calcareous soil. It is distributed in the open ground of oak forest, summer dry grassland, short shrub grassland, abandoned land, erosion land, farmland edge, and roadside.

25. ***T. triunciale* (L.) Raspail, 1825. Ann. Sci. Nat. Ser. 1,5: 435.** (Fig. 8.41)

Synonyms: *Ae. triuncialis* L., 1753. Sp. Pl.: 1051;
Ae. elongata Lam., 1778. Fl. Fr. 3: 632;
Ae. echinata Presl, 1820. Cyp. et Gram. Sic.: 47;
Aegilopodes triuncialis (L.) Á. Löve, 1982. Biol. Zentralbl. 101: 207.

Morphological characteristics: Annual or biennial. Tillers less, prostrate, stem knee bent upward after elongation, 20–35 cm tall, the first rachis long, leaves concentrated in the middle and lower parts of plants. Leaves linear, 2–6 cm long, usually hairy. Spike narrow lanceolate, 3–6 cm long, vestigial basal spikelets 3, seldom 2, developed spikelets 3–8, usually 4–5, umbrella-like abscission at maturity. Spikelet broadly lanceolate, usually with 4 florets, upper 2 sterile florets, middle and lower spikelets large, gradually smaller toward upper end; middle and lower spikelets longer than the adjacent rachis internodes, upper spikelets shorter than rachis internodes. Glume leathery, short hairs, 3 awns, a short central awn or a spiny teeth-like; glume awn of upper spikelets long, especially for apcial spikelet; the central awn with broad base, longer (4.5–7 cm) and larger than the others. Lemma longer than glume, lemma with short awns or awnless. Palea membranous, two ridges. Caryopsis naked.

Cytological characteristics: 2n = 28. Genome UC.

Distribution: Portugal, Spain, southern France, Italy, Yugoslavia, Bulgaria, Albania, Greece, Crimea, southern Ukraine, Caucasus, Transcaucasia, Turkey, Iraq, Iran, Syria, Lebanon, Kuwait, Saudi Arabia, Cyprus, Israel, Algeria, Morocco, Afghanistan, and Pakistan. It grows in a variety of soils in the Mediterranean evergreen oak forest land and edge, summer dry grassland, shrub grassland, abandoned lands, grave land, farmland edge, and roadside. Altitude 150–1800 m.

26. ***T. peregrinum* Hackel, 1907. Ann. Scott. Nat. Hist. Quart. Mag. 62: 102.**

Synonyms: *Ae. kotschyi* Boiss., 1846. Diagn. Pl. Orient., N. S. 1,7: 129;
Ae. geniculata Figori et Notaris, 1851. Agrost. Aegypt. Phrag. Paris 1: 18, non *Ae. geniculata* Roth, 1787;

Fig. 8.41 *T. triunciale* (L.) Raspail
1. Adult plant; 2. glume of apical spikelet; 3, 4. glume of fertile lateral spikelets at lower parts; 5. the first, second, third, and fourth floret of fertile spikelet; 6. glume of fertile spikelet; 7. lodicule; 8. lodicule, stamens, feathery stigma, and palea of the first floret of fertile lateral spikelet

Ae. glabriglumis Gandoger, 1881. Oesterr. Bot. Zeitschr. 31: 82;
T. kotschyi (Boiss.) Bowden, 1959. Canad. J. Bot. 37: 675;
Ae. triuncialis ssp. *kotschyi* (Boiss.) Zhuk., 1928. Tr. Prikl. Bot. Genet. Sel. 18,1: 499;

Fig. 8.42 *T. peregrinum* Hackel var. *Kotschyi* (Boiss.) Yen et J. L. Yang
1. Adult plant; 2. glume with 4 awns; 3, 4. glume; 5. lemma of the first floret; 6. lodicule, stamens, feathery stigma, and palea; 7. the first, second, and third floret

Aegilemma kotschyi (Boiss.) Á.Löve, 1982. Biol. Zentralbl. 101: 207.

var. kotschyi (Boiss.) **Yen et J. L. Yang, comb. et stat. nov. according to *Ae. kotschyi* Boiss., 1846. Diagn. Pl. Orient., N. S. 1,7: 129** (Fig. 8.42)

Synonym: *Ae. triuncialis* ssp. *kotschyi* (Boiss.) Zhuk., 1928, Tr Prikl. Bot. Genet. Sel. 18,1: 499.

Morphological characteristics: Annual or biennial. Multiple tillers, prostrate, stem knee bent upward after elongation, culms 15–25 cm tall. Leaves linear, usually hairless. Spike narrow lanceolate, 2–3 cm long, vesitigial basal spikelets 2–4, usually 3, developed spikelets 2–6, usually 4; lower spikelets larger than upper spikelets, lower spikelets longer than the adjacent rachis internodes, upper rachis internodes longer than the adjacent spikelets; spike tapering toward the apex, umbrella-like abscission at maturity. Spikelets containing 3–4 florets, upper 1–2 florets sterile, the whole spike umbrella-like abscission. Glume with numerous parallel veins, leathery, glume apex with the 2 or 3 awns, awn broad and flat at base, gradually tapering toward the apex, flat expansion outward at maturity. Lemma longer than glume, 1–3 awns, as long as or slightly shorter than glume awn, lemma of apical floret usually with 1 awn and 1 teeth, or 2 teeth. Palea membranous, two ridges. Caryopsis hulled.

Cytological characteristics: 2n = 28. Genome UB^1.

Distribution: Transcaucasia, Afghanistan, Pakistan, Iran, Iraq, Kuwait, Saudi Arabia, eastsouthern Turkey, Syria, Lebanon, Cyprus, Israel, Jordan, Lower Egypt and Sinai, Libya, Tunisia. It grows on gray calcareous grassland, white limestone soil, loess and sandy soil. It is distributed in summer dry grassland, short shrub grassland, farmland edge and roadside. Altitude 100–1100 m.

var. variabile (Eig) **Yen et J. L. Yang, comb. et stat. nov. according to *Ae. variabilis* Eig, 1929, Feddes Repert. Beih. 55: 121, non *T. variabile* Markgraf, 1932.** (Figs. 8.43 and 8.44)

Synonyms: *Ae. peregrina* (Hackel) Eig, 1929. Feddes Repert. Beih. 55: 121, in adnot; *Aegilemma peregrina* (Hackel) Á. Löve, 1984. Feddes Repert. 95: 499.

Morphological characteristics: Annual or biennial. Multiple tillers, prostrate, stem knee bent upward after elongation, culms 15–40 cm tall. Leaves linear, hairy or hairless. Spike oval, narrow lanceolate or nearly cylindrical, 1.5–7.5 cm long, vestigial basal spikelets 1–4, usually 3, and developed spikelets 2–7, usually 3–5, oblong-oval shape, lower spikelets larger than upper spikelets, lower spikelets longer than the adjacent rachis internodes, upper rachis internodes slightly longer than the adjacent spikelets, spike abruptly or gradually tapering, umbrella-like abscission at maturity. Spikelets usually fertile, containing 3–6 florets, usually 4–5 florets, upper 1–3 florets sterile, whole spike with umbrella-like abscission. Glume with numerous parallel veins, leathery, apical spikelet glume with 3 awns, lateral spikelets glume with 2–3 awns, for 2 awns the central awn only developed into a small tooth or bulge, awn base broad flat, gradually tapering toward the apex, inclined upward at maturity, awns length not equal to each other. Lemma longer than glume, with 1–3 awns, short or awnless. Palea membranous, two ridges. Caryopsis hulled.

Cytological characteristics: 2n = 28. Genome: UB^1.

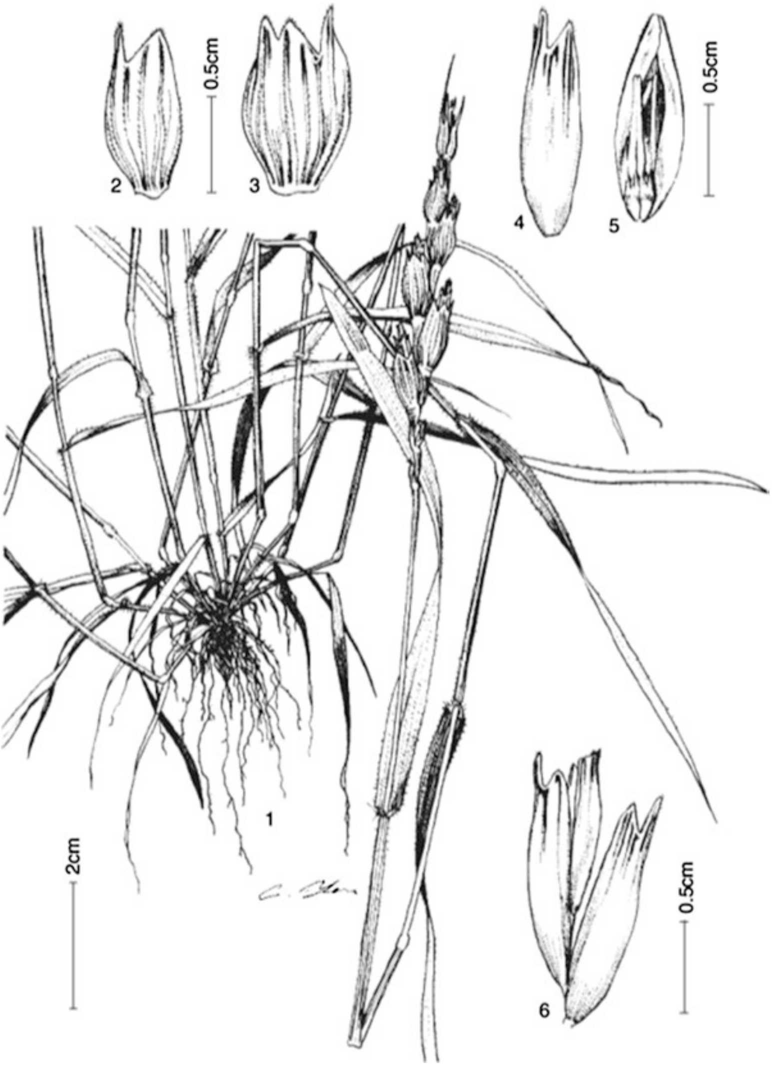

Fig. 8.43 *T. peregrinum* Hackel var. *variabile* (Eig) Yen et J. L. Yang
1. Adult plant; 2. the first glume; 3. the second glume; 4. lemma; 5. lodicule, stamens, feathery stigma, and palea; 6. the second, third, fourth florets and the fifth hypoplasia floret

Distribution: Southern Italy, Sicily, southern Greece, southern Turkey, lower Mesopotamia, Syria, Lebanon, Cyprus, Israel, Jordan, lower Egypt, Libya, Tunisia, Algeria, Morocco. It grows in a variety of soils. It is distributed in oak forest open ground, summer dry grassland, short shrub grassland, abandoned land, farmland edge, and roadside. Altitude 0 ~1 600 m.

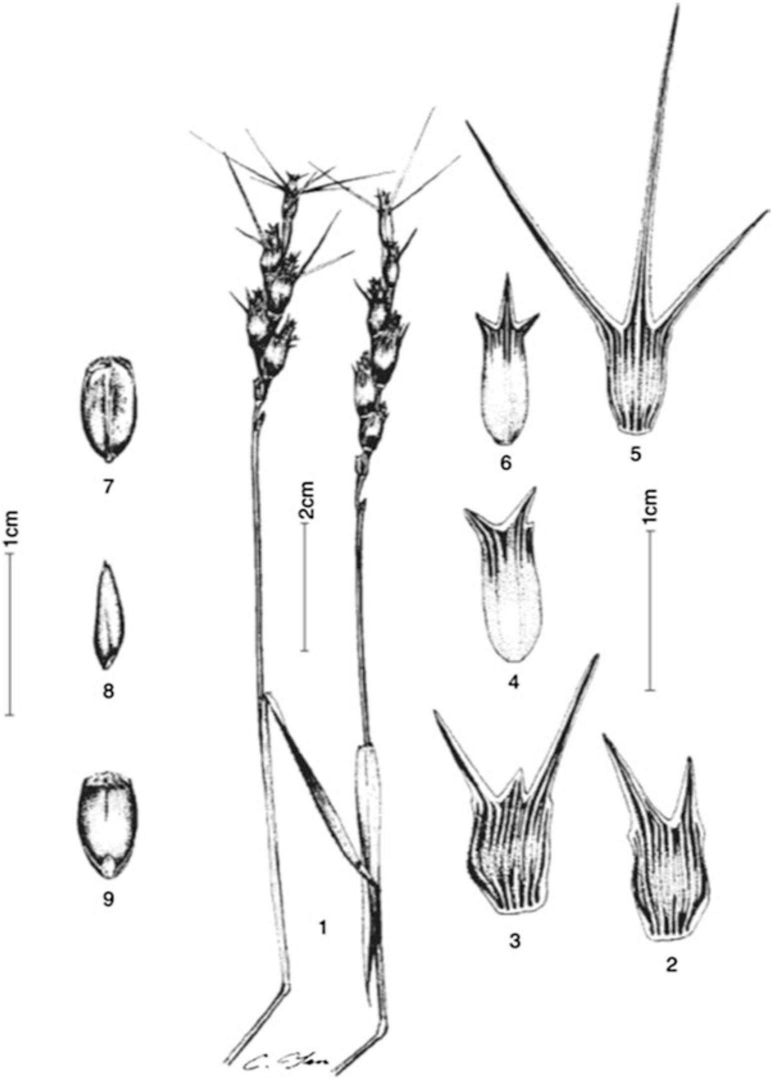

Fig. 8.44 *T. peregrinum* Hackel var. *variabile* f. *aristatum* Yen et J. L. Yang
1. Leaf, stem, spike of adult plant; 2. the first glume; 3. the second glume; 4. lemma; 5. upper spikelet glume with long awn; 6. lemma of upper spikelet; 7. caryopsis ventral view; 8. caryopsis lateral view; 9. caryopsis dorsal view

Amblyopyrum (Jaub. et Spach) **Eig, 1929. in P. Z. E. Agric. et Nat. Hist., Agric. Rec. (Tel-Aviv) 2: 199.**

Am. muticum (Boiss.) **Eig, 1029. in P. Z. E. Inst. Agric. et Nat. Hist., Agric. Rec. (Tel-Aviv) 2: 200.** (Fig. 8.45)

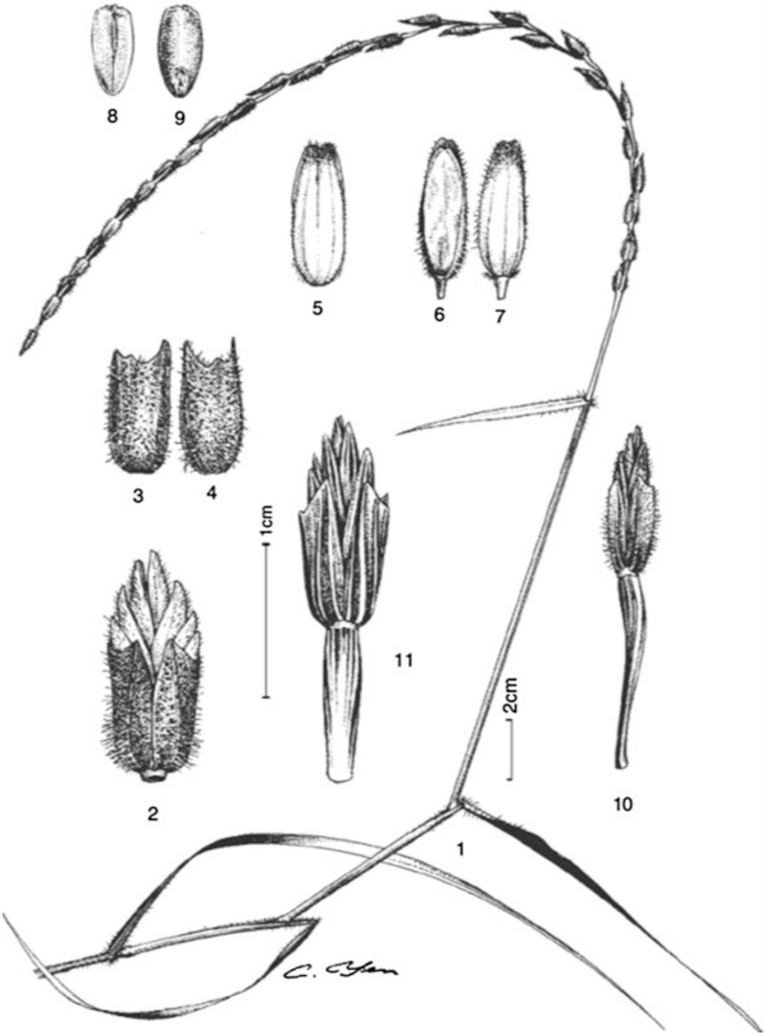

Fig. 8.45 *Amblyopyrum muticum* (Boiss.) Eig
1. Leaf, stem, spike of adult plant; 2. spikelet dorsal view; 3, 4. glume; 5. lemma of the first floret; 6. the second floret ventral view; 7. the second floret dorsal view; 8. the second caryopsis ventral view; 9. the second caryopsis dorsal view; 10. apical spikelet; 11. hairless glume, lemma, and rachis internode for the hairless forma

Synonyms: *Ae. mutica* Boiss., 1844. Diagn. Pl. Or., N. S. 1,5: 73;
Ae. tripsacoides Jaub. et Spach, 1847, Ill. Pl. Or. 2: 121, tab. 200;
T. muticum (Boiss.) Hackel, in Fraser, 1907. Ann. Scott. Nat. Hist. 1907: 103, non *T. muticum* Rode, 1818, Char. et Descr. Cereal Hort. Tubingen: 10–11 (incertae sedis);
T. tripsacoides (Jaub. et Spach) Bowden, 1959. Canad. J. Bot. 37: 666.

Morphological characteristics: Annual or biennial. Less tillers, culms 70–80 cm tall. Leaves linear, hairy or hairless. Spike slender, linear, 25–30 cm long; rachis internodes longer than spikelets length, 1 spikelet per rachis node, 10–15 spikelets per spike, arrangement very sparse. Spikelet rectangular, flat, with 5–8 florets, upper 1–3 florets sterile. Glume leathery, trapezoid, the upper wider than the lower parts, with 2–4 blunt teeth, usually hairless or sparsely short bristles. Lemma leathery, nearly as long as glume length, hairless, with a blunt tip. Palea with two ridges, membranous. Cross-pollination, self-sterility. Caryopsis hulled.

Cytological characteristics: 2n = 14. Genome T.

Distribution: Turkish Anatolian plain, Turkey-Armenia, South Caucasus, Transcaucasia, western Iran, northeastern Syria, northern Iraq border. It grows in sandy soil, gravel land, and gray steppe soil. It is distributed in abandoned lands, farmland edges, and roadsides. In eastern Turkey, many dense clusters are scattered.

var. *loliaccum* (Jaub et Spach) **Eig, 1929. Agric. Rec. (Tel Aviv) 2:200. hairless varietas**

Synonyms: *Ae. loliacea* Jaub. et Spach, 1850–1853. Illustr. Pl. Orient. 4: 23. pl. 317;
Ae. mutica subsp. *loliacea* (Jaub. et Spach) Zhuk., 1928.
Bull. Appl. Bot. Pl. Breed. 18: 546
Am. muticum subsp. *loliacea* (Jaub et Spach)
Á. Löve, 1984. Feddes Repert. 95: 494

Except for hairless, the morphological characteristics, distribution, ecological environment, and cytological characteristics of this varietas are same as the original species.

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Chapter 9
Taxon Within a *Triticum* Species

In the second half of the nineteenth century, many works on taxa and classifications below species were carried out on the genus *Triticum*. For instance, Alefeld used characteristics of spike and grain to classify varietas. Kornicke further developed and made a number of varietas names, some of which are still used by some people. They identified varietas using the characteristics such as spikes with awns or awnless, hairy or hairless glumes, spike color (white, red, black), and grain color (white, red). In the twentieth century, such artificial classification was adopted by Вавилов, Фляксбергр, Туманян, Якубцнер of the former Soviet union school and some scientists in other countries, for example Percival, making classification very complicated. In our opinion, over-complex classification is not necessary in scientific theory and useless in productive practice. The classification on the basis of simple phenotypic traits cannot effectively reflect the naturally phylogenetic relationships in many cases. However, in cultivated crops, cultivar that is developed by artificial selection on human economic purposes is a useful unit with economic significance. Correspondingly, in the natural environment, varietas formed by natural selection is the natural unit of evolutionary adaptation.

Are there any objective units below species? Yes, cultivar and varietas are. As mentioned above, a cultivar with desirable economic characteristics is selected by breeders, while varietas (and forma) is formed by natural selection. Latin name should not be used for a cultivar according to International Code of Botanical Nomenclature and International Code of Nomenclature for Cultivated Plants. Instead, fancy name or popularized Latin name should be used for a cultivar. Although it seems appropriate to use the same nomenclature for varietas with the same grade as cultivar, Latin names should be used for varietas in accordance with the provisions of the above-mentioned international code and historical customs.

The difference of traits between cultivars/varietas is originated from DNA mutation in natural conditions. Genetic recombination resulting from cross-fertilization between cultivars/varietas will produce diverse individuals with different gene constitutions to favor the generating of favorable traits. Under artificial selection, a group (cultivar) with desirable economic traits and consistent in genetics will be

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formed, while under natural selection, a group (varietas) with good adaptation to certain ecological conditions was formed.

Interspecific/generic hybridization often can have a similar function to hybridization between cultivars. Homoeologous chromosomes between species can pair sometimes and genetic recombination will occur, especially under the inactive condition of Ph gene. Therefore, genetic materials can be exchanged between species. The introduction of exogenous genes can confer a species new inheritable characters. For example, Sears introduced the leaf rust resistance gene from *T. umbellulataum* into common wheat, resulting in high resistance to leaf rust. Zhensheng Li (personal communication) introduced the blue grain trait from *Lophopyrum ponticum* into common wheat. However, none of the common wheat has the character of blue grains in the past. We introduced the amber-grain character of tetraploid Polish wheat into common wheat by hybridizing Polish wheat with common wheat line Fan 33, and developed the series of NPFP resources with the character. Stankov and Tsikov (1974) transferred the round-grain gene on chromosome 3D of *T. aestivum* concv. *sphaerococcum* to *T. durum*. We also introduced multispikelets genes of rye into common wheat, making that the number of spikelets increased from 18–25 up to 26–35 (Yen et al. 1993). Bluthner and Mettin (1973) observed the replacement of chromosome 1B with Rye 1R in the selected line 153/63 that was absent for the satellites on 1B. Similarly, cultivars Orlando and Saladin are similar to 153/63 with the substitution of 1R(1B). The short-arm chromosomes of 1B (1BS) of cultivars Аврора and Кавкаэ, derived from cultivar Neuzucht, were replaced by 1RS of rye. Авроа and Кавкаэ inherited resistance to powdery mildew from rye, and had important significant in production. In addition, Agrus is a highly resistant cultivar to leaf rust, derived from the introduction of an alien chromosome of *Lophopyrum elongatum* (= *Agropyron elongatum*). However, all the mentioned cultivars are still *T. aestivum.*

On the other hand, because of the introduction of genetic materials from alien species, a new interaction relationship will be established, which can generate transgressive traits absent in parents; or because of the meiotic abnormalities caused by distant hybridization, chromosomal structure variations, such as repetition, deletion, inversion, translocation, etc., may occur, which may also affect gene expression and produce novel trait. The interspecific hybridization hence can generate some special traits for concultivar. For example, we used Polish wheat as the female to cross common wheat line ya-an-ai 2, and found that some F3 plants were highly like the Ruo-qiang-gu-mai wheat, which was an ancient wheat found in Xinjiang, China. However, Ruo-qiang-gu-mai was susceptible to stripe rust races 18 and 19, but these F3 plants were immune to the races. In the hybridization combination, plants resembling *T. turgidum* concv. *carthlicum* (both glume and lemma having long awn) and dwarf durum wheat with dense spikes were also obtained. In addition, from the cross of common wheat line Fan 33 with tetraploid Polish wheat, we also obtained non-tiller common wheat that was not found in our previous wheat population, besides the common wheat with amber-colored grain derived from Polish wheat. Taken together, hybridization might have played a role in the production of concultivars and varietas. Hybridization pathway for the production of *T.*

turgidum concv. *carthlicum* was also indicated by the genetic analysis of Ohtsuka (1983).

Gene mutation and genetic recombination during hybridization, especially for interspecific hybridization, have greatly enriched the genetic diversity of species. However, there is no reproductive isolation between different groups despite of diverse phenotypes. The hybridization between populations within a species will bring new genetic recombination to naturally select for better adaptation to ecological environments. Such intraspecies hybridization is hence helpful to form new varietas. There are usually a series of intermediate types without clear boundary among populations. The production process of a new cultivar is similar to the intraspecific hybridization. However, under the artificial selection, the intermediate types were eliminated, and the cultivar with wanted economic characters is selected according to people's economic purposes. Those cultivars with minor differences are called a cultivar group or concultivar.

On the other hand, although there are distinct phenotypes among populations, the intraspecies differences do not cause reproductive isolation and lead different genomes. However, the quantitative accumulation of genetic variations could result in qualitative change, thus probably contributing to the formation of new genomes and the production of new species. There are many reports on the effects of gradual variation accumulating on species divergence. For example, Sachs (1953) observed that the semi-lethal effects of *T. macha* depends on cultivar groups of other *Triticum* species. In another example, Riley and Bell (1958) observed similar phenomenon using *T. monococcum* var. *boeoticum* and var. *thaouder*. Hybrids of *T. monococcum* var. *boeoticum* with tetraploid wheat die at the third or fourth leaf stage, but hybrids of var. *thaouder* with tetraploid wheat grow normally.

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Chapter 10
Geographic and Historical Origin of Wheat

The investigation on the wild wheat in the past 100 years have found wild wheat including *T. monococcum* var. *boeoticum*, *T. monococcum* var. *thaoudar*, *T. urartu, T. turgidum* var. *dicoccoides*, and *T. timopheevi* var. *araraticum.* However, the wild type of common wheat has been not found yet. The wild *T. monococcum* is distributed in the Middle East and nearby regions, including Balkans, Turkey, Syria, Jordan, Lebanon, Palestine, northern Iraq, Northwestern Iran, Armenia, Azerbaijan, the Transcaucasia, the northern coast of the Black Sea, and southern coast of the Sea of Azov to the Crimean Peninsula. *T. urartu* is distributed in the mountains of Armenia, Israel, Syria, Palestine, northwest Iran, southeastern Turkey, and other Fertile Crescent areas. *T. turgidum* var. *dicoccoides* is distributed in the eastern coast of the Mediterranean Sea, namely northern Palestine, Lebanon, western and northwestern of Syria, southeastern Turkey, northeastern Iraq, and adjacent areas of northwestern Iran, Armenia, Azerbaijan, and Transcaucasia. *T. timopheevi* var. *Araraticum* is only distributed in Armenia, Azerbaijan, Naxçivan, and Iran. Apparently, these wild species had existed before humans began farming. The primitive humans selected wheat as a food resource, probably due to the relatively big grains with high quality. After the primitive humans knew how to cultivate, *T. monococcum* and *T. turgidum* were then cultivated and spread.

Archaeological study found circular stones and pebbles in Paleolithic cultural relics in the Middle East around 7500 BC. They were probably used to mill grains. One of the important discoveries from Middle Eastern cultural relics in the Middle Stone Age around 9000–7000 BC was that there were stone sickles, bone sickles, and bone hoes in the Erwad cave culture of the Camel Mountains. This finding indicates that primitive humans in the Middle East had harvested grains or forages using these tools at that time. It not only shows that harvest had played an important role in life, but also there were special cultivation tools such as bone hoes. Although peoples at that time might still live mainly by hunting and collecting wild plants, the existence of bone hoes indicates that they had known how to coarsely grow plant crops.

After 7000 BC, carbonized, especially dry or muddy, wheat grains and spikes have been found in many places. At present, the earliest specimens for carbonized

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wheat spikes and wheat spikelets preserved in dry clay were found at Jammu area in Iraq, identified as relics from 6700 BC. Spikelets of *T. monococcum*, *T. turgidum* var. *dicoccoides*, and resembling *T. turgidum* concv. *dicoccon* have been clearly identified from the carbonized relics. *T. turgidum* concv. *dicoccon* from 6000 BC was discovered at Matarrah in Iraq. Lots of wheats were found in the relics from 5000 to 4000 BC. Cultivated *T. turgidum* and *T. monococcum* were unearthed from the Halafian Communities of the upper Euphrates Tigris in Iraq. Cultivated *T. turgidum* were unearthed at Alluvial plain in Iraq. Cultivated *T. turgidum* and occasionally *T. aestivum* concv. *compactum* were found in Fayum of Egypt, Merimbde beni Salame, and El Omari. From the Loess Plain of Danube Delta to Rhine Estuary in Europe, wheats assembling, cultivated *T. turgidum* and *T. monococcum* were unearthed. In 3000 BC, the inhabitant site of Swiss Lake, France, northern Italy, Spain, Britain, Central Europe, and Scandinavia Peninsula unearthed cultivated *T. turgidum* and *T. monococcum*. *T. aestivum* cocnv. *compactum* were found in Switzerland and Denmark. During this period, most of the wheat found in the ancient tombs of Egypt was cultivated *T. turgidum*. Unger found *T. aestivum* cocnv. *compactum* at the pyramid brick of Dashur in Egypt. In Europe about 2000–1000 BC, in the north of the Alps, cultivated *T. turgidum* was replaced by *T. aestivum* concv. *spelta*, and then replaced by naked *T. aestivum* L. concv. *aestivum*. Taken together, from archaeological history, the discovery of wheat in primitive human cultural relics was first in Iraq and regions around, then in Egypt, and then in Europe.

In China, the Zhoukoudian (Chinese ape man and upper cave man) site in Beijing has a large number of fruits of trees but without wheat; the Banpo Village in Xi'an unearthed millet stored in pottery pots, also without wheat (around 5000 BC). However, common wheat appeared in the burial bags of the ancient corpses at the Peacock River in Xinjiang with more than 4000 years ago (Fig. 10.1). The inner walls of the chanting hall of the Loulan Ancient City Site still contain whole florets of common wheat (Fig. 10.2). The carbonized grains of cultivated *T. turgidum* were found at Neolithic Longshan cultural relics of the Diaoyutai Site in Bo County, Anhui Province (2000 BC ago). Around 2700 BC, barley and wheat had been widely cultivated in the Reaches of Yellow River. There was the record of Chinese characters "Gao Mai" in Wu Ding's oracle inscriptions. “Mai” is wheat in English. There are Chinese characters "Lai" and "Mou" in the inscriptions on bones and tortoise shells of Yin Ruins, "Lai" and "Mou" is barley and wheat, respectively. It seems that wheat has spread gradually from the Middle East to North Africa, Europe, and East Asia, as suggested by de Candoll (1886). On the other hand, there were only einkorn and *T. turgidum* in the relics of 5000 BC, while common wheat did not exist at that time. In Europe, the first type of cultivated hexaploid wheat was hulled *T. aestivum* concv. *spelta*, and then the naked types including *T. aestivum* cocnv. *compactum*.

It is now possible to arrive at the notion that the primitive peoples of the Middle East began to take wild *T. monococcum* and wild *T. turgidum* as foods. Around 7000 BC, humans understand agricultural cultivation, and then began to plant wild *T. monococcum* and wild *T. turgidum*. Human’s activities made the growing area of wheat far beyond the original wild wheat distribution and spread wheat to North

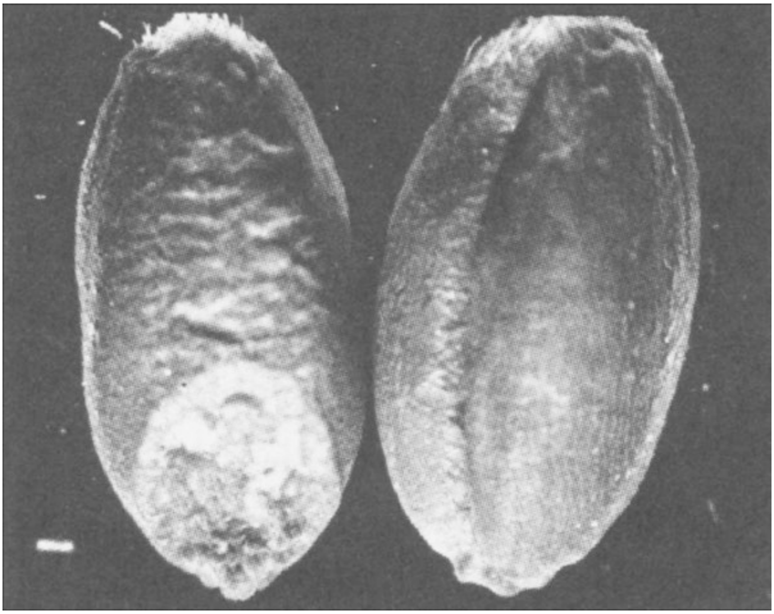

Fig. 10.1 Common wheat (*T. aestivum*) grains in a burial bag of a female mummy at the Peacock River in Xinjiang. They were determined by ^{14}C as relics of 4200–4500 years ago. It is the oldest common wheat found in China. The burial bag was woven using *Apocynum venetum*. Specimens are extant in Urumqi Museum, Xinjiang, identified by Chi Yen and Junliang Yang in 1986.

Africa, Europe, and East Asia. During the process of human cultivation, many cultivars of cultivated *T. monococcum* and *T. turgidum* were produced through artificial and natural selection. The cultivated *T. turgidum* in northwestern Iran and the Transcaucasia was naturally crossed with the weed *T. tauschii* var. *strangulate* (Dvorak et al. 1998), and the spontaneous chromosome doubling of the hybrids resulted in the production of hexaploid wheat (Xu and Dong 1992). The process is possible to occur many times in northwestern Iran and the Transcaucasia. Some of the hexaploid wheat materials with excellent features were selected by human and developed into common wheat (Kihara 1958). It is likely that the earliest common wheat was the hulled *T. aestivum* concv. *spelta*, which was first spread into Europe, and that mutation lead to the production of naked-grain common wheat. It is also possible that the naked-grain common wheat was formed by crossing different naked *T. turgidum* and *T. tauschii* var *strangulata*, similar to the artificial synthesis of common wheat by crossing naked-grain *T. turticum* concv. *carthicum* with *T. tauschii* by Kihara and Lilienfeld. However, available experiments indicated that all the hybrid progenies of *T. turgidum* with *T. tauschii* are hulled, since hulled traits in *T. tauschii* is dominant (Chen et al. 1998). Although the two pathways of origins are possible, both need a mutation process to produce naked-grain common wheat. The long rachilla of *T. aestivum* concv. *vavilovii*, found in Armenia, should also derive from natural mutations. In concert, long rachilla was produced from common wheat

Fig. 10.2 The florets of *T. aestivum* in the inner walls of the chanting hall of the Loulan Ancient City Site in Xinjiang. Palea, lodicule, ovary, and pistil were clearly visible. It was a relic of 2000 year ago, determined by ^{14}C. It is probably the oldest floret specimen preserved today. The specimen was identified by Chi Yen and Junliang Yang in 1986. It is extant in Urumqi Museum, Xinjiang.

cultivar Xifu 1 by ^{60}Co radiation mutation. *T. aestivum* concv. *Macha,* found in Georgia, was probably originated from the natural introgression of rye gens by distant hybridization. Springness and semi-springness wheat adapts the ecological condition of warm areas in the Mediterranean subtropical summer-drought ecological area. Winterness is a new ecological adaptability, formed by natural/artificial selection, after spreading to northern of the North Temperate Zone.

There are still wild species of diploid and tetraploid wheat. They were formed before human cultivation, and their origins are well known, namely in the Fertile Crescent Zone of the Middle East. As mentioned above, common wheat was formed from interspecific hybridization of tetraploid wheat and diploid *T. tauschii*, followed by spontaneous chromosome doubling, in the common distribution area of the two species. However, the common distribution area is very large, from the Middle East, Central Asia to the central part of the Reaches of Yellow River in China. Therefore, scholars have different opinions on the origin of common wheat. For a long time in the past, many scholars believed that the primitive common wheat was the spelta wheat with hulled grains and that naked grain common wheat were produced by its mutation (McFadden and Sears, 1946; Kuckuck 1959; Kihara et al. 1965; Kerber and Rowland 1974). Spelta wheat is mainly distributed in Europe. However, genetic studies and archaeological data suggest that European spelta wheat is probably derived from the introgressive hybridization between naked grain common wheat and hulled *T. turticum* (Tsunewaki 1968; Liu and Tsunewaki 1991). In the1950s, it had been found that Asian spelta wheat has primitive chromosome constitutions, also different from European spelta wheat in some other genetic characteristics (Kuckuck and Schiemann 1957; Kuckuck 1959; Tsunewaki 1968). It is hence possible that Asian spelta wheat was formed by the hybridization between primitive *T. turgidum* and *T. tauschii*, and then Asian spelta wheat was evolved into naked grain common wheat.

Yang et al. (1992) found that naked grain common wheat cultivar Chinese Spring also contained three sets of primitive ABD chromosomes. The primitive chromosome structure of Chinese wheat probably suggests a relatively short evolutionary history. In addition, *T. aestivum* concv. *yunnanense* and *T. aestivum* concv. *tibetanum,* specially distributed in China, show primitive morphological traits such as hulled grains (Shao et al. 1980). However, they are distinct from spelta wheat in morphology. Chinese common wheat landraces are different from western common wheat in some characteristics. For instance, Chinese wheat has a high crossability with rye and the seed setting rate of inter-genus cross as high as 90% (Backhouse 1916; Zeven 1987; Luo et al. 1992, 1993a, b, 1994), due to having 1–4 recessive crossability genes of kr1, kr2, kr3, and kr4 (Zheng et al. 1992). Besides high crossability, oriental common wheat contains dwarf genes *Rht1* and *Rht2*. Based on these observations, some scholars put the possibility that China is also a place of wheat origination. If common wheat was formed in China, *T. turgidum* and *T. tauschii* in China should exhibit a similar genetic structure to Chinese common wheat. The synthetic hexaploid wheat "RSP" derived from a cross between Chinese *T. turgidum* cv. Ailanmai and Chinese *T. tausschii* is highly similar to *T. aestivum* concv. *Yunnanense* in morphology (Lan and Yen 1992). However, crossability genes are located on chromosomes 5A, 5B, 5D, and 1A in oriental common wheat, but on chromosomes 1A, 6A, and 7A in Chinese *T. turgidum* (Liu et al. 1999). Molecular genetic analysis of the D genome of *T. tauschii* and common wheat showed that the D genome of all common wheat including Chinese wheat was derived from *T. tauschii* var. *strangulatum*, not from the *T. tauschii* distributed in China (Lagudah et al. 1991; Ward et al. 1998). Therefore, it can be said that Chinese common wheat is more likely to be introduced from the West, although it has some unique special traits such as high crossability, ground glume, multifloret, and primitive chromosomal structure.

Primitiveness of chromosomal structure and traits may relate to the absence of artificial selection. In Tibet, some common wheat landraces are often mixed with the weed type wheat *T. aestivum* concv. *tibetanum* that has hulled grains and brittle rachis, indicating little artificial selection. Similarly, weed *Hordeum vulgare* “agriocrithon” is distributed in Tibet. The existence of the weed barley was once regarded as the evidence that six-rowed barley was originated in Tibet (Shao et al. 1975; Xu 1975, Shao et al. 1980). Weed barley (including six-/two-rowed, hulled/naked) in Tibet is also mixed in primitive landraces. However, both weed wheat and barley have no independent groups in natural vegetation. They share some common morphological and physiological characteristics with the symbiotic landraces. Weed wheat and barley could be derived from the genetic combinations or gene clustering dispersed in primitive landrace individuals. The gene pool of primitive landraces may contain primitive traits without being eliminated by consciously artificial selection. Therefore, the existence of primitive landraces does not indicate their origin in this region.

The distribution area of primitive varieties is often found at the edge of the outward expansion from the center of origin, because the new successor varieties formed in the center of origin would replace the primitive one, gradually from the origin center to the edge over time. The primitive varieties at edge of distribution areas would be replaced at last. Therefore, if primitive varieties still exist, they usually exist at the edge of the distribution area, where it is often relatively closed, usually in mountain areas. Such places were existed in Tibet several decades ago, and thus some of primitive varieties are preserved there.

Cultivated crop variety is the product of agricultural culture, formed by human unconscious or conscious selections. It is also one of the means of agricultural production. It arises neither in the cultural and technological lagging areas, nor in the wilderness areas occupied by wild species. Cultivated variety should appear in the cultural region, where it is adjacent to the wild species distribution area. If no wild species exists, the emergence of cultivated varieties is also impossible. The great agronomist Vavilov has put forward the origin center of eight major crops. He thought the origin center of China is located in southwestern mountain areas, according to the distribution of wild characteristics and genetic diversity. Vavilov's opinion is one of reasons that affected some scholars to consider Tibet as the origin center of crops. In China, some wheat groups have unique and primitive characteristics, such as in Sichuan white landrace group, *T. aestivum* concv. *yunnanense* and *T. aestivum* concv. *tibetanum*. This observation raises the question if China is an origin center of common wheat. In China, there are many cultivated tetraploid varieties. However, *T. tauschii* var. *strangulatum* has not been found in China, which is the D-genome donor varietas of common wheat.

The following question is: Where did Chinese common wheat come from? The results of molecular markers showed that the D genome of common wheat was derived from *T. tauschii* var. *strangulatum*, not from *T. tauschii* var. *typicum*. *T. tauschii* var. *strangulatum* is only distributed in the two separated areas: southwest of the Caspian Sea (northern Iran) and the Transcaucasia. Jaaska (1980) thought that the Transcaucasia is the possible origin place of common wheat. However, Nishikawa et al. (1980) suggested that northern is the birthplace of common wheat based on the α-amylase isozyme patterns. This suggestion was supported by RFLP analysis from different groups (Lagudah et al. 1991; Ward et al. 1998). More and more evidences have indicated that common wheat originated from northern Iran, at the distribution area of *T. tauschii* var. *strangulatum*. About 5000 years ago, the group containing special traits such as high crossability, round glumes, multiflorets, and primitive chromosome structure was eastwardly spread to the Han culture Center in the Reaches of Yellow River, then to Yunnan and Tibet in China, and Korea and Japan. In the secondary center, oriental wheat cultivars share many common traits but formed novel diversity by artificial selection. Due to the blockade of high mountains, lagging culture, and technology in Tibet and northwest Yunnan, the original varieties still conserved their primitive states, thus wild-type traits such as brittle rachis were preserved.

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Chapter 11
Artificially Synthesized Species and Genera

The artificial colchicine treatment or spontaneous chromosome doubling of interspecific/intergeneric hybrids can generate amphiploids that can set seeds. Using this strategy, many newly synthetic species or genus was produced. Some species, such as rye (*Secale*), *Haynaldia*, and *Lophopyrum*, are very easy to cross with wheat to produce hybrids even without special treatments such as embryo rescues. Generally, seedlings of intergeneric hybridization in Triticeae can be obtained by rescues of immature embryos at 14 days (sometimes 7 days) after cross-pollination. More distant hybridization such as wheat-maize can be also possible (Laurie and Bennett, 1986, 1987). Some successful examples of interspecific and intergeneric hybridization are shown in Table 11.1.

As early as the nineteenth century, humans generated synthetic hexaploid triticale (BBAARR)—*Tritiosecale rimpui* Wittmack—which is the first new species made by human. It is also a new genus *Tritiosecale*, and a man-made new crop. It has some uniquely fine traits emphasized by people. For example, the lysine content of grain is very high, about 2 times higher than that of wheat. It is a particularly excellent forage. After genetic improvement, it can also be used for human consumption.

Synthetic wheat and amphiploids using related species/genera of wheat may contain excellent genes which are not found in modern wheat and have been used in improving wheat varieties. There are many examples, such as introducing leaf rust resistance genes from *Aegilops* into common wheat. Synthetic hexaploid wheat has not been directly used in commercial production for a long time, because it contains many undesirable agronomic traits which do not meet the requirements of commodity production. However, Wuyun Yang of Sichuan Academy of Agricultural Sciences used “large population limited backcross” technology to improve synthetic hexaploid wheat that was derived from the crossing of durum wheat and *T. tauschii,* as materials via. After 15 years of breed selection, Chuanmai 42 and other several varieties were released in recent years. They have been applied in commercial production, and exhibited better yield potentials and disease and stress resistance compared to other varieties. It is also the first commercial variety derived from synthetic hexaploid wheat in the world. Since there is such an example, of course, there are successors.

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Table 11.1 Artificially synthesized species and their genome in Triticeae

Cross combination	Genome constitution	Pioneers of synthesis
T. turgidum × *Secale cereale*	**AABB/RR**	
T. monococcum × *Dasypyrum villosum*	**AA/VV**	
T. turgidum × *Das. villosa*	**AABB/VV**	Tschermak (1930)
T. aestivum × *S. cereale*	**AABBDD/RR**	Левитский and Бенецая (1931)
T. turgidum × *T. ovatum*	**AABB/UUM^{o}M^{o}**	Kihara and Katayama (1931)
T. triaristatum × *T. aestivum*	**UUX^{t}X^{t}/AABBDD**	Oehler (1934a, b)
T. caudatum × *T. turgidum*	**CC/AABB**	Oehler (1934a, b)
T. longissimum ×*T. turgidum*	**B^{1}B^{1}/AABB**	Sando (1935)
T. timopheevi× *T. monococcum*	**AAB^{sp}B^{sp}/A^{m}A^{m}**	костов (1936)
T. monococcum × *T. uniaristatum*	**AA/NN**	
T. triunciale × *T. turgidum*	**UUCC/AABB**	Oehler (1936)
T. turgidum × *Lophopyrum intermedium*	**AABB/E^{b}E^{b}E^{e}**	Хижняк (1937)
T. turgidum × *T. monococcum*	**AABB/A^{m}A^{m}**	Жебрак (1939)
T. turgidum × *T. turgidum*	**AABB/AABB**	Жебрак (1940a, b)
T. turgidum × *T. timopheevi*	**AABB/AAB^{sp}B^{sp}**	Жебрак (1941a, b, c)
T. timopheevi × *T. aestivum*	**AAB^{sp}B^{sp}/AABBDD**	Жебрак (1941a, b, c)
T. speltoides × *T. monococcum*	**B^{sp}B^{sp}/A^{m}A^{m}**	Sears (1941a, b)
T. bicorne × *T. monococcum*	**B^{b}B^{b}/A^{m}A^{m}**	Sears (1941a, b)
T. monococcum × *T. tauschii*	**A^{m}A^{m}/DD**	Sears (1941a, b)
T. monococcum × *Ae. umbellulatum*	**A^{m}A^{m}/UU**	Sears (1941a, b)
T. turgidum × *T. speltoides*	**AABB/B^{sp}B^{sp}**	Britten and Thompson (1941)
T. triaristatum var. *columnare* × *T. timopheevi*	**UUX^{t}X^{t}/AAB^{sp}B^{sp}**	
T. aestivum × *Lo. elongatum*	**AABBDD/ E^{b}E^{b}E^{b}E^{b}E^{e}E^{e}E^{e}E^{e}StSt**	Armstrong and Mclenna (1944)
T. cylindricum × *T. turgidum*	**CCDD/AABB**	Sears (1944)
T. turgidum × *T. aestivum*	**AABB/AABBDD**	Жебрак (1944a, b)
T. aestivum × *T. aestivum*	**AABBDD/AABBDD**	
T. turgidum × *T. tauschii*	**AABB/DD**	McFadden and Sears (1944)
T. turgidum × *T. caudatum*	**AABB/CC**	McFadden and Sears (1946)
T. timopheevi × *T. umbellulatum*	**AAB^{sp}B^{sp}/UU**	McFadden and Sears (1947)
T. timopheevi × *T. caudatum*	**AAB^{sp}B^{sp}/CC**	McFadden and Sears (1947)
T. timopheevi × *T. tauschii*	**AAB^{sp}B^{sp}/DD**	McFadden and Sears (1947)
T. timopheevi × *T. speltoides*	**AAB^{sp}B^{sp}/B^{sp}B^{sp}**	McFadden and Sears (1947)

(continued)

Table 11.1 (continued)

Cross combination	Genome constitution	Pioneers of synthesis
T. timopheevi × *T. bicorne*	$\mathbf{AAB^{sp}B^{sp}/B^{b}B^{b}}$	Li and Tu (1947); McFadden and Sears (1947)
T. timopheevi × *T. uniaristatum*	$\mathbf{AAB^{sp}B^{sp}/NN}$	McFadden and Sears (1947)
T. ventricosum × *T. turgidum*	**DDNN/AABB**	Сорокина (1937)
T. turgidum × *Leymus racemosus*	**BBAA/NsXm**	
T. timopheevi × *T. longissmum*	$\mathbf{AAB^{sp}B^{sp}/B^{1}B^{1}}$	Kaschiri (1975)
T. aestivum × *Lo. intermedium*	$\mathbf{BBAADD/E^{e}E^{e}E^{e}E^{e}StSt}$	Cauderon (1966)
T. aestivum × *Lo. ponticum*	$\mathbf{BBAADD/E^{b}E^{b}E^{b}E^{b}E^{e}E^{e}E^{e}E^{e}StSt}$	Cauderon (1966)
T. monococcum × *S. cereale*	$\mathbf{A^{m}A^{m}/RR}$	Knobloch (1968)
T. turgidum × *Hordeum brevisubulatum*	**BBAA/HHHH**	Knobloch (1968)
T. timopheevi × *Ag. cristatum*	**BBAA/PP**	Knobloch (1968)
T. timopheevi × *Lo. intermedium*	$\mathbf{B^{sp}B^{sp}AA/E^{e}E^{e}E^{e}E^{e}StSt}$	Knobloch (1968)
T. timopheevi × *Lo. ponticum*	$\mathbf{B^{sp}B^{sp}AA/E^{b}E^{b}E^{b}E^{b}E^{e}E^{e}StSt}$	Knobloch (1968)
T. timopheevi × *Elymus repens*	**StStStStHH**	Knobloch (1968)
T. timopheevi × *S. vavilovii*	$\mathbf{B^{sp}B^{sp}AA/RR}$	Knobloch (1968)
T. timopheevi × *Das. villosum*	$\mathbf{B^{sp}B^{sp}AA/VV}$	Knobloch (1968)
T. monococcum × *H. vulgare*	$\mathbf{A^{m}A^{m}/II}$	Kruse (1973)
T. turgidum × *H. vulgare*	**BBAA/II**	Kruse (1973)
T. aestivum × *H. vulgare*	**BBAADD/II**	
T. aestivum × *H. vulgare var. spontaneum*	**BBAADD/II**	Bates et al. (1976)
T. aestivum × *H. chilense*	**BBAADD/HH**	Martin and Chapman (1977)
T. timopheevi × *H. vulgare*	$\mathbf{B^{sp}B^{sp}AA/II}$	Cauderon et al. (1978), Kimber and Abubaker (1979)
T. monococcum × *Lo. intermedium*	$\mathbf{A^{m}A^{m}/E^{e}E^{e}St}$	Kimber and Abubaker (1979)
T. monoicoccum × *Lo. ponticum*[a]	$\mathbf{A^{m}A^{m}/E^{b}E^{b}E^{b}E^{b}E^{e}E^{e}E^{e}E^{e}StSt}$	Kimber and Abubaker (1979)
T. turgidum × *H. chilense*	**BBAA/HH**	Martin and Laguna (1980)
T. timopheevi × *Lo. junceiforme*	$\mathbf{B^{sp}B^{sp}AA/E^{b}E^{b}E^{e}E^{e}}$	Kimber and Abubaker (1979)
T. timopheevi × *S. cereale*	$\mathbf{B^{sp}B^{sp}AA/RR}$	Kimber and Abubaker (1979)
T. timopheevi × *S. africanum*	$\mathbf{B^{sp}B^{sp}AA/RR}$	Kimber and Abubaker (1979)

(continued)

Table 11.1 (continued)

Cross combination	Genome constitution	Pioneers of synthesis
T. timopheevi × *H. bogdanii*	**B^{sp}B^{sp}AA/HH**	Kimber and Abubaker (1979)
T. aestivum × *H. bulbosum*	**BBAADD/I^{b}I^{b}**	
T. aestivum × *H. pusillum*	**BBAADD/HH**	Finch and Bennett (1980)
T. aestivum × *Le. racemosus*	**BBAADD/NsXm**	Mujeeb and Rodriguez (1980)
T. aestivum × *Lo. podperae*	**BBAADD?**	Dewey (1981)
T. aestivum × *Das. villosum*	**BBAADD/VV**	

Note: Modified and updated according to Kihara et al. (1954)

[a] The Latin name "*Elytrigia elongata*" is used by Armstrong and Mclennan. "*elongata"* should be a diploid. The decaploid species may be *Lophopyrum ponticum* (Podp.) A. Löve

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Appendix: Taxon Directory of *Triticum-Aegilops* complex

Aegilops L.

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Triticum polonicum var. *compactum* Link, Berol. 1: 28. 1827.

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Triticum polonicum subsp. *compactum* var. *elongatum* Koern., in Koern. et Wern. Handb. Getreideb. 1: 102. 1885.

Triticum polonicum subsp. *compactum* var. *halleri* Koern., in Koern. et Wern. Handb. Getreideb. 1: 104. 1885.

Triticum polonicum subsp. *componactum* var. *intermedium* Koern., in Koern. et Wern. Handb. Getreideb. 1: 104. 1885.

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Triticum polonicum subsp. *oblongum* var. *anomalum* Koern., in Koern. et Wern. Handb. Getreideb. 1: 100. 1885.

Triticum polonicum subsp. *oblongum* var. *incertum* Koern., in Koern. et Wern. Handb. Getreideb. 1: 100. 1885.

Triticum polonicum subsp. *oblongum* var. *rubrovelutinum* Koern., in Koern. et Wern. Handb. Getreideb. 1:100. 1885.

Triticum polonicum subsp. *oblongum* var. *rufescens* Koern., in Koern. et Wem. Handb. Getreideb. 1: 100. 1885.

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Triticum polonicum subsp. *quadratum* var. *nigrescens* Koern., in Koern et Wern., Handb. Getreideb 1: 101. 1885.

Triticum polonicum subsp. *quadratum* var. *seringei* Koern., in Koern. et Wern., Handb. Getreideb. 1: 101. 1885.

Triticum polonicum subsp. *quadratum* var. *vilmorini* Koern., in Koern. et Wern. Handb. Getreideb. 1: 101. 1885.

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Triticum repens var. *arenosum* Spenner, Fl. Friburg. 1: 162. 1825.

Triticum repens var. *arenosum* Meinshaus, Fl. Ingr. 425. 1878. Not. Spenner 1825.

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Triticum repens var. *aristatum* Parnell, Grasses Sootl. 11: 137. pl. 63. 1842. Not Suter, 1802 or Stokes, 1812.

Triticum repens var. *aristatum* Doell, Fl. Bed. 1:128. 1855. Not Suter, 1802.

Triticum repens var. *aristatum* Doell, Fl. Grossh. Baden 128. 1857. Not Suter, 1802.

Triticum repens var. *aristatum* Neilreich, Fl. Nieder-Oesterr. 85. 1859. Not Suter, 1802.

Triticum repens aristatum Blytt, Morges Fl. 163 [err. 363.] 1861. Not Stuer, 1802.

Triticum repens var. *aristatum* Hein, Graeserfl. 152. 1877. Not Suter, 1802.

Triticum repens subvar. *aristatum* Coss. et Germ., Fl. Env. Paris ed. 2. 852. 1861.

Triticum repens var. *aristatum* 1. *dumetorum* (Schreb.) Doell, Fl. Grossh. Baden 128. 1857.

Triticum repens var. *aristatum* 4. *pubescens* Doell, Fl. Grossh. Baden. 129. 1857.

Triticum repens var. *aristatum* 3. *sepium* (Thulll.) Doell, Fl. Grossh. Baden 129. 1857.

Triticum repens var. *aristatum* 2. *vaillantinum* (Wulf.) Doell, Fl. Grossh. Baden. 129. 1857.

Triticum repens arundinaceum Fries, Summ. Veg. Boand. 250. 1846.
Triticum repens var. *arvense* (Schreb.) Mutel., Fl. Franc. 4: 145. 1837.
Triticum repens var. *arvense* Hartm., Handb. Scand. Fl. ed. 5. 283. 1849. Not. Mutel, 1837.
Triticum repens var. *arvense* (Schrank) Hausm., Fl. Tirol 2:1018. 1852. Not Nutel 1837.
Triticum repens var. *arvense* Meinshaus, Fl. Ingr. 426. 1878. Not Nutel, 1837.
Triticum repens var. *boreale* Laestad, Nya Bot. Not. 1856: 77. 1856.
Triticum repens var. *caesium* (Presl) Laestad, Nya Bot. Not. 1856: 78. 1856.
Triticum repens var. *caesium* Doell, Fl. Grossh. Baden 130. 1857. [same as (Presl) Laest., 1856]
Triticum repens var. *capillare* Pers., Syn. Pl. 1: 109. 1805
Triticum repens var. *compactum* Vasey in Wheeler, Rep. U. S. Surv. W. 100th Merid 6: 293. 1878. No description.
Triticum repens var. *dasystachyum* Hook., Fl. Bor. Ame. 2: 254. 1840.
Triticum repens var. *domesticum* Laestad, Nya Bot. Not. 1856: 78. 1856.
Triticum repens var. *dubium* Laestad, Nya Bot. Not. 1856: 77. 1856.
Triticum repens var. *dumetorum* (Hoffm.) Mutel., Fl. Franc. 4: 145. 1837.
Triticum repens var. *dumetorum* Guss. Fl. Sic. Syn. 1: 67. 1843.
Triticum repens var. *dumetorum* (Schrank) Hausm., Fl. Tirol. 2:1018. 1852. Not (Hoffm) Mutel, 1837.
Triticum repens dumetorum Blytt, Norges Fl. 163. [err. 363.] 1861. Not (Hoffm. Mutel, 1837.
Triticum repens var. *elymoides* Spenner, Fl. Friburg. 1: 161. 1825.
Triticum repens subsp. *eu-repens* var. *barbatum* Duval-Jouve ex Syme, in Sowerby, Engl. Bot. ed. 3. 11: 179. 1873.
Triticum repens subsp. *eu-repens* var. *litoreum* "aendert ab." *aristatum* Aschers. et Graebn. Syn. Mitteleur. Fl. 2: 1802. 1901.
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Triticum repens subsp. *eu-repens* var. *salinum* (Hack.) Aschers. et Graebn. Syn. Mitteleur. Fl. 2: 649. 1901.
Triticum repens subsp. *eu-repens* var. *stenophyllum* Aschers & Grasbn. Syn. Mitteleur. Fl. 2: 636. 1901.
Triticum repens f. *firmum* (Presl.) Mutel., Fl. Franc. 4: 146. 1837.
Triticum repens [subsp. II. *T. pungens*] var. *genuium* Syme, in Sowerby, Engl. Bot. ed. 3, 11: 180. p1. 1811. 1873.
Triticum repens var. *glaucescens* G. Meyer, Chloris Hanov. 611. 1836. No description.
Triticum repens var. *glaucescens* Aschers. et Graebn., Syn. Mitteleur. Fl. 2: 650. 1901.
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Triticum repens var. *glaucum* Gray, Gram. & Cyp. 2: 128. 1835. nom. nud.
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Triticum repens var. *glaucum* Blytt, Norges Fl. 363. 1863. Not. Neilreich 1859.

Triticum repens var. *glaucum* Vasey in Whealer, Rep. U. S. Surv. W. 100th Merid. 6: 293. 1878. No description.

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Triticum repens Hegetschw. et Heer, Fl. Schweiz 101. 1840. Not L. 1753.

Triticum repens var. *hirsutum* Grun., Bull. Soc. Nat. Moscou 42: 32. 1869.

Triticum repens var. *imbricatum* (Lam.) Guss., Suppl. Fl. Sic. Prodr. 1: 34. 1832.

Triticum repens var. *intermedium* Wahlenb., Fl. Suec. 1: 77. 1824.

Triticum repens var. *junceum* (Reih.) J. E. Smith, Bogl. Fl. 1: 183. 1824. without descr.

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Triticum repens × *junceum* subsp. *megastachyum* (Lange) Aschers. et Graebn., Syn. Mitteleur. Fl. 2: 665. 1901.

Triticum repens × *junceum* I. *microstachyum* (Fries) Aschers. et Graebn., Syn. Mitteleur. Fl. 2: 665. 1901.

Triticum repens × *junceum* B I. *normale* Aschers. et Graebn., Syn. Mitteleur. Fl. 2: 665. 1901.

Triticum repens × *junceum* B II. *obtusiusculum* (Lange) Aschers. et Graebn., Syn. Mitteleur. Fl. 2: 666. 1901.

Triticum repens var. *leersianum* Guss., Suppl. Fl. Sic. Prodr. 1: 34. 1832.

Tritifum repens var. *leersianum* (Schrank.) Hauem., Fl. Tirol. 2: 1019. 1852. see Guss. 1832.

Triticum repens var. *leersianum* Moinshaus, Fl. Ingr. 426. 1878. see Guss. 1832.

Triticum repens var. *litoreum* Anderss., Pl. Scand. Gram. 5. 1852.

Triticum repens litoreum (Schumach.) Hook. f. Stud. Fl. Brit. Isles 454. 1870. see An-derss. 1852.

Triticum repens var. *littorals* (Host) Mutal., Fl. Franc. 4: 146. 1837.

Triticum repens var. *littorale* Hartm., Handb. Skand. Fl. ed. 5. 283. 1849. Not (Host) Mutal. 1837.

Triticum repens var. *littorale* Bab., Man. Brit. Bot. Ei. 3. 400. 1851. Not. *T. repens-var*. littorale (Host) Mutal.

Triticum repens littorale Blytt, Morges Fl. 163. [err. 363] 1861. see same (Host) Mutel 1837.

Triticum repens [subsp. II. *T. pungens*] var. *littorale* (Host) Syme, in Sowerby, Engl. Bot. ed. 3. 11: 180. 1873.

Triticum repens var. *magellanicum* E. Desv., in Gay, Fl. Chil. 6: 452. 1853.

Triticum repens var. *maius* Doell ex Domin, Sitzungsb. Akad. Wiss. Math. Naturw. (Wien) 1904: 74. 1905. see Doell 1855.

Triticum repens var. major Doell, Rhein. Fl. 69. 1843. var. majus Doell, Fl. Badenh. 129. 1855.

Triticum repens var. *maritisum* Smith ex Roth, Neue Beitr. 1: 137. 1802.

Triticum repens var. *maritimum* (Koch and Ziz) Doell, Rhein Fl. 69. 1843. Not Smith ex Roth 1802.

Triticum repens var. *minus* Hook., Fl. Bor. Amer. 2: 254. 1840.

Triticum repens var. *mucronatum* Stokes, Bot. Nat. Ned. 1: 181. 1812.

Triticum repens var. *muoronatum* Hartm., Handb. Skand. Fl. 283. 1849. Not Stokes 1812.

Triticum repens var. *multiflorum* Pers., Syn. Pl. 1: 109. 1805.

Triticum repens var. *mutica* Bodl., Ann. Wien Mus. Naturgesch. 1: 158. 1836, no description. Not var. *muticum* Schvebl. & Martens. 1824.

Triticum repens var. *muticum* Schuebl. et Nartens, Fl. Wurtemberg 47. 1834.

Triticum repens var. *nanum* Hook., Fl. Bor. Amer. 2: 254. 1840.

Triticum repens var. *nemorale* Anderss., Pl. Scand. Gram. 4. 1852.

Triticum repens var. *nodosum* Stev. ex Griseb., in Ledeb. Fl. Ross. 4: 341. 1853.

Triticum repens var. *obtusiflorum* Spenner, Fl. Friburg. 1: 161. 1825.

Triticum repens [subsp. I. *T. eu-repens*] var. *obtusum* Syme, in Sowerby. Engl. Bot. ed. 3. 11: 179. 1873.

Triticum repens var. *pauciflorum* Nerat., Fl. Par. ex. 4. 2: 17. 1836.

Triticum repens [subsp. *pungens*] var. *pycnanthum* Syme, in Sowerby. Engl. Bot. ed. 3. 11: 180. 1873.

Triticum repens remificum Link, Linnaea 9: 133. 1835.

Triticum repens var. *scabrifolium* Doell, in Mart. Fl. Bras 23: 226. 1880.

Triticum repens var. *scabrifolium* f. vulgaris Doell, in Mart. Fl. Bras. 23: 226. 1880.

Triticum repens var. *sepium* (Thuill.) Borbas, Math. Termesz. Kozles 15: 342. 1878.

Triticum repens var. *strictum* G. Meyer, Chloris Hanov. 611. 612. 1836.

Triticum repens var. *subconvolutum* Link, Linnaea 17: 397. 1843.

Triticum repens var. *subulatum* (Schweigger) Guss., Suppl. Fl. Sic. Prodr. 1: 34. 1832.

Triticum repens var. *subulatum* Mutel., Fl. Franc. 4:145. 1837.

Triticum repens var. *subulatum* Meinshaus., Fl. Ingr. 436. 1878. Not. Guss. 1832.

Triticum repens var. *subvillosum* Hook., Fl. Bor. Amer. 2: 254. 1840.

Triticum repens var. *tenerum* Vasey, in Wheeler, Rep. U. S. Surv. W. 100th Nerid. 6: 293. 1878. No description.

Triticum repens var. *vaillantianum* G. Meyer, Chloris Hanov. 611. 1836. No description.

Triticum repens var. *vaillantianum* (Wulf.) Hauss., Fl. Tirol 2: 1019. 1852.

Triticum repens var. vaillantii Meinshauson, Fl. Ingr. 426. 1878.

Triticum repens var. *violaoceum* Hartm., Handb. Skand. Fl. ed. 4. 43. 1843.

Triticum repens var. *vulgare* Spenner, Fl. Friburg. 1: 161. 1825.

Triticum repens var. *vulgare* Doell, Fl. Baden 1: 128. 1857.

Triticum repens var. *vulgare* Neilreich, Fl. Mieder-Oasterr. 85. 1859.

Triticum repens [Clairv.] Man., Herbor. 26. 1811.

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Triticum richardsoni Schrad., Linnaea 12: 467. 1838.

Triticum rigidum Schrad., Sem. Nort. Gotting (1803): 23. Fl. Germ. 1: 392. 1806.

Triticum rigidum var. *banaticum* Heuff., Varh. Zool-Bot. Ges. Wien 8: 235. 1858.

Triticum rigidum var. *ruthenicum* Griseb., in Ledeb. Fl. Ross. 4: 342. 1853.

Triticum rigidum var. *stipaefolium* Trautv. ex Fedtsch., Bull. Jard. Bot. Pierre Grand 14 (Suppl. 2): 96. 1915, as syn. of *Agropyron elongatum* var. *stipaefolium* Fedtsch.

Triticum rigidum var. *tomentosum* Regel, Acta Hort. Petrop. 7: 592. 1881.

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Triticum roegnerii Griseb., in Ledeb. Fl. Ross. 4:339. 1853.

Triticum rossicum Flaksb., Bull. Appl. Bot. Pl. Breed. 8: 501. 1915. nom. nud. The synonym for *T. dicoccum* var. *ferrugineum* Al..

Triticum rottboellia Lam. et DC., Fl. Franc. 3: 86. 1805.

Triticum rottboellioides Duval-Jouve ex Aschers. et Graebn., Syn. Mitteleur. Fl. 2: 660. 1901.

Triticum rouxii (Gren. & Duval-Jouv.) Nym. Consp. 842. 1882.

Triticum rufescens Hort. ex Steud., Nom. Bot. ed. 2. 2: 717. 1841, the synonym for *T. spelta* L..

Triticum rufinflatum Flaksb., Bull. Appl. Bot. Pl. Breed. 8: 501. 1915. nom. nud; the synonym for *Triticum dicoccum* var. *milturum* Al..

Triticum rupestre Link, Enum. Hort. Berol. 1: 98. 1821.

Triticum rupestre Turcz. ex Ganewin, Trav. Mus. Bot. Acad. Sci. Petrograd 13: 33. 1915. No description. Not Link,1821.

Triticum sabulesum (Marsch-Bieb.) Hera., Ver. Bot. Ver. Brand. 76: 43. 1936.

Triticum salinum Salzm. ex Steud., Nom. Bot. ed. 2. 2: 717. 1841, nom. nud.

Triticum sanctum (Janka) F. Hermann, Repert. Sp. Nov. Fedde 44: 159. 1938.

Triticum sadinicum Koel. ex Spreng., Syst. Veg. 1: 323. 1825. The synonym for *Triticum vulgare* var. *turgidum* Spreng..

Triticum sartorii (Boiss. & Heldr.) Boiss. er Heldr. ex Nym., Consp. 840. 1882.

Triticum sativum Lam., Fl. France 3: 625. 1778.

Triticum sativum var. *aestivum* (L.) Wood, Classbook. ed. 2. 619. 1847.

Triticum sativum var. *aristatum* Coss. et Germ, Fl. Env. Paris 2: 658. 1845.

Triticum sativum brigantiacum Desv., Opusc. 164. 1831.

Triticum sativum capense Desv., Opusc. 163. 1831.

Triticum sativum × *cereale* Aschers. et Graebn., Syn. Mitteleur. Fl. 2: 719. 1902.

Triticum sativum subsp. *compactum* Hiitcoen, Sucmen. Kasvis 224. 1933.

Triticum sativum compactum (Host.) Desv., Opusc. 164. 1831. Same (Host) Book. 1890.

Triticum sativum var. *compactum* (Host) Book, Fl. Nieder-Osterr. 1: 116. 1890. Refer to Desv. 1831.

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Triticum sativum var. *erythrospermum* (Koern. et Wern.) Degen, Fl. Veleb. 1: 575. 1936.
Triticum sativum etruscum Desv., Opuec. 160. 1831.
Triticum sativum etruscum griseum Desv., Opusc. 160. 1831.
Triticum sativum etruscum lutesoens Desv., Opusc. 160. 1831.
Triticum sativum herinaceum (Hornem.) Desv., Opusc. 349. 1834.
Triticum sativum var. *hybernum* (L.) St. Amans., Fl. Agen. 53. 1821.
Triticum sativum var. *monococcum* (L.) Vilm., Blunengartn. 1218. 1896.
Triticum sativum × *monococcum* Aschers. et Graebn., Syn. Mitteleur. Fl. 2: 702. 1901.
Triticum sativum var. *mutica* alba Bayle-Barelle, Monogr. Agron. Cereali 46. pl. 3. f. 14. 1809.
Triticum sativum var. *muticum* Coss. et Germ., Fl. Env. Paris 2: 658. 1845.
Triticum sativum neapolitanum Desv., Opusc. 164. 1831.
Triticum sativum × *ovatum* Aschers. et Graebn., Syn. Mitteleur Fl. 2: 713. 1902.
Triticum sativum pictatianum Desv., Opuec. 163. 1831.
Triticum sativum var. *pilosa* (Dalz. & Giba) Cooke, Fl. Bombay 2: 1052. 1908.
Triticum sativum × *polonicum* Aschers. et Graebn., Syn. Mitteleur. Pl. 2: 700. 1901.
Triticum sativum pyramidale Delile,Fl. Aeg. 178. p1. 14. f. 3. 1812.
Triticum sativum rubeolarium Desv., Opusc. 165. 1831.
Triticum sativum rubescens Desv., Opusc. 163. 1831.
Triticum sativum var. *ruffa aristata* Bayle-Barelle, Monogr Agron. Cereali 48. p1. 3. f. 16. 1809.
Triticum sativum var. *ruffa muticum* Bayle-Barelle, Monogr. Agron. Cerali 49. p1. 3. f. 17. 1809.
Triticum sativum semi-barbatum Desv., Opusc. 159. 1831.
Triticum sativum siculum Desv., Opusc. 160. 1831.
Triticum sativum sinense Desv., Opusc. 159. 1831.
Triticum sativum spartheum Desv., Opusc. 160. 1831.
Triticum sativum var. spelta (L.) Richt. Pl. Eur. 1: 129. 1890.
Triticum sativum tenax Hack., in Engl, & Prantl, Pflanzenfam. 22: 85. 1887.
Triticum sativum trimestre Desv., Opuac. 162. 1831.
Triticum sativum trimestre nanum Desv., Opusc. 164. 1831.
Triticum sativum × *triunciale* Aschers. et Graebn. Syn. Mitteleur. Fl. 2: 714. 1902.
Triticum sativum var. *turgidum* (L.) Delile, Fl. Aeg. 177. pl. 14. f. 2. 1812.
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Triticum tenax var. *africanum* (Koern.) Aschers. et Graebn., Syn. Mitteleur. Fl. 2:695. 1901.

Triticum tenax var. *albiceps* (Koern.) Aschers. et Graebn., Syn. Mitteleur. Fl. 2: 689. 1901.

Triticum tenax var. *albidum* (Alefeld) Aschers. et Greebn., Syn. Mitteleur. Fl. 2: 684. 1901.

Triticum tenax var. *albirurum* (Koern.) Aschers et Graebn., Syn. Mitteleur. Fl. 2: 684. 1901.

Triticum tenax var. *alexandrinum* (Koern.) Aschers. et Graebn., Syn. Mitteleur. Fl. 2: 694. 1901.

Triticum tenax var. *apulicum* (Koern.) Aschers. et Graebn., Syn. Mitteleur. Fl. 2: 695. 1901.

Triticum tenax var. *arrasseita* (Hoochst.) Aschers. et Grern, Syn. Mitteleur. Fl. 2: 693. 1901.

Triticum tenax atriceps (Koern.) Aschers. et Gaebn., Syn. Mitteleur. Fl. 2: 688. 1901.

Triticum tenax var. *barbarossa* (Alefeld) Aschers. et Graebn., Syn. Mitteleur. Fl. 2: 686. 1901.

Triticum tenax var. *barbarum* Aschers. et Graebn., Syn. Mitteleur. Fl. 2: 693. 1901.

Triticum tenax var. *buccale* (Alefeld) Aschers. et Graebn., Syn. Mitteleur. Fl. 2: 691. 1901.

Triticum tenax var. *caesium* (Alefeld) Aschers. et Graebn., Syn. Mitteleur. Fl. 2: 685. 1901.

Triticum tenax var. *campylodon* (Koern.) Aschers. et Graebn., Syn. Mitteleur. Fl. 2: 693. 1901.

Triticum tenax var. *candidissimum* (Arduinj.) Aschers. et Graebn., Syn. Mitteleur. Fl. 2: 693. 1901.

Triticum tenax var. *centigranium* Aschers. et Graebn., Syn. Mitteleur. Fl. 2: 692. 1901.

Triticum tenax var. *cervinum* (Alefeld) Aschers. et Graebn., Syn. Mitteleur. Fl. 2: 691. 1901.

Triticum tenax var. *circumflexum* (Koern.) Aschers. et Graebn., Syn. Mitteleur. Fl. 2: 695. 1901.

Triticum tenax var. *clavatum* (Alefeld) Aschers. et Graebn., Syn. Mitteleur. Fl. 2: 688. 1901.

Triticum tenax var. *coeruleivelutinum* Aschers. et Graebn., Syn. Mitteleur. Fl. 2: 686. 1901.

Triticum tenax var. *coeruleacsens* (Bayle-Barelle) Aschers. et Graebn. Syn. Mitteleur. Fl. 2: 695. 1901.

Triticum tenax var. *columbinum* (Alefeld) Aschers. et Graebn., Syn. Mitteleur. Fl. 2: 691. 1901.

Triticum tenax var. *compactum* (Host.) Aschers. et Graebn., Syn. Mitteleur. Fl. 2: 686. 1901.

Triticum tenax var. *crassiceps* (Koern.) Aschers. et Graebn., Syn. Mitteleur. Fl. 2: 688. 1901.

Triticum tenax var. *creticum* Aschers. et Graebn., Syn. Mitteleur. Fl. 2: 687. 1901.

Triticum tenax "Q" [var.] *cyanothrix* (Koern.) Aschers. & Graebn. Syn. Mitteleur. Fl. 2: 685. 1901.

Triticum tenax var. *delfii* Aschers. et Graebn., Syn. Mitteleur. Fl. 2: 684. 1901.

Triticum tenax var. *dinurum* (Alefeld) Aschers. et Graebn., Syn. Mitteleur. Fl. 2: 691. 1901.

Triticum tenax var. *dreischianum* (Koern.) Aschers. et Graebn., Syn. Mitteleur. Fl. 2: 690. 1901.

Triticum tenax var. *dubium* (Koern.) Aschers. et Graebn., Syn. Mitteleur. Fl. 2: 691. 1901.

Triticum tenax subsp. *durum* (Desf.) Aschers. et Graebn., Syn. Mitteleur. Fl. 2: 692. 1901.

Triticum tenax subsp. *durum* var. *fastuosum* (Leg.) Aschers. et Graebn., Syn. Mitteleur. Fl. 2: 694. 1901.

Triticum tenax subsp. *durum* X polonicum Aschers. et Graebn., Syn. Mitteleur. Fl. 2: 692. 1901.

Triticum tenax var. *echinodes* (Koern.) Aschers. et Graebn., Syn. Mitteleur. Fl. 2: 689. 1901.

Triticum tenax var. *erinaceum* Aschers. et Graebn., Syn. Mitteleur. Fl. 2: 688. 1901.

Triticum tenax var. *erthroleucon* (Koern.) Aschers. et Graebn., Syn. Mitteleur. Fl. 2: 685. 1901.

Triticum tenax var. *erythromelan* (Koern.) Aschers. et Graebn., Syn. Mitteleur. Fl. 2: 694. 1901.

Triticum tenax var. *erythrospernum* (Koern.) Aschers. et Graebn., Syn. Mitteleur. Fl. 2: 685. 1901.

Triticum tenax var. *ferrugineum* (Alef.) Aschers. et Graebn., Syn. Mitteleur. Fl. 2: 685. 1901.

Triticum tenax var. *fetisowii* (Koern.) Aschers. et Graebn., Syn. Mitteleur. Fl. 2: 688. 1901.

Triticum tenax var. *fuliginosum* (Alefeld) Aschers. et Graebn., Syn. Mitteleur. Fl. 2: 686. 1901.

Triticum tenax var. *gentile* (Alefeld) Aschers. et Graebn., Syn. Mitteleur. Fl. 2: 689. 1901.

Triticum tenax var. *graecum* (Koern.) Aschers. et Graebn., Syn. Mitteleur. Fl. 2: 685. 1901.

Triticum tenax var. *hererae* (Koern.) Aschers. et Graebn., Syn. Mitteleur. Fl. 2: 690. 1901.

Triticum tenax var. *hordeiforme* Aschers. et Graebn., Syn. Mitteleur. Fl. 2: 694. 1901.

Triticum tenax var. *hostianum* (Clem. y Rubio) Aschers. et Graebn., Syn. Mitteleur. Fl. 2: 685. 1901.

Triticum tenax var. *humboldtii* (Koern.) Aschers. et Graebn., Syn. Mitteleur. Fl. 2: 687. 1901.

Triticum tenax var. *hystrix* Aschers. et Graebn., Syn. Mitteleur. Fl. 2: Lief. 26: 82. 1903. 2: 688. 1901.

Triticum tenax var. *icterinum* (Alefeld) Aschers. et Graebn., Syn. Mitteleur. Fl. 2: 688. 1901.

Triticum tenax var. *iodurum* (Alefeld) Aschers. et Graebn., Syn. Mitteleur. Fl. 2: 691. 1901.

Triticum tenax var. *italicum* (Alefeld) Aschers. et Graebn., Syn. Mitteleur. Fl. 2: 695. 1901.

Triticum tenax var. *leucomelan* (Alefeld) Aschers. et Graebn., Syn. Mitteleur. Fl. 2: 693. 1901.

Triticum tenax var. *leucurum* (Alefeld) Aschers. et Graebn., Syn. Mitteleur. Fl. 2: 693. 1901.

Triticum tenax var. *libycum* (Koern.) Aschers. et Graebn., Syn. Mitteleur. Fl. 2: 695. 1901.

Triticum tenax var. *linaza* (Koern.) Aschers. et Graebn., Syn. Mitteleur. Fl. 2: 687. 1901.

Triticum tenax var. *linnaeanum* (Alefeld) Aschers. et Graebn., Syn. Mitteleur. Fl. 2: 692. 1901.

Triticum tenax var. *lusitanicum* (Koern.) Aschers. et Graebn., Syn. Mitteleur. Fl. 2: 689. 1901.

Triticum tenax var. *lutescens* (Alefeld) Aschers. et Graebn., Syn. Mitteleur. Fl. 2: 684. 1901.

Triticum tenax var. *martensii* (Koern.) Aschers. et Graebn., Syn. Mitteleur. Fl. 2: 690. 1901.

Triticum tenax var. *megalopolitanum* (Koern.) Aschers. et Graebn., Syn. Mitteleur. Fl. 2: 691. 1901.

Triticum tenax var. *melanatherum* (Koern.) Aschers. et Graebn., Syn. Mitteleur. Fl. 2: 689. 1901.

Triticum tenax var. *melanopus* (Alefeld) Aschers. et Graebn., Syn. Mitteleur. Fl. 2: 695. 1901.

Triticum tenax var. *meridionale* (Koern.) Aschers. et Graebn., Syn. Mitteleur. Fl. 2: 685. 1901.

Triticum tenax var. *mirabile* (Koern.) Aschers. et Graebn., Syn. Mitteleur. Fl. 2: 692. 1901.

Triticum tenax subsp. *molle* Aschers. et Graebn., Syn. Mitteleur. Fl. 2: 685. 1901.

Triticum tenax var. *murciense* (Koern.) Aschers. et Graebn., Syn. Mitteleur. Fl. 2: 694. 1901.

Triticum tenax var. *nigribarbatum* (Desv.) Aschers. et Graebn., Syn. Mitteleur. Fl. 2: 690. 1901.

Triticum tenax var. *nigrum* (Koern.) Aschers. et Graebn., Syn. Mitteleur. Fl. 2: 685. 1901.

Triticum tenax var. *niloticum* (Koern.) Aschers. et Graebn., Syn. Mitteleur. Fl. 2: 695. 1901.

Triticum tenax var. *obsourum* (Koern.) Aschers. et Graebn., Syn. Mitteleur. Fl. 2: 694. 1901.

Triticum tenax var. *pavoninum* (Alefeld) Aschers. et Graebn., Syn. Mitteleur. Fl. 2: 691. 1901.

Triticum tenax var. *plinianum* (Koern.) Aschers. et Graebn., Syn. Mitteleur. Fl. 2: 692. 1901.

Triticum tenax var. *provincial* (Alefeld) Aschers. et Graebn., Syn. Mitteleur. Fl. 2: 694. 1901.

Triticum tenax var. *pseudocervinum* (Koern.) Aschers. et Graebn., Syn. Mitteleur. Fl. 2: 691. 1901.

Triticum tenax var. *pyrothrix* (Alefeld) Aschers. et Graebn., Syn. Mitteleur. Fl. 2: 684. 1901.

Triticum tenax var. *reichenbachii* (Koern.) Aschers. et Graebn., Syn. Mitteleur. Fl. 2: 693. 1901.

Triticum tenax var. *rubriatrum* (Koern.) Aschers. et Graebn., Syn. Mitteleur. Fl. 2: 691. 1901.

Triticum tenax var. *rubriceps* (Koern.) Aschers. et Graebn., Syn. Mitteleur. Fl. 2: 689. 1901.

Triticum tenax var. *rubrum* (Koern.) Aschers. et Graebn., Syn. Mitteleur. Fl. 2: 688. 1901.

Triticum tenax var. *rufulum* (Koern.) Aschers. et Graebn., Syn. Mitteleur. Fl. 2: 687. 1901.

Triticum tenax var. *salomonis* (Koern.) Aschers. et Graebn., Syn. Mitteleur. Fl. 2: 691. 1901.

Triticum tenax var. *sardoum* Aschers. et Graebn., Syn. Mitteleur. Fl. 2: 685. Lief. 26: 82. 1903.

Triticum tenax var. *schimperi* (Koern.) Aschers. et Graebn., Syn. Mitteleur. Fl. 2: 694. 1901.

Triticum tenax var. *sericeum* (Alefeld) Aschers. et Graebn., Syn. Mitteleur. Fl. 2: 689. 1901.

Triticum tenax var. *seringei* Aschers. et Graebn., Syn. Mitteleur. Fl. 2: 693. 1901.

Triticum tenax var. *speciosissimum* (Koern.) Aschers. et Graebn., Syn. Mitteleur. Fl. 2: 690. 1901.

Triticum tenax var. *speciosum* (Alefeld) Aschers. et Graebn., Syn. Mitteleur. Fl. 2: 690. 1901.

Triticum tenax var. *splendens* (Alefeld) Aschers. et Graebn., Syn. Mitteleur. Fl. 2: 688. 1901.

Triticum tenax var. *submuticum* (Aschers.) Aschers. et Graebn., Syn. Mitteleur. Fl. 2: 685. 1901.

Triticum tenax var. *subvelutinum* Aschers. et Graebn., Syn. Mitteleur. Fl. 2: 686. Lief. 26: 82. 1903.

Triticum tenax var. *turcicum* (Koern.) Aschers. et Graebn., Syn. Mitteleur. Fl. 2: 686. 1901.

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Triticum vulgare bauhini (Lag.) Alefeld, Landw. Fl. 332. 1866.

Triticum vulgare bidens Alefekd, Landw. Fl. 334. 1866.

Triticum vulgare brunneum Alefeld, Landw. Fl. 331. 1866.

Triticum vulgare buocale Alefeld, Landw. Fl. 326. 1866.

Triticum vulgare var. *caesiodes* Flaksb., Bull. Appl. Bot. Fl. Breed. 20: 104. 113. 124. 1929.

Triticum vulgare var. *caesio-speltiforme* Tuman., Bull. Appl. Bot. Fl. Breed. 222: 310. 1929.

Triticum vulgare caesium Alefeld, Landw. Fl. 330. 1866.

Triticum vulgare var. *caesium* Schweinf., Bull. Herb. Boiss. 2 (appendix 2): 45. 1894, no description.

Triticum vulgare [Gruppe 4. *T. durum*] var. *campylodon* Koern., in Koern. Wern. Handb. Getreidebau. 1: 70. 1885.

Triticum vulgare var. *caspium* K. Koch, Linnaea 21: 426. 1848.

Triticum vulgare [Gruppe 3. *T. turgidum*] var. *centigranium* Koern., in Koern. et Wern. Handb. Getreidebau. 1: 63. 1885.

Triticum vulgare cervinum Alefeld, Landw. Fl. 327. 1866.

Triticum vulgare var. *cinerescens* Flaksb., Bull. Appl. Bot. Fl. Breed. 20: 101. 110. 123. 1929.

Triticum vulgare var. *cinerosum* Flaksb., Bull. Appl. Bot. Pl. Breed. 20: 104. 113. 123. 1929.

Triticum vulgare [Gruppe 4. *T. durum*] var. *circusflexum* Koern., in Koern. et Wern. Handb. Getreidebau. 1: 72. 1885.

Triticum vulgare cladure Alefeld, Landw. Fl. 333. 1866.

Triticum vulgare clavatum Alefeld, Landw. Fl. 328. 1866.

Triticum vulgare coeleste Alefeld, Landw. Fl. 327. 1866.

Triticum vulgare [Gruppe 3. *T. turgidum*] var. *coelestoides* Koern, in Koern. et Wern. Handb. Getreidebau. 1: 64. 1885.

Triticum vulgare var. *coeruleo-velutinum* Koern., Syst. Uebers Cereal. 12. 1873. nom. seminud.

Triticum vulgare var. *coerulescens* Link, Handb. Gewachee 1: 10. 1829.

Triticum vulgare coeruleum Alefeld, Landw. Fl. 335. 1866.

Triticum vulgare columbinum Alefeld, Landw. Fl. 327. 1866.

Triticum vulgare compactum (Host) Spenner, Fl. Priburg. 1: 163. 1825.

Triticum vulgare subsp. *compactum* (Host)Link, Hort. Berol. 2: 182. 1833.

Triticum vulgare 2. *compactum* 16. *humboldti* Koern., Syst. Uebers. Cereal. 12. 1873. No description.

Triticum vulgare var. *compositum* (L.) Wood, Class-Book ed. 3. 802. 1861.

Triticum vulgare subsp. *compositum* var. *vavilovi* Tum. ex Vav., Theoret. Bases. Pl. Breed. 2: 7. 50. f. 6. 1935. Russian.

Triticum vulgare compositum var. *vavilovi* Tum., Chron. Bot. (N. I. Vavilov writed *The Origin, Variation & Breeding of Cultivated Plants*). 13(1/6): 336. 1949/1950.

Triticum vulgare [Gruppe 2. *T. compactum*] var. *compressum* Koern, in Koern., et Wern. Handb. Getreidebau. 1: 55. 1885.

Triticum vulgare [Gruppe 2. *T. compactum*] var. *copticum* Koern, in Koern., et Wern. Handb. Getreidebau. 1: 55. 1885.

Triticum vulgare [Gruppe 2. *T. compactum*] var. *crassiceps* Koern, in Koern., et Wern. Handb. Getreidebau. 1: 53. 1885.

Triticum vulgare var. *creticum* Seringe, Descr. Fig. Cer. Eur. 142. pl. 3. f. 3. 4. 1842.

Triticum vulgare [Gruppe 1. *T. vulgare*] var. *cyanothrix* Koern, in Koern. et Wern. Handb. Getreidebau. 1: 46. 1885.

Triticum vulgare [Guppe 1. *T. vulgare*] var. *deifii* Koern., in Koern. et Wern. Handb. Getreidebau. 1: 46. 1885.

Triticum vulgare var. *dicoccocides* Koern., Niederrh. Ges. Bonn. 21. 1889.

Triticum vulgare dicoccum (Schrank) Alefeld, Landw. Fl. 331. 1866.

Triticum vulgare 6. *dicoccum* 49. *krsusei* Koern., Syst. Uebers. Cereal. 14. 1873. No description.

Triticum vulgare 6. *dicococum* var. 45. *majus* Koern., Syst. Uebers. Cereal. 14. 1873. nom. seminud.

Triticum vulgare dinura Alefeld, Landw. Fl. 326. 1866.

Triticum vulgare [Gruppe 3. *T. turgidum*] var. *dreiechisnum* Koern, in Koern., et Wern. Handb. Grtreidebau. 1: 60. 1885.

Triticum vulgare [Gruppe. 3. *T. turgidum*] var. *dubium* Koern., in Koern.,et Wern. Handb. Getreidebau. 1: 62. 1885.

Triticum vulgare duhamelianum Alefeld, Landw. Fl. 335. 1866.

Triticum vulgare subsp. *durum* (Desf.) Link, Hort. Pl. Berol. 2: 182. 1833.

Triticum vulgare durum (Desf.) Alefeld, Landw. Fl. 324. 1866.

Triticum vulgare 4. *durum* 28. *barbarium* Koern., Syst. Uebers. 13. 1873. nom. nud., Koern. et Wern. Handb. Getreidebau. 1: 70. 1885. as syn. of T. vulgare [Gruppe 4. *T. durum*] var. *leucurum* Alefeld.

Triticum vulgare [Gruppe. 2. *T. compactum*] var. *echinodes* Koern., in Koern. et Wern. Handb. Getreidebau. 1: 54. 1885.

Triticum vulgare var. *erinaceus* (Hornen.) Link. Hort. Berol. 2: 182. 1833.

Triticum vulgare erion Alefeld, Landw. Fl. 325. 1866.

Triticum vulgare [Gruppe 1. *T. vulgare*] var. *erythroleucon*. Koern., in Koern. et Wern. Handb. Getreidebau. 1: 47. 1885.

Triticum vulgare [Gruppe 4. *T. durum*] var. *erythromelan*. Koern., in Koern. et Wern. Handb. Getreidebau. 1: 71. 1885.

Triticum vulgare [Gruppe 1. *T. vulgare*] var. *erythrospermum* Koern., in Koern. et Wern. Handb. Getreidebau. 1: 46. pl. 1. f. 3. 1885.

Triticum vulgare var. *erythrospermum irkutianum* Pissarev., Bull. Appl. Bot. Pl. Breed. 14: 133. 135. 1924. Russian.

Triticum vulgare [Gruppe 6. *T. dicoccum*] var. *erythrurum* Koern., in Koern. et Wern. Handb. Getreidebau. 1: 91. 1885.

Triticum vulgare subsp. *eu-vulgare* Brand, in Koch, Syn. Deutsch Schweiz. Fl. ed. 3. 3: 2792. 1907.

Triticum vulgare subsp. *eu-vulgare* f. *aestivum* (L.) Brand, in Koch, Syn. Deutsch. Schweiz. Fl. ed. 3. 3: 2792. 1907.

Triticum vulgare subsp. *eu-vulgare* f. *hibernum* (L.) Brand, in Koch, Syn. Deutsch. Schweiz. Fl. ed. 3. 3: 2792. 1907.

Triticum vulgare farrum (Bayle.) Alefeld, Landw. Fl. 331. 1866.

Triticum vulgare ferrugineum Alefeld, Landw. Fl. 330. 1866.

Triticum vulgare var. *ferrugineum rossicum* Flaksb., Bull. Appl. Bot. Fl. Breed. 8: 861. 1915. No description.

Triticum vulgare var. *ferrugineum sibiricum* Flaksb., Bull. Appl. Bot. Fl. Breed. 8: 861. 1915. No description.

Triticum vulgare [Gruppe 2. *T. compactum*] var. *fetisowii* Koern., in Koern. et Wern, Handb. Getreidebau. 1: 54. 1885.

Triticum vulgare var. *flexuosum* Link, Hort. Berol. 2: 182. 1833.

Triticum vulgare [Gruppe 6. *T. dicoccum*] var. *flexuosum* Koern., in Koern. et Wern. Handb. Getreidebau. 1: 88. 1885.

Triticum vulgare fringillarum Alefeld, Landw. Fl. 335. 1866.

Triticum vulgare fuchsii Alefeld, Landw. Fl. 332. 1866.

Triticum vulgare fulginosum Alefeld, Landw. Fl. 330. 1886.

Triticum vulgare var. *fusoescens* Link, Hort. Berol. 1: 24. 1827.

Triticum vulgare gentile Alefeld, Landw. Fl. 326. 1866.

Triticum vulgare var. *graeco-imarginatum* Stolet., Bull. Appl. Bot. Pl. Breed. 23(4): 84. 337. 1930.

Triticum vulgare [Gruppe 1. *T. vulgare*] var. *graecum* Koern., in Koern. et Wern. Handb. Getreidebau. 1: 46. 1885.

Triticum vulgare var. *griseum* Vav., Bull. Appl. Bot. Pl. Breed. 131: 225. 1923.

Triticum vulgare var. *gunticum* Vav., Bull. Appl. Bot. Fl. Breed. 131: 231. 1923.

Triticum vulgare var. *hamadanicum* Vav., Bull. Appl. Pl. Breed. 131: 227. 1923.

Triticum vulgare var. *heraticum* Vav. et Kob., Bull. Appl. Bot. Fl. Breed. 191: 89. 1928.

Triticum vulgare [Gruppe 3. *T. turgidum*] var. *herreraeKoern.*, in Koern. et Wern. Handb. Getreidebau. 1: 60. 1885.

Triticum vulgare hordeiforme (Host) Alefeld, Landw. Fl. 325. 1866.

Triticum vulgare var. *horogi* Vav., Bull. Appl. Bot. Fl. Breed. 131: 230. 1923.

Triticum vulgare hostianum Fikry, Egypt. Agr. Rev. 17: 13. 1939.

Triticum vulgare [Gruppe 2. *T. compaotum*] var. *humboldti* Koern., in Koern. et Wern. Handb. Getreidebau. 1: 52. pl. 1. f. 4. 1885.

Triticum vulgare var. *hybernum* (L.) Spenner, Fl. Friburg. 1: 163. 1825.

Triticum vulgare hystrix Seringe., Descr. Fig. Cer. Eur. 140. pl. 3. f. 2. 1842.

Triticum vulgare icterinum Alefeld, Landw. Fl. 328. 1866.

Triticum vulgare intermedium Seringe, Descr. Fig. Cer. Eur. 139. 1842.

Triticum vulgare var. *iranicum* Vav., Bull. Appl. Bot. Fl. Breed. 131: 226. 1923.

Triticum vulgare italicum Alefeld, Landw. Fl. 325. 1866.

Triticum vulgare jodura Alefeld, Landw. Fl. 326. 1866.

Triticum vulgare var. *kabulicum* Vav., Bull. Appl. Bot. Pl. Breed. 131: 231. 1923.

Triticum vulgare var. *kazvinicum* Vav., Bull. Appl. Bot. Pl. Breed. 131: 227. 1923.

Triticum vulgare var. *kermanshachi* Vav., Bull. Appl. Bot. Pl. Breed. 131: 227. 1923.

Triticum vulgare var. *khorassanicum* Vav., Bull. Appl. Bot. Pl. Breed. 131: 229. 1923.

Triticum vulgare [Gruppe 6. *T. dicoccum*] var. *krausei* Koern., in Koern. et Wern. Handb. Getreidebau. 1: 91. 1885.

Triticum vulgare var. *kurdistanicum* Vav., Bull. Appl. Bot. Fl. Breed. 131: 226. 1923.

Triticum vulgare leptura Alefeld, Landw. Fl. 325. 1866.

Triticum vulgare leucochiton Alefeld, Landw. Fl. 332. 1866.

Triticum vulgare leucocladua Alefeld, Landw. Fl. 332. 1866.

Triticum vulgare leucoaelan Alefeld, Landw. Fl. 324. 1866.

Triticum vulgare [Gruppe 1. *T. vulgare*] var. *leucospermum* Koern., Koern. et Wern. andb. Getsidebau. 1: 44. 45. 1885.

Triticum vulgare leucura Alefeld, Landw. Fl. 324. 1866.

Triticum vulgare [Gruppe 4. *T. durum*] var. *libycum* Koern., in Koern. et Wern. Handb. Getreidebau 1: 73. 1885.

Triticum vulgare [Gruppe 6. *T. dicoccum*] var. *liguliforme* (Koern.) Koern., Koern. et Wern. Handb. Getreidebau. 1: 90. 1885.

Triticum vulgare [Gruppe 2. *T. compactum*] var. *linaza* Koern., in Koern. et Wern. Handb. Getreidebau. 1: 53. 1885.

Triticum vulgare linnaeanum Alefeld, Landw. Fl. 327. 1866.

Triticum vulgare var. *luristanicum* Vav., Bull. Appl. Bot. Pl. Breed. 131: 227. 1923.

Triticum vulgare [Gruppe 3. *T. turgidum*] var. *lusitanicum* Koern., in Koern., et Wern. Handb. Getridebau. 1: 59. 1885.

Triticum vulgare lutescens Alefeld, Landw. Fl. 329. 1866.

Triticum vulgare var. *lutescens* subvar. *lutinflatum* Flaksb., Bull. Angew. Bot. St. Petersb. 4: 18. 1911.

Triticum vulgare var. *lutescens poltawense* Flaksb., Bull. Appl. Bot. Pl. Breed. 8: 861. 1915. No description.

Triticum vulgare var. *lutescens praecox* Pissarev, Bull. Appl. Bot. Pl. Breed. 14: 134. 135. 1924. Russian.

Triticum vulgare var. *lutinflatum* (Flaksb.) Vav., Bull. Appl. Bot. Pl. Breed. 131: 229. 1923.

Triticum vulgare [Gruppe 6. *T. dicoccum*] var. *macratherum* (Koern.) Koern., in Koern. et Wern. Handb. Getreidebau. 1: 89. 1885.

Triticum vulgare [Gruppe 3. *T. turgidum*] var. *martensii* Koern., in Koern. et Wern. Handb. Getreidebau. 1: 60. 1885.

Triticum vulgare [Gruppe 3. *T. turgidum*] var. *megalopolitanum* Koern., in Koern. et Wern. Handb. Getreidebau. 1: 60. 1885.

Triticum vulgare var. *melanopogon* Chiov., Monogr. Rapp. Colon. Rome No. 19: 13. 1912.

Triticum vulgare melanopus Alefeld, Landw. Fl. 325. 1866.

Triticum vulgare var. *melano-rubrum* Tuman., Bull. Appl. Bot. Pl. Breed. 222: 310. 1929.

Triticum vulgare melanura Alefeld, Landw. Fl. 333. 1865.

Triticum vulgare var. *meridionale* Koern., in Koern. et Wern. Handb. Getreidebau. 1: 47. 1885.

Triticum vulgare var. *mesopotamicum* Vav., Bull. Appl. Bot. Pl. Breed. 131: 226. 1923.

Triticum vulgare metzgeri Alefeld, Landw. Fl. 332. 1866.

Triticum vulgare michauxi Alefeld, Landw. Pl. 334. 1866.

Triticum vulgare miltura Alefeld, Landw. Fl. 329. 1866.

Triticum vulgare var. *milturum khogotanse* Pissarev, Bull. Appl. Bot. Pl. Breed. 14: 133. 135. 1924. Russian.

Triticum vulgare var. *milturum* subvar. *rufinflatum* Flaksb., Bull. Angew Bot. St. Petersb. 4: 19. p1. 8. f. 190. 1911.

Triticum vulgare [Gruppe 3. *T. turgidum*] var. *mirabile* Koern, in Koern., et Wern. Handb. Getreidebau. 1: 63. 1885.

Triticum vulgare monococcum (L.) Alefeld, Landw. Fl. 333. 1866.

Triticum vulgare [Gruppe 4. *T. durum*] var. *murciense* Koern., in Koern. et Wern. Handb. Getreidebau. 1: 71. 1885.

Triticum vulgare var. *murgabi* Flaksb., Bull. Appl. Bot. Pl. Breed. 20: 101, 111,123. 1929.

Triticum vulgare var. *muticum* Schuebl. & Martens, Fl. Wurtemberg 44. 1834.

Triticum vulgare var. *muticum* subvar. *glabrum* Schuebl. et Martens. Fl. Wurtemberg 44. 1834. No description.

Triticum vulgare var. *muticum* subvar. velu*t*inum Schuebl. & Mertens, Fl. Wurtemberg 45. 1834. No description.

Triticum vulgare [Gruppe 5. *T. spelta*] var. *neglectum* Koern., in Koern. et Wern. Handb. Getrdebau. 1: 80. 1885.

Triticum vulgare [Gruppe 3. *T. turgidum*] var. *nemausense* Wittm, in Koern. et Wern. Handb. Getreidebau. 1: 59. 1885. “Wittmack in lit. ”

Triticum vulgare var. *nigrencens* Liuk, Hort. Berol. 1: 24. 1827.

Triticum vulgrare var. *nigroaristatum* Flaksb., Bull. Appl. Bot. Pl. Breed. 8: 195. 1915.

Triticum vulgrare var. *nigro-erythrosparcum* Jakusb. ex. Percival, Journ. Bot. Brit. & For. 64: 209, 210. 1926.

Triticum vulgrare var. *nigro-graecum* Percival, Journ. Bot. Brit. & For 64: 209, 210. 1926.

Triticum vulgrae var. *nigroinflatum* Vav., Bull. Appl. Bot. Fl. Breed. 131: 230. 1923.

Triticum vulgrare var. *nigro-meridionale* Percival, Journ. Bot. Brit. & For. 64: 209. 210. 1926.

Triticum vulgare [Gruppe 1. *T. vulgare*] var. *nigrum* Koern., in Koern. et Wern. Handb. Getreidebau. 1: 46. 1885. Not Link 1829.

Triticum vulgare forna. *nigrum* Link, Handb. Gewachse 1: 10. 1829.

Triticum vulgare [Gruppe 4. *T. durum*] var. *niloticum* Koern., in Koern., et Wern. Handb. Getreidebau. 1: 73. 1885.

Triticum vulgare var. *casicolum* Ducell., Bull. Soc. Hist. Nat. Afr. Nord 11: 91. 1920.

Triticum vulgare [Grupp 4. *T. durum*] var. *obsourum* Koern, in Koern., et Wern. Handb. Getreidebau. 1: 72. 1885, nom. semi-nud.

Triticum vulgare var. *cxianum* Vav., Bull. Appl. Bot. Pl. Breed. 131: 230. 1923.

Triticum vulgare var. *pamiricum* Vav., Bull. Appl. Bot. Pl. Breed. 131: 230. 1923.

Triticum vulgare pavoninum Alefeld, Landw. Fl. 327. 1866.

Triticum vulgare phaeoladum Alefeld, Landw. Fl. 332. 1866.

Triticum vulgare [Gruppe 3. *T. turgidum*] var. *plinianus* Koern. in Koern. et Wern. Handb. Getreidebau. 1: 63. 1885.

Triticum vulgare provinciale Alefeld, Landw. Fl. 325. 1866.

Triticum vulgare var. *pseudobarbarossa* Vav., Bull. Appl. Bot. Pl. Breed. 131: 225. 1923.

Triticum vulgare [Gruppe 3. *T. turgidum*] var. *pseudocervinum* Koern., in Koern. et Wern. Handb. Getreidebau. 1: 63. 1885.

Triticum vulgare var. *pseudo-erythroleucon* Percival, Journ. Bot. Brit. & For. 64: 209, 210. 1926.

Triticum vulgare var. *pseud-graecum* Flaksb., Bull. Appl. Bot. Pl. Breed. 20: 104. 112, 123.1929.

Triticum vulgare pseudo-hostianum Flaksb., Bull. Appl. Bot. Pl. Breed. 8: 196. 1915.

Triticum vulgare var. *pseudomeridionale* Flaksb., Bull. Appl. Bot. Pl. Breed. 8: 196. 1915.

Triticum vulgare var. *pseudoturcicum* Vav., Bull. Appl. Bot. Pl. Breed. 131: 225. 1923.

Triticum vulgare var. *pseudo-turkomanicum* Vav. et Kob., Bull. Appl. Bot. Gen. Pl. Breed. 191: 89. 1928.

Triticum vulgare var. *pubescens* K. Koch, Linnaea 21: 436. 1848. without. descr.

Triticum vulgare pycnura Alefeld, Landw. Fl. 333. 1866.

Triticum vulgare pyrothrix Alefeld, Landw. Fl. 329. 1866.

Triticum vulgare var. *quasi-rufinflatum* Flaksb., Bull. Appl. Bot. Pl. Breed. 20: 102, 114, 123. 1929.

Triticum vulgare var. *quasi-turcicum* Flaksb., Bull. Appl. Bot. Pl. Breed. 20: 102, 114, 123. 1929.

Triticum vulgare [Gruppe 5. *T. spelta*] var. *recens* Koern, in Koern., et Wern. Handb. Getreidebau. 1: 80. 1885.

Triticum vulgare [Gruppe 4. *T. durum*] var. *reichenbachii* Koern., in Koern. et Wern. Handb. Getridebau. 1: 71. 1885.

Triticum vulgare var. *rubescens* Link, Hort. Berol. 1: 24. 1827.

Triticum vulgare [Gruppe 2. *T. compactum*] var. *rubriceps* Koern., in Koern. et Wern. Handb. Getreidebau. 1: 54. 1885.

Triticum vulgare [Gruppe 3. *T. turgidum*] var. *rubroatrum* Koern., in Koern. et Wern. Handb. Getreidebau. 1: 61. 1885.

Triticum vulgare [Gruppe 5. *T. spelta*] var. *rubrovelutinum* Koern., in Koern. et Wern. Handb. Getreidebau. 1: 80. 1885.

Triticum vulgare [Gruppe 2. *T. compactum*] var. *rubrum* Koern., in Koern. et Wern. Handb. Getrdidebau. 1: 53. 1885.

Triticum vulgare var. *rufescens* Link, Handb. Gewachs 1: 9. 1829.

Triticum vulgare var. *rufinatum* (Flaksb.) Vav, Bull. Appl. Bot. Pl. Breed. 131: 229. 1923.

Triticum vulgare [Gruppe 2. *T. compctum*] var. *rufulum* Koern, in Koern. et Wern. Handb. Getreidebau. 1: 52. 1885.

Triticum vulgare var. *rufum* Link, Hort. Berol. 1: 24. 1827.

Triticum vulgare rufum Alefeld, Landw. Fl. 335. 1866.

Triticum vulgare var. *rufum* subvar. *velutinum* Link. Hort. Berol. 1: 25. 1827.

Triticum vulgare [Gruppe. 3. *T. turgidum*] var. *salomonia* Koern., in Koern. et Wern. Handb. Getreidebau. 1: 61. 1885.

Triticum vulgare var. *sardoum* Koern., in Koern. et Wern. Handb. Getreidebau. 1: 47. 1885.

Triticum vulgare var. *scabriusculum* K. Koch, Linnaea 21: 427. 1848. without descr.

Triticum vulgare [Gruppe 5. *T. spelta*] var. *schenkii* Koern., in Koern. et Wern. Handb. Getreidebau. 1: 80. 1885.

Triticum vulgare [Gruppe 4. *T. durum*] var. *schimperi* Koern., in Koern. et Wern. Handb. Getreidebau. 1: 71. 1885.

Triticum vulgare sericeum Alefeld, Landw. Fl. 328. 1866.

Triticum vulgare serotinum Alefeld, landw. Fl. 331. 1866.

Triticum vulgare var. *shugnanicum* Vav., Bull. Appl. Bot. Pl. Breed. 131: 230. 1923.

Triticum vulgare [Gruppe 3. *T. turgidum*] var. *speciocissimum* Koern., in Koern. et Wern. Handb. Getreidebau. 1: 60. 1885.

Triticum vulgare speciosum Alefeld, Landw. Fl. 326. 1866.

Triticum vulgare spelta (L.) Alefeld, Landw. Fl. 334. 1866.

Triticum vulgare var. spelta 35. Alefeldi Koern., Syst. Uebers. Cereal. 13. 1873, without descr.

Triticum vulgare 5. *spelta* 38. *erubescens* Koern., Syst. Uebers. Cereal. 14. 1873. nom. seminud.

Triticum vulgare 5. *spelta* 39. *rubrovelutinum* Koern., Syst. Uebers. Cereal. 14. 1873. No description.

Triticum vulgare splendens Alefeld, Landw. Fl. 328. 1866.

Triticum vulgare sub-afghanicum Flaksb., Bull. Appl. Bot. Pl. Breed. 20: 104. 111. 123. 1929.

Triticum vulgare var. *subbarbarossa* Vav., Bull. Appl. Bot. Pl. Breed. 131: 228. 1923.

Triticum vulgare var. *subcaesium* Flaksb., Bull. Appl. Bot. Pl. Breed. 20: 106. 113. 124. 1929.

Triticum vulgare var. *suberythroleucon* Vav., Bull. Appl. Bot. Pl. Breed. 131: 228. 1923.

Triticum vulgare var. *suberythrospernum* Vav., Bull. Appl. Bot. Pl. Breed. 131: 227. 1923.

Triticum vulgare var. *subferrugineum* Vav., Bull. Appl. Bot. Pl. Breed. 131: 228. 1923.

Triticum vulgare var. *suhfuliginosum* Vav., Bull. Appl. Bot. Pl. Breed. 131: 228. 1923.

Triticum vulgare var. *subgraecum* Vav., Bull. Appl. Bot. Pl. Breed. 131: 227. 1923.

Triticum vulgare var. *subgunticum* Vav., Bull. Appl. Bot. Pl. Breed. 131: 231. 1923.

Triticum vulgare var. *sub-hamadanicum* Tuman., Bull. Appl. Bot. Pl. Breed. 222: 311. 1929.

Triticum vulgare var. *sub-hostianum* Vav., Bull. Appl. Bot. Pl. Breed. 131: 228. 1923.

Triticum vulgare var. *sub-iranicum* Tuman., Bull. Appl. Bot. Pl. Breed. 222: 311. 1929.

Triticum vulgare sub-kabulicum Flaksb., Bull. Appl. Bot. Pl. Breed. 20: 104. 111. 123. 1929.

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Triticum vulgare var. *submeridionale* Vav., Bull. Appl. Bot. Pl. Breed. 131: 228. 1923.

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