

Plant Genetics and Genomics: Crops and Models

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Genetics and Genomics of the *Triticeae*

Foreword by Ronald L. Phillips

 Springer

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Foreword

At this writing, a strain of stem rust of wheat is threatening production around the world, reminiscent of the North American stem rust epiphytotic in 1903 and 1905 and from 1950 to 1954. Norman Borlaug is saying that every commercial wheat variety in the world will need to be replaced with a resistant type. This situation highlights why genetics and genomics information for the Triticeae is so important. Because about half of the yield advances in our major crops generally is the result of genetic advances, any information that can be obtained about genes and gene expression of our rich plant genetic resources is extremely valuable.

Reading this up-to-date book reminds one as much of a textbook as a reference book for learning about plant genetics and systematics as well as the structural and functional organization and evolution of the Triticeae. The book is forward-looking in many ways, including a review of the value of model species to speed genetic understanding of the various crops. The advantages of *Brachypodium* as a model species are described including the fact that it has more traits in common with other Triticeae than other model systems; given that *Arabidopsis* has been a valuable model for all plant species, *Brachypodium* may offer a leap forward for the Triticeae. The large and complex genome of wheat, for example, made initial progress rather slow and made funding agencies wary of investing. This book shows that those days are or at least should be over.

The Triticeae is made up of numerous relatives of approximately 350 species (about 30 genera) among which there are 101 species of 19 genera that are either cultivated or otherwise useful as wild species. Fortunately, the 294 ex situ genebanks in 83 countries holds 1,278,000 accessions. This book provides a well-organized summary of what is held in these genebanks and points out the need for a global database. Two databases, however, are recommended – the Mansfield Database and the USDA online system.

Because the Triticeae has so many relatives, wide hybridization using modern methods for enhancing introgression is especially important. Introgression of specific chromosomes from related species into barley has provided resistance to several diseases. The extensive cytogenetic stocks in the Triticeae have and continue to be important in genomic analysis.

The genomic structure of Triticeae is large and complex, and composed of genes interspersed by huge amounts of repetitive elements. The main repetitive elements in Triticeae are retroelements – principally Copia and Gypsy superfamilies – and can compose 55–70% of the total genomic DNA. Evolution of the genomes reflects a “conservative portion” mainly of genes and single copy DNA, and a “dynamic” portion of transposable elements, duplicated genes and gene fragments. Gene density is shown to be positively correlated with recombination rate. The sequence of *Puccinia graminis*, the causal agent of stem rust, also is now available and even it has 47% of its genome in repetitive elements.

Mapping with Triticeae species is extensively discussed in the book. Although impressive maps exist, it is mentioned that they are not dense enough to foster detailed map-based cloning; interestingly, about half of the genes cloned in the Triticeae (10 out of 19) are disease resistance genes. Relatively few SNP markers are available, and there is a call for further development of such markers. In the book, here are many excellent tips on mapping in terms of appropriate mapping populations, detection of linkage methods, Radiation Hybrid mapping, QTL analysis, and use of multiple environments. An extensive and useful discussion of association mapping provides the needed future directions while reviewing the reported studies and indicating how Association Mapping can compensate for lower marker numbers where whole-genome scans are of low resolution.

Chromosome and chromosome-arm sorting are emphasized in terms of the potential to simplify genome sequencing in the Triticeae. One needs to remember that many chromosome arms in wheat have more DNA than the entire rice genome. Chromosome-arm-specific BAC libraries (the book reports 14 to date) will aid in the study of the structure and evolution of individual chromosomes. The Wheat GeneChip contains one-third of all wheat genes – 55, 052 transcripts. Other new tools available for functional gene analysis in barley and wheat include VIGS (Virus Induced Gene Silencing), RNAi (RNA interference), and TIGS (Transient Induced Gene Silencing). Other useful parts of the book include an extensive discussion on scientific name nomenclature, an excellent accounting of the various species and their origins, and the genetics of many traits especially important in domestication.

Finally, information is presented on a number of quality traits such as B-glucan content, B-amylase, and QTLs for malting quality. Interestingly, the terminal segment of 5HL of barley is reported to carry genes for seed dormancy, pre-harvest sprouting, high malt extract, diastatic power, alpha amylase, and other traits. The genetic analysis of many abiotic stress traits such as drought, cold and heat tolerance, and salinity are reviewed. Also included is a chapter on the genetics of flowering. Experience with flowering shows that the variation in a trait may be due to a sequence far away, such as the Vgt1 QTL in maize that is 70 kb upstream from a flowering effector gene (Ap2-like). Sequencing of Triticeae genomes will allow a detailed scan around such regions of interest and greatly advance the identification of regulatory sequences controlling traits that influence productivity.

Wheaties boxes have used the phrase “Breakfast of Champions”. This book shows that Triticeae genetics is now ready to be the main course. Many genetic resources are now readily available in the Triticeae and molecular genetics tools have been demonstrated to be effective in this set of genomically-complex species. These facts together with the economic value, the ever-present biotic and abiotic stresses, and the greatly increased prices for the Triticeae commodity crops, provide the basis and need for increased investments in research and development.

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Preface

Cereals constitute over 50% of total crop production worldwide (<http://www.fao.org/>) and cereal seeds are one of the most important renewable resources for food, feed, and industrial raw materials. Crop species of the Triticeae tribe that comprises wheat, barley, and rye are essential components of human and domestic animal nutrition. Wheat is grown on 17% of all crop area and represents the staple food for 40% of the world's population. Barley ranks fifth in the world production and is widely used for animal feed and food industry. Rye is second after wheat among grains most commonly used in the production of bread and is also very important for mixed animal feeds and as a source of new alleles for biotic and abiotic stress tolerance in wheat breeding programs. Their domestication in the Fertile Crescent 10,000 years ago ushered in the beginning of agriculture and signified an important breakthrough in the advancement of civilization.

The economic importance of the Triticeae has triggered intense cytogenetic and genetic studies in the past decades that resulted in a breadth of information and tools that have been used to develop wheat, barley and rye varieties with increased yield, improved quality and enhanced biotic and abiotic stress tolerance. In contrast, genomics in the Triticeae lagged behind other plant species, hampered by the size (17 Gb for the bread wheat genome, i.e., 40× the rice genome; 5 Gb for barley and 8 Mb for rye) and complexity (high repeat content, polyploidy) of their genomes. Recently, however, the situation has changed dramatically and the convergence of several technology developments led to the development of a “Genomic toolbox” with new and more efficient resources that supported the establishment of robust genomic programs in the Triticeae. These new capabilities will permit a better understanding of the Triticeae plants biology and support the improvement of agronomically important traits in these essential species.

In this book internationally recognized experts summarize advances of the past decades, synthesise the current state of knowledge of the structure, function, and evolution of the Triticeae genomes and describe progress in the application of this knowledge to the improvement of wheat, barley and rye. The taxonomy, origin and conservation of the huge amount of genetic resources present in the Triticeae families are first reviewed together with basic information about

the genetics and cytogenetics of the three main representatives of the family (wheat, barley and rye). A second section provides the state of the art in the development of tools, resources and methods that have revolutionized our knowledge about the structure, function and evolution of the Triticeae genomes followed by a third section that illustrates the application of these resources to study and improve agronomically important traits such as biotic and abiotic stress resistance, plant development and quality. Finally, three chapters open perspectives into the deployment of new genetic approaches to identify traits and how a better understanding of the organisation of the Triticeae genomes and the ongoing development of new sequencing technologies will support future genome sequencing of these essential crops.

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Part I
Genetics of the Triticeae

Chapter 1

Scientific Names in the *Triticeae*

Mary E. Barkworth and Roland von Bothmer

Abstract The grass tribe *Triticeae* has been the focus of many research programs because its inclusion of wheat, barley, and rye makes it of critical importance to the world's food supply, an importance that is enhanced by the many other species that are important for forage and soil stabilization. One consequence of the tribe's importance is that scientists throughout the world are engaged in its study, particularly its cultivated species. The crop species are also used as model organisms in research. This is leading to a rapid accumulation of knowledge about the cultivated species and their close relatives and a slower accumulation of knowledge about the other species. For this reason, and because the tribe grows in almost all temperate regions of the world, many different taxonomic treatments have been proposed for its members. As a result, many of its members have more than one correct scientific name and some names have multiple interpretations. Examples are provided of how such situations arise. This is followed by a discussion of the criteria used in selecting a treatment to be used, brief characterizations of the generic interpretations adopted, and summaries of some alternative interpretations.

1.1 The *Triticeae*

Triticeae is the scientific name for the tribe (group) of grasses that includes the cereals *Triticum aestivum* (bread wheat), *T. durum* [\equiv *T. turgidum* ssp. *durum*] (*durum* wheat), *Secale cereale* (rye), and *Hordeum vulgare* (barley), the modern cereal \times *Triticosecale* (triticale), plus about 350 other species (Löve 1984) [Authors for all names mentioned in this chapter are given in the Appendix]. The cereals are undoubtedly the tribe's best known members, but many of the other species are important for forage and soil stabilization. The cereal and annual species are most abundant in western Asia and around the Mediterranean, but the

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other species are found in almost all temperate regions of the world, the country with the greatest concentration being China (Barkworth et al. 2005).

Morphologically, the *Triticeae* differ from other grasses in their combination of open leaf sheaths, membranous ligules, sessile to almost sessile spikelets, and ovaries with a hairy top. Within the tribe, as in other grass tribes, there is variation in many respects including morphology, life cycle, reproductive behavior, ploidy level, genomic constitution, habitat preference, and phenotypic plasticity. Where the *Triticeae* differ from other tribes are in their economic importance and the extent to which they hybridize, forming at least partially fertile hybrids. Because of their economic importance, the *Triticeae* are the focus of research studies by scientists in diverse disciplines and many different countries; because of the rather low barriers to hybridization, almost all members of the tribe are potential resources for development of genetically improved strains and cultivars (e.g., Verushkine and Shechurdine 1933; Anamthawat-Jonsson et al. 1997; Pinto et al. 2003). Even so, most studies have focused on the cereal species or their close relatives (e.g., Dhaliwal et al. 1990), with the result that there is more information available about them than about other members of the tribe.

1.2 Why so Many Names?

A taxonomic treatment is an attempt to partition the observed variation in a group of organisms into a hierarchical set of units or *taxa* [singular form, *taxon*]. Within the *Triticeae*, the commonly used ranks are, in descending order: genus, species, subspecies, and variety. Early taxonomists relied solely on morphological characters in deciding how to partition the tribe into taxa. Today, although people (including taxonomists) like to be able to distinguish taxa morphologically, information from other disciplines is used in developing taxonomic treatments. As more information becomes available, taxonomic treatments need to change to reflect this information, but how, when, and to what extent such changes should be made is often a matter of dispute. Consequently, there are often multiple taxonomic treatments for a group in use at any given time. This is particularly true of widely distributed and well-studied groups such as the *Triticeae*.

The existence of multiple taxonomic treatments means that many taxa have multiple correct scientific names—and that some scientific names have multiple meanings—because the correct scientific name for a taxon depends on the taxonomic treatment adopted. Most taxonomic treatments of the *Triticeae* are incomplete. Many are regional in scope (e.g. Tsvelev 1976; Edgar and Connor 2000; Wu et al. 2006; Wu and Raven 2007; Barkworth et al. 2007); others treat only one genus (e.g., Dorofeev et al. 1979; Frederiksen 1986, 1991a,b; Bothmer et al. 1995; Baden 1997; Baden et al. 1997; Frederiksen and Peterson 1998). A few discuss the genera to be recognized but not the

delimitation of species in each genus (Dewey 1984; Yen et al. 2005a). Löve's (1984) treatment of the *Triticeae* is the only one that treats all members of the tribe. His work is incredibly valuable and shows considerable insight. Nevertheless, it contains aspects which all, or almost all, of those working with the tribe now reject. This is, however, true of most taxonomic treatments—and taxonomists themselves will change their treatment of a group as new information is obtained or because of changing generic or species concepts (cf. *Elytrigia* in Dewey 1982, 1984; *Critesion* in Barkworth and Dewey 1985; Barkworth et al. 2007).

There are no rules for making taxonomic decisions. The primary goal of the International Code for Botanical Nomenclature (henceforth, "Code"; McNeill et al. 2006) is to ensure that there is one, and only one, correct name for each plant. It provides rules, called Articles, for creating names or deciding among existing names for a taxon, but these come into play only after a taxon's circumscription (i.e., its taxonomic treatment) has been decided.

1.2.1 Impact of New Technologies on the Taxonomy of the Triticeae

The current taxonomic tradition, in which an attempt is made to place related organisms together, dates from around Theophrastus' time (Pavord 2005). The use of binomials for naming species was introduced by Bauhin in 1650 (see Lawrence 1968), but the first *International Code of Botanical Nomenclature* was not published until 1930 although there had been several earlier attempts to reach agreement (see Lawrence 1968). Early taxonomists placed plants that were evidently distinct in different species; genera comprised species that resembled each other more than species of another genus. Thus Bentham (1882), Hackel (1887), and Hitchcock (1951) interpreted *Agropyron* as including all the species of the tribe with solitary spikelets. As knowledge accumulated, it became evident that some of the evidently distinct genera included a mix of closely and distantly related species which, as understanding of evolution developed, was seen as undesirable, and led to the preparation of revised taxonomic treatments.

Nevski (1934) was the first to attempt realigning the genera of the *Triticeae* so that they more closely reflected the evolution of the tribe. At that time, the impact of the ability to stain chromosomes was reflected in such works as Avdulov's (1931) caryosystematic study of grasses. Nevski was aware of Avdulov's work but he noted that he had to make his generic decisions while there was still only minimal cytological data available for the tribe.

In 1984, the accumulated cytogenetic data led Löve and Dewey to propose, independently of each other, that generic circumscription in the tribe be based on genomic constitution. Each noted, however, that as additional species were studied it might become necessary to recognize more genera. These ideas were

greeted with considerable criticism at the time (Barkworth 2000; Barkworth and Bothmer 2005 for review), but many of circumscriptions accepted today reflect the impact of cytogenetic information.

Since 1984, molecular tools have become the “new technology”. They have been employed in a wide range of studies of the *Triticeae*, some focusing on elucidation the relationships among the tribe’s members, others on obtaining information that will aid plant breeders. Integrating such information into the taxonomy, and hence the names used, is still in progress. It has confirmed many, but not all, of the conclusions reached on the basis of cytogenetic information. In some instances, it has made it easier to understand why some taxonomic decisions are problematic. For instance, some molecular studies support treatment of *Triticum* and *Aegilops* as a single genus; others suggest that they should be separate but that *Amblyopyrum* should be included in *Triticum*; others suggest that, if genera are to be monophyletic, the tribe should be reduced to a very small number of genera (see Petersen et al. 2006 for a review).

Once again, a new technology is providing greater insight into the evolution and phylogeny of the tribe. Like other technologies, it is helping us better understand the complexity of the evolutionary and phylogenetic processes that are reflected in the diversity of the tribe. Integrating the implications of such information into the taxonomic treatment of the tribe is an ongoing process.

1.2.2 Integrating New Information into the Taxonomy of the Triticeae

Taxonomists vary in the rate with which they incorporate new information into their treatments. There are many reasons for this, such as differences in the rate at which information comes to the attention of taxonomists and the importance they attach to different kinds of information. Some taxonomists attach considerable importance to having morphologically distinct entities; others think reflecting genetic similarity more important; others consider molecular phylogenetic information paramount. At the generic level, some consider that supraspecific groups such as genera must be monophyletic, that is, have a single common ancestor, a requirement that would reduce the perennial *Triticeae*, if not the whole tribe, to a single genus. Others (e.g., Löve 1984; Dewey 1984; Yen et al. 2005a) emphasize the importance of genomic constitution, seeing this as a measure of genetic relatedness. This is only feasible in the very few groups, the *Triticeae* being the prime example, for which this information is available. Still others emphasize stability. This last is an understandable desire, but one that can require ignoring the implications of new knowledge. All these variables affect the extent to which a taxonomic treatment reflects existing information.

In the remainder of this chapter, we first illustrate why some taxa have multiple names and some names have multiple meanings. We then outline the

guidelines that we followed in deciding on the taxonomic treatment (and hence the names) we currently recommend for use. We conclude with a brief characterization of the genera that we recognize and a summary of alternative treatments. The index includes all the names used in this volume, plus some of their frequently encountered synonyms.

1.3 Interaction of Taxonomy and Nomenclature—Some Examples

In this section, we illustrate why taxonomic treatments change, and the impact of such changes on names, by considering three examples from the *Triticeae*. In the process, we discuss a few of the intricacies of the Code and the reason why it is sometimes important to cite the authors of a scientific name.

1.3.1 Multiple Names at the Generic Level: *Pseudoroegneria*

The impact of different generic treatments on the names of species and lower ranks is easier to follow than differences in the treatment of species and lower ranks. In most instances, all that is involved is replacement of the generic name and, possibly, a change to the ending of the specific epithet so that its gender agrees with that of the generic name. There is often no choice in the specific epithet because the Code (McNeill et al. 2006, Art. 11.4) requires that one use the first specific epithet available. This is the Principle of Priority. Thus, the western North American species now known as *Pseudoroegneria spicata* was originally called *Festuca spicata* by Pursh (1813). In *Agropyron*, it becomes *Agropyron spicatum* (Scribner and Smith 1897), the ending of the epithet changing because *Agropyron* is neuter whereas *Festuca* is feminine. Other nomenclaturally correct names for the taxon are *Elymus spicatus*, published by Gould (1947) and *Elytrigia spicata*, published by Dewey (1983). Which name is used depends on the taxonomic treatment adopted for the genera in the tribe (see Table 1.2). If authors of names are being cited, the citations for the combinations mentioned above are: *Festuca spicata* Pursh, *Agropyron spicatum* (Pursh) Scribn. and J.G. Sm., *Elymus spicatus* (Pursh) Gould, *Pseudoroegneria spicata* (Pursh) Á. Löve, and *Elytrigia spicata* (Pursh) D.R. Dewey. The decision to include both awned and unawned plants in *Pseudoroegneria spicata* was based on ecological, and experimental studies (Daubenmire 1939, 1960; Carlson 2007).

Note that the name of a species is a binomial; the word(s) in roman type that follows the name of a species refer to the author(s) of the name. The Code (McNeill et al. 2006, Art. 46) states that “In publications, particularly those dealing with taxonomy and nomenclature, it *may* be desirable . . . to cite the author(s) of the name concerned” [Emphasis added]. In practice, most editors require citation of the author(s) for all names used at the species level; some

require it for higher ranks. When doing so, it is best to follow the recommendations of Brummitt and Powell (1992) on how, and whether, to abbreviate them. Their recommendations are also available at <http://www.ipni.org>. The Web site also enables one to find the accepted abbreviation for one that is no longer in use. For instance, searching for the abbreviation “Linn.” will bring up the name Linnaeus and its accepted abbreviation, “L.”.

1.3.2 Multiple Names at the Generic Level: Elymus

In some cases, it is impossible to retain the original specific epithet when moving a species to a different genus. For instance, when the western North America species *Agropyron dasystachyum* is included in *Elymus*, it has to be called *Elymus lanceolatus* because, when Gould went to transfer the species in 1949, he found that Trinius (1829) had already used the combination *Elymus dasystachys* for a central Asian species, one now known as *Leymus secalinus* (Wu et al. 2006). When he made the transfer, Gould had three names to consider: *Agropyron dasystachyum*, *A. lanceolatum* and *A. subvillosum*. The authors of these names believed that they referred to three different species, but Gould thought that all three names referred to variants of a single species. Of the three epithets, “*dasystachyum*” was unavailable because it had been used by Trinius. Of the other two epithets, “*lanceolatum*” was first used at the species level by Scribner and Smith in 1897, “*subvillosum*” by Nelson in 1904. Thus, “*lanceolatus*” was the earliest available epithet at the species level so, in accordance with the Principle of Priority, *Agropyron dasystachyum* became *Elymus lanceolatus*, the author citation being (Scribn. & J.G. Sm.) Gould.

1.3.3 Additional Problems with Generic Changes

Determining the correct combination to use when transferring a species from one genus to another is only one of the problems associated with changing generic boundaries. Another is that one must also change descriptions and identification keys. Descriptions of *Agropyron* that reflect its current interpretation usually refer to its closely spaced spikelets with keeled glumes, characteristics that were not true of the majority of the species included in the genus by Bentham (1882). Similarly, the expansion of *Elymus* to include many, but not all, species that are now excluded from *Agropyron* has led to changes in its generic description.

Generic changes also require that care must be taken in interpreting such statements as “*Elymus* is the most widespread genus in the tribe, being native in both the northern and southern hemispheres”. This is true if one accepts the interpretation of Löve (1984) or Edgar and Connor (2000), even though Edgar and Connor interpreted the genus somewhat differently from Löve. It is not

true if one adopts the interpretation of Yen et al. (2005a) because these authors place the Australasian species into other genera.

At a practical level, a greater problem is presented when a generic change is proposed but, for one reason or another, new names are published for only some of its species. For instance, Church (1967) demonstrated that *Hystrix patula*, the type species of *Hystrix* is genetically close to species of *Elymus*. For this reason, it is now included in *Elymus* and is known by the name first given to it by Linnaeus (1753), *E. hystrix*. This does not mean that all the other species that used to be included in *Hystrix* belong in *Elymus*. Indeed, Zhang and Dvorák (1991) and Jensen and Wang (1997) demonstrated that the species known as *Hystrix californica* is genetically more closely related to species of *Leymus* than species of *Elymus*; it was transferred to *Leymus* by Barkworth in 2006. The problem is that most species of *Hystrix* grow in eastern Asia. The authors of the *Flora of China* and Bothmer et al. (2005) decided to recognize *Hystrix* as a genus, consequently there are no names for most of the Chinese and Japanese species in *Elymus* or *Leymus*. Moreover, because few of the species of *Hystrix* have been examined by those who consider that the genus should not be recognized, there is no way of knowing where the species should be placed. All that is clear is that, according to the Code, if *Elymus hystrix*, the type species of *Hystrix*, is included in *Elymus*, *Hystrix* cannot be used as a generic name. A similar problem exists with respect to *Elytrigia*. The matter can only be addressed by studying the species involved.

1.3.4 Multiple Names at the Species Level and Below: The *Triticum monococcum* Complex

Recent changes in the taxonomic treatment of the *Triticum monococcum* complex will illustrate their impact on the names used and the meaning of those names. The focus is on plants associated with five epithets, “*monococcum*”, “*aegilopoides*”, “*boeoticum*”, “*thaoudar*”, and “*urartu*”. Each of these epithets refers to a group of plants that at least one taxonomist has considered worthy of recognition as a taxon.

Four of the five taxa have nomenclaturally correct names as species of *Triticum*: *T. boeoticum*, *T. monococcum*, *T. thaoudar* and *T. urartu* (Table 1.1, column 1). Note that the name of each species is a binomial; the word(s) in roman type that follows the name of the species refer to the author(s) of the name. In the table, the date when each name was published is shown in parentheses after the author’s name.

There is no nomenclaturally correct name for the “*aegilopoides*” taxon as a distinct species of *Triticum* even though taxonomists now agree that it belongs in *Triticum*. The binomial *Triticum aegilopoides* has been published by two different people, Forsskål (1775) and Körnicke (1885), but they used the name for different taxa. Forsskål applied it to a group of plants that are now

Table 1.1 Names of four close relatives of *Triticum monococcum sensu stricto* under different taxonomic interpretations. The dates show the year that the name was published by the author concerned. Forsskål published the name *Triticum aegilopoides* in 1775, but the specimen that shows what he meant by the name belongs to a different genus

Five equal entities		Two species, <i>T. monococcum</i> with two subspecies (adopted by Slageren [1994])		Three species, <i>T. boeoticum</i> with two subspecies (see Ciaffi <i>et al.</i> 1998)
All species	All subspecies of <i>T. monococcum</i>			
<i>T. monococcum</i> L. (1753)	<i>T. monococcum</i> L. (1753) subsp. <i>monococcum</i>	<i>T. monococcum</i> L. (1753)	<i>T. monococcum</i> L. (1753) subsp. <i>monococcum</i>	<i>T. monococcum</i> L. (1753)
<i>Crithodium aegilopoides</i> Link (1834) (No legitimate name in <i>Triticum</i> at species level for this entity.)	<i>T. monococcum</i> subsp. <i>aegilopoides</i> (Link) Thell. (1918)		<i>T. monococcum</i> subsp. <i>aegilopoides</i> (Link) Thell. (1918)	<i>T. boeoticum</i> Boiss. subsp. <i>boeoticum</i> (effectively 1853) [not <i>T. boeoticum</i> subsp. <i>aegilopoides</i> (Link) E. Schiem. (1939); see text for explanation]
<i>T. boeoticum</i> Boiss. (1854)	<i>T. monococcum</i> subsp. <i>boeoticum</i> (Boiss.) Á. Löve & D. Löve (1961)			
<i>T. thaouadar</i> (Hauskn.) Jakubz. (1932)	<i>T. monococcum</i> subsp. <i>thaouadar</i> (Hauskn.) Flaksb. (Flaksberger 1913)			<i>T. boeoticum</i> subsp. <i>thaouadar</i> (Hauskn.) E. Schiem (1939)
<i>T. urartu</i> Thumanjan <i>ex</i> Gandilyan (1972)	<i>T. monococcum</i> subsp. <i>urartu</i> Á. Löve & D. Löve (1961)	<i>T. urartu</i> Thumanjan <i>ex</i> Gandilyan (1972)		<i>T. urartu</i> Thumanjan <i>ex</i> Gandilyan (1972)

known as *Elionurus hirsutus* (Clayton et al. 2002) that do not belong in the *Triticeae*. Körnicke applied it to the same group of plants that Link called *Crithodium aegilopoides* but, according to the Code (McNeill et al. 2006), if there have been two different uses of a name, its meaning is fixed by its first use, no matter how incorrect later taxonomists may find that use to be. This means that Körnicke's use was illegitimate.

If one wants to mention both uses of the name in an article, one can distinguish between them by the author citation: *T. aegilopoides* Forssk. is the taxon now included in *Elionurus*; *T. aegilopoides* (Link) Balansa ex Körn. refers to the taxon that was first described and named by Link; this is indicated by the presence of his name, in parentheses, immediately after the scientific name. Link's name is followed by the abbreviation of the name of the person who published the new combination, Körnicke. In doing so, however, Körnicke acknowledged that he was publishing the combination based on information provided by Balansa; this is indicated by the "Balansa ex" portion of the authorship. *Ex* is Latin for "from within" or "out of" so the citation is saying that Körnicke obtained information from within Balansa's work that made him decide to publish the combination *Triticum aegilopoides*. Balansa may have made notes on herbarium specimens or discussed the matter with Körnicke, but he did not formally publish the name.

In most papers, there is no scientific need to cite the author of the scientific names used although it is usually an editorial requirement. It is, for instance, hard to imagine a paper, other than one about nomenclature, in which both uses of *Triticum aegilopoides* would be employed. If the "*aegilopoides*" taxon is to be named as a species of *Triticum* distinct from the other four species, a different epithet must be used. So far as we know, no one has published such a name.

Each of the five entities discussed in this section has also been named as a subspecies of *Triticum monococcum* (Table 1.1, column 2), but most scientists no longer consider this treatment appropriate. For instance, Slageren (1994) concluded that the "*urartu*" epithet referred to a taxon that should be recognized as a species whereas the "*aegilopoides*", "*boeoticum*", and "*thaouadar*" epithets referred to taxonomically insignificant variants of a single taxon that are best treated as one of two subspecies of *T. monococcum*, the other subspecies being *T. monococcum* subsp. *monococcum*. The correct name at the subspecies level for the combined "*aegilopoides-boeoticum-thaouadar*" entity is *T. monococcum* subsp. *aegilopoides*, because the Code (Art. 11) states that, when combining species or lower ranks, the correct epithet is the one that was first used at the desired rank, in this case subspecies.

This is not the end of the story. Ciaffi et al. (1997, 1998) argued, on the basis of information presented in their papers, that three of the entities should be recognized as species: *T. monococcum*, *T. boeoticum*, and *T. urartu*. They stated that the "*thaouadar*" entity should be treated as a subspecies of *T. boeoticum*, for which they used the name *T. boeoticum* subsp. *thaouadar*. This name was published by Grossheim in 1939 and is nomenclaturally correct, but the name of the other subspecies should be *T. boeoticum* subsp. *boeoticum*, not *T. boeoticum*

subsp. *aegilopoides*, as used by Ciaffi et al. The reason for this is that Ciaffi et al. state: “Two morphological types of *T. boeoticum* are recognized: subsp. *aegilopoides*. . .and subsp. *thaouidar*. . .” (p. 124). Whenever a species is subdivided, one automatically creates a subdivision that includes the type specimen of the species. The name of this subdivision repeats the specific epithet, in this case, “*boeoticum*”. (The type specimen is the specimen, usually chosen by the name’s author, that anchors the meaning of a name). Thus, the correct name of the second subspecies recognized by Ciaffi et al. is *T. boeoticum* subsp. *boeoticum*. Although “*aegilopoides*” was the first epithet used at the subspecies level, the autonym (i.e., the automatically generated name) has priority. Note that the primary findings of Ciaffi et al. are not affected; one merely needs to substitute *T. boeoticum* subsp. *boeoticum* for *T. boeoticum* subsp. *aegilopoides* when reading their papers.

There is one more wrinkle to this story. The simplest concerns the spelling of “*boeoticum*”. Boissier (1854) used two different spellings for this epithet, “*boeoticum*” and “*baeoticum*”. Because the type specimen was collected in Boeotia, Greece, the correct spelling is “*boeoticum*”.

In the above paragraphs, we showed how different taxonomic treatments resulted in taxa having multiple nomenclaturally correct names. Equally importantly, it means that some names have more than one meaning. For instance, the name *Triticum monococcum* may refer to only one of the five entities treated; to all but the “*urartu*” entity, as in Slageren (1994); or to all five of them (because it was the only one in existence until Link published *Crithodium aegilopoides*). How can one determine which usage an author was adopting? Sometimes it is made clear by the other names used, as in the article by Ciaffi et al. (1998). Another approach, and one that will enable people to interpret what group is intended even if there are further changes in the taxonomic treatment of these entities after publication of a paper, is to prepare herbarium specimens from representative mature plants of the material used in the study and deposit these voucher specimens in a herbarium that will loan them to other researchers on request. A third approach is to cite the taxonomic treatment being followed, but this will not resolve all problems. For instance, if an author follows Slageren, it may be impossible to determine, without looking at voucher specimens, whether references to *T. monococcum* subsp. *aegilopoides* mean *T. boeoticum* subsp. *boeoticum* or *T. boeoticum* subsp. *thaouidar*.

The above paragraphs are about nomenclature. What is not discussed is which of the three taxonomic treatments is best, nor the criteria to be used in deciding what is “best”. Those are the questions that must be answered if a single taxonomic treatment is to be adopted. We are recommending acceptance of the treatment based on the findings of Ciaffi et al. (1997, 1998), because their treatment best reflects what is now known about the genetic relationships within the complex. If, however, a paper is published in which van Slageren’s treatment is followed, one needs to bear in mind that statements about *T. monococcum* subsp. *aegilopoides* may be referring to either, or both, *T. boeoticum* subsp. *boeoticum* and *T. boeoticum* subsp. *thaouidar*.

1.4 Taxonomic Treatment in this Chapter

As stated earlier, there are no universally accepted rules for making taxonomic decisions. The reproductive behavior of plants tends to make a mockery of attempts to develop such rules. For instance, a frequently heard suggestion is that genera should be monophyletic. This means that a genus should include all species derived from the same common ancestor. This works well in groups where diversification is primarily the result of lineage splitting; it is difficult to follow in a group such as the *Triticeae* that exhibits complex patterns of reticulation and polyploidy.

Another approach to generic classification that has been strongly advocated for the *Triticeae* (Löve 1984; Dewey 1984; Yen et al. 2005a) is to base generic circumscription on genomic composition. Difficulties with strict application of this approach include our ignorance of the genomic composition of several species and the imperfect correlation between morphology and genomic composition. Nevertheless, to the extent that it has been investigated, genomic composition tends to indicate the groups of species to which the primary ancestors of allopolyploid species belong (Svitashev et al. 1996; Mason-Gamer 2001; Liu et al. 2006; Sun et al. 2006). It may, however, underestimate the contribution of hybridization to the tribe's diversity.

Still another approach emphasizes the value of morphologically distinguishable genera. One problem with this approach is that no taxonomist is equally familiar with all the species of the tribe. Groups of species may be evidently distinct to those familiar with them, but indistinguishable to those encountering them for the first time. The ease and low cost of sharing digital images should reduce the extent to which this differing familiarity is a problem in the future. Another question is whether all morphologically distinguishable species groups should be recognized as genera. If they are, *Sitanion* Raf. undoubtedly merits recognition at the generic level.

Taxonomists rely heavily on each other's work when preparing generic descriptions or prepare descriptions based solely on the species occurring in their region of interest. The first approach tends to preclude the adoption of new characters in delimiting genera. It may also lead to the perpetuation of errors. The value of regional descriptions depends on how much of the diversity within the genus is represented in the area concerned. Developing useful circumscriptions of new generic interpretations requires developing detailed species descriptions for a high proportion of the species in each genus.

An additional concern with generic delimitation in an economically important group such as the *Triticeae* is tradition. Changes in generic circumscription should be made if the resulting classification is a substantially closer fit to the evolutionary history of a group. On the other hand, if what is involved is breaking a well-known, easily identified genus into two or more sister genera, or the combination of two long-established sister genera into a single genus, the