

# Hitoshi Kihara, Áskell Löve and the modern genetic concept of the genera in the tribe Triticeae (Poaceae)

<sup>1</sup>YEN Chi\* <sup>1</sup>YANG Jun-Liang <sup>2</sup>YEN Yang

<sup>1</sup>(Triticeae Research Institute, Sichuan Agricultural University, Dujiangyan, Sichuan 611830, China)

<sup>2</sup>(Department of Biology and Microbiology, South Dakota State University, Brookings, SD 57006, USA)

**Abstract** Taxonomy is a tool for organism recognition, an understanding of phylogenetic relationships among organisms, a guide for germplasm utilization, and a common language for communication. Therefore, a taxonomic treatment needs to reflect our current understanding of such relationships. In nature, there are only two absolute units of living organisms: individuals and species. A species is a group of individuals who are connected to each other as a unit by their indispensable relationships of breeding. Reproductive separation is an essential boundary between species, and the only factor to form independent gene pools during organismal evolution. Since there is no absolute boundary among taxa above species, any taxonomic treatments above species cannot avoid arbitrariness. Nevertheless, some classification should be made for the convenience of their description, utility and/or study. This paper classifies the biosystematic relationships among taxa in Triticeae on the basis of genetic studies. The principles for our taxonomic treatment are: (1) reflecting the current understanding of the phylogeny among the species involved, (2) being convenient for germplasm utilization, and (3) avoiding unnecessary radical change apart from the tradition.

**Key words** Taxonomy, genus, classification principle, biosystematics, genome.

Taxonomy is a tool for organism recognition. It tells us which species an individual belongs to as well as how it is related to others. Taxonomy is also a guide for germplasm utilization. People use it to identify the adequate gene pool. Therefore, a taxonomic treatment needs to reflect the current understanding of such relationships based on multidisciplinary researches, and yet be convenient for using.

Triticeae is economically the most important tribe in Poaceae. It contains major cereal crops and forage grasses such as wheat, barley and rye. Because of their economic importance, Triticeae plants are far more frequently used for applied and theoretical researches than any other tribes of the Poaceae are. However, confusions have often arisen about which species the authors were talking about due to variety of taxonomic classification systems followed by different authors. Hence, a taxonomic treatment that reflects our current understanding of the phylogenetic relationship is needed to be adapted so that we can have a common language when talking about Triticeae plants.

## 1 Historical account and current situation in Triticeae taxonomy

From the eighteenth to the twentieth centuries, Triticeae taxonomy was basically based on morphological and phytogeographic studies. Binary nomenclature of species, systematic

ranks, and International Code of Botanical Nomenclature were established during this period. These achievements have helped to resolve the chaos in plant recognition by arranging individuals into systematic ranks. Now, it is well known that morphological characters are phenotypes of the individuals directed by their genetic make-ups. It is also known that phenotypes result from the interactions among environmental and hereditary factors. Morphologic similarities may reflect a close phylogenetic relationship among individuals. However, two phylogenetically closely related species can also be morphologically different to each other when they grow up in different environments. Thus, a taxonomic treatment solely relying on morphological analysis cannot avoid misclassification.

Following the pioneer work by Rosenberg (1909), Kihara (1930) proposed his genome theory and introduced his cytogenetic method for studying the phylogenetic relationships among species and genera in higher plants. He brilliantly expounded the origin of auto- and allo-ployploids. He made a clear classification of the genus *Aegilops* L. He also clarified the origin and the relationships among species of the genus *Triticum*. Since then, genetic studies and, particularly, cytogenetic studies have strongly influenced taxonomic treatments of Triticeae species. Examples are the taxonomic treatments by Sears (1948, 1956), Mac Key (1954, 1963, 1968a, b), Bowden (1959), and Morris and Sears (1967). Dewey and his colleagues (Dewey 1967a, b, 1968a, b, 1969, 1970, 1971, 1972, 1981; Dewey & Holmgren, 1962) carried out cytogenetic studies in perennial Triticeae grasses for many years and made great contributions to the basic knowledge of the genomic constitutions in most plants of this group (Dewey, 1982, 1984). These achievements created a favorable environment for developing cytotaxonomy of tribe Triticeae, and prompted Löve (1982) to propose his generic taxonomy of tribe Triticeae on the basis of his rigorously genomic concept by recommending that each genome (or haplome as he called) or combination should be the base to define a genus. His “Conspectus of the Triticeae” (Löve, 1984), as he said, is “a taxonomical and nomenclatural survey of the more than 500 biological taxa of the Triticeae tribe of grasses in a system of thirty-seven genomically defined genera based on twenty-three single-haplome taxa as recently validated elsewhere”. He regarded the genomic approach as being “crucial for studies of the evolution and definition of the basic taxonomical categories” (Löve, 1984). We generally agree with Löve’s viewpoint that “genome analysis that identifies haplomes has become widely accepted as a method for studies of polyploids and their ancestry”. However, we also recognize that some species on Löve’s list had never been cytogenetically studied at that time. Many of these species are Asiatic perennial species. The treatment of the group that is traditionally classified as the genus *Roegneria* is a good example. The Y genome in these plants was not well studied at that time. Hence he treated *Roegneria* as a synonym of *Elymus*.

Although many scientists have favored Löve’s conspectus of Triticeae (Bothmer & Salomon, 1994; Lu, 1994), nobody has exactly abided by his principles. For example, he divided *Aegilops-Triticum* group into 16 genera. So far, *Aegilops* or *Triticum* has still been a favorite as the genus name for this group. Most botanists in Europe and North America deviate from Löve’s principles and put six genomic combinations into one genus, the *Elymus* sensu lato. Löve put these taxa together into the genus *Elymus* due to his limited knowledge of their genomic constitutions in his era. Now, we have known that these groups consist of multiple genomes and need to be further divided if Löve’s principle is followed. However, those botanists who believe they are Löve’s followers still unfortunately follow Löve’s inadvisable classification and ignore his essential principles of generic definition.

As Yen et al. (1997) pointed out, there are only two absolute units of living organisms in nature: individuals and species. A species is a group of individuals who are connected to each other by their indispensable relationships of breeding. No absolute boundary exists among genera, families and the taxa above. Taxonomic treatment above species cannot avoid

arbitrariness. Classification at genus level can be made on different bases. For example, the genus *Triticum* L. was defined as having the **A**, **B** and **D** genome combination (Löve, 1984), possessing an **A** genome (Kihara, 1954, 1982; Mac Key, 1963, 1968a, b), or having close genomic relationships (Morris & Sears, 1967; Kimber & Feldman, 1987).

Species is very important in theoretical and applied biology. This is because that a species represents an independent gene pool in the evolutionary system. Reproductive separation is the only factor for the formation of such independent gene pools in organismal evolution. Although there are many concepts about how to define a species, from the viewpoint of evolutionary genetics, a species is an independent gene pool, and reproductive separation is the only standard for species identification. The factor(s) causing the reproductive separation is the causal force of speciation. How the reproductive separation has been achieved, however, varies among species. It may be caused by a gene mutation, such as the rDNA mutation that separates *Triticum monococcum* L. and *T. urartu* Thumanjan ex Gandilyan; by an chromosomal aberration, such as the translocation between *Secale montanum* Guss. and *S. cereale* L.; or by a genomic convergence, such as in the origin of *Triticum timopheevi* Zhuk., an amphidiploid derived from the hybrid between *T. urartu* and *T. speltoides* Flaksb. From these, we can see that reproductive separation might be achieved at different levels of genetic constitution, such as being genic, chromosomal or genomic, but the result is the same. Formation of reproductive isolation is the pathway by which each species has evolved, and it may differ one species from others. Therefore, the fact that speciation has followed multiple routes in the nature needs to be kept in mind when we do taxonomic treatment. Obviously, it will be wrong to use a single uniformed formula to classify a group of diverse species such as Triticeae species. And this is the exact mistake made by Löve (1984).

Plant taxonomy is a science dealing with classification of plants for facilitating their utility for human benefits. Although we hope that a taxonomic treatment can truly reflect the natural relationships of the taxa concerned, it also should be convenient for utilization. If a taxonomic classification goes too extreme, resulting in too many monotypic genera or too many species in one giant genus, it will become useless. The treatment of *Aegilops-Triticum* complex of Löve (1984) and the treatment of the genus *Elymus* by some others just represent such a mistake.

## 2 The major problems of Triticeae taxonomy

One of the hot disputes in the genus classification in Triticeae is the treatment of the genera *Elymus* and *Roegneria*. These perennial grasses are naturally divided into several groups according to cytogenetic studies, molecular analyses, phytogeographic observations, and ecological and morphological survey. These natural groups were validly identified as several genera based on the International Code of Botanical Nomenclature. One of them is the genus *Roegneria*, which was established on the basis of the type species *Roegneria caucasica* C. Koch and based upon priority of publication (Koch, 1848 in *Linnaea* 21: 413). Phytogeographically, this group of plants has their own special distribution area. Morphologically, they have short and broader palea. Hence, *Roegneria* should be a valid genus according to the Code. Cytogenetically, these species possess **St** and **Y** genomes (Jensen & Wang, 1991; Lu, 1993), unlike *Elymus sibiricus* L., the type species of the genus *Elymus*, which has an **St** and **H** genome combination (Dewey, 1974). If we follow Löve's principles, *Roegneria* should also be a genus.

The so-called genus *Elymus* recognized by many botanists is in fact a medley of various combinations of the **H**, **P**, **St**, **W** and **Y** genomes (Bothmer & Salomon, 1994). If we follow the genomic group concept which Morris and Sears (1967) applied to genus *Triticum*, the

genus *Elymus* sensu lato should include the diploid related taxa as well. Hence, *Agropyron*, *Australopyrum* (Tzvelev) Á. Löve, *Hordeum* section *Campestris*, and *Pseudoroegneria* should be grouped into this genus, and *Elymus* would be a giant genus, with more than 200 species! This genus still would have more than 150 species even if the diploid taxa were excluded.

Jensen (1996) proved that genomes **P**, **St** and **Y** were possessed by *E. alatavicus* (Drobov) Á. Löve, *E. batalinii* (Krasn.) Á. Löve, *E. grandiglumis* (Keng) Á. Löve, *E. kengii* (Tzvelev) D. F. Cui, *E. kokonoricus* (Keng) Á. Löve, *E. melantherus* (Keng) Á. Löve and *E. thoroldianus* (Oliver) G. Singh. And, he combined these species into section *Hyalolepis* (Nevski) Á. Löve of the genus *Elymus*. Also, the genus *Elymus* proposed by Bothmer and Salomon (1994) and Lu (1994) is composed of more than 150 taxa. They all claimed that they followed Löve. As mentioned above, a taxonomic treatment above the species level cannot avoid arbitrariness. If there exist natural groups we should embody them into our classification. The genus *Elymus* of Löve's needs to be revised to embody the natural groups indicated by cytological, morphological and eco-phytogeographical surveys on the basis of the International Code of Botanical Nomenclature. And we can do so by just following Löve's principles. Figure 2 shows such a treatment. Of the taxa, *Australoroegneria* (**StStWWYY**, Torabinejad & Mueller, 1993), and *Douglasdeweya* (**PPStSt**, Wang et al., 1986) are newly established genera.

Some natural groups were formed by ecological condition, and have some distinguished morphological characteristics for adaptation. For example, *Hystrix* Moench is a disputed group. It has broadly lanceolate leaves to adapt the dim sun light under forests and reduced glumes. Based on their preliminary cytological observation, Church (1967a, b) and Dewey (1982, 1984) believed that this group of species had the same **H** and **St** genomes as *Elymus* and *Sitanion* Raf. So, Löve (1984) put both *Sitanion* and *Hystrix* species into *Elymus* as section *Hystrix* (Moech) Á. Löve, and section *Sitanion* (Rsfm.) Á. Löve, respectively. However, recent molecular analyses (Jensen & Wang, 1997; Zhou et al., 1999; Zhou et al., 2000; Zhang et al., 2002) showed that *Hystrix californica* Kuntze, *Hystrix duthiei* (Stapf) Bor, *Hystrix duthiei* ssp. *longearistata* (Hack.) C. Baden and *Hystrix coreana* (Honda) Ohwi do not have the **H** and **St** genomes, but the **Ns** and **Xm** genomes. As a result, these *Hystrix* species should belong to the genus *Leymus* Hochst. (Jensen & Wang, 1997; Svitashv et al., 1998) and should thus be reclassified as a section under the genus *Leymus*. On the other hand, *Hystrix patula* Moench morphologically looks like *H. duthiei* ssp. *longearistata* very much. However, recent cytogenetic study suggested that these two forest grasses share no genome with each other (Hai-Qin ZHANG, personal communication), and thus cannot be classified in the same genus. Obviously, *Hystrix* can no longer be recognized as an independent genus.

According to the traditional, morphological treatment, the genus *Hordeum* consists of 37 species. Löve (1984) separated *Critesion* Rafin. from *Hordeum*. From the viewpoint of cytotaxonomy, this treatment is right, but few people follow this treatment in practice because of the force of habit. Recent researches (Bothmer et al., 1986, 1987, 1988a, b; Jaaska, 1992, 1994) suggested that two groups in the genus *Critesion*, namely *H. murinum* L. (=section *Trichostachys* (Dumortier) Á. Löve) and *Hordeum marinum* Huds. (=section *Marina*) are different from other *Critesion* species. These species have an **Xu** or an **Xa** genome, respectively. Their crossibility with *Critesion* species is very low, and chromosome pairing has not been observed in the hybrids. All these indicated that these two groups of species have no close phylogenetic relationships with other taxa of *Hordeum* or *Critesion*. Based on Löve's principles, these two groups must be treated as separate genera: *Trichostachys* and *Marina*, in addition to *Hordeum* and *Critesion*. If we consider the force of habit, they would better be treated as sections, or subgenera under *Hordeum* instead.

Another problem in these taxa is the existence of chromosome pairing control genes

(Sadasiyaiah & Kasha, 1971; Yen & Yang, 2004). The action of such genes overshadows the real phylogenetic distance between *Hordeum vulgare* L. and *H. nodosum* L. Their hybrids were found to have seven ring bivalents at MI of the pollen mother cells but quite sterile. Chromosomes from *H. nodosum* L. were often eliminated after several cell cycles. It seems that the two taxa share the same I genome (Dewey, 1984), but differentiation did occur. Therefore, we propose here to designate the genome of *H. nodosum* as the  $I^p$ . Obviously, this taxon should belong to *Hordeum* but not a member of *Critesion*.

Löve (1984) divided traditional *Elytrigia* Desv. into three genera: *Lophopyrum*, *Thinopyrum* Á. Löve, and *Elytrigia*. Recent investigations (Wang, 1985; Liu & Wang, 1989, 1992, 1993a, b; Xu & Conner, 1994) indicated that genome J is very close to genome E, and the two can be regarded as two modified forms of the later and thus designated as  $E^b$  and  $E^c$ , respectively (Wang et al., 1994). Since *Thinopyrum* and *Lophopyrum* have the same basic genome, these two genera should, according to Löve's principles, be combined. *Elytrigia repens* (L.) Nevski (the type species of the genus *Elytrigia*) was observed to have the StStH genome combination (Dewey, 1980; Assadi, 1994; Assadi & Runemark, 1995; Vershinin et al., 1994), and thus should be combined into genus *Elymus*. *Elytrigia* section *Trichophorae* has been found to possess an  $E^cSt$ ,  $E^cE^cSt$  or  $E^bE^cSt$  combinations. If Löve's principles are followed, this taxon should be raised to the genus level and, together with *Thinopyrum* and *Lophopyrum*, designated as a new genus *Trichopyrum* Á. Löve. Figure 1 shows the phylogenetic relationships of these groups.

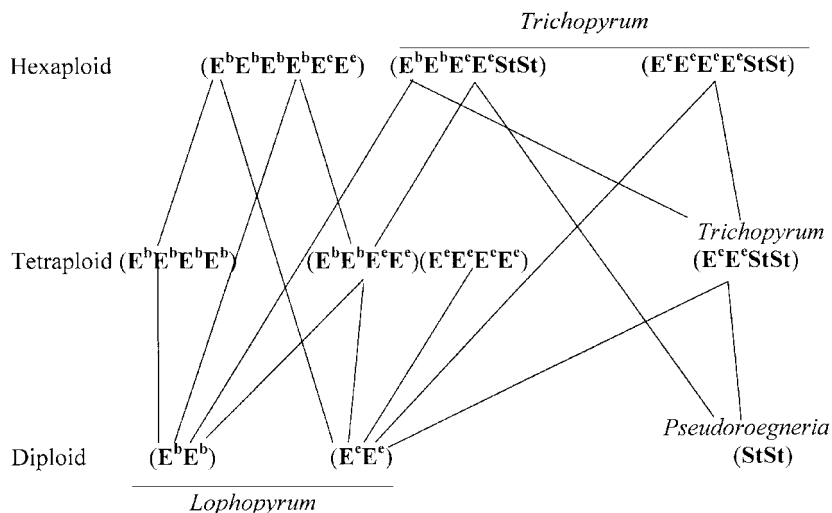


Fig. 1. A diagram of phylogenetic relationships of *Lophopyrum* group and their genomic donors.

The *Aegilops-Triticum* group is special because that it consists of only about 28 species but has eight different genomes plus more than five modified versions. Every diploid taxon has its own genome. These diploid species are very easy to cross with each other resulting in many allo- or auto-allopolyploid species. Löve (1984) divided this group into 16 genera, with 10 being monotypic. Nevertheless, the great majority of wheat scientists have never accepted Löve's treatment. Instead, *Aegilops* or *Triticum* is still used as the generic name for these taxa.

*Aegilops mutica* Boiss. has a T genome, which has never been found in any polyploidy species. It seems that this species has no close phylogenetic relationship with other *Aegilops* taxa. In fact, Eig (1929) separated this taxon from *Aegilops* and treated it as a genus, *Amblyopyrum* Eig. Obviously, Eig's treatment seems to reflect the phylogenetic relationships

and follow the International Code of Botanical Nomenclature. *Amblyopyrum*, therefore, ought to be a valid genus name. Hence, *A. muticum* (Boiss.) Eig is undoubtedly a valid species name for this taxon. Löve (1984) and Tzvelev (1989) followed Eig's suit and we fully agree with them.

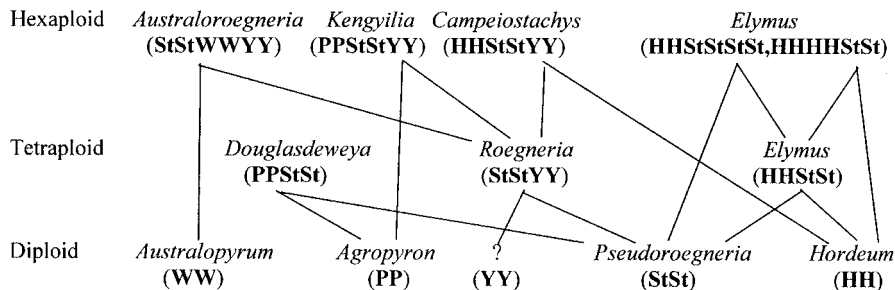


Fig. 2. A diagram of phylogenetic relationships among genera *Agropyron*, *Australopyrum*, *Australoroegneria*, *Elymus*, *Hordeum*, *Kengyilia*, *Campeiostrachys*, *Douglasdeweya*, *Pseudoroegneria*, and *Roegneria*.

According to Kihara (1930, 1954), whether the uniqueness of a genome in a diploid species is defined by the degree of its difference from other genomic analysers is judged by chromosome pairing in meiosis of the hybrids. However, there is no consistent standard for this judgement. For example, although genome **B** of the *Triticum* species obviously has some differences from genomes **G** and **S**, Löve still designated **B** for the latter two. Certainly, the differences among the **B**, **G**, and **S** genomes may not be as great as those among the **S<sup>b</sup>** genome of *Aegilops bicornis* Jaub. & Spach., the **S<sup>l</sup>** genome of *Ae. longissima* Schweinf. & Muschl., and the **S<sup>s</sup>** genome of *Ae. searsii* Feldman & Kislev ex Hammer. Are they qualified to be independent genomes or only modified versions of **B** genome? There has been no clear answer. Tsunewaki (1988) showed that *T. timopheevi* shared its cytoplasm with *Ae. speltoides* Tausch, and thus proved that the **G** genome of *T. timopheevi* has very closely relationship to the **S** genome of *Ae. speltoides*.

Yen and Kimber (1990) used the variable  $\log_e(x/y)$  to measure of the genomic distance among the **S**-genome groups (Fig. 3). The results showed that *Aegilops longissima* and *Ae. speltoides* have the most distant relationship; that *Ae. sharonensis* Eig. is equally and most closely related to *Ae. longissima* and *Ae. speltoides*; that *Ae. bicornis* is closer to *Ae. speltoides*

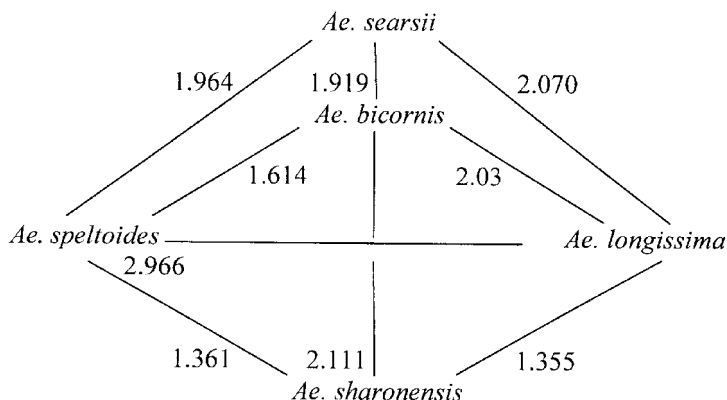


Fig. 3. The variable relationships among the **S**-genome of diploid *Aegilops* species, measured by  $\log_e(x/y)$ . (From Yen & Kimber, 1990)

than to any other species and almost equally but closely related to *Ae. longissima*, *Ae. sharonensis* and *Ae. searsii*; and that *Ae. searsii* is almost equally but distantly related to *Ae. longissima*, *Ae. speltoides* and *Ae. bicornis*. These results suggested that the **S**-genome species share a same basic genome but each has a unique variety.

Results of molecular analyses have also shown that genomes **S**, **B**, **D**, and **A** are much more closely related to each other than to other genomes (Monte et al., 1993; Dvorak & Zhang, 1990; Dvorak et al., 1998). Molecular analyses of cytoplasm genomes reported by Tsunewaki (1996) suggested that *Triticum timopheevi* has the same cytoplasm as some races of *Aegilops speltoides* do and the cytoplasm of *T. turgidum* L. is very similar to that in some races of *Ae. speltoides*. All these suggested that genomes **S**, **B** and **G** are basically the same genome. Therefore, Löve was right when he applied the genome symbol "**B**" to all of these modified versions previously designated as **S**, **G** and **B**, respectively. On the other hand, the International Committee on Genome Designation of International Triticeae Symposium kept the traditional designations for the corresponding genomes in its "Genome Symbols in the Triticeae (Poaceae)" (published in 1994, Logan, Utah, U.S.A.). This is a good example showing that designating a genome symbol is very arbitrary and is strongly influenced by the force of habit. Although the suggestion by the International Committee on Genome Designations of the Second International Triticeae Symposium will be followed here, we, considering their real phylogenetic distances, still regard genomes **B**, **G**, and **S** just as different versions of the same genome. Hence Fig. 4 shows the relationships among the taxa within the *Aegilops-Triticum* group.

As shown in Fig. 4, *Aegilops-Triticum* species have been basically formed around three pivotal genomes, **A**, **D**, and **U**. Phylogenetically, speciation in this group is quite different from that in the **St** genomic groups (*Elymus-Kengyilia-Roegneria* ... etc.). Speciation in the **St** genomic groups is mainly based on genomic modification. For example, 23 species and five varieties in the genus *Kengyilia* share the same basic genome combination but differ by minor

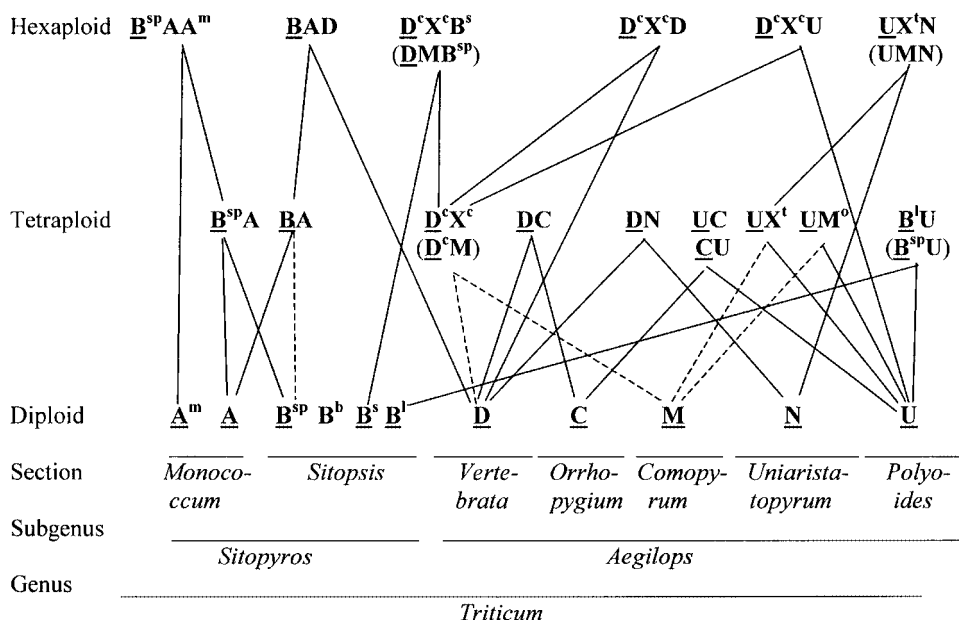


Fig. 4. A diagram of phylogenetic relationships within the genus *Triticum*.

modifications; and so is the speciation in the genera *Elymus*, *Campeiostrachys* and *Roegneria*. Now we are in a scenario that Löve's rigorous genome concept of classification is suitable for the **St** taxa but not for the **A**, **D**, and **U** taxa. If we applied Löve's concept to the **A**, **D**, and **U** taxa, we can not avoid making too many monotypic genera in the classification. Philosophically, things will go to their opposite if they are too extreme. Krause (1898) combined *Elymus*, *Hordeum*, *Elytrigia* (= *Agropyron*), *Secale* L., and *Triticum* together and established a giant genus, *Fruentum* Krause. On the other hand, Löve classified 11 monotypic genera for the *Aegilops-Triticum* group. Practically, nobody but themselves have accepted these extreme treatments no matter how good the reasons did they have.

### The proposed classification of the genera in Triticeae

Obviously, a new classification of Triticeae species at the genus level is badly needed to clear up the chaos. Here, we propose the following principles for the genus classification:

(1) A treatment of genera should reflect not only the phylogenetic relationships among the species involved, but also the convenience of its applications.

(2) Genus treatment must follow the principles and articles of the International Code of Botanical Nomenclature.

(3) The force of habit needs to be considered whenever possible to avoid adding more chaos.

(4) Since speciation of different species group may follow different pathways, different standards should be applied to their classification to better reflect their phylogeny.

(5) Nuclear and cytoplasmic genome constitutions are important factors for the genus classification and so are ecological factors.

(6) A genus classification needs to be revised if more knowledge about the phylogenesis is obtained.

As we mentioned above, Triticeae taxonomy was first established on the basis of morphology, phytogeography and ecology before the era of experimental sciences. Nevertheless, morphological taxonomy can only serve as the first step to approach a taxon. The preliminary morphological taxonomy has to be revised if adequate data from experimental sciences are available. We consider that we now have the adequate data to revise the taxonomy of the tribe Triticeae at the genus level and mostly at species level. With Löve's conspectus in mind and on the basis of the principles we proposed above, we herewith propose the following generic reclassification of the tribe Triticeae:

#### 1. *Hordeum* and its sections

*Hordeum* L., Sp. Pl.: 84. 1753.

Section *Cerealia* Anderson, Skand. Gram.: 8. 1852.

Genome: **I** and its modified versions.

Section *Trichostachys* Dumortier, Observ. Gram. Belg.: 92. 1823.

Genome: **Xu** and its modified versions.

Section *Marina* (Nevski) Jaaska in Hereditas 116: 30. 1992.

Genome: **Xa** and its modified versions.

Section *Campestria* Anderson, Skand. Gram.: 8. 1852.

Genome: **H** and its modified versions.

#### 2. *Lophopyrum*

*Lophopyrum* Á. Löve in Taxon 29: 351. 1980.

Section *Lophopyrum*

Genome: **E<sup>e</sup>**, **E<sup>b</sup>**.

Section *Trichophorae* (Nevski) Dubovik in Nov. Sist. Vyssh. Nizschikh Rast. 1976:



7. 1977.

Genome: **St, E<sup>e</sup>, E<sup>b</sup>**.

### 3. *Elymus* and the related genera

*Agropyron* J. Gaertn. in Nov. Comm. Acad. Sci. Petrop. 14: 539. 1770.

Genome: **P**.

*Hordeum* L., Sp. Pl.:84. 1753.

Section *Campestris* Anderson, Skand. Gram.: 8. 1852.

Genome: **H**.

*Australopyrum* (Tzvelev) Á. Löve in Feddes Repert. 95: 442. 1984.

Genome: **W**.

*Pseudoroegneria* (Nevski) Á. Löve in Taxon 29: 168. 1980.

Genome: **St**.

*Elymus* L., Sp. Pl.: 83. 1753.

Genome: **H, St**.

*Roegneria* C. Koch in Linnaea 21: 413. 1848.

Genome: **St, Y**.

*Campeioctagys* Drob., Fl. Uzbek. 1: 540. 1941.

Genome: **H, St, Y**.

*Kengyilia* C. Yen & J. L. Yang in Can. J. Bot. 68: 1894-1897. 1990.

Genome: **P, St, Y**.

*Douglasdeweya* C. Yen, J. L. Yang & D. Q. Baum in Can. J. Bot. 2005 (in press).

Genome: **P, St**.

*Australoroegneria* C. Yen & J. L. Yang (ined.).

Genome: **St, W, Y**.

### 4. *Aegilops-Triticum* complex

*Triticum* L., Sp. Pl. : 85. 1753.

Subgenus *Aegilops* Hackel in Engler & Prantl, Nat. Pflanzenfam. II : 80. 1887.

Genome: **D, D<sup>c</sup>; C; M (X<sup>c</sup>, X<sup>t</sup>), M<sup>o</sup>; N; U**.

Subgenus *Sitopyros* Hackel in Engler & Prantl, Nat. Pflanzenfam. II : 81. 1887.

Genome: **A, A<sup>m</sup>; B, B<sup>sp</sup>, B<sup>l</sup>, B<sup>b</sup>, B<sup>s</sup>; D**.

We understand that this reclassification does not solve all the problems we have. Some problems, such as the treatment of the taxa at the rank of species and below, and the validity of some nomenclatures in the tribe Triticeae other than genetic reasons, such as the invalid genus name *Dasypyrum* (Coss. & Durieu) T. Durand, etc. have been discussed in another monograph (Yen & Yang, 1999, 2004).

## References

- Assadi M. 1994. Experimental hybridization and genome analysis in *Elymus* L. Sect. *Caespitosae* and Sect. *Elytrigia* (Poaceae: Triticeae). In: Wang R R-C, Jensen K B, Jaussi C eds. Proceedings of the Second International Triticeae Symposium. Logan: USDA-Forage and Range Laboratory. 23-28.
- Assadi M, Runemark H. 1995. Hybridization, genomic constitution and generic delimitation in *Elymus* s. l. (Poaceae: Triticeae). Plant Systematics and Evolution 191:189-205.
- Bothmer R von, Salomon B. 1994. Triticeae: a tribe for food, feed and fun. In: Wang R R-C, Jensen K B, Jaussi C eds. Proceedings of the Second International Triticeae Symposium. Logan: USDA-Forage and Range Laboratory. 1-12.
- Bothmer R von, Flink J, Landström T. 1986. Meiosis in interspecific *Hordeum* hybrids I. Diploid combinations. Canadian Journal of Genetics and Cytology 28: 525-535.
- Bothmer R von, Flink J, Landström T. 1987. Meiosis in interspecific *Hordeum* hybrids II. triploid combinations. Evolutionary Trends in Plants 1: 41-51.

- Bothmer R von, Flink J, Landström T. 1988a. Meiosis in interspecific *Hordeum* hybrids III. Tetraploid ( $2x \times 6x$ ) combinations. *Hereditas* 108: 141-148.
- Bothmer R von, Flink J, Landström T. 1988b. Meiosis in interspecific *Hordeum* hybrids IV. Tetraploid ( $4x \times 4x$ ) combinations. *Genome* 30: 479-485.
- Bowden W M. 1959. The taxonomy and nomenclature of the wheat, barley, and ryes and their relatives. *Canadian Journal of Botany* 37: 657-684.
- Church G L. 1967a. Taxonomic and genetic relationships of eastern North American species with setaceous glumes. *Rhodora* 69: 121-162.
- Church G L. 1967b. Pine Hills *Elymus*. *Rhodora* 69: 330-351.
- Dewey D R. 1967a. Synthetic hybrids of *Elymus canadensis* × *Sitanion hystrix*. *Botanical Gazette* 128: 11-16.
- Dewey D R. 1967b. Genome relations between *Agropyron scribneri* and *Sitanion hystrix*. *Bulletin of the Torrey Botanical Club* 94: 395-404.
- Dewey D R. 1968a. Synthetic hybrids of *Agropyron caespitosum* × *Agropyron dasystachyum* and *Sitanion hystrix*. *Botanical Gazette* 129: 316-322.
- Dewey D R. 1968b. Synthetic hybrids of *Agropyron dasystachyum* × *Elymus glaucus* and *Sitanion hystrix*. *Botanical Gazette* 129: 309-315.
- Dewey D R. 1969. Synthetic hybrids of *Agropyron albicans* × *A. dasystachyum*, *Sitanion hystrix*, and *Elymus canadensis*. *American Journal of Botany* 56: 664-670.
- Dewey D R. 1970. Hybrids of South American *Elymus agropyroides*, with *Agropyron caespitosum*, *Agropyron subsecundum*, and *Sitanion hystrix*. *Botanical Gazette* 131: 210-216.
- Dewey D R. 1971. Synthetic hybrids of *Hordeum bogdanii* with *Elymus canadensis* and *Sitanion hystrix*. *American Journal of Botany* 58: 902-908.
- Dewey D R. 1972. Genome analysis of South American *Elymus patagonicus* and its hybrids with two North American and two Asian *Agropyron* species. *Botanical Gazette* 133: 436-443.
- Dewey D R. 1974. Cytogenetics of *Elymus sibiricus* and its hybrids with *Agropyron tauri*, *Elymus canadensis* and *Agropyron caninum*. *Botanical Gazette* 135: 80-87.
- Dewey D R. 1980. Morphological, cytological and taxonomic relationships between *Agropyron repens* and *A. elongatiforme* (Gramineae). *Systematic Botany* 5: 61-70.
- Dewey D R. 1981. Cytogenetics of *Agropyron ferganense* and its hybrids with six *Agropyron*, *Sitanion*, and *Elymus* species. *American Journal of Botany* 68: 216-225.
- Dewey D R. 1982. Genome relationships and taxonomy of the perennial grasses related to wheat. *Agronomic Abstract* 1982: 63.
- Dewey D R. 1984. The genome system of classification as a guide to intergeneric hybridization with perennial Triticeae. In: Gustafsson J P ed. *Gene Manipulation in Plant Improvement*. New York: Plenum. 209-279.
- Dewey D R, Holmgren A H. 1962. Natural hybrids of *Elymus cinereus* × *Sitanion hystrix*. *Bulletin of the Torrey Botanical Club* 89: 217-228.
- Dvorak J, Luo M C, Yang, J L. 1998. Genetic evidence on the origin of *T. aestivum* L. In: Damania A B, Willcox G, Quallsat C O eds. *The origin of agriculture and domestication of crop plants in the Near East: An International Symposium of Plant Biologists and Archaeologists*. Aleppo: ICARDA. 235-251.
- Dvorak J, Zhang H B. 1990. Variation in repeated nucleotide sequences sheds light on the phylogeny of the wheat B and G genomes. *Proceedings of the National Academy of Sciences USA* 87: 9640-9644.
- Eig A. 1929. Monographisch-kritische Uebersicht der Gattung *Aegilops*. *Repertorium Speciorum Novarum Regni Vegetabilis, Beihefte* 55: 1-228.
- Jaaska V. 1992. Isoenzyme variation in barley genus *Hordeum* L. 2. Aspartate aminotransferase and 6-phosphoglyconate dehydrogenase. *Hereditas* 116: 29-35.
- Jaaska V. 1994. Isoenzyme evidence on the systematics of *Hordeum* section *Marina* (Poaceae). *Plant Systematics and Evolution* 191: 213-226.
- Jensen K B. 1996. Genome analysis of Eurasian *Elymus thoroldianus*, *E. melantherus*, and *E. kokonoricus* (Triticeae: Poaceae). *Genome* 33: 563-570.
- Jensen K B, Wang R R-C. 1991. Cytogenetics of *Elymus caucasicus* (Koch) Tzvelev and *E. longearistatus* (Boiss.) Tzvelev (Poaceae: Triticeae). *Genome* 34: 860-867.

- Jensen K B, Wang R R-C. 1997. Cytological and molecular evidence for transferring *Elymus coreanus* and *Elymus californicus* from the genus *Elymus* to *Leymus* (Poaceae: Triticeae). *International Journal of Plant Sciences* 158: 872-877.
- Kihara H. 1930. Genomanalyse bei *Triticum* und *Aegilops*. *Cytologia* 1: 263-284.
- Kihara H, Nishiyama I. 1930. Genomanalyse bei *Triticum* und *Aegilops*. I. Genomaffinitäten in tri-, tetra-, und pentaploiden Weizenbastarden. *Cytologia* 1: 270-284.
- Kihara H. 1954. Consideration on the evolution and distribution of *Aegilops* species based on the analyser-method. *Cytologia* 19: 336-357.
- Kihara H. 1982. Wheat studies — retrospect and prospects. Tokyo: Kodansha.
- Kimber G, Feldman M. 1987. Wild wheat, an introduction. Special Report 353. Columbia: College of Agriculture, University of Missouri-Columbia, U.S.A.
- Krause E H L, 1898. Floristische Notizen II. Gräser. *Botanisches Centralblatt (Jena)* 73: 337-343.
- Liu Z W, Wang R R-C. 1989. Genome analysis of *Thinopyrum caespitosum*. *Genome* 32: 141-145.
- Liu Z W, Wang R R-C. 1992. Genome analysis of *Thinopyrum junceiforme* and *T. sartorii*. *Genome* 35: 758-764.
- Liu Z W, Wang R R-C. 1993a. Genome constitutions of *Thinopyrum curvifolium*, *T. scirpeum*, *T. distichum*, and *T. junceum* (Triticeae: Gramineae). *Genome* 36: 641-651.
- Liu Z W, Wang R R-C. 1993b. Genome analysis of *Elytrigia caespitosa*, *Lophopyrum nodosum*, *Pseudoroegneria geniculata* ssp. *scyyhica* and *Thinopyrum intermedium*. *Genome* 36: 102-111.
- Löve Å. 1982. Generic evolution of the wheatgrasses. *Biologisches Zentralblatt* 101: 199-212.
- Löve Å. 1984. Conspectus of the Triticeae. *Feddes Repertorium* 95: 425-521.
- Lu B R. 1993. Biosystematic investigations of Asiatic wheatgrasses—*Elymus* L. (Triticeae: Poaceae). Doctoral thesis. Department of Plant Breeding Research Dissertation, the Swedish University of Agricultural Sciences, Svalöv, Sweden.
- Lu B R. 1994. The genus *Elymus* L. in Asia. Taxonomy and biosystematics with special reference to genomic relationships. In: Wang R R-C, Jensen K B, Jaussi C eds. *Proceedings of the Second International Triticeae Symposium*. Logan: USDA-Forage and Range Laboratory. 219-225.
- Mac Key J. 1954. The taxonomy of hexaploid wheat. *Svensk Botanisk Tidskrift* 48: 579-590.
- Mac Key J. 1963. Species relationship in *Triticum*. In: *Proceedings of the Second International Wheat Genetics Symposium*. *Hereditas Supplement* 1966, 2: 237-276.
- Mac Key J. 1968a. Relationships in the Triticeae. In: Finlay K W, Shephard K W eds. *Proceedings of the Third International Wheat Genetics Symposium*. Canberra: Australian Academy of Sciences. 39-50.
- Mac Key J. 1968b. Genetic basis of systematics and wheat. *Agrobiologia* 1: 12-25.
- Morris R, Sears E R, 1967. The cytogenetics of wheat and its relatives. In: Quisenberry K S, Reitz L P eds. *Wheat and Wheat Improvement*. Madison: American Society of Agronomy. 19-87.
- Monte J V, McIntyre C L, Gustafsen J P, 1993. Analysis of phylogenetic relationships in the Triticeae tribe using RFLPs. *Theoretical and Applied Genetics* 86: 649-655.
- Rosenberg O. 1909. Cytologische und morphologische Studien an *Drosera longifolia* × *rotundifolia*. *K. Svensk Vetenskaps Akademiens Handlingar* 43: 1-64.
- Sadasivaiah R S, Kasha K J. 1971. Meiosis in haploid barley—an interpretation of non-homologous chromosome associations. *Chromosoma (Berlin)* 35: 247-263.
- Sears E R. 1948. The cytology and genetics of the wheats and their relatives. *Advances in Genetics* 2: 239-270.
- Sears E R. 1956. The systematics, cytology and genetics of wheat. *Handbuch der Pflanzenzuchtung*. Berlin & Hamburg: Verlag Paul Parey. Band II: 164-187.
- Svitashev S, Bryngelsson T X, Li M, Wang R R-C. 1998. Genome-specific repetitive DNA and RAPD markers for genome identification in *Elymus* and *Hordelymus*. *Genome* 41: 120-128.
- Torabinejad J, Mueller R J. 1993. Genome constitution of the Australian hexaploid grass *Elymus scabrurus* (Poaceae: Triticeae). *Genome* 36: 147-151.
- Tsunewaki K. 1988. Plasmon diversity in *Triticum* and *Aegilops* and its implication in wheat evolution. *Genome* 31:143-154.
- Tsunewaki K. 1996. Plasmon analysis as the counterpart of genome analysis. In: Jauhar P P ed. *Methods of Genome Analysis in Plants*. New York: CRC Press. 271-299.

- Tzvelev N N. 1989. The system of grasses (Poaceae) and their evolution. *Botanical Review* 55: 141-204.
- Vershinin A, Svitashv S, Gummesson P-O, Salomon B, Bothmer R von, Bryngelsson T. 1994. Characterization of a family of tandemly repeated DNA sequences in Triticeae. *Theoretical and Applied Genetics* 89: 217-225.
- Wang R R-C. 1985. Genome analysis of *Thinopyron bessarabicum* and *T. elongatum*. *Canadian Journal of Genetics and Cytology* 27: 722-728.
- Wang R R-C, Dewey D R, Hsiao C. 1986. Genome analysis of the tetraploid *Pseudoroegneria tauri*. *Crop Science* 26: 723-727.
- Wang R R-C, von Bothmer R, Dvorak J, Fedak G, Linde-Laursen I, Muramatsu M. (Committee on Genome Designations). 1994. Genome symbols in the Triticeae (Poaceae). In: Wang R R-C, Jensen K B, Jaussi C eds. *Proceedings of the Second International Triticeae Symposium*. Logan: USDA-Forage and Range Laboratory. 29-34.
- Xu J, Conner R L. 1994. Intravarietal variation in satellites and C-banded chromosomes of *Agropyron intermedium* ssp. *trichophorum* cv. Greenleaf. *Genome* 37: 305-310.
- Yen C, Yang J L. 1999. *Biosystematics of Triticeae*. Vol. I. Beijing: Chinese Agricultural Press.
- Yen C, Yang J L. 2004. *Biosystematics of Triticeae*. Vol. II. Beijing: Chinese Agricultural Press.
- Yen C, Yang J L, Yen Y. 1997. The history and the correct nomenclature of the D-genome diploid species in Triticeae (Poaceae). *Wheat Information Service* 84: 56-59.
- Yen Y, Kimber G. 1990. Genomic relationships of *Triticum searsii* to other S-genome diploid *Triticum* species. *Genome* 33: 369-378.
- Zhang H-Q (张海琴), Zhou Y-H (周永红), Zheng Y-L (郑友良), Yang R-W (杨瑞武), Ding C-B (丁春邦). 2002. Morphology and cytology of intergeneric hybrids between *Hystrix duthiei* ssp. *longearistata* and *Psathyrostachys huashanica* (Poaceae: Triticeae). *Acta Phytotaxonomica Sinica (植物分类学报)* 40: 421-427.
- Zhou Y-H (周永红), Yang J-L (杨俊良), Yen C (颜济). 1999. Biosystematic studies on *Hystrix longearistata* from Japan and *Hystrix duthiei* from China (Poaceae: Triticeae). *Acta Phytotaxonomica Sinica (植物分类学报)* 37: 386-393.
- Zhou Y H, Zheng Y L, Yang J L, Yen C. 2000. Relationships among species of *Hystrix* Moench and *Elymus* L. assessed by RAPDs. *Genetic Resources and Crop Evolution* 47: 191-196.

# 木原均, A. 洛夫与小麦族(禾本科)的现代 遗传学属的概念

<sup>1</sup>颜 济\* <sup>1</sup>杨俊良 <sup>2</sup>颜 旻

<sup>1</sup>(四川农业大学小麦研究所 四川都江堰 611830)

<sup>2</sup>(Department of Biology and Microbiology, South Dakota State University, Brookings, SD 57006, USA)

**摘要** 分类学是认识生物体的一种工具,对生物体间系统关系的理解,种质资源利用的指南,也是一种交流用的普通语言。因此,分类处理需要反映这些关系的近期认识。在自然界,生物体只有两个绝对的单位:个体与种。一个种是一群个体被不可缺少的生殖关系相互联系成为一个绝对单位。生殖隔离是种与种间的基本界限,同时也是生物演化过程中形成独立基因库(gene pools)的惟一因素。既然在种以上的分类群没有绝对界线,在种以上的任一分类处理都不可能避免人为性。虽然如此,仍然必须作出某些分类适应它们的描述、利用与(或)研究。这篇文章对小麦族分类群间生物系统关系的划分是基于遗传学的研究。我们分类处理的原则是:(1)反映这些种系统演化现今的理解;(2)便于种质资源的利用;(3)避免与传统处理有不必要的剧烈改变。

**关键词** 分类学; 属; 分类原则; 生物系统学; 染色体组