Chi Yen · Junliang Yang

Biosystematics of Triticeae

Volume V. Genera: Campeiostachys, Elymus, Pascopyrum, Lophopyrum, Trichopyrum, Hordelymus, Festucopsis, Peridictyon, and Psammopyrum

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Preface

This is the fifth and final volume of "Biosystematics of Triticeae." Volume 5 includes the remaining genera in Triticeae, which were not introduced in volumes 1–4. It involves nine genera, namely *Campeiostachys* Drobov; *Elymus* L.; *Pascopyrum* Á. Löve; *Lophopyrum* Á. Löve; *Trichopyrum* Á. Löve; *Hordelymus* (Jessen) Haez.; *Festucopsis* (C. E. Hubbard) Melderis; *Peridictyon* O. Seberg, S. Frederiksen, and C. Baden; and *Psammopyrum* Á. Löve.

Campeiostachys Drobov was established by the Soviet plant taxonomist Василий Петрович Дробов, which was published in the first volume of the Uzbekistan Flora (Флора Узбекский ССР) in 1941. The type species is *Campeiostachys schrenkiana* (F. and M.) Drob. containing the **H**, **St**, and **Y** genomes. The classification of *Campeiostachys* is according to the principles of phylogenetic based natural biosystematics based on genomic analysis. After discussion with our long-time collaborator Dr. Bernard R. Baum, we decided to use the genus *Campeiostachys* Drobov, which we think is the best systematic treatment approach to objective reality. We have proposed *Hordeo-Roegneria* (the combination of two genome donors) as the name of the genus; however, the name of *Campeiostachys* was proposed by Василий Петрович Дробов prior to *Hordeo-Roegneria*. Thus, according to the International Botanical Synonym, the name of *Campeiostachys* Drobov should be used for these taxa.

Elymus L. is an old genus founded by Carl Linné in 1753. The type species is *Elymus sibiricus* L. with the **St** and **H** genomes. *Elymus* is a large genus including 83 species, 20 varieties, and some taxa called variants. (We believe that there is no difference between variety and variant in nature. Both variety and variant are different combinations of different alleles, which belong to the same level. Variant is a classification of artificial determination. Thus, we only recognize variety in this book.) *Elymus* is distributed from South America to North America, Eurasia, and Africa, which is the most widely distributed genus in the tribe Triticeae. Because of the differences in ecological environment, morphological variation of *Elymus* species is also very large. Like the genus *Leymus*, *Elymus* is a genus of polymorphism. Therefore, past morphological taxonomists divided it into several genera, such as

Elymus, *Sitanion*, and *Elytrigia*. Meanwhile, some species with a single spikelet were treated in the genus *Agropyron* or *Roegneria*. However, all of these taxa contain the **St** and **H** genomes, and they should be treated as in the same genus, *Elymus* L. This is a taxonomy mistake merely on morphology.

From the morphological point of view, *Campeiostachys* is similar to *Elymus*. They are cryptic genera, but their origins were totally different. For the karyotype of 11 species of *Campeiostachys*, there are two pairs of satellite chromosomes, namely 40th and 42nd, respectively. The satellite in 40th was large, while that in 42nd was small. This is the karyotype characteristic of the **Y** genome. Genera *Roegneria* (**StStYY**) and *Anthosachne* (**StStYYWW**) contain the **Y** genome, but the donor of **Y** genome is still unknown. That is to say, the genus *Campeiostachys* (**StYH**) is formed by the hybridization between *Roegneria* (**StY**) and *Hordeum* (**H**). The origin of *Campeiostachys* has no association with *Elymus*, although these two genera are similar in morphology. The genus *Elymus* (**StH**) is formed by the hybridization between *Pseudoroegneria* (**St**) and *Hordeum* (**H**). The **St** and **H** genomes in *Campeiostachys* and *Elymus* were same, and they were dominant in species of these two genera. The **Y** genome in *Campeiostachys* was recessive and was not expressed. Thus, both *Campeiostachys* and *Elymus* expressed the **St** and **H** genomes in morphology, and this led to the morphological similarity of these two genera. To distinguish between *Campeiostachys* and *Elymus*, we only use cytogenetic or molecular genetics methods. Here, we can see the limitations of morphological taxonomy. Morphological observations are important in taxonomy. We recognize species from their phenotypes firstly, that is, to understand them from their morphological characteristics. In the preface of volume 3, we have pointed out that phenotype (P) is the product of the interaction between heredity (H) and environment (E). It is a variable function relationship between heredity and environment. Coupled with the dominance-recessive relationships between pairs of genes as determined by the law of genetic display, it is possible to get the wrong result of heredity from the phenotype. This is "The inverse theorem is often untenable" on logic. Because of the dominance-recessive relationships in genetics, morphological taxonomists do not see the existence of recessive **Y** genomes. That is the reason why morphological taxonomists often confuse *Campeiostachys* and *Elymus*. Phenotypic differences due to different environmental adaptations often resulted in morphological taxonomists erroneously classifying *Elymus* with the same genome into different genera. Furthermore, while combining *Campeiostachys* and *Roegneria* with *Elymus*, some people mistakenly placed some species of *Anthosachne*, *Stenostachys*, and *Leymus* in *Elymus*. In this volume, we will correct these by the results of the experimental data.

Pascopyrum Á. Löve is one of the important pasture wild grasses in northwestern North America. It is a heterologous octoploid formed by hybridization between *Elymus* and *Leymus* and contains four genomes of **St**, **H**, **Ns**, and **Xm**. It is one of the main species that constitute the grassland vegetation in northwestern North America. It is a unique genus involving only one species.

Lophopyrum Á. Löve and *Thinopyrum* Á. Löve were two genera published by Á. Löve in 1982. He believed that *Lophopyrum* is a genus containing the **E** genome

while *Thinopyrum* is a genus containing the **J** genome. These two genera were published in the same article, so there is no question of which is prioritized. The **E** and **J** genomes were very similar based on the results of experimental analysis, and they should be treated as two subtypes of the same genome. Thus, species with the **E** and **J** genomes should be combined into one genus. Most people used the **E** genome so far, so the name of the genus should be *Lophopyrum*. However, someone used the name of *Thinopyrum*. Here, we recommend the genus *Lophopyrum* for species containing the **E** genome.

Trichopyrum Á. Löve was published by Á. Löve in 1986. It was an allopolyploid genus that was separated from the Section *Trichopyrum* (Nevski) Dubovik of the genus *Elytrigia*. It contained the **E** and **St** genomes. Obviously, it is originated from the species of *Lophopyrum* with the **E** genome and the species of *Pseudoroegneria* with the **St** genome.

Many taxonomists consider *Elytrigia* as an independent genus, but it consists of many taxa with different genomes. It is also a "hodgepodge" or "trash bin" created by morphological taxonomists (Davis and Heywood, 1963). The type species *Elytrigia repens* L. contains the $\mathbf{HHSt^1St^1St^2St^2}$ genomes and should be combined into the genus *Elymus*. The genus *Elytrigia* should not be existed for its type species *Elytrigia repens* has been included in *Elymus*. Furthermore, *Elytrigia elongata* is a species containing the **E** genome, which should be included into *Lophopyrum*. *Elytrigia intermedia* is a species containing the $\mathbf{E^eE^bSt}$ genomes, which should be treated as *Trichopyrum*. *Elytrigia* is a genus that is established based on morphology, which does not fit with the natural biological system. Thus, it is a wrong classification. In "Conspectus of the Triticeae" (Löve, 1984), *Elytrigia* was a genus with the **E**, **J**, and **S** (**St**) genomes, which should be included in the genus *Trichopyrum*. Therefore, *Elytrigia* as a genus will not be recognized in this book. Classification treatment of species in *Elytrigia* should be based on its genomic constitutions. For example, the type species *Elytrigia repens* (L.) Nevski, which contained the $\mathbf{St^1St^1St^2St^2HH}$ genomes, should be treated in *Elymus* L. *Elytrigia intermedia* (Host) Nevski, which contained the $\mathbf{E^bE^bE^eE^eStSt}$ genomes, should be classified as *Trichopyrum* Á. Löve. Since the **E** and **J** were two variants of the same genome, namely $\mathbf{E^e}$ and $\mathbf{E^b}$, species containing the **E**, **J**, and **S** (**St**) genomes should be treated as *Trichopyrum* Á. Löve.

Hordelymus (Jessen) Haez. is a monotypic understory genus distributed 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 *Taeniatherum* and understory *Hordeum*, possibly containing the **H** and **T** genomes. In 1994, R. von Bothmer et al. suggested a distant relationship of *Hordelymus* with either of the two genera based on the 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.

All together, five volumes (volumes 1–5) of "Biosystematics of Triticeae" have included 30 genera, 2 subgenera, 464 species, 9 subspecies, and 186 varieties in Triticeae. 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 and supplement the results of Áskell Löve. This is also a summary of the results of the pioneers of O. Rosenberg, H. Kihara, E. R. Sears, D. R. Dewey, etc. Just as "Atomic Table of the Elements" proposed by Mendeleev, our books explain the tribe Triticeae at biological level. The genus of Triticeae is clear so far, although some species have not completed the experimental test. We should study species with unknown genomic constitutions further, which makes the biosystematics of Triticeae more perfect. We attempted to maintain the truth and remove the false for deriving a more natural biosystematics of Triticeae. We wish that these books would serve as a useful reference for Triticeae scientists such as taxonomists, breeders, and geneticists. This is the purpose of these books—to create new knowledge for humans and to provide reliable support for technical design.

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

Translators' Biodata

Hai-Qin Zhang, Yong-Hong Zhou, and Dan-Dan Wu focus on studies of biosystematics of Triticeae, especially for the perennial Triticeae species. They have carried out extensive research into the perennial Triticeae species, including clarifying the genomic constitutions of species, the phylogeny of Triticeae species, and their breeding utilization.

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This translation commemorates the authors of this book Prof. Chi Yen (1924.5.12–2021.2.6) and Prof. Junliang Yang (1930.8.30–2018.5.5) at Triticeae Research Institute, Sichuan Agricultural University, China!

Translators
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Wenjiang, Chengdu, China

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Contents

About the Authors

Chi Yen and **Junliang Yang** are botanists, crop geneticists, and breeders. They are famous in promoting the research of the systematics of Triticeae in the world and has made outstanding contributions to the study of Triticeae germplasm resources.

Professors Chi Yen and Junliang Yang **revealed the transfer of cell nuclear material according to conjugation tube** in higher plants. They found the original mechanism of homologous-heterogenous polyploids and non-integrated polyploids. Thus, they **set up a classification system of the genus and species with genome and sub-genome combinations, respectively**. It was known as a significant contribution after Mendel's law of inheritance, Morgan's chromosome theory of heredity, and Hitoshi Kihara's genome theory in Triticeae. And they also revised Åskell Löve's classification system. Based on this study, they re-classified about 6100 Triticeae germplasms collected by them, including 193 species from 21 genera. They characterized the chromosome numbers of 40 species, found ten new species, and named two new genera *Kengyilia* and *Douglasdeweya*.

Professors Chi Yen and Junliang Yang used these germplasms to improve wheat varieties with high yield, multi spikelet, and the resistance of pre-harvest sprouting, such as "Yaanzao", "Datouhuang", "Zuyeqing" and "Fan 6". He improved the strategy of convergent hybridization and selected excellent variety "Fan 6" that became the critical parents of wheat in China. The durable resistance to stripe rust of "Fan 6" remained for more than 20 years.

Professors Chi Yen and Junliang Yang **proposed the multiple secondary axis theory**. This theory described the essential nature of organs in Gramineae and other plants.

Chapter 1
Biosystematics of Genus *Campeiostachys*

Campeiostachys Drobov is a new genus published by the Soviet botanist Василий Петрович Дробов in Volume 1 of the *Uzbekistan Flora* (*Флора Узбекистана CCP*). The type species is *Campeiostachys schrenkiana* Drobov. It is allohexaploid containing the **H**, **St**, and **Y** genomes (Lu & von Bothmer, 1992). Currently known, there are 11 species and 14 variants containing the **H**, **St**, and **Y** genomes in Triticeae, including *Campeostachys schrenkiana* Drobov. Since the type species of *Campeostachys* Drobov is characterized by containing the **H**, **St**, and **Y** genomes, it should be appropriate to classify the grasses containing the **H**, **St**, and **Y** genomes into the genus *Campeostachys*.

1.1 Classical Morphology Taxonomy of *Compeiostachys*

In 1845, the Russian German botanists Friedrich Ernst Ludwig von Fischer and Carl Anton Meyer published a new species *Triticum schrenkianum* Fisch. et C. A. Mey. (p. 305) in Volume 3 of the *Bulletin of the Academy of Sciences* based on a specimen taken by A. Schrenk in Tacheng, Xinjiang, China in 1841. This is the earliest published taxon of *Campeiostachys*.

In 1852, two new species, *Elymus dahuricus* Turcz. and *Elymus excelsus* Turcz., were collected and named by the Russian botanist Николаи Степанович Турчанинов. The German botanist August Heinrich Rudolph Grisebach published these two species in Volume 4, page 331, of *Flora Rossica*, which was edited by Carl Friedrich von Ledebour, and named as *Elymus dahuricus* Turcz. ex Griseb. and *Elymus excelsus* Turcz. ex Griseb, respectively.

In 1868, Grisebach published *Elymus nutans* Griseb., which was collected from the high mountains of northern India and with spikes nodding, in Volume 3 of the *Nachr. Ges. Wiss. Gottingen*, page 72.

In 1881, the German botanist Eduard August von Regel, director of the St. Petersburg Botanical Garden in Russia, published a new variant, *Triticum*

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strigosum planiflolium Regel, in the *Journal of the Petersburg Botanical Garden* (Труды Петербургского Ботанического Сада), Volume 7, Issue 2, page 591. This new variant is the same taxon as *Triticum schrenkianum* Fisch. et C. A. Mey.

The French missionary Armand David (he was also a botanist who made great achievements in plant survey and collection in China) who lived in Beijing from 1862 to 1874 collected a grass specimen in Beijing. In 1884, the specimen named as *Elymus dahuricus* var. *cylindricus* Franch. by the French botanist Adrien René Franchet., was published in the *Natural History Museum of Paris*, Nouv. Arch. Mus. Hist. Nat II.7: 152. It was also recorded in the Volume 1 of the *Plantae Davidianae ex sinarum imperio*, which was published in December of the same year on page 342.

In 1891, American botanist and agronomist Samuel Mills Tracy named a grass from Japan as *Agropyron joponicum* Tracy, which was published in Issue 6 of the *U.S. Department of Agriculture* (U. S. Dept. Agr. Div. Bot. Ann. Rep.)—the same taxon, which is earlier 51 years than *Roegneria kamoji* Ohwi named by J. Ohwi in 1942. However, *Agropyron joponicum* Tracy is a nomen nudum and is invalid.

In 1901, the Greek botanist C. A. Candargy combined *Triticum strigosum planifolium* Regel (which was named by Eduard August von Regel in 1881) into *Agropyron* and renamed it as *Agropyron pseudostrigosum* Candargy in his book *Monogr. tēs phyls tōn Krithōdōn* on page 40. On page 41 in this book, he also combined *Triticum schrenkianum* Fisch. et C. A. Mey. (which was named by Friedrich Ernst Ludwig von Fischer and Carl Anton Meyer in 1845) as *Agropyron schrenkianum* (Fisch.et C. A. Mey.) Candargy. Actually, these two combinations were the same taxon.

In 1903, the Austrian grass scientist Eduard Hackel published a variant named *Agropyron semicostatum* var. *transiense* Hack. in page 507 of II. 3 of the *Bull. Herb. Boiss*. *Agropyron semicostatum* (Nees) Candargy, which is also known as *Triticum semicostatum* Nees ex Steud, is a tetraploid species ($2n = 28$). However, now we know that "var. *transiense*" is a hexaploid species ($2n = 42$). Thus, they were not the same species.

In 1923, the Soviet botanist Ромаии Юлиевич Рожевиц downgraded *Elymus excelsus* Turcz. ex Griseb. as *Elymus dahuricus* var. *excelsus* Turcz. ex Griseb. Roshev. in page 138 of Volume 4 of the *Botanical Research* (Ботанические Материалы) published in Leningrad.

In 1923, the Soviet botanist Вассилий Петрович Дробов published a new species named *Agropyron turkestanicum* Drobov (p. 41) in the *Tashkent Plant Identification Manual* (Определител Растений Окресности Ташкента).

In 1927, the Japanese botanist Honda published a new species named *Agropyron mayabaranum* Honda in page 384 of Volume 41 of the *Journal of Botany* published in Tokyo, Japan. It is according to the No. 1032 specimen collected by Nakajima in Kumamoto in 1902, the No. 5 specimen collected in Kumamoto in 1924, and the No. 95 specimen collected in Kumamoto in 1925.

In 1930, Honda renamed *Elymus dahuricus* var. *cylindricus* Franch., the cylindrical variant of the French botany Adrien René Franchet named, to *Elymus*

cylindricus (Franch.) Honda. published in *the Journal of Tokyo Imperial University* (*Journ. Fac. Sci. Univ. Tokyo*), Part III, Botany, Volume 3, page 17.

In 1931, the Japanese botanist J. Ohwi published a new species named *Elymus villosulus* Ohwi in the Issue 45 of *the Journal of Botany* (pp. 183–184), published in Tokyo, Japan.

In 1932, the Soviet botanist Сергей Арсениевич Невский published two new species and three new combinations in Volume 30 of the *Museum of the Botanical Garden of the USSR Academy of Sciences* (Известия Ботанического Сада Академий Наук СССР): *Agropyrum drobovii* Nevski (p. 626), *Clinelymus dahuricus* (Turcz. ex Gresib.) Nevski (p. 645), *Clinelymus excelsus* (Turcz. ex Gresib.) Nevski (p. 640), *Clinelymus nutans* (Gresib.) Nevski (p. 644), and *Clinelymus tangutorum* Nevski (p. 647).

In 1934, the Soviet botanist Сергей Арсениевич Невский combined *Triticum schrenkianum* Fisch. et Mey (which was named by Friedrich Ernst Ludwig von Fischer and Carl Anton Meyer) in *Roegneria* and renamed it as *Roegneria schrenkiana* (Fisch. et C. A. Mey.) Nevski (p. 68). He also combined *Agropyrum drobovii* Nevski in *Roegneria*, and named it as *Roegneria drobovii* (Nevski) Nevski (p. 71). A new species named *Roegneria himalayana* Nevski was published in 1934. However, this new species was officially published in the *Journal of the Institute of Botany of the Soviet Academy of Sciences* (Туды Ботанического Института Академий Наук СССР) in 1936. Judging from the current experimental data, these three hexaploid grasses should not be included in *Roegneria* but in *Campeiostachys*.

In 1936, the Austrian botanist Heinrich, Freiherr von Handel-Mazzett combined *Clinelymus tangutorum* Nevski in the genus *Elymus* and renamed it as *Elymus tangutorum* (Nevski) Hand.—Mazz. in his "Symbolae sinicae Botanische Ergebniss Expedition der Akademie der Wissenschaften in wien nach Südwest-China," Volume 7, Fascicle 5 (p. 1292).

In 1936, Japanese botanist Honda grouped *Elymus cylindricus* (Franch.) Honda into *Clinelymus cylindricus* (Franch.) Honda according to the classification of C. A. Невский, which was published in *the first Manchurian scientific investigation record* (Rep. First Sci. Exped. Manch.), Sect. IV. (Index Fl. Jehol), on page 101.

In 1936, Honda published a new species called *Elymus tsukushiensis* Honda in Volume 50 of *the Journal of Botany* (p. 391). It was based on the No. 9 specimen taken by K. Nakajima in the northern region of Fukuoka Prefecture, the No. 6 specimen obtained from the Hososhima Island in Fukuoka Prefecture in 1933, and the No. 96 specimen collected in Nagasaki Prefecture in 1935.

In the same year, *Elymus tsukushiensis* Honda was recombined into *Clinelymus tsukushiensis* (Honda) Honda in the "Japanese Plant 28" (p. 572), which was published in Volume 50 of *the Journal of Botany*. On the same page, *Elymus villosulus* Ohwi named by J. Ohwi was combined into *Clinelymus villosulus* (Ohwi) Honda.

In 1937, Ohwi published a new species named *Elymus osensis* Ohwi in Volume 13 of *the Journal of Plant Research*, No. 5 (p. 334).

In the same year, he combined *Elymus tsukushiensis* Honda, which was named by Honda in the Volujme 6 of *Acta Phytotax. & Geobot*. (p. 54), in *Agropyron tsukushiense* (Honda) Ohwi.

In 1941, the Soviet botanist В. П. Дробов combined *Agropyrum drobovii* Nevski, which was named by С. А. Невский in Volume1 of the Uzbek Flora (Флора Узбекистана), into *Semiostachys drobovii* (Nevski) Drobov (p. 284).

In this flora, В. П. Дробов published a new genus called *Campeostachys* Drob. The type species is *Campeiostachys schrenkiana* (Fisch. et C. A. Mey) Drobov, which was *Triticum schrenkianum* Fisch. et C. A. Mey named by F. E. L. von Fischer and C. A. Meyee (pp. 300, 540).

In 1941, Ohwi combined *Agropyron mayabanum* Honda as *Roegneria mayabanum* (Honda) Ohwi, and record is as a synonym of *Agropyron mayabanum* Honda. Meanwhile, Ohwi combined *Elymus tsukushiensis* Honda as *Roegneria tsukushiensis* (Honda) Ohwi, and record is as a synonym of *Agropyron tsukushiensis* Honda (in Volume 10 of *Acta Phytotax. & Geobot*., p. 99).

In 1942, Ohwi published a new species called *Agropyron kamoji* Ohwi based on the type specimen of *Roegneria kamoji* Ohwi. in "Japan's Grasses Fourth" of the "*Plant Classification and Plant Geography*," Volume XI, No. 3, p. 179. This species was named based on Japanese Folk called the grasses as Kamoji-gusa.

In the same year, Ohwi upgraded *Adapyron mayabaranum* var. *intermedium* Hatusima to a species, and named it as *Agropyron hatusimae* Ohwi in *Plant Classification and Plant Geography* No. 4, page 258.

In 1953, Ohwi published a new variant named *Agropyron tsukushiense* (Honda) Ohwi var. *transiense* (Hack.) Ohwi in his book *The Flora of Japan* (p. 106).

In 1960, the British botanist A. Melderis published a new variant named *Elymus dahuricus* Turcz.ex Gresib var. *micranthus* Meld. in the book *The grasses of Burma (Ceylon, India and Pakistan*, edited by N. L. Bor (pp. 669, 697). In this book, he also recombines *Roegneria himalayana* Nevski into *Agropyron himalayaum* (Nevski) Meld. (p. 662).

In the same year, the Soviet botanist Никоай Николаевич Цвелев published a new species named *Elymus pamiricus* Tzvel. in Volume 20 of *Botanical Research (Leningrad)* (Ботанические Материалы [Ленингград]) (p. 425). In addition, *Triticum schrenkianum* Fisch. et C. A. Meyer. was combined in *Elymus* as *Elymus schrenkianus* (Fisch. et C. A. Meyer.) Tzvel. (p. 428).

In 1963, Chinese botanists Yili Geng and Shouliang Chen published a new species named *Roegneria aristiglumis* Keng et S. L. Chen (pp. 55–56) and a new variant called *Roegneria kamoji* Ohwi var. *macerrima* Keng (p. 17) in the article "Correction of *Roegneria* C. Koch" in *the Journal of Nanjing University (Biology)*, Issue 3, 1963, No. 1. Both of these two taxa are hexaploids and should belong to the genus *Campeostachys*.

In 1964, the Japanese botanist Ohwi and the cytogeneticist and grass scientist Sakamoto published a Triticeae grass *Agropyron humidorum* Ohwi et Sakamoto that was grown in Japanese rice fields in *Plants Research Journal*, Volume 39, page 124.

In 1965, Ohwi downgraded *Elymus villosulus* Ohwi into a variant and named as *Elymus dahuricus* var. *villosulus* (Ohwi) Ohwi, which was published in the *Flora of Japan* (page 155).

In 1968, the Japanese botanist Masao Kitagawa published a new species named *Elymus franchetii* Kitag. in the *Journal of Plant Research*, Volume 43, Issue 6, page 189.

In 1971, the Soviet botanist H. H. Цвелев downgraded *Elymus excelsus* Turcz.ex Griseb. into a subspecies and named *Elymus dahuricus* ssp. *excelsus* (Turcz. ex Griseb.) Tzvelev in Новости Систематики Высших Растений, Volume 8, page 63. This treatment was determined by morphological classification, but no experimental data.

In 1972, H. H. Цвелев combined *Roegneria himalayana* Nevski and *Roegneria drobovii* (Nevski) Nevski into *Elymus himalaynus* (Nevski) Tzvel. and *Elymus drobovii* (Nevski) Tzvel. in the Новости Систематики Высших Растений, Volume 9, pages 61 and 62, respectively. Meanwhile, he downgraded *Elymus pamiricus* Tzvel. to *Elymus schrenkianus* ssp. *pamiricus* (Tzvel.) Tzvel. on page 62.

In 1978, H. C. Пробатова published a new subspecies named *Elymus dahuricus* Turcz. ex Griseb. ssp. *pacificus* Probatova in the Новости Систематики Высших Растений, Volume 15, page 68. This treatment was determined by no experimental data.

In 1980, the Chinese botanist Xilin Yang from Inner Mongolia Normal University published two new variants: *Roegneria aristiglumis* Keng et S. L. Chen var. *liantha* H. L. Yang and *Roegneria aristiglumis* Keng et S. L. Chen var. *hirsute* H. L. Yang in the *Journal of Plant Taxonomy*, Volume 18, No. 2, page 253. The difference between *R. aristiglumis* var. *liantha* and its original variant is that the glume and the lemma of *R. aristiglumis* var. *liantha* are smooth and glabrous. The difference between *R. aristiglumis* var. *hirsute* and its original variant is that the former had hard bristles in leaves.

In 1984, Löve upgraded *Elymus dahuricus* var. *villosulus* (Ohwi) Ohwi to subspecies, and named *Elymus dahuricus* ssp. *villosulus* (Ohwi) Löve in the article "Conspectus of Triticeae," which was published in Volume 95 of *Feddes Repertorium*. He also combined *Agropyron humidorum* Ohwi et Sakamoto into *Elymus*, and treated it as *Elymus humidorus* (Ohwi et Sakamoto) Löve (p. 457). Löve upgraded *Elymus dahuricus* var. *villosulus* (Ohwi) Ohwi to subspecies, which is also subjectively determined without any experimental data.

In the same year, Chaopin Wang from Inner Mongolia Agriculture and Animal Husbandry College and Xilin Yang from Inner Mongolia Normal University published a new variant called *Elymus dahuricus* Turcz. ex Gresib. var. *violeus* C. P. Wang et H. L. Yang in *Plant Research*, Volume 4, Issue 4, page 86.

In 1985, H. C. Пробатова published a new species named *Elymus woroschilowii* Probatova in the *Far East Vascular Plant* (Сосуд. Раст. Сов. Дальн. Вост.), Volume 127, page 113.

In 1988, Shouliang Chen combined all *Roegneria* species into *Elymus*, and combined the hexaploid *Roegneria aristiglumis* Keng et S. L. Chen to *Elymus aristiglumis* (Keng et S. L. Chen) S. L. Chen (p. 8), which was published by Yili

Geng and herself in *Nanjing Zhongshan Botanical Garden Bulletin*. This is a subjective classification, which makes *Elymus* as a "hodgepodge" away from the natural system (see P. H. Davis and V. H. Heywood, 1963. *Principles of Anigiosperm Taxonomy*. D. van Norstrand Co., Princeton, NJ/New York).

In 1994, the authors discovered a grass with special morphology in Qinghai. It was named *Roegneria tridentata* Yen et J. L. Yang according to the concept of classification at that time. It was published in the *Novon*, Volume 4, pages 310–313. It is a hexaploid plant, and now it should belong to *Campeiostachys*.

In 1997, according to the subjective morphology classification of H. H. Цвелев, Shouliang Chen combined two *Roegneria* variant identified by Xilin Yang into *Elymus*: *Elymus aristiglumis* (Keng et S. L. Chen) S. L. Chen var. *hirsutus* (H. L. Yang) S. L. Chen and *Elymus aristiglumis* (Keng et S. L. Chen) S. L. Chen var. *lianthus* (H. L. Yang) S. L. Chen, which were published in *Novon*, Volume 7, Issue 3, page 227. *Roegneria tridentata* Yen et J. L. Yang, which was named by the authors, was also combined into *Elymus tridentatus* (Yen et J. L. Yang) S. L. Chen (p. 229).

In 2002, Guanghua Zhu, who worked at the Missouri Botanical Garden, published a variant called *Elymus kamoji* (Ohwi) S. L. Chen var. *macerrimus* G. Zhu in *Novon*, Volume 12, Issue 3, pages 426–427.

These taxa mentioned above are hexaploid plants and the genome constitution is **HHStStYY**, and should be included in the genus *Campeiostachys*.

1.2 Experimental Biological Research on *Campeiostachys*

Sakamoto from the National Institute of Genetics, Japan, conducted a cytogenetic observation study on the common weed *Agropyron tsukushiense* (Honda) Ohwi var. *transiens* (Hack.) Ohwi from Japan, North Korea, and China, and determined that it is a hexaploid plant containing 42 chromosomes (*Japanese Journal of Genetics*, 1964). A haploid plant containing 21 chromosomes was found in the valley adjacent to Mishima, Japan. It was dwarf but tiller was vigorous. According to the meiosis metaphase I (MI) of pollen mother cells (PMCs), there are no trivalent and quadrivalent, but only 0.2% of bivalents, and 20.6% of univalents, indicating that it is an allopolyploid, including three different genomes. It is neither an autopolyploid, nor a homologous heteroploid.

In 1966, Sakamoto and Muramatsu published two series of papers: "Cytogenetic studies in the tribe Triticeae. II. Tetraploid and hexaploid hybrids of *Agropyron*" and "Cytogenetic studies in the tribe Triticeae. III. Pentaploid *Agropyron* hybrids and genomic relationships among Japanese and Nepalese species" in the *Japanese Journal of Genetics*, Volume 41, Issues 2 and 3. They analyzed the genomic relationships between the tetraploid and hexaploid species from Japan and China. The hybrid combinations and the meiotic metaphase I chromosome pairing of the F_1 hybrids in these two papers are shown in Tables 1.1, 1.2, 1.3, and 1.4, respectively.

Table 1.1 The results of interspecific hybridizations (Adapted from Sakamoto and Muramatsu (1966a), Table 2)

Hybrids (♀ × ♂)	Years of hybridization	No. of emasculated florets	No. of seed obtained	No. of sow seeds	No. of germination	No. of hybrid plants
Tetraploid in Japan × tetraploid in Japan						
Ag. Yezoense × *Ag. ciliare* No. 1	1952	12	4	4	2	R170
Ag. ciliare No. 1 × *Ag. yezoense*	1955	–	10	10	9	S11
Ag. Gemekini × *Ag. ciliare* No. 3	1957	8	0			
Tetraploid in Japan × tetraploid in Nepal						
Ag. ciliare No. 1 × *Ag. semicostatum*	1956	24	16	16	16	5731
Ag. Semicostaum × *Ag. ciliare* No. 4	1956	10	1	1	1	5731
Ag. Semicostatum × *Ag. yezoense*	1956	12	10	9	4	5743
Ag. ciliare No. 4 × *Ag. gemilinii* (Nepal)	1967	20	1	1	1	5878
Ag. gemilinii (Nepal) × *Ag. ciliare* No. 4	1957	14	0			
Tetraploid in Nepal × tetraploid in Nepal						
Ag. gemilinii (Nepal) × *Ag. semicostatum*	1957	6	2	2	1	5887
Tetraploid in Japan × tetraploid in Americas						
Ag. ciliare No. 1 × *Ag. trachycaulum*	1956	15	11	5	5	5733
Hexaploidy in Japan × hexaploidy in Japan						
Ag. humidurum No. 1 × *Ag. tsukushiense* No. 1	1956	14	5	5	5	5741

(continued)

Table 1.1 (continued)

Hybrids (♀ × ♂)	Years of hybridization	No. of emasculated florets	No. of seed obtained	No. of sow seeds	No. of germination	No. of hybrid plants
Ag. humidurum No. 1 × *Ag. tsukushiense* No. 2	1956	76	28	28	17	5751

Table 1.2 Chromosome pairing of the F_1 hybrids at metaphase I (Adapted from Sakamoto and Muramatsu (1966a), Table 7)

Hybrids (♀ × ♂)	No. of cells observed	amplitude of bivalents	No. of bivalents	Chromosome pairing				
				V	IV	III	II	I
Tetraploid in Japan × tetraploid in Japan								
Ag. Yezoense × *Ag. ciliare* (R170)	45	10–14	14		0.356	0.200	11.289	2.289
Tetraploid in Japan × tetraploid in Nepal								
Ag. ciliare × *Ag. semicostatum* (5731)	408	5–14	12	0.002	0.135	0.150	11.336	4.196
Ag. semicostatum × *Ag. yezoense* (5743)	69	10–14	12		0.043	0.043	12.261	3.174
Tetraploid in Japan × tetraploid in Americas								
Ag. ciliare × *Ag. trachycaulum*	325	2–9	5	0.015	0.065	5.329	17.095	
Hexaploids in Japan × hexaploids in Japan								
Ag. humidurum × *Ag. tsukushiense* (5751)	46	20–21	21			0.022	20.739	0.457

In 1948, Murakami observed the above grasses and named the two genomes of *Ag. ciliare* as **II** and **KK**. *Ag. humidurum* is **II**???, and *Ag. tsukushiense* is **II KK LL**. According to the data provided in this paper, *Ag. ciliare* and *Ag. yezoense* were tetraploids and containing the **II KK** genomes, while *Ag. humidurum* and *Ag. tsukushiense* contained the **II KK LL** genomes.

The observation of the haploid *Ag. tsukushiense* var. *transiens* by Sakamoto (1964) showed that the chromosome pairing rate in PMCs is very low with chromosome association of $0.0_{IV} + 0.0_{III} + 0.2_{II} + 20.06_{I}$. The results suggested that it is an allohexaploid plants.

In two sets of genomes of *Ag. ciliare* and *Ag. trachycaulum*, one set is totally different while the other set is homologous. According to Stebbins and Snyder (1956), chromosome pairing of the triploid hybrid between *Ag. trachycaulum* and *Ag. spicatum* was 7 II + 7 I or 1 IV + 5 II + 7 I, suggesting that *Ag. trachycaulum* and

Table 1.3 Interspecific hybridization combination between tetraploids and hexaploids (Adapted from Sakamoto and Muramatsu (1966b), Table 2)

Hybrids (♀ × ♂)	Years of hybridization	No. of emasculated florets	No. of seed obtained	No. of sow seeds	No. of germination	No. of hybrid plants
Ag. tsukushiense No. 1 × *Ag. ciliare* No. 1	1956	24	12	11	10	5734
Ag. tsukushiense No. 2 × *Ag. ciliare* No. 5	1956	64				
Ag. tsukushiense No. 2 × *Ag. ciliare* No. 3	1958	26	3	3	3	5930
Ag. tsukushiense No. 1 × *Ag. Yezoense*	1956	22	14	14	12	5736
Ag. yezoense × *Ag. tsukushiense* No. 1	1956	24	17	17	6	5742
Ag. Gmelini (Japan) × *Ag. tsukushiense* No. 2	1957	20	1	1	1	5888
Ag. humidurum No. 1 × *Ag. ciliare* No. 5	1956	100	29	29	19	5752
Ag. humidurum No. 1 × *Ag. ciliare* No. 2	1956	18	0			
Ag. yezoense × *Ag. humidurum* No. 2	1958	22	0			
Tetraploid in Nepal × hexaploid in Japan						
Ag. tsukushiense No. 1 × *Ag. semicostatum*	1956	24	19	16	14	5737
Ag. humidurum No. 1 × *Ag. semicostatum*	1957	18	7	7	2	5886
Ag. Gemilinii (Nepal) × *Ag. tsukushiense* No. 2	1957	20	12	12	4	5884
Ag. tsukushiense No. 1 × *Ag. gemilinii* (Nepal)	1956	20	2	2	2	5735
Ag. tsukushiense No. 2 × *Ag. gemilinii* (Nepal)	1957	20	0			

(continued)

Table 1.3 (continued)

Hybrids (♀ × ♂)	Years of hybridization	No. of emasculated florets	No. of seed obtained	No. of sow seeds	No. of germination	No. of hybrid plants
Ag. Gemilinii (Nepal) × *Ag. humidurum* No. 1	1957	20	2	2	1	5885
Ag. humidurum No. 2 × *Ag. gemilinii* (Nepal)	1957	28	0			

Ag. spicatum shared one set of genome. Meanwhile, chromosome pairing in *Ag. ciliare* No.1 × *Ag. trachycaulum* showed that one set of genome between these two species were homologous.

According to the data listed in the above tables, the three tetraploid species and two hexaploids in Japan have the same two sets of genomes, which were the same as those of tetraploid species from Nepal. The genomic constitutions of these species are shown in Table 1.5.

Sakamoto published a paper, "Cytogenetic studies in natural hybridization among Japanese *Agropyron* species," in *Japanese Journal of Genetics*, 1964, Volume 41, Issue 3, pages 189–201. He found some natural hybrids of *Agropyron*, which included some pentaploid and some hexaploid, on the outskirts of Mishima, where the National Genetic Research Institute is located. A remarkable feature of these hybrids is that they are sterile or have a very low seeding rate, so the spikes are erect. The pentaploid is a natural hybrid of *Ag. ciliare* and *Ag. tsukushiense.* The hexaploid is a natural hybrid of *Ag. humidurum* and *Ag. tsukushiense*. From 1956 to 1962, 34 hybrid plants were found near footpaths or canals or in paddy fields.

Takemasa Osada from Fukuoka High School also collected some hybrid plants in Fukuoka-Ken, and compared the morphological characteristics and chromosome pairing behavior of perennial natural hybrids and artificial hybrids (Table 1.6).

In 1955, based on morphological identification, Ohwi identified the natural hybrid from Fukuoka, Kyushu, which, collected by T. Osada, should be *Ag* × *mayebaranum* Honda. The morphological characteristics of the natural hybrids from Mishima are very similar to the hybrid from Fukuoka. So it means that *Ag* × *mayebaranum* Honda is an interspecific hybrid containing the **II KK LL** genomes.

To explain here, there is no uniform naming rule in the name of genome at that time. The **II**, **KK**, and **LL** genomes named by Murakami are the **StSt**, **YY**, and **HH** genomes suggested by the Genomics Nomenclature Committee in 1994.

In 1980, Dewey made karyotype analysis on *Agropyron drobovii* (PI 314194, PI 314196, PI 314201, PI 314203), which was identified by H. H. Цвелев and collected by the Quentin Jones and Wesley Keller (plant collectors of U.-S. Department of Agriculture) in the region 70–80 km northeast of Astana, the capital of the Republic of Kazakhstan, in 1965. The results were published with the title of "Cytogenetics of *Agropyron drobovii* and five of its interspecific hybrids" in the *Botanical Gazette*, Volume 141. To detect the genomic constitutions of

Table 1.4 Chromosome pairing of F_1 hybrids at metaphase I (Adapted from Sakamoto and Muramatsu (1966b), Table 6)

Hybrids (♀ × ♂)	No. of cells observed	Amplitude of bivalents	No. of bivalents	Chromosome pairing				
				V	IV	III	II	I
Tetraploid in Japan × hexaploid in Japan								
Ag. tsukushiense × *Ag. ciliare* (5734)	107	9–15	14		0.056	0.075	10.056	8.439
Ag. tsukushiense × *Ag. yezoense* (5736)	87	7–15	14		0.149	0.333	12.241	8.805
Ag. yezoense × *Ag. tsukushiense* (5742)	55	13–15	14	0.036	0.128	0.291	12.600	8.010
Ag. gmelini (Japan) × *Ag. tsukushiense* (5888)	50	11–15	13		0.180	0.160	12.280	8.840
Ag. humidurum × *Ag. ciliare* (5752)	53	12–16	14		0.094	0.019	13.170	6.453
Tetraploid in Nepal × hexaploidy in Japan								
Ag. tsukushiense × *Ag. semicostatum* (5737)	156	6–14	11		0.110	0.161	9.800	14.052
Ag. humidurum × *Ag. semicostatum* (5886)	47	8–14	10			0.021	10.660	13.617
Ag. gemilinii (Nepal) × *Ag. tsukushiense* (5884)	97	3–15	12		0.113	0.113	11.299	11.567
Ag. gemilinii (Nepal) × *Ag. humidurum* (5885)	25	9–15	11		0.040	0.080	11.920	10.760

Table 1.5 Genome composition of tetraploid and hexaploid of several *Agropyrons* in Japan and Nepal (Adapted from Sakamoto and Muramatsu (1966b), Table 7)

Species	2*n*	Genome
Japan		
Ag. ciliare var. *minus* Ohwi	28	**II KK**
Ag. gmelini var. *tenuisetum* Ohwi	28	**II KK**
Ag. yezoense Honda var. *yezoense*	28	**II KK**
Ag. humidurum Ohwi et Sakamoto	42	**II KK LL**
Ag. tsukushiense var. *transiens* Ohwi	42	**II KK LL**
Nepal		
Ag. gmelini Scribn et Smith	28	$\mathbf{I^nI^n\ K^nK^n}$

Table 1.6 Chromosome pairing of artificial and natural hybrids and their parental species (Adapted from Sakamoto (1966), Table 4)

Chromosome pairing				*Ag. humidurum* No. 1	Artificial hybrids (5751)	Natural hybrids		*Ag. tsukushiense* No. 2
IV	III	II	I			Mishima (H1)	Fukuoka (a-7)	
		21		114	35	56	73	132
1		19		0	0	1	1	0
		20	2	0	10	5	3	3
	1	19	1	0	1	0	1	0
		19	4	0	0	1	0	0
Total				114	46	63	78	135

A. drobovii, Dewey (1980) made hybridization between *A. drobovii* with the diploid *A. libanoticum* Hackel with **SS** genomes, the tetraploid *A. dasystachyum* (Hack.) Scribn. and *A. mutabile* Drobov with **SSHH** genomes, and the *A. ugamicum* Drobov with **SSYY** genomes, and *A. leptourum* (Nevski) Grosssh. containing the **SSSSHH** genomes. The hybridization results are shown in Table 1.7 and Fig. 1.1.

Dewey (1980) performed cytological observations on the four materials of *A. drobovii*: 85% of PMCs at meiotic metaphase I are with 21 bivalents, and 95% of which are ring bivalents (Fig. 1.1a). Also, 15% of PMCs contain 2–4 univalents. The meiosis anaphase I is basically normal; only 5% of PMCs have lagged chromosomes, and the tetrads have paranucleus. After the meiotic metaphase I, the periods are very normal, indicating that some univalents observed in the meiotic metaphase I may be separated bivalents. The pollen fertility is 70–95% with an average of 90%.

The F_1 hybrids of *A. libanoticum* (diploid, **SS** genomes) and *A. drobovii* (hexaploid) are tetraploids with 28 chromosomes. In the meiotic metaphase I, each PMC has a large number of univalents with an average of 13.91. Most PMCs have 16 univalents and 6 bivalents (Fig. 1.1b). The PMCs contained a large number of lagged chromosomes with an average of 10.43. Bridge fragment was formed in 39% of cells, and in some cells were up to five. The formation of chromosome bridge means that paracentric inversion occured. More than 99% of the tetrads have paranucleus. All pollens are empty particles that cannot be dyed. From these test

Table 1.7 Meiosis of *Agropyron drobovii* and five interspecific hybrids (Adapted from Dewey (1980), Table 2)

Species or hybrids	2*n*	Number of plants		Metaphase I								Anaphase I		Tetrads	
				I	II	III	IV	V	VI	No. of cells observed	Ring bivalents (%)	No. of lagging chromosome	No. of cells observed	No. of micronucleus	No. of cells observed
A. drobovii	42	15	Amplitude	0–4	19–21	–	–	–	–	211	95	0–3	345	0–3	350
			Average	0.32	20.83	–	–	–	–			0.05		0.06	
A. libanoticum × *A. drobovii*	28	15	Amplitude	5–22	2–10	0–4	0–1	–	–	579	37	0–19	388	0–12	425
			Average	13.91	5.85	0.73	0.05	–	–			10.43		6.39	
A. dasystachyum × *A. drobovii*	35	9	Amplitude	5–25	4–14	0–4	0–1	–	–	312	44	2–20	244	0–6	250
			Average	15.58	9.03	0.42	0.03	–	–			11.13		2.15	
A. mutabile × *A. drobovii*	35	10	Amplitude	13–29	3–11	0–2	0–1	–	–	534	22	0–9	250	0–9	250
			Average	20.84	6.59	0.29	0.03	–				2.12		3.12	
A. ugamicum × *A. drobovii*	35	4	Amplitude	6–18	5–14	0–3	0–1	0–1	0–1	193	8	0–12	100	2–10	100
			Average	10.56	10.4	0.77	0.14	0.07	0.05			4.50		5.42	
A. drobovii × *A. leptourum*	42	9	Amplitude	6–26	1–14	0–7	0–2	–	–	142	12	2–17	200	0–7	200
			Average	17.57	8.32	2.43	0.12	–	–			9.47		2.35	

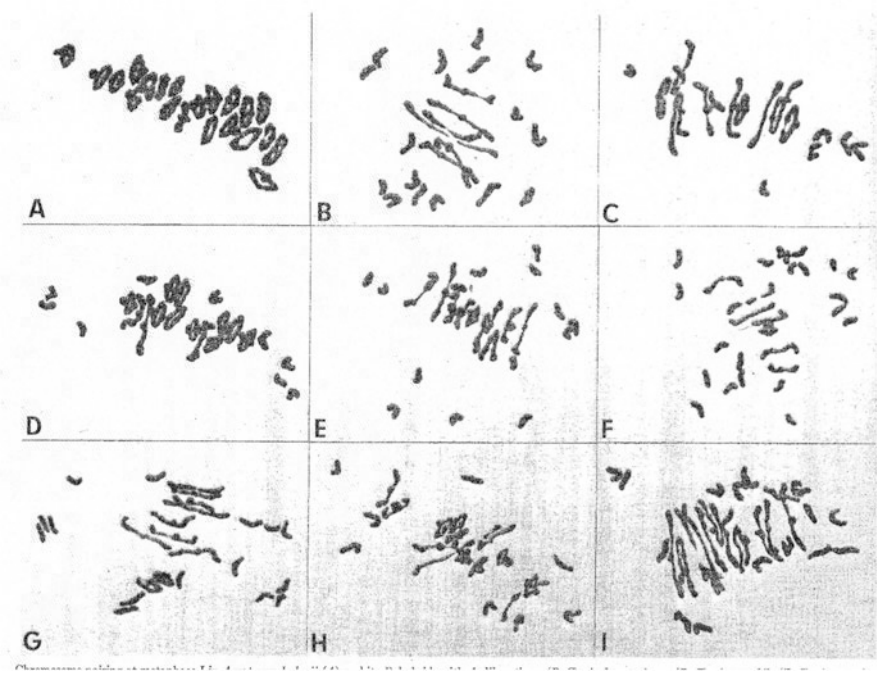

Fig. 1.1 The meiotic pairing of *Agropyron drobovii* and the F_1 hybrids at metaphase I. (**a**) *A. drobovii* with 21 ring bivalents; (**b**) *A. libanoticum* × *A. drobovii* with 16 univalents and 6 rod-bivalents; (**c**) *A. libanoticum* × *A. drobovii* with 7 univalents, 6 bivalents (3 ring), and 3 trivalents (V-shaped); (**d**) *A. dasystachyum* × *A. drobovii* with 9 univalents and 13 bivalents (10 ring); (**e**) *A. dasystachyum* × *A. drobovii* with 13 univalents, 9 bivalents (2 ring), and 1 trivalent (V-shaped); (**f**) *A. mutabile* × *A. drobovii* 21 univalents and 7 divalents (1 ring); (**g**) *A. mutabile* × *A. drobovii* with 15 univalent, 10 bivalents (2 ring); (**h**) *A. ugamicum* × *A. drobovii* with 8 univalents, 12 bivalents, and 1 trivalent (V-shaped); (**i**) *A. drobovii* × *A. leptourum* with 17 univalents, 8 bivalents, and 3 trivalents (V-shaped). (Adapted from Dewey (1980), Fig. 2)

data, it is showed that *A. drobovii* and *A. libanoticum* shared one set of genome with some differences.

The F_1 hybrid between *A. dasystachyum* (tetraploid) and *A. drobovii* are pentaploids with 35 chromosomes and their meiosis is not normal in each period. All PMCs contain univalents with an average of 15.58 per cell; 43% of PMCs have more than 10 bivalents, whereas some have up to 14 bivalents (Fig. 1.1d). PMCs containing multivalent were up to 34%. Lagged chromosomes were observed in meiosis anaphase I. However, the tetrads were obviously more normal than the meiosis anaphase I with an average 2.15 of paranucleus. Among the 10 hybrid plants, 9 produced a few (0.1–1.0%) of large-sized dyeable pollen, and obtained 1 fertile seed in 50 open-pollinated hybrid florets.

There are many morphological variations in *A. mutabile* produced in Asia, and H. H. Цвелев divides it into subspecies and varieties. Dewey believed that *A. mutabile* (PI 314622) used in this experiment was identified as *A. mutabile* subsp. *mutabile*

var. *eschense*, and was determined to be a tetraploid plant containing the **SSHH** genomes by Dewey. The F_1 hybrid between this variety and *A. drobovii* has spikelets purple, the spikelets on the side axis, and the spike larger than their parents. Its meiotic chromosome pairing is similar to the hybrids between *A. dasystachyum* and *A. drobovii*, except that the paired chromosomes are apparently less (Table 1.7). The most common pairing patterns were 21^{I} and 7^{II}, accounting for 17% of the number of observed PMCs. The bivalents were up to 11 in few cells, whereas more cells contained 10 bivalents (Fig. 1.1g). Meiosis anaphase I was relatively normal. About 25% of the meiosis anaphase I cells did not have lagged chromosomes with an average of 2.12 per cell. Most (94%) of the tetrads contain paranucleus. All pollens are sterile, and none of hybrids produced seeds.

A. ugamicum also is a species distributed in Central Asia. Its distribution is essentially identical with *A. drobovii*, and their habits are very similar. Although their distributions and habits are similar, their morphology is different. In *A. ugamicum*, spikelets are dense and on the side axis is found evidently, glume glabrous and lemmas with short awn (less than 5 mm), and the genome constitutions is **SSYY**. The flowering period of *A. ugamicum* is usually less than two weeks, plus it is self-pollinated, so it is difficult to hybridize in natural habitats. However, secondary spikes occasionally grow in a few plants, and then they were hybridized with *A. drobovii* by Dewey. The F_1 hybrid of *A. ugamicum* and *A. drobovii* is pentaploid with 35 chromosomes. The meiotic chromosome pairing was better than the other hybrid combinations with the ring bivalents accounting for 68% of PMCs. The meiosis metaphase I PMCs had 12–14 bivalents in more than 25% of PMCs (Fig. 1.1h). More than 75% PMCs at metaphase I have a multivalent composed of 3–6 chromosomes, indicating significant structural difference between the chromosomes of *A. ugamicum* and *A. drobovii*. The meiosis abnormality phenomena persists in the meiosis anaphase I, 90% of the cells have lagged chromosomes, and 18% of the cells have bridge fragments. All tetrads contain paranucleus and all pollens are aborted.

A. leptourum (Nevski) Grossh. is a Central Asian perennial grass distributed in the Caucasus Mountains, passing through the Alborz Mountains in northern Iran, directly to Pamir Alai and the Tianshan Mountains. C. A. Невский classifies it into *Roegneria* with its small anther, self-pollination, and the **SSSSHH** genomes. Dewey (1972) using *A. libanoticum* (**SS**) hybridized with *A. caninum* (**SSHH**), then doubled the F_1 hybrid and produced a new plant. It is very easy to hybrid with *A. drobovii*. Fifty-six florets of *A. drobovii* (PI 314203) were hybridized with the amphidiploid, and obtained 32 hybrid seeds, of which 20 are germinated into seedlings. The morphology of the hybrid was intermediate of the parents while its spikes are longer than their parents. The F_1 hybrid is a hexaploid with 42 chromosomes. The chromosomes are very long and become small in the meiosis metaphase I, making the pairing relationship difficult to interpret. There is no normal syndesis. There are 60 different combinations of univalent, bivalent, and multivalent in 142 observed PMCs. *A. drobovii* × *A. leptourum* hybrids are characterized by high frequency of trivalents. Approximately 93% of PMCs contain 1–7 trivalents with an average of 2.43 per cell. All cells in meiosis anaphase I have lagged chromosomes.