Cytologia Focus:

History and New Developments on the 90th Anniversary of Cytologia: On the Occasion of the Publication of “Dawn of Modern Wheat Genetics”

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Summary This year marks the 90th anniversary of *Cytologia*. Modern wheat genetics began 16 years prior to the first issue of *Cytologia* in 1929. Flaksberger's wheat stocks, which were sent to Minami in October 1913, were used by Sakamura to determine the number of chromosomes in wheat. Flaksberger's death in prison in September 1942 was a tragedy for the research community. The Russian and Soviet contribution to modern wheat genetics is immeasurable, but its decline during and after the era of Lysenko was pitiful. This is made clear by the number of publications from each country since the first issue of *Cytologia*. The publication of *Cytologia* continued during World War II; after the war, the contribution of India, which became independent at that time, was considerable. Recently, India's contribution has been relativized, and contributions from other Asian countries including Thailand and Japan, the Middle East and South America have increased, and *Cytologia* has been supported by increasingly diverse countries.

Key words 90th Anniversary of Cytologia, Flaksberger's wheat stocks, Wheat genetics, Indomalayan region, Ichthyology, Cereal cytogenetics, Karyotype.

The review entitled “Dawn of Modern Wheat Genetics: The Story of the Wheat Stocks That Contributed to the Early Stage of Wheat Cytogenetics” by Koichiro Tsunewaki was published in *Cytologia* last year (Tsunewaki 2018). Tsunewaki, a Professor Emeritus at Kyoto University, expanded Kihara's alien cytoplasm to plasmon analysis of the *Triticum*–*Aegilops* complex. This story began in October 1913, when Konstantin Flaksberger, Bureau of Applied Botany, Russia, wrote to Yuzo Hoshino, Hokkaido University, Japan, requesting seeds of Japanese cereals. This was 16 years before the first issue of *Cytologia*, which included an introductory paper titled “Conjugation of homologous chromosomes in the genus hybrids *Triticum*×*Aegilops* and species hybrids of *Aegilops*” by Hitoshi Kihara (Kihara 1929). This year marks the 90th anniversary of *Cytologia* and in this review I focus on its birth and subsequent development based on the above-mentioned review article by Tsunewaki.

Wheat stocks that contributed to the early stage of wheat cytogenetics

Four wheat researchers played major roles in Tsunewaki's story: in chronological order these are Konstantin Flaksberger, Takajiro Minami, Tetsu Sakamura, and Hitoshi Kihara.

The wheat stocks sent from Flaksberger to Minami, who initially propagated them at Hokkaido University, left St. Petersburg, Russia, sometime in October 1915, then passed along the 9300 km of the Trans-Siberian Railway during World War I, and reached Sapporo, Japan, sometime before May 19, 1916. Flaksberger's wheat stocks were sent to Minami, who initially propagated them at Hokkaido University and then provided them to Sakamura, who observed chromosome numbers at the root-tip and pollen mother cell (PMC), and produced crosses in four combinations between 4x and 6x species in the summer of 1917. These postulated events fit the hypothesis that the wheat stocks sent by Flaksberger to Minami were used by Sakamura to determine the number of chromosomes of wheat.

Tetsu Sakamura had been a graduate student in the Faculty of Agriculture, Hokkaido University, since 1913, carrying out chromosome studies of leguminous species, but he switched to wheat in 1916 and asked Minami to provide wheat seeds. He determined the correct number

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Fig. 1. Number of publications by country at the 90th anniversary of *Cytologia*; data are percentages.

of chromosomes of eight wheat species, among which he discovered polyploidy of $2n=14$ ($2x$), 28 ($4x$), and 42 ($6x$). These results were published in July 1918; in December of that year Sakamura left Japan to study overseas for 2 years (Sakamura 1918).

Hitoshi Kihara entered the graduate school of Hokkaido University in August 1918. He accepted Sakamura's offer to take over his materials and in 1918 started working on the $5x$ hybrids growing in the field of Hokkaido University. In addition to the F_1 hybrids produced by Sakamura, Kihara himself performed crosses to produce two triploid F_1 hybrids, *T. dicoccum* ($4x$ species) $\times$ *T. monococcum* ($2x$), and *T. aegilopoides* ($2x$) $\times$ *T. dicoccum* ($4x$). He analysed the meiotic chromosome behaviour of these hybrids and the number of somatic chromosomes of their offspring, and thus determined their genome constitution; this work opened a new era of genomic analysis. When Kihara moved to Kyoto University in October 1920, he received from Hokkaido University all of the wheat species studied by Sakamura, as stated above, and extended his genomic analyses to encompass all species of the genera *Triticum* and *Aegilops*. The genomic analysis of the genus *Triticum* was completed in 1951 (Lilienfeld and Kihara 1934, Kihara 1951, Lilienfeld 1951), as well as that of the genus *Aegilops* by Kihara (1949), the latter complemented by a study of its four hexaploid species by Kihara and Tanaka (1970).

In 1973, Tsunewaki's group at Kyoto University started an investigation of differentiation of plasmon in the *Triticum-Aegilops* complex; plasmons of this complex were introduced into 12 wheat genotypes, including three of Flaksberger's stocks. This resulted in the generation of 552 alloplasmic lines; their phenotypes and restriction fragment patterns of organellar DNAs were compared. The maternal and paternal lineages of most species in this complex were determined based on the results of that plasmon analysis and Kihara's genomic analysis (Tsunewaki *et al.* 2019).

The era of Flaksberger and Lysenko

The following brief biography of Flaksberger was taken from Tsunewaki's review (Tsunewaki 2018). Upon graduating in 1907 from the Department of Physics and Mathematics, Imperial Yuriev University, Russia, Flaksberger was immediately appointed Vice Director of the Bureau of Applied Botany, Ministry of Agriculture, Russia, where he worked throughout his life on the agrobotanical study of wheat. He published four editions of "Wheat Taxonomy," in 1915, 1922, 1928, and 1939. He was arrested on June 28, 1941, about one year after the arrest of Nikolai Vavilov and, sadly, died on September 13, 1942, in Zlatoust Prison Hospital in the Ural District at the age of 62 years.

N. Vavilov was a prominent Russian and Soviet agronomist, botanist, and geneticist best known for

identifying the centres of origin of cultivated plants. He devoted his life to the study and improvement of wheat, corn, and other cereal crops that sustain the global population. Vavilov visited Japan in 1929 and met Kihara, a wheat geneticist at Kyoto Imperial University, and delivered, in English, a lecture entitled “The Origin of Cultivated Plants.” However, Vavilov’s work was criticised by Trofim Lysenko, whose anti-Mendelian concepts of plant biology had won favour with the Soviet dictator, Joseph Stalin. As a result, Vavilov was arrested and in July 1941 was sentenced to death. Although his sentence was commuted to 20 years’ imprisonment, Vavilov tragically died of starvation in prison in 1943.

Lysenko’s theory assumed the heritability of acquired traits, denied Mendel’s inheritance and the concept of genes, and deviated from Darwinian evolution but, with Stalin’s support, gained power rapidly (Soyfer 2001). In 1936 he became a director of the Kiev Agricultural Institute and fought a fierce battle with orthodox geneticists, and in 1939 he became a member of the Soviet Academy of Sciences and won a decisive victory at the debate that year. From 1940 to 1965, Lysenko served as director of the Institute of Genetics of the Soviet Academy of Sciences, and the defeated orthodox geneticists were arrested, expelled, or forced to change their views. The farming methods advocated and practiced by Lysenko devastated Soviet agriculture, but this reality was hidden from the wider world. *Cytologia* published 34 articles from the Soviet Union from 1930 to 1940; however, after 1941, when the German–Soviet war began, no article from the Soviet Union appeared. The last article was from the Cytological Laboratory of the Institute of Plant Industry in Leningrad-Pushkin (Lewitsky 1940).

Post-war trajectory and a new ichthyologic trend

A series of wheat genome studies by Kihara and co-workers is one of the highlights of *Cytologia*. The decade in which *Cytologia* had been launched was passing; the Second World War began in September 1939, the German–Soviet War in June 1941, and the Pacific War in December 1941, which affected *Cytologia* greatly. Submissions from the West, but not the Soviet Union, reappeared after the end of the Second World War. In addition, submissions from India, which became independent in 1947, saved *Cytologia* from a crisis. However, in the 1990s, the Indian economy stagnated while those of other Asian countries increased. In fact, numerous articles have been submitted from three regions: North India (including Himalaya), Bangladesh downstream of the Ganges and Brahmaputra Rivers and around their delta, and Thailand (including Indochina and the northern Malay peninsula) (Kawano 2018).

In Thailand, including Indochina and the northern Malay peninsula, Alongklod Tanomtong and co-workers have recently focused on fish karyotype analysis and have published 15 reports in *Cytologia* over the

last 2 years on the following fish species: Humpback cardinalfish, *Fibramia lateralis* (Kasiroek *et al.* 2017a); Banggai cardinalfish, *Pterapogon kauderni* (Kasiroek *et al.* 2017b); triangle butterflyfish, *Chaetodon triangulum* and yellow butterflyfish, *C. andamanensis* (Supiwong *et al.* 2017a); Indian vagabond butterflyfish, *Chaetodon decussatus* and Lined butterflyfish, *C. lineolatus* (Supiwong *et al.* 2017b); Nile tilapia, *Oreochromis niloticus* (Sriuttha *et al.* 2017); three-spot damselfish, *Dascyllus trimaculatus* (Getlekha *et al.* 2017); ocellated dragonet, *Synchiropus ocellatus* and picturesque dragonet, *S. picturatus* (Kasiroek *et al.* 2017c); crystal eye catfish, *Hemibagrus wyckii* (Supiwong *et al.* 2017d); Chevey’s sheetfish, *Micronema cheveyi* (Pinthong *et al.* 2017); F₁ hybrid catfish: Mekong giant catfish, *Pangasianodon gigas*×striped catfish, *P. hypophthalmus* and spot pangasius, *Pangasius larnaudii*×*Pangasianodon hypophthalmus* (Sreeputhorn *et al.* 2017); whitecheek monocle bream, *Scolopsis vosmeri* (Supiwong *et al.* 2017c); snakehead fishes, *Channa marulius* and *C. maruloides* (Sarasan *et al.* 2018); Hihgfin barb fish, *Cyclocheilichthys armatus* (Chaiyasan *et al.* 2018); black lancer, *Bagrichthys majusculus* (Supiwong *et al.* 2018); and longfin carp, *Labiobarbus leptocheilus* (Saenjun-daeng *et al.* 2018).

In response to these reports from Thailand, *Cytologia* recently published several analyses of fish karyotypes from the Middle East and South America. Ayata *et al.* (2018) reported the diploid chromosome number, karyotype, and chromosomal-banding properties (C-banding and Ag staining) in *Cobitis phrygica* and *C. simplicispina* from Turkey. At least 18 species of the genus *Cobitis* of the family Cobitidae are known in Turkey. The endemic species *C. phrygica* is distributed in the watersheds of the Acıgöl, Salda, and Söğüt Lakes in Turkey and *C. simplicispina* is distributed in the Sakarya and Kızılırmak basins and around Tuz Lake. The distribution of *Cobitis* in Turkey was revised recently because of complex problems regarding their systematics and phylogeny.

Chromosomal investigation is useful for solving systematic and taxonomic problems in fish. However, the difficulty in obtaining chromosomes from fishes, the small size and the large number of their chromosomes, and the lack of a standard method has hampered such investigations. Studies published in *Cytologia* typically aim to evaluate chromosomal properties by conventional cytogenetic (Giemsa, Ag-NOR, and banding-C staining) and cytomolecular (fluorescence *in situ* hybridization using 5S, 18S rDNA, Rag1, Rex3, Rex6, and telomeric probes) markers in the following endemic loach species: *Cichla kelberi* and *C. piquiti* from Brazil (de Freitas Mourão *et al.* 2017); the *Astyanax scabripinis* population in the São Francisco River, Brazil (Klassmann and dos Santos 2017); and the *Moenkhausia sanctaefilomenae* population in the Upper Paraná River

basin, Brazil (Fernandes and Alves 2017).

Recent developments in cereal cytogenetic research

Several reports on Poaceae have been published in *Cytologia* over the past 2 years (Gupta, *et al.* 2018, Khah and Verma 2017, Rani *et al.* 2017, Kaur and Gupta 2018, Özer *et al.* 2018, Shiogai *et al.* 2018). A useful review on the wheat genome was published by Tsunewaki in 2018, and the expression profiles of two long non-coding RNAs in salt-stressed barley roots were detailed by Karlik *et al.* (2018) in the same year.

Gupta and coworkers at Punjabi University and Khalsa College in 2017 reported male meiotic studies of 20 species belonging to 14 genera of the tribe Andropogoneae from the State of Haryana in northern India and its adjoining hills, and some parts of Rajasthan. Haryana encompasses an area of 44212 km² and is bordered to the south by Rajasthan. The Shivaliks are also known as sub-Himalaya or 'the foothills' and typically range in altitude from 900–1500 m, while a few exceed 2000 m. Few studies have assessed the cytological diversity of grasses in these hills. The tribe Andropogoneae is commonly known as Sorghum. One Andropogoneae species is grown for grain, and others for fodder, and are cultivated in warm climates worldwide or have become naturalised in pasture lands.

Khah and Verma (2017) reported a case of multiple translocation heterozygosity in an M₁ population following gamma irradiation of pearl millet (*Pennisetum glaucum* L.). *P. glaucum*, a member of the grass family, is the most widely cultivated type of millet. It is an important cereal crop and is a good material for cytological analysis as it has comparatively few suitably sized chromosomes ($2n=14$), which facilitates their staining. Pearl millet is rich in essential compounds such as proteins, fibre, phosphorous, magnesium, and iron. Because of its composition, pearl millet has health benefits and is a staple food for many people worldwide, particularly in Africa. The generation of mutants of this important cereal crop using physical or chemical mutagens is important for genetic studies and plant breeding programs. Rani *et al.* (2017) performed pachytene analyses of 18 accessions of three genera of minor millet: *Eleusine indica*, *Panicum antidotale*, and *Setaria italica*.

The genus *Setaria* is economically important for grain and forage. The genus falls under the tribe Paniceae and the family Poaceae. Kaur and Gupta (2018) investigated the cytological features of eight species and 16 accessions. *S. geniculata* ($2n=54$), *S. homonyma* ($2n=18$), and *S. italica* ($2n=36$) were the first reported euploid cytotypes, and the cytological studies of *Setaria barbata* ($2n=54$), *S. glauca* ($2n=54$), *S. pumila* ($2n=54$), and *S. verticillata* ($2n=108$) were the first from Rajasthan.

Perennial ryegrass (*Lolium perenne*), which is cultivated across large areas in the temperate regions of the world, was the first cultivated and widely used grassland

plant. The natural flora of Turkey is rich in *Lolium* species. Özer *et al.* (2018) proposed that Turkish perennial ryegrass populations may be relevant to chromosomal variation in the karyotype relationships between cytotypes, which could facilitate the development of new cultivars.

Poaceae species use the C₄ photosynthetic pathway, as do 46% of grasses; together, these account for 61% of C₄ species. Such species include the food crops maize, sugar cane, millet, and sorghum. Maize (*Zea mays*) is a representative C₄ plant, but its senescing leaves exhibit C₃-like photosynthetic properties. Under the culture conditions of Shiogai *et al.* (2018), first leaves of maize finished maturation by day 9 after sowing and subsequently began to exhibit a considerable degree of O₂ inhibition, a C₃-like photosynthetic property. They proposed that preferential senescence in the mesophyll cells (MCs) may cause insufficient CO₂ pumping into the bundle sheath cells (BSCs) and lead to C₃-like photosynthetic properties in senescing maize leaves.

The two main types of commercial grain crops are cereals and legumes. Grains and cereals are synonymous with caryopses, the fruits of the grass family, Poaceae. In agronomy and commerce, seeds or fruits from other plant families are called grains if they resemble caryopses. Cereal grain crops are grown in greater quantities and provide more food energy worldwide than any other type of crop and are, therefore, staple crops. Edible grains from other plant families, such as buckwheat (Polygonaceae) (Gupta *et al.* 2018), quinoa (Amaranthaceae), chia (Lamiaceae), and sesame (Pedaliaceae) (Das *et al.* 2018) are referred to as pseudocereals. In addition to these plants, a large number of papers on legumes have been published in *Cytologia*, indicating the diversity of food available in India (Ghosh *et al.* 2017, Chaudhary and Kumar 2017, Gosavi *et al.* 2017, Kumar and Singh 2018), Egypt (Siddiqui *et al.* 2018), and Mexico (Tapia-Pastrana *et al.* 2018). The 90-year history of *Cytologia* shows that karyotype analysis is an excellent tool for diversity research.

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