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Some taxonomical adjustments in eurasiatic wheatgrasses

Einige taxonomische Änderungen bei eurasiatischen Quecken

by

Askell LÖVE

1. INTRODUCTION

In the classical tradition of the Linnaeans, contrary to the approach of the Bentham-Hookerians, a biological genus is defined as a cluster of reproductively isolated species that could have evolved from a single prototype by linear branching or autoploidy. Genetically oriented evolutionists have construed this to mean, that all the species of a biologically defined genus share a single and essentially similar chromosome set, termed haplome (HEILBRONN and KOSSWIG 1966, LÖVE and LÖVE 1975), or, in case of alloploidy, a complex genome; it follows that a well circumscribed genus is characterized by one basic chromosome number only, either monoploid for single haplome genera or addititiuous for complex genome taxa. That characteristic is typical also of the tribe (AVLUDOV 1931), whereas the evolutionary family and higher categories must be defined by various other phylogenic characteristics, frequently beyond

the approaches of cytogenetics (cf. DAHLGREN et al. 1985). The essential cytological processes involved in this evolutionary sequence have been studied in greatest detail in the economically important grasses of the Triticeae tribe (cf. KIHARA 1975, DEWEY 1982, 1984) in which a system of 24 single-haplome and 13 complex-genome genera was recently proposed by LÖVE (1982, 1984). In these grasses, complete or at least very strong incompatibility between haplomes of generic status is maintained by extensive rearrangement in at least four and frequently all the seven pairs of the chromosomes of related haplomes. This disturbs and prevents hybridization, but the remaining three or less pairs stay as homologous or homeologous. When more than a single species constitute a haplome genus, their reproductive isolation is maintained by meiotic disturbances in their hybrids caused either by secondary and moderate linear changes in some chromosomes within the limits of homeology, or simply by differences in autoploidy. The processes involved in this generic and specific differentiation based on the chromosomes were termed macroevolution by GOLDSCHMIDT (1940), as contrasted to microevolution based on gene mutation and recombination followed by natural selection. These processes are generally recognized as distinct in their evolutionary importance by experimental geneticists, though the powerful neodarwinian and molecular lobbies still maintain that the processes of microevolution alone suffice as an explanation of evolution at all levels. The theory of the single basic chromosome number of the genus and the single chromosome number of the biological and Linnaean species has been recognized by cognizant taxonomists since the ascent of cytogenetics (cf. WILSON 1900), but the observation of the generic significance of the haplome was only recently carried to its taxonomical conclusion through the new subdivision of the more than 500 wheatgrasses (DEWEY 1982, 1984, LÖVE 1982, 1984).

Although the haplomic or genomic genera are ultimately defined on basis of their karyomorphological constitution essential for their reproductive incompatibility, gross morphology, geography and a strict nomenclatural typification remain important components. Therefore, the methods of genome analysis based on studies of meiosis in hybrids may be augmented or even replaced by several other more or less subjective procedures. Utilizing either or both herbarium or live material, comparison of descriptions and specimens are sometimes enhanced by a variation of methods of extrapolated correlates that was invented by ANDERSON (1949)

for the search of parents of hybrids, and later applied for finding the approximate characterization of the diploid components of a polyploid genome (SARKAR 1955, SARKAR and STEBBINS 1956). The next step may be either a detailed chemical analysis (JAASKA 1972, NAKAI 1982) or a careful study of the mitotic karyotype, which has proven to be among the most conservative characteristics of a genus and a species (LEVITSKIY 1976, CHENNAVEERAIAH 1960). Each of these methods may give a conclusive evidence of the haplomic relationship of diploids and polyploids, though in some cases the results from a study using a single approach are inconclusive so that a more complex analysis is needed.

2. TWO MINOR DISSENTS

The most reliable conclusions from genome analysis are based on studies of hybrids between diploids and polyploids with two or more heterologous haplomes. Although in some cases hybrids between polyploids give some indication of relationship, a certain risk of misinterpretation is inevitable. Such difficulties seem to have been the cause of repeated claims of autoploidy in the genus Gigachilon (cf. DHALIWAL and JOHNSON 1976), and also of the assumption that two haplomes "B" and "C", were involved in the two sections of that genus (KIHARA and LILIENFELD 1934). More recently, similar ambiguities have resulted in some remarks on the relationship of Critesion bulbosum, of the "H" haplome, and Hordeum vulgare, of the "I" haplome, and led DEWEY (1984) to the conclusion that the former taxon should be transferred to the genus of the latter. Also, such disturbances have caused some arguments about a possible identity of the genera Lophopyrum and Thinopyrum and an alloploid group traditionally included as a part of the then unnatural genus Elytrigia (DEWEY 1984). The two haplome groups "E" and "J" were separated as well-defined genera Lophopyrum and Thinopyrum by LÖVE (1982, 1984); geneticists and taxonomists agreed that they are biologically distinct, though CAUDERON (1958, 1966) had declared them to be closely related but also emphasizing their distinction. That dissent has ultimately been settled by recent observations by WANG (in press) of hybrids between the diploid L. elongatum and the diploid T. bessarabicum that differ in four heterologous chromosome pairs whereas the remaining three chromosomes are homeologous or homologous and responsible for the relationship claimed by CAUDERON (1958,

1966) and others studying triploid hybrids of L. elongatum and T. junceiforme. That shows that the taxonomical merger of these genera need to be regarded as a fallacy.

3. TYPICAL ELYTRIGIA

The Elytrigia genus, as defined by LÖVE (1982, 1984), is a polyploid assemblage of three sections, Elytrigia, Lolioides and Trichophorae. DEWEY (1976, 1984), supported by own genome analyses and those of CAUDERON (1958, 1966) and others, concluded that the genomic formula of E. repens must be "SSX", the first two haplomes deriving from some Pseudoroegneria and the "X" perhaps from Thinopyrum, an idea contradicted by the observations of OESTERGREN (1940) and HENEEN (1963) and by the fact that crushed E. repens leaves do not emit the smell characteristic of "J" haplome taxa. My old karyotypic measurements confirm the partaking of two "S" haplomes. But the third set remains unidentified, and the method of extrapolated correlates could neither confirm nor exclude the assumption that the "N" haplome of Psathyrostachys or the "G" haplome of Festucopsis might be involved. Until that problem is solved the formula proposed by DEWEY (1984) is the most reasonable.
Studies of hybrids between ssp. repens and spp. arenosa confirm that these are fully interfertile major races; that may be supposed also for ssp. calcarea, though live material has not been available. The ssp. pseudocaesia, an endemic of southeastern Ukraine, is likely a hybrid of E. repens and Pseudoroegneria cretica, since DRULEVA (in PROKUDIN et al. 1977) and PETROVA (1967) found it to have 2n=35 chromosomes, and completely sterile specimens furnished by Professor Y.N. Prokudin in 1963 were morphologically intermediate; the 42-chromosome material reported by LÖVE (1984) from a roadside in Greifswald in East Germany has proven to be a glaucous form of E. repens. Since hybrids of E. elongatiformis and E. loliodes of the section Lolioides and between these and ssp. repens are as fertile and with similar meiosis as those of repens and arenosa, it seems reasonable to regard them as equivalent subspecies of E. repens, whereas the endemic E. kasteki from the Tyan-Schan may be better placed as incertae sedis. Our hexaploid number for E. elongatiforme from southeastern Ukraine furnished as seed by Professor Prokudin, confirms reports by DRULEVA (in PROKUDIN et al. 1977) and PETROVA (1972), but is

at variance with the observation by DEWEY (1980) of octoploid material with an entire hexaploid set from E. repens and an additional diploid set of unknown origin.

4. THE ELYTRIGIA INTERMEDIA - VARNENSIS COMPLEX

Four species of Elytrigia were hesitatingly placed by LÖVE (1984) in the section Trichophorae, i.e. its hexaploid type species E. intermedia with nine subspecies, the dodecaploid E. varnensis, and E. pycnantha and the E. pungens complex. DEWEY (1984) placed E. intermedia and its races gentryi and podperae as equivalent species in his collective Thinopyrum, but left E. varnensis, E. pycnantha and E. pungens untouched in Elytrigia s.str.

A critical morphological scrutiny shows that E. varnensis is likely an autoploid of E. intermedia. The subspecific nature of nine races of the latter taxon seems to be substantiated by the observation that their various hybrids are as fertile as are hybrids between different provenences of the typical subspecies, with similarly disturbed meiosis.

Hybrids between E. intermedia and E. repens are relatively frequent where both taxa occur within the same area (PROKUDIN et al. 1977, TZVELEV 1976 and MELDERIS 1980). Such hybrids were studied by CAUDERON (1958, 1966), who found them to have much disturbed meiosis, an observation I can confirm. She concluded that both are complex alloploids that share only her hypothetical haplome "Z" with Critesion secalinum, in addition to the haplomes "EE" and "RR", respectively. DEWEY (1984), however, designated these latter genomes as "EEX" and "SSX", the "X" being unknown but not identical. My own incomplete results are consistent with these tentative conclusions. Since hybrids between E. intermedia and Lophopyrum flaccidifolium (EE) had up to 14 bivalents and seven univalents in 56 cells, or, in four cells, two quadrivalents and ten bivalents plus seven univalents, the formula proposed by DEWEY (1984) seems to be confirmed. As to the identity of the "X" haplome, crosses between E. intermedia and diploid Pseudoroegneria strigosa or tetraploid P. cretacea, grown from Ukrainian seeds, consistently showed up to seven ring bivalents or up to seven trivalents, respectively, in addition to numerous univalents and some supposedly autosyndetic and loose bivalents. Therefore it may seem logical that the "Z" haplome of CAUDERON

(l. c.) or the "X" haplome of DEWEY (l. c.) actually is the "S" haplome of Pseudoroegneria, a conclusion consistent with results from comparison of extrapolated correlates that by itself was less decisive. Therefore, I venture to propose that the genomic formula of the typical taxa of the section Trichophorae is "EES", or so distinct from that of Elytrigia s.str. as to warrant its acceptance as a complex genome genus in its own right. That new genus is to be validated below as Trichopyrum, to which belong the species T. intermedium with its nine subspecies, and T. varnense.

5. THE ELYTRIGIA PUNGENS - PYCNANTHA COMPLEX

Four additional taxa classified as two species and three subspecies of Elymus by MELDERIS (1978) were transferred as such to Elytrigia sect. Trichophorae by LÖVE (1984), i.e. E. pycnantha and E. pungens with the subspecies pungens, campestris and fontqueri. CAUDERON (1958, 1966) reasoned from preliminary studies that the hexaploid E. pycnantha might be regarded as a complex alloploid for which she proposed the genomic formula "NNY" in a system of her own. For reasons not revealed, DEWEY (1984) translated this formula into "SSX". The genomic formula "KKEE" suggested by CAUDERON for the octoploid ssp. campestris of E. pungens, was altered by DEWEY (1984) into "SSXX"; in these cases "X" may represent the "J" haplome of Thinopyrum. That suggestion may be supported by the differences in chromosome size, an observation in line with that of OESTERGREN (1940) and HENEEN (1963), also, the smell of the crushed leaves of these taxa is similar to that of other "J" haplome species. In addition, hybrids of each of the hexaploid and octoploid species with the tetraploid T. junceiforme formed several multivalents of the larger chromosomes and also some rod bivalents and multivalent chains supposedly produced by autosyndesis of the smaller chromosomes. It may, thus, seem safe to conclude that the "J" haplome plays a part in the genomic constitution of the series under discussion.

Tetraploid plants grown from seeds collected by the late Dr. P. Font Quer in the early 1960's on the shores of Mallorca were not identified as the taxon fontqueri until two decades later. The incomplete notes of our crosses reveal, however, that hybrids with some of the "S" haplome diploids and tetraploids from the Crimea-Caucasus region produced highly

disturbed meiosis, one or two distinct ring-bivalents being observed in many cells. This we interpret now as indicating that although the additional haplome of the tetraploid under discussion is not the "S" haplome, it is apparently related to the latter. On the other hand, sterile hybrids of the tetraploid and the "G" haplome of the diploid later named Festucopsis festucoides, grown from Moroccan seeds furnished by the late Professor L. Emberger, were found to produce seven bivalents and seven univalents in almost every cell. This, admittedly incomplete, evidence seems, nevertheless, sufficient for the conclusion that the unidentified haplome of the tetraploid from Mallorca indeed represents the "G" haplome, and that the genomic constitution of the taxa fontqueri, pycnantha and pungens forms the homeogenomic series of the "GJ", "GGJ" and "GGJJ" complexes in a distinct genus for which the name Psammopyrum is proposed and validated below, with appropriate name transfers.

6. NOMENCLATURE

Elytrigia Desv., restricted to the genomic constitution SSX.

E. repens (L.) Nevski, 2n=42, with ssp. repens, arenosa (Petif)A.Löve, calcarea (Cernjav.) A.Löve, elongatiformis (Drobov) Tzvelev, and lolioides (Kar.et Kir.) A.Löve.

Trichopyrum A.Löve, gen.nov., based on Elytrigia ser. Trichophorae Nevski 1936, Trudy Bot.Inst.Akad.Nauk SSSR, ser. 1/2, 83. Genomic constitution EES, EEEESS.

Typus generis: Trichopyrum intermedium (Host) A.Löve.

Name from Greek tricho-, comb.-form of thrix, hair, and pyros, wheat.

T. intermedium (Host) A.Löve, comb.nov., based on Triticum intermedium Host, 1805, Gram.Austr. 3, 23, with ssp. intermedium, afghanicum (Melderis) A.Löve, barbulatum (Schur) A.Löve, epiroticum (Melderis) A.Löve, graecum (Melderis) A.Löve, gentryi (Melderis) A.Löve, podperae (Nabelek) A.Löve, pouzolzii (Godron) A.Löve, pulcherrimum (Grossh.) A.Löve, all comb. nov.; for basionyms and synonyms, cf. LÖVE (1984), 486-487. All 2n=42.

T. varnense (Velen.) A.Löve, comb.nov., based on Triticum varnense Velenovsky 1894, Sitz.-Ber.Böhm.Ges.Wiss. 28. 2n=84.

Psammopyrum A.Löve, gen.nov. Gramen perenne, pruinosum, usque ad 120 cm altum, plus minusve caespitosum, rhizomate longe repente. Foliosum laminae planae vel marginibus involutae, supra nervis crassiusculis, scabris, pungentes, ubi obtritus propria olidus. Spicae erectiusculae vel laxiusculae; rhachis dorso glabrata vel brevissime puberrula, marginibus spinoso-cialiata. Spiculae 3-10 florae. Glumae oblongae vel oblongo-lancelolatae, coriaceae, apice acutae vel mucronatae, 5-6-nerves. Antherae 4-7 m longae. Genomic constitution GJ, GGJ, GGJJ. Typus generis: Psammopyrum pungens (Pers.) A.Löve.
Name from Greek psammos, beach-sand, and pyros, wheat.

Psammopyrum pungens (Pers.) A.Löve, comb.nov., based on
Triticum pungens Pers. 1805, Syn.Pl. **1**, 109, excl.syn. Smith. 2n=56.
ssp. pungens
ssp. campestre (Gren. et Godron) A.Löve, comb.nov., based on
Agropyron campestre Gren. et Godron, 1856, Fl.Fr. **3**, 607, excl. syn. Reichenb.
Psammopyrum athericum (Link) A.Löve, comb.nov., based on Triticum athericum Link, 1844, Linnaea **17**, 365. 2n=42. Syn. Triticum pycnanthum Godron. 1854, cf. NYMAN (1854/55)
Psammopyrum fontqueri (Melderis) A.Löve, comb. et stat. nov, based on Elymus pungens ssp. fontqueri Melderis, 1978, Bot.J.Linn.Soc. **76**, 380. 2n=28.

For some synomyms and references see LöVE (1984, 484-488).

SUMMARY

1. The genera Critesion and Hordeum as well as Lophopyrum and Thinopyrum are to be maintained as distinct genera based on their different haplomes.
2. Elytrigia s.str. has the genomic constitution SSX and is restricted to the hexaploid complex of its type species, E. repens (L.) Desv. It comprises the five subspecies repens, arenosa, calcarea, elongatiformis and lolioides.
3. Trichopyrum is validated as a new genus of the genomic constitution EES and EEEESS, comprising the hexaploid T. intermedium and the dodecaploid T. varnense, the former including nine subspecies.
4. Psammopyrum is described as a new genus for the homeogenomic series GJ, GGJ and GGJJ, comprising the tetraploid species P. fontqueri, the hexaploid P. athericum, and the octoploid P. pungens with its ssp. campestre.

ZUSAMMENFASSUNG

1. Die Gattungen Critesion und Hordeum sowie Lophopyrum und Thinopyrum müssen aufgrund ihrer unterschiedlichen Haplome beibehalten werden.
2. Elytrigia s.str. hat die Genom-Konstitution SSX und ist beschränkt auf den hexaploiden Komplex seiner Typus-Art E. repens (L.) Desv., welche die fünf Subspecies repens, arenosa, calcarea, elongatiformis und lolioides umfasst.
3. Trichopyrum wird als neue Gattung mit der Genom-Konstitution EES und EEEESS bestätigt, welche die hexaploide T. intermedium und die dodekaploide T. varnense umfasst. T. intermedium umfasst neun Unterarten.
4. Psammopyrum wird als neue Gattung für die homeogenomischen Serien GJ, GGJ und GGJJ beschrieben. Sie umfasst die tetraploide P. fontqueri, die hexaploide P. athericum und die octoploide P. pungens mit ssp. campestre.

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