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From the desk of

Mon 22/5/89

PREM P. JAUHAR, PH.D.

Do you have a spare list of your publications?

Many thanks

Prem

To a great cytogeneticist and evolutionist Professor Áskell Löve
Prem
5/9/89

AN EVALUATION OF BAUM ET AL.'S ASSESSMENT OF THE GENOMIC SYSTEM OF CLASSIFICATION IN THE TRITICEAE

PREM P. JAUHAR AND CHARLES F. CRANE

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中国主要植物圖說

禾本科

主編 耿以礼

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1965

A. — Therefore, it has been the main reason for ~~the~~ one of the chief [?] confusion and disagreement as to the generic classification of the perennial wheatgrasses (g. [illegible]), in addition to the fact that most of its components have been combined by most botanists classifying the wheatgrasses because it is [illegible] similarly a complex of Asiatic [illegible] groups. [illegible]

The genus Elytrigia as circumscribed by Nevski ( ) and later authors, but not in its original sense, is a heterogeneous complex, morphologically as well as cytologically, some of the constituents of which ~~being~~ being entirely incompatible.

In the strict sense, the genus includes a few distinct complexes ~~which~~ the genome of which ~~are~~ is known to be ~~[illegible]~~ an allohexaploid assemblage of three pairs of distinct haplomes each of which representing a morphologically distinct group of diploids and their autoploids. In addition, there are two allotetraploid groups uniting two of the three diploid haplomes. ~~one of which is morphologically~~ ~~and~~ The groups ~~[illegible]~~ the genomes of which are made up of a single haplome at the diploid or higher levels are almost incompatible and morphologically so distinct that there can be no doubt that each of them constitutes a well-defined genus in its own right ~~[illegible]~~.

~~[illegible]~~ The oldest and most widespread we identify as the (densely caespitose) genus Festucopsis (Hubb.) Melderis, and include in it ~~[illegible]~~ .... diploid ~~species~~ and a few ~~[illegible]~~ autotetraploid species, distributed mainly in the mountains of central Asia but also met with as far west as in North Africa, North America and Australia. We designate the ~~[illegible]~~ primary haplome of this genus as S; it ~~is one of the haplomes of the genus of Elymus of one of the tetraploid genera this haplome is met with~~ Since the group certainly is at least of early Tertiary age, the haplome has differentiated somewhat during speciation within the group, so ~~the secondary haplome is [illegible]~~ that it may be divided into ~~[illegible]~~ different secondary haplomes, but ~~it is met with as an essential constituent of the genome of the allotetraploid Asiatic group that we name Elytrigodes~~ (NS), ~~also of the widespread allotetraploid genus Elymus in its strict sense~~ none of which have as yet been clearly distinguished.

Another ~~[illegible]~~ haplome characterizes the ~~[illegible]~~ mainly Mediterranean and Black Sea section Junceae which is also widespread on the coasts of western Europe and occurs in the Cape region of South Africa as do numerous other Mediterranean plants of late Tertiary origin. This haplome we designate as N and ~~[illegible]~~ distinguish the group as the rhizomatous genus Junceopyrum; it includes of two variants of the haplome and of genomes representing the tetraploid, hexaploid and ~~A third haplome~~ an autoploid series at least up to the (octoploid level ~~[illegible]~~).

A third haplome is typical of the mainly Southwest Asiatic, eastern Mediterranean ~~[illegible]~~ section Elongatae. This haplome we call E and ~~distinguish the group~~ designate the group as the caespitose ~~[illegible]~~ steppe genus Lophopyrum, alluding to its tufty appearance; it consists of an autoploid series from the diploid to the decaploid level. ~~These haplomes~~ It is the ability of these three haplomes to combine with various other haplomes to form genomes of more or less distinct genera that has caused much of the difficulty encountered in the classification of the perennial wheatgrasses. ~~The S haplome is the a component of the very large and widespread genus Elymus in the strict sense, the N haplome is possibly identical with the the [illegible] haplome~~ The E and N haplomes combine to form the genome of the group of the ~~[illegible]~~ section Caespitosae of the collective genus Elytrigia that we distinguish as the ~~[illegible]~~ Southwest Asiatic, southeast European genus Proselytrigia which apparently is a step towards the origin of the hexaploid ENS ~~genus Elytrigia~~

We find it most logical to distinguish as genera ~~these~~ groups that are characterized by ~~a morphologically distinct [illegible] [illegible]~~ haplome so distinct that at least most of its chromosomes are unable to pair with those of other such haplomes at the same time as their genome, and therefore ~~[illegible]~~ morphological and physiological characteristics ~~or~~ make ~~the~~ ~~the~~ taxon easily recognized and distinguish ~~[illegible]~~ it from other such groups, irrespective of if the haplome forms autoploid series or has taken part in the production of alloploid taxa ~~[illegible]~~ with which it is able to form sterile hybrids with certain degree of meiotic pairing. Instead of including such alloploids in a genus with either or both its parental haplomes, ~~we find~~ we believe it is wiser to regard ~~them~~ them as representatives of a complex genus of their own, rather than to include all in an unworkably [illegible] genus. (Usually, ~~[illegible]~~ the chromosomes of the distinct haplomes have been so rearranged by aid of inversions and reciprocal translocations that they are unable to pair, although the [illegible] of the same primary genus still makes for a certain [illegible].)

rightly to genetic Eurasiatic steppe genus Elytrigia in its strict sense. ~~The N hyplone~~ ~~the~~ On morphological grounds it may be assumed that the N hyplone could be identified with the cytologically still not certainly identified so-called X genome that together with the J genome of Platystachys seems to have given rise to the widespread but moderately strong rhizomatous genus Leymus, ~~but~~ (cf. thus, it may be one of the Jane hyplones of the complex polyploid monotypic North American genus Pratopyrum.) ~~The N hyplone~~ is also a likely component, ~~of the genus~~ Elytrigia together with the S hyplone, of the mainly Eurasiatic ~~and~~ exception genus Elytrigia (NS) which was tentatively placed in the series Stipifolium of Elytrigia by Newski ( ). Whereas the S hyplone has entered with the H hyplone of the perennial ~~genus Elymus~~ it very large ~~a~~ widespread genus Elymus in its wide sense. And both the S and N hyplones share a place with the ~~H~~ H and J hyplones of the ~~polyploid~~ cytologically genome of the polyploid monotypic North American prairie grass genus Pratopyrum, ~~which~~ the distribution of which seems to indicate an origin as late as during the last part of the Pleistocene.

Since all the species concerned have not as yet been ~~studied~~ hybridized ~~in order to~~ for an analysis of their genomes & hyplones, and several still remain even cytologically unknown, their classification is, in these cases based on morphological observations only. ~~This is~~ However, usually ~~is~~ possible by aid of morphological observations alone, ~~since~~ because each hyplone, as well as each polyploid genome, are characterized by distinct characters of a diagnostic significance. Nevertheless, some uncertainty may prevail, & then especially ~~as~~ as to the classification of the ~~genus~~ section Hyalolepis as a section of Elytrigia s. str. because the genome constitution ~~of~~ ~~these species is~~ of these species as being ENS as in Elytrigia proper is deduced from morphological evidence alone, since only one? a few? species has been cytologically studied, more involved in hybridization experiments, & we have seen only a limited ~~material~~ herbarium material of some, not all, the taxa involved. But in that conclusion, as in possible misinterpretations of cases of which experimental & cytological evidence is lacking, we stand corrected when ~~better~~ more reliable evidence becomes available.

The grasses that we call Wheatgrasses, or the relatives of cultivated wheat that taxonomist classify in the tribe Triticeae of the family Poaceae, are plants of meadows of various sizes in mountains and on steppes on all the continents. Some of them are common over wide areas and are gregarious so they may alone cover almost endless plains with fodder for livestock, but most straddle alone or in low numbers as parts of various plant associations. These grasses are most numerous at most variable on the mountains & steppes in the lands of southwestern Asia which the ancients called the Orient, or from India to Turkey & from the southern Siberian steppes to the Indian Ocean, but they are foreign arctic climates & a few live in tropical mountains, & some are even found on isolated oceanic islands like Norfolk & Réunion.

The wheatgrasses are characterized by being either annual or perenial grasses of various height, with flat, convolute or sometimes linear leaves. Their leaf-sheaths usually have small auricles at the mouth & the ligule is membranous & often short and blunt (truncate). The leaf-blades have the anatomy characteristic of the so-called festucoid grasses, or...

Huxley 74: J. Linn 1760?

Here I must make a long methodological digression. The method of approach to any scientific problem is clearly of extreme importance, & will to a large extent determine the type of discovery made

The hybridization led to the discovery that ~~one~~ one species of the same genus, in this case Agropyron, reacted very differently when crossed with wheat, ~~so that~~ —.

In the past, the wheatgrasses have been recognized as wheat, rye & barley by the ancients, but although they may have been aware of some of the non-cultivated species & named them, later generations have not been able to identify such names. Linnaeus named 28 species which he placed in the genera Triticum, Elymus, Secale, Hordeum & Aegilops, and then misplaced one species in the genus Bromus; in modern opinion these taxa represent only 22 biological species. Since his time numerous taxa have been described from within this group, so that presently we recognize almost 500 taxa of which about 320 seem to be at least reasonably good biological species. It may be of interest at this stage to mention that of these taxa 328, or almost 70%, are known as to their chromosome no., that the karyotype or idiogram has been determined for 226, or 45% of them, and that about 100 of these taxa (or 20%) have taken part in about 300 artificial hybrid combinations that have been analyzed as to their meiosis. No other tribe or group of comparable size has been so intensely studied.

Here I would like to make a brief methodological deviation before continuing a discussion of the classification of these grasses, which since Linnaeus have been periodically [illegible] into fewer or more genera on basis of various considerations.

The method of approach to a scientific problem of this kind is clearly of extreme importance & so is the philosophical thinking behind the conclusions to be drawn, because they will to a large extent determine the type of discovery made or the classification proposed. Putting the matter the other way round, the method of approach is itself largely dictated by the type of answer you want to obtain: it is, in fact, a kind of a question. Furthermore, the question will alter with time & the progress of discovery: when one method has yielded the main crop of answers that it could be expected to provide, it is time to ask another kind of question, by adopting a new method.

The original approach to plant taxonomy inevitably was descriptive because botanists set out to describe as fully & accurately as possible the variation of plants & the phenomena which they exhibit. This approach

is designed to answer the basic question about what are the facts in the wider sense of the word so the plant can be classified and again identified by simple observational methods as inevitably are used by non-specialists and by floristic botanists, who do not require more exact information. Though this fundamental approach needs categories as do all kinds of studies, these may be rather arbitrarily chosen and hardly need to be more closely defined.

When scientific knowledge advances, so the requirements of exactness the descriptive approach is supplemented by the comparative. This is first focused around the grouping or classification because we need to know what pattern or system an assemblage of plants has in common, and what distinct types there are at various levels of characterization. In the wheatgrasses, this lead to a somewhat confused state, since a considerable degree of arbitrariness cannot be avoided as long as the morphological method is supplemented only by anatomical and geographical considerations that hardly are sufficient for conclusions as to the grade of physiological relationship. Since, following the morphological method Schur concluded that many of the more than 100 species that were discovered during the century following Linnaeus were correctly classified in small genera many of which more than fifty were described, whereas others used the same method as a basis for lumping this variation into only the German botanist Host used the same method as a basis for lumping all the wheatgrasses into a single genus, which he called Frumentum, an illegitimate name also according the nomenclatural rules of his time. More moderate lumpers, however, selected a few distinct morphological traits as a basis for placing all these species in the genus Triticum, small genus Triticum, Secale and Aegilops and the large genus Hordeum, Agropyron and Elymus, an arrangement that was generally accepted all over the world until half a century ago and still is predominant in even the modern manuals for the English-speaking nations, though not in the conservative Flora Europaea. Implicit in this system was the idea of physical

IV.

relationship, although its nature remained diffuse and dim. With the acceptance of the fact of evolution, this implicit postulate became explicit, and the question posed by the comparative method became correspondingly altered: behind common patterns we were searching for common origins. The result ~~was a more phylogeny~~ is a more phylogenetic classification, a classification intended to express evolutionary descent and relationships rather than just a convenient pigeon-holing system. When such a classification was first attempted for the wheatgrasses, by the Russian ~~taxonomist~~ (Roshevitz, and especially by his student) Nevski (in the Flora USSR in 1934) in the 1930ies, it was based on morphology, geography and anatomy and a little cytology, ~~it resulted~~ but no experiments, and it resulted in the acceptance of almost 30 genera, some of which were extremely narrowly defined while others remained collective. Nevertheless, this led to extensive experimentation that has resulted in [illegible] ~~crossing combining~~ hybridization of all these genera in various ~~ways~~ directions, studies of the meiotic divisions of these hybrids (and thus of the ~~[illegible]~~ possible genetical relationship of these genera, and to ~~investigations of~~ cytological investigations of 70% of the about 500 taxa now recognized. ~~That has made it~~ An evaluation of ~~these extensive~~ the results of these extensive investigations ~~has led to some which have to a considerable extent been based on~~ [illegible] which for practical reasons have to a considerable degree been directly or indirectly based on the Nevski conclusions, has led to (several) new revisions of the classification of the wheatgrasses at the specific and generic levels and also of the limits of the tribe Triticeae itself ~~to which even Nevski had[?]~~ to which some botanists, even Nevski, had attached ~~[illegible]~~ a few genera that the new methods have found to be unrelated to the group. It must be mentioned that ~~[illegible]~~

[~~Before [illegible] discussing the [illegible] taxonomical conclusions that various students have made on basis of the results of the new methods, I would like to review briefly the methods themselves.~~]

the new approach has universally accepted the socalled biological species concept so its main discussions concern the generic classification of the taxa, not their basic circumscription or delimitation.

V.

Before discussing the taxonomical conclusions that various students have drawn on basis of the results arrived at by aid of the new methods, I would like to review briefly the methods themselves.

1) The morphological method. I can be brief about this approach, which is based on description and comparison of morphological traits. Although some characters are important for the classification of the Poaceae as a group or for the distinction at the generic level, a strong emphasis is laid upon the study of minute floral characters on basis of which especially Hackel described his many genera. They concern the

To this method belong the observation of the growth habit of the plant, its being annual or perennial, the tough or fragile character of the rhachis, the number of spikelets at each node of the rhachis, the morphology of each spikelets, the number of florets in each spikelet, the shape of the glumes and lemmas and relation of the glumes to the lemmas or presence or absence of type of the awns. Although considering of these characters undoubtedly lead to more genera than [illegible] were accepted by the Deutsche school that still dominates in the floras of the English-speaking world, this approach can logically lead to rather different results, as we can see on the following table that is reproduced from Schanzle (1973, p. 12). Table II

The variation is not only in the number of genera circumscription of genera but also in the delimitation of the subtribes.

Schanzle (1973, p. 13) disregarded the subtribal classification which he found to be misleading, and instead classified the morphologically distinguished groups on basis of their distribution, growth habit, and the number of spikelets at the node of the rhachis (figure!). Table II

VI.

~~2) Anderson's [illegible] diagram~~

As a result of the morphological method, our group in Uppsala in the early 1950's made ~~[illegible]~~ comparisons of critical (polyploid groups) of wheatgrasses by aid of the method of extrapolated correlation proposed by Edgar Anderson & his book « Introgressive hybridization » published in 1949, since we believed that this method might reveal relationships & differences that the conventional morphological approach ~~could not~~ could not easily discover. By aid of this tedious method we could convince ourselves that the group of Elymus ~~and the~~ circle around the species arenarius is unrelated to other species then classified either as Elymus ~~&~~ or Agropyron & then concluded that it ~~was~~ would be wise to accept for it the generic name Leymus that had been ignored since its publication by Hochstetter (1855?). The method found its proper use, however, in the work by our student Sarbua aided by Stebbins, when they could demonstrate that the so-called B-genome of tetraploid & hexaploid wheat ~~was not but~~ ~~it is in it~~ is similar to the genome of the Sitopsis group of the collective genus Aegilops (Cyt. of Sarbua & Stebbins p. 258).

Fig. II

By aid of this method it has also been possible to demonstrate that the genus Elytrigia is unrelated to Elymus ~~and also of~~, that the genus Hordelymus ~~has~~ is an allotetraploid of ~~the genus~~ a genus Hordeum, & that the perennial species of the genus Leymus are most likely ~~to be of the genus~~ Psathyrostachys ~~& species of~~ a diploid species of the Central Asiatic genus Psathyrostachys, & the tetraploid species related to the so-called Agropyron junceum.

VII.

2) Another variation of the morphological approach uses computer techniques for socalled character analysis. Since the computer does not think, he must be fed the available data and then programmed ~~to analyse them in such~~ to ~~and~~ cluster (them) and analyse them to evaluate them in various ways. Although this technique has been tried for parts of the Triticeae by some botanists, it has been employed for ~~all the taxa~~ most of the taxa only by Bernard Baum of Ottawa, who advocated on basis of a detailed cluster analysis the acceptance of 28 genera that form at least four distinct groups. The perhaps most remarkable results of this analysis ~~which~~ is that the ~~—~~ cultivated ~~—~~ *Hordeum* is widely distant from the species of the subgenus *Hordeastrum*, and that the ~~isolated~~ supposedly isolated genus *Henrardia* may be closely related to *Triticum* and *Aegilops*. It ought to be pointed out, ~~however,~~ that no experimental or cytological observations were used in this analysis, ~~so which might~~ and that whereas most of the genera were narrowly defined, some others were very collective, but it is ~~nevertheless remarkable~~ that the results seem to support a wide splitting rather than extensive lumping of these grasses.

Fig. 7-9. Table 3 Baum 1978, p. 2553

3) The cytological approach is based on studies of the number ~~of~~ of the chromosomes and ~~—~~ of the socalled karyotype or idiogram. The number itself, which has been determined for 70% of the taxa, is of ~~little~~ interest as a distinction between diploid taxa and their auto- and alloploid derivatives, whereas the karyotype or idiogram is important for the identification of socalled haplomes and their variations and for the recognition of auto- and alloploidy based on these haplomes. This method was first used in big scale on the genera *Aegilops* and *Triticum* ~~by Senyaninova-Korchagina~~ by Senyaninova-Korchagina in 1930, (she was a student of Levitsky in Leningrad), and we and our students in Winnipeg and Montreal made great efforts to ~~analyse~~ analyse as many species as ~~could~~ possible, especially the diploids. ~~—~~ We succeeded in analyzing the karyotype of 45% of the wheatgrasses, or in 226 taxa, but so far only the results of studies on the wheats and *Aegilops* and a few other annual genera have been published by Sarkar ~~and~~ and by Chennaveeraiah.

VIII.

~~When analyzing karyotypes, it is of an utmost importance that the material is [illegible] carefully fixed so that the chromosomes swell as little as possible and their primary and secondary constrictions be clearly visible.~~

I may perhaps add here within parenthesis that when we decided to analyse the karyotypes or haplomes (a useful term coined by Heilbronn & Kosswig in their Principia Genetica), of the wheatgrasses, we were influenced by two factors. First, I had studied extensively the distribution in Europe of twelve socalled karyotypes that occur within the ~~genus~~ dioecious genus, *Acetosa* which ~~and~~ had ~~[illegible]~~ been analysed earlier in Japanese material by Kihara and Yamamoto (1931) and by Ono (1935). Second, I was aware that in the search of the socalled D-genome of cultivated wheat, Pathak (1940) had compared the karyotype of numerous cereals and their relatives and came to the conclusion that one of the chromosome sets of hexaploid wheat seemed to be ~~[illegible]~~ morphologically identical ~~[illegible]~~ with the chromosome set of the diploid socalled *Aegilops squarrosa*; this was the species which McFadden and Sears, and independently Kihara in 1944 used ~~[illegible]~~ for ~~producing~~ synthesizing *Triticum spelta* ~~by aid of hybridization of tetraploid emmer wheat and~~ through allopolyploidy from a hybrid with tetraploid emmer wheat. It was, thus, evident, that ~~[illegible]~~ karyotype analysis could render useful results also for the study of the relationship of the wild wheatgrasses, although we were aware that the direct relationship ~~of the taxa~~ or the lack thereof could not be established by ~~morphology~~ karyotype studies alone.

When analyzing karyotypes, utmost care must be taken in the fixing of the material, which by necessity is selected from mitotic divisions, either pollen mitosis or, more easily, mitosis in root tip cells.

Kagawa 1926, 1927; Jenkins, Aegilops chr.

but also to the cytological conjecture, by Kagawa (1926) of the occurrence of three distinct karyotypes of 7 chromosomes each in the polyploid series of wheat species. In 1944 the search led to the discovery, by Kihara and McFadden and Sears independently, of the socalled D-genome in the diploid species *Aegilops squarrosa*, or nomenclaturally more correct *Aegilops Tauschii* of the Vertebrata section of the genus. For one reason, the B-genome evaded discovery for twelve more years and was first discovered, in the Sitopsis section of *Aegilops*, by Sarkar and Stebbins (1956), not by aid of the methods of Kihara but through the application of the socalled method of extrapolated correlation, proposed for discovery of one hybrid parent when another is known, by Edgar Anderson in 1949.

The karyotypic studies ~~[illegible]~~ combined with ~~[illegible]~~ the results of genome-analysis were used by Chennaveeraiah and Sarkar in support of the reinstatement of the genera Amblyopyrum, Eremopyrum and Agropyron s. str. and we based our ~~[illegible]~~ ~~our~~ revival, in 1961, of the genus Leymus as distinct from Elymus on the observation that both its haplomes are significantly distinct from both ~~the~~ the haplomes of any Elymus, in addition to morphological distinctions — which Hochstetter (1848) had made his ~~[illegible]~~ wise splitting of these genera that ~~since~~ had been ignored for over a century. As for other ~~polyploid~~ genera described by past taxonomists, ~~it was found that homogenous distinct ~~ haplomic constitutions characterize the genera~~ and presently accepted by at least some taxonomists

but felt that some additional morphological and hybridization evidence was needed before that step could be taken without some hesitation. That evidence has since become available. [illegible] there seems to be only the classical resistance of our inherent conservatism that may counter ~~[illegible]~~ the acceptance of such a proposal, and the ~~[illegible]~~ its ~~[illegible]~~ general ratification is only a matter of time and convenience.

ABDUM,

HTJNES

auto: A Aegilops
F ~~R~~ ~~P~~ Eremopyrum
H Critesion
PR Agropyron
E Lophopyrum
N Thinopyrum
S Pseudoroegneria
V Dasypyrum
X Festucopsis

11a.

by becoming what Zohary and Feldman (1962) appropriately termed pivotal for further evolution,

~~Although only a few of the haplomes,~~

Only six of the 24 haplomes were found to have taken ~~[illegible]~~ part in allopolyploid evolution, but 8 haplomes have formed autoploid series, even up to the octoploid and decaploid levels. ~~[illegible]~~ As indicated by this, most of the diploid taxa and many of the polyploid ones have a very low crossability, although ~~all have [illegible]~~ it has been possible to form hybrids between at least some of them so that there is no doubt that the entire tribe can be regarded as a single comparium in the sense of Danser, whatever that may mean. I take it to signify that the tribe Triticeae is a natural unit that has evolved by chromosomal rearrangement from a single original haplome or karyotype ~~but that still retains~~ ~~the chromosomes~~ so that although the chromosomes of the ~~[illegible]~~ present haplomes pair only slightly or not at all, they retain essentially the same major genes so some crossability is maintained. Others may interpret this differently. ~~without~~ ~~without ignoring~~ It is my opinion also that the ~~genomic system~~ discovered in the Triticeae both by aid of hybridization and karyotype study makes it possible to divide the tribe into evolutionarily and genetically well defined genera in a manner more logical than any such groups have ever been classified, and thus point the way for future evolutionary classification at the generic level of other such complexes.

II 6.

[It is of certain interest to note ~~that of the~~ the different success of the various allopolyploid ~~constitution~~ haplome constitutions]

We could spend hours on speculations as to the place and time of origin of the Triticeae and of the course of evolution that ~~has~~ characterizes its genera and species. There is no geological evidence of any of its members, but the wide distribution of the genomic constitution HS in the circumpolar ~~Arctic~~ arctic and boreal zone ~~of~~ the mountains of North Africa eastward to the Himalayas, Java, in Australia and New Zealand. Phytogeographers would doubtlessly conclude from this observation, that this genomic constitution hardly can be younger than from the middle Tertiary, perhaps even older. ~~That~~ ~~the~~ ~~the primary haplomes H and S~~ The primary haplome H is distributed in the northern hemisphere and in South America, and the haplome S is characteristic of species presently growing in ~~Eastern~~ southeastern Europe, southern and central Asia and North America.

That allows us to suggest that the primary haplomes H and S must be at least from the early Tertiary. ~~This~~ — suggestion is perhaps supported by the fact that S is presently ~~distributed~~ known to occur in diploid and tetraploid species met with in southeastern Europe, ~~eastern Mediterranean~~ and the stretching from the mountains of Asia Minor east to the Himalayas and northwards to the Siberian mountains and to ~~North A~~ eastern North America; whereas the H haplome is known to occur in the temperate and boreal parts of Asia and North America as well as in the South American mountains.

~~Although~~ The concept of the generically defined genus inevitably leads to the splitting of some ~~ancient~~ genera of the past, ~~such as~~ as, e.g., the genera Aegilops, Triticum, Hordeum, ~~Secale~~ Elymus s.l. ~~and~~ Elytrigia, ~~and~~ Agropyron s.l. However, it also dictates the ~~grouping~~ lumping of some such groups into a single genus because of their close generic relationship, ~~such as for instance~~ as for instance the genera Anthoxanthum, Cockayne, Hystrix & Sitanion, all of which are characterized by the generic constitution HS typical of Elymus s. str., the by far the largest genus of the tribe.

If the genetic classification by genomic constitution is adopted, extensive ~~splitting seems to be required only for~~ new splitting seems to be required only for the *Agilops-Triticum* group and for ~~[illegible]~~ *Agropyron* and *Elymus* as defined by those ~~adhering to the Bent~~ still adhering to the Bentham concept of the wheatgrasses, ~~[illegible]~~ the *Elytrigia* complex as still defined by the Russians. ~~[illegible] [illegible] the wheat-Agilops group~~ the *Elytrigia* group as still defined by most authors who separate it from *Elymus* and *Leymus*. At the same time, the smaller genera ~~into which~~ of the Elymineae accepted by Nevski and ~~American authors and~~ some older authors have been found to be composed of the ~~haplomes [illegible] [illegible] from Critesion and [illegible] from Psathyrostachys~~ same haplomes as *Elymus* s. str., so they must be united with that genus; the groups in question are *Anthosachne*, *Asperella*, *Clinelymus*, *Cockaynea*, *Hystrix*, *Roegneria*, *Sitanion* and *Terrellia*.

If the generic description by genomic constitution is adopted, it will strengthen the delimitation of several natural genera already described & accepted. This will be the fact with the ~~[illegible] adopted~~ genus Amblyopyr (genus ..), which Eig (1929:) separated from Agilops & all later authors have accepted, Aegilops in the strict sense (genus ...), Secale (genus ..), Dasypyr (genus ..), Eremopyr ( ), Heteranthelium ( ), Henrardia ( ), ~~[illegible]~~ Crithopsis ( ), Taeniatherum ( ), Hordeopsis ( ), Psathyrostachys ( ), Agropyr s. str. ( ), Leymus ( ), & Elymus s. str. ( ). It will also support the separation of the wild barleys ~~of the cultivated ones~~ as the genus Critesion, which is widely distinct from the cultivated barleys of the genus Hordeum ( ). It will, likewise, require that genera ~~as widely accepted~~ as Anthosachne, Elionurus, Cochlearia, Hystrix, Roegneria, Setaria & Tarrella be sunk into the natural genus Elymus, since they are all characterized by the genomic constitution HS.

Triticeae: Triticale 1979 ... : Gebrüder Borntraeger, c. 125 pp. Langdon

Böcher, Holmen, Jakobsen, Fredskild, Grønlands Flora 3. udg. 1978?

Since none of us seems to appreciate to have to change names that we have become used to,

(To propose any change in classification inevitably seems to make even some scientists angry because they disagree without being able to directly say why — but it makes them think. The proposal to define genera phylogenetically by aid of their genomic constitution ~~...~~ certainly offers hope for the future of evolutionary classification with bold new perspectives and new ideas and new approaches to problems that taxonomists have dreamt of solving but frequently surrender (capitulate) to as being unsolvable. ~~But~~ And although this evolutionarily soundest of solutions sometimes is inevitably radical in its extensive splitting (as in Agropyron, Elytrigia), and sometimes equally conservative in its stringent lumping (as in Elymus), it is always logical and therefore just what has to be done. It is rather matter that its ~~may require~~ acceptance may have to wait for our nephews, the generation of our grandchildren, as even the great Linnaeus found when he presented his classical Species Plantarum. But it has to be done now nevertheless

This is probably not the ultimate solution of the ~~great~~ problem of generic definition, since none of our solutions is more than preliminary. And ~~you~~ nobody is forced to swallow it forthright and not even after long chewing. It is also likely that one will want to accept the genomic genera for one group and reject them for another. That is your privilege. But I am ~~convinced~~ in no doubt that it will be accepted for most plants by our nephews, the generation of our grandchildren, who ~~will then~~ always are ~~must be~~ the ~~our~~ ultimate judges of our efforts and ideas.

Hymenophyllum: x = 13: Arabidopsis thaliana 2n = 10, Cardaminopsis ~~[illegible]~~ arenosa 2n = 32: 16 x 10 [illegible] = 26.
Pleurogyne [illegible] 2n = 40, [illegible] [illegible]
[illegible] Aster 7, 8, [illegible] 7, [illegible] 8.

(1)

When the system of classifying ~~[illegible]~~ living beings into genera and species was invented, few biologists had thought of an evolutionary process. Nevertheless, even the earliest systems were based on the idea that a genus should include species that are related in one way or another, although this idea was dim and not easily clarified at ~~that~~ that stage of knowledge. ~~Classification~~

Biology started ~~[illegible]~~ with classification, and it may well be said to be as old as human thought. In a sense classification may perhaps be regarded as having originated with reacting organisms, since even the lowest of ~~life forms res~~ living beings respond differently to a varied environment and effectively order their own world. It is but reasonable to expect that such an ancient and universal activity, vital to the most primitive tribes and the most advanced stages of knowledge alike, should have developed to a precise and undisputed technique. It may, therefore, be astonishing that it still is not uncommon for different students of the same material to arrive at altogether different classifications, and these may at times seem to be evaluated more by the reputation or vociferation of their ~~authors~~ proponents than ~~[illegible]~~ on their approximation to reality. One of the reasons for this fact is probably the fact that even truly observational science has not yet reached more than a fraction of the biota of the world and that ~~[illegible]~~ our knowledge of even the ~~[illegible]~~ most studied of biota is only partial. ~~Empirical studies must still predominate with their inevitable tendency~~ Steadily increasing knowledge requires constant revision in classification, although empirical studies long will predominate with their inevitable tendency toward authoritarianism.

It must necessarily be realized that the (philosophy and) method of approach to any scientific problem is clearly of extreme importance, and will to a large extent determine the type of classification arrived at. Or, to put the matter the other way round, the method of approach is itself largely dictated by the type of answer one wants to obtain; it is, in fact, also a kind of a question. Furthermore, the question will alter with time and the progress of discovery, so that when one method has yielded the main crop of answers that it could be expected to provide, then it is time to ask another kind of question, by adopting a new method.

This is just what has happened in the field of botany, where the original approach is inevitably descriptive, because botanists set out to describe as fully and accurately as possible the variety of organisms and the phenomena which they exhibit. ~~The approach~~ ~~The descriptive approach soon is supplemented by the comparative, which is~~ This original approach is designed to answer the basic question about what are the facts; though it needs categories as do all kinds of studies, these are rather arbitrarily chosen and hardly need to be more closely defined.

The descriptive approach soon is supplemented by the comparative, which is focused around the question of grasping that mirrors the patterns that an assemblage of organisms has ~~together~~ in common, and what distinct types there are at various levels of characterization. This leads to classification of organisms in a hierarchical system of categories which have to be more or less exactly defined, although some degree of arbitrariness cannot be avoided.

When the comparative method becomes connected with the theory of evolution, it soon requires still a new procedure, an approach which is best termed differential analysis. This seeks to clarify the question about the cause of differences between the members of a related group and also between the related groups themselves. This is just, in the model ~~method~~ of ~~phylogenetics~~, making analysis of the hybridization and studying the mechanisms of cell division. It is primarily associated with studies of the internal structure and total pattern of each system of detectable components and the history of evolutionary divergence and its causes. ~~It goes without saying that this treatment~~ It is from this treatment combined with comparative morphology that we have been able to conclude that

It would be interesting to speculate about the age and evolutionary history of the complex, but this time we must confine ourselves only to state that the largest group of polyploids (in the genus Elymus in the strict sense) consists of a combination of the H and the S haplomes from the genus Pseudoroegneria. It has a circumpolar arctic and boreal distribution and reaches south to Tierra del Fuego as well as to Australia and New Zealand. Although no fossils have been studied so far, a careful phytogeographer would likely regard this distribution as an evidence of an origin prior to the Miocene, so the separation of the also rather widespread H and S haplomes alone could be suggested to be of an early Tertiary age. These plants are perennial. At the other end of the evolutionary line are the wheats and their relatives which seem to have been in a state of rapid evolution in the Middle East during the period during and after the Pleistocene glaciations of the northlands, and the hexaploid bread wheat with its ABD genomic constitution may perhaps only be a few thousand years old. The same is also true for the most important hay producer of the tribe, a grass of the North American prairies south of the last Pleistocene ice, which has been shown, by careful studies by Dewey, to combine the HS genome and characteristics of one of the polyploid species with the JN genome and characteristics of another still existent species of restricted distribution.

It is also tempting to speculate over possibilities of breeding experiments (with polyploidy) that could be more successful than those tried in various places during the past few decades, nowhere with proper success. The lack of success of the so-called rye-wheat or Triticale combination may be connected with the fact that rye is an allogamous species, wheat autogamous, and that much genetic variation is inevitably lost during the process that is based on hybridization (between these two fundamentally different breeding systems) followed by chromosome number duplication — perhaps

group of the wheatgrasses that is characterized by a single haplome needs to be accepted as a genus in its own right.‡ As a matter of fact such a definition was recently advocated by the wheat geneticist MacKey (1968) ~~when reviving the generic name~~ (Crithodium) for the Einkorn wheat. [illegible] ~~It was also contemplated by Chennaveeraiah (1960) in connection with his studies~~ The same idea,# with the addition of proposing that groups produced by different ~~compositions~~ alloploid compositions of intersterile haplomes also be regarded as distinct genera, was ~~(also)~~ contemplated by Chennaveeraiah (1960) in connection with his thorough studies on *Aegilops*, though he hesitated to propose it in view of the fact that some additional morphological and hybridization evidence still was not available. That evidence has since been amply added so ~~that seems to be left only the classical resistance~~ the only logical resistance left, as far as splitting of the Aegilops-Triticum complex is concerned, must be based on our inherent conservatism, ~~and~~ which, fortunately, changes with new generations, ~~in taxonomy and genetics no less than in other sciences, [illegible] the violent exchanges~~.

This leads to the conclusion that I have found it logical to propose, ~~that~~ to follow MacKey in accepting generic status for each ~~grouping of~~ haplomic group, be it large or only of a single species, and also for each of the ~~distinct genomic~~ haplomic complexes of alloploids. This proposal would make no changes in most of the genera accepted by Nevski and modified by Tzvelev, ~~[illegible]~~ and result in strengthening of the definition of genera as *Amblyopyrum* (T), *Aegilops* s.str. (MU or MMU), *Secale* ( ), *Dasypyrum* ( ), *Eremopyrum* ( ), *Heteranthelium* ( ), *Henrardia* ( ), *Crithopsis* ( ), *Taeniatherum* ( ), *Hordelymus* ( ), *Psathyrostachys* ( ), *Agropyron* s.str. ( ), *Leymus* (JN), *Festucopsis* (F), and *Elymus* (HS).

~~Exogiting the~~

It would take too long to review the influence that the acceptance of the genomic concept as a general dogmatic in the wheat grasses would have on the annual group of Triticeae

For the sake of time I must refrain from detailed discussion of the status of nomenclature of the taxa that are characterized by haplomes that have taken no part in the evolution of the cryptic & instead additional part in the evolution of the cryptic & instead only mention briefly the effects that this concept will have on the ~~genetic haplome~~ classification of the pivotal haplomes & of the taxonomy of the polyploid complexes. (The essential pivotal haplomes of the annual wheatgrasses D in the haplome A, which is characteristic of the so-called Einkorn or monococcum wheats; at the generic level its current name is Nivisa, ~~that~~ of which the same species is diploid, & less well known are ~~the~~ autotetraploid. Another pivotal haplome is D, which is typical of the genus Sitopsis, which originally was devised as a subgenus of Aegilops, ~~The third pivotal haplome is D~~ & includes seven ~~species~~ all of which have been classified as subspecies only of the eight species. The third annual pivotal haplome is D, which is characteristic of the genus Patropyrum which has been classified as the species tauschii (or wrongly as the species squarrosa) of the ~~sect~~ monotypic section Vertebrata of Aegilops. Two of these haplomes, A & D, have united to form the ~~Emmer or macaroni wheats~~ single species & ten subspecies of the Emmer or macaroni wheats with their ~~many~~ more than 5000 cultivars, ~~& these two haplomes & the D haplome are the~~ & Emmer wheat ~~of~~ plus the D haplome produced the important Durhum or bread wheat & its six subspecies which are known to comprise over 3500 cultivars.

The ~~genus~~ genus Secale, the rye, is characterized by a haplome of its own that has not taken part in further evolution though it has recently formed alloploids after hybridization with wheats, by aid of plant breeders. Other annual ~~non~~-pivotal haplomes need not to be mentioned since their distinction has rarely been doubted. The genus Hordeum, in the usual circumscription, ~~that includes both the~~ however, has been found to include, in the annual cultivated group, the genus Hordeum in its strict sense,

the haploid I, which has not taken part in further evolution, & the haploid H, which is typical of the diploid cultivated barleys which are more correctly classified in the genus Criteria; that haploid has been very active in the evolution of other cereal groups.

Wellknown genera that are characterized by a single haploid each that have not taken part in further evolution, are the rye, or Secale, Dasypyrum, Eremopyrum, Heteranthelium, Hordeum, Critopsis, Taeniatherum, & Agropyrum s. str., all natively distributed in the mountains & grasslands of the Middle East. The genus Hordeum, or barley, also is innocent of pivotal action, whereas its relative, Critesion, or the wild barleys, is characterized by the pivotal haploid H, which has actively contributed to allopolyploid evolution that led to generic development. One of its offspring genera is the monotypic European Hordelymus with the generic constitution HT, the T being derived from the annual weed Taeniatherum of western Asia & eastern Europe. Another offspring but its essential offspring, with the S-genome of the old genus Pseudoroegneria of southern Europe & Asia Minor & the North American is the genus Elymus which includes almost 200 taxa distributed all over the northern & boreal areas, & reaching Tierra del Fuego, Natal & East Africa, Java, Australia & New Zealand. Its generic constitution is HS, & it comprises, in addition to the restricted diploid genus Elymus, also groups that until recently have been recognized as the genera Asthenatherum, Clinelymus, Cochlearia, Hystrix, Roegneria, Sitanion & Taeniatherum.

The genus Elytrigia, which Nevski (1934) recognized as a split out of the then conventional Elymus as delimited by Bentham, has proven to be a complex made up of five distinct diploid or autoploid (haploid) taxa of which three haploids are pivotal, or E characteristic of Lophopyrum, which comprises the genus Elymus elongatus group, N that is typical of Thinopyrum & the genus Agropyrum sect. Junceum, & S of Pseudoroegneria mentioned earlier. There are also two small tetraploid genera, Psathyrostachys, with

the genomes E and N, and *Elytrigoides* with the genomes E and S, which may lead to the hexaploid *Elytrigia* s. str. with its E, N and S genomes. Also the classification of *Elytrigia* remains tentative because too little is still known about its many Arctic species of the section *Hyalolepis*, but its other sections, *Elytrigia*, *Trichophorae*, *Lolioides* and *Caespitosae* ~~...~~ all include the E, N and S genomes and seem to be reasonably well defined.

Leymus. ~~The remaining~~

~~Then it remains to mention the group which circles around the species which Linnaeus named *Elymus arenarius*. On morphological grounds alone, Hochstetter (1848) had ~~already~~ distinguished it as the genus *Leymus*~~

Then it remains to mention ~~the~~ two ~~groups~~ taxa that both are represented on the

No or few hybrids between haplomes of annuals and perennials?
But possible ~~[illegible]~~ polyploids of wheat, and those with S or N of the perennials?
Also between barley and Leymus and Elymus; or Critesion?, where one haplome is the same in both.
Leymus x Elytrigia, Elytrigia x Triticum,

Karyotype: method invented by Levitsky, little used and much misunderstood by those who have accepted it as an additional morphological ground, not based on the integration ... [illegible]

If we at this stage summarize the results from the karyotype and genome analysis as far as their effects — the ~~taxonomy~~ conformed taxonomy of the wheatgrasses are concerned, the first assertion must be that they clearly ~~confirm the~~ contradict the still widely accepted morphologically based classification of this variation into wide genera as was advocated by Bentham and Hackel almost a century ago, since these assemblages are genetically and karyologically so variable that they could not have evolved from a single original type by only linear branching! the classical definition of a good biological genus. At the same time, however, these assertions must ~~be~~ be interpreted as contradictory to some of the splitting made by Nevski, and as an evidence of that ~~[illegible]~~ even some of the genera he accepted still remained much too inclusive. Let us look at the "individual" cases systematically and begin with the youngest group and most restricted in distribution, the annual genera of the Triticeae:

1)

Haplomes — basic.

Soon after the discovery of chromosomes and their numbers it became evident to those who worked with them, that they are of utmost significance for evolution and thus taxonomy and plant breeding. Still, after almost a century, there are ~~[illegible]~~ cytologists, who know next to nothing in taxonomy, who gabble about... and taxonomists, and other floristic botanists.

Haplome not constant more than other biological phenomena...

There are those who expect to be able to find the exact haplome that went into the making of macaroni wheat 10.000 wheat generations ago, and seem to be astonished that it is not found in the material they collect by chance in one locality in the Near East. Although chromosomes and haplomes are among the most constant objects on earth, they change at least slightly, ~~this~~ although the haplomes of wheat have clearly changed so little, that they remain essentially identical in all the tetraploid and hexaploid taxa of wheat, they nevertheless are not exactly identical.

1) Huxley.

x) Heidelberg. Jena

~~[illegible]~~ Name adjustments and changes are unavoidable because we do not have the absolute truth on which to define the categories and because ~~[illegible]~~ our concepts of the categories unavoidably change with increased knowledge. Although we at least try ~~to avoid radical replacements~~ ~~[illegible]~~ to counteract drastic name changes by aid of the Code so that correct names never fade away though they may shift from a comprehensive taxon to a more distinct one whenever the former has to be split.

[illegible] [illegible] [illegible] [illegible]
Haplome [illegible]
[illegible], [illegible], [illegible]   [illegible], [illegible]

Origin.

The origin of the Triticeae tribe remains unknown, and no ~~of~~ paleobotanical remains have so far been discovered, not even pollen grains. Through comparative studies of the morphology of the diploids, however, it is possible to postulate that the earliest members of the tribe were plants with the following characteristics: 1) diploid ~~[illegible]~~ (autogamous?) with large fusiform chromosomes with at least predominantly median centromeres; 2) allogamous; 3) the spike with three spikelets at each node; 4) more than two florets in each spikelet; 5) endosperm with single starch grains; 6) distributed in ~~[illegible]~~ S.W. & Asiatic mountains. Therefore, it seems reasonable to assume, that this plant may have been similar to ~~[illegible]~~ some of the species of Pseudoroegneria (Psathyrostachys). ~~[illegible]~~ Since the distribution of the ~~[illegible]~~ advanced Elymus species, which is characterized by tetra-hexa- and octoploidy, shows that it must have been formed before the ~~Atlant~~ North Atlantic was formed ~~before~~ the middle Tertiary, it is reasonable to suggest that the first diploids ~~[illegible]~~ evolved in the early Tertiary or ~~[illegible]~~ late Cretaceous. From this earliest haplome evolved the other genomic haplomes, ~~[illegible]~~ most likely the E and N that are ~~[illegible]~~ closer related than others and have a connection with S on one side and U and C? on the other.

Leymus x Secale: Östergren 1959 (Wa[illegible])
L. x
A. junceiforme x [illegible] (–).
– x rigens
Leymus x A. junceiforme
Se

Compensatory – qualitative changes: X + 10X.

Terminology.

It is convenient to base the study of relationships of taxa on the characteristics of meiosis in hybrids combined to the concept of the genome, an approach that has been especially successful in investigations of wheats & their relatives, first carried out by Kihara ( ) & his associates. That method, termed genome-analysis by Kihara (1930), is based on the observation, first made by Rosenberg (1909) on Drosera, that in triploid hybrids (3x) between a tetraploid (4x) & one of its putative diploid parents, (2x), the chromosomes at meiosis roughly produce 2x bivalents & x univalents, presumably because homologous chromosomes pair, leaving unpaired the chromosomes of the set lacking partners.

Cytological & Taxonomic: Rose

Cytological & Taxonomic: Tritic

B:

$S_e H_e$ — $2n = 28$, $n = 14$

$S_k H_k H_k$ — $2n = 42$, $n = 21$

F_1 $2n = 35$

$S_e S_k \to 7_{II}$

$H_e H_k \to 7_{II}$ ~~…~~ ; 7_{III} ($H_e H_k H_k$) at [illegible].

maximum $_{II} \to 14_{II} + 7_{I} = 35$, no ~~…~~ autosyndesis; max. with: $20_{II} + 1_{I}$

$7_{III} + 7_{II} = 35$

$4_{III} + 11_{II} + 1_{I} = 35$

21, 12, 9 = 4+1; 23, 12, 35

agelaeus = gregalis, = gregarius → belonging to a flock or herd

flock = grex, gen. gregis (L.)

herd = agele (Gr.), nomeuma

armentum, grex, pecus, -coris, -pecus (cattle) L.

homocorous = same art, same genome (2 …) — core: a body of people, company, group of … shift.) Oxf. dict.

~~homoeocorous~~ = same genus, … , [illegible] adj. [illegible].

heterocorous = olika genom, olika; släktens … .

homologous = same, kromosompar.

homoeologous = likartade, ej samma ursprung.

heterologous = olika.

[När 5 (eller fler) kromosomer är homoeologa, då blir hybriden och karyotypen heterocorous? / heterogenome?

Homoeology.

Reduced pairing due to some homoeology, as documented by an increased number of rod-bivalents and decreased number of interstitial chiasmata.

gräns : hybrid : urskilja-, skilja-åt. (distinguish; separate, distinguish from each other, differentiate, discriminate between) (bestämma = determine)

Canon analysis — interpretation of structure — d.

& his co-workers studying the evolution of wheats & their relatives, & later applied to studies of other wheat grasses & their relationships by various workers, notably Stebbins & his students & associates ( ), Anderson ( ), Hansen & Runemark ..... Dewey ... Dvořák ...

~~Flat method~~ Flat method is based on the observation, first made by Rosenberg (1909)

In cases of large genera, it may be so convenient with whole to recognize some morphologically distinct sections, some of which have been regarded as distinct genera in the past, though such a division is more convenient than biologically justifiable as long as available cytogenetical results may seem to be an insecure basis for such a division, but these sections are geographically distinct.

Sensu!

by keen taxonomists in the past, though less critical authors of manuals have preferred to ignore them and instead perpetuate the confusion, and so most need only to be revived and defined strictly on basis of their correct typification. Thus, the ~~[illegible]~~ generic genera ~~commonly united [illegible] under the collective names~~ ~~Elymus, Agropyron, Elymus and Hordeum, Triticum~~

X) t. p. 29.

The second most important category is that of species, which is biologically defined by its reproductive isolation and morphological distinctness (e.g. Mayr 1942, Löve & Löve 1942), but only occasionally is it found to be necessary to recognize as its intraspecific subdivisions the subspecies, which is equivalent to a major geographical race, and the variety, which designates a minor geographical race (e.g. Hultén 1962, 1968, ~~Hylander [illegible]~~, Löve & Löve & Kapoor 1971), whereas more local populations are grouped as demes or ecotypes, without a formal Latin name.

~~Thus, the single-haplome genera of the perennial wheatgrasses subtribe are Critesion (haplome H), typified by C. jubatum (L.) Nevski,~~

Thus, the single haplome genera of the subtribe Elymiinae are
Critesion Rafin. (haplome H), typified by C. jubatum (L.) Nevski,
Taeniatherum Nevski (haplome T), typified by T. caput-medusae (L.) Nevski,
Psathyrostachys Nevski (haplome J), typified by P. lanuginosa (Trin.) Nevski,
Agropyron Gaertn. (haplome P), typified by A. cristatum (L.) Gaertn. P. Beauv.
Lophopyrum Löve (haplome E), typified by Lophopyrum elongatum (Host) Löve,
Thinopyrum Löve (haplome N), typified by T. junceum (L.) Löve,
Festucopsis ((C.E. Hubbard) Melderis (haplome G), typified by F. serpentinii ((C.E. Hubbard) Melderis
Pseudoroegneria (Nevski) Löve, (haplome S), typified by P. strigosa (M. Bieb.) Löve.
Whereas the perennial ~~polyploid~~ genera formed by allopolyploidy from some of the haplomes are:
Hordelymus (Jessen) Harz (genome HT?), typified by H. europaeus (L.) Harz.
Leymus Hochst. (genome JN), typified by Leymus arenarius (L.) Hochst.,
Elytrigia Desv. (genome ENS, ENSS and ENNS), typified by Elytrigia repens (L.) Nevski,
Elymus L. (genome HS, HHS and HSS), typified by E. sibiricus L.,
Pascopyrum Löve, (genome HJNS), typified by P. smithii (Rydberg) Löve, and one Australian and two Siberian groups the genomic constitution of which remain insufficiently known. The single haplome genera are Eurasiatic steppe or coastal

c.

Studies on polyploids and their diploid relatives led to the ~~coining~~ concept of the ~~term~~ genome (Winkler 1920) ~~to designate~~ for the sum total of the genes in which each allele occurs only once, or, in cytological ~~manner~~ terms, the haploid chromosome complement and the sum total of its genes, irrespective of polyploidy. ~~From this At that time several studies, followed At that time, several studies, by hybrids between polyploids and The concept of the genome~~ It had become increasingly evident since the studies by Rosenberg (1909) on Drosera ~~hybrids~~, ~~that~~ in hybrids ~~between a polyploid and one of its~~ ~~This led to a new interest in~~ Morphological: Hurst, Anderson, ~~cytogenetic...~~. ~~It was evident that a genome of a polyploid must be somewhat ... Rosenberg (1909) Morphological studies of various hybrids between various levels of polyploids had at that time~~

Anderson

This concept soon ~~caused~~ resulted in renewed efforts in the study of ~~polyploid~~ polyploids through hybridization ~~with~~ to their putative diploid ancestors, ~~which was at an impasse at that time, and~~ ~~these~~ leading to ~~two~~ three new methods of study. The first ~~was~~ combined ~~taxonomic~~ morphological and taxonomical observations with cytological studies and resulted in that Hurst (1925), studying the genus Rosa, demonstrated that there are five different ~~diploid~~ groups of diploid species in this genus, which, in addition to their cytological ~~characteristics~~ peculiarities when hybridized, are each ~~characterized~~ set apart by ~~definite~~ definite traits ~~combinations~~ of morphological characteristics. ~~By aid of detailed studies of extensive material,~~ Hurst (l.c.)]

One of these is purely comparative and morphological and led to the observation by Hurst (1925) that the genus Rosa is composed of five ~~diploid diploid~~ species ~~...~~ with ~~...~~ seven haploid chromosomes, ~~termed~~ called septets, each set apart by definite morphological traits, and various ~~...~~ ~~polyploid~~ combinations of the septets and their characteristics into a series of alloploid genomes. The comparative method for hybrid studies was later ~~...~~ developed in considerable detail for studies on introgressive hybridization by Anderson (19...) and then applied for identification of one of the basic haplomes of ~~...~~ polyploid wheats by Sarkar & Stebbins (1956?). ~~The other method is cytological and ...~~ ~~...~~ The second method is cytological and morphological and involves detailed studies of the ~~...~~ karyotype of the species of a genus; it was worked out by ~~...~~ Levitsky (19) and his school and led, among others, to the identification of the karyotypes that characterize the various haplomes and polyploid genomes of the collective genus Aegilops, by Chennaveeraiah (1960?). The third and most successful approach is that ~~of ...~~ termed genome-analysis by Kihara (   )

Pairing between homologous or homoeologous chromosomes in diploid hybrids is said to be autosyndetic if chromosomes from the same gamete or parent are involved, but allosyndetic if they derive from different gametes or parents (Ljungdahl 1922, 1923?). The same terms are frequently used in a wider sense for pairing in polyploids, autosyndesis then meaning pairing between the chromosomes that derive from one of the parents only, or between homocore chromosome sets in polyploids above the tetraploid level, and allosyndesis denoting pairing between chromosomes deriving from two or more parents or belonging to heterochore haplomes. On basis of this kind of consideration, Kihara & Ono (1926) distinguished two kinds of polyploids, autopolyploids when essentially the same haplome has been multiplied permitting the formation of multivalent chromosome associations through autosyndesis at meiosis, and allopolyploids, when the taxon has been produced by duplication of the chromosomes of a hybrid of two or more heterocore haplomes; these terms were abbreviated to autoploids and alloploids by Clausen, Keck & Hiesey (1945). When in complex polyploids the alloploid taxon has derived from different numbers of haplomes of each kind, e.g. from a diploid AA and a tetraploid DDDD, or when it has been produced by an autoploid duplication of a single alloploid, e.g. AABD becomes AAAADDDD, the term autoalloploid is used (Kostoff 1939). Stebbins (1947, 1950) recommended that the alloploids be divided into two groups, segmental alloploids and true alloploids, the former being defined as containing two pairs of haplomes which have in common a considerable number of homologous chromosomal segments or even whole chromosomes, but differ from each other in respect to a sufficiently large number of genes or chromosome segments, so that the different haplomes produce sterility when present together at the diploid level. Kihara (1951) rejected this terminology and proposed instead the terms isosyndetical and iso-anisosyndetical alloploids, whereas Löve & Löve (1949) divided the autoploids into panautoploids or strict autoploids the chromosome sets of which are completely homologous, hemiautoploids which are formed from hybrids between populations some chromosomes of which are homoeologous, hemialloploids which are produced from partially hybrids between homoeocore haplomes, and pseudalloploids which derive from completely sterile hybrids between heterocore haplomes

The genetic system of the diploid Triticeae
(G. Nevski (1933).

Terminology.

It is a basic fact of cytology that a diploid chromosome complement is made up of two monoploid sets two monoploid sets of a certain basic no. of chromosomes each pair of which form bivalents at meiosis so its chromosomes are said to be homologous, whereas the other, heterologous chromosomes of heterologous pairs do not. Diploid species of the same genus tend to have similar but somewhat pairs that one or more of which differ somewhat in their linear arrangement so their pairing is deficient or lacking. That is usually caused by changes termed segmental interchange, viz inversion, duplication, deficiency or plainly by small or diffuse molecular alterations that occur that involve only the same chromosome pair, or segmental interchanges that involve a chromosome pair or two different chromosome pairs. The result is new chromosomes that are said to be homoeologous (similar) to the pair from which they originated. When successive changes have altered a set so that all or at least most of its chromosomes have become homoeologous or heterologous so their pairing is reduced, or heterologous so they are no longer able to pair when hybridized, the chromosome complement is said to have become homoeochore (homoeo, similar, chore, (group). Homoeochore chromosome complements characterize species of the same genus, which because of reduced mutability whereas the complement of a species of its interfertile congeners is said to be homoeochore, when further differentiation has taken place, so that the entire chromosome complement most of the chromosomes or the entire chromosome complement has become differentiated beyond the possibilities of meiotic pairing, it is said to be heterochore, & likely represents related but distinct genera (the species with reduced cytological stability in that rarely cross in nature or never cross in nature though they may occasionally be artificially crossed to form an offspring the chromosomes of which never pair or pair only slightly at meiosis. Reproductive Efficiency, Reproductive barriers (are also formed by numerical differences caused by aneuploidy or heteroploidy between homoeochore of the same homoeochore set or of homoeochore complements). Such monoploid (chromosome sets are also called haplomes (Hamilton 2 Hermig...).

A proposal to solve the problem by aid of ~~the results available~~ ~~this~~ genus-analysis was made by MacKay ( ) in connection with studies of ~~the~~ the wheats & their relatives, though . . .

[illegible]

11a.

~~Generic analysis~~

It is evident from the many attempts at a new generic classification of the wheatgrasses, especially those that have traditionally been grouped as the collective genera *Agropyron* and *Elymus*, that taxonomists generally agree that these complexes are unnatural and highly heterogeneous and therefore not expedient and frequently even impractical and misleading for evolutionists and practical agronomists alike, irrespective of the nomenclatural legitimacy of the generic names accepted.

~~Some botanists, who perhaps have believed in taxonomy as an art rather than as an important scientific discipline, have concluded that the best~~ ~~Recent proposals include the extreme idea of the prolific floristical botanist and physician Krause, who in 1899 drew the conclusion from the observed natural hybrids of the wheatgrasses, that the most logical solution of their taxonomy would be to lump them into a single genus, which he named Frumentum without validation; this idea has more recently been repeated by Stebbins, who with his associates has contributed significantly to the analysis of the genomes of the cereal taxa; besides of~~

These attempts reach all the scale from the extreme lumping of all the species of the tribe into a single genus, because of the apparent crossibility, as advocated by Krause (1898) and recently revived by Stebbins and his associates ( ), to the extreme splitting of the cereal taxa into small genera sometimes distinguished by aid of doubtfully selected characters, as proposed by Nevski (1933?). In between these extremes have been various proposals by Melderis (1950-1953? . . . .), Bor ( ), Runemark? & Heneen (1968?), Tzvelev (1973?, 1976) and others, who have accepted some morphologically and genetically heterogeneous genera for certain groups but left untouched the critical heterogeneity of others.

~~As pointed out most recently by Dewey (1980?), the results of the generic analysis have at last~~

Symptomatic complete weakening or set out of function through hybridization, so no pairing starts; gradually other relationships ... [illegible] ...

Elymus x Leymus: natural hybrids in Greenland - Iceland?, implied by Pascopyrum.

Autosyndesis: 42 x 14

---

s. 24 redraft:

Numerous ~~empty~~ empty or ~~slightly filled~~ only slightly filled seeds were obtained. Of the latter, four germinated in a Knops solution and gave rise to plants which formed rosettes during the three years when they were kept, but only one formed a weak and small culm during the third summer. The spikelets were ~~[illegible]~~ empty except a few ~~[illegible]~~ middle ones that formed small anthers which did not dehisce. In the few pollen mother cells that could be analysed only univalents were observed.

s. 25 - : Set in:

A. ~~[illegible]~~ ~~[illegible]~~ [illegible] x Elytrigia repens, Leymus ~~[illegible]~~ Thinopyrum ~~[illegible]~~ [illegible] [illegible], Pseudoroegneria, Critesion.

(above "Elytrigia": Leymus combinations)

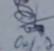
Although minor chromosomal changes are frequently discovered in the laboratory, especially in studies of allogamous and thus heterozygous organisms, these are not the results of recent rearrangements but rather accumulation of survival through the millions of ~~harmless aberrations~~ genetically and evolutionarily harmless aberrations. More important changes are extremely rare, as can be seen by the fact that on an average less than one species of higher plants has been created per century since the emergence of the angiosperms more than 180 million years ago (as [illegible] by the number of species past and present). The chromosomes are among the most conservative phenomena known, and the hybrids are considerably more so, so that most of the species presently known have been there when mountain ~~[illegible]~~ chains rose and eroded away. Nevertheless, they change, though within very narrow limits as documented by the distribution, limited or wide, of the species themselves.

(Hemsleyeae)

The distinction of the hybrids (of each genus group) is so straight, that their hybrids have never been observed in nature though such combinations can, with difficulty, be made experimentally. Their occurrence, single?, in the past is implied by their allopolyploids. A hybrid can, however, hybridize, even in nature, with ~~genome~~ an allopolyploid genome of which it is a part, & polyploids can hybridize even when none of the hybrids are the same of Elaeagnus × Elaeagnus in Graebn.

Hemsleyeae genus, generally accepted, first proposed by Mackay?

homoeo = homoios = like



homoeo - stem
haemo = haemo- = ~~[illegible]~~ = blood — hemi = half. logos = ratio (of homologue in Oxf. Dict.)

hetero = other, different

homo = same

homologous haplomes — same: i.e. a tetraploid genome that is autoploid, or haplomes of related taxa that have not become homeologous, and only a little morphologically different. — i.e. cytologically identical as to pairing, with normal Mendelian genetical variation

homeologous haplomes — like: i.e. ~~homologous or essentially the [illegible]~~ ~~essentially the same~~ inter- and intrachromosomal changes ~~making~~ of one chromosome impairing pairing; i.e. in closely related species, usually only 1–4 pairs involved, the other unchanged. Species not still related

heterologous haplomes — unlike; i.e. all chromosomes so rearranged as to reduce pairing to a minimum, though the essential genetical complement ~~[illegible]~~ remains similar and crossability has not ceased. Genera

genome

septet — haplome A monoploid or basic chromosome set and its genetical complement was named a septet by Hurst (192..) studying roses, ~~[illegible] a haplome by but we find~~ ~~[illegible]~~ which are characterized by seven chromosomes, but we find it more appropriate to use the ~~[illegible]~~ neutral term haplome proposed by Hailbronn & Ulonnig (1961, 1966) in ~~[illegible]~~ their review Principia Genetica. ~~[illegible]~~ It is ~~[illegible]~~ equivalent to Wahl's (19..) term genome only in diploids, although it also covers the [illegible] components of polyploid genomes.

The results from the hybridization experiments indicate that all the present variation within the tribe ~~originates~~ has evolved from a single taxon with the diploid chromosome number 2n=14. This original haplome or chromosome complement has differentiated and varied by aid of various chromosomal rearrangements ~~to form~~ ~~to form~~ through various stages of homeological ~~[illegible]~~ complements to haplomes that are designated heterologous ~~[illegible]~~ because their chromosomes have differentiated beyond pairing possibilities, though they still are made up of essentially the same genes, and still have not become completely incompatible [illegible]... 24? such heterologous ~~[illegible]~~ diploid sets have been identified or are implied, and have been given identifying letters. Subsequent evolution of ~~each~~ ~~[illegible]~~ some of the haplomes has resulted in a few or many homoeological series of ~~[illegible]~~ ~~[illegible]~~ haplomes ~~the~~ some of the chromosomes of which still are able to pair; these series, ~~which~~ between the members of which there is a more or less strong reproductive barrier because of reduced pairing, are identified by aid of superscripts of each haplome letter.

Species within each haplome group are formed either by consecutive differentiation or homeology, or ~~only~~ autoploidy. ~~[illegible]~~ New basic genomes ~~[illegible]~~ are formed by alloploidy, which then is followed by further homeologous differentiation. Examples of the first: ~~the~~ Critesion.... the second Nivirin with two species, third Gigachilon, ~~[illegible]~~ Triticum and Elymus.

I should have said at once that although I enjoy the bibliography itself, your excellent preface about What is a visionary? pleased me no less, not only because it is so well written but also since it is so true in every detail. There you, perhaps unwittingly, make another observation that shows how Icelandic he remained, when you tell about the books he gave you: that is the secret of the great amounts of books published in Iceland, because they replace the valueless flowers and expensive jewelry preferred as gifts by those who do not appreciate culture.

I hope this reaches you. My Hanover friend did not know your exact address, but I found it in Who's Who of American Women, in which I also see that you have not been able to avoid continuing your own cultural activities. And I am sure you enjoy Washington, though you probably also miss the quiet of Hanover. We did not visit you the last few years of Vilhjálmur's life because the usual aversion against those who dare to differ forced us to leave Montreal when the French became more belligerent. Then we went to Colorado, unaware of the bigotry of the conservatives in the prairies that after a dozen years forced us, in a way I thought was the speciality of Hitlerland and the Communists, who also were supported by that all your socalled friends turn chicken and swallow their whistles, to go further west, where our older daughter lived and our younger daughter intended to live, [as we of little fighting as Vilhjálmur was in a fight it was wise to withdraw.] and enjoy the California climate, though our conditions may not be those we expected in "the land of the free" when we first made the same mistake as most immigrants. But that is another story which may be told in my biography, in Icelandic, who knows?

I see that you were lucky to marry another great scientist, who understands cultivated thinking but also more economy than we Icelanders seem to do, as I understand from that you have together formed a foundation for securing future works. Perhaps we ought to do the same — but we know nothing about how that is done and nobody who has done it — though we continue to work on a basis of a library smaller than that of Vilhjálmur but still one of the best in our field.

Evelyn Stefansson Nef.
2726 N. St. ~~Washington~~ NW, Washington DC. 20007.

Dear E.

A good friend in Hanover showed me the thoughtfulness to send me a copy of the chronological bibliography of Villhjálmur's works, and excused himself for not having done this at once when it was published two years ago. ~~I have enjoyed this so much that it [illegible] the [illegible]~~ He needed no excuse, since I have rarely enjoyed so much a bibliography of any of my friends, but Villhjálmur was also such a special man, who grows in the memory of those who knew him and ~~[illegible]~~ also in the minds of those who were too young to know him, as do all those great men who dare to express ~~controversial~~ ideas that their contemporaries regard as controversary because they did not see them first, ~~[illegible]~~ and then live forever. Villhjálmur was the greatest Icelandic scientist of all times, and you gave him the complete all happiness that helped him immensely in his achievements. I ~~[illegible]~~ remember that he was proud of his fellowship in the Explorers Club.

I hope you still remember me as the Icelander, then in Montreal, who visited you sometimes at Hanover, ~~[illegible]~~ with my Swedish wife, who then conversed with you when I listened to Villhjálmur [who wanted me to call him Villi, the name of his childhood, and called me Halli, my old nickname ~~[illegible]~~ (Icelanders together of course)]. These were bright points in our emigrant lives, and we were sorry when he passed away and we lost the contact with you. Especially when I now observed that he had completed his biography that he then said he was working on; I have been trying to locate a copy in the libraries here, but still in vain. He left some of his great books as a gift when he visited us in Montreal, and it would have pleased him to know that not only we both but also our daughters and sons-in-law enjoyed them, and that now they have all been read, no, devoured, by our three granddaughters, who have become highly interested in stories of explorations and of the biographies of great men found in our library.

[Margin insertion: I am also proud of that, ~~[illegible]~~, I was the second and only other Icelander who has been fellow of the Explorers Club, which he had told me about with pride long ago.]

One of my nephews in Reykjavík, ~~[illegible]~~ a young librarian at the University Library, which once lacked some wise man and funds to get you to send Villhjálmur's library to there, where it would have been inexhaustibly useful, has been ~~[illegible]~~ pushing me to compose my own bibliography so that he or others would later be saved the efforts all ~~[illegible]~~ surviving bibliographers always have to spend when they try to make such compilations after the fact. ~~I decided to try to follow Mattila's scheme, [illegible]~~ This I am trying to do, following Mattila's scheme. You ~~[illegible]~~ will be astonished to hear, that also my creative works began with Icelandic poetry as did Villhjálmur's — it probably has been typical for many who were educated in Icelandic tradition, on either side of the Atlantic.

Parodi, L.R. 1940: Estudio crítico de las gramíneas Austral-Americanas del genero Agropyron. — Rev. Mus. La Plata, N.S. 3, Secc. Bot.: 1-63.

(~~[illegible]~~) [illegible] Hole

Hystrix, [illegible] Cockaynea [illegible] Roegneria [illegible] (cf. [illegible])

Krause, E.H.L. 1898: Floristische Notizen. II. Gräser. Bot. Centralbl. 73: 337-343. ([illegible])

Hyg[illegible] — Hamber

Among the grasses of New Zealand with boreal relationships are two groups, belonging to the tribe Triticeae, which for a long period have been classified in the genera Agropyron and Asprella, ~~respectively~~ (or in the genera Anthosachne and Cockaynea.) ~~The former group was investigated. Both groups have been. The former group was revised by Connor (1954), who concluded that it comprised four species~~ In the last treatment of the latter group, Zotov (1943) concluded that the latter group would be most correctly accommodated in the ~~austral~~ genus Cockaynea comprising two species from New Zealand and one from Tierra del Fuego, whereas Connor (1954) placed the ~~other~~ former complex ~~[illegible]~~ as four species of the then very collective genus Agropyron, ~~[illegible]~~ with the remark that two of the species could belong to the genus Anthosachne, as suggested by Nevski (1934), whereas according to his opinion the two others might fall into the genus Roegneria as adopted by Nevski (1934)?. ~~[illegible]~~ Connor (1956, 1962a, b) made considerable hybridization experiments between the New Zealand populations of his Agropyron, whereas Hair, Beuzenberg and Pearson (1967) reported the chromosome numbers of the four New Zealand species of Agropyron ~~[illegible]~~ and the two species of Cockaynea. ~~[illegible]~~ Nevski (1934) and Connor (1954) ~~[illegible]~~ touched upon the relationship of these taxa ~~to~~ with species from Australia and elsewhere, but no reports have so far been made on hybridization comparisons between the New Zealand taxa and related species from Australia or elsewhere, nor on hybridization experiments or karyological comparisons between any representatives of the austral and boreal groups of perennial wheatgrasses.

When Connor visited Löve in Montreal in 1958, considerable time was spent on discussions of the austral wheatgrass problem, since at that time Löve ~~had considerable studies~~ and his associates were involved in ~~had going considerable~~ studies of the cytotaxonomy ~~boreal variations~~ of the ~~perennial~~ wheatgrasses. During these discussions ~~it was concluded that~~ it was agreed that before revisions could be made of the taxonomy of the austral populations, experimental hybridization ~~followed by cytogenetical studies~~ of these and boreal taxa was needed, followed by cytogenetical and other biological investigations. ~~[illegible]~~ Therefore, seed samples of the New Zealand populations were sent to Montreal by Connor and Hair so that Löve could include these taxa in his hybridization experiments and study their relationships to ~~[illegible]~~ other wheatgrasses for a more ~~[illegible]~~ exact classification. This paper may be regarded as a result of these studies, though it is also an outgrowth of a general ~~[illegible]~~ cytogenetically founded revision of the wheatgrasses of the world which is being worked out by the senior author.

The basic genome, or the same total of genes of the original chromosomes, has been reshuffled in various ways without any major gain or loss, whereas the reshuffling of chromosome parts within a set has, first, caused speciation, and second, resulted in genic differentiation followed by further speciation. The genes, similar in all the species though their effects are somewhat varied by their progressive other effects, are the cause of the morphological & physiological variability, whereas the actual evolution is caused by chromosome reshuffling & polyploidy.

MacKey (Moscow) has advocated to designate the genes by three-pointed genomes, so that those with A will be written — that would lead to confusion, because at least the D genome also occurs in more than one species, & also O etc. Actually only two logical solutions, either to include all the taxa as a single genus, perhaps subdivided into subgenera & sections on genic lines, or to designate [illegible] Both solutions are extremely correct, but depending upon points of view, but any intermediate solutions must be regarded as illogical & evolutionarily fallacious & misleading, for various reasons (which?), as shown, e.g., in the description of Elymus by Gould (1942?).

Essentially the same genes & genomes variously activated through chromosomal rearrangements

Same genomes with modified haploses, gradually from within species, to represent the isolation of species & necessary to absolute crossability barriers of genera.

A genus is designated as a group of species that have evolved from the same ancestral species by linear branching. Similar designation for a tribe.

As in all cases of taxonomy, the dendrogram proposed should be considered only as a step towards solving the problem a solution that can't be considered to must inevitably remain tentative at least so long as all the taxa have not been sufficiently investigated or as a hypothesis that may serve as a point of departure for further discussion & elucidation.
(Lubimenko — Aleksandrov)

Three taxonomically and evolutionarily acceptable possibilities:

1) All a single large genus — not practical

2) Reduce number to as many genera as are Nevski's etc. subtribes — ~~[illegible]~~ — not easy since the subtribes are not well enough defined.

3) The generic system — most logical and most practical in the long run.

Status quo unacceptable, be it that of Bentham still used in America, ~~[illegible]~~ that of Hylander ~~[illegible]~~ in the Scandinavian floras, Rothmaler in the German flora, Melderis in Flora Europaea, or Nevski as modified by Tzvelev in the Soviet flora.

Dig[illegible] to phylogeny

Although Tzvelev (l.c.) lists uncritically chromosome numbers for many species so studied in his flora, he explicitly ignores their message. His taxonomy, therefore, is thoroughly phenetic rather than phylogenetic, but nevertheless it is the most perfect classification available for the wheatgrasses.

Although the morphological method is, for various reasons, severely limited as an approach to phylogenetic classification, it long was the only method available and many of its ~~results~~ ~~remain classical~~ conclusions have stood the tooth of time.

Sarkar 1955, 1956, 1958; 1957?
Fravisky 1935 (Secale [illegible] x Agropyron [illegible])
Myers & Hill 1940,
Peto 1930
Simonet 1935, a, b,
Stebbins & Pun 1953: V. — Stebbins & Singh 1950, + Snyder 1955, + Vaarama 1954, + Valencia & Valencia 1946, + Walters 1943.
Cauderon 1956, 1954?, 1962a, b,
Hunziker 1954, 1966a, b, 1953, 1965, 1955
Hunziker & Covas 1955,
Hunziker & Mauromicale 1964, 1963,
Hunziker, Naranjo & Zeiger 1973
Heneen & Runemark 1972, 1962,
Heneen 1963a, b, c, 1962,
? Runemark & Heneen 1968
Cauderon 1958, 1966,
Evans 1962,
Matsumura & Sakamoto 1956,
Schulz-Schaeffer & Jurasits 1963,
Cauderon & Saigne 1961,
Godley 1947, 1951?
Östergren 1940a, b,
Simonet & Guinochet 1938,
Dewey 1961 —
Knowles 1955,
Rajhathy, Morrison & Symko 1964
Sakamoto 1965 etc. — 1973, + 1974, 1972, & & Muramatsu 1965
Schooler 1966
Shiotani 1968
Boyle & Holmgren 1955
Chmelovich & Sehm 1959 (W/S)
Morrison & Rajhathy 1959 (III).

Clinton,
Sears etc.

phenetic – [illegible]
[illegible]

Introduction.

It has been claimed, with considerable reason, that classification or taxonomy of living beings is as old as ~~human thought~~ reacting ~~organisms~~ creatures, since even the lowest of organisms respond differently to a varied environment and effectively order their own world. It is reasonable to expect that such an ancient and universal activity, vital to the most primitive human tribes and scientists alike, should have developed into a precise and undisputed technique. ~~It is, therefore, surprising that it still is not uncommon~~ It is, therefore, surprising that despite a general agreement as to the categories represented by the biota of the earth, it is still not uncommon for different students of the same material to arrive at altogether different classifications at the generic & specific levels, and these may at times seem to be evaluated more by the reputation of their authors than on their approximation to reality. One of the reasons for this is probably the fact that even truly observational science has not yet reached more than a fraction of the biota of the world, so that empirical studies still predominate with their inevitable tendency towards authoritarianism.

It must necessarily be realized that the method of approach to any scientific problem is clearly of utmost importance and will to a large extent determine the kind of discovery made. Or, to put the matter the other way round, the method of approach is itself largely dictated by the type of answer one wants to obtain; it is, in fact, also a kind of a question. Furthermore, the question will alter with time and the progress of discovery, so that ~~we~~ when one method has yielded the main crop of answers that it could be expected to provide, then it is time to ask another kind of question by adopting new methods.

This is just what has happened in the field of plant taxonomy, where the original approach is inevitably descriptive, because botanists set out to describe as fully and accurately as possible the variety of plants and the phenomena which they exhibit. This approach is designed to answer the basic question about what are the facts; though it needs categories as do all kinds of studies, these are rather arbitrarily chosen and hardly need to be more closely defined.

The descriptive method is soon supplemented by the comparative. This is first focused around the question of grouping or classification because we need to know what pattern or system an assemblage of organisms has in common, and what distinct types there are at various levels of characterization. This leads to classification of organisms in an hierarchical system of categories which have to be more or less exactly defined, although some degree of arbitrariness cannot be avoided.

Implicit in such a system is the idea of physical relationship. With the acceptance of the fact of evolution, this implicit postulate becomes explicit, and the question posed by the comparative method becomes correspondingly modified, because behind common patterns we must reach for common origins. The result is a phylogenetic classification, or a grouping intended to express evolutionary descent and relationship. For this classification the definition and delimitation of at least the basic categories is extremely vital. So is also the selection of characters to be used, because in such a system, that also must be basic for ~~intentional breeding of pl~~ various utilization of the plants for human purposes, it is essential that only truly genetically directed traits be selected, ~~and not~~ not those that are mainly phenotypical and thus determined by environmental influences as were many characters accepted by taxonomists of past centuries.

The comparative method connected with the theory of evolution soon requires still a new procedure, an approach which is best termed differential analysis. This seeks to clarify the question about the cause of ~~differences~~ variation between the members of a related group and also between the related groups themselves. This, in fact, is the modern method of cytogenetics, making analyses of the hybridization and studying the mechanism of cell division, and it forms one of the main pillars of what we term biosystematics or cytotaxonomy. It is firmly associated with studies of the [illegible] pattern of each group [illegible] and the history of evolutionary divergence and its causes. It is evident that this treatment requires exact definition of all its categories, since it sees in them important evolutionary steps that are repeated endlessly by all kinds of organisms. It is from this approach that we have been able to conclude that there are ~~four~~ certain essential and independent processes that shape variation within each gene pool or species, and others that isolate species and mold genera, tribes and families. ~~[illegible]~~ 2nd st.

Progressive as it is, taxonomy tends toward a greater exactness, as indicated by the sequence of the different methods mentioned. However, the extent of the material to be classified counteracts the use of the more advanced methods inasmuch as most ~~trop~~ plants are still ~~known~~ only known ~~from a few~~ to botanists from a few specimens. ~~from a foreign land.~~ Or, in other words, as long as the material available for taxonomical studies stretches over a complete range in a gentle gradient, from the empirical art of classifying a single specimen from a remote land to the exact ~~scienti~~ logical evaluation of data and measurements from most experiments with well-known plants, it is not possible and indeed ~~illogical~~ unreasonable to require the same exactness of all taxonomic work. Every approach is useful for its time, every study carries us closer to the truth. The only requirement that ought to be made is that whenever a more advanced stage of knowledge is reached for a plant this ought to replace a less exact classification based on less advanced methods. This is the single principle of progressive science and other procedures must be branded as reactionary and unscientific.

It has been said, that there are as many concepts of the basic categories of plant classification as that a distinct definition of each of these is not necessary. That is a truth with considerable modification, ~~although that~~ although it may fit for much of the application of the descriptive method when used for little known taxa. Although Linnaeus never directly defined his categories, it is implicit in his work that he was thinking of ~~categ~~ a certain degree of relationship & phylogeny at the levels beyond the genus, & such an idea has been increasingly basic to most taxonomical work by later generations. ~~But the reading the Comparative approach based on the theory of evolution is the old~~ But when the knowledge of a taxa has reached the level of the comparative method based on the theory of evolution, the distinct definitions of the basic categories become imperative. ~~Because~~ Therefore, ~~& cytotaxonomists~~ taxonomists applying the experimental methods as additional to morphology for the exact biological classification of thoroughly known taxa ~~might~~ may accept the family in its traditional sense as a collection of genera ~~[illegible]~~ to have evolved from a common ancestor, although frequently this cannot be proven by aid of safe cytogenetical indications. For the other categories, or the genus, species, subspecies & variety, however, ~~the~~ the biological concept ~~biological or evolutionary concept is (fairly) decisive. According to that concept, a taxa at the basic level is biological or evolutionary~~ biological or evolutionary modification of the Linnaean concept is modified in such a way that a taxa at these levels is defined biologically or cytogenetically but identified morphologically, primarily by aid of characters of flowers, fruits or flowering branches as advocated by Linnaeus (1736), since these attributes are less affected by phenetic influences than are ~~the~~ common vegetative characteristics. The biological approach supports that natural genera are separated by restrictions or barriers to crossability tending towards total incompatibility (Gustafsson 1975a Arthur Allen) Such clusters of related species should, as far as possible, demonstrate morphological, cytogenetical & other evidence of linear branching evolution within the group & therefore common phylogeny ~~& restricted reproductive isolation without~~ without reticulation to the earlier stages of relationship, as well as restricted crossability ~~& or other~~

with closely kindred groups at the same level and a complete barrier of miscibility towards more remotely related taxa of the same family. Genera so defined are usually identical to genera carefully described by critical classical botanists. They are characterized by a single basic chromosome number that may be secondary if more than one distinct morphotype is involved in the evolution of the taxon, when its origin derives from hybridization. Their chromosomes also are characterized by a similar chromosome morphology of all the species involved and by a definite phylogenic (chromosomal) and generic (genetic) relationship (cf. Löve and Löve 1975b). From the same point of view, a separate biological species is made up of a single genepool of individuals and groups that are completely miscible with each other, irrespective of the magnitude of morphological variation and distribution of its races, but it is reproductively isolated by aid of cytological attributes that prevent effective interbreeding with related taxa at the same level. Based on the same logic, subspecies and varieties are defined as interfertile major and minor geographical races which are capable of interbreeding freely wherever they meet, as clearly distinguished from the purely morphological and geographical definitions of those categories by earlier botanists (cf. Du Rietz 1930; Hultén 1968 [illegible]).

Progressive as it is, taxonomy tends toward a greater exactness, because genetical exactness is of an utmost importance not only for the purposes of breeding new plants for a hungry mankind and its animals but also because only evolutionarily strictly defined and homogeneous categories form a safe background for good geobotanical and other advanced studies related to the history and kinship of the plants concerned (cf. Rothmaler 1944, Löve & Löve 1954). However, the amplitude of the material to be classified counteracts the logical use of the more advanced concepts for most plants since many taxa are still only known to botanists from a few specimens, and next to nothing is known about their variation and biological characteristics. Or, in other words, as long as the material available for taxonomical studies stretches over a complete range in a gentle gradient, from the empirical art of classifying a single specimen from a remote land to the logical evaluation of extensive data and measurements of experiments with well-known plants, it is not possible and indeed preposterous to require the same exactness of all taxonomic work. Every approach is right for its time and stage of knowledge, every study carries us closer to the truth. The only requirement that ought to be made is that whenever a more advanced stage of knowledge is reached for a taxon this ought to require the replacement or adjustment of less exact qualifications based on less advanced methods. That is the single logical principle of progressive science, and other procedures must be branded as reactionary and unscientific.

3a

Although several small genera of plants have been extensively studied by aid of experiments, only a single group of genera or a tribe of over 200 species has actually reached the stage of knowledge making it available for proper evolutionary classification, despite the fact that all its taxa are not thoroughly known from these points of view. This taxon is the tribe Triticeae of the grasses, a group of genera that contains the world's most important annual cereals, wheats, barleys and rye, as well as many perennial forage grasses of temperate meadows and semidesert steppes. Because of this, botanists and agronomists alike have spent more efforts on studies of these plants than on all others since the dawn of agriculture and plant science. Therefore, these plants were reasonably well known already by Theophrastos and Plinius, and no other group had been as exactly defined and gained as many vernacular names in the languages of the lands where they grew wild or were cultivated before the scientific era commenced a few centuries ago. Nevertheless ---- 3b.

3.5.

It is inevitable that botanists have spent more efforts on understanding the plants on which human survival and progress ~~depend than on~~ depend than on the other lilies ~~of the field~~ roses of Sharon and the lily of the valleys, although much understanding of the useful is based on observation of the wild. ~~[illegible]~~ Therefore, from times immemorial more observations have been made on the socalled wheatgrasses, or the group of the essential cultivated grains ~~[illegible]~~ and their wild relatives, than on all other grasses together. These plants were reasonably exactly known already by Theophrastos and Plinius, and no other group had gained as many and exact vernacular names before the scientific era commenced ~~in the~~ a ~~few centuries ago~~. Nevertheless, when ~~Linnaeus (1753)~~ reviewed then available knowledge of these grasses and classified them into his mainly phenetically system, ~~he recognized only a few ill-defined genera with a limited number of species.~~ that was based on his believe in fixed genera of species which had evolved from an originally created prototype, ~~gradually~~ he recognized only a few genera often grouped with a limited number of species, most of which had been recognized by plain folks for centuries. Because his preoccupation with the ~~[illegible]~~ system, he ~~[illegible] did not recognize~~ [illegible] the relationship of his genus Aegilops and its three then known annual species with the other groups so he placed them far apart, but the three genera Elymus, with five perennial species, Secale, with four annual species, Hordeum, with seven annual and perennial species, and Triticum, with seven annual and perennial species, were all placed together, evidently as an appreciation of their relationship. Later botanists, ~~the~~ however, found it necessary to delimit ~~[illegible]~~ the Linnaean genera ~~more exactly~~ differently and and to shuffle his species between these and other genera on basis of a ~~[illegible]~~ similarly phenetic concept, although all these original genera still are regarded as valid, though more strictly defined.

~~It is evident that although Linnaeus (1753 and later) recognized relationships ~~ ~~[illegible] relationship between species of a genus, he based this category on the belief~~ The generic concept of Linnaeus was diffuse and so was that of ~~his successors~~ most of his successors. Nevertheless, with increased knowledge of these grasses and their relatives, botanists choose to add new genera and to shuffle the species between them in various ways, based on differently selected characters. An historical review of these nomenclatural manipulations (e.g. [illegible]...) would carry us too far from the purpose of this report, ~~[illegible]~~ but ~~they~~ although they were based exclusively on morphological explanations, they went into two opposite directions, ~~that~~ that reached their extremes in the lumping of ~~the Triticeae [illegible] of the presently known recognized 300-odd (east)~~

by Hitchcock & Chase (1951) of all the Triticeae in the Manual of the grasses of the United States into the genera *Agropyron*, *Triticum*, *Aegilops*, *Secale*, *Elymus*, *Sitanion*, *Hystrix*, and *Hordeum*, and in the splitting by Nevski (1934) of the same tribe in the Flora SSSR, ~~into the genera~~ into the genera *Brachypodium* and *Trachynia*, which later have been segregated in the unnatural tribe Brachypodieae, and the true Triticeae genera *Anthosachne*, *Roegneria*, *Agropyron*, *Eremopyrum*, *Haynaldia*, *Secale*, *Aegilops*, *Triticum*, *Heteranthelium*, *Clinelymus*, *Asperella*, *Elymus*, *Aneurolepidium*, *Malacurus*, *Psathyrostachys*, *Taeniatherum*, *Cuviera*, *Critesion*, and *Hordeum*. Intermediate between these treatments are the recent groupings of the tribe ~~in the genera~~ by Melderis, Tutin and others in the Flora Europaea into the genera *Festucopsis*, *Leymus*, *Elymus*, *Crithopsis*, *Taeniatherum*, *Psathyrostachys*, *Hordeum*, *Hordelymus*, *Secale*, *Dasypyrum*, *Aegilops*, *Triticum*, *Agropyron*, *Eremopyrum*, and by Tzvelev (1976) in his Soviet grasses into the genera *Elymus*, *Elytrigia*, *Agropyron*, *Eremopyrum*, *Heteranthelium*, *Amblyopyrum*, *Aegilops*, *Triticum*, *Dasypyrum*, *Secale*, *Hystrix*, *Leymus*, *Psathyrostachys*, *Hordeum*, *Hordelymus*, *Taeniatherum*, and *Henrardia*.

~~Both~~ These last treatments are basically morphological. Their phylogenetical significance is strengthened by consideration of anatomical investigations but weakened by the fact that although chromosome numbers ~~are mentioned~~, ~~their meaning~~ and also recent crossing experiments, their meaning is explicitly ignored or misunderstood. But they ~~are~~ both ~~the~~ represent the most perfect nomenclaturally classification available for the wheatgrasses.

Despite the fact that the (among the) two last-mentioned systems proposed for the Triticeae considered some observations of phylogenetic importance, neither system ~~the~~ is satisfactory from that point of view because several of the genera accepted remain ~~heterogeneous~~ artificial and heterogeneous, and thus do not reflect present genetical knowledge concerning the true relationships of the species involved. Classification based on such relationships is especially important for cultivated plants and their wild relatives because without a thorough recognition of the evolutionary status of each category, experiments to ~~improve and~~ produce new and useful combinations and to improve those already established by aid of planned hybridization are likely to fail. Therefore, time certainly is ripe for incorporating into the taxonomy of these grasses the results of numerous truly phylogenetic observations that have been performed in many lands since the discovery of the polyploid series among the cultivated wheats by Kihara (1919) and Sax (1922) and the observation of the relationships of polyploid wheats and certain ~~species~~ species of the weedy collective genus *Aegilops* by Kihara (1930) and several later authors.

L.B. Johnson [illegible]

5.

Methods for studying phylogeny.

Although several methods have been invented to gain insight in the phylogenetic history of plants in general, ~~of the wheatgrasses~~ only two have been extensively used for the wheatgrasses. The classical approach is a detailed ~~morphological~~ gross morphological comparison of the species concerned that later has [frequently] been enhanced [for establishing higher categories] with anatomical and histological ~~studies~~ observations. A variation of this method is the study of hybrids or allopolyploids with one known parent for which exact morphological measurements are tabulated and ~~my~~ extrapolated in order to reveal the possible characteristics of the unknown parent. That method was first used by Anderson (1949, 1953) in the study of hybrids of wild plants ~~[illegible]~~ and then successfully applied in the search of the B-genome of tetraploid wheat by Sarkar (~~1955~~) ~~[illegible]~~ and Stebbins (1956a, b). Serological or immunological and chemical variations of the ~~[illegible]~~ comparative method have been applied on some wheatgrasses with positive results, but since ~~they have never been extensively [illegible]~~ these observations have been limited to a genus or two, ~~they have~~ their significance for the classification of the tribe into genera and species ~~[illegible]~~ still remains negligible.

~~The first breakthrough in the studies of wheatgrass phylogeny~~
~~Hybridization experiments of some species of wheatgrasses~~
~~It has been long known~~

Natural hybrids between several ~~species~~ genera of annual and perennial wheatgrasses ~~and between them~~ have been known to botanists for centuries, and artificial ~~[illegible]~~ generic hybrids were ~~produced by~~ reported several times in the past century (e.g. Focke 1881). Sterile hybrids between common wheat and rye were observed by plant breeders in Europe late last century, and ~~[illegible]~~ fertile allopolyploid offspring from such hybrids was obtained only by German and Russian scientists (e.g. Müntzing). ~~The~~ ~~The observations~~ Although these preliminary observations on some crossability between the conventional genera were too incomplete for ~~any conclusions~~ any drastic conclusion as to their relationship, Krause (1898) used them as a basis for the extreme lumping of the Triticeae in the single genus Frumentum, a nomenclaturally illegitimate and taxonomically highly doubtful proposal which has been thoroughly ignored, although it has ~~been [illegible]~~ perhaps been favorably received by some botanists (e.g. Stebbins 1956).

A real breakthrough in the study of wheatgrass phylogeny came with the combined studies of polyploidy and artificial hybridization that were commenced by Kihara (1919, 1921) and Sax (1921) and led to

the discovery that cultivated wheats represent a polyploid series ~~of~~ [meiotic studies in hybrids] ~~are diploid~~ from the diploid to the hexaploid stage, ~~and that the two polyploids are alloploids.~~ Soon it was shown, by [illegible] mainly by Kihara (1924), that the two non-diploid species were alloploids of which one set of chromosomes derived from diploid wheat, the others from then unknown species that were suspected ~~to~~ by many to belong to the genera *Aegilops* and *Agropyron* (cf. Schiemann 1948). Continued hybridization [descriptive] experiments performed by Kihara and his [coworkers] cooperators led to the invention by Kihara (1930) of his so-called genome analysis ~~of wheat and~~ ~~in which~~ ~~to be used as~~ in which observations of chromosome pairing at meiosis in artificial hybrids are used to identify homology of the chromosome sets of the parents (cf. Liljefeld 1951, Kihara 1954, 1965, 1966). ~~It is based on~~ ~~The terminology of this method is based on the~~ This method and its name is based on the concept of the genome (Winkler 1920), which the sum total of the genes in which each allele occurs only once. In the case of a diploid or an autoploid, a genome is identical with the lowest haploid, or monoploid, set of chromosomes, whereas in an alloploid the genome constitutes the sum of the [illegible] haploid sets [illegible] involved.

Kihara and his associates and some later authors have used the term genome also for these haploid sets that are identified by aid of studies of meiotic pairing in hybrids, or by karyotype studies at mitosis (Chennaveeraiah 1960), ~~the correct genome analysis~~ they are more exactly termed haplomes, as proposed by Hellbrand and Hossing (1938, 1966) but ignored by most others. The genome of a diploid species is ~~identical~~ the same as its haplome, an autoploid series is made up of as many single haplomes and a single genome as its ploidy degree decides, whereas alloploid genomes are composed of two or more ~~haplomes~~ distinct haplomes. A single letter formula is used to designate these groupings so that, e.g. diploid wheat is said to be composed of the AA genome or haplome, its autotetraploid is denoted as AAAA, whereas the genome of tetraploid wheat is AABB, ~~and its haplomes~~ ~~made up of the haplomes A and B~~, and hexaploid wheat is named AABBDD from the haplomes A, B and D, ~~which are known to have be typical of diploid *Triticum monococcum*, of the diploid genus *Aegilops* group *Sitopsis* and *Aegilops squarrosa*, respectively.~~

~~It is a well-known fact that pairing in hybrids within the same species frequently is disturbed by~~

based on the haplome B typical of the *Sitopsis* section ~~of A~~ of the genus *Aegilops* and the haplome D of *Aegilops tauschii*.

~~For any genome analysis~~
~~It is important to notice, when discussing the that~~
~~At this stage it may be worth while to~~

The basic assumption of genome analysis is that haploid or monoploid sets of (homologous) chromosomes of allopolyploids and their diploid relatives will remain identical or so slightly changed for a long period of time that their individual chromosomes will pair more or less normally and more or less completely in artificial hybrids between the carriers of the genome, be they diploid or polyploid (e.g. Löve & Löve 1975), an assumption that has been strongly supported by numerous observations.

A triploid hybrid between an allotetraploid, AADD, and either of its diploid progenitors, AA or DD, is expected to form 2x bivalents and x univalents, or $X_{II}+X_{I}$, x being the basic number of chromosomes which in the wheatgrasses is 7. The univalents are supposed to represent the chromosomes of the diploid progenitor that does not take part in the hybridization. It is, however, not rare to observe some reduction in the frequency of bivalents in such hybrids, as a result of some changes in the chromosomes of the genome, presumably in the polyploid, that have rendered them homeologous or only partially homologous, a process that also is responsible for the evolution of new genomes the chromosomes of which are, however, never strictly non-homologous in groups like the Triticeae in which crossability is met with at a variably low degree even between the most distinct of genera, and the most distinct of genomes, although meiotic pairing may be practically nil.

Genome analysis becomes difficult when one or both participants in the hybridization, because it may sometimes be difficult to discern between progenitial pairing of the chromosomes of both parents and the autosyndetic pairing of chromosomes derived from the same parent. A skilled observer will, however, rarely for this reason have difficulty in identifying the essential bivalents, although such a possibility always must be kept in mind. Nevertheless, these and other problems in the observation of pairing are frequently encountered, as discussed in certain detail by Gaul (1958).

During the past three decades considerable information has been obtained by aid of genome analysis ~~(in hybrids)~~ between genera and ~~[illegible]~~ annual Triticeae species. (Sarkar ~~1956, 1958;~~ 1955, 1956, 1958,

Although biological definitions of the basic taxonomic categories have been aimed at by leading botanists since the times of Linnaeus, and although such definitions were in fact furnished already by the pre-Darwinian evolutionist DeCandolle (1813), tools to test the ~~status~~ ~~category~~ biological status of these units ~~became available~~ did not emerge until the rise of genetics, and even then they were cumbersome and timeconsuming ~~so they have still reached~~ because genetical experiments require considerably more time and facilities than do phenetical identifications.

(Although the grass tribe Triticeae is predominantly a boreal taxon, it is represented in the austral hemisphere ~~both~~ in ~~[illegible]~~ Australia and New Zealand as well as in South America.

The group of ~~grasses~~ wheatgrasses represented in New Zealand by the genus Agropyron as delimited by Connor (19...) and Cockayne as described by...

The tribe Triticeae of grasses is a taxon that apparently has originated in the mountains of Central Asia ~~from where it has dispersed~~ where it has evolved ~~[illegible]~~ and differentiated into ~~numerous~~ genera, species and subspecies since in the middle Cretaceous. ~~The genus~~ The main bulk of this variation are perennial grasses ~~which are typical of~~ of boreal and arctic mountains of Eurasia and North America, with a tongue reaching throughout the Andes to Tierra del Fuego and another stretching in the temperate Asiatic mountains westward to ~~West~~ Africa and east and southward to Australia and New Zealand. A smaller number of taxa are annual and ~~[illegible]~~ restricted to the mountains of the ~~Near East~~ classical Orient with outposts in eastern Africa; ~~these latter groups~~ they embrace ~~[illegible]~~ some of the most important of ~~[illegible]~~ grains that have evolved during the emergence of ~~[illegible]~~ man ~~[illegible]~~ ~~at the [illegible]~~ through his influence ~~[illegible]~~ and influenced his cultural evolution, ~~[illegible]~~ as the barley, rye and the three species of wheat.

Although the taxa at species and subspecies level of this tribe ~~[illegible]~~ surpass half a thousand, only ... species have dispersed in prehistoric times to Australia and New Zealand, where they have traditionally been recognized as species of the genera Agropyron and Hystrix or Cockaynea.

Wheatgrasses. 1.

Some wise men have said, that human life & human culture is based on grasses, & there can hardly be any doubt that the grass family plays a larger role in the wellbeing of man & his animals than any other family of plants. All grasses are not equally important, so that man & domesticated animals utilize only a fraction of the perhaps 650 genera & more than 10 000 species of the grass family. ~~I have seen no scientific estimate as to the exact~~ Be it as it may, but although bread grasses of the tribes Festuceae and Aveneae may seem to furnish the bulk of the fodder for domesticated animals in the northern hemisphere, the ~~growing~~ grasses of greatest concern for the affluence of man & his stock in historical times all seem to belong to the tribe Triticeae, or ~~what to what~~ the so-called wheatgrasses, or cultivated wheat & its relatives. It has even been claimed with ~~considerable reason~~ that without wheat there would have ~~been no~~ been little human culture, although the fact that most cultivated plants were first bred & domesticated by Stone age Indians in America, from which the ~~cultivated~~ wheatgrasses that gave rise to the ~~ancient~~ Old World bread wheat are absent.

Botanists have by known that wheat, ~~is related to rye~~ rye & barley are related to numerous wild grasses, & that ~~they~~ these grasses occasionally hybridize with one of these. The nature of this relationship, however, have remained obscure for various reasons, so that even the ~~true~~ ~~study~~ ~~was still recently~~ limits of the tribe Triticeae were unclear & allowed the inclusion of even the very collective taxa ~~recently~~ of the ~~group~~ collective genus Bromus. In recent decades, however, extensive studies of artificial hybridization & chromosome morphology have revealed that this latter genus itself, apart from the other units, not only by its much smaller chromosomes but also by its inability to cross with any of the wheatgrasses, even those that morphologists agreed ~~seemed~~ looked closely related to its species. The wheatgrasses as we now define the tribe, consist of ~~about~~ 320 species of ~~grass~~ a number of variable genera which all are characterized by a zigzag spike, laterally compressed spikelets with two glumes, single starch grains, & perhaps most important, rather large chromosomes the basic number of which is x=7. It is also important to note, that

natural hybrids between several of the classically defined genera are not rare when these taxa come into contact, and that it has been found possible to cross every genus with any of the other genera under experimental conditions, though sometimes this is connected with considerable difficulties. It ought also to be emphasized that many of these hybrids are not only completely sterile but also completely free of even the slightest meiotic pairing, though the success in crossing them certainly is indicative of relationship that may be masked by considerable rearrangement of all the chromosomes, and of relationship of the cytoplasm of all the taxa involved. The fact ~~that~~ of the crossability has confused some taxonomists ~~[illegible]~~ before its variations and relationships to meiotic pairing or lack of it became evident, but it has also stimulated plant breeders to experiment widely with many of these grasses and to express in that connection dreams so wild that they are perhaps unlikely ever to become true — or perhaps they will nevertheless?

~~Work that has been done on the hybridization of wheatgrasses~~

When a large group of plants demonstrates such a wide variation in morphology and also has no absolute crossability barriers, it can be expected that taxonomists have come to various conclusions when trying to classify its taxa at various levels, ~~depending upon the point of view of the~~ since Solomon's justice depends upon how Solomon was raised, as Mark Twain is said to have said. Those raised on the classical morphological philosophy tend to overlook the significance of the hybridizations ~~at [illegible]~~ and the chromosomes and look mainly at the few distinct morphological characters; they are likely to conclude that only a single or a few genera are involved. Whereas those brought up on genetics and evolution experimentation might lean towards emphasizing the variable crossability and the meiotic pairing ~~to the distinct~~ ~~[illegible]~~ as well as certain distinct ~~[illegible]~~ combinations of ~~morphological~~ the few morphological distinctions and thus conclude that the genera are many. As a matter of fact, modern morphological taxonomists have represented both these points of view and everything between them, and they have repeatedly become confused by what they claimed to be a lack of distinct generic delimitation due to the occurrence of transitional spike characteristics that others have solved by simply moving critical taxa from one group to another.

~~During the past half a century, when plantbreeders have been in a dire need of taxonomical advice on which to base experiments of transferring useful genes between taxa or producing novel generic combinations, several systems of classification of the wheatgrasses has been presented. The previous classification that was strongly affected by the opinion of the great British taxonomist Bentham, is the one still predominant in American publications. In this system, as presented by A. S. Hitchcock ~~in 1950~~ and ~~slightly modified by Frank Gould in 1968~~, and Agnes Chase in 1951, these grasses are classified in the ~~large~~ genera *Agropyron*, *Triticum*, *Aegilops*, *Secale*, *Elymus*, *Sitanion*, *Hystrix* and *Hordeum*, of which *Agropyron*, *Elymus* and *Hordeum* are the largest; Frank Gould, in 1968 follows a similar system but adds the small genus *Taeniatherum* and sinks *Aegilops* into *Triticum*.~~

~~That European authors~~

The classification of the wheatgrasses as presented by Linnaeus in 1753 simply included ~~the [illegible]~~ the 39 ~~genera~~ taxa that he recognized into the ~~[illegible]~~ genera *Aegilops*, *Elymus*, *Hordeum*, *Secale* and *Triticum*. During the next century, when many more species became known, several authors split and rearranged the Linnean genera in various ways, but at the end of the last century, the British taxonomist Bentham claimed that the ~~entire [illegible]~~ of these grasses was best accommodated in the five Linnean genera, ~~[illegible]~~ the more recently ~~Agropyron~~ described ~~[illegible]~~ large genus *Agropyron*, and the two smaller western hemisphere genera *Sitanion* and *Hystrix*. This classification is still predominant in America, ~~[illegible]~~ although Gould in 1968 ~~[illegible]~~ proposed that *Aegilops* be united with *Triticum*, and it was also widely used in Europe and elsewhere prior to the last world war.

Fig. 1

A widely different classification of these grasses was proposed ~~[illegible]~~ in the early 1930's by the Russian agrostologist Nevski, who recognized 25 genera in the tribe mainly because of an extensive splitting of the classically delimited groups *Agropyron*, *Elymus* and *Hordeum* into more restricted genera. His system was mainly used in the Soviet Union but also in the Scandinavian flora by Hylander (1953) who revised the material in question in cooperation with Melderis, who in 1953 proposed a modification of the Russian system based on the available information on crossability and chromosome characteristics. Melderis modification accepted only 22 genera. ~~He has later (1978) further revised his point of view for the Flora Europaea in which~~

9 Elymus
4 Secale
8 Hordeum
12 Triticum
6 Aegilops
39

Fig. 1

Fig.

Fig. More recently, the Swedish botanists Runemark and Heneen (1968) recognized only 14 genera in the tribe and followed a proposal by Gould (1947?) in uniting the collective genera *Agropyron* and *Elymus* into a single genus with the latter name. ~~The~~ A recent ~~but~~ comprehensive approach is that of the Japanese geneticist

Fig. Sakamoto (1974), who accepted 15 genera which he classified into ~~two~~ a Mediterranean-Central Asiatic group of 10 genera and an Arctic-Temperate group of 5 genera on basis of their distribution and their perennial or annual growth habits, as well as on observations on their crossability and chromosome characteristics.

Fig. The last revision is by the Russian agrostologist Tzvelev in his (Soviet Grassflora of 1976 in which he adopts a modified system based on that of Nevski but with only 13 genera.

This review may serve as a demonstration of the confusion among taxonomists as to the generic division of the wheatgrasses, though it ~~hardly there~~ ~~mentions the extreme~~ did not mention the extreme views of Krause (1898), recently supported by Stebbins and some of his cooperators, who felt that the morphological uniformity, and later the general crossability, supported the inclusion of all the tribe in a single genus *Frumentum*, a taxonomical absurdity and a nomenclatural misunderstanding, because ~~an illegitimate replacement of *Triticum* that must be so widened~~ the name of the collective genus is *Triticum*, if such a point of view is entertained. But let us leave ~~on that note for awhile~~ the taxonomy for a while on that note.

European taxonomists have long been aware that hybrids between certain species of wheatgrasses occur occasionally, and that some of the wild taxa may casually cross with the cultivated grains. ~~One of the great botanical controversies of the last century concerned a plant which some~~ Several natural hybrids have been listed in European manuals, and one of the great botanical controversies of the last century concerned a plant which was discovered close to cultivated fields in Southern France in 1830 and soon found also in Italy from where Bertolini described it in Flora Italiana in 1833 as the hybrid *Ægilops triticoides*. ~~Some others claimed it to be a new introduction from the Orient~~ After a lengthy discussion it was indeed proven to be a hybrid between an *Ægilops* ~~...~~ species and maccaroni wheat. Even before the rediscovery of Mendel's laws,

Different chromosomal changes towards homeology — still one hybrid.
New generic name for Hybrids for same reason.

plant breeders in Europe tried to ~~transfer~~ cross various wheatgrasses with ~~the~~ ~~[illegible]~~ cultivated wheat in order to transfer to it various positive traits. ~~E. [illegible] von Tschermak, one of the [illegible] rediscoverers of founders of modern genetics, was one of the most ardent exponents in this field and [illegible] been succeeded in producing fertile allopolyploids from some such crosses in the early of Aegilops and Triticum in the early twenties After the clarification, by Kihara and his cooperators, of the~~ After the ~~discovery~~ establishment of modern genetics, ~~hybridization~~ studies of these grasses were intensified, especially when Kihara and his cooperators around 1920 had been able to clarify the origin of the cultivated wheats. These studies involved ~~the discovery~~ also the discovery ~~of the important of naturally~~ of ~~natural~~ hybrids of wheat and rye that lead to the natural creation of allopolyploid ryewheat and various other observations with which plant breeders are well acquainted.

The studies of the relationships of the wheatgrasses ~~are~~ ~~[illegible]~~ continued in two directions. First by ~~hybridization~~ artificial hybridization that at once indicated that although some of the genera of the taxonomists were an assemblage of taxa of very various relationships, some of these groups ~~were~~ are closely related and easily ~~[illegible]~~ hybridized, ~~whereas still others are [illegible]~~ These experiments were mainly performed by agronomists who used doubtfully identified material of these grasses, ~~[illegible]~~ the natural areas of which are predominantly within the vaste ranges of the Soviet Union and Southwestern Asia, but they led to the discovery, by Kihara and his cooperators, of the fact that

Although it may seem convenient to use only a few comprehensive generic names, that convenience diminishes when these groups become unwieldly large so that even a critical key ceases to be useful for their identification.

Exact biological classification that reflects the processes of evolution is especially important for plants of economical importance, because it is basic for various methods used for their improvement in the strictly plant breeding, which is mainly based on the application of the processes of subspeciation and rarely includes the hybridization of good species or well established genera for the simple reason that well defined species or genera do not mix although occasionally if by human assistance they sometimes may cross. That is the reason for that the most advanced system of classification has been employed for the cultivated plants in the strictly the most essential of them, the grain-producing grasses and their relatives that are grouped together in the tribe Triticeae.

Since the tribe Triticeae ~~is~~ includes one of the ~~most~~ economically most important ~~grain~~ annual cereal crops and numerous forage grasses, or ~~especially~~ of ~~semidesert~~ temperate grasslands and semidesert steppes, its ~~[illegible]~~ ~~is of considerable~~ ~~that~~ ~~[illegible]~~ its classification into a distinctly phylogenetic system is highly desirable. ~~Although numerous geneticists and taxonomists have made or have made efforts to~~ ~~[illegible]~~ Crossability between the various diploid and polyploid species of the complex is considerable under experimental conditions, and many such hybrids have long been known to occur under natural conditions (Focke 1881). During the past three or four decades many geneticists have ~~not only produced an increasing number of such~~ studies these hybrids cytologically and morphologically and frequently employed for this studies either karyomorphology or, more often, the ~~so-called genome-analysis~~ technique of so-called genome-analysis invented by and successfully applied by Kihara (1930 and later) and his collaborators in ~~analyzing~~ explaining the evolution of wheats and their relatives. This method is based on the assumption

5.

The phylogenetic observations alluded to in the last ~~paragraph are in part connected with studies of the ... type of chromosomes in various~~
paragraph are of various kinds, but their bulk is connected with ~~crossings between~~ hybridization between species that have traditionally been placed either in the same genus or in different genera. It has been observed by several workers, e.g., that whereas some species of the traditional genus Agropyron hybridize frequently under natural conditions, others hardly ever cross, ~~the genus is the and still others seem unable to form hybrids with other~~ Likewise, certain species classified in the genus Elymus and known to have the same chromosome number ~~and~~ ~~unable hybridize~~ never hybridize in nature and ~~are~~ rarely in experimental gardens, whereas they cross easily with taxa that are classified in different genera. Many of these observations have been ~~the~~ made by plantbreeders interested in combining ~~per~~ the perennial habit and drought resistance of certain [illegible] species to the superior ~~grain quality of~~ quality of the flour of the grain producing species, though only a few of such experiments have met with success. ~~The~~ For a time, these hybridizations puzzled some taxonomists, who believed this crossability to be an indication of a relationship, so close that the assumed generic limits might ~~be unnatural~~ be fictional. Others interpreted the results

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Many of the results obtained have been interpreted wrongly by taxonomists (Melderis, Tzvelev . . . —)

Agropyrum, Elymus, ~~Elytrigia~~.

Elytrigia Smithii Nevski, Act. Inst. Bot. AN SSSR I. 1:25 (1935) — Am.

~~A. [illegible] R. & S. Syst. II: 751: Ecuador~~
~~A. [illegible] R. & S. l.c.~~ Syria
~~A. [illegible] Boiss.~~ Hausskn. ex Boiss. Fl. Or. 5: 663: Persia.
~~A. [illegible] Boiss. Diagn. I. 5: 75:~~ Persia
~~A. [illegible] Presl, Rel. Haenk. 1: 266: Chile~~
~~A. dasystachyum Scribn. [illegible] (1883): USA.~~
~~A. [illegible] D.C. Agrost. 102: S. Afr.~~
~~A. divaricatum Boiss. [illegible]: Orient.~~
~~A. divergens Nees ex Steud.: Am. bor.~~
A. filiforme Poir. ~~[illegible]~~ Syst. 2: 760: ~~[illegible]~~ [illegible] Ind. A.
~~A. [illegible] Boiss. Fl. Or. 5: 661: Al. [illegible].~~
~~A. [illegible] Boiss. Fl. Or. 5: 660: Orient.~~
~~A. [illegible] Nees, ex Steud. Syn. Pl. Glum.: 342: [illegible]~~
~~A. [illegible] R. & S. Syst. 2: 753. Batavia~~
~~A. orientale R. & S. Syst. 2: 757. Orient, Afr. bor.~~
~~A. [illegible] Gren. [illegible]: Egypt.~~
~~A. pectinatum D.C. Agrost. 102: Austral. N. Zeal.~~
~~A. peruvianum R. & S. 2: 761: Peru~~
~~A. [illegible] Presl, Rel. Haenk. 1: 267: [illegible]~~
~~A. [illegible] Boiss. Fl. Or. 5: 662. Caucasus~~
~~A. Richardsonii Schrad. Linnaea 12 (1838): 467: Am. bor.~~
~~A. [illegible] De Not. [illegible]: Liguria~~
~~A. [illegible]~~
~~A. scribneri Vasey, Bull. Torrey Bot. Club 10 (1883): 128: Am. bor.~~
~~A. secundum Presl, Rel. Haenk. 1: 266:~~ Chile
~~A. [illegible] Nees ex Steud. Syn. Pl. Glum.: 346: Afghan.~~
~~A. strigosum Boiss. Fl. Or. 5: 661: Orient.~~
~~A. [illegible] R. & S. Syst. 2: 761: Aleppo (Syria)~~
~~A. [illegible] Boiss. [illegible]: [illegible]~~
~~A. [illegible] Vasey, Bot. Gaz. 10 (1885): 258: Am. bor.~~
~~A. [illegible] D.C. Agrost. 102, Australia.~~
~~A. [illegible] Vasey, Contr. U.S. [illegible]: Am. bor.~~
~~A. [illegible] Vasey, in A. Gray [illegible]: Am. bor.~~
~~A. [illegible]~~
~~A. [illegible]: Tibet~~
~~A. [illegible] Hook. f. Fl. Brit. Ind. 7: 370: Ind. or.~~
~~A. [illegible]~~
~~A. [illegible]~~
~~A. [illegible]~~
~~[illegible] Hook. f. Fl. Brit. Ind. VII: 370: Ind. or.~~
~~A. [illegible]~~
~~A. [illegible]~~
~~[illegible]~~
~~[illegible]~~
~~[illegible]~~
~~[illegible]~~

one page ↓

~~E. [illegible] Presl, Rel. Haenk. 1: 265: Chile~~
~~E. [illegible] Am. [illegible]~~
~~E. [illegible] Presl, Rel. Haenk. 1: 264: Peru~~
~~E. [illegible] Hook. f. [illegible]: Reg. Magell.~~
~~E. [illegible] Nees, ex Steud. Syn. Pl. Glum.: 347: Chile~~
E. caesius Boiss. Fl. Or. 5: 691: Afghan.
~~E. cappadocicus Boiss. [illegible]~~ Cappadoc. (Armenia).
~~E. [illegible]: Am. bor.~~
~~E. [illegible] Phil. Linnaea 29 (1857-58): 104: Chile~~
~~E. [illegible]: Am. bor.~~
~~E. [illegible] Presl, Rel. Haenk. 1: 265: Am. bor.~~
~~E. [illegible] Phil. Linnaea 33 (1864-65): [illegible]: Chile~~
~~E. [illegible] Presl, Rel. Haenk. 1: 265: Sinus Nootka~~
~~E. [illegible]: Am. bor.~~
~~E. [illegible]: Chile~~
~~E. [illegible] Phil. Linnaea 33 (1864-65): [illegible]: Chile~~
~~E. [illegible] Presl, Rel. Haenk. 1: 264: Sinus Nootka~~
~~E. [illegible]: As. [illegible]~~
~~E. [illegible] (1856): [illegible]~~
~~E. [illegible] Phil. Linnaea 33 (1864-65): [illegible]: Chile~~
~~E. [illegible] Phil.: Chile~~
~~E. [illegible]~~
~~E. [illegible]~~
~~E. [illegible] Vasey, Bot. Gaz. 10 (1885): 258: [illegible]~~
~~E. [illegible] Phil. Fl. Atac. 56: Chile~~
~~E. [illegible] Phil. Linnaea 33 (1864-65): 301: Chile~~
~~E. [illegible]: Am. bor.~~
~~E. [illegible]~~
~~E. Sandbergii Vasey, Bull. Torrey Bot. Cl. [illegible] (1884): 126: Am. bor.~~
~~E. [illegible]: Austral.~~
~~E. [illegible] Phil. Linnaea 33 (1864-65): [illegible]: Chile~~
~~E. valdiviae Steud. Syn. Pl. Glum.: 349: Chile~~
~~E. [illegible] Phil. [illegible] Chile (1892): [illegible]:~~ Chile
~~E. [illegible]~~
~~E. [illegible]: Reg. Argent.~~
~~E. [illegible] Speg. [illegible] (1897): 632: Patag.~~
~~E. [illegible] Speg. [illegible]: Patag.~~
~~E. [illegible]: Chile~~
~~E. [illegible]~~ — Chile
~~E. patagonicus Speg. [illegible] (1897): 630~~ — Patag.
~~E. [illegible]~~
~~E. [illegible]: Reg. Argent.~~
~~E. [illegible] Hook. f. Fl. Brit. Ind. 7: 377: Ind. or.~~
~~E. [illegible]: Chile~~
~~E. [illegible]~~ Argent.
~~E. [illegible]: N. Z.~~
~~E. [illegible]~~
~~E. [illegible]~~
~~E. [illegible]~~
~~E. [illegible]~~ — Japan
~~E. [illegible] Ohwi, Bot. Mag. Tokyo 45 (1931): 185~~ — Japan
~~E. [illegible]~~ (= Clinelymus [illegible])
~~E. [illegible] Ohwi, [illegible] (1937): 374~~ — Japan
~~E. [illegible]~~ Clinelymus [illegible]
~~E. [illegible]~~ — Japan
E. [illegible] Ohwi, Act. Phytotax. Geobot. 6 (1937): 54 (Clinelymus [illegible]).

See: Clinelymus Nevski! & Elytrigia, Roegneria

↓ 2 pages:

Elymus: (U. l. '41–'50)

Roegneria

~~E. chinensis (Trin. ex Bunge) Keng, Sungkiang 6 (1941): 66, in obs. = Triticum chinense)~~

~~E. [illegible] Keng, l.c.: 55. (Kiangsi)~~

~~E. [illegible], Tzvelev, Not. Syst. Herb. Inst. Bot. 20 (1960): 425. [illegible] Agropyron [illegible]~~

Symb. Sin. Pt. 7. (1936): 1292.

Clinelymus (Nevski 1932 Bull. Jard. Bot. AN SSSR 30: 640.)

~~[illegible] Nevski~~: l.c.: 644: China (Manchuria) = E. [illegible] (N.) Hand.-Mazz.

~~[illegible] (Buckley) Nevski~~, l.c.: 648: = E. glaucus, N. Am.

~~[illegible] (Steud.) Nevski, l.c.: 649 = Elymus [illegible]~~

~~[illegible] (Honda) Honda, Bot. Mag. Tokyo 1936: 571 = E. [illegible]~~

~~[illegible] (Franchet) Honda Rep. Manchoukuo IV, 4: 101 (1936): E. dahuricus v. cylindricus~~

~~[illegible] (Honda) Honda, Bot. Mag. 1936: 572 = E. [illegible]~~

~~[illegible] (Ohwi) Honda, l.c. = E. [illegible]~~

~~[illegible] Honda, l.c.~~

Elymus [illegible] (Nevski) Hand.-Mazz. l.c.: 1192 (China)

E. [illegible] Keng, 1941, Sungkiang 6: 88 ((China, Sikang)).

Elytrigia

~~[illegible] (Baumg.) Nevski, 1933, Act. Inst. Bot. AN SSSR I, 1: 26 (1933); Agr. [illegible]~~ = Elytr. [illegible]

~~[illegible] (Ohwi) Tzvelev [illegible]~~ = Agropyron [illegible]

~~[illegible]~~ [illegible] 7 (1957): X = A. [illegible]

~~dasystachya~~ [illegible] 1954: [illegible] 81: 33 (a T. [illegible] v. dasystachyum)

: ~~[illegible]~~ (Roggi) Probatova, Not. Syst. Herb. [illegible] 16 (1954): 63, in obs. = Agr. [illegible]

~~[illegible]~~ (Moench) Tzvelev, Novit. Syst. Pl. Vasc. 1964: 28 = T. [illegible] v. [illegible]

Leymus Arenaria [illegible]

~~Elytrigia~~

[illegible] (Ohwi) [illegible] (1971): 122 (Agropyron)

~~[illegible] (1956): 24 = E. [illegible]~~

Roegneria

~~[illegible]~~

~~[illegible]~~

~~[illegible]~~

~~[illegible]~~

~~[illegible]~~

~~[illegible]~~ [illegible] Bot. 17 (1940): 235 (Manchuria)

~~[illegible]~~

~~[illegible]~~ 16 (1954): 58, in obs. (Agropyron [illegible])

~~[illegible]~~

~~[illegible]~~ (1957): 175 = Brachypodium [illegible]

~~[illegible]~~ l.c.: 187 = A. [illegible]

~~[illegible]~~ (1959): [illegible] = Agropyron [illegible]

~~[illegible] Keng, Clavis: 185, = Agr. [illegible]~~

~~[illegible]~~

[illegible]

STAGE II
26 July,1976

Leymus Hochst. *

Rhizomatous perennials. Leaves flat or convolute, glaucous, densely and shortly hairy on veins above, glabrous beneath; ligule short. Inflorescence a spike; rhachis tough. Spikelets subsessile, usually imbricate, with 3-5(-6) florets; rhachilla disarticulating above the glumes and beneath each floret. Glumes narrowly lanceolate to linear-subulate, covering the sides of the lower florets, 1- to 5-veined, glabrous or hairy, not or shortly awned. Lemma lanceolate, 5-veined, not or shortly awned. Palea nearly as long as the lemma, 2-keeled. Stamens 3. Lodicules 2. Ovary hairy at the top.

1 Glumes 2.2-3.2 mm wide, with 3-5 distinct veins; spikelets in pairs at each node of the rhachis
 2 Upper part of stems and rhachis glabrous .. .. 1. arenarius
 2 Upper part of stems and rhachis densely pubescent 2. mollis
1 Glumes not more than 2 mm wide, with 1-3 obscure veins
 3 Spikelets solitary at each node of the rhachis .. 8. ramosus
 3 Spikelets in groups 2-4(-6) at each node of the rhachis
  4 Keels of the palea glabrous or aculeolate only near the apex; spike robust; spikelets usually in groups of 3-4(-6) at each node of the rhachis .. 3. racemosus
  4 Keels of the palea spinose-ciliate at least in the upper half; spikes not robust; spikelets in groups of 2-3 at each node of the rhachis
   5 Basal part of glumes narrowly lanceolate, the lower glume with its basal part covering that of the upper; lemma 10-15 mm .. .. 4. karelinii

* By A. Melderis.

5 Basal part of glumes linear, the lower glume with its basal part not covering that of the upper; lemma 4-9 mm

6 Plants with long, creeping rhizomes, not forming tufts; leaves usually flat, with thin, distant veins above .. .. 7. multicaulis

6 Plant with shortly creeping rhizomes, forming small tufts connected by a rhizome; leaves flat or convolute, with prominent, approximate veins

7 Lemma glabrous on the back, with an awn 1-2 mm; glumes scabrid on the margins and on the middle vein towards the apex .. .. 5. akmalensis

7 Lemma more or less hairy on the back, with an awn 0.5-1 mm; glumes usually hairy .. .. 6. paboanus

1. L. arenarius (L.) Hochst., Flora (Regensb.) 7: 118 (1848) (Elymus arenarius L.). Glaucous perennial with long, creeping rhizomes. Stems usually 50-150 cm, robust, glabrous. Leaves 8-15 mm wide, flat, with convolute margins, densely and minutely scabrid or hairy on veins above, glabrous beneath. Spikes 15-35 cm x 10-25 mm, dense; rhachis glabrous except for spinose-ciliate main angles. Spikelets 20-32 mm, with 3-4(-5) florets, in pairs at each node of the rhachis. Glumes 15-25 x 2.2-3.2 mm, narrowly lanceolate, tapering to an acuminate-subulate point, with 3-4 distinct veins, keeled, glabrous or shortly hairy, especially on the keel. Lemma 12-25 mm, 5- to 7-veined, densely hairy, with short, soft hairs. Palea sparsely ciliate on keels near the apex. Anthers 7-8 mm. 2n=56. Maritime sands and sandy shores of large lakes. N. & W. Europe, from the Arctic to N.W.Spain; an occasional casual elsewhere. Be Br Da Fa Fe Ga Hb Hs Ho Is No Rs(N,B,C) Su.

2. L. mollis (Trin.) Hara, Bot. Mag. (Tokyo) 52: 232 (1938)(Elymus mollis Trin.). Like 1 but stems usually shortly hairy below the spikes; rhachis hairy; spikelets 18-25 mm; glumes 3- to 5-veined, hairy;

palea shortly ciliate on the keels; anthers c. 6.5 mm. 2n=28. Sand-dunes. Iceland. Is. (North America, N.E. Asia.)

3. L. racemosus (Lam.) Tzvelev, Not. Syst. (Leningrad) 20: 429 (1960)(Elymus giganteus Vahl.). Perennial with long, creeping rhizomes. Stems 50-100 cm, up to 10 mm in diameter in the basal part. Leaves up to 15 mm wide, scabrid on the veins above and on the margins, glabrous beneath. Spikes 15-35 cm x 10-20 mm, gradually tapering towards the apex. Spikelets 15-20 mm, with 4-6 florets, compressed, in groups of 3-6. Glumes 15-25 mm, linear-lanceolate, acuminate-subulate above, glabrous. Lemma 10-14 mm, 7-veined, acute, softly hairy in the lower part, glabrous towards the apex. Anthers c. 5 mm. Dry, sandy soils. S.E. Europe. Bu Rm Rs(C,W,K,E) Tu.

1 Stems nearly always shortly hairy below the spikes; spikes very dense, with spikelets in groups of 3-5(-6); glumes 1-veined .. .. (a) subsp. racemosus

1 Stems nearly always glabrous below the spikes; spikes fairly lax, with spikelets in groups of 3

2 Glumes 2- to 3-veined; keels of the palea glabrous or with a few cilia in the upper part .. .. .. (b) subsp. sabulosus

2 Glumes 1-veined; keels of the palea with numerous cilia in the upper part .. .. (c) subsp. klokovii

(a) Subsp. racemosus: Stems nearly always shortly hairy below spikes. Spikes dense, with spikelets in groups of 3-5(-6) at each node of the rhachis. Glumes 1-veined. Keels of the palea glabrous or with a few cilia in the upper part. 2n=28. S.E. Russia. (Caucasus to C. Asia.)

(b) Subsp. sabulosus (Bieb.) Tzvelev, Nov. Syst. Pl. Vasc. (Leningrad) 8: 65 (1971)(Elymus sabulosus Bieb., Leymus sabulosus (Bieb.) Tzvelev): Stems nearly always glabrous below the spikes. Spikes fairly lax, with spikelets in groups of 3 at each node of the rhachis. Glumes 2- to 3-veined. Keels of the palea glabrous or with a few cilia in the upper part. 2n=28. Throughout the range of the species.

~~Early~~ obscure

The origin of the Triticeae tribe is as obscure as that of the grass family itself, although we may surmise, from the present distribution of its members, that its ~~basic diploid~~ primary diploid genome of seven haploid chromosomes first became differentiated in the mountains of what now is southeastern Asia, probably already in the Jurassic but not later than in the Cretaceous. Since there is no fossil record to suggest any ~~such~~ hypothesis ~~as to~~ on the age of grasses in general and the wheatgrasses in particular, this suggestion remains only speculative. ~~but it is not contradicted~~ It is, however, not necessarily contradicted by the complete absence of gramineous fossils even through most of the Tertiary, because only the seeds of such plants are likely to ~~be~~ have been ~~so preserved~~ satisfactorily preserved. ~~But the suggestion is indirectly supported~~ ~~Since all the genera of this tribe~~ Since several genera of the tribe ~~have~~ ~~these distribution~~ ~~are~~ include a relatively low number of species of limited distribution centered in southwestern Asia, it seems reasonable to assume that the primary diploid wheatgrass ~~that~~ was a perennial plant, probably of mesophytic localities rather than of forests or deserts. It is likely to have been a caespitose plant 50–150 cm tall that had linear leaves perhaps up to half a centimeter broad, somewhat tapered at the base but without leaf-stalks. ~~The culms certainly were herbaceous and the plants have flowered at least once a year. The biseriate spikelets have been arranged inside a broadly ovoid or spheroid sheaths ~~ ~~but it~~ may or may not have been somewhat spiny. The glumes of the rather large biseriate spikelets may have been somewhat spiny, and have formed a somewhat extracted spi and the spikelets have formed a somewhat extracted spike~~
The rather large biseriate spikelets, which likely were surrounded at the base with small hairs, ~~are~~ were arranged into ~~somewhat~~ extracted spikes ~~at~~ ~~or~~ near the tops of the culms, which was without apical leaves. The glumes were ~~likely~~ probably spineless, ~~but the~~ and the leaks of superior paleas were without awnlike appendages, and the superior paleas and anthers were without an apical awn. The rachis has been non-branched (non-ramified), the spikelets sessile or on very short stalks and formed regular longitudinal rows on the culms. The gynoecium and caryopsis were terminally naked but thickly pilose near the top.

pedicels 0.5-2 mm, smooth, terete. Spikelets 4-15(-22) mm, narrowly ovate, with 5-16(-22) florets. Glumes obtuse to acute, sometimes mucronate, smooth, with thick, prominent veins; lower 2.8-3.3 mm, 1-veined; upper 3.1-3.5 mm, 3- to 5-veined. Lemma 3.3-3.8 mm, smooth, obtuse to acute, with a wide insertion and partly enfolding the next higher rhachilla-segment and lemma, with an apiculum up to 0.3 mm. Rhachilla-segment 1-1.5 mm, smooth.
[illegible] the sands. Mediterranean region and Iberian peninsula. Bl Co Cr Ag Gr Hs It Lu Sa Si.

4. C. [illegible] (Boiss.) [illegible] (Festuca [illegible] Boiss.). Stems up to 30 cm, ascending to erect, somewhat rigid. Inflorescence a sparingly branched panicle 3-12 cm, mostly with 1-3 spikelets or short branches and 1 longer branch at each node; branches and pedicels patent, divaricate at maturity; pedicels 0.5-2 mm, subclavate, sharply angular. Spikelets 5-14 mm, narrowly linear, with 2-6 florets. Glumes obtuse to acuminate or somewhat [illegible], mucronate, smooth or slightly scabrid; lower 1.1-2.5 mm, 1/2-3/4 as long as upper, 1-veined; upper 2.3-4 mm, 3-veined. Lemma 3-5 mm, acuminate or mucronate, ciliate to emarginate at apex but lacinate not enfolding the next higher rhachilla-segment, sometimes mucronate. Rhachilla-segment 2.5-2.5 mm, pubescent. Rocky places on hills. Aegean region (Macedonia and Peloponnesus). Gr Cr.

5. C. divaricata (Desf.) Bentham, Jour. Linn. Soc. London 19: 118 (1881) (Scleropoa divaricata (Desf.) Parl.). Stems up to 35 cm, procumbent to erect, somewhat rigid. Inflorescence a rather sparingly branched panicle 5-15 cm, mostly with 1 spikelet and 1-2 branches at each node; branches and pedicels patent, divaricate at maturity; pedicels 0.5-1 mm, subclavate, sharply angular. Spikelets 5-17 mm, linear-oblong, with 5-8(-12) florets. Glumes obtuse to rounded, rarely cuspidate, not mucronate, smooth or slightly scabrid, with 1 thick, prominent vein; lower 2.8-4.1 mm; upper 3.3-5 mm. Lemma 4.7-5.3(-6) mm, glabrous, obtuse or rounded to emarginate, not enfolding next higher rhachilla-segment,

14 NN
14 JN

2

seeds of the former even germinated, whereas several of the 24 seeds of the latter even germinated [illegible] though only two plants survived ~~to [illegible]~~ and flowered. They were, naturally, highly sterile, although most of the 28 chromosomes were unpaired at meiosis, it was possible to observe from five to nine bivalents at metaphase. ~~I interpreted this as indicating that some autosyndesis of the Agropyron chromosomes might occur, although it was also that one haplome of the but also~~ Studies of the tetraploid *Agropyron* parent had shown the occurrence of chiasmata that I interpreted as an indication of autoploidy, so I took the occurrence of more than seven bivalents in the hybrid to mean that some autosyndesis of the *Agropyron* chromosomes occurred, whereas I explained the occurrence of 5–7 bivalents as indicating that one of the two haplomes of the *Elymus* species must be identical or closely related to the two *Agropyron* haplomes. I believe this conclusion was supported by the much later observation of 5–7 bivalents in hybrids between *Elymus mollis* and *Agropyron* from the diploid *Agropyron* bessarabicum produced by aid of one of my students in a greenhouse in Boulder some twenty years later, ~~but that is another story~~ to ~~but to tell that love is~~ but that is another story.

These first experiments convinced me that any successful experiment in producing useful alloploids in the wheatgrasses must be preceded by detailed taxonomical studies and by cytogenetical analyses of the kind done by Kihara and his associates in their studies of relationships of the wheats and *Aegilops*, and by aid of exact analyses of the karyotypes of species and their races, so that unnecessary consuming time by hopeless hybridization could be avoided.

We moved to ~~Winnipeg in the spring of 1951, to the heart of the~~ Winnipeg in the heart of the Canadian wheatbelt in 1951, and although experimental facilities were limited, as at most botanical institutions in America, we accepted this as a challenge to widen considerably the studies that had begun in Iceland and planned a taxonomical and genetical review of the wheatgrasses as a whole. Although these grasses are mainly Arctic, ~~many have been~~ many have been introduced into North America for various purposes, and others are easily available from experimental stations and seed exchanges. ~~One of our graduate students in Winnipeg and later Montreal worked with~~ We made plans for closer studies of certain of these grasses and reviewed their general taxonomy as the first step (Love 1954), and some of our graduate students in Winnipeg and later Montreal studied certain critical groups (Chmurowicz 1960; Sarkar …, Brown …). But our own incomplete investigations were kept unpublished except for certain taxonomical conclusions (Love , Love & Love), at the same time as we followed the promising results of independent studies of the tribe performed elsewhere (Stebbins … Gould, …

The first steps of the author of this report towards the problems it is concerned with were taken in connection with planning of plant breeding in Iceland, an arctic country with a mild oceanic climate and short summers where the cultivation of grain crops has repeatedly been attempted with limited success. Although my efforts were to be directed towards the ~~breeding~~ introduction of a few garden plants and the breeding of some of the grasses cultivated for hay production, I was affected by the perhaps futile dream of the arctic inhabitants of self sufficiency also in grain production, and by the historical record of utilization of the wild species of strandwheat (lymegrass) in areas in southeastern Iceland where these plants cover considerable areas of sandy soils. My dream was also stimulated by enthusiastic reports of Russian success in hybridizing wheat and wild wheatgrasses in the hope of producing perennial hay producing grasses that also would furnish annual crops of grain. According to available information at that time, only a single ~~mostly~~ Eurasiatic species of lymegrass, Elymus arenarius, was then known from Iceland, and its being octoploid of a complex ~~composition~~ alloploid composition dampened my expectations, which, however, were rekindled when my Czech friend Emil Hadač in 1948 discovered ~~another~~ in the highlands specimens of the circumpolar ~~tetraploid~~ E. mollis, which I had the pleasure of finding later myself and observe its being tetraploid, a fact then not known from elsewhere. Although the native character of this latter species has been disputed by others, who even seemed to be skeptical as to my ever having counted its chromosome number which then had been confirmed from America and Greenland, I cultivated some specimens of both the tetraploid and octoploid at our experimental station at Úlfarsá. In the early spring of 1949, Swedish colleagues, by aid of officials of the Icelandair, ~~made it possible~~ furnished me with live specimens of some grain crops that ~~were planted in the greenhouse~~ furnished us with pollen. ~~either so that it could be preserved for the flowering of the wheat plants~~ The barley plants flowered earlier than the lymegrass so their pollen had to be preserved for a couple of weeks, whereas the flowering of the limegrass and tetraploid and hexaploid wheat almost coincided. Despite of ample pollination of both the limegrasses, only ~~a few~~ fourteen seeds developed from the ~~hybridization attempts~~ attempted cross with diploid barley, but none were obtained from the pollination of the wheat species. Further, none of the seeds germinated.

My interest in the wheatgrasses goes back to my youth in Iceland, an arctic oceanic country with short summers, where the cultivation of grains is at best a lottery played only by a few optimists. When I began my botanical collection in 1931, a few wild grasses belonging to the tribe of wheatgrasses were known to occur in the country, and the ubiquitous quackgrass had, of course, become one of its most noxious weeds. I could not avoid to learn about the fact that my forefathers in ~~southern~~ the early ages of southeastern Iceland had had some success in the past in utilizing the grains of the lymegrass, and I believe some tidings about certain Russian success in ~~hybridizing and~~ stabilizing hybrids between this perennial of little use with some of the useful grain crops was a factor influencing my decision to pursue further education in genetics and plant breeding. During my studies in Sweden, however, other interests took most of my time, although the fact that my colleague Gunnar Östergren ~~had been~~ was studying the cytogenetics of certain wheatgrass hybrids kept my interest alive.

When returning to Iceland in 1945 my interest in the possibility of ~~producing~~ combining the ~~hardiness~~ hardiness and perennial characters of the arctic lymegrasses with the ~~useful~~ agriculturally important characters of barley or wheat was revived, although most of my time had to be spent on other ~~projects~~ activities. However, I succeeded in gathering some live material of the two Icelandic species of lymegrasses, Elymus arenarius (2n=56), E. mollis (2n=28), for cultivation at an experiment station on Úlfarsá, and also to cultivate for a year a few seedlings of *Hordeum vulgare* (2n=14), *Triticum turgidum* (2n=28), *Triticum aestivum* (2n=42), *Secale cereale* (2n=14), and ~~*Hordeum maritimum*~~ *Agropyron junceum* (2n=28), thanks to valuable help by my Swedish colleagues Sven Ellerström and Axel Tonje and officers of Icelandair, which transported live material from Sweden in the spring of 1948. The transplants did not seem to suffer much from the considerable climatical change, except for a marked delay in flowering which made it possible to pollinate the material profusely in all directions. Though the results were perhaps not encouraging because no seeds were obtained from crosses involving the lymegrasses on the one hand and the wheats and rye on the other, they nevertheless resulted in six seeds from the cross *Elymus mollis* x *Hordeum vulgare*, and in 24 seeds from the cross *Elymus mollis* x ~~*Hordeum maritimum*~~ *Agropyron junceum*. None of the six

Although all taxonomical categories originally were subjective units that by necessity were based on morphological groupings for the sake of convenience, it has long been a tendency among botanists to superimpose them with some kind of phylogenetic relationship. [Thus, the highly subjective classical trend to accept as species all genera units that - (e.g. Willis, Ref.).
was in the last century replaced by the Austrian school by a dogmatism of the species by aid of geographical distribution, etc].
Since such connections at the best have at the best been speculative for the genera, at least only minor readjustment of the admittedly insufficient classification of most plants has been accepted, although in a few significant cases considerable changes have been proposed.

At about the same time an evolutionary line of annuals ~~was~~ commenced in southwestern Asia ~~at last this~~ later leading to the differentiation of ~~at least~~ sixteen clearly distinct ~~species~~ Lagolones, some of which formed an tetraploid series. Within both the annual & perennial ~~series~~ Lagolones a certain degree of hybridization followed by allopolyploidy also created new ~~species~~ & successful grasses each of which has differentiated further ~~into~~ at the species & lower levels & dispersed to areas widely separating those of the original diploids.

We interpret the results from the hybridization experiments of the Triticeae as a strong support of the theory that opinion that all the wheatgrasses derive from a single diploid haploid primary haploid which characterized a species that for some reason evolved from a primitive member of the Festuceae in the late Cretaceous or early Tertiary in the mountainous regions which now forms the Asian Australasian; some of a part of the heterogeneous tribe Brachypodieae may have also branched from this early Triticeae like, whereas other taxa presently included in the genus Bromus tribe or even in the collective genus Brachypodieae bear no relationship to these grasses. The original haploome is likely to have been identical to the present S haploome. Although it has although the identity of this haploome have evolved, first, several this haploome has, by aid of inversions, segmental interchanges of various more or less diffuse. This haploome, as characterized not only by a distinct combination of certain regular morphological characters but also by minor changes in the morphology of genital arrangement of its chromosomes, thus causing the genetic by isolating barriers reproductive isolation between species of their interfertile races, which presently are distributed in isolated areas from North Africa in the west through the Asiatic mountains to Central mountains of Asia North America and in the Eurasiatic of North American mountains, perhaps also reaching North Africa of southern Australia. It has For the sake of some certain uncertainty caused by limited experience we also given rise also to by aid of drastic chromosomal rearrangements, proyect to keep these provided species from the restriction gene transfer to new haplotypes of haploomes so distinct that they are unable to pair with the original those of the primary haploome, though a certain degree of crossability has been retained because of genetical & cytoplasmic relationship. By aid of drastic more or less diffuse chromosomal rearrangements The taxa belong to this haploome has a few times given rise to new autoploid species, but it has more frequently changed, by aid of more or less diffuse chromosomal rearrangements, into new haploomes so drastically distinct from the primary haploome that they rarely are able to cross at all then their chromosomes can't pair; these changes have apparently mostly taken place mainly in the mountains of southwestern Asia where in the early Tertiary the new haploomes new presumably formed the haploome that we designate as S, at least five new primary haploomes were formed, that furthers also produced new series of autoploid species.

Diffuse chromosome rearrangements = not clear segmental or interchange or inversion, but rather mixed. Occurs in some genus hybrids?

There is a reason to believe that the evident morphological relationship of all the grasses of the tribe Triticeae is caused ~~by common descent~~ not only by common ~~desc~~ descent from ~~a single diploid genome~~ [illegible] ~~a haplome of haplome~~ a single species with a haplome of seven large chromosomes but also by retaining the primary genes of this original taxon through reshuffling by aid of various chromosomal rearrangements that have resulted in new haplomes that sometimes ~~have been developed~~ have almost developed beyond the possibility of crossability. ~~Some of~~ These ~~genomes~~ haplomes have evolved further by the same kind of chromosomal rearrangement ~~to form an array of diploid species that remain retain their crossability~~ between and within some of their chromosomes to form an array of diploid species that retain their crossability but are effectively ~~isolated~~ separated from each other by a certain degree of reproductive isolation; by aid of natural selection some of these species have later formed interfertile but geographically distinct geographical races. ~~Some of the haplomes have formed an autoploid series~~ When the ~~diff~~ partial differentiation of a haplome [illegible] has not reached a stage ~~when~~ that precludes some ~~genetic~~ genetical interchange or prevents the pairing of most of the chromosomes when hybridized, it is reasonable to regard this only as variation of the same [illegible] primary haplome [illegible] which then is designated by a letter and a subscript (or superscript). Polyploids formed from such haplomes are, then, autoploids, either panautoploids when [illegible] consisting of the same unrearranged haplome, or hemiautoploids when slightly ~~variable~~ different variations of the same haplome are involved. ~~Such polyploids are met~~ Polyploids of both these kinds are met with in some groups of the wheatgrasses, and since they certainly have originated by branching from the same original haplome, there is ~~no reason to~~ a good reason to retain them in the same ~~genus~~ strict genus as the original haplome. However, when, ~~[illegible] is formed~~ perhaps more rarely in the wheatgrasses, a taxon is formed by hybridization of two distinct haplomes followed by polyploidization and, thus, alloploidy, this does not constitute a case of linear branching but rather by a kind of reticulation. . . .
Not one genus.

(Formed. . . from the Festuceae . . . but as long as paleobotanical evidence is not available in support of the assumption that the ~~wheatgrasses~~ Triticeae are younger than the former, ~~the~~ [illegible] evolution in the opposite direction cannot be logically excluded.)

Hylander (Wien discussion, p. 208): Must avoid the false circumscription and delimitation of genera.

Gutin + Pilger: Small, well delimited genera.
(No real intermediates)
Love: Hylander 1961, p. 212: intermediate position.

The karyotype of the Balkan plant is morphologically similar to that of F. festucoides from Morocco and E. strigosa from the Crimea; since the Moroccan ~~plant~~ and the Balkan plants could be hybridized with . . . they may contain the S haplome, although the study could not be completed by aid of a meiotic analysis of the hybrids, for reasons unbelievable.

If all [accepted] in one genus, then not Frumentum but Triticum, but since there is a marked preference to crossability within the annual and perennial groups, respectively, and very much less between these groups, the same logic might perhaps also lead to the acceptance of the annual genus Triticum s. latiss., and the almost exclusively perennial Elymus s. latiss. — however, neither of these solutions is biologically reasonable or agronomically practical so further splitting certainly is to be preferred.

Accepting less comprehensive genera inevitably leads to the need to define them more exactly. Since some crossability is met with even between groups as definitely distinct as, e.g. Agropyron junceum, elongatum, spicatum — although the sterility of the offspring is complete because of a total lack of pairing between the chromosomes involved, that cannot be utilized as a reasonable criterion. The crossability of the allopolyploids to both the diploid groups from which they clearly have arisen would also be a useless characteristic, since then as unrelated as the diploid Agropyron tauri and the diploid perennial species of Hordeum would have to be put into either the same genus as Elymus s. str. or . . .

Although the same reasoning could and ought to be used as a basis of a thorough biologically based revision of the annual group, which presently is constituted of the very collective genera Triticum and Aegilops and the biologically strict genera Heteranthelium, Dasypyrum, Secale, Eremopyrum, Taeniatherum, Hordeum s. str., Crithopsis and Henrardia, we prefer to defer such a revision to a later occasion. It ought to be mentioned, however, that earlier botanists have [split into more restricted genera already] the two first groups, as e.g. Nivieria Seringe (1818) or Crithodium Link (1834), [originally by Thellung] Amblyopyrum (Jaub. & Spach) Eig, [originally by the ...] but since even that is insufficient on basis of our present knowledge of their genomic constitution, . . .

Secale L.
cereale L.
ssp. cereale
ssp. montanum (Guss.)
~~ssp. silvestre (Host)~~
ssp. Vavilovii (Grossh.)
sylvestre Host

ssp. segetale (Zhuk.)

Boris Yurtsev.
Kom. Bot. Inst.,
Popov Street 2,
Leningrad 197022

Dasypyrum (Coss. & Dur.) Borbás (= Haynaldia Schur 1866, non Schulzer 1866)
villosum (L.) Borb. (Secale villosum L.). annual; [illegible] (perenn.?)
hordeaceum (Boiss.) Coss. & Dur. (= H. hordeacea (Boiss.) Hack. = Agropyron hordeaceum Boiss.)

Dear Boris:

Many thanks for the two reprints — Chukotka and especially for the book from the symposium — the Arctic floristic region that the mail needed over two months to get from Leningrad to San José! Although it always is one struggle ~~involved~~ with dictionaries involved when we read Russian papers, you write ~~such~~ in such a way that we believe we get the ~~meaning~~ out rather easily. ~~though we~~ However, ~~both~~ we and many others would have preferred to read this in English — ~~than~~ but it is written more for Russians than for others for the simple reason that many times more those study the Arctic than here — and also ~~[illegible]~~ botanists with a better training and wider knowledge than students even from Harvard, the contribution by Young is like sticking out one's tongue ~~after reading~~ compared to your paper, and so is that of Rönning, but [illegible] reviews what he has reviewed before and does it well as always. I enjoyed especially your ~~list of~~ analytic list of species, which is perhaps not as good for extra-Soviet areas because you had only secondary knowledge of these floras and not too good information to base it on, but the Soviet part is especially interesting to us. We are pleased to see that our Atlas has influenced even your "conservative" morphological ideas somewhat, and that you have accepted our "cryophyte" term, although Aleksandrova seems to think it is your creation rather than mine! And I disagree with your attempts to explain away the distinct tundras in Iceland and Greenland, they are no less arctic than those you accept in Alaska which you also have not seen — we have a paper about that disagreement in Phytocoenologia, the Festschrift for Tüxen this spring. You probably have heard that Doris has translated Aleksandrova's good book on ~~A~~ the Arctic and Antarctic for the Cambridge University Press, which only then [illegible] been interested in a translation of your arctic symposium, too.

When I looked through your list of arctic plants, I was sorry to see that you did not list the names of authors, because several of the species are apparently of recent description by you and your colleagues so they are listed nowhere yet. Or at least we cannot find the publications and do not have the appropriate reprints.

And in that connection I would like to remind you of my old wish for pieces of fruiting specimens of your ~~two~~ Rumex ~~species and~~ beringensis and Krausei and of the Rumex aschyrifolia of Tolmatchev, since the descriptions are insufficient for identification even by me. ~~I have a reason to believe that at least one may be~~ Please, do not forget it any longer!

Perhaps Michael Kirpicznikov could help you to get the specimens to me through ~~the~~ W. A. Weber of the Herbarium at Boulder? I understand that Kirpicznikov has not been well but hope he is better — give him my best regards and tell him that if he has sent the last volumes of the two European Russian floras he mentioned in the fall, and the Novitates for 1978, the package is still not here. But I hope it has not been lost in the mail.

~~We are presently working on the [illegible]~~ [illegible] together with Douglas Dewey in Utah, and are finding much pleasure from the thorough grass flora by Tzvelev, ~~although he, as also Fedorov, [illegible] Flora Europaea, has little cytogenetical understanding because of the Lysenko dominance which still prevents you from having more than a handful of cytologists, none as great as Navashin and Levitsky, and he and Fedorov also have missed a good deal in direct names~~ although his morphological concepts are clearly affected by the lack of genetics caused by the loudspoken agronomist Lysenko. But much of what Tzvelev did for these grasses is solid and will not be changed by time — nor by us.

We have been invited ~~to [illegible]~~ by Prokudin to come and speak at a botanical symposium at ~~[illegible]~~ Khabarovsk at the Pacific Science Congress — but we got no formal papers from the Congress and the invitation came after the deadline given in it had passed. And since the miscarriage of justice we have experienced here — no less than that of your Jewish "dissidents" — prevents us from getting any financial support and we have to save every cent for the same reason, we do not expect to be able to come. And those scientists sent in "exchange" to the Union apparently must be Americans, and then it does not matter [illegible] as you have seen, except Bill Weber who was [illegible] we would like to visit the entire country [illegible]

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sagenioides (Mett.) Ching
Syn. Heterogonium sagenioides
2n = 80
80 Manton 1954b

sinii (Ching) Ching
see Ctenitis sinii

3850. Heterogonium Presl
x = 10,(40)?

pinnatum (Copel.) Holttum
2n = 160?
160-164 Manton 1954b

sagenioides (Mett.) Holttum
see Ctenitopsis sagenioides

3860. Stenosemia Presl
x = 10,(40)

aurita (Swartz) Presl
2n = 80
80 Friebel 1933
80 Walker, T. G. 1973

3870. Pseudotectaria Tardieu
no information

3880. Tectaria Cav.
x = 10,(40)

amplifolia (v. Ald. v. Ros.) C. Chr.
2n = 80
80 Manton 1954b
80 Manton & Sledge 1954

angelicifolia (Schum.) Copel.
2n = 320
c.320 Manton 1959

please see

This is the last installment in Texas of the chromosome number lists, which were initiated in 1964 by Ashell Love and Otto Solbrig as a facility for a rapid publication of chromosome numbers that otherwise might have remained unpublished.