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About the Institute
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Hunt Institute was dedicated in 1961 as the Rachel McMasters Miller Hunt Botanical Library, an international center for bibliographical research and service in the interests of botany and horticulture, as well as a center for the study of all aspects of the history of the plant sciences. By 1971 the Library's activities had so diversified that the name was changed to Hunt Institute for Botanical Documentation. Growth in collections and research projects led to the establishment of four programmatic departments: Archives, Art, Bibliography and the Library.

~~The selection of the topic of this seminar course was perhaps made in the light of the widespread doomsday prophecies that even respectable scientists have supported in recent years.~~

The selection of the topic of this seminar course was perhaps made in the light of the widespread doomsday prophecies that tell us that pollution by smog, industrial waste, insecticides, defoliants and other widely used chemicals, is leading to a catastrophe that soon will extinguish ~~the human~~ life on the earth, or at least substantially reduce the health of the human population. It is the opinion of those who organized the seminar that although there is some reason for concern, most of this is to be regarded as fantasies that employ the common instinct for the macabre which may have sprung from the rich literature of medieval legend and the largely shallow but ~~widespread~~ unfortunately widespread literature of science fiction. Even moderates, are sometimes driven to conclude that if science and technology cannot make much headway with the problems of technological waste, then attention should better be directed elsewhere. It is only fair to say that those who go further in their despair about the solution of urgent problems can only infrequently be shown evidence that the problems which oppress them may yet be solved — if that were possible, immediate solutions would be preferable to discussion. It does not follow from this, however, that some kind of disaster is ~~inescaple~~ inescapable. ~~Certainly there is~~ The seminar was organized in order to help the new generation to realize that certainly there is no warrant for the strange prophecies which frequently suggest that disaster will spring from science and its technological applications. The truth is doubtlessly the opposite, since there is ~~a~~ much greater reason to believe that science will contribute to the enlightenment and prosperity of the future as it has helped in the past.

In our highly technological society many of the difficulties that trouble the followers of the Doomsday Fallacy are caused by the fact that our biological understanding of our environment has developed slower than the technology which has improved human life more in the last 100 years than all the human struggle for existence could do for millions of years. Others will discuss important aspects of this problem, but I would like to introduce to you the concept of the ecosystem, which is frequently discussed but rarely properly understood.

Classification at the levels of
a/ subspecies and lower: phenetic,
b/ species and higher: genetic.

A. Historical background.
B. Taxonomic principles?
C. Conclusion: Suggestions.

Biosystematics I 1. 7/2 '69.

1) Introduction

Biosystematics = classification based on study of living material.
Genecology – cytotaxonomy – evolution – phytogeography.

Orthodox taxonomy: herbarium studies, classifies material on morphology alone.
This is the starting material even for biosystematists.
Studies on living material result in splitting or lumping.

A biosystematist needs to know the principles of cytogenetics, taxonomy, geography, ecology, horticulture, field botany etc. biometrics.

We know more than million species of animals, 150 – 200 000 higher plants.

The genetic aspect works with a small group; the cytological aspect may work with large groups; in which the specialist studies breeding mechanisms, hybridization in nature and in experiment, habitat variations; isolation barriers, both external and internal, if the plant is still evolving and then how, – and adds, to this laboratory experiments and biometrics

In order to be able to work in biosystematics, the scientist must be a good geneticist at the same time as a good taxonomist. The genetic point of view starts by studies of the variability of the individual and the population. This variability is of two fundamentally different kinds: genotypic and phenotypic.
M. p. 66 – 71; Winge

We will later discuss some details of inheritance, but at this stage it is appropriate to state, that the hereditary constitution of each individual is composed of a large number of different genes. The total sum of all these genes of the individual is called the <u>genotype</u>, (a term coined by the Danish botanist Wilhelm Johansen) and thus the genotype is identical to the hereditary constitution. The term <u>phenotype</u> indicates the appearance and condition of an individual at a certain moment. This condition is the result of the interaction between the genotype and the environment. A less well defined term for genotype used around the turn of the century was <u>id</u>, which was coined by the biologist Weismann, based on the greek word <u>idos</u>, that which is seen, form, shape, or kind; it survives in the combinations haploid, diploid, polyploid.

During the development of the individual from the fertilized egg cell to the adult organism, the genotype will constantly direct the developmental processes. but this will occur during a continuous interplay with the multitude of different environmental influences, to which the growing organism is exposed.
<u>Thus, the properties of an individual are conditioned by two fundamental factors</u>: the genotype and the environment.

External differences that result from environmental influences are called <u>modifications</u>: a starved cow or pig. a starved plant, intelligence of a person starved for certain amino acids when baby; Primary cause of all variation is genotypic, but the molding of the individual by the environment is also important, how [illegible] is displayed by the [illegible].
~~Modifications of twins.~~ Vegetative reproduction: identical genotype - <u>clone</u>.
Some modifications are permanent for the lifetime of the individual: Hedera helix leaves (English ivy), identical twins differing looks + life habits?
<u>Dauermodification</u> — or permanently induced modifications.
Environmental plasticity: some species rigid and little affected by the environment, whereas others are more or less plastic.
<u>Summarize</u>: What is inherited are not definite characters, but a norm of reaction, or a special mode of reaction to different external influences. Certain red-flowered <u>Primula sinensis</u> cultivated in a humid greenhouse at 30-35°C forms white flowers. When returned, back to red flowers. — no change in the genotype.

We will discuss genetical variability next time, and then also the difference between allogamy (cross-fertilizing, outbreeding) and autogamy (self-fertilizing, inbreeding) on variability and the genetical constitution. Since biological variation is a very complexed phenomena which is affected by the genotype and the environment, it is advisable to study it first in groups that have the same ~~[illegible]~~ genotype, either because they reproduce asexually or because they ~~are~~ belong to what we call pure lines, which are progenies produced by ~~selfing~~ ~~self-ferti~~ inbreeding from single homozygous mother plants. Within each such line all individuals will have the same genotype, and if they have not been modified by environmental conditions, they will have generally ~~the same~~ a very similar appearance. Nevertheless, certain characters will vary, and when pure lines of beans are assorted into classes of size, even they will show a variation in size following the normal curve; the same applies to physiological and certain morphological characters, the variation of which thus are modifications only.

Different pure lines are, however, different from each other, since they do not belong to the same genotype. Sometimes the differences in external appearance are small or none, but the lines may nevertheless differ in physiological properties, such as, earliness of flowering or maturity, winter hardiness, or resistance to disease. In order to understand this more clearly, we must become familiar with two new terms, biotype and population. A biotype is the sum total of all the individuals having the same genotype, whereas a population is a group of individuals belonging to more than one ~~biotype~~ genotype.

→

With other words, a population is a mixture of individuals with different genotypes.

The individuals within a pure line belong to the same biotype as long as the inbreeding is perfect and no mutations have occurred. If two different pure lines are derived from two genotypically identical mother plants, a rare phenomenon, both lines will belong to the same biotype. "Pure line" is consequently a genealogical concept, whereas biotype is a term referring to the genotypical constitution.

Populations of self-fertilizing plants usually consist of a multitude of homozygous biotypes. In cross-fertilizing plants, and in most animals, and in man, the situation is quite different. One of the basic characteristics of cross-fertilization is perpetual hybridization between different individuals comprising the population. Since these individuals are genotypically dissimilar, the result will be ~~a~~ a continuous segregation and recombination of genes in the population. Every individual is heterozygous for a large number of genes, and its sex cells will, therefore, have an extremely variable constitution. When a heterozygous plant is crossed with another strongly heterozygous individual, a progeny will be formed in which practically every individual has a different genotype.

If we compare stands of self-fertilizing plant species, for instance barley and wheat, with stands of cross-fertilizers, such as rye or timothy, it can be fairly easily seen that the cross-fertilizers are more variable than the self-fertilizers, especially if the plants have been subjected to breeding. The contrast between a stand of a ~~homozygous biotype~~ homogeneous biotype of a self-fertilizer and of a heterogeneous population of a cross-fertilizer is always striking.

More ostensibly than by direct observation of the population, the variability in cross-fertilizers may be unravelled by employing vegetative propagation. In a perennial grass such as timothy, or in rhubarb, this is very easily accomplished by dividing the clump into several parts, which upon replanting develop again into new plants. As pointed out earlier, such plants constitute a clone, i.e. a progeny formed by vegetative division. If clones from several different individuals within a population are raised and are cultivated in the same field, characteristic differences among the clones will appear, whereas the plants within each clone are strikingly similar. This demonstrates very well the presence of hereditary variability in the population. The differences among the clones depend on their different genotypes; the similarity between the plants within each clone on the fact that they are *isogenic*, or that they have the same genotype.

Typical clones of gigantic size are met with in fruit trees and potatoes, in which propagation is purely vegetative so that each variety represents a clone. As long as propagation occurs in a vegetative fashion, the clone will remain constant; but if seed reproduction is allowed, an immense variation will be the result.

↓

During Darwin's time, it was generally believed that all organisms have an inherent tendency to vary. This would imply that in the offspring of certain organisms some individuals are plus variants, others minus variants, with regard to a certain property. If natural selection acts upon a variable population and favors the plus variant, then the mean value of the character in question would gradually be shifted in a positive direction. Since the individuals, changed in this way, would still retain the ability to vary just as much in the plus as in the minus direction, the character in question should be able to evolve in a positive direction indefinitely, or at least as long as this would be valuable for the species or the strain. In other words, there would be no limit to the displacement of the type that natural selection would be able to induce through selection from the existing variability.

Recent research has verified that natural selection is an extremely important instrument in nature. Of the enormous multiplicity of individuals that are constantly being produced, only a few are so well equipped in genetic respects that they are able to compete successfully and assure the continued existence of the species or strain. On the other hand, it has now become clear that Darwin's view concerning the inherent tendency for directionless variation and the attendant capacity for continuous and unlimited displacement of the type is erroneous.

One of the notable results of genetics is the demonstration that biological variation is a complex phenomenon that is due to several quite different causes. This had actually been demonstrated by the German zoologist A Weismann before the turn of this century, when he cut off the tails of his mice for generations, though it was convincingly and particularly well elucidated by the Danish botanist Wilhelm Johansen during the first quarter of this century. Johansen's selection experiments in populations and pure lines of beans belong to the classical works of genetics. Johannsen was able to show that selection had an effect only as long as the material represented a population i.e. a genetically hetrogeneous material. Selection within a pure line, on the other hand, fails completely because variation within the line is only modificatory, i.e. caused by environmental influences. Thus, any number of generations of planting the largest or smallest beans, respectively, within a line will not change the characteristic mean value of the bean size of the line.

Within each of the lines there is a plus and a minus series. Over a period of six years, the largest and smallest beans were chosen as seed material. The progenies of the plus series, however, did not have a greater mean weight than the progenies in the minus series, and the same was true of both lines investigated. Selection in a bean population in which several homozygous biotypes are represented will, on the contrary, rapidly lead to a change in the mean value; but further displacement will not occur after the selection has ~~had~~ led to a pure line representing the most extreme bean size.

In a cross-fertilizer, selection has a much greater chance to give rise to development in a certain direction than in a population of a self-fertilizer. In the cross-fertilizing population there is, of course, a high degree of heterozygosity, and ~~therefore~~ thereby extensive variation arises by recombination. However, in spite of the almost infinite number of different gene combinations, which can be found within a population of this kind, there are also limits in this category that cannot be exceeded. These limits are set by the genes which were present in the population when selection was started. When these genes have been combined in the most favorable ways, corresponding to the kind of selection to which the population is exposed, it will be impossible to proceed any further.

There is one more possibility, however, new genes may be formed by mutation, which is not caused by recombination of genes. We will discuss this later, but can summarize this by stating that biological variation has three main causes: 1) environmental influences, 2) recombination, and 3) mutation.

1) What do the terms genotype and phenotype signify?

2) How can two individuals with different genotype have the same phenotype?

3) What is the difference between environmental modification and environmental plasticity?

4) Are all kinds of characters equally susceptible to environmental influences?

5) Reaction norms rather than characters are inherited. Why?

6) Are nonidentical twins mono- or dizygous?

7) Examples of clones? Humans?

8) Result of selection in a/a cross-fertilizer, b/a self-fertilizer, c/a pure line?

9) The difference between a biotype and a pure line?

10) The major causes of biological variation?

11) Why are individuals of the same clone isogeneous?

12) What is a population?

13) Why are varieties of fruit trees and potatoes uniform?

14) What is the difference between clones and pure lines?

(~~Next: not on Friday!~~ also Fr. kl. 10. 14/2 '69.

Biosystematics II.

(prevalence)

Last time we discussed variability of the phenotype, and defined some basic terms. We will add today a discussion about inherited variability, as this has been clarified through mendelism.

According to earlier views, the hereditary substance should consist of a homogeneous and indivisible matter, which to a certain extent represented an extract of the physical constitution of the parent. Charles Darwin believed that the different parts of the body were able to form small matter, which he called gemmules, (Pangenesis theory) which were accumulated and concentrated into hereditary substance in the eggs and sperms. According to this view, ~~the~~ ~~acquired~~ environmental ~~eff~~ influences on for instance body size caused by overeating or starvation, would be inherited to the offspring, exactly as Lamarck had postulated, and hybrids should be intermediate between the parents and would produce a uniform progeny similar to itself. In this hybrid the hereditary substances of the parents were supposed to be mixed; and when the hybrid formed sex cells, these would contain a homogeneous mixture of the hereditary constitutions of the original parents. With other words, it was believed that the hereditary substances of the parents were mixed as thoroughly as any two soluble liquids. In animals and in man it was believed that the hereditary substance had something to do with the blood — a view reflected in such expressions as "half-blood", "full blood", and "blue blood".

During the latter part of the 19th century observations were made that demonstrated that this view must be based on some fallacy. As to the inheritance of acquired characters through gemmules, the German biologist August Weismann showed its incorrectness through detailed experiments with mice and their tail length . . . . . -
But the gemmules-hypothesis was most thoroughly contradicted by some simple experiments performed by the Moravian monk Gregor Mendel, who worked with different pure lines of garden peas, which were constant thanks to their being almost obligate inbreeders, but differed in single conspicuous characters: yellow or green seeds; ~~non~~ ~~filled~~ ~~and~~ round or wrinkled seeds; white or colored flowers; yellow or green pods; etc. When Mendel crossed lines differing in these characters, he found that the ~~characters~~ hybrids were not at all intermediate between the parents, but in most cases corresponded to one of them. Inevitably dominant - recessive. (later: prevalence for intermediate).

The experimental hybrid between two pure lines is F_1 (= Filial = progeny; P = parental). Self pollination → F_2 never uniform or constant; on the contrary, some plants showed the dominant character, others the recessive. Mendel counted these individuals from large-scale experiments, and found that, on an average, 3/4 of a progeny had the dominant character, 1/4 the recessive. F_3: all recessive constantly recessive, 1/3 ~~some~~ dominant also constant, but 2/3 ~~others~~ showed the same segregation as the F_2 plants or 3:1. . . etc. . .

Mendel realized that his results could only be explained by the assumption that the hereditary differences between the intercrossed parents depended on individual and constant units of heredity, which he called factors but we name genes (a term coined by Johannsen 1909: Elemente der exakten Erblichkeitslehre — from Genetics: Bateson 1906 — gene = genos = sex = genus). The genes are transmitted in unchanged condition by the sex cells from one generation to the next — ~~Mendel found this theoretically, we call them unknown~~.

Mendel introduced letter designations for what he called pair of factors, or alleles, dominant by capitals, recessives by lower case (or small) letters. Coloured gen flower A, the white flower, a. Mendel assumed that the sex cells contain only one member of a pair of alleles, thus assuming that — genetic reduction takes place when sex cells are formed. Self pollination: A + A = AA, or a + a = aa. Hybrids A + a = Aa; since A dominates, the coloured flower F_1.

Mendel indicated the F_2 procedure:

♀ sex cells	♂ sex cells A	a
A	AA	Aa
a	Aa	aa

$1 : \underbrace{2 : 1} = 1 : 3$.

[~~Procedure: 1:2:1~~]. Aa × aa or Aa × AA = backcross; preferably to the recessive. 1:1

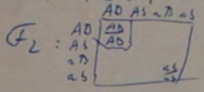
Central point of Mendel's discovery: A hybrid forms more than one kind of sex cells, and that dominant and recessive are distributed with equal frequencies in male as well as female sex cells, i.e. <u>not</u> as Darwin and others thought; they never disappear but are hidden when recessive if a dominant gene is present.

This is for diploid organisms — in haploid-diploid, like mosses, 1:1 segregations instead of 3:1 = backcrosses or rather Aa → a and A.

3.

This example is for monohybrid combinations of one gene pair only, and it explains mainly the inheritance of single variations.

Dihybrid: red flowers + round seeds, white flowers + wrinkled seeds, = AABB, aabb. Sex cells or gametes: AB and ab. F_1 AaBb, (red, round).

F_2 :


$\Rightarrow$ 9 AB : 3 Ab : 3 aB : 1 ab = 16 combinations.

Backcrossed by Mendel: AaBb : aabb = four categories, in same frequency: 1:1:1:1, because the F_1 forms four kinds of gametes in the same frequency: AB, Ab, aB and ab. aabb only one kind of gametes ab.

$\frac{AB}{ab}$. $\frac{Ab}{ab}$. $\frac{aB}{ab}$. $\frac{ab}{ab}$ are externally different: red, round, red wrinkled, white round, white wrinkled.

The genes may be recombined in the hybrids — a very important discovery that explains increase in variation — two new and constant combinations. AAbb and aaBB. The genes are the same, but recombined, and now form true-breeding lines. A basis of breeding.

Hybridizing also AAbb and aaBB → same results: 9:3:3:1.

More complicated if prevalence instead of dominance, but the all intermediates are heterozygotic → versus homozygotic.

introduced by Bateson 1906.

Trihybrid segregation; general formulas.

In crosses between parents differing in more than two pairs of genes, the principle is the same but the segregation more complicated. In a typical *trihybrid segregation*, in which three pairs of genes are involved (Aa, Bb, Cc), the segregation ratio in the F_2 will be 27:9:9:9:3:3:3:1=64. The 27 combinations will contain A, B, and C in a single or double dose; the three nines will correspond to the combinations ABc, AbC, and aBC, with the dominant genes occurring either in single or double dose; the three threes will have the combinations Abc, aBc, and abC (with the dominants single or double), and the remaining one will represent the triple recessive and homozygous combination aabbcc.

In monohybrid segregation, the hybrid forms two types of gametes (A and a); in dihybrid four (AB, Ab, aB and ab), in trihybrid eight (ABC, ABc, AbC, aBC, Abc, aBc, abC, and abc). To study the trihybrid segregation more closely, we can use these for a checkerboard, and then will see that the 64 squares will form the segregation sum of 27:9:9:9:3:3:3:1.

If the number of genes is larger than three, the recombination possibilities are greatly increased. This may be clarified by aid of two very simple formulas, the first of which is $\underline{2^n}$, indicating how many different kinds of gametes a hybrid that is heterozygous for $\underline{n}$ different genes is able to form. If $n=1$, then $2^n = 2^1 = 2$ different kinds of gametes, A and a; if $n=2$, then $2^2=4$, if $n=3$, then $2^3 = 2 \times 2 \times 2 = 8$. If $n=10$, then $2^{10} = 1024$. If we count with that human beings have 5000 gene~~s~~ pairs, which certainly is a very low number, much too low, then 2^{5000} = (Pierre can tell us).

↓

Still more important, but just as simple, is the formula $\underline{3^n}$ in which n again indicates the number of genes for which a certain hybrid is heterozygous. This formula denotes the number of genetically different combinations in the offspring of the hybrids. In monohybrid, n=1, $3^1 = 3$ = in F_2 three genetically different categories: $\underbrace{AA, A-}_{3}, \underset{1}{aa}$.
Dihybrid: $\underline{3^2} = \underline{9}$ = AABB, A-BB, AABb, A-Bb, AAbb, A-bb, aaBB, aaBb, aabb.
This is more easily understood if we start from the typical dihybrid segregation ratio 9:3:3:1 of 9 AB combinations (= 1AABB, 2A-BB, 2AABb, 4A-Bb): 3A (1AAbb, 2A-bb), 3B (= 1aaBB, 2aaBb), 1ab (= aabb).

With trihybrid segregation 3^3 = 27 genetically different categories. And with higher n-values the degree of genetical variation is enormously increased. If n = 10, then 3^{10} = 59,049 different combinations of genes may be formed; and if n = 50 or 100 or even 5000, the numbers are astronomical, explaining why no two human individuals, other than monozygotic twins, ever have been genetically similar.

Mendel's Versuche über Pflanzenhybriden, classical like Darwin's work. Unknown when M. died 1884, rediscovered 1900 by Hugo de Vries, Carl Correns, and Erich von Tschermak-Seysenegg. 1900 therefore the birthyear of genetics and modern views of evolution and modern animal and plant breeding.

Deviating segregation ratios.

Dominance often incomplete = prevalence, the Aa intermediate.
E.g. red × white = light red.
(~~Mutant effect; close to the mother, discuss later.~~)
A famous example of prevalence: Andalusian chicken, which have a bluish or speckled color tone because of a mosaic of white and black feathers, = a cross between a white and a black race.
Andalusian never breed true, but always 1 : 2 : 1 = black, Andal. white : AA.Aa aa.
Closer to dominant than recessive, not quite intermediate:
~~Mutant effect~~: two-rowed and six-rowed barley, the hybrid is more similar to the two-rowed parent

Frequently, there are complications by what is called interaction, so that the dihybrid segregation may be changed to other dihybrid segregation ratios such as 9 : 7, 9 : 3 : 4, 12 : 3 : 1, and 15 : 1.

In the first case, 9 : 7 segregation, we are dealing with what is called complementary genes, a term that implies, that each gene per se is without effect, but when both genes occur together, a certain character is developed or expressed. In the classical case it was a question of a cross between two white-flowered varieties of sweet peas, in which the F_1 hybrid had red flowers, and the F_2 segregated into 9 red : 7 white. In this instance the parents had the constitution AAbb and aaBB, i.e. one dominant gene each. A and B did not have any effect when they were alone, and the parental flowers were, therefore, white. In the F_1, AaBb, both dominants together, thus red — as when two colorless liquids are mixed to give rise to a colored solution. In the F_2 9/16 with A and B, whereas the 7 white are 3Ab + 3aB + 1ab).

9 : 3 : 4 = one of the dominant genes effectless when alone, (not both).
E.g. A = red, B = changes red to purple. Without A the white only.
9AB purple, 3Ab red, 3aB white, 1ab white.

↓

12:3:1: arises when a dominant gene prevents another dominant gene from being expressed. In oats certain dominant genes for black and gray kernels are known = A and B. Parental types may be $AAbb$ and $aaBB$, former parent black kernels, latter gray. $F_1 = AaBb$; since kernels cannot be black and gray at the same time, they are black, the gray is masked by black. This is called epistasis, i.e. A is epistatic over B, – or B is hypostatic to A: in F_2:

9 AB = black + gray = black, 3 Ab = black (cannot be distinguished),
3 aB = gray, 1 ab = white.

Epistasis is not dominance, and they should be clearly distinguished. Rather interaction or cooperation, since dominance refers to the relation between alleles of the same pair.

13:3 will rise from inhibiting factors or inhibitors, which prevent certain dominant genes from exerting their normal action.

For instance, R = red flowers, r = white flowers. Inhibitor H prevents R from producing color, thus HR = white. H alone = white. The cross $\underset{\text{present}}{\underline{H}HRR} \times \underset{\text{absent}}{hh\underline{rr}}$ (both parents white flowered). F_1: $HhRr$ white because of H. F_2: 3/16 red flowered because of presence of R and absence of H. Segregation:
9 HR: white because of H; 3 Hr white because of absence of R,
3 hR: red because of R and absence of H, 1 hr: white because of absence of R.
Fairly uncommon, but observed in plants and animals.

15:1 is a special case of polymeric or multiple genes = cooperation between different genes with similar effects. R_1 and R_2 = (red color). $R_1R_1R_2R_2 \times r_1r_1r_2r_2 = R_1r_1R_2r_2$ F_1. – F_2 = 15 red : 1 white ($r_1r_1r_2r_2$).
~~There are other deviations, but these~~ Polymeric genes are of interest to quantitative inheritance studies.

Pleiotropism = several different effects of one gene, e.g. at different times of development; two or more things.

Do not confuse ~~multi~~ polymeric or multiple genes affecting the same character with *multiple alleles*, which are ~~ge~~ more than two genes at the same locus affecting the same external character, e.g. eye color in Drosophila.

A special case of pleiotropism is when a gene for a certain morphological character, e.g. (R/r red veins in *Oenothera*, stimulates the pollen ~~grain~~ tube to grow faster so that ~~the~~ higher frequency of *R* fertilizes the egg than do *r*. The phenomenon of various speed of pollen tube growth is also connected with chromosome size and sex chromosomes. It is called *certation*, from certatio = race. Named by N. Heribert-Nilsson.

Before leaving this field, we can remember that a gene is made up of DNA.

1) What is the difference between genetics and mendelism?

2) Difference between dominance and epistasis?

3) Pleiotropism?

4) Try different dihybrid gene combinations, with and without complementary genes, epistasis, inhibitors, and polymeric genes.

23/2 69.

Biosystematics 3.

It was demonstrated by a number of students of minute anatomy during the 17th and 18th centuries that the tissues of organisms have a cellular organization. The earliest published picture of such a structure appeared in 1665 in a book by Robert Hooke. He called this structure a cell, which meant simply cavities bounded by walls, like cells in a honeycomb, or globules of numerous unrelated things. For most part they were looked upon as subordinate components of tissues rather than important individualized units. Dutrochet ([illegible]) In 1837, Schleiden (plants) and 1839, Schwann, (animals,) showed that all plants and animals are made of cells, whereas in 1831 Robert Brown had shown that all cells have not only a ~~proto~~cytoplasm but also a nucleus. The first observation of a cell division was made by Wilhelm Hofmeister in 1848; he drew correct pictures of the pollen divisions in Tradescantia. Protoplasm (von Mohl 1844; Cytoplasm + nucleoplasm: Strasburger 1882) The discovery of fertilization as the fusion of two nuclei was made in 1875 by Richard Hertwig, working on the sea urchin egg. Chromosome research, however, did not start effectively until in the 1880's, and since then a very large species of plants and animals have been very carefully studied with regard to the number and morphology of the chromosomes. 90% since 1937, when the general book by Darlington was published, ~~the 3rd edition in [illegible] Cytology (earlier Recent advances in Cytology)~~.

Literally, chromosome means "color body". The name was chosen by Waldeyer (1888) because the chromosomes absorb and retain certain dyestuffs to a higher degree than other parts of the cell. It is, therefore, relatively easy to make them clearly visible and to study them in detail with the aid of the microscope. They are, as a rule, invisible in cells that do not divide but appear as distinct bodies with definite form only during cell division.

Since the chromosomes represent the material substance that conditions the similarities between generations and that also underlies biological variation, it is of cardinal importance to study how the chromosomes behave during the different stages of the life of the individual.

Before we proceed further, it may be convenient to introduce two terms, which cytogeneticists use frequently, namely gamete and zygote, terms proposed by Bateson (1902). Gamete means sex cell and is formed from the Greek ~~word~~ gamikos, of or for marriage; whereas zygote is the cell that arises as a result of the fusion of the male and female gametes, i.e. fertilized egg cell. Zygote is from Greek zygotos = yoked.

An ordinary nuclear division = mitosis (Flemming 1882: from mitos = thread)

Reduction division = meiosis (Farmer & Moore 1905): maiotic phases; from ~~meiot~~ meioun = to lessen.

Somatic; soma = body (Weismann 1882?).
(contra: germ cells, or Keimzellen: Engler & Prantl (1897).

Mitosis — begins with interphase, previously called resting stage which is a misnomer.

Prophase: long and slender chromosomes, each divided into two chromatides, with a centromere.
the centromere is a moving body, perhaps the site of life itself?
In Interphase and prophase a nuclear membrane; disappears late in prophase.

Metaphase: Orientation and shortening of chromosomes; spindle formed.

Anaphase: Chromatides separated and move towards opposite poles, after centromere division.
(backwards) Two identical sets of chromosomes.

Telophase: Chromosomes less dense, disappear into a new interphase.

The end
Cell number at the beginning of embryonic development is 2^n, where n is the number of mitosis — obviously a fairly low number of divisions leads to the large number of cells in multicellular organisms.

Meiosis:

In ordinary mitoses, the daughter cells receive exactly the same chromosome complement as originally possessed by the mother cell. On the other hand, in meiosis, which occurs before the formation of sex cells, a halfing of the chromosome number occurs.

1st division Begins with interphase; then a long prophase:

1. Leptotene: Chromosomes as single (not double as in mitosis) threads, with beads = chromomeres. Threads dispersed evenly in the nucleus.
2. Zygotene: Chromosomes pair, corresponding chromomeres side by side. First near the centromere or at one end. Association extends, until the whole complement are present as double or bivalent threads, in the haploid number.
3. Pachytene: Paired threads coil around one another and their proximal chromomeres increase in size. Differential condensation in different parts.
4. (Early Diplotene: Each chromosome falls apart into two chromatids, which remain in close association. Exchange partners, at points where they are held together: crossing-over — chiasmata where the chromatids have broken. (chiasma = two lines placed crosswise, as an X; Janssens 1909).
5. Late Diplotene: Spiralization continues, chromosomes straighten and successive loops between chiasmata come to lie at right angles.
6. Diakinesis: Chromosomes shorten, spiralization reaches a maximum, chiasmata move out towards the ends.
7. First Metaphase: Paired chromosomes arrange themselves with their pairs of centromeres evenly distributed on either side of the equatorial plane of the spindle.
8. First Anaphase, Centromeres of each pair pass to opposite poles — with a pair of attached chromatids so that the chiasmata are separated.
9. First Telophase: From two daughter nuclei at poles, uncoil and form a short interphase, two separate cells formed. Each nucleus is haploid.

IInd division;

10. Metaphase-II: The two chromatids widely separated, more than at mitosis, held together by centromere. Later stages look like mitosis.
11. Anaphase-II: Separation like in ordinary mitosis.
12. Telophase-II: Four daughter nuclei are formed.

Meiosis results in that each of the four new cells will contain one representative of each chromosome pair, either maternal or paternal, but not both, and distributed by haphazard.

In all organisms with sexual reproduction there is a perpetual alternation between two phases with different chromosome numbers; these phases are called haplophase and diplophase. Haplophase is represented by the lower chromosome number and diplophase by the higher number. By aid of these cytological informations the processes of alternation of generations, which are still much used in lower plant morphology, are easily understood.

The haplo- and diplophases develop differently in different organisms. In most animals the haplophase is greatly reduced and practically limited to the gametes or sex cells. In many lower plants just the opposite occurs; the diplophase is limited to the fertilized female gamete, or zygote, which undergoes meiosis and forms spores, from which the haplophase will then develop. In certain algae, for instance, the haplophase and diplophase are about equally developed and even have about the same external appearance. In mosses the haplophase is more prominent than the diplophase. The moss plants are haploid, while the diplophase is limited to the less conspicuous spore capsule and its stalk, which grows up from the fertilized egg. Meiosis in mosses occurs in the spore capsules and leads to the formation of haploid spores that give rise to new haploid moss plants.

In ferns the diplophase dominates and is represented by the fern plants themselves upon which the spores are formed. As usual the spores are haploid as a result of meiosis. With germination of the spores, prothallia are formed that together with the spores represent the haplophase of the ferns. The prothallia are usually small and insignificant but they are free-living organisms, on which the male and female sexual organs are developed. The sex cells in these organs are formed without meiosis, since the prothallia are already haploid. The fertilized egg-cell, on the other hand, will be diploid, and from it a diploid fern plant will develop.

In flowering plants the haplophase is still more reduced and is only represented by the pollen grains and embryo sac. The pollen grains are, to a certain extent, independent organisms, whereas the embryo sacs are not liberated but live in the mother plant. The pollen grains are formed in the anthers, which at an early stage usually contain a large number of pollen *mother cells*, or *microspore* mother cells. Meiosis takes place in the p.m.c., which are changed into *tetrads* (dyad, not quintet, – duetto!), i.e. groups of four haploid cells, or *microspores*. These cells eventually separate from each other (exception: Ericaceae, Cyperaceae, ~~etc.~~ Orchidaceae: all together: pollinium), and develop into pollen grains. Initially these pollen grains have only one nucleus, but by a mitosis they soon develop into binucleate pollen grains, containing one *vegetative* and one *generative* cell. The *vegetative* nucleus, which also is called the *tube nucleus*) is situated in the middle of the pollen grain and does not divide again; the *generative* nucleus, on the other hand, divides once more and gives rise to two *sperm nuclei*, each of which is surrounded by a small amount of cytoplasm. The sperm nucleus and its cytoplasm constitute a small sperm cell. When they have been formed, the pollen grain is mature and ready for fertilization.

The embryo sac is formed from a megaspore (or macrospore) mother cell in the ovule. Such a cell undergoes meiosis and gives rise to four *megaspores* (or macrospores) with reduced chromosome numbers. Usually only one of these megaspores will develop into an embryo sac, the other three degenerate. The embryo sac develops in different ways in different groups of flowering plants, but as a rule, there will be *three* consecutive mitoses leading to an embryo sac containing eight nuclei. Three of these nuclei are located in the proximal end of the embryo sac and form the socalled *egg apparatus*, which consists of one *egg cell* and two so-called *synergids*. Of the five other nuclei, three form *antipodal cells*, in the distal end of the embryo sac, whereas the remaining two nuclei, the *polar nuclei*, remain lying in the middle of the embryo sac. Strangely enough, the two polar nuclei usually fuse to form a *fusion nucleus*, which contains twice as many chromosomes as the other nuclei in the embryo sac.

Before fertilization – pollen grains must land – the stigmatic surface of the pistil, germinate, form *pollen tubes*, reaches the embryo sac. Each tube transmits *two* sperms, one fertilizing the *egg* cell, the other uniting with the *fusion* nucleus. *Double fertilization* in higher plants. Embryo develops from the zygote, *endosperm* (albumen) from the fusion nucleus, which is triploid. The embryo is the beginning of the diplophase – but the endosperm is triploid.

In the higher animals, including man, the sex cells are formed in a similar way as in flowering plants. In the male sex there exist a large number of cells in the testicles (primary spermatocytes), which undergo meiosis and give rise to four cells or spermatids, each with the haploid chromosome number. These cells, which are comparable to the young mononucleate pollen grains in a flowering plant, are transformed, without further nuclear division, into sperms.

In the female, meiosis occurs in the ovaries. As in flowering plants, every mother cell, primary oocyte, gives rise only to one functional cell with a reduced chromosome number. The other three cells degenerate. ~~(polar bodies)~~. This occurs in such a way that the egg mother cell first forms a polar body as a result of the first meiotic division. This body contains a nucleus and a small part of the cytoplasm of the egg mother cell. The polar body is completely detached from the egg mother cells and ~~[illegible]~~ degenerates, ~~A second polar body~~ after having divided and formed two cells, and at the same time the secondary oocyte forms another polar body which is also dissolved. Only one cell remains, and it develops into the egg. The egg nucleus is haploid and the cell contains a substantial quantity of nourishment, especially in reptiles and birds. The ostrich egg is ~~[illegible]~~ a single cell and its yolk is the largest animal cell known.

The haploid egg cells of animals are fertilized by the haploid ~~spermato~~ sperms after various kinds of copulation, and form the zygote which grows into the embryo and into the new diploid individual.

Let me mention that the units of Mendelian inheritance are located on the chromosomes. This has been demonstrated satisfactorily ~~[illegible]~~ by aid of numerous early experiments so this claim is without dispute. By aid of studies of linkage, which are connected with observations of genetical crossing-over and cytological chiasmata, it is possible to map the genes on a chromosome, though this requires facilities which never have been available ~~in Cla~~ at this University. Such phenomena have significance in evolution and ~~[illegible]~~ biosystematic studies, but since they are only periferal, they can be left out of the present discussion in the hope that you get information about them in other courses in genetics.

A process that is of a greater importance to ~~our~~ the phenomena we must consider is that of meiosis, ~~As mentioned before~~, and then especially the formation of chiasmata and its results. In this connection, however we must restrict us to the statement that chiasma formation has a double function, one of which is genetic crossing-over and consequent recombination of genes, the other other a mechanical attachment of the homologous chromosomes during that part of meiosis which ranges from diplotene to first metaphase. It ought to be pointed out, however, that the mechanism of ~~[illegible]~~ chiasma formation is not an absolute requisite for meiosis — it is, e.g. not met with in males of Drosophila, who, therefore, show no genetical crossing-over — and in some other insects it is known that pairing is a case of attraction between homologous chromosomes without an exchange of chromosome segments.

Genetically, meiosis is important because alleles comprising allelic pairs separate. But it is also important as a stage at which we can easily discover changes that are of basic evolutionary importance. Since a discussion of structural chromosome alterations require ~~[illegible]~~ a whole lecture, we will wait with them until next time, and instead we might discuss one of the phenomena already mentioned.

7/4 '69.

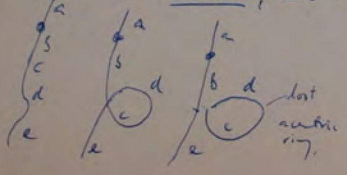
Biosystematics IV.

Structural chromosome alterations.

Chromosomes are extremely constant, as is ~~the~~ necessary for material on which so much important matter depends, but they are not entirely unalterable, and on their changes depends evolution itself or one of its most important processes. Their structure may be changed in different ways, either spontaneously, (~~i.e. by unknown causes~~) by internal causes, or as a consequence of different external agents. If we wish to bring about structural chromosome alterations, the most effective method is to irradiate the animal or plant with X-rays or other kinds of radiation with great ionizing power. Certain chemicals also have a similar effect. After treatment of this kind, it often happens that the chromosome is broken transversely at one or several places. This process of breaking is called <u>fragmentation</u>. ([illegible], aging).

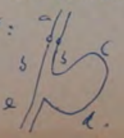
The simplest kind of fragmentation is, of course, when the chromosome is divided into two pieces. If the breakage does not occur precisely in the centromere, which in exceptional cases may occur, fragmentation leads to two chromosome segments, one of which carries the centromere, whereas the other is <u>acentric</u>, i.e. lacks a centromere. Since the acentric fragment is no longer able to participate in the process of mitosis, it will, as a rule, remain in the cell in which it arose and will gradually disintegrate there. The „<u>centric</u>" fragment, with the centromere, is, however, able to continue to divide in a normal way like an ordinary chromosome. It differs from a normal chromosome in that the breakage surface, where the fragmentation first occurred, has properties other than those of a typical chromosome end. Gradually, however, „healing" will take place, and the new shortened chromosome will then, in all respects, behave like a normal chromosome. Fragmentation, in this case, has led to a <u>deficiency</u>, i.e. a loss of a distal portion of the chromosome, including a chromosome end. Deficiencies may be long or short, but those most frequent include only a few chromomeres.

A loss of a segment does not necessarily need to be at the end of a chromosome, and it is at least as frequent that an interior or middle part of a chromosome is lost. Such a structural alteration is called a <u>deletion</u>, and it usually arises through the formation of a loop:



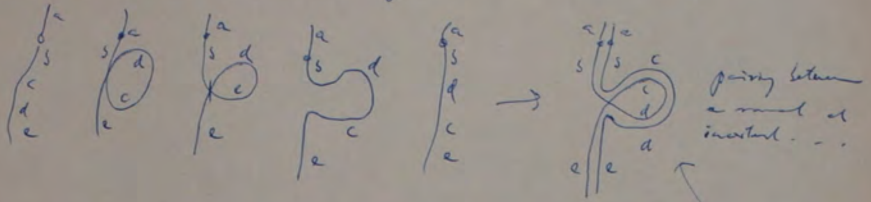
Loop in the original a<u>bcde</u> chromosome; break and union where the chromosome strands are in contact. Ring-shaped and a rod — the latter survives.

Pairing of this deleted part:



Much studied in Drosophila salivary gland chromosomes, corn, rye.

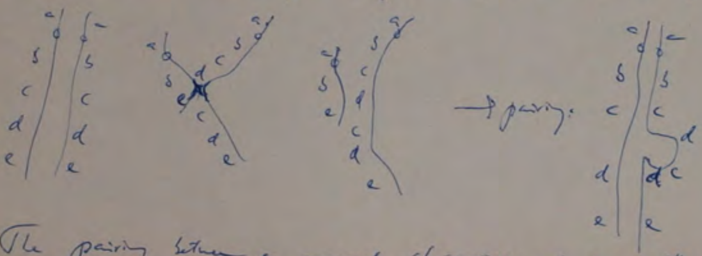
The formation of a chromosome loop may also lead to the origin of an <u>inversion</u>, i.e. a reversal of the position of an interior or middle chromosome segment. This is schematically so:



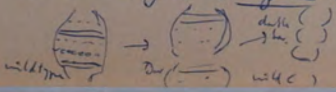
Also in this case, four broken surfaces are formed; these surfaces will have a strong tendency to unite in pairs. This may either occur in such a way that a deletion and an acentric ring are formed, or that the cd segment will be reversed or inverted, so that the original chromosome, abcde, will be replaced by the new abdce. (Same genes but in another order, position effect).

The pairing between a normal and a chromosome with an inverted segment requires the formation of a rounded bulge by one and a loop by the other.
Well known from Drosophila and pachytene ~~[illegible]~~ stages of corn and rye.

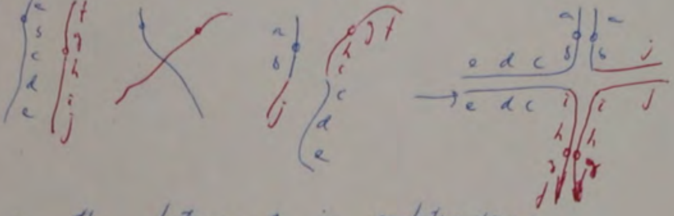
The opposite of a deletion is called a <u>duplication</u>. It signifies, as indicated by the name, that a certain chromosome segment is duplicated. Duplications may arise in various ways, but they are probably most frequently produced when two homologous chromosomes ~~to~~ come to lie across each other and break at the points of contact, followed by possible recombinations of the four chromosome ends. The result will be two new chromosomes, one of which (abe) representing a deletion, and the other (abcdcde) a duplication, in which the segment cd is present twice:



The pairing between a normal chromosome and one with a duplicated segment must lead to the formation of a loop similar to one found in a deletion heterozygote. Well known from <u>Drosophila</u> etc. <u>Bar</u>, Dou<u>ble Bar</u> — (eye form):



The last major type of structural chromosome alterations is known as a *translocation* or *segmental interchange*. It is the result of that segments of chromosomes belonging to different pairs exchange places. This may occur as a consequence of a contact between two non-homologous chromosomes, and at a certain point where they lie across each other breaks may occur followed by a new kind of chromosome reunion:



Pairing in the heterozygote in pachytene stage):

It was originally assumed that translocations might at least sometimes be single, a segment from one chromosome being attached to the end of another unaltered chromosome. At present it seems clear that such translocations do not occur and that all such changes are double, so that the segments are always exchanged, thus more correctly called segmental interchanges. A precondition for the origin of a structural alteration is that the *two* newly broken chromosome ends are near each other. In cases of single translocations only one end would be available, and in such a case the broken segment does not have any possibility of becoming permanently attached to an unbroken chromosome. A translocation, however, may appear to be single when a very small segment of one chromosome has been interchanged with a larger segment from another chromosome.

With the formation of deletions, *ring-shaped chromosomes* arise. If they lack centromeres, they will soon be eliminated. On the other hand, if they are provided with a centromere, they are capable of division. Such chromosomes, which are well investigated in *Drosophila* and corn, often divide in a deviating way and may give rise to rings of double size with two centromeres through abnormal chiasmata formation and crossing-over. At anaphase these rings will be disrupted, after which the four broken ends often recombine and form two new rings of smaller size. These in their turn may be doubled and dissociated in subsequent mitotic cycles, resulting in a large number of structurally different ring types. If genes with known genetic effects are located in these rings, a combined genetic and cytological analysis may lead to interesting results.

The effects of structural chromosome alterations.

Structural alterations induce certain phenotypic changes, which we will not discuss in this connection, but they have also different effects on chromosome pairing and fertility of the organism.

Let us start with deficiencies and deletions, which actually represent a single category, characterized by the loss of a larger or smaller chromosome segment. Such a loss will, as a rule, have very marked effects, but with a considerable difference between homo- and heterozygotes. In a heterozygote with one normal and one deficient chromosome, vigor is usually rather good if the missing segment is small; but the larger the piece that is missing, the poorer the vigor will be. Fertility in these heterozygotes is usually reduced. In flowering plants, gametes carrying a deficiency are, as a rule, nonfunctional in the pollen but are occasionally transmitted by the ovules. In animals the gametes will all function normally; but the resulting zygotes, which are heterozygous for the deficiency, are usually unable to develop if the deficiency is large. — In most cases homozygosity for deficiencies and deletions has a deleterious effect and leads to death, even if the lost segments are quite small. Thus, chromosomes, as a rule, are so highly differentiated that every small part has an indispensable function.

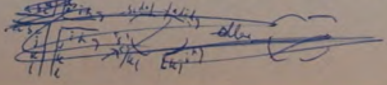
Duplications have more benign effects than the loss of chromosome substance; but even in this category, there is a disturbance of chromosome balance that in instances of larger duplications causes a reduction in fertility and vigor.

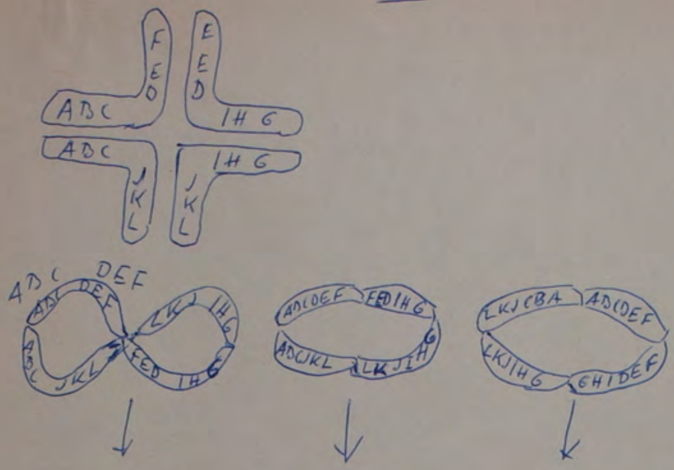
Segmental interchanges.

what happens for dicentrics (dizentrische) Chr. cf. Rieger & Michaelis p. 103 (Cytogenetik).

In contrast to heterozygotes for duplications, deficiencies and deletions, heterozygotes for segmental interchanges are easy to find. I mentioned that at meiosis in a segmental interchange heterozygote the two interchanged chromosomes and the corresponding original chromosomes form a crosslike configuration during pachytene. If at least one chiasma is formed in each arm — which as a rule is the case — an association of four chromosomes will arise, and it is easy to distinguish during diplotene, diakinesis, and first metaphase. The occurrence of a ring of four chromosomes in a diploid organism, which otherwise forms only ordinary chromosome pairs, is a reliable indication of heterozygosity for a segmental interchange.

As a rule, a segmental interchange heterozygote has a reduced fertility — which is another, though less reliable, indication that segmental interchange between non-homologous chromosomes has occurred. The reason for reduced gametic viability is the formation of gametes in which certain chromosome segments are lacking, whereas other segments occur in a double dose. : scheme: other side;





ABCDEF	ABCDEF	ABCDEF
GHIJKL	FEDIHG	ABCJKL
ABCJKL	ABCJKL	LKJIHG
FEDIHG	LKJIHG	FEDIHG.

Original chromosomes: ABCDEF and GHIJKL.
Segmental interchange: ABCJKL and GHIDEF

Only two of six gametes will be balanced or contain all four segments: (ABCDEF. GHIJKL) and (ABCJKL. FEDIHG). the other four unbalanced. ~~and die~~.

In flowering plants, where the effects of segmental interchanges are well investigated, pollen grains with an unbalanced chromosome complement are killed by their own hereditary constitution. Dead or bad grains contra living or good — easy to see under a microscope after simple staining — empty or filled. Also, the embryo sacs are unable to function.

If the chromosomes in a segmental interchange ring of four are distributed at random two by two at first metaphase, only two of six possible combinations will be balanced and viable. Good pollen is then expected to be 33.3%. However, fertility is usually higher and sometimes like normal, because segmental interchange rings are most frequently arranged in zigzag fashion at first metaphase, resulting in balanced genetical distribution.

In a zigzag case every alternate chromosome in the ring will move to the same pole, so that the anaphase groups, and the gametes, will receive a balanced chromosome complement and be functional. ~~If, on the other hand, adjacent chromosomes in the ring~~

The decisive factor for fertility in a translocation heterozygote is the frequency of figure-eight configurations at first metaphase. If this frequency amounts to 100%, such a heterozygote will be quite fertile. Such cases are well-known, for instance in Oenothera(14), ~~and~~ Datura(14), Rhoeo(12), Campanula(20). More frequently, however, part of the pollen mother cells and megaspore mother cells contain regular interchange rings, in which the adjacent chromosomes pass to the same pole, resulting in about 50% sterility which indicates that the frequency of figure-eight and regular rings at first metaphase is about the same.

In animals the haplophase is still more reduced than in higher plants; this is probably the reason why the short-lived sex cells in animals are, as a rule, quite functional even if they have received a very unbalanced constitution. However, the sterility comes at the zygotic stage, so that fertilized eggs or embryos with unbalanced chromosome constitutions are killed by their own unsuitable hereditary constitutions.

Inversions.

Inversions are ~~somewhat more~~ difficult to demonstrate than translocations but lead to characteristic deviations in individuals having one normal and one inverted chromosome. The effect of such heterozygosity at the pachytene stage and in salivary chromosomes has already been mentioned.

In addition, inversions can be demonstrated at the first anaphase — if the inverted segment is large enough to allow a relatively high frequency of crossing-over. Diagram: result → dicentric chromatid and acentric fragment. = bridge & fragment. Dicentric chromatid will be broken, resulting in larger or smaller deficiencies and duplications. In plants this disturbs the genetic equilibrium and leads to partial sterility, especially of pollen.

Inversions are common — Paris quadrifolia (non-Trillium), Drosophila, etc. Several consecutive inversions in Drosophila . . .

14/3 69

Biosystematics V.

If we accept the biological species concept, which regards each species as representing a single gene pool, isolated from other such pools by a reproductive barrier against mixibility, then it is evident that every species is characterized by a single and specific chromosome number. The fact that only in a few number of described species have more than one such numbers been observed, demonstrates the skill with which non-experimental taxonomists of the past have been able to distinguish these gene pools; whenever such an exceptional case is discovered, its observation ought to be followed by a detailed taxonomical study that will result in the description of a new species.

When the chromosome numbers of different species of a genus are compared, three different possibilities are met with: 1) all the species may have the same chromosome number; 2) the species may have various chromosome numbers, which do not show any obvious relationship to each other; and, 3) the chromosome numbers of the species may form a multiple series. This third possibility is of general occurrence, especially among flowering plants, and it is of a great importance. Therefore, it deserves to be discussed in detail.

Definition — ~~If we look at the species of wheat, which is the most important of all cultivated plants, some taxa have~~ Taxon – taxa (taxon, taxa, Lam 1948: – to indicate taxonomic groups of any rank). Originally from Meyer 1926: Logik der Morphologie im Rahmen einer Logik der gesamten Biologie; from taxonomy, as phylon (Haeckel 1866) from phylogeny).

If we look at the species of wheat, which is the most important of all cultivated plants, some taxa have $2\underline{n} = 14$ chromosomes, others $2\underline{n} = 28$, and still others $2\underline{n} = 42$. These numbers are multiples of seven, and ~~thus seven is said to be~~ since seven is the lowest haploid number of the series, it is said to be the basic number ~~(x)~~ of wheat. The basic number is the ~~[illegible]~~ monoploid number of the series, and it is usually indicated with the letter $\underline{x}$, as contrasted to the haploid $\underline{n}$ and diploid $2\underline{n}$. A polyploid series is indicated by $2x, 3x, 4x$ etc. — a haploid may be a polyploid: $\underline{n} = 28 = 4x$.

In other genera there may be other basic numbers. In *Chrysanthemum* x = 9, and in this genus, species and hybrids are known with all multiples of 9 from 18 to 90. In the potato and tobacco genera (*Solanum* and *Nicotiana*) x = 12, and the somatic numbers are, for instance, 24, 48 and 72. In the apple genus, *Malus* x = 17; in poplars and willows, (*Populus* and *Salix*) x = 19. Most basic numbers, however, are lower than 12, and higher numbers are usually secondary.

The occurrence of a multiple chromosome number series is known as *polyploidy* (Winkler 1916) and it represents a highly interesting regularity. This phenomenon occurs in about 1/3 of all higher plants known; it is more frequent under extreme conditions, and is typical of many of our cultivated plants. In the wheats, the diploid wheats are most primitive and of little use at present (einkorn), the tetraploids (macaroni emmer) formed the basis for the ~~Mediterranean and~~ Egyptian civilization, whereas the hexaploids are the modern breadwheats (dinkel).

In several other cases, for instance in oats (*Avena*), we meet with similar conditions. As a rule, those species in a polyploid series that have the highest chromosome numbers are also the most valuable as cultivated plants. Besides wheat, and oats, this is true for potato, tobacco, white clover, alfalfa, timothy, Kentucky bluegrass, ~~oat~~ orchard grass, and the banana, apple, orange, sugarcane, and figs. On the other hand, rye, barley, and beets have low, nonpolyploid or diploid chromosome numbers.

It is known that most ferns, which are the oldest of presently living higher plants, are highly polyploid, and so are also the mosses, whereas polyploidy is quite rare in the conifers. In animals the phenomenon is also frequent, though it is often masked by chromosomal variations connected with sex.

The origin of a polyploid series has been elucidated by experimental investigations. It is known, for instance, that species representing high levels in a series have arisen from older species with lower chromosome numbers. It has also been found that polyploids may be of three different kinds, which we designate as *autopolyploidy*, and *allopolyploidy* ~~and endoploidy~~. With *autoploidy* we are concerned with a purely quantitative increase in the number of chromosome sets, that originate from the same species or from a hybrid between two races. *Alloploidy*, involves a summation of chromosome sets from different species. Whereas *endoploidy* signifies an increase in the number of chromosomes within a cell. In connection with autoploidy, it may also be appropriate to mention *haploidy*, which is the occurrence of individuals with half the number of chromosomes of the species in question. It may be best to discuss these phenomena separately and each in its turn.

Autoploidy.

The first observed autoploid was the so-called gigas mutant of *Oenothera* (erythrosepala) *Lamarckiana*, which was studied by de Vries and later found to have 2n = 28, instead of 14 chromosomes. Another similar case was observed by American workers in the Jimson weed, *Datura stramonium*. Also in this species, the deviating type was initially thought to be a mutant, which on account of its deviating external properties and its inability to intercross with the initial form was assigned the name „New Species". Upon cytological examination, the chromosome number was found to be 48 instead of 24.

During recent decades so many autoploids have been produced that the effects of such alterations are easy to characterize. Starting with such cases as those just mentioned, in which the chromosome number of the autoploid is exactly twice that of the original taxon, it is convenient to designate the original diploid as AA, the new tetraploid as AAAA. Each A denotes a chromosome set, a so-called genome, i.e. the chromosome complement present in the gametes of the lowest level, monoploid level, in the polyploid series (Winkler 1920). Haploid - diploid. — Monoploid - diploid, ~~tetr~~, tri, tetra, penta, hexa, hepta, octo, nono, deca, ... dodeca- - -

With regard to their external characters, ~~autotetraploids, are~~ true autotetraploids, or panautotetraploids (L. & L. 1949) are characterized by a certain degree of gigantism; stems, leaves, and seeds having greater dimensions than in the original material. These changes, which are often very striking and which have, therefore, been of great importance for the production of new types of ornamental plants, are primarily due to the fact that the cells are considerably larger in the tetraploids. This is because there is fairly strong relationship between chromosome number and the size of the cell nucleus, and also between nucleus size and cell volume. Thus, tetraploids are built of larger „building blocks" than diploids; and, if the cell number is unchanged, this will lead to an increase in the size of the organs. The changes in size may also be in part gene conditioned. When the chromosome number has been doubled, the entire set of genes has also been duplicated — which, of course, must have fairly far-reaching genetical consequences.

At any rate, doubling the chromosome number usually leads to an increase in the size of various organs, and in many cases but certainly not always, to an increase in the size of the entire plant. Different species react differently to chromosome doubling, and often the new chromosome number is above the optimum; the tetraploids have certain gigas properties, but may not be as well developed or vigorous as the original diploid. This is especially true when the primary material already has a relatively high chromosome number. Thus, in common wheat, products with 84 chromosomes instead of the usual 42, display poor vigor. On the other hand, rye with 28, instead of 14, is an unusually successful tetraploid that is superior to ordinary rye with respect to vegetative development.

Another fact that should be stressed in this connection is that primarily the tetraploids are often weaker and more disharmonious than those tetraploids that eventually may be derived from them after a period of gene recombination and selection. Just as a new mutation will not show its optimal properties until recombination has had an opportunity to grind off its initial effects and to fit it into the general genotype in the best possible way. New tetraploids are „raw" tetraploids, which may be improved in different ways, if genetic recombination is given an opportunity to act upon them. In cross-fertilizers this will occur spontaneously, whereas in self-fertilizers different primary tetraploids must be crossed in order to achieve such a recombination effect.

Chromosome doubling also has physiological consequences. Thus, autoploids often have a lower osmotic pressure, or perhaps rather a wider adaptability of the osmotic pressure, a retarded rate of cell division, and a longer vegetative period than the corresponding diploids. Lower osmotic pressure leads to reduced frost hardiness, but a wider adaptability of the osmotic pressure is always positive. In several cases, differences in the contents of vitamins, drugs, and in other chemical composition of the cells have also been found.

The physiological effects of autoploidy may also be responsible for the fact that the numbers of flowers that are embryologically formed and developed are often lower in the tetraploids than in the original diploid material.

VI. 21/3.

Meiosis, fertility, chromosomal variation

A very characteristic and unfavorable property of autotetraploids is that their fertility is usually reduced. This may in part be due to purely genic causes, which may be removed by recombination and selection. Much of the sterility, however, is caused by the fact that meiosis in an autotetraploid follows a course quite different from that in a diploid. This is due to the presence of four homologous chromosomes of each kind instead of two. Assuming that the primary material is a diploid species with 14 chromosomes (AA), there will form seven bivalents (Haecker 1892) at meiosis, which may be called a_1-a_1, $a_2-a_2 \ldots a_7-a_7$. In the tetraploid (AAAA), there will be four chromosomes of each type, and at meiosis these seven groups of four chromosomes may form seven <u>quadrivalents</u> (tri, quadri, penta, hexa, hepta, octo, etc.). A quadrivalent is an association of four homologous chromosomes.

Not always, however, do the four homologous chromosomes succeed in finding each other, and the quadrivalents are not formed. Sometimes, the homologous chromosomes are represented by an association of three chromosomes, called a trivalent, and a univalent, or by two bivalents. As a rule, therefore, the average number of quadrivalents per cell is, therefore, lower than the maximum possible number. Autotetraploids of different species behave differently in this respect. Some of them have a very high frequency of quadrivalents, others a low number, and in some cases bivalents are found almost exclusively. In most cases about half of the chromosomes form quadrivalents.

The occurrence of trivalents and univalents at meiosis in an autotetraploid leads to disturbances in chromosome distribution and to the formation of gametes with deviating chromosome numbers. In an autotetraploid with 28 chromosomes all the gametes would receive 14 chromosomes if meiosis were regular. On account of the disturbances mentioned, however, many of the gametes will have chromosome numbers that diverge somewhat from 14, mainly 13 or 15 but even wider deviations. These gametes are often inviable due to their deviating constitution or they are less vigorous than the gametes with 14 chromosomes. This is the principal cause for the high degree of sterility in an autotetraploid.

Generally, sterility is more pronounced in the pollen than in the ovules, and at least part of the gametes with deviating numbers usually function on the female side. This will give rise to <u>aneuploidy</u>, i.e. the occurrence of individuals with chromosome numbers falling outside the strict polyploid series. (euploidy, aneuploidy: Täckholm 1922.)

In the example given above, aneuploidy will occur in individuals with 27 or 29 instead of 28 chromosomes. Such deviating plants have poorer vigor and lower fertility than those having the exact tetraploid number of 28. This fact is of great interest, since it demonstrates clearly that a chromosome set is a well-balanced unit, the function of which is disturbed by deviation from the normal chromosome number. In spite of the fact that a plant with 27 chromosomes has three normal chromosome sets, the absence of a single chromosome in the fourth set brings about a reduction in vigor and fertility of the plant; and the same is true also when there is one wheel too many in the "machinery", or 29 instead of 28 chromosomes. Wider deviations from the tetraploid number may have still more marked effects.

In such circumstances it is possible to understand why polyploid series may be preserved in nature. In many genera a sensitivity to aneuploid deviations is so pronounced that only individuals with precise multiples of the basic chromosome sets occur in nature — sometimes in series that range from the diploid to the decaploid or even 100-ploid or more (Ophioglossum 240-480-720, 1440; Rumex: 20-200; Antennaria 14-56;

Crossing barriers.

Another essential factor that contributes towards preserving the polyploid series is the fact that an autotetraploid is often more or less separated from the original diploid form by a crossing barrier. Thus, it is extremely difficult to produce hybrids between ordinary diploid barley with 14 chromosomes and the autotetraploid with 28 chromosomes. The same difficulty was observed already by de Vries in *Oenothera gigas*, and it is met with again in the autotetraploid taxa of *Datura*. As mentioned previously, this taxon was called a "New Species", especially because it could not be crossed with the original diploid.

The isolation between diploid and autotetraploid taxa is manifested in part by checked pollen-tube growth, in part by certain disturbances during embryo development. The causes of these disturbances are not yet fully clarified, but the basic cause is known to be of a purely quantitative nature. Such quantitatively conditioned crossing difficulties are also of importance for natural species formation by polyploidy.

It should be mentioned in this connection that when common rye with 14 chromosomes and tetraploid rye with 28 chromosomes are cultivated in closeby fields, pollen from the diploid will strongly reduce seed setting in the tetraploid. This is caused by the fact that hybrid embryos with 14+7=21 chromosomes are formed, but they succumb at an early stage except in a few cases, which give rise to seeds with 21 chromosomes. Plants derived from the latter will have three genomes and are said to be *triploid*.

Autotriploids.

With regard to their external phenotypes, autotriploids have properties similar to ~~[illegible]~~ autotetraploids, i.e. they are often gigas forms as compared to the corresponding diploids. Sometimes the optimum for an increase in the chromosome number is evidently situated at the triploid rather than at higher levels. The so-called giant aspens with 3x19 = 57 chromosomes occur spontaneously in nature and have also been experimentally produced. They are autotriploid clones displaying rapid growth and large vegetative and floral dimensions. Autotetraploid aspens, on the other hand, are not known in nature; and those experimentally produced are not as vigorous as the natural triploids. Triploid sugar beets (with 3x9 = 27), which, contrary to the general rule, may easily be produced by crosses between tetraploids and diploids, are superior to both parental taxa. Several of our most valuable apple varieties are triploid with 3x17 = 51 chromosomes. On an average, the triploid varieties seem to have better storage qualities and a higher vitamin C content than the ordinary diploid apple varieties with 34 chromosomes.

A circumstance that limits the economic exploitation of the autotriploids is their pronounced sterility. This sterility is primarily caused by strong chromosomal disturbances in meiosis, which are generally characteristic of individuals having three homologous sets of chromosomes. During meiosis these identical chromosomes tend to form trivalents.

When the three chromosomes of a trivalent separate at first anaphase, two chromosomes will move to one pole and one to the other. If all seven trivalents are oriented in the same way, with one chromosome directed to the upper pole and two to the lower one, the interphase nuclei will have 7 and 14 chromosomes, respectively. After the second division, gametes will be produced with these chromosome numbers. This, however, is an extreme case, which rarely occurs. The orientation of the trivalents is usually at random so that the most frequent chromosome distributions will be 10 and 11, corresponding to about half the somatic triploid number, but other numbers between 7 and 14 will also occur. Of these chromosome numbers, only 7 and 14 represent multiples of the basic number, whereas the numbers 8-13 are aneuploid. Gametes with these aneuploid numbers will usually succumb, especially on the male side, and only pollen grains and ovules with 7 or 14 chromosomes will function normally. Similar conditions are met with in other autotriploids, and it is therefore understandable that autotriploids generally have very poor fertility. It should also be remembered that meiotic irregularities in a triploid are increased by the presence of univalents, which are distributed at random at anaphase and often eliminated.

Besides triploidy and tetraploidy, higher levels of autoploidy are also known. Thus, a doubling of the chromosome number in an autotetraploid will lead to an octoploid with eight times the basic number. These extreme autoploids are rarely viable in experiments, though some are, and even much higher polyploids of ~~this way~~ autoploid origin are known in nature.

Autoploidy may be induced by meiotic disturbances due: 2 = 21 → 14+7 ∂ 14+7 = 28.
Also by a treatment with various narcotics (colchicine), higher or low temperatures.

Haploidy.

In flowering plants the diplophase dominates, and the haplophase is normally limited to the pollen grains and embryo sacs. It is interesting to note, however, that in exceptional cases plants may arise that are entirely haploid. Since these haploids only carry one genome, they will have the same chromosome number as the gametes in a diploid; in spite of this, they may develop into relatively normal plants with essentially the same morphological appearance as the corresponding diploids, except for that they are smaller and weaker. The weakness is particularly evident in haploids of cross-fertilizers, in which the general occurrence of recessive and deleterious genes directly afflicts the haploids, because there is only one set of chromosomes so the recessive defect will immediately emerge. In diploids this effect will be buffered by the homologous chromosome.

Meiosis in a true haploid is very irregular, because chromosome pairs cannot be formed, and the chromosomes are distributed at random. Therefore, they are usually completely sterile, except if unreduced gametes are formed.

In <u>polyhaploids</u>, i.e. haploids obtained from polyploid species, conditions will be more complicated because these haploids will contain more than one genome. If the genomes are homologous or partially homologous, bivalent formation and good fertility in the polyhaploid may be the consequence.

Haploids may be produced spontaneously, but in very low frequencies. They can be produced experimentally with considerable effect by aid of some methods. The first is <u>delayed pollination</u>, i.e. pollination is delayed until the egg starts to divide without fertilization, and then the formation of a triploid endosperm after pollination will stimulate the growth of the embryo. – Pollination with heavily X-rayed pollen also may result in haploidy. – Pollination with pollen of a different species is a third method. – Fourth method is the twin method: perhaps 5 %oo haploids.

8.

Alloploidy.

The Danish geneticist Øjvind Winge formulated in 1917 the theory that polyploid series in nature arise by species hybridization and summation of the diploid chromosome sets of the intercrossed species. Let us, for example, assume that species I and species II have 14 chromosomes each, but of different kinds. The genomes of the two species may be denoted by AA and BB, each letter indicating a set of seven chromosomes. If hybrids are produced, they are AB.

Winge assumed that the chromosome number in such species hybrids, is sometimes doubled at an early stage and presumably in the zygote. This would occur because the chromosome replication would be disturbed in such a way that cells with 28 instead of 14 chromosomes would arise. These polyploid cells would give rise to individuals with a double chromosome number, i.e., in the example given, to plants in which all the cells would have AABB instead of AB. At meiosis, A genomes would pair with each other and form seven bivalents, 7_{II}; and the B genomes would also form 7_{II}. Meiosis should become quite regular and give rise to gametes with 14 chromosomes each — the AABB then would breed true and be a new species with 28 chromosomes, representing a synthesis of the original AA and BB parents.

Wingé's theory has been thoroughly verified by thousands of observations in nature and experiment. The best example is the wheat genus:

T. monococcum (einkorn): 2n = 14 = AA; *T. dicoccum* (emmer wheat): 2n = 28 = AABB.
T. aestivum (dinkel, breadwheat): 2n = 42 = AABBDD;
Aegilops squarrosa 2n = 14 = DD; *Ae. speltoides* 2n = 14 = BB.
Ryewheat = AABBRR = 42; AABBDDRR = 56.
This is genome analysis. Made difficult by partial homology or homeology.
Nicotiana tabacum 2n = 48 = *N. sylvestris* + *N. tomentosiformis* 2n = 24 + 24.
Brassica napus (rape): 2n = 38 = *B. campestris* (field mustard) 2n = 20 + *B. oleracea* (cabbage) 2n = 18.
Raphanobrassica: *Raphanus* (radish) + *Brassica* (cabbage). 18 + 18 = 36.

From these examples and many more it is save to conclude that not only quantitative, autoploid alterations in chromosome number, but, perhaps to a still higher degree alloploidy by species hybridization and summation of the different genomes has played an important role in the origin of polyploid series in wild plants as well as in the origin of many cultivated plants.

Actually hybridization — the less related the parents the more successful the polyploids.
Panauto → doubling of the genome of an individual or pure line: ca. 3-5% in all populations; usually very little vitality (most common, rarely survives) (~~[illegible]~~
Hemiauto → doubling of a hybrid between races of the same species → less common, survives better).
Hemiallo → doubling of hybrids between subspecies; rare, highly successful.
Panallo → doubling of very distant hybrids; hybrids very rare, alloploid highly successful.
full fertility in hybrid for 2 first → low fertility for hybrid.
little success ⟶ high success.

9.

28/3'69.
(just in — [illegible])

Aneuploidy. (Täckholm 1922)

In connection with the discussion of autotriploids and autotetraploids, the phenomenon that is called aneuploidy was mentioned. Aneuploidy is the occurrence of chromosome numbers that deviate from exact multiples of the chromosome sets. Gametes ~~that~~ and individuals with numbers that are not strictly polyploid have reduced vigor or are markedly inferior to normal individuals in one respect or another. This is also the case with haploids, in which only unreduced gametes are viable, because they alone contain a complete set of chromosomes.

Our knowledge of aneuploidy and its effects are to a large extent based on the classical investigations of trisomics (Blakeslee 1921), which in the 1920's were carried out by the Americans A.F. Blakeslee and J. Belling, on Datura stramonium, the Jimson weed. It is a diploid species with 2n = 24 chromosomes. Blakeslee and Belling obtained in their material plants with 2n = 25 chromosomes, which they termed trisomic because they had three chromosomes of one kind, instead of two, and gradually they obtained trisomics of each of the 12 chromosome pairs, which they called the twelve apostles; and each was found to be morphologically distinct and easily distinguishable from one another. This is a nice demonstration of the fact that the genes are carried in the chromosomes.

The trisomics are less vigorous than the normal diploids, but various trisomics are different in this respect, and pollen grains with an extra chromosome are less vigorous than normal ones, in plants. (Their segregation ratio is frequently 2:1, but rarely 17:1). Downe's syndrome: mongolism.

Monosomics _ nullisomics — more viable in polyploids, lethal in diploids. Used for analysis of genes and in plant breeding.

I have mentioned that it is evident that evolution has combined entire chromosome sets from two species to form an allopolyploid. It is also possible to bring together parts of different genomes. If, for instance, crosses are made between wheat with 42 chromosomes and ryewheat with 56 chromosomes, a hybrid with 49 chromosomes (42 wheat + 7 rye) will be obtained. If such a hybrid is backcrossed to wheat, it is possible to get plants with 42 wheat chromosomes and single rye chromosomes and among them plants having two rye chromosomes of the same kind. In lines from such plants it is possible to add economically important properties as disease resistance.

It has even been possible to substitute one wheat chromosome pair for one rye pair. Though this is only used rarely in plant breeding, with considerable effects, it is at least possible that something similar may also have taken place rarely in nature.

The deleterious effect of aneuploidy is most pronounced when the absolute chromosome number is low, and it grows weaker with an increased polyploidy.

In species with high chromosome numbers, there is often a certain variation around that high number without any distinct effect. In plant genera with high basic numbers, the sensitivity to aneuploidy is also less pronounced. This is probably caused by that the high basic numbers (19: *Populus*, 17: *Pomoideae*) are actually polyploid, so the plants are secondary polyploids (Darlington & Moffett 1930). Example also: *Brassica napus* $2n=38$ $x=19$; from $x=10$ fr. *B. campestris* + $x=9$ fr. *B. oleracea*.

Agmatoploidy: *Luzula*, *Carex*, insects.

B-chromosomes:

Everything that has been said so far about chromosomes has demonstrated that these bodies are indispensible for living organisms. Strangely enough, there are also chromosomes that have been found to be indifferent or even deleterious in their effects.

In papers published in 1927 and 1928 A. E. Longley and L. F. Randolph reported the occurrence of what they called B-chromosomes in corn. This designation was used for a kind of small chromosome that occurred in varying numbers in some individuals of corn in addition to the ordinary chromosome complement. All normal corn plants have 20 so-called A-chromosomes, and alterations in the number or structure of these chromosomes have just as acute effects as in *Drosophila* and *Datura*. The B-chromosomes, on the other hand, are only present in some corn plants and occur in varying frequencies in different strains. Plants without B-chromosomes have quite normal properties, and there is no evidence that the plants containing B-chromosomes are in any way superior to plants without B-chromosomes. On the contrary, it is clear that plants with many B-chromosomes are weaker and less fertile than other plants. This effect, however, will not be obvious unless the number of B-chromosomes is fairly large. This number may range from one to more than 20. An interesting property of the B-chromosomes in corn is that they are heterochromatic, i.e., they have rather sticky surfaces and stain somewhat differently from A-chromosomes.

Before the discovery of B-chromosomes in corn, rye plants in different countries were observed to have 16 instead of 14 chromosomes. The latter number is the normal one, and at the outset it was assumed that the increase from 14 to 16 was due to a transverse division of one of the ordinary rye chromosomes. However, from investigations by Japanese and Russian workers it became gradually clear that the 16-chromosome rye carries two supernumerary chromosomes of a quite specific type, and also that these supernumerary chromosomes behave in a deviating way during the first mitosis of the pollen grains.

Since 1940 these phenomena in rye, and similar phenomena in other plant genera, have been investigated more closely, especially in Sweden. Rye plants with two extra chromosomes of the kind just indicated — later on called *standard B-chromosomes* as distinguished from other altered B-chromosome types that have arisen in culture — were first observed in two Swedish rye varieties. Later on, seeds of primitive strains of rye were obtained from Turkey, Afghanistan, Iran, eastern Siberia, and Korea, and in most of the samples B-chromosomes were found to occur in various frequencies. Exceptional was the material from Korea, which had B-chromosomes in no less than 90% of the plants studied.

The results obtained from ~~[illegible]~~ very detailed analyses of the pachytene chromosomes at meiosis have shown that B-chromosomes of different origin have the same organization, though they may differ in certain structural details. In spite of these minor differences, it is evident that this chromosome type is essentially the same in all plants so far studied since they all have the same peculiar property: They are able to double their number (at minimum) once during each generation. During the first division of the pollen grain (and at the corresponding stage on the female side, the two chromatids of the B-chromosomes do not separate and move to opposite poles, but instead both pass to the same pole and are included in the generative nucleus that gives rise to the sperm or the egg cell.

In the offspring of plants with two standard B-chromosomes, the majority of the plants will have four such chromosomes; and in their offspring the numerical increase will continue. This increase in number is, however, checked by the deleterious effect of these chromosomes on fertility and vigor. That effect is obvious already in plants with two B-chromosomes, and it clearly increases with an increase in their number. No rye plants with more than 8 B-chromosomes are viable, and those with more than 6 B-chromosomes are completely sterile. Nevertheless, this deleterious effect is much weaker than that of supernumeraries of A-type, since even one extra A-chromosome has a very strong negative effect. The B-chromosomes in rye are *sub-inert*, i.e., have a markedly reduced genetic effect.

B-chromosomes are generally deleterious though ~~[illegible]~~ never as strongly as ordinary chromosomes. ~~Evidence has been [illegible]~~ In some plants, like *Festuca pratensis* and *Centaurea scabiosa*, a low number of B-chromosomes has a benign effect on vitality and plant vigor in certain ecological circumstances. It is possible that they have played a certain role in evolution, though this still is a matter that is insufficiently known, mainly because of the lack of a systematic search for these chromosomes in the entire floras under various ecological conditions. It is a phenomenon worth looking at much closer, though this mentioning of it must suffice in this connection.

Biosystematics VI.

Hereditary adaptation – ecotypes.

Quantitative properties are usually conditioned by a large number of genes. It is important to recognize this fact when we try to interprete the adaptations which organisms undergo under different environmental conditions.

All organisms manifest a certain degree of environmentally induced plasticity. In times when variation through gene recombination was unknown, it was believed that all biological variation depended on the fact that variable environmental conditions directly affected the individual characteristics. Such views were accepted not only by Lamarck in 1809 but also by Darwin in 1859, and several others. We do not need to go into details of the discussions of the possible inheritance of acquired characters, which dominated biology in the last century, though it is worth while to mention that some biochemists, even some of those who call themselves molecular geneticists, have a difficulty in abandoning such explanations, and you have probably all heard about Lysenko.

It is natural selection that is the cause of what we call adaptations in the living world. These adaptations are in part environmental, but they are most frequently genotypic. Genotypical adaptation is initially brought about by an interaction between gene recombination and natural selection. This is particularly evident in species which occur in different kinds of habitats or which live under different climatic conditions. In such cases it is possible to establish that a species is differentiated into groups of biotypes that are genetically adapted to a certain environment. A group of biotypes having certain adaptive properties in common is called an ecotype.

The term ecotype was coined by Göte Turesson in 1922 on basis of broad experimental investigation of Swedish plants. Similar investigations of ecotypes in large scale have later been carried out by James Gregor in Edinburgh and Clausen, Keck & Hiesey at Stanford, but at present no facilities for such transplantation studies are available anywhere. The principal method employed in ecotypic investigations involves the collection of plants from a large number of different localities within the distribution area of each species. This material is cultivated in the same experimental field, where it is often possible to observe surprisingly marked differences among plants from different habitats or climatic areas.

Turesson's classical material was *Hieracium umbellatum*, a hawkweed, which he collected from a series of localities along the coast and from the interior of the province of Scania in southern Sweden. The plants from the sandy seashores were characterized by a prostrate growth habit, long shoots, and narrow, hairy leaves, whereas the same species collected in cliff localities was represented by an ecotype with broader and more shiny, green leaves, short shoots and a compressed growth habit. Lastly, the inland type was late flowering, tall and erect, and had distinctively narrow leaves.

Hieracium umbellatum represents a good example of differentiation into ecotypes that depends on more or less sharp edaphic (soil) differences between habitats. Another species, *Solidago virgaurea*, was found to be differentiated into ecotypes by climatic differences. When plants from the alpine regions of northern Sweden were transplanted to an experimental garden in southern Sweden and cultivated together with plants from the southern province of Scania, the differences in development were very striking. The northern ecotype was of low stature and flowered very early, whereas the southern ecotype was several times taller and flowered much later in the summer. These ecotypes are well adapted to their areas of origin. In the north, *Solidago* must rapidly reach the flowering and seed-setting stages if the seeds are to mature before the short summer has passed. The southern ecotype, on the other hand, has more time to its disposal and is therefore able to attain greater dimensions. A large number of similar observations in other species have clearly demonstrated that differentiation induced by the habitat or the climate really represents a favorable adaptation to the environment. In certain cases

(clines) this has also been verified by plant physiological and biochemical investigations.

When differentiation is conditioned by the habitat, the ecotype differences are usually more distinct than in climatic ecotypes. The differences among habitats are often quite abrupt and pronounced as, for instance, in the transition from cliffs to beaches or from moors to forests. Climatic differences, — temperature and day length — are more continuous, and ecotypic differentiation in these cases ~~at~~ may thus represent a gradual transition between the extreme types. In the latter case it may be more appropriate to speak of ecoclines rather than of ecotypes. (Cline: Huxley 1939, Gr. klinein, to slant). But still both of these concepts are expressions of a hereditary adaptation to the environment.

When a collection of ecotypes is cultivated together in an experimental garden, all the ecotypes, of course, will be modified by the environment of the experimental garden; but the essential thing is that characteristic differences determined by the hereditary differences between the various ecotypes will remain.

Turesson demonstrated by raising seed progenies and by making artificial crosses, that these differences are really genetic. The new generations raised from seed retain, in general, the characteristic properties of the ecotype; but after crosses between different ecotypes within the same species the F_2 will display a complex segregation, demonstrating that many genes are involved. Evidently, polymeric genes cause the quantitative differences observed among different ecotypes or members of an ecocline.

All ecotypes have arisen from an interaction between genetic recombination and natural selection. Only those gene combinations that confer an advantage in the struggle for life can produce viable individuals that are able to reproduce themselves. The average genotype in a population of plants or in a stock of animals will, therefore, with great exactness respond to the demands made by the specific environment. That hereditary adaptation may arise is easy to understand when we know that such quantitative characters as winter hardiness, earliness, specific mode of growth, etc., are conditioned by many polymeric genes or multiple genes (factors). The recombination mechanism has a very large gene pool to work with and will lead to an almost unlimited number of different biotypes. Thus, nature has much to select from when meeting the demands made by a particular environment.

Although genetic adaptation will most easily occur in cross-fertilizing (allogamous) organisms that continuously produce a large number of new gene combinations, populations of homozygous self-fertilizers are also usually rich in different biotypes. This multitude of biotypes in autogamous biota is, in part, caused by the fact that self-fertilization is seldom absolute. Now and then spontaneous crosses between different biotypes may occur and give rise to swarms of new biotypes in the F_2 and later generations.

The occurrence of spontaneous mutations, i.e. sudden alterations of single genes, may also contribute to ~~[illegible]~~ this variability. Cross-fertilization is, however, the safest way to produce hereditary variation; and in nature there are a multitude of different mechanisms favoring cross-fertilization and, hence, variation through gene recombination. The most effective means is, of course, the separation into two sexes. But even in ~~[illegible]~~ hermaphroditic (bisexual) organisms self-fertilization may be precluded by special mechanisms; in plants, for instance, by different adaptations to insect pollination and through the presence of self-sterility genes.

Ecotypic differentiation may sometimes be so pronounced that it may be doubtful whether the ecotypes should be considered as belonging to the same species. According to Turesson we should speak of different ecotypes when these can be intercrossed without difficulty and produce fertile hybrids. When dealing with different species, however, crossing difficulties and reduced fertility in the hybrids are met with.

Turesson's data on ecotypic differentiation are comparable with similar experiences and conclusions drawn from investigations of cultivated plants. Winter wheat varieties from Sweden, i.e. old land varieties, were found to have better winter hardiness than British varieties, but to be less hardy than Finnish land wheats, which are extremely hardy. The degree of winter hardiness in wheat is clearly proportional to the degree of winter cold.

Other plant species behave in a similar way, and, as a consequence, plant breeding is most successfully carried out as a *local* breeding. When selection is carried out in a cross-fertilizer, or in a cross population of a self-fertilizer, the breeder will automatically be assisted by the local environmental conditions, which will eliminate certain recombinations, whereas others representing more successful constellations of genes will be preserved.

In man a certain ecotypic differentiation can be traced with regard to skin color. Dark skin color with its protective pigmentation is most prevalent in the warmest and sunniest parts of the earth. People native to the colder regions do not need so much pigment and thus are lighter colored. A Swede will be ~~[illegible]~~ ~~too~~ suntanned in Africa, but he will never become as dark as a negro. The modification, i.e. suntanning, has less protective value than the genotypically conditioned pigmentation. If a negro lives in more northern countries, his color will be somewhat modified towards lighter pigmentation, but an obvious difference in skin color between the Swede and the Negro will remain, whether the comparison is made in Sweden or in Africa. There is good reason to believe that this difference in pigmentation is not incidental but represents an adaptation to the different environments — it is clearly a case of ecotypic differentiation. (With its changing in the skin carotene to D-vitamins).

Hereditary adaptation to different environments is a fundamental biological fact that is not only valid with regard to differentiation *within* a species, but there is also much evidence that it is also of primary importance in the differentiation of species, and, indeed, for all those alterations of living organisms that is usually called evolution.

On the other hand, it is also known that a certain degree of differentiation may arise initially that does not involve any hereditary adaptation. This may occur if a small part of a population is detached from the main population and becomes isolated. In such an event it is highly improbable that the small daughter population will contain all the genes present in the mother population. By pure chance certain genes may be absent, or others may be present in higher frequencies. These gene differences also cause external and internal differences, which consequently do not result from natural selection and adaptation.

A good example of this type of differentiation is represented by a species of snail that is indigenous in certain mountain valleys of Hawaii. These valleys extend radially from volcanic summits, and are sharply isolated from each other by the steep valley slopes. Every valley has its specific type of snail, which may be distinguished from the snail forms from the other valleys by some definite morphological character. Since the habitats as well as the climate are practically identical in the valleys, the differentiation into different races cannot *per se* represent hereditary adaptation, it must instead be a question of differentiation due to random distribution of genes, socalled *genetic drift* (Sewall Wright 1931) or the *Sewall-Wright effect*.

Biosystematics VII

Species hybrids

I have mentioned previously that although plants with different chromosome numbers, sometimes may be crossed, ~~they~~ these hybrids are actually sterile, so that their genes cannot be mixed or recombined. With other words, chromosome number differences may allow crossability but not mixibility. Chromosome numbers may vary from $2n = 2$ in ~~the~~ *Ascaris*, which is ~~[illegible]~~ intestinal worm of the horse, ($2n = 4$, the Compositae *Haplopappus gracilis*), to $2n = 1260$, ~~which~~ in the Indian fern *Ophioglossum reticulatum*, though most animals and plants have less than 100 chromosomes. Nevertheless, there are so many species, that it is unavoidable that many unrelated animals and plants have the same chromosome number.

The shape of the chromosomes and their size differs considerably, ~~[illegible]~~ from chromosomes of *Scirpus* and *Luzula* which are just visible in the light microscope since they are a little more than 0.2 μ long, to those of lilies which may be more than 30 μ long! We distinguish chromosomes on basis of their size but more frequently on basis of their morphology, or *karyotype* (Levitsky 1931), usually by aid of the localization of their centromere. If the centromere is situated in the middle of the chromosome, the chromosome is *metacentric*. Submetacentric, subtelocentric, acrocentric (near end), telocentric (exactly at the end; very rare). Also said that the centromere is median, submedian, subterminal, terminal. Often *secondary* constrictions occur and make the identification of the chromosome easier; especially when satellites occur, connected with the formation of nucleoli, which are dense, spherical bodies rich in RNA and visible only or mainly in the interphase.

Even if different species have the same chromosome number and are related, they rarely cross if their chromosome morphology is not similar. And the grotesque combinations reported in mediaeval times have not been experimentally verified, as, e.g. the report of the creation of the ostrich from a hybrid between a sparrow and a camel! In animals, hybridization is often prevented because the *individuals* of different species do not *wish* to pair with each other. In *Drosophila* this has been studied in detail by bringing together females of one species with males ~~[illegible]~~ belonging in part to the same species and in part to a more or less closely related species. The females almost always prefer their own males. Hybridization is, also, often prevented by the fact that the sexual organs in the two species are so differently constructed that pairing is excluded.

In flowering plants species crosses are often prevented from the outset by the fact that pollen from one species is unable to germinate on the stigmas of the other. In other cases the pollen may germinate, but pollen tube growth is so slow that fertilization cannot take place. In certain instances, however, this difficulty may be experimentally prevented by stimulating pollen tube growth through moderate X-ray doses or by repeated pollinations.

If the egg is fertilized and a hybrid embryo is formed, the embryo may degenerate during its development, resulting in an inviable seed. In several cases of this kind it has been found that embryo death is not caused by an unsuitable embryo constitution, but by a physiological disharmony between the embryo and the mother plant. In other words, the mother is a "bad nurse" for the hybrid seed. This has been demonstrated by excising the embryo from the ovule, followed by culture of the excised embryo on an artificial nutrient medium. The technique for artificial embryo culture has been gradually improved, and it is presently possible to raise a considerable number of species hybrids that otherwise would not have survived.

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In most cases hybrids between closely related species are quite vigorous, showing socalled hybrid vigor or luxuriance. However, if the parental species differ markedly from each other, the hybrids may be weaker than the parents, and more or less abnormal. Such F_1 hybrids may, for instance, have a tendency for tumor formation or phenotypic variegation; the latter phenomenon depends on the fact that genes may be differently expressed in different parts of the same individual. It arises either from a disturbed of normal gene reproduction or by somatic elimination of certain chromosomes.

Frequently the cross is ~~[illegible]~~ successful but only a part of the F_1 are viable. This is sometimes explained as caused by that one of the parents is heterozygous for an allelic gene pair, which has no effect when segregating within this species, but which reacts in a special way with genes from the other species. Then, the dominant allele gives normal hybrids, whereas the recessive gene has a lethal effect when combined with genes from the other species. Since the gametes with the dominant and recessive genes are equally frequent, viable and nonviable hybrids will also arise in a ratio of 1:1. This phenomenon is best known from Crepis and Lamium.

Sterility.

Hybrids between different species as a rule have a reduced fertility or are even completely sterile. This sterility may have several different causes. In certain cases genes from one of the species combine so poorly with the genes from the other species that the sexual organs become defective. In species hybrids of plants the anthers are often abnormal and do not dehisce. Also the female reproductive organs are often nonfunctional or abortive. In other cases the disturbances do not occur until at a later stage and are then usually expressed as chromosomal irregularities during meiosis.

Numerous inversions, forming bridges, segmental interchanges resulting in rings and chains.

Progeny of F_1 (partially sterile hybrids is extremely variable, often abnormal, usually sterile, frequently much less viable than the F_1 and the parents.

Possible to transfer genes from one species to another, even chromosomes, if the species are not too far related: rye and wheat, through synthetics.

Cytotaxonomy studies the taxonomy by aid of chr. counts and morphol. chr. studies. Cytogeography studies cytol. phenomena connected with geography. Experimental ~~[illegible]~~ cytogenetics adds hybridization experiments and solves especially taxonomical and evolutionary problems of genera and species which do not differ markedly in chromosome morphology and number.

The only cytology done in [illegible], is based on observations of mainly mitosis and morphology of somatic chromosomes – still lacking all the fine techniques of meiotic investigations.

Biosystematics VIII.

Taxonomic categories and their definition.

~~Biosystematics~~

Before we go into detail of the methods of classification which are based on longer tradition than those of any other branch of science, I want to emphasize that taxonomy is at the same time the most elementary and most inclusive part of biology — most elementary because living beings cannot be discussed or treated in a scientific way until some classification has been achieved, and most inclusive because taxonomy in its various branches gathers together, utilizes, summarizes, and implements everything that is known about animals and plants, whether morphological, physiological, psychological, ecological, cytological or genetical or you name it. Most of all, taxonomy is what taught us about the fact of evolution, which has penetrated our knowledge during the past hundred or so years, in such a way that it has given us an understanding of the history of the universe and of the natural laws that decide about living and dead matter.

Biosystematics is the classification of living beings in categories in an evolutionary hierarchy. Such a hierarchy is closely connected with real relationships, and relationships can be studied with certainty only by aid of cytogenetical methods. Thus the big background discussions which we will try to incorporate in the following reports. It is evident that morphology is of a great importance to all classifications, but since it is determined by genes as is evolution at all stages, it should be clear that genetics is no less basic for taxonomy ~~the~~ and evolution than taxonomy is for these two fundamental sciences of the living world.

The twenty or more categories which the taxonomist uses in classification are of unequal value and of different significance. They fall quite naturally into three groups:

1) The species category
2) Categories for distinguishable populations within species.
3) Categories for higher taxa, that is for grouping of species.

The species, in a number of different ways, occupies a unique position in the taxonomic hierarchy.

Let us first discuss

The Species Problem.

It seems to be one of man's most elementary urges to want to identify things and name them. Even the most primitive people have names for kinds of birds, fishes, flowers, and trees. If only individuals existed, and the diversity of nature were continuous, it would be difficult to sort them into groups and distinguish "kinds". Fortunately, the diversity of nature is discontinuous, consisting in any local fauna and flora of more or less well-defined "kinds" which we call species. In the American southwest, for instance, there are about 7000 "kinds" of higher plants. These are the species of the taxonomist. Primitive natives in the mountains of New Guinea will distinguish the same kinds of organisms as, quite independently, does the specialist in the big national museums.

The concept of species seems so absurdly simple that it always comes as something of a shock to a beginning taxonomist to learn how voluminous and seemingly endless the debate about the species problem has been. In zoology there is now fair agreement on the species concept, but heterodox views are still vigorously defended in botany.

The species problem has been made to appear more difficult than it is by a confusion of the concepts underlying the terms phenon, taxon, and category. The working taxonomist sorts specimens or individuals into phena and decides which of these are members of populations each of which belongs to a single taxon of the species category. To be able to undertake the ranking of taxa, the taxonomist must have a clear conception of the category species. If he defines it in such a way that it coincides with the phenon, he may facilitate his task of sorting specimens, but his activity will result in species that are biologically and hence scientifically meaningless. The objective of a scientifically sound concept of the species category is to facilitate the assembling of phena into meaningful taxa on the species level. A short survey of the history of species concepts will show how different the species taxa are which one is forced to distinguish if one adopts different species concepts.

Species concepts.

Taxonomic literature reports innumerable species concepts. By their philosophical basis, all these concepts fall into three groups. The first two, the typological and the nominalistic species concepts, have mainly historical significance, but are still upheld by a few contemporary authors, whereas the third, the biological species concept, is based on evolutionary considerations and is being used by increasingly more biologists.

Typological species concept. According to this concept the observed diversity of the universe reflects the existence of a limited number of underlying "universals" or types (*eidos* of Plato). Individuals do not stand in any special relation to each other, being merely expressions of the same type. Variation is the result of imperfect manifestations of the idea implicit in each species. This species concept, going back to the philosophies of Plato and Aristotle, was the species concept of Linnaeus and his followers. Since this philosophical tradition is sometimes referred to as essentialism, the typological definition is also sometimes called the essentialist species definition. Various attempts at a purely numerical or mathematical species definitions are logical equivalents of this species concept. It must be emphasized that there is a complete difference between basing one's species concept on morphology and using morphological evidence as inference for the application of a biological species concept.

Two practical reasons exist for the now almost universal rejection of the typological species concept: (1) Individuals are frequently found in nature that are clearly conspecific with other individuals in spite of striking differences in structure owing to sexual dimorphism, age differences, polymorphism, and other forms of individual variation. Although often described originally as different species, they are deprived of their species status, regardless of the degree of morphological difference, as soon as they are found to be members of the same breeding population. Different phena that belong to a single population cannot be considered different species. (2) Sibling species differ hardly at all morphologically, yet are good biological species. Degree of difference is not the decisive criterion in the ranking of taxa as species.

Its own adherents abandon the typological species concept whenever they discover that they have named as a separate species something that is nothing but a conspecific phenon. At present the typological species concept is still defended by some writers adhering to Thomistic philosophy, which is ~~the scholastic phi~~ based on the scholastic doctrine of Thomas of Aquinas (+ 1274).

Nominalistic species concept. The nominalists deny the existence of real universals. For them only individuals exist, while species are man-made abstractions. (When they have to deal with a species, they treat it as an individual on a higher plane). The nominalistic species concept was popular in France in the eighteenth century (Buffon, Robinet, Lamarck) and has adherents to the present day. The American botanist Bessey expressed this viewpoint particularly well in 1908: „Nature produces individuals and nothing more, . . . species have no actual existence in nature. They are mental concepts and nothing more . . . . Species have been invented in order that we may refer to great numbers of individuals collectively".

The biological species concept. In the late eighteenth century it began to be realized that neither of the medieval species concepts discussed was applicable to species of living beings. An entirely new species concept began to emerge after about 1750. It is supported by statements of many naturalists and taxonomists of the nineteenth century. The German biologist K. Jordan (1905), however, was the first who clearly formulated the concept in all of its consequences. It combines elements of the typological and nominalistic concepts by stating that species have independent reality and are typified by the statistics of populations of individuals. It differs from both by stressing the populational aspect and genetic cohesion of the species, and by pointing out that it receives its reality from the historically evolved, shared information content of its gene pool.

As a result, the members of a biological species form (1) *a reproductive community*. The individuals of a species of animals recognize each other as potential mates and seek each other for the purpose of reproduction. A multitude of devices ensures intraspecific reproduction in all organisms. The species is also (2) *an ecological unit* which, regardless of the individuals composing it interacts as a unit with other species with which it shares the environment. The species, finally, is (3) *a genetic unit* consisting of a large, intercommunicating gene pool, whereas the individual is merely a temporary vessel holding a small portion of the contents of the gene pool for a short period of time. These three properties raise the species above the typological interpretation of a „class of objects". The species definition which results from this theoretical species concept is, as formulated by Ernst Mayr (1942):

Species are groups of interbreeding natural populations that are reproductively isolated from other such groups.

The development of the biological concept of the species is one of the earliest manifestations of the emancipation of biology from an inappropriate philosophy based on the phenomena of inanimate nature. This species concept is called biological not because it deals with biological taxa, but because the definition is biological. It utilizes criteria that are meaningless as far as the inanimate world is concerned.

When encountering difficulties it is important to focus on the basic biological meaning of the species: A species is a protected gene pool. It is a Mendelian population which has its own devices, called isolation mechanisms, which protect it against harmful gene flow from other gene pools. ~~These isolation mechanisms~~ Within the gene pool, so-called subspecies, varieties and forms may be formed on basis of gene mutation, genetic recombination and natural selection or genetic drift; although this kind of evolution, or subspeciation, may be favored by geographical or seasonal or edaphic isolation, it has no influence on the speciation processes, which are based on chromosomal differences, numerical and structural. If ~~[illegible]~~ internal reproductive barriers are formed by structural changes, like inversions and segmental interchanges, they become gradually stronger until they become an effective barrier to gene exchange and even to crossability; whereas those formed by numerical changes are abrupt. Abrupt speciation: panauto, hemiauto, hemiallo, panalloploidy. (discuss).

Genes of the same gene pool form harmonious combinations because they have become coadapted by natural selection. Mixing the genes of two different species leads to a high frequency of disharmonious gene combinations; mechanisms that prevent this are therefore favored by selection. This makes it quite clear that the word species in biology is a relational term: A is a species in relation to B and C because it is reproductively isolated from them. It has its primary significance with respect to sympatric and synchronic populations, and these are precisely the situations where the application of the concept faces the fewest difficulties. The more distant two populations are in space and time, the more difficult it becomes to test their species status in relation to each other because of diminished crossability, but the more irrelevant biologically this also becomes.

The biological species concept also solves the paradox caused by the conflict between the fixity of species of the naturalist and the fluidity of the species of the evolutionist. It was this conflict which made Linnaeus ~~to~~ deny evolution and Darwin the ~~not~~ reality of species. The biological species combines the discreteness of the local species at a given time with an evolutionary potential for continuing change.

The unique position of species in the hierarchy of taxonomic categories has been pointed out by many authors. Taxa of the species category can be delimited against each other by operationally defined criteria (interbreeding versus noninterbreeding of populations). It is the only taxonomic category for which the boundaries between ~~taxa~~ the taxa at that level are defined objectively.

Logicians do not always fully appreciate that the terminology of "a class" and "a member" fails to bring out the complete difference between, on one hand, the relation of individuals to the species and, on the other hand, ~~the relation of individuals~~ of species taxa to higher taxa. The statement that something is "a member of a class" has an entirely different meaning for an individual which through its genotype is a member of a species, and a species taxon which is included in a higher taxon. A category is not a class in the same sense as a higher taxon, but a designation of rank. Logicians do not appreciate that the "higher" and "lower" rank of taxa is a relative, not an absolute property. One can compare taxa in a single phyletic line, but one cannot say that the genus is the same thing in all kinds of plants and animals. Again, the species is an exception because (at least in sexual species) the species is an equivalent phenomenon in all groups of animals and plants.

Intraspecific categories designate groupings of populations within species. Normally, however, the species is the lowest category used in routine taxonomy. The higher categories are groupings of species. In view of this key position of the species and the fact that in nature one encounters individuals and phena, the assigning of individuals and phena to species taxa is one of the key problems of taxonomy.

26/x '69.

From phenon to taxon to category.

A failure to understand the meaning of the three terms, phenon, taxon, and category, has lead taxonomists into much confusion. It has been the cause of most attacks on the biological species concept. When an author says: "As a paleontologist I cannot employ the biological species concept because I cannot test the reproductive isolation of fossils," he reveals his lack of understanding. What the taxonomist observes directly are individual phenotypes which he sorts into phena, which are samples of phenotypically similar specimens, or a phenotypically reasonably uniform sample. On the certain biological concepts and information, such as an awareness of the possibility of sexual dimorphism, growth, alternation of generations, nongenetic modifications of the phenotype, etc., he assigns the phena to populations ~~which in~~ which are made up of the individuals of a given locality which potentially form a single interbreeding community. In turn, he classifies these populations into taxa, which are taxonomic groups that are sufficiently distinct to be worthy of being distinguished by name and to be ranked in a definite category. The ranking of a taxon into categories, which designate rank or level in a hierarchic classification, as subspecies, species, genus or family, is based on inferences drawn from the available data. This methodology of evolutionary classification bases inferences on evidence and uses, for the most part, concepts and definitions for which the data are not directly observable, as do most of the inductive sciences. Here it is necessary to emphasize the distinction between definition – and the evidence that the definition is met. We propose to define taxonomic categories in evolutionary and phylogenetic terms, but to use evidence that is almost entirely non-phylogenetic when taken as individual observations. In spite of considerable confusion about this distinction, even among some taxonomists, it is really not particularly difficult. The well-known example of monozygotic twins is explanatory and is something more than an analogy. We define such twins as two individuals developed from one zygote. No one has ever seen this occur in humans, but we recognize when the definition is met by evidence of similarities sufficient to sustain the inference. The individuals in question are not twins because they are similar but, quite to the contrary, are similar because they are twins. Precisely so, individuals do not belong in the same taxon because they are similar, but they are similar because they belong to the same taxon. Linnaeus was quite right when he said that the genus makes the characters, not vice versa, even though he did not know what makes a genus. This statement is a central element in evolutionary taxonomy, and the alternative clearly distinguishes it from non-evolutionary taxonomy. Another way to put the matter is to say that categories are defined in phylogenetic terms but that taxa are defined by somatic relationships that result from phylogeny and are evidence that the categorical definition is met.

The reproductive isolation of a biological species, the protection of its collective gene pool against pollution by genes from other species, results in a discontinuity not only of the genotype of the species, but also of its morphology and other aspects of the phenotype produced by this genotype, because mutations in one gene pool cannot be transferred into another. This is the fact on which taxonomic practice is based. Reproductive isolation cannot, of course, be directly observed in samples of preserved specimens. However, it can be inferred on the basis of various types of evidence, as for instance the presence of a discontinuity, a bridgeless gap, between two correlated character complexes. In living species, of course, such inferences can be tested by observation and experiment.

The crucial difference between the reasoning of the typologist and the adherent of the biological species concept is as follows: The typologist says: „There is a clear-cut morphological difference between samples a and b, therefore they are, by definition, two morphospecies, that is, two species." Any list of synonyms will quickly reveal how often this philosophy has led to the description of phena as species. The biological taxonomist asks: „Is the morphological difference between samples a and b of the kind one would expect to find between two reproductively isolated populations, that is, between two biological species?" In other words, he uses the amount and kind of morphological difference only as an indication of reproductive isolation, only as evidence to draw an inference. This is a legitimate and reliable technique. Where the typologist would recognize phena as species, the biologist will draw the right inferences from largely morphological evidence, and his species are usually confirmed by subsequent researches. When competent taxonomic work based on morphological evidence is re-examined in the light of the finding of behavior or biochemistry, it is usually confirmed in its entirety.

It is not always realized that the classification of phena is based on entirely different evidence than the classification of species. The classification of species is based on weighted similarity, evaluating all sorts of comparative data, be they morphological, physiological, behavioral or what not. The classification of phena is based on their relation to the gene pool of the population to which they belong. Ultimately this can be established only by breeding behavior. This in turn can be either observed in nature or studied experimentally. It does not matter whether one deals with strikingly different sexes in birds, insects or higher plants; breeding alone will establish ~~that~~ what phena together form a population. The experienced taxonomist knows what variation to expect within a biological species. No computer method seems yet to be found that would empirically assign phena to species. The taxonomist does this rapidly and with a high degree of precision on the basis of his accumulated knowledge of the biology of the species concerned. In this taxonomic operation the classical methods still reign supreme because they are enormously faster than presently known numerical methods.

The fact that difficulties sometimes arise when the biological species concept is applied to natural taxa does not mean that the concept as such is invalid. Many generally accepted concepts face similar difficulties when they have to be applied in a particular situation or to a specific sample. The concept *tree*, for instance, is not invalidated by the existence of spreading junipers, dwarf willows, giant cacti, and strangler figs. One must make a clear distinction between a concept and its application to a particular case.

The three most serious difficulties in the application of the biological species concept, are those caused by the lack of pertinent information, those caused by apomictic reproduction, and those caused by evolutionary intermediacy of gradual speciation.

Insufficient information. Individual variation in all of its forms often raises doubt as to whether a certain morphotype is a separate species or only a phenon within a variable population. Sexual dimorphism, age differences, polymorphism, and other such types of variation can be unmasked as individual variation through a study of life histories and through population analysis. The taxonomist working with recent animals and plants and normally deals with preserved material is confronted by the same problems as the paleontologist, who likewise must assign phena to species.

Apomixis: In many organisms systems of reproduction are found that are not based on the principle of an obligatory recombination of genetical material between individuals prior to the formation of a new individual. Self-fertilization, parthenogenesis, apomixis, pseudogamy, and vegetative reproduction are some of these forms of uniparental reproduction.

A population, as defined in evolutionary biology, is an interbreeding group. By definition, therefore, an asexual population is a contradiction, even though the word population has other usages in which a combination with asexual is not contradictory. The biological species concept based on the presence or absence of interbreeding between populations is therefore inappropriate for uniparentally reproducing organisms.

Attempts to define asexual species or agamospecies, with or without using the word population, have not been particularly successful. Fortunately, there are usually well-defined morphological discontinuities among kinds of asexually reproducing organisms. The discontinuities are apparently produced by natural selection among the various mutants, which occur in the asexual clones. It is customary to utilize the existence of such discontinuities, and the amount of morphological difference among them, to delimit species among asexually reproducing animals and plants. Depending upon the strength of such discontinuities, competent taxonomists classify some agamics as species, when no sexual species is known from which it might have branched off, whereas other such taxa are better classified as agamospecies at the subspecies level, or as agamovarieties or even agamoformae.

Evolutionary intermediacy: Although apparent morphological intermediacy may occur between alloploids and their diploid parents, and between members of an autoploid series, closer investigations always result in the discovery of strong reproductive isolation and an observable gap of discontinuity, which is characteristic of a newly formed abrupt species. In the case of gradual speciation, however, the situation is different as long as the reproductive gap has not become absolute so that it prevents crossibility, or at least strong enough to exclude mixibility. Populations will be found under these circumstances which are in the process of becoming separate species and have acquired some but not yet all of the attributes of distinct species. In particular, the acquisition of morphological distinctness is a subspecific process which may not be correlated with the speciation process of the acquisition of reproductive isolation. The most common difficulties ~~of~~ for the taxonomist which may result from evolutionary intermediacy ~~[illegible]~~ are caused by:

1/ Acquisition of reproductive isolation without equivalent morphological change. Such entities are named sibling species. In all cases of this kind that have been reported before ~~[illegible]~~ superficial studies reveal none or very small differences at the first sight, whereas detailed investigations usually result in the discovery of numerous otherwise overlooked morphological differences. Sibling species are frequently discovered first by experimental methods, though they are also often observed by aid of careful measurements of characters which display bimodal characteristics, and the two modes originally discovered can then be correlated with additional characters.

2/ Acquisition of strong morphological difference without reproductive isolation. A number of genera of plants and animals are known in which morphologically very different populations interbreed at random wherever they come in contact. The typological solution of calling every morphologically distinct population a distinct species is clearly inappropriate in such situations. Conversely, there are genera in which the isolating mechanisms between any two species may break down occasionally. To consider such species conspecific would be going to the opposite extreme. No generalized solution is possible where morphological divergence and acquisition of reproductive isolation do not coincide. The only recommendation to the specialist is that he delimit his species in such a way that they form biologically meaningful, natural entities. ~~The difficulty posed by the rapid morphological divergence of populations without acquisition of reproductive isolation~~

3) The occasional breakdown of isolating mechanisms (hybridization).

Reproductive isolation may break down occasionally even between good species. Most frequently this will lead only to the production of occasional hybrids that are either sterile ~~of~~ or of lowered viability, and this will not cause any taxonomic difficulty. More rarely, there is a complete local breakdown of isolation resulting in the production of hybrid swarms and more or less complete introgression.

Hybrid individuals are sometimes described as species before their hybrid nature is discovered. Such names lose their validity as soon as the hybridism is established. Only populations are recognized as taxa, and hybrid individuals are not populations.

Taxonomically more difficult are situations where new populations are formed as ~~results~~ a result of hybridization, ~~in all instances in which the~~ ~~the~~ though this is usually also caused by lack of reproductive barriers. Even when the two parental populations maintain their genetical integrity over a more or less wide area in which they occur together, it seems advisable to uphold their species status even though in a portion of their range there is an apparent breakdown of isolation, which frequently is the result of crossibility under special conditions, not followed by mixibility. Whereas populations of morphological and geographical distinctness that ~~meet but~~ hybridize and mix into a hybrid swarm where they meet occasionally apparently have high mixibility and ought to be regarded as subspecies only.

Conclusion:

Species: Groups of interbreeding natural populations that are reproductively isolated from other such groups.

Subspecies: A geographically defined aggregate of local populations which differ morphologically from each other. Major geographical race.

Variety: Minor geographical race.

Preliminary Note on the cytotaxonomy of the American Acorus.

One of the several Araceous plants growing in eastern North America from the subtropical south to the subarctic north is a species of *Acorus*. It was mentioned from this continent already by Schoepf (1787) and listed by Michaux (1803) and Pursh (1814) as being common in the east. These pioneers and almost all later botanists mentioning this plant regarded it as conspecific with the European taxon *Acorus Calamus* L., and most observers also felt certain that it had been introduced from Europe already by the earliest ~~settlers~~ colonists. None went farther in this claim than Merrill (1954), who even gave the exact dates and places for this introduction: Jamestown in 1607, and Plymouth in 1620, and suggested that it could even have arrived a few years earlier with the Mayflower, or at the French settlements in Canada.

Only one American botanist has clearly observed that the American *Acorus* is not identical with the European plant but should be classified as a taxon of its own. In his Medical Flora, Rafinesque (1828) pointed out that although all botanists regarded the American and European *Acorus* to be similar, they differ as much from each other as the Chinese *Acorus* differs from each of them. He described the common taxon as *A. calamus* var. *americanus*, but later (Rafinesque, 1832) described a plant of the southeast from Texas to Tennessee as the species *A. flexuosus* Raf. and still a few years later (Rafinesque, 1836) gave a description of still another species, *A. floridanus*, from Florida to Carolina, at the same time as the more common and northern plant was named as the species *A. americanus*. Rafinesque (l.c.) regarded all three taxa to be equally distinct, and his descriptions seem to indicate that while the two southeastern taxa may be ~~similar~~ only modifications of the same species, the northern taxon is distinct.

For some years, the present writers have collected cytological material of the ~~Amer~~ *Acorus* of the ~~centr.~~ prairies, and plains, and made some preliminary studies as to its morphology and distribution, and studies on the sterility of the plants by aid of herbarium specimens. These studies, which still are in their initial phases only and are aimed at an ultimate understanding of the evolution of the genus *Acorus*, have already resulted in such observations that the origin of the American *Acorus* and its taxonomical position as compared to the European plant is no longer a guess. ~~In these studies the writers~~ Therefore this preliminary paper.

It has been shown by Wulff (19. . . - - - -), in a series of papers that the European *Acorus Calamus* is a triploid and sterile plant, while fertile plants from ~~Botanical~~ ~~in~~ ~~Bot~~ the Botanical Gardens in Leningrad and Copenhagen, were found to be Tetraploid and diploid respectively. The diploid number 2n=24 was also reported by Wulff (19- - - -) from plants grown from seeds from Montreal, and by - - —

author even goes as far as claiming the following „facts which any real searcher for the truth could easily have determined by writing a few letters": .... „The common sweet flag was introduced from Europe by our earliest colonists, arriving, very likely, in Jamestown in 1607 and in Plymouth in 1620: it may have been a Mayflower passenger, or it may have arrived, a few years earlier, at the French settlements in eastern Canada. It was, in turn, unquestionably introduced into Europe from Asia. The only other known species of *Acorus* occurs in eastern Asia. Once introduced here, it immediately established itself".

The present writer has made some preliminary studies on the cytotaxonomy of the genus *Acorus*, in connection with biosystematic investigations on endemism and vicariism in the American flora. Much needs to be added to these studies before their completion, but since several ~~already~~ observations already made on this genus are of a great interest in connection with the controversy on the origin of the American *Acorus*, a preliminary publication at this stage of the studies seems justified.

~~It is known (Matth. etc.) that~~

Although it is likely that Acorus Calamus has been introduced to southern Russia and Poland and from there to Denmark already at the middle of the 13th? 14th century (cf. - - - - -), it is known for sure that it was not grown in central Europe prior to 1562, when Mattiolo received plants to Prag from Constantinople (cf. Mücke, etc.). It spread ~~firstly to other~~ rather fast to other Botanical Gardens, but did not become common elsewhere in central and western Europe until about a century later. Already the early European authors observed that the plant was completely sterile, but although many philosophical explanations to this phenomenon were given through the ages, it was not fully understood until ~~when~~ Wulff (1939, - - -) demonstrated that the plant is an autotriploid with 2n = 36 chromosomes. [illegible] Indian material is also triploid and sterile. ~~and~~

Already Linnaeus (1753) observed certain morphological variations within the species, and on the basis of differences between south- and north-Indian plants, he described two varieties, var. vulgaris and var. verus. Wulff (. . .) ~~later~~ was able to demonstrate that these variations are climatical modifications of no taxonomical significance, and the same is certainly true of all the many varieties and species described from India westwards by several authors of the past two centuries.

Although the great majority of species of Acorus described in the past was based on material from regions, where the triploid ~~has been~~ only is met with, some taxa distinct from it have been observed by botanists studying the plants of eastern Asia. ~~Solander (in ... 1789) described a species, A. gramineus, from southeastern Asia,~~ Solander (in .. 1789), studying plants from southeastern Asia, described a species, A. gramineus, which later was named A. humilis by Salisbury (1796) and A. pusillus by Siebold (1830), and besides some distinct morphological differences it was also reported to be fully fertile. Loureiro (1790) described a more restricted southeast Asiatic species Orontium cochinchinensis, which was correctly transferred to the genus Acorus by Schott (in Schott & Endlicher, 1832). It is morphologically ~~not, especially~~ distinct from A. gramineus but closely related to A. Calamus, but differs from the latter mainly in being fully fertile. ~~Lastly, we move~~ ~~Still further north, or in northern in eastern Siberia~~ ~~Manchuria, China, Korea, and Japan grows the east~~ Another fertile ~~species~~ taxon from eastern Asia was described as A. ~~calamus or~~ species by Schott (1864-), A. Calamus var. angustatus by Engler (1905), and A. asiaticus by Nakai (1936). It differs from the other three species in several characters, but its variability, which is even wider than that of ~~A. gramineus~~ A. Calamus clearly falls within the variability of the Siberian plant (cf. Wein, 1939), which had ~~already~~ been described already by Turczaninow (18...) as A. triquetra. This was understood as early as 1879 by Engler, and stressed especially by Wein (1932-..).

The cytology of the species A. gramineus was studied by Nakajima (1933), who found the plant to be a diploid with $2n = 24$ chromosomes. This number was later confirmed by Wulff (1940) and Ito (1941-42), while Murakubo (1940) counted only $2n = 22$ chromosomes. This latter number and the number $2n = 18$ reported for the species by Malvesin-Fabre (1945) are certainly to be regarded as inexact counts for $2n = 24$, ~~which has been confirmed lately on seed material by the present writers~~

No direct reports are available on the cytology of A. cochinchinensis. As far as can be seen from the pictures and descriptions of and diploid fertile material obtained by Wulff (194..) from the Botanical Garden at Copenhagen, these plants are referable to this southeast-Asiatic species. It has been cultivated in Copenhagen since the last part of the 19th century (cf. Mücke, 1908) and has probably been brought directly from its original area by some of the many Danish ships of the East-Asiatic Company. The Copenhagen plants were distinctly different from the other diploids, but ~~closer~~ ~~related~~ most closely related to the triploid A. Calamus.

The ~~[illegible]~~ chromosome nbr. for the species *A. triqueter* was reported ~~by Wulff (1940)~~ — as *A. calamus* from ~~from~~ the Botanical Garden of Leningrad, or *A. calamus* var. *spurius* — by Wulff (1940, 1954). It is 2n = 48, ~~or also~~ ~~first by~~ although 2n = 44 was reported for the ~~variety~~ synonymous var. *angustatus* by Kurakubo (1940) and for the synonymous *A. asiaticus* by Ito (1941-42).

~~There can be no doubt~~

The cytological ~~reports~~ and morphological studies by Wulff (l.c.) allow us to draw the conclusion that four distinct taxa of *Acorus* are met with on the Eurasiatic continent. Two of these taxa are diploid species ~~and~~ confined to relatively restricted areas in southeastern Asia, while the third has a wider area in the north and is a tetraploid. The fourth taxon is *A. calamus* which is triploid and sterile and ~~has it~~ has been dispersed mainly by ~~the~~ aid of ~~at~~ human activities. The studies made by Wulff (l.c.) have demonstrated without doubt that it is an autotriploid plant, and its morphological resemblances to ~~A.~~ the diploid *A. cochinchinensis* indicate that it is a triploid of that species. Triploids occur in a very low frequency in all plants (cf. Löve, 1944; Darlington, 19...) ~~at~~ but do not survive ~~very~~ for a long time except when vegetative propagation is possible. All the species of *Acorus* propagate vigorously by vegetative means, ~~but~~ ~~it~~ but in addition to this the triploid included considerably more than the diploid of the etheric oil used for medical purposes in the past (cf. Wolff. ——) ~~so that~~ ~~it has~~ making it more desirable ~~f~~ to man than the diploid itself. It has been ~~produced~~ ~~found~~ originally produced somewhere in Tonkin(?) but carried westwards for cultivation by the white —— to India, and, much later, all the way to Europe.

Although the American *Acorus* was identified by the early botanists with *A. Calamus*, Rafinesque (1828) pointed out that ~~although~~ "the European *Acorus* is deemed by all Botanists similar to the North American," and yet differs as much from it as the Chinese" (*A. gramineus*). He described it as "our American variety or species", but named it *A. Calamus* var. *americanus*, with the remark that the "distinctions hardly amount to specific difference." Later on, however, Rafinesque (1836) regarded the estival plant growing "from Canada to Missouri and Virginia" as the species *A. americanus*, while a vernal and dwarfish plant met with "from Florida to Carolina" was named *A. floridanus*, and, a little earlier, (Rafinesque, 1832?) a likewise vernal plant with short and narrow leaves, medial spadix, and long scape with flexuose and triangular awl-like leaf with one concave side, had been given the name *A. flexuosus*. The two last-mentioned taxa are doubtlessly identical, while only detailed experiments can ~~show~~ demonstrate if the differences between them and *A. americanus* are real or only based on climatical modifications.

Despite Rafinesque's (l.c.) ~~[illegible]~~ observations as to the differences between the European and American *Acorus*, later authors continued to regard both taxa as being identical. This was maintained, e.g. by Engler (1879, 1905, 1933?), who even went as far as naming the American *Acorus* var. *vulgaris*. Many later authors have followed this lead, although nobody has supported it as strongly as did Merrill (1954).

~~The first cytological reports based on American material of *Acorus* were published by Dudley (1937) and Buell (1938), who both reported the number 2n = 18 counted by Dahl from Minnesota. That this number was too low was demonstrated by Wulff (1950, 1954), who counted 2n = 24 chromosomes in plants from~~

The American *Acorus* is always fully fertile, with abundant seeds ~~(cf. Marie-Victorin, 1931)~~. This fact alone should have been enough indication of the incorrectness of the hypothesis of its introduction from Europe. However, the reason for this difference was~~, however, known~~ became known only recently, when it was found that it is a diploid species with 2n = 24 chromosomes, as determined by Wulff (1950, 1954) on material from Minnesota and Quebec. The same number has been counted by the present writers from several localities in Canada, and ~~the~~

herbarium material from elsewhere on the continent shows no sterility and, thus, no indication of being triploid as it must be if introduced from Europe.

~~[illegible]~~ No discussion is needed as to the lack of distinctiveness, ~~identity~~ of the American ~~[illegible]~~ diploid and ~~to~~ the European A. calamus or the Asiatic A. triquetra, since this is evident not least from their ~~[illegible]~~ differences in chromosome number, creating a secure barrier of sterility. Since hybridization experiments between it and the other diploids remain to be performed, ~~[illegible]~~ the cytogenetical relationships ~~[illegible]~~ of the three diploids remain unknown, although the morphological differences between them as well as the developmental dissimilarities ~~[illegible]~~ observed by Wulff (~~[illegible]~~) (l.c.) are strong indications of that the three diploids cannot be conspecific. There is ~~little~~ no doubt, however, that Sauer (1950) is right in ~~[illegible]~~ suggesting a dispersal of Acorus to North America from eastern Asia, although his timing of this dispersal is somewhat in error. As a matter of fact, the diploid American Acorus has been met with on this continent constantly since Eocene (cf. Berry), ~~it~~ ~~it is morphologic~~ or considerably longer than all the period since human beings were first met with in eastern Asia.

As a conclusion of this preliminary report it ~~can be said, that~~ is to be pointed out that the genus Acorus is represented in Asia by the two diploid species A. gramineus and A. cochinchinensis and the tetraploid A. triquetra. Outside the~~ir~~ natural areas of these species it is represented by the triploid and sterile A. Calamus, which most probably is an autotriploid (hybrid) of A. cochinchinensis. The North American Acorus is an indigenous ~~plant~~ taxon, which may be composed of two species, the diploid, estivan A. americanus (Raf.) Raf. of the temperate, ~~and~~ boreal and even subarctic region of the ~~eastern part continent~~ land east of the Rocky Mountains, and the erect and dwarfy A. flexuosus Raf. in the temperate to subtropical southern parts of the continent. This latter taxon remains cytologically unknown.

The present writers would greatly appreciate to receive fresh seeds and ~~roots~~ living rootstocks of all the species mentioned, but especially of the Asiatic diploids and the most southern and dwarfy representative of the genus in North America. ~~for further studies~~

Nakai, T., Honda, M., Satake, Y., and Kitagawa, M. 1936:

Index Florae Jeholensis, cum Appendice: Plantae novae vel minus cognitae ex Manshuria. — Rep. First Sci. Exp. to Manchoukuo. Section IV, Part IV., 1936, pp. 1—108 (Appendix 73–108):

p. 105:

76) Acorus asiaticus Nakai in sched. Herb. Univ. Imp. Tokyo.

Acorus Calamus (non Linnaeus) Thunberg, Fl. Jap. p. 144 (1784); Franchet & Savatier,
Enum. Pl. Jap. II, p. 10 (1876); Franchet, Pl. David. I, p. 313 (1884); Komarov in
Act. Hort. Petrop. XX, p. 412 (1901) [Fl. Mansh. I (1901)] saltem pro parte; Forbes &
Hemsley in Journ. Linn. Soc. XXXVI, p. 187 (1903) saltem pro parte; Matsumura, Ind.
Pl. Jap. II. 1. p. 168 (1905); Yabe, Enum. Pl. S. Mansh. p. 22 (1912) saltem pro parte;
Mori, Enum. Pl. Cor. p. 78 (1922) pro parte; Komarov & Klob.-Alisova, Key Pl.
Bild! Far East Reg. USSR I, p. 330, t. 101, 102 (1931) pro parte?; Kuzeneva in
Komarov, Fl. URSS III, p. 479 (1935) pro parte?

Acorus Calamus Linnaeus var. vulgaris (non Linnaeus) Engler, Pfl.-reich.
IV. 23B (Heft 21) p. 309 (1905) pro parte.

Acorus Calamus Linnaeus var. angustatus (non Besser) Engler, l. c. p. 312 (1905) pro parte;
Makino & Nemoto, Fl. Jap. ed. 1. p. 1311 (1925) pro parte, ed. 2. p. 1494 (1931) pro parte.

Rhizoma crassum longe repens radices fibrosas simplices atro-fuscas emittens. Folia longe linearia apice ensiformia vel falcato-ensiformia longitudine nervosa medio prominente 1-carinato-nervia viridula glaberrima nitida basi sensim dilatata vaginantia et margine anguste tenuiter scarioso-membranacea usque 105.5 cm longa et 18 mm lata. Pedunculus foliis brevior ultra spadicem in spatham phyllodioideam pedunculo longiorem-breviorem productus laevissimus. Spatha foliis conformis apice ensiformis. Spadix sessilis erecto-patens cylindricus sursum sensim angustatus apice obtusus usque ad 6.8 cm. longus circa 1cm. latus. Tepala circa 1.8–2 mm longa 0.5–1 mm lata oblongo-elliptico-quadrata apice dilatata et incrassata pallida fusco-maculata dorso 1-carinato-nervia. Filamenta complanata lata linearia — linearia 1-nervia inferne pallida superne fusca toto fusco-maculata glaberrima. Antherae luteae 0.5–0.9 mm longae glabrae. Ovarium viride fusco-maculatum glabrum superne fere conicum inferne breviter cylindricum [illegible] vero sterile nunquam in baccam maturum usque ad 6 mm. longum. Stigma sessile punctiforme.

Sm!!

Hab. Japonia:

Prov. Su-wô: O-uti-mura (Z. NIKAI n. 82. 14. Mai. 1892. – Typus).

Manshuria:

Prov. Lung-chiang: circa T'ao-nan (M. Kitagawa Jul. 12, 1931).

Prov. Fêng-t'ien: circa Lao-hu-t'an (" – Jul. 12, 1931).

Prov. Jê-Hô: ~~Ch~~ Ch'êng-tê & 2 ca. Ch'ai-hê-k'ou.

Korea:

Prov. Kan-hoku: Ho-dyô-dô (T. Nakai 1918).

Prov. Kan-nan: San-sui – Kei-gan-tin (T. Nakai 1914).

Prov. Zen-nan: In insula Sai-syû-tô (– 1913).

Distr. Manshuria, China, Korea & Japan.

Affinis Acorus Calamus Linnaeus, sed exquo ovariis sterilibus nunquam maturis, spathis multo longioribus apice ensiformibus discrepat.

(vilket betyder, att A. C. aldrig bildar frö, men att A. a. gör det).

Schott, H.W. 1859: Aroideen-Skizzen. - Oesterr. Bot. Zeitschr. 9: 98 - 101:

p. 101:

Acorus Nilaghirensis. Spadix sesquipollicaris, diametro 4-lineari, Spatha longissima (sesquipedali), medio subdilatata superatus. Ovaria in stylum conicum fere producta. Ovula paraphysibus fertil? illis longioribus circumposita, primina (testa) modice fimbriata, secundina (tegmine) producta, obiter-fimbriata. —
India orientalis (Nilaghiri montes). (south India).

Synon. Acorus terrestris. Hohenacker pl. Ind. orient.

Acorus Tatarinowii. Folia 1½ - 2 pedes et ultra longa, ¼ pollicis lata. Spadix sesquipollicaris, diametro trilineari. Spatha longissima. Ovula paraphysibus longis immo praelongis velata, primina breviter-fimbriata, secundina valde-producta brevius fimbriata. — China (Pekin). Tatarinow.

(= asiaticus ?)
= cochinchinensis?

(Gray Index?)

Acorus.

Scientific Exp. to Manchoukuo, 1st, Rep. (Congr. Libr.)

A. asiaticus Nakai, in Rep. First Sci. Exp. Manchoukuo, Sect. IV. 4 (Index Fl. Jehol.) 105 (1936): Manchur., Corea, China, Japan.

Museum Botanicum Lugduno Batavum – Annales. 1 (1863)

A. angustifolius Schott, in Ann. Mus. Bot. Lugd. Bat. I, 284 (c. 1860). ~~Ann Arbor.~~ Univ. of Minn.

A. Belangeri Schott. – – –

A. cochinchinensis Schott, H.W. Melet. I, 22. Cochinchina. Gray & N.Y.

A. flexuosus Raf. New Fl. Tell. 29., Atl. Journ. 178

A. Griffithii Schott, Oestr. Bot. Zeitschr. 1858, 351. Minnesota Univ. MnV.

A. nilaghirensis Schott, Oestr. Bot. Zeitschr. 1859, 101.

A. spurius Schott, in Miq. Ann. Mus. Bot. Lugd. Bat. I, 284.

A. Tatarinowii Schott, in Oestr. Bot. Zeitschr. 1859, 101.

A. triquetra Turcz. ex Schott, Prodr. 578 Gray & N.Y.

„Der Anzeiger der Entdeckungen in der Physik, Chemie, Naturgeschichte und Technologie", 1831, utg.: N. Schtscheglof (Shsheglov?), VIII, 3. Hefte. : Turczaninow: A. triquetra. Leningrad.

Ledebour: Flora rossica, 1853, (s. 12, 13.)

Besser: Über die Flora des Baikals. – Flora XVII, Bd. I, 1834, Beiblatt 1 – (inte nödvändigt).

~~Schott, H. W. Aroideae Maximilianae. [illegible]~~

Rafinesque, C. S.: Atlantic journal, and friend of knowledge.

1832-1833 1-8 [illegible] 212 pp.

Autikon botanikon. (1840?) 1815-1840

(bilder [illegible] names).

Schott, H.W. 1858: Aroideen-Skizzen. – Oesterr. Bot. Zeitschr. 8: 349–357.

p. 351:

Acorus Griffithii folia 15–18-pollices longa 3 lineas lata. Spadix vix ~~seq~~ sesqui pollicaris, spatha 4–5-pollicari comitatus, cuneato-lanceolata, acuminata. Habit. in Bootan (Griff. in Herb. Hooker).

Durch die kurze Spatha und dem kleine Spadix ausgezeichnet, und dadurch eben von Acorus terrestris, wo die Spatha sehr lang und schmal ist, verschieden.

(Bhutan är : östra delen av fjällen, just öster om Nepal).

Acorus Calamus L. 3x

Acorus gramineus Sol. 2x

Acorus americanus (Raf.) Raf. 2x

Acorus cochinchinensis Schott 2x

Acorus triqueter Turcz. 4x

A. asiaticus Nakai 4x

1: Diploider:

A. gramineus Soland. 1789.
(= A. humilis Salisb. 1796; A. pusillus Siebold 1830)

&

A. cochinchinensis ~~Schott~~ (Lour. 1790) Schott 1832

A. americanus (Rafin.) Rafin. 1836
(= A. flexuosus Rafin.?, A. angustatus Rafin. 1840, A. floridanus 1836).
(A. verus Houttuyn 1777).

2. Tetraploider:

A. triqueter Turcz. 1831; Schott 1860
(= A. Tatarinowii Schott 1859, A. spurius Schott 1864; A. asiaticus Nakai 1937)

3 Triploider:

A. Calamus L. 1753
(= 3x A. cochinchinensis)
↑
A. angustifolius Schott 1864
~~(= 3x A. gramineus ?)~~