March 4, 1954

Interpretation of origin and behavior of the controlling systems.

I. Review of previous discussion.

1. Purpose was to show that systems present that control genic action in manner not quite like that of Ds - Ac or that of a_1 - Dt, (which are much alike).

2. These other systems, have basic pattern however that is similar -- control of genic action; evidence suggests that segregations of controlling units occur. Meiotic segregations obtained and linkages noted. Results of somatic segregations similar to those of meiotic segregations.

II. Controlling systems revealed by the b.f.b. cycle. Concluded that they do not arise denovo but are present in the normal nucleus -- function in some precise way during the development of the organism.

a). Somatic segregations occur, changing the constitutions of the sister nuclei with respect to the controlling unit.

b). These changes result in subsequent controls of the action of specific genes.

c). For the genes to become active, some change must occur at the locus of the gene.

d). Some mechanism must be present in the nucleus that initiates these changes in nuclear organization and constitution.

e). Believe this mechanism associated with the heterochromatic elements of the chromosomes -- primary initiators of the changes that subsequently occur.

f). The pattern controlling genes, the "switch" genes, etc., may be expressions of their action.

III. The recent studies of others showing the mechanism outlined in this series of discussions:

1. Work of Brink and students on the var. P locus in maize: Have come to same conclusions regarding the controls of the patterns of variegation expressed. Have found the transposing units. Have found the twin sectors of the types described in this series and have investigated the progeny derived from them. Confirms the story here presented.

2. Peterson, in maize, has found system controlling variegation that also appears to follow the main conditions here discussed -- the controls of genic action; transpositions of the controlling unit comparable, in many respects to Ac but not Ac.

3. The studies of the "Hi" mutation factor in Drosophila by Ives and Hinton -- suggests controlled changes at certain gene loci and controlled types of chromosomal alterations that occur at specific loci.

4. Somatic crossing-over as observed by Stern. Some cases strongly suggest a controlled system in operation here to give precise types of exchanges between certain chromosome components.

5. Many suggestive cases in literature. The cytological cases are most instructive in this respect. Review will be given of representative cases

IV. According to interpretation given -- that the effects described represent those normally occurring in development -- we must account for their appearance in the stocks used here.

1. If the processes described of control of genic action occur in standard strains, their presence not readily revealed. This is because they are active at particular times, controlled in this respect, and therefore not observed as specific units unless they are called modifiers.

2. If the controls not regulated, a chaoitc situation would occur, regarding gene action, the regulation of development, the maintainence of species, etc.

3. The pattern controlling genes -- look very much like the systems outlined
a). The patterns in flowers: strikingly controlled in many cases.
b). The patterns of pigmented areas in the Lady Beetle -- again, a striking case of control of when the gene for pigment formation, or involved in it, is effective.

4. If one of these systems of control becomes "out-of phase" -- starts working at a different time in development, the results would be apparent. Altered times of gene action would be noted. Variegation would result.

5. The mechanism of change, as here outlined in the discussions, would make it clear that once such a system becomes "out-of-phase", it would continue to be so, and would result in the appearance of new changes in genic action, elsewhere, which then would be put "out-of-phase".

V. The interpretation described would require that in the normal development of an organism, somatic segregations should occur. The nuclei should not all be alike. Again, changes at particular gene loci should occur at specific types, leading to nuclei with different potentialities for genic action.

1. What do we know about somatic segregations? About differences in genic action in different nuclei of an organism? Is there any evidence to support the above interpretations?

2. There is a vast wealth of information in support of the ideas given. These are mainly in the area of investigation known as "cytology" and much of it is purely descriptive. Many of the papers in this field are not examined by geneticists because of their highly technical nature. Most are not seen at all by biologists in other fields. The observations, however, are of vast significance. The field has only been tapped and a wide opportunity is present for experimental investigations.

3. A brief review will be given of the nature of this evidence, with examples selected for illustrations. Will cover the following topics:

(1) Differences in nuclei of organism with respect to sets present.
(2) Differences in nuclei of organisms with respect to particular chromosomes present.
(3) Differences with respect to component parts of the chromosome itself:
(a) Large segments to (b) the minutest segments known -- the bands in the salivary gland type chromosome.

VI. Differences in nuclei of an organism with regard to the number of sets of chromosomes present:

1. Zygote -- starts out with two sets of chromosomes, one from male and one from female. During development, changes occur in the number of sets of chromosomes within the nuclei. These are controlled changes: certain types of cells having certain specific types of changes in sets. The set may increase -- poly ploid nuclei; or the set may be reduced -- to haploid nucle. These changes occur at specific times during the development of the organism. Also, different mentods of change in set number occur.

The increases in numbers of sets: By means of endomitosis -- no mitotic division figures. Various methods of accomplishing this endomitosis. Fusions

a). The degrees of increase: From tetraploid to 2,000 ploid.

b). The type of appearance of chromosomes: Polytene type - salivaries or diffuse type -- frequent; Or, combination of both.

The decreases in number of sets: Some interesting examples:

a). Tail of Rana (frog). Epidermis is diploid (Swan, 1952)
Mesenchyme is haploid (Ludford, 1953)

b). Sea Urchin: A "reduction division" in certain cells early in cleavage stage: 16 cell stage -- 4 micromeres present. These are 2n. In division of micromeres, reduction of chromosome number occurs to haploid. These haploid cells become skeletal components of organism.

b). Increase of sets followed by decrease of sets: Culex. Very well examined case to show the mechanism involved. Reduction occurs during metamorphosis period.

VII. Differences in nuclei with regard to certain chromosomes of the complement: Loss of chromosomes at specific divisions: Non-disjunctions of certain chromosomes in certain divisions; Other methods of accomplishing the same.

1. Best worked case that of Sciara: Outline on board.
Loss of chromosomes at mitosis
Non-disjunction of particular chromosome at certain division
Pasage of chromosome through nuclear membrane -- highly controlled.
The experiments that show which part of chromosome is responsible for the phenomena.
When is this effect impressed on centromeres?
What mechanism makes the impression so precise?

2. The B-type chromosomes in plants. Very highly controlled non-disjunctio of these chromosomes. Occur at specific times and with specific consequences.
a). Example of this behavior -- the B chromosome in maize:
Diagram on board.

Control exerted at centromere region of B-chromosome, as in the X chromosomes in Sciara. The translocation studies showing this.

3. Ascaris - loss of parts of chromosomes - [illegible] ends.

VIII. Differences in behavior of sets of chromosomes within same nucleus:
Ch. no. condensed = 28.
White . Monarthropalpus. Spermatogenesis:

→ Sperm receives chromes in condensed set.

IX. Differences in appearance of different chromosomes of a set in different stages.

a). The small chromosome in salivary glands of White. "elland

b). The alternation in condensation of particular chromosomes:

Type 1 Type 2

X. Differences expressed by individual parts of chromosomes in different cells of an organism:

1). The chromocenter regions -- heterochromatin in Drosophila -- too well known to comment on.

2). Condensed versis diffuse condition of segment of a chromosome:

Type 1 Type 2

3). Most exciting recent case -- that of Pavan on Rhyndhisciara -- two different species studied.

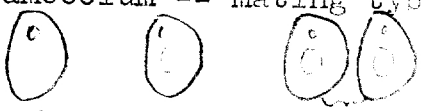
a). All eggs laid at one time -- within 45 mins.
b). "early all larve of one sex
c). All develop at same rate - 42 days to pupation. Common puparius formed
d). The changes occurring to specific bands at certain times in development in the different tissues; change at particular band specific for the tissue involved.
e). One type: at certain time, increase in D.N.A. and swelling of particular band; Separation of components of the polytene bands -- Large Puff region formed. At certain stage, shrinkage of puff region. Return to dense band, but now bad very much wider than before the process started. Increase in D.N.A. remains. Interpretaion: Multiplication of genes of this band, specifically. Differential behavior.

XI. Conclusions on nuclear compositions in organisms: Wide differences among the cells of an organism with regard to the nuclear composition. Differs with respect to sets, parts of set, parts of chromosomes, even parts of so small as a band in the salivary type chromosome.

Mechanisms : Differential behavior at certain mitoses: Losses of certain chromosomes; Non-disjunctions of controlled type at certain divisions. Passage of chromosome through nuclear membrane.

XII. Differential nuclei resulting from specific divisions: on genic level.

1. Paramoecium -- mating type reaction:



→ segregation division. Macronuclei differ in mating type. Micronuclei unchanged.

2. Tetrahymena -- mating type reaction: Same as paramoecium except the division is not as precise -- first or second division of macronucleus.

3. Case in Glomerella where mating type "mutation" occurs at specific time in development of ascogenous hyphae.

XIII. The effects of species crosses: Often quite bizaar.

1. Changes in the chromosome complement: Various polyploid conditions, reductions, occur in tissues that do not show such reactions in the individual species involved.

2. Case of Metz in Sciara: Cross of S. x S.

The mosaic salivary gland:

3. Species cross in Nicotiana. A. x B. Backcrossed to A

A.A B complement: B chromosomes eliminated somatically.

3. Altered genic action often noted; Variegation appears.

XIV. The constitution of differentiated nuclei -- as shown when these cells forced to divide.

a). Treatment of root -- chemical (indol-acetic acid. does not affect behavior of chromosomes in the nuclei that regularly divide. Forces nuclei that are fully differentiated to divide. Theh show a variety of chromosomal aberrations. One type observed in cell that had undergone endomitotic division:

The effects observed are very much like those produced by Ds.

XV. Ds type behavior in other organisms than maize:

1. Metz - Sciara. Certain chromosome, certain band region -- break seen in all salivary gland cells. Showed that this was genetically controlled.

2. Hyacinthus - Darlington. Break in a particular chromosome late in development of the sporocytes. Genetic control

3. Vicia - Levan. With certain treatment, break occurs at the nucleolus organizer quite predictably.

4. Dreyfus -- break in arm of particular chromosome at certain division in the spermatogenesis of

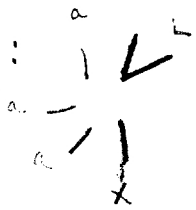
5. Catcheside - Oenothera. His case of position effect following translocation: Evidence much like that found for Ds. Chromosome breaks; chromosome duplications and deficiencies of certain region of a chromosome in the translocation complex.

XVI. Conclusions:

1.

on board

Sarva -

Egg:  × Sperm

Zygote

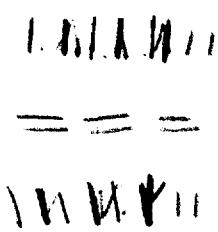
First 4 cleavages = ordinary mitoses

Separation of germ line + sarva

sarva

germ line

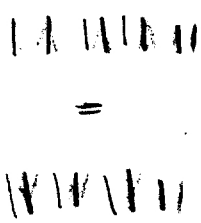
5th or 6th div



elimination of 1 V not known

7th div.

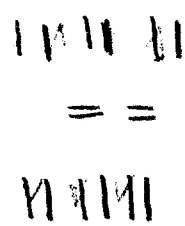
To become ♀



origin

1 x = 1 ♀ : 1 ♂

To become ♂

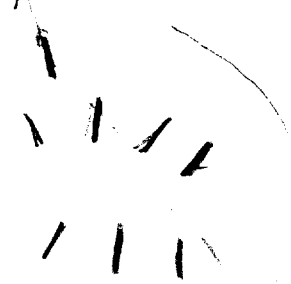


origin

1 x = ♀

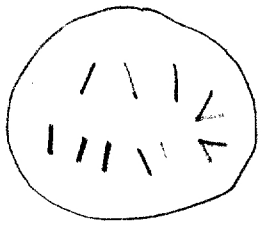
elimination of 1 x chr.

passes through nuclear membrane



The spermatogenesis – meiotic diversion.

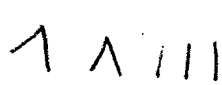
Prophase: no synapses



anaphase I

→ Bud; complement from ot of autosomes and x
Does not develop sperm

Anaphase II



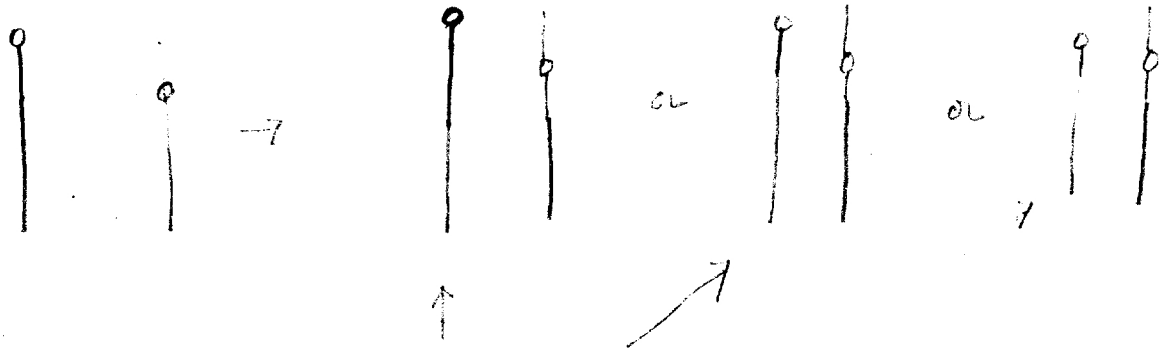
→ non functional cell.

→ sperm nucleus

1 set of autosomes from mother
2 x chromosomes from mother
2 limited chromosomes.

Sciara - The translocation studies of Crouse.

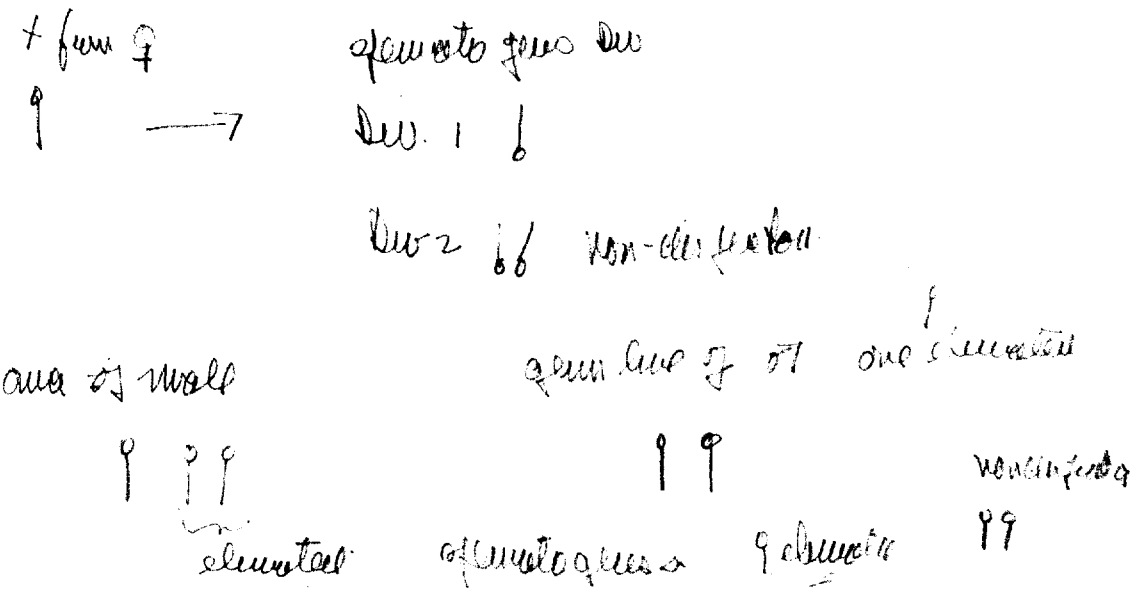
1. Series of x - autosome translocations



1) non-disjunction in fem
2) Eliminated in cleavage divisions in soma; through nuclear membrane in germ line

2. The control exerted on or by the centromere (or closeness) of x chromosome. not a component of the chromatin in this chromosome as a whole.

3. Alteration of controls in alternate generations: not the effect of a particular centromere which remains differentiated. It becomes differentiated at some time.



4. Differences must be impressed on the homologues at some time during development and this at the centromere of x chromosome which prepares it for the eventualities.

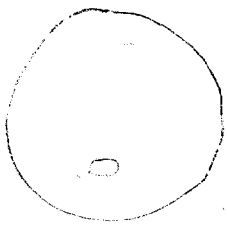
The B-type chromosomes in maize -

1. Nature of B-type chr. Extra chromosome; not like any in normal complement. Found in various strains of maize

2. The internal morphology of the B-type chr.

3. Behavior of B-type in mitoses -
   Divides in each mitoses along with regular set of chromosomes.
   Occupies a particular position on plate at edge of plate.

4. Behavior in pollen grain division: Differential division

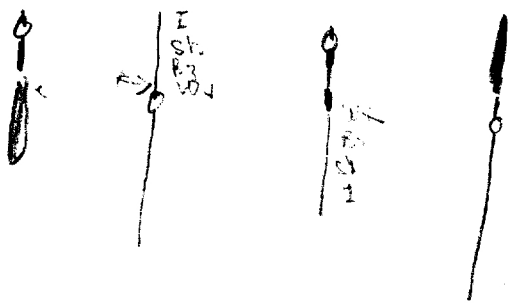


generative cell

Bs = sister chromatids

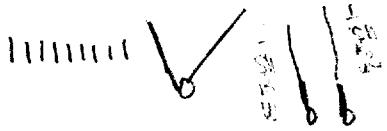
5. 2 species: one with no B; 1 with 2 Bs.

6. Translocations between A-type + B chromosomes:



7. The differential division in pollen

a) no I Sh R_3 Wx

b) 

8. Fruit wing of sperm in cross with C sh Gyx:

Endosperm with a = C sh Gyx in phenotype
Zygote " b) = Dup. of I Sh R_3 Wx

Endosperm with b) = I Sh R_3 Wx
Zygote " a) = Plant = $\underline{b}$

9. Again, region of centromere responsible for the non-disjunction in the pollen division.

The mosaic salivary gland in Sarara species cross. - Metz

1. S. Ocellaris ♀ x S. Reynoldsi ♂.
2. Salivary band structure of each recognizable.
3. The hybrid - one individual -
   2 composite of gland

← all cells have expected hybrid constitution
1 set of O. + 1 set of R.

mosaic party
gland.
29 cells.

16 cells = expected chromosome constitution.

1 cell = " " " + 1 extra chromosome from O.

12 cells = all have 2n but all are ocellaris chromosomes

4. Distribution of 12 cells = not contiguous. Appears as if same event occurred in number of different cells.

a) None of cells were all Reynoldsi = ♂ complement

b) Interpretation Metz: Is this an example of out-of phase action normally occurring at meiosis? Expression of chromosome complement of ♂?

Mark 4 [illegible]

I. In studies presented, have shown that units appear in the nucleus that differ in quite recognizable ways from those usually projected for the gene:

1) We have in the past considered the gene as an indivisible entity, occupying a specific locus in a specific chromosome

2) We have considered that this gene operates in a particular way - it is responsible, at some level, for the organization of molecular components which influence the course of biochemical reactions in the cell.

3) We have considered that each gene function to this extent in its own particular way

4) We have considered in the past that during the mitotic cycle, each gene is reproduced, usually accurately, so that two sister chromatins are alike in their genic genetic constitution.

5) We have not been so precise in our thinking of the changes that occur at the genic level when a mutation occurs.

a) A few geneticists have desired to consider a mutation as a change in structure of the gene entity in such a way that it subjectively functions to produce a modified molecular component which then enters into the biochemical sequence. This would be a real gene change

b). The studies in Drosophila of position effects, first appreciated and defined by Sturtevant, opened up a wide field of research. Knowledge gained from these studies, a ~~complex~~ series of modifications of this view of mutation as a permanent change in structure of the gene entity, and superimposed caution in projections of the nature of change at the genic level that is responsible for the observed mutation.

c). The position of gene entities along the chromosome remained. We knew that if some alteration occurs at a near a particular known locus in the chromosome, a particular general type of alteration could occur.

d). Many regions in the chromosome, however, where no changes of a mutational type could be obtain. Instead, changes produced letters: alteration of many regions result in inviability. This leaves a big blank in our knowledge of genic composition of the chromosomes.

II. In the many studies, here discussed, a second system of chromosome + molecular control is superimposed on the older recognized system of stationary genes.

1. This system is composed of recognizable, specific genetic units, but these units are not stationary. They can move from one location to another

2. These units differ from the stationary units, in that they can control the action of the stationary units.

3. These movable units have specificity: There are different types of these units, forming specific systems, such as the Ds - Ac system, the "a_1" unit - Dt system; the "pg" - En unit of petunia. The action of a gene, in the case of the various mutable genes, reflects the behavior and specificity of the particular controlling system in action at the locus of the stationary unit - Examples of A_1:

1) System "a_1" - Dt
2) " Ds - Ac
3) " a_1^{m-1}
4) " a_1^{m-2}

Each system differs in its mechanism of control of the genic expression of the stationary A_1 unit.

II. We outlined the evidence of the kinds of changes that occur to chromosomes when a chromosome of the complement is undergoing the b.f.b. cycle and discussed that certain chromosomal components - the centromeres, the knobs + the nucleoles of Ginger, were being altered by this process.

1). We have indicated that in plants that underwent this cycle, the systems controlling genic action were made evident

2). We outlined one test that supported the assumption that the b.f.b. cycle could expose such units - the a_1/a_1 b.f.b. cycle stage

to induce mutation at a_1.

3) We have shown that new mutable genes can arise in plants having a mutable gene and that often the system operating at this new locus is the same as that known to be present in the plant -- the numerous cases of origin of Ac controlled mutability when Ds + Ac are present.

4). We have outlined our knowledge of the events that occur at the locus and came to the conclusion in the Ds. Ac case, that the change in phenotypic expression was not due to a change in the gene ~~gene was not mutating~~ but that the changes occurring were associated with changes of the Ds unit which controls the degree + type of action of the gene.

5) We have given the evidence which suggests that the type of change is a result of some physical alteration in the chromatin material of or at the Ds unit.

III. We are left with the problem of accounting for the appearance of these gene controlling systems: Where do they come from? Why and they appear in these plants that underwent the I.S.G. cycle?

IV. My speculations on them run somewhat as follows:

1. These gene controlling systems are always present in maize
2. They operate in "normal" maize just as they do in our mutable strains. Controlling the action of some genes during development in the same manner + until the same precision.

3. They were made evident to us because their time of operation was thrown "out-of-phase" during the developmental cycle: They are active at times not associated with the normal cycles.

4. The mechanism responsible for this is associated with the alterations induced in the heterochromatic elements of the chromosomes

5. Changes in the quantities and mutual associations of the heterochromatic elements in some manner initiates changes in the times of action of the mobile gene controlling units. These mobile units need not be composed of the materials of the heterochromatic elements but changes in these elements affect the action of the mobile units, putting them "out-of-phase" in the periods of action; Once out-of-phase, they remain that way, allowing their mode of operation to be discovered.

6. On this view, we are not creating any new phenomena, nor have we introduced a new condition, such as a virus, that would be responsible for the results obtained.

7. Do not patterns in development suggest the presence of new units? Such simple patterns as the position, the size, + the inheritance phenomena of the pigmented spots on the of the Lady Beetle? Why does pigment appear only at certain places + at certain times in the formed endosomes which regulate the control of such pigment formation in development? What about the Kleenes in maize that shows such

precise controls in the distribution + intensity of pigment in different tissues and parts of tissues in an organism? Why are there so many alleles of this locus, each showing specific action with respect to these differences, intensity + distribution within the same plant? Could there be reflection of the nature of action of controlling units? Are changes occur during development at specific times + in specific cells and at specific loci that control where + how much pigment will be formed in the descendant cells?

8. If the assumptions made above were true, then, the cells of an organism should not be alike but should differ from one another in very precise + controlled ways.

9. The evidence for differences in the genetic constitution of males, and the evidence of how these arise is vast. To adequately consider this evidence would require a whole series of lectures.

10. I will try, nevertheless, to outline some of this evidence, in order to indicate the range of differences that are among developed and the nature of their origins, when this is known. Only examples of some types, by no means all types, can be given at this time.

11. These range from differences involving number of sets of chromosomes to differences involving known genes, on both morphological and physiological levels.

changes in chromosome constitutions at certain times during development.

I. Polyploidy – "normal" individuals

1. Widespread phenomenon. Certain cells of organisms are polyploid –

Degree varies from 1 n to 2,000 n.

Disposition of chromosomes in nuclear vacuoles – ① polytene, ② individual strands. ③ combination.

2. Mode of producing polyploidy – varies: Endomitosis; nuclear fusion; suppression of nuclear separation.

3. Expressions – a) Polytene chromosomes in Diptera – very well known

b) Polyploid cells in plants – " " " characterize certain cells in a tissue

c). Same applies to animals.

4. Not only increases in chromosome constitutions characterize particular stages, but also decreases in chromosome constitution

a) Most familiar = meiotic division

b) Less " = Reductions in early developmental stages =

Frog (Green, 1953) – In tail of frog, the mesenchymal cells have reduced chromosome number. Those of epidermis show the 2n number.

Sea Urchin – (Lindahl, 1953) – 16 cell stage, 4 micromeres present at veg. pole. All with 2n = 36.

Division of micromeres: reduction = cells found have 18 cbs; (prime [illegible])

II. Changes in constitution during development - specific chromos.

1. Best case because best studies - Pavan.

Outline: the origin of sperm constitution
" " " egg "
The fusion = Soma
a) Loss of limited chr
b) " " extra x chr - which ones
Losses in germ line: extra x chr -
The region controlling loss = centromeres.

2. Others - Cesidrosyndrome - White -

3. Differences within mulei having polytene chromos:

a). Whole chromos - White, Millard, Barnes.

b). Parts of chromos at certain times during development -
Beermann, Mechelke, Pavan.

① The Pavan studies: Outline.

c. Schultz - the Y chr in mus cells.

III. The changes in constitution of mulei at specific times -

a) the B type chr: many organisms.

b) the component responsible in maize. A-B translocation. The
centrum region or close to it = as in Pavan.

IV. The changes in genic action occurring at specific divisions -

a) Mating type: in Paramecium

b) " " : in Fungus Glomerella.

V. Alterations induced by Di-Type behavior - breaks at specific loci

1. Sciarra - Metz - genetic transmission
2. ~~Campanula~~ Hyacinthus - breaks at specific loci - late in development
3. Vicia - Levan - breaks at specific loci when seedling from with low oxygen content.
4. Drey fus: breaks at specific loci during spermatogenesis
5. Oneothera - Catchside: " " " region (locus) in a translocation chromosome.

VI. Specific associations of chromosomes in cells -

1. Maize - associations of knobs - 9+5 very high at pachytene - S. Petersen

" " centres - non-random " " " "

2. In differentiated cells of plants: treatments: force differentiated cells to divide: Bridges + fragments. Their relations to one another in polyploid cells

same flow
sine flow

Reflect associations: in working nucleus.

VI. Differences in behavior of chromosomes within a nucleus:

a). One set of chromosomes = all condensed = stain very differently from the other set

b). " chromosomes = " " at one stage; differences like other ones at another stage.

c). One region or band of a set - differences at different stages of development without chromosomes of nucleus.

VII. Conclusions:

1. The different nuclei of an organism can vary in their genic constitutions in a very wide range of possible ways: From differences in organism & behavior at specific loci to differences in whole chromosomes, to differences in whole sets:-

Presence or absence; increase in quantity or decrease in quantity; differences in divergent roles; differences in structure - at all levels from a band to a whole set of chromosomes.

2. In the light of this knowledge, the origin and behavior of mutable genes, as outlined, is not a fantastic projection, but a working hypothesis with much latitude for future experimentation to define, modify and refine our appreciation of the various systems within the nucleus which operate to control the expression of genes during the developmental process.

1953

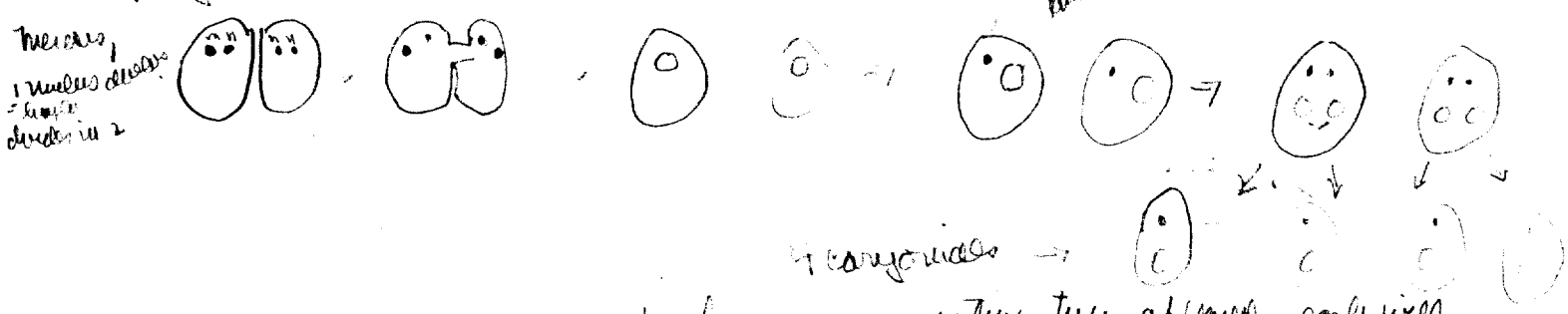
Nanney, D.L. + P.A. Caughey

Mating type determination in Tetrahymena pyriformis.

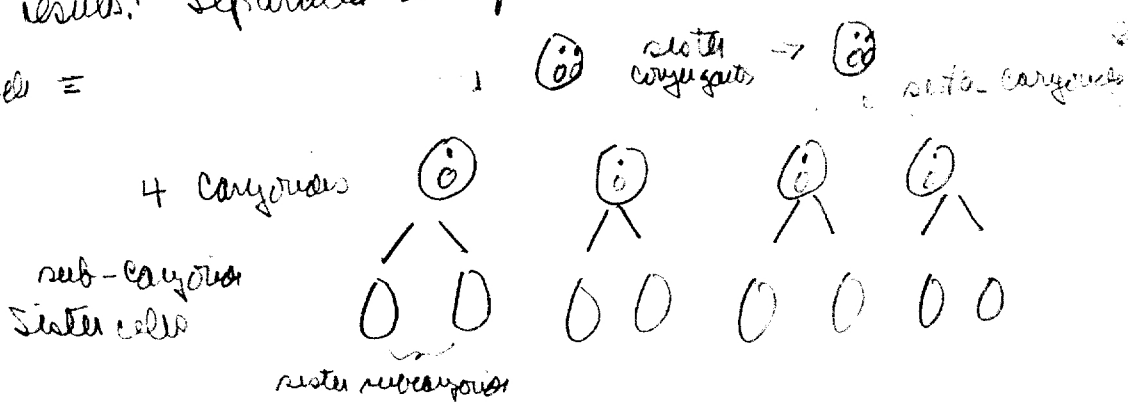
Proc. Nat Acad. Sci 39: 113-119

—

1. M. Paramoecium bursaria, multiple mating types occur.
   " aurelia, no more than 2 mating types found within a variety (given I : II, III : IV etc.
2. Tetra. pyriformis: wide variety of forms.
   1) amicronucleate, no known sexual form.
   2) "selfing" lines
   3) crossing clones. This type used: Woods Hole 14, Woods Hole 6: mating type I
   mating type II
3. Life cycle:



4. Among 500 F_1 F_2 + F_3 and back crosses, 7 mating types appeared, each will mate with another type but not with itself
5. Selfing clones also appeared. These give as many as 4 mating types within clone, but individual isolates give rise to pure mating type
6. M P. aurelia (Sonneborn) mating type within individuals of caryonides are usually able but mating type produced by sisters (sister caryonides) often differ. Mating type "segregates" at 1st division of macronucleus. Time of change.
7. The Tetrahymena results: Separated cells from ex conjugates up to three produced by caryonides ≡



all possible comparisons of mating typs in related clones tested. Results of 3 exp. shown in table 2.

Table 2 of paper

Cross	Sister sub-caryonides alike	Sister sub-caryonides different	Sister caryonides alike	Sister caryonides different	Co-conjugant caryonides alike	Co-conjugant caryonides different
1	7	6 (1)	16	28	18	73
2	7	1 (1)	6	12	10	27
3	13	4 (1)	10	22	14	59
Totals	27	11 (3)	32	62	42	159

( ) = number of sub-caryonides in which different pure line typs were found: Relayed segregations, delayed changes in nuclear constitution

Nearly all possible combinations were found within sister caryonides: [illegible]

8. Crossing same mating types, - III × V from F2 individuals, as examples -- yielded very different mating types. And, different alleles of II or V give different spectra of types

Table 3 of paper:

Cross	Temperature	mating Types of caryonides from III × V F2 individuals I	II	III	IV	V	VI	VII	Selfing culture	Total
4	16°C	2	5	4	0	5	13	0	9	38
	26°C	12	3	4	0	3	4	0	9	35
5	16°C	0	5	4	11	2	0	2	14	38
	26°C	0	11	1	9	2	0	4	16	43

Interpretation (mine)

Results suggest an unstable locus determining substance responsible for mating type. In P. aurelia, time of change at locus occurs, usually, at first division of macronuclei in sister conjugants, each to two parental type. In Tetrahymena, time of change has greater spread, going into sub-conjugant divisions but mainly at first division of macronuclei. Here, type of change can give a number of new mating types, not formed in parents reaction types.

Time and type of change in nuclear constitution illustrates. Related to mitotic event.

Auto - mutagenesis in the mushroom, Schizophyllum commune

John R. Raper, Univ. of Chicago. Science 118 pg 574, 1953 (Nov).

1. Tetrapolar sexuality; obligate crossmating imposed and controlled by incompatibility factors at two loci, A + B.
2. Each fruit produces progeny of 4 distinct mating types
3. Fertile matings occur between strains of these diverse mating types only in those combinations which yield the double heterozygote.
4. In other combinations having A + B factors in common, heterokaryons of a unique type are formed.
5. The common - A heterokaryon, which is stable and capable of indefinite vegetative growth, induces mutation in its component nuclei in frequencies up to 10^{-6} times the spontaneous rate for the same mutations in homokaryotic strains.
6. Mutants belong to a limited number of distinct morphological types (about 10) each differing from the wild by a single, characteristic, altered locus.
7. Age of heterokaryon + genetic history of its component strains determine mutation frequency and, to a lesser extent, the type of mutation induced.
8. Auto-induced mutagenic agent(s) suspected which preferentially affects a limited number of loci in a regular and predictable manner.

Hinton, T., P. T. Ives & A. T. Evans

Changing the gene order and number in natural populations

Evolution 6 : 19-28

1.

1. 13 × Chr. mutant stocks examined. Derived from hi of Ives.
2. Each carries inversion from c.o. studies
3. Arose in hi stock with frequency of 4.8% of tested lethal-bearing chromosomes
4. Kept in stock by balancing with Δ-49.
5. Crossed to normal & salivaries examined.

			Breaks	
Breaks.	m (1) hi	1	12 E	20
	"	2	1 F	20
	"	3	4 D	20
same locus	"	4	4 C	20
		5	1 F	20
same locus	"	6	4 C	20
	"	7	12 E	20
same locus	"	8	3 C	20
	"	9	8 F	20
	"	10	4 E 2, 3	8 A, 1, 2
	"	12	1 C 3	20
	"	13	4 E	20

Transposition (hi 11) Break at 5C, 7E, 20. Region between 5C and 7E inserted into 20.

nearly 1/2 of breaks occur in region 4.
Regions involved coincide with positions of hetero chromatin given by Kaufmann
Break positions in 20 not determined cytologically. Crossover studies suggest sufficiency of positions of breaks in 20.

Species crosses - alteration in chr. complements

I. Many examples - changes in gene action,
appearance of variegation
changes in chromosome constitution - reductions
Metz - Scarce change in set - Mosaic
salivary gland. Species A × B.
Same cells = Hybrid
" " = cell species B
" " = Part of A + B.

Nicotiana - eliminating change in set in
f.c. A × B × A = B also
eliminate connection

Ds type behavior – Besides maize.

1. Hyacinthus – Darlington. Particular chromosome – breaks late in development at specific region of a specific chromosome.

2. Sciara – Metz. Strain showing break at specific region of specific chromosome in strain of Sciara. Genetically controlled.

3. Dryfus – Break at specific region of certain chromosome during spermatogonial divisions

4. Vicia – Levan – Breaks at specific regions m.o. in chrs. in early development – cause environmental.

5. Oenothera – Catchesides. Evidence strongly suggests Ds type behavior in chromosome arising from translocation. Breaks at or close to heterochromatin

Differential segregations – genetic expressions, non-mendelian [illegible]

1. Paramecium – mating type reaction – Two nuclei, mono + differ following this division. At certain time in development

2. Tetrahymena – same as Paramecium as next following division

3. Case in Glomerella where "mutation" is genetically controlled in the development of the ascogenous hyphae. At certain time in dev.

4. Control of patterns - why pigment forms at certain position

5. Wing of Eyelestia - differential mitosis required.

Differences in number in different cells of an organism: Morphological Studies

1. Zygote = 2n = 2 sets of chromosomes.

a). Increasing number of sets ① – definite degrees in certain cells of tissue
② Nucleus – varying considerably: Polytene
Widespread phenomenon
strands remain together

Diffuse: strands separated

combination of both

b). Decreases in sets of chromosomes – at particular time in development

① Frog – Tail Mesenchyme cells haploid in
Epidermis: diploid

② Sea Urchin – Somatic reduction in division of certain, clearly differentiated cells of 16 cell stage of embryo – the micromeres.
all 4 micromeres nuclei = 2n (36
During their division = reduction in molecular chromosomes. (18)

③ Culex (mosquito)

2. Differences in different cells of organism with regard to certain chromosomes of the complement: a) Sciara [the centromere action]

b) Maize – B type chromosomes. [the centromere action]

c). Plants + Animals – many cases like that of both Sciara + Maize.

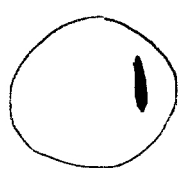
3. Differences in behavior of sets of chromosomes within in a nucleus – Reflect differences in function.

one set condensed = become chromosomes in sperm (white –

one set extended.

4. Differences in behavior of individual chromosomes in complement at different times & in different cells of tissue

a) White – salivary; Photo Trillard – salivary.

b). Some cells  others

Different same

5. Differences in behavior of individual parts of chromosomes.

cells

a) Large ↙ or ↘

segment

b). Chromocentric regions – Drosophila

Somatic cells – Newsalls

Salivaries.

b) Smallest segment known - the bands in salivary glands - Pavan.

Rhyndrisarra:

1) all eggs laid within 45 min

2). larvae = all of 1 sex

3) " develop all at same time 42 days to pupae.

4). Extraordinary good salivary glands type chr in several of the tissues

5). Can follow differential behavior of individual bands at any one time.

6). Showed: certain minimum bands in particular tissue of all larvae undergo same type of change during development + same sequences of changes. Reflects differential action at certain times in development. Pavan interpretation of some changes: increase in DNA, or of gene components, differentially in a particular band. Always same bands, in same tissue at same time in development.

March 4th.

I. Review of previous discussion.

1. Purpose is to show that other systems present that control genetic expressions besides the Ds-Ac + Ai-Dt systems, which are much alike

a) To show that some basic similarities are present - that controlling genic expressions + showing the clear-cut somatic segregations + meiotic segregations that give the same change in genic expression. Also, that initial evidence suggests transposition of the controlling factors.

c) Such transposition have also been proposed to account for genetic changes in expression of the var. P loca in many of Bray + another case of varying the pale green by Peterson.

II Since these controlling systems have made themselves evident in cells whose nuclear composition has been altered, we infer that they were present in the nucleus before the alteration occurred. Performing in same manner -- controlling genic action and doing so at specific times + in specific cells during development

How can we account for their appearances:

If we take the view that they are present in the nucleus before alteration, then they must be functioning in normal nuclei -- (1) They serve to control specific genic actions at certain stages in development (2) That the somatic segregations likewise occur during normal development. (3) That the cells in which such segregations occur do not give rise to the genic cells but to cells which will be differentiated

in one "set line of determined course. (4). Redifferentiation, T building vegetating will not arise from cells which have lost components by the segregation process but can arise only from specific cells within this tissue, which have not been altered by somatic segregations.

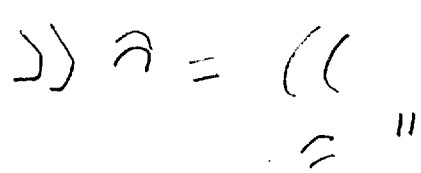
The reasons we have been able to see this process is because the segregation process has "been put - out of phase" by the alteration occurring to the heterochromatic elements by the b.f.b. cycle.

We can therefore examine this process because it is "out of phase" and determine the factors involved and how they operate.

This by pothers would require that in normal development the nucleus of different cells of an organism would vary genetically. They would not be equivalent to one another genetically. It would be given controlled types of somatic segregation at special divisions during development. It would suggest that chromosome alterations - translocations etc - might accompany some of these changes. What evidence do we have that such events occur in normal development? There is a vast amount of cytological evidence pointing in this direction. Some representative examples will be chosen.

III. The "dedifferentiation" of differentiated plant cells:

1. Cells in root fully differentiated normally would not undergo a division
2. These forced to undergo a division by chemical treatment - (This treatment does not induce chromosome alteration in the dividing cells)
3. The chromosome complement -- chromosome alterations, present in malleus, made evident in these cells. The polyploid cells arising from endomitosis:



The anaphase. Bridges + fragments. Two homologues] ⊂] ⊂
Same aberration in each homologue. Expresses controlled event at same position in each homologue.

4. Such cells not capable of developing a new organism because of many aberrations present that are expressed at anaphase -

5. Conclude that the chromosome aberrations are of a controlled nature - association of particular complexes of the malleus in particular cells.

IV. The controlled segregations of nuclear components during normal development. These occur on all levels - from chromosome sets to components of chromosomes.

1. Best analyzed case - Sciara . Many others with same general pattern.

2. The B-type chromosomes in plants - Many cases - Examples B. type chs.

3. Genetic non-equivalence - Differential segregations

Paramecium mating type

Glomerella " "

V. Non-equivalence of chromosome components in normal development - all levels. from sets, to nature chromosomes, to parts of chromosomes, to individual bands - genes - in chromosomes.

See sheet.