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The Role of Chromosome Mutation and Aberration in Species Formation and Differentiation

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THE ROLE OF CHROMOSOME MUTATION AND ABERRATION

IN SPECIES FORMATION AND DIFFERENTIATION

A Thesis

Presented to

the Graduate Faculty

Central Washington State College

In Partial Fulfillment

of the Requirements for the Degree

Master of Education

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by

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CHAPTER I

DEFINITION OF PROBLEM

In recent years new knowledge of genetics has developed so rapidly that it is difficult for any individual to remain cognizant of all its various aspects and related fields. New discoveries in the fields of cytology, chemistry, cytogenetics, physics, botany and zoology have contributed greatly to this very rapid growth. New techniques of measurement, microscopy, electronic-device development, and light and sound wave manipulations have given scientists tools for exploring areas of genetics that heretofore were unavailable to them.

One result of these new techniques was the revelation of the structure of a molecule that is not only capable of reproducing itself, but is arranged in such a manner as to control physiological functions of the living cell. It was also shown that the method of molecular replication could allow sudden change that lended itself to the observed laws of heredity. The structure of this molecule, deoxyribonucleic acid (DNA), unlocked many scientific doors, but it also introduced new problems for the geneticists and scientists in closely allied fields.

To understand the principles of genetics and evolution as they are applied in all organisms, it is necessary to integrate the new knowledge in its proper perspective within that already incorporated into the concepts of species formation and differentiation. The events of chromosome replication and alteration, together with their basic role in genetics, become extremely important as a basis for understanding organic evolution. The occurrence of chromosome mutation or aberrations has an effect on the evolution of new species. The analysis of these chromosome functions is the purpose of this paper.

In this paper the chromosomes and their areas of genetic influence represent the materials which are passed from the parent to the offspring. The term gene will be used to designate a specific area or locus on a chromosome. These genes express themselves in the organism in a characteristic manner. Alteration of a chromosome or of a particular locus in a chromosome, resulting in a different expression of the characteristic phenocopy, will be considered a mutation.

Mutations will be considered to be of two types; (1) point mutations, which concern genes or loci of specific genic traits on a chromosome and (2) chromosome aberrations, which are gross alterations of large chromosome segments or entire chromosome.

The term species applies to any group of similar organisms making up a population of interbreeding individuals that will not ordinarily interbreed with any other population occupying the same ecological niche.

CHAPTER II

REVIEW OF THEORY

Evolution has always been an area of conjecture and disagreement. Even today, though new knowledge is being gained very rapidly, there is much disagreement about the nature of these processes and the likelihood of agreement seems quite remote.

Before the publication of Alfred Wallace's and Charles Darwin's combined theory, and Darwin's subsequent book Origin of Species in 1859, only one theory of evolution and species formation of any importance had been proposed (24:1-10). LaMarck's theory of acquired characteristics had much acceptance during the early 19th century and even during the 20th century there were scientists who used this approach to species formation and differentiation. The group, known as the Michurinists in Russia with Lysenko as their bellwether, is the only group at the present time following this theory (24:11-12).

LaMarck based his theory on environmentally induced adaptations occurring in animals and plants. His explanation was that mutations were not only induced by the environment, but that the mutations were also somewhat selected by the environment before they occurred. He stated that pressure applied by the environment caused the development of adap-

tive structures which were passed to the following gener-
ations. He made no attempt at explaining how the variation
of individuals within the same ecological area occurred.
This theory was accepted by many biologists until 1858.

In 1858, Charles Darwin and Alfred R. Wallace read
their co-developed theory of natural selection to the Royal
Society of London (7:preface). The next year Darwin's
book Origin of Species was published. The repercussions
of this book were tremendous. The book created a furor
among the philosophers and theologians of the day. Even
today the name Darwin precipitates many heated discussions,
and it is still almost universally connected with the proc-
esses of evolution and species formation.

Darwin's theory proposed that all organisms reproduced
at a much greater rate than the food supply would support and
that only those "most fit" were able to survive. Darwin's
basic idea was formulated when he read Malthus' On
Population (7:428-429).

The primary fault in Darwin's theory was the lack of
an explanation for the difference between environmentally
induced individual variation and variations that occurred
due to genetic changes. During the last part of the 19th
century when Darwin's theory was so vehemently attacked, he
alluded more heavily to LaMarck's theory of acquired charac-
teristics to help explain the gaps in his own theory (17:233-
235).

During the 1860's some brilliant work was done by Gregor Mendel, an Austrian monk, with hybrids produced by crosses of the common garden pea, Pisum sativa. From his observations of the phenotypic ratios that occurred, Mendel formulated the laws of segregation and independent assortment that form the basis of modern genetics (12:31-77). The importance of Mendel's work was not realized immediately, and it was not until the beginning of the 20th century that these findings were rediscovered and their value reasessed (11:Preface).

Mendel's experiments were rediscovered by Hugo DeVries. This information together with experimentation of his own, prompted DeVries to formulate his own theory called the mutation theory. DeVries' hypothesis was based on the theory that the substance of the heritable materials could and did undergo sudden, abrupt changes that produced changes in the developing individual (11:1-3). These sudden changes he called mutations (11:4).

While the mutation theory is the most widely accepted of all the theories proposed, it has had much refinement since its formulation. Work performed by scientists on the many varieties of Drosophila, on the fungi Neurospora, and recently on the bacteriophages and viruses, has provided new knowledge of chromosome and gene mutations that partially negates some aspects of DeVries' original theory.

DeVries proposed that mutations were of such a nature and of sufficient magnitude that a new species was formed in one sudden, catastrophic change (11:5-6). However, it is now known that most of the larger or more drastic mutations that occur are of a lethal or semi-lethal nature and that the mutant individuals die before they reach sexual maturity.

Since large mutations caused lethality, the role of mutations in species formation had to be redefined. Scientists such as Fisher, Haldane, Cheverikov, and Sewall Wright were instrumental in the redesign of this modified mutation theory (13:16). These men, working independently, developed a genetic theory of evolution or species formation. The genetic theory limits the mutations or changes occurring in the chromosomes or genes to very small changes or to changes that do not necessarily have a lethal effect. The interaction of the environment with these small changes, which may be accumulated by segregation and recombination to have a larger effect in their accumulative form, brings about new or different species. (14:12-15).

Since this refinement of the mutation theory of species formation was proposed, other refinements have also been suggested. Some scientists, such as Richard Goldschmidt, insist that new species cannot be developed by the process of small mutations, which he calls micro-evolution (19:94). These proponents of the macro-evolution

form of species differentiation insist that new species can
be produced only by larger, systemic mutations which would
help to segregate the various species within a given area.
They feel that the new "species" produced by the micro-
evolution process must be considered as varieties only.
Without isolation of these new species true speciation has
not occurred (25:115-116). However, the micro-evolutionists
feel that the factors or types of isolation are just as
readily found in small mutations as they would be found in
larger mutations.

The only other theory proposed at the present time
is followed by the Michurinists. They feel that environment-
induced changes similar to the changes of the LaMarckian
theory are responsible for any new species that occur. The
promotion of Lysenko as head of the Russian Academy of
Science in 1948 contributed to the rise of this concept
which is apparently based more on present Russian political
ideology and philosophy than on scientific fact.

Organic diversity and the development of new types
of individuals have their most concrete bases on the muta-
tions occurring in all populations. The differentiation
of these new species is determined then by (1) the occur-
rence and rate of mutations and their appearance in a
population, (2) the selection pressure that is applied by

the environment, and (3) the size of the group making up the interbreeding population.

The problem then arises as to how these mutations and aberrations occur and what are their more precise roles in species formation and differentiation.

CHAPTER III

THE HEREDITARY MATERIAL

Through the development of better microscopes, the
processes of cellular division and propagation became more
evident. Schleiden, Schwann and Virchow, over a period of
time (1838-1855), proposed the Cell theory (12:152-153).
This theory holds that all organisms are composed of cells
and that any new cells arise from pre-existing cells. Germ
cells are derived from divisions of certain cells in the
parent and in turn produce the cells of the off-spring's
body. Thus multi-cellular organisms are derived from a
single cell or from the fusion of two specialized cells
that each carry half of the chromosome complement of the
parent organisms.

The microscope also permitted discovery of cellular
structure that heretofore had gone unrecognized. Cell
nuclei were first seen and named by Robert Brown in 1831,
but the cellular importance of the cell nucelus was not
recognized until Eduard Strasburger (1875) and Butschli
(1876) proposed that the cell nucleus developed exclusively
from previous cell nuclei by a process called "mitosis",
the name given it by Walter Fleming in 1822 (12:153-154).

Mitosis is the process of cell division during

the chromosomes duplicate themselves and a full complement
of chromosomes is segregated to each daughter cell. This
is different from the process of meiosis where the single
duplication of the chromosomes is followed by two cellular
divisions with the segregation of allelic pairs so that
each gamete developed has half the full complement of
chromosomes of the parent organism.

With the discovery of the mitotic process, it was
realized that the heredity and the controlling mechanism of
the cells were controlled by the materials found within the
nuclei of the cells. The most obvious structures within
the nuclei are the chromosomes, so called because of their
staining qualities with certain dyes. Sutton and Boveri
(1902) proposed that the chromosomes carried the hereditary
units (46:231-251).

The realization that the chromosomes were the car-
riers of the hereditary materials gave impetus to the study
of these structures. Their movements during mitosis and
meiosis, and any changes that occurred which would explain
the presence of organic diversity among the individuals
making up a population were studied.

However, the smallness of the chromosomes and their
integral parts made it extremely difficult to study them
even with the powerful electron microscope used in modern
research. Certain facts have been ascertained though,

through some brilliant research by many scientists.

Under the compound light microscope the gross struc-
ture of the chromosomes is observable and the position of
their centromeres may be ascertained by the configuration
of the chromosomes as they are pulled from their position
on the equatorial plane toward the cell polar regions. The
function of the centromeres is to direct the chromosomes
toward the cell poles by becoming attached to the spindle
fibers extending from these polar regions.

The chromosomes may be grouped according to the
location and type of centromere. These groups are:
(1) pericentric chromosomes, which have a single centromere
near either end of the chromosome, (2) metacentric chromo-
somes, where the centromere is located near the center of
the chromosome, and (3) diffuse, which is unusual in that
a distinct centromere constriction is not found on the
chromosome and is thought to be scattered along the chromo-
some in several points (10:251-261).

Under a more powerful microscope, such as the electron
microscope, the smaller details of gross structure may be
more readily observed. In a shortened condition, such as
is formed during mitosis, dark bands that have been stained
with certain dyes, can be observed. These bands are pos-
sibly made up of large macromolecules of deoxyribonucleic
acids, which stain a very dark color by Feulgen technique.

These bands are thought to be attached to each other by
protein molecules which do not stain dark by the above tech-
nique. These dark-staining bands show a unique individuality
in each chromosome, and electron photographs of chromosomes
can be compared and their differences noted. In the case
of certain morphological changes in the individual chromo-
some band arrangement, these changes may be noted by these
photograph comparisons and are thought to be evidence for
mutation occurrence.

The somatic cells and germinative cells (before
spermatogenesis or oogenesis) have a genome or set of chro-
mosomes that have two gene loci on homologous chromosomes
that make up a pair for at least each characteristic of
that cell or organism. However, these homologous chromo-
some pairs may contain genes or gene loci that number into
the hundreds and possibly into the thousands. Each gene
locus may affect only one phenotypic characteristic, but
several loci may have a multiple effect on one or more
characteristics. The electron microscope is not forceful
enough to show separate deoxyribonucleic acid molecules,
but the bands found on giant chromosomes, such as the
Drosophila salivary chromosomes, are considered to be the
sites where these macromolecules are found.

It is known that the elongated, dark-staining chro-
mosome bodies are made up of three types of materials:

deoxyribonucleic acid (DNA), ribonucleic acid (RNA), and proteins, primarily histones and protamines (2:8). Of these three chromosome materials, all are found in most organism's chromosomes, but in certain bacteria, bacterio-phages and viruses, only DNA and proteins are found (50:93-107). In some bacteria and bacteriophages the DNA that is present is found to be made up of only one strand of sugar-phosphate-nucleotide radicals.

With the knowledge that the chromosomes contain DNA, RNA, and certain proteins, scientists began work on the possible integration of the known facts about DNA with the hope of developing a working hypothesis for the determin-ation of the DNA structure. It was known that the heritable materials must possess three qualities to conform to the known facts. First, the material must be of such a nature that it is capable of reproducing itself with fidelity. Second, it must be possible for sudden, discreet changes in structure to occur in order to account for the appearance of mutants within a population. Third, it must be capable of transmitting the necessary information to the developing organism or cell in order to control its development.

While the proposal that the hereditary material must be DNA with known chemical properties, it was not until 1953 that a workable hypothesis was proposed for its

molecular structure (6:54-61). A English chemist, F.H.C. Crick, and an American geneticist, James Watson, proposed a double-helix configuration that provided a possible basis for observations that several other scientists had also recognized. They derived this structural model from observations of X-ray diffractions of fibrous DNA material (6:54).

The DNA molecule, as proposed by Watson and Crick, is made up of two separate chains of pentose sugar molecules connected by phosphate radicals. These separate chains of sugar and phosphate molecules are connected to each other by hydrogen bonds occurring between "side molecules" of amino acids attached to each pentose sugar molecule. The direction of the chain formation of each separate sugar-phosphate-nucleotide chain is opposite to that in its complementary strand with which it forms the double helix.

The phosphate group bonding between sugar molecules is from the 3rd carbon atom of one radical to the 5th carbon atom of its neighbor. These pentose-nucleotide radicals are held at a 90 degree angle by the phosphate groups and parallel to its neighboring pentose-nucleotide groups. The shift in vertical plane by the 3 to 5 carbon bonding gives a spiral or helical twist to the DNA molecule. The degree of twist is affected by the amount of water present and varies from 17 to 24 degrees (6:56). Therefore, it takes approximately 9-15 phosphate-pentose-nucleotide groups

to make up a complete 360 degree twist in the double helix strand. This was one of the more difficult problems that the Watson-Crick model clarified, since the X-ray diffraction pictures did not give the clear structural crystal hoped for (30:247-260). The helical twist caused the distortion of the crystalline structure.

The strands of phosphate-sugar-nucleotide chains are held parallel and together by the hydrogen bonds formed by amino acids. These proteins are of two main types: Purines, which have the larger molecular size, and pyrimidines which are smaller. The two purines found in DNA are thymine and quanine. The pyrimidines are cytosine and adenine (47:407-410).

One purine and one pyrimidine combine by hydrogen bonds to form each coupling nucleotide base. This combination of one purine and one pyrimidine in each nucleotide base was deemed necessary by Watson and Crick because any other type of coupling would cause distortion of the parallel strands due to the molecular size difference of the amino acids. Previous chemical analysis had shown that the ratio of quanine (purine) to cytosine (pyrimidine) was very close in all DNA tested, although the total amounts of these proteins differed from DNA in different species of organisms. The amount of thymine to adenine showed a similar relationship (47:407).

The Watson-Crick structure gave a basis on which new hypotheses could be formulated. The DNA molecule is thought to reproduce itself by breaking the weak hydrogen bonds between the nucleotide pairs. Each complementary strand replicates itself by attachment of new sugar-phosphate-nucleotide molecules which would be the replicated of the complementary strand that had detached itself (6:54-61). This hypothesis of molecular reproduction or assimilation into DNA macromolecules cannot be explicitly proven, but it does offer a workable model for further research.

The method of information coding, and the transferring of that information from the DNA molecules of the chromosomes has had much investigation since the Watson-Crick model was presented. The nucleotide base-pair sequence of the DNA molecule was found to be quite uniform within a species and this gives a method of information coding (45:35-42). Various codes have been proposed by George Gamow, F. Crick, and Noboru Sueoka (18:70-78). The type of code that these men proposed was one made up of a sequence of at least three nucleotide base-pairs called "triplets". Since the possible combinations of three pairs of nucleotides would give a total of 64 possibilities, a system of "non-overlapping" lowered the possible number down to 20, which is the number of known amino acids recognizable today.

If each triplet corresponds to a particular amino acid and the RNA functions to transfer this information to the amino acid producing structures of the cell, the triplet could conceivably be considered as a gene. However, it is fairly obvious that in many cases a cellular process is a complex functional unit and no one triplet would have complete control over it even though the lack of that triplet of base pairs could very well inhibit the process.

Further experiments with the use of synthetic RNA molecules have shown that only two of the 20 known amino acids need all three nucleotide base-pairs present before the amino acid or protein will be synthesized (33:80-85). These experiments, carried out in cell free systems in the laboratory, show that the triplet may not be necessary for the formation of most of the amino acids which are used to produce the cellular proteins. Probably there is a higher integration including many or several triplets for the formation of these larger protein molecules.

The RNA molecule was found to be composed of a single chain of ribose sugar-phosphate-nucleotide radicals, with the difference between DNA and RNA of only the sugar molecule and one of the four amino acids of the nucleotide bases. Instead of thymine, the RNA has uracil, plus the other three amino acids found in DNA. Also, the nucleotide-base-pair sequence was found to be very similar to the base

sequence found in the DNA molecules from the same organism. This relationship is presumed to be part of the basic system of genetic information transfer from the chromosomes to the rest of the cell.

The method of genetic transfer can be more readily seen by the action of certain bacteriophages. The phages are composed of a head region which contains the hereditary materials, a tail region which is hollow, and a structure at the tip of the tail region for attachment to a bacteria wall.

Upon attachment to a bacterium, the phage punctures the wall with its hollow tail section and injects the hereditary materials of the head region into the bacterium. At this point, the DNA of the phage takes over control of the protein synthesis of the bacteria. The DNA of the phage induces the ribosome structures of the bacteria to produce proteins which are incorporated into new phage systems (22: 41-49; 43:76-79).

Thus the production of new amino acids and proteins by the use of the coded information of the DNA molecule, under the direct control of the RNA molecules which are in turn controlled by the DNA, is apparent. Investigations into the RNA molecules of the various organisms show that there are different types of RNA and that each of these different types has a different function. At present

these RNA function groups are divided into messenger RNA
(m-RNA) and transfer RNA (t-RNA).

Messenger RNA is concerned with the formation of the
sequence of nucleotide base-groups similar to the base-
group of the DNA of the system. The t-RNA attaches itself
to specific amino acids and attaches these to other amino
acids in the order prescribed by the m-RNA (33:83-84).
The amount of t-RNA is found to be much greater than the
m-RNA and their specific functions were shown by an
experiment with a cell free system.

The experiment consisted of removing an atom of
sulfur from a molecule of cysteine. The removal of the
sulfur atom changes the molecule from cysteine to alanine.
The removal of the sulfur atom was performed after the t-
RNA had attached itself to the cysteine molecule. The
t-RNA proceeded to place the "now" alanine molecule into
a protein where normally a cysteine molecule was found
(33:91-92). This indicates that the m-RNA acts as a tem-
plate and that the t-RNA acts as the catalyst to attach
the separate amino acids into a larger molecule.

It is now quite evident that the basic material of
the chromosomes which carries the genetic coding of the
heredity of the parents to the offspring is the DNA mole-
cule. The different types of RNA molecules probably set up
a complex enzymatic system, which controls the formation of

the cellular products and the development of that organism. Any change in the basic molecular structure of the deoxyribonucleic acid during its replication or in the passage from the parent to the offspring would have a profound effect. How much of the basic DNA molecule would correspond to a gene cannot be ascertained, but it may vary and the gene's control of the phenotype may be changed by a change in that amount of DNA material.

CHAPTER IV

MEIOSIS AND CROSSING OVER

The importance of the meiotic and mitotic processes
in the germination and development of any organism has been
realized for many years. Since it has been noted that many
of the lower forms of life have a different relationship
between mitosis and meiosis than in the higher forms, it
has been conjectured that the meiotic process has developed
from a modification of the mitotic processes.

Wilson classifies the meiotic processes as (1) game-
tic or terminal and (2) zygotic or initial (49:484-492).
Gametic meiosis is found in most animals and zygotic meiosis
in lower plants. In the alternation of generations in plants
it is found that the zygote is the only diploid cell in the
life cycle of lower plants. In higher plants meiosis takes
place to form haploid megaspores and microspores which then
go through a series of somatic (mitotic) divisions to form
female and male gametophytes respectively (34:3).

The first meiotic stage is of a greater duration
than that of somatic prophase and also it is typified by
a marked increase in nuclear volume and hydration (10:
318-319). This increased duration of time and increase of
nuclear size denotes a physiological change in the cyto-
plasm (34:3-4).

The meiotic behavior of chromosomes is important since the chromosomes contain the "genes" which are inherited and segregated by the mechanism of chromosome segregation (48:17). The main differences in chromosome behavior are due to the function of the centromeres or the kinetochores. The "standard" type of meiosis is accompanied by a centralized centromere, with the exception of the diptera, whether the centromere is metacentric or pericentric (34:4). An atypical meiotic process is accompanied by nonlocalized centromeres. Some orders of insects having this type of meiosis are Hemiptera and Lepidoptera. Also the Arachnida or spiders have nonlocalized centromeres (14:129-130). Certain of the lower plants are also thought to have this type of meiotic activity.

The first prolonged stage of meiosis is called the prophase. It can be further broken down into (1) the preleptonema and leptonema, (2) zygonema, (3) pachynema, (4) diplonema, and (5) diakinesis. These later divisions are arbitrary and it is impossible to separate the later stage of one from the early stage of the next subdivision.

The onset of meiotic prophase is marked by an increase in nuclear volume followed by gradual modifications in nuclear structure (10:318-319). The gradual evolution of the diffused chromatin reticulum into a set of condensed chromatin bodies takes place. In some plants these con-

densing bodies begin to take on a spiral or coiled shape.
In animals the spiral stage is not evident, but the en-
larged chromatin areas are considered to be prochromosomes
or prochromocenters (34:14).

The preleptotene spiral is lost as the leptonema
stage begins to develop and the chromosomes unravel to
become greatly extended. However, not all organisms show
a loss of spiralization, and there is considerable conjec-
ture that the spiralization of the chromosomes produces
the banding appearance of many chromosomes. Bridges states
that, "The gross structure of salivary gland chromosomes is
somewhat like that of an accordian, and unless these chro-
mosomes are stretched, the doubleness of most bands is not
visible" (3:61-64). The larger gyres of the spiral then
may cause this close appression (23:113-118). Another
idea is that the bands are large macromolecules of DNA or
a series of DNA molecules and that the non-staining zones
between these bands are connecting protein structures (29:
118-121).

Chemical analysis of the leptotene chromosomes shows
that the doubling of the DNA and histone content occurs be-
fore zygonema. Also, in some organisms the doubling of the
chromosomes can be observed (3:63). The chromosomes begin
to shorten and thicken toward the end of the leptonema stage.

There is no noticeable homologue pairing and it is during the following zygonemic period that the homologous pairing begins.

The zygonema stage of meiotic development finds the chromosomes thicker and shorter, and electron microscope photographs show some very interesting structural detail. Many cytologists feel that the polytenic structure of these chromosomes is very evident and have made proposals for the explanation of the individual repetition of chromomeres located in separate bands on the chromosomes.

One such proposal by Bridges is that the multi-fibril structure seen in Drosophila salivary chromosomes represents 8 chromomeres from each parent or a total of 16 chromomeres to make up one gene loci (3:64). Reduplication of the thinner bands on the chromosome could give rise to the heavier and thicker bands that are readily observed. Under good preparation, the heavier bands sometimes may be seen as separate parallel bands that are closely appressed.

Hans Ris states that the chromosomes of meiotic prophase are bundles of microfibrils which are uniform in thickness of about 500-600 Angstroms (35:133). This microfibril bundle is approximately twice the size of interphase chromosomes. Some cytologists feel that the number of microfibrils making up the chromosomes of different species is varied (32:290-309).

The coiling that appears to cause the shortening of the zygotene chromosomes does not seem to have any noticeable effect upon the pairing of the homologous chromosomes. The pairing continues until the homologues are found in close proximity to each other, but the mechanism for this has not been ascertained.

When zygotene pairing ceases, the nucleus is considered to be at pachynema. Pairing has occurred and it has been called a "stable" stage by Swanson (47:65). The chromosomes at this time are made up of two chromatids, or 4 chromatids for each homologous pair. This condition is called the tetrad stage. These bivalents continue to shorten and in many instances the homologous pair may be twisted around each other. This relation coiling may have an essential role in crossing over (34:19).

Linear differentiation in chromosome morphology is best observed at pachynema and is the stage that is widely exploited in cytogenetic studies (34:19).

The development of the diplonema stage is evidenced by the tendency of the chromosomes to begin to separate. The separating chromosomes may be held together at one or more points between the homologues. It is thought that the formation of these chiasmata is brought about by the crossing over between chromatids.

Crossing over and chiasma formation is the result of the exchange of chromatin materials between non-sister or non-homologous chromatids (10:364). The importance of this lies in the formation of new individuals with reshuffled paternal and maternal genes. Without this exchange, which is not an orderly process by any means, the reshuffling would not occur and consequently the traits received from any one parent would reflect the set of traits or genes that they had received from their parents.

The explanation for the exchange of genic material is not definitely known, but several hypotheses has been proposed. One of the most recent hypotheses is that as the DNA doublestrand material divides to build a complementary strand (see above), the developing strand may accidentally copy a section of each of the closely situated, but separated strands. This would cause a single chiasma to be formed. This process is called "copy choice" (43: 84-87).

While the single crossover is the most common type, the crossing of materials in two closely linearly associated areas is known. If the two complementary strands of the DNA molecule were in close proximity to each other, it is feasible that a "double-cross" could occur, or even that an "illegitimate" or sister-chromatid crossover could occur, too.

Other earlier hypotheses were proposed by (1) Sax, and a modified version of this theory by Matsuura and Haga; (2) The partial-chiasmatypy theory of Janssens and its modification by Darlington; and (3) the Belling hypothesis which considers crossing over and chromosome replication to be intimately associated (47:285-289).

The theory proposed by Sax, which is often called the Classical theory, is based on the assumption that a chiasmata does not represent a crossover (37:601-603). He assumes that crossing over occurs when a chiasma is ruptured and a reunion of broken ends or parts occurs with a recombination of the various parts of the chromatids. The chiasma formation is considered to have been produced by relational looping or twisting between either sister or non-sister chromatids.

A modified version of Sax's two plane theory has been proposed by Matsuura and Haga (28:48-57). However, since they suggest that crossing over is accomplished by the transformation of a relational spiral into a parallel spiral system, the number of chiasma formed would be greater than any evidence seems to warrant.

The partial-chiasmatypy or one-plane theory was originally proposed by Janssens. This theory has been further supported by many others, especially Darlington (26:248). This hypothesis is based on the assumption

that chiasma formation is the consequence of crossing over, or the exchange of chromatin materials. It has been proven by Stern, Creighton and McClintock, that crossing over is accompanied by chromatin exchange. However, in some cases where chiasma-like structures are found, there is no crossing-over occurring. In male Drosophila melanogaster, Cooper showed that (1) chiasma formation does not represent a crossover and (2) that some chiasmata may be formed by the opening out of loops found in the chromosome configuration as proposed by Sax (37:601-603).

Belling's proposal was only partially accepted because he considered that the crossovers were due to strand formation between chromomeres of non-sister chromatids that were in a relational coil in close proximity to each other (1: 388-413). The only difficulty with this hypothesis is the explanation of three- and four-strand crossovers and the positive proof that chromosome replication and fibril connections occur at the proper time during chromatid replication. The three- and four-strand crossovers can be explained by the presence of sister chromatid crossovers. The time of fibril connection formation is a matter for question as yet, but the disagreement should be settled by new DNA information that should be forthcoming.

The "copy-choice" between the chromatids during DNA replication and the subsequent formation of two-, three- and four-strand crossovers is very feasible. Also the relationship between crossovers and chiasma formation seems more definite with the copy-choice process.

While the reconciliation of these quite opposite hypotheses seems hopeless, there is definite agreement on the importance of crossovers as a means for the breaking up of linkage systems in maternal or paternal chromatids so that a reshuffling of genes can take place. This has a two-fold effect. First, the process of evolution of new varieties and species is speeded up. Second, new combinations with more favorable genetic complement may be the result of this unorganized recombination process.

CHAPTER V

MUTATIONS AND CHROMOSOME ABERRATIONS

It is evident that there exists much diversity
within the higher plants and animals. This diversity is
used by many scientists as the means for the classifica-
tion of these groups. However, the awareness of the dis-
continuity or separateness of the groups should also be
evident. The discontinuity of one form and the advent
of another form is usually spoken of as evolution.

An understanding of evolution becomes important
for the clarification of how these new forms are derived.
The change in the hereditary material (mutations and
chromosome aberrations), together with its dynamic
interaction with the envrionment, give rise to the
development of new forms. These new forms may differ
from the parent organisms in varying degrees, but the
more drastic the change the greater the likelihood of
the mutation being of a lethal nature. Most mutations
that do occur are considered to affect the new organism
adversely, especially if it has a dominance over the old
trait (27:20).

Also, the environment has much to do with the
development of any organism. Two organisms may have dis-
similar genotypes but appear closely related in many ways

due to the environmental factors (14:196-202). The environmental factors reach an important position in the process of evolution since they actually provide the "selection" factors even though they cannot produce the specific changes or mutations for that factor within the organisms. The environment can only modify the phenotypic appearance but can not control the genotypic potential.

The process of genetics or genic transmission (meiosis and mitosis) then must provide the raw materials for the evolution of new species. The raw materials that occur do so by chance to a very large degree.

The Mutation theory that was developed by DeVries and Korjinsky was favored by at least two facts. First, the existence of at least apparently useless characteristics in many organisms. Second, the absence of transitional forms or the fact of discontinuity from the wild type form to the mutated form in many instances. This holds true in almost all cases except where there is an interaction between genes to produce a transitional form of that characteristic (11:69).

The existence of apparently useless, non-detrimental genes within a population becomes more significant when the selection factor of the environment changes. Usually the pressure occurs slowly over an extended period of time.

However, man has upset nature's balance in many ways. An example of selection pressure, possibly through the use of one of these heretofore useless characteristics, is the use of insecticides for the control of insects. The apparent resistance that many insects seem to acquire for many of these insecticides must be due to the presence of a mutation that allows them to develop in spite of the changed environment which now includes the factor of the insecticides.

With each new insecticide developed, a selection factor changes. When a mutation occurs or the increase in frequency of an already existent mutated gene allowing the individual to survive more readily in its new environment, the adjustment to the environment occurs.

The types of changes or mutations have been grouped into two categories by Dobzhansky (14:21). These categories or types are (1) point or gene mutations, and (2) chromosomal aberrations. Of these two groups the gene or point mutation is considered to occur most frequently.

The gene can be defined as the smallest unit of a chromosome that affects or controls a specific trait and is segregated in a Mendelian ratio during the meiotic process. This is a functional definition which is used simply because the exact nature of the gene is not known.

The only workable explanation at the present time is the possible change in sequence of the nucleotide bases within the DNA molecule (see Chapter III). If the genetic codes are provided for by the sequence of these bases, then any alteration of that sequence would affect the phyenotypic appearance or the physiological function controlled or affected by that gene.

The rate or frequency at which mutations occur is quite difficult to determine since the change that occurs may be extremely small or the physiological function is not important for the survival of the individual. However, it has been found that certain gene loci seem to be more stable than other gene loci (9:469-478). These gene loci or genes do not mutate as often, or the appearance of the trait that they control is not altered as often as other traits. Whether this stableness is due to the molecular structure or whether it is due only to the position on the chromosome of these particular genes is a question beyond present-day knowledge.

If we consider the structure of the genetic material to be common in all DNA material then the most obvious answer would be the position on the chromosome. (By common we mean that the same four nucleotide bases are present in varying amounts or ratios). However, we cannot be sure that the cause of a point mutation is merely the reshuffling of the nucleotide bases. It may also entail

the altered structure of part or all of a DNA molecule.

The other type of genetic change is due to a physical change in the gross morphology of the chromosome set or some smaller part of that set. The chromosomes are made up of a linearly arranged sequence of DNA, RNA and protein macromolecules. We presume that the DNA materials are the inherent genetic materials that control the RNA and its role in protein synthesis. The DNA and RNA materials are implanted on a protein matrix. The best information for this assumption is the observance of experiments on bacteriophages that have been done by many scientists, primarily Beadle, Tatum, Sueoaka and others. Also there have been comparisons of DNA, RNA and protein content between organisms of the same species and they have been found to occur in a constant or near constant ratio (45: 35-42).

In the previous chapter it was noted that the results of crossingover were the formation of chiasmata and the subsequent chromatid breakage that occurred when the chromatids pulled apart in the anaphase stage. Also, organisms can be found where chiasma-like structures form but do not lead to nor are the cause of crossingover (10:35). These chiasma-like structures may well cause subsequent chromatid breakage just as well as chiasmata formed by crossingover.

Whenever there is chromatid breakage there are several possible ways in which the chromosome may be affected. If the broken chromatid has a meta- or pericentric centromere, there is the possibility that the broken fragment may not come into contact with rest of the chromatid or another chromatid, may not re-fuse with a chromatid, and consequently is often lost since it does not become attached to the spindle fiber due to the lack of a centromere (39:134-142). The broken fragment usually becomes lost during the later stages in the meiotic process and leaves a chromosome with a different configuration.

The loss or deletion may have several effects on the developing cell or organism. If the amount of material lost is great enough or if the gene or genes included are critical for the organism's survival, death of the organism is very likely to occur. This lethal effect is very common in a deletion or loss of chromosome material (21: 58-61). In a study by M. Demerec, it was found that of the 11 deficiencies noted, 10 were lethal. The deficiency that was not lethal showed that the tissue in which it was found was decidedly weaker (8:354-359). The general conclusion reached by Demerec was that most deletions or deficiencies show a possible lethal effect when it occurs in loci that control activities associated with early ontogenetic development.

However, one example of a homozygous deficiency which is not lethal is Bar-eye, a condition known in Drosophila flies. There may be other examples that are not known at the present time since in many cases the deletion of a single gene or gene locus may have the appearance of a point mutation.

Another structural change that can occur is a reduplication. A reduplication results in the presence of two genes or gene loci where normally there is only one such gene. A reduplication can occur in the process of recombination where multiple breaks have occurred in two or more chromatids. There is the possibility that during the process of replication one or more gene loci can be reduplicated by the "copy choice" in closely situated chromosomes. This would most likely cause a deletion to occur in one chromatid and a reduplication in the other chromatid. Since there is no proof that the replication of homologous chromosomes occurs at the same rate or at the same instant, there could be a reduplication occurring by copy choice where there is no deletion in the corresponding chromatid. The most important evolutionary aspect of the process of reduplication is the possibility of the development of new, larger linkage systems from smaller systems. While there is no iron-clad rule that an increase in size or number of component parts brought about

by increased chromosome material content (38:523-533).

Also in cases where the phenotypic characteristic is controlled by multiple genes or alleles, any reduplication of the gene or gene loci involved would cause a change in the appearance of that character. Examples of this type of condition are skin color in man and Bar-eye in Drosophila.

Other conditions that may arise from breakage and recombination are rearrangement of the fragment(s) into a new sequence or linear arrangement. An inversion may be the result of a multiple or a single break within a single chromosome or chromatid. If a break occurs, the fragment may become inverted and produce the new sequence or chromosome configuration. When a multiple break occurs there may be an inversion formed in an intercalary position. The results may be similar or they may be due to the "position effect". Also the new configuration may not be as stable as the former configuration and the rate of mutation may be affected.

The other type of rearrangement is called a translocation. A translocation is the product of multiple breakage and the fragments are shifted away from their former positions. It is a chromosomal rearrangement by which (1) fragments are exchanged between non-homologous chromosomes or (2) a portion of one chromosome is transferred to a

different part of the same chromosome or another chromosome. In organisms which reproduce by self-fertilization, apogamy, parthenogenesis, or asexually, translocations can develop and become established more readily than in obligatory cross-fertilizing organisms (41:252-253). Since there is difficulty involved in any cross-fertilizing organisms developing the lasting chromosome configurations by translocations, the evolutionary importance of translocations would be restricted to asexually reproducing organisms.

In plants and some animals, another type of mechanism has produced many new species. This process is sometimes called "ploidy" because it involves the loss or gain of entire sets of chromosomes or genomes. The primary effect of polyploidy is a change in size. An enlarging effect occurs when the diploid conditions are heterozygous. This enlarging effect may be most obvious in plants where their various organelles such as sepals, petals, anthers, etc., become greatly exaggerated (41:301-308). In many plants where seeds are produced, the opposite effect may occur with a reduction in cell size. In an experiment performed with sugar beets, Beta vulgaris, the ploidy effect caused an increase in chloroplast number and very little effect on cell size. (31:358-366)

Secondary results include (1) water content of the cell, which is vitally affected by the surface-volume ratio

of the cell; (2) changes in the rate of growth (autopoly-
ploids especially grow more slowly); and (3) the viability
or reproductive capacity is usually greatly affected.

Polyploid individuals may occur in many ways. They
may occur by the combining of a dissimilar genome or chro-
mosome set with a normal genome through hybridization.
This is called "alloploidy". Another method is by the as-
similation of a similar genome to give a double set of
chromosomes and is called "autoploidy" (4:177-193).

The problem of reproduction in polyploids is usually
the determining factor affecting the successful development
of these ploidy individuals in the breeding population.
The polyploids with an even number of chromosome sets have
a greater chance of becoming implanted in the population
because they are able to go through the meiotic processes
of synapsis and pairing with a greater chance of success-
fully performing these operations (40:441).

The results of a fertile, successfully reproducing
polyploid are the same as the results obtained from gene
mutation (4:95-110). As in any other type of mutation
that appears, if the condition causes a better chance for
survival in the environment than the former condition, then
it has a very good chance of becoming implanted into the
breeding population barring accidental loss through the

death of the individual or loss through subsequent gene
reversion.

The evolution of new species is controlled by the
environment to the extent that only those individuals that
can successfully survive and reproduce will form the breed-
ing population. The raw materials for this environmental
selection are provided by gene mutations, chromosomal
aberrations or alterations and the gain or loss of parts
or complete sets of chromosomes.

CHAPTER VI

EVOLUTION WITHIN THE NATURAL POPULATION

The occurrence of mutations and chromosomal aberrations that make up the raw materials for the evolution of new forms and characteristics within the population do not necessarily bring about the development of these new forms. Several factors affecting the populations determine the successful mutations and their integration into the breeding population. These factors, (1) mutation pressure, (2) immigration pressure, and (3) selection pressure determine the evolutionary change that occurs within any population (51:382-389). Likewsie, each of these factors is affected by population size and methods of reproduction.

Mutation pressure may be defined as the presence of mutant forms within a population and the rate at which it appears or is lost by genetic drift. Genetic drift, as defined by Sewall Wright, "includes all variations in gene frequencies which are indeterminate in direction" (15:311-319). As would be suspected, the effect of mutation and genetic drift is most severe or noticeable in small populations. The heterogeneity is significantly greater in the populations descended from small numbers of founders than in those descended from large numbers of founders (15:311-319).

Gene reversion occurs in all populations and the direction of this gene reversion tends to be toward the wild type. Theories have been developed for this phenomenon. It would seem that since each mutation has a characteristic rate of reversion that the stableness of the mutations on a molecular level would enter into this observed fact.

In some cases there is an interaction between the dominant and recessive alleles. This interaction is called gene conversion and usually results in a modified phenotypic appearance or a changed physiological activity. However, if the definition of a gene is that it must independently segregate and be passed on in heredity by Mendelian principles, then there should be no actual loss of genetic material through this process.

The gene frequency within the breeding populations is important since the evolution that occurs will be brought about by its selection and propogation. The evolutionary factors affecting gene frequencies are (1) mutation (2) cross breeding (3) selection and (4) inbreeding.

In large, freely interbreeding populations with no secular change in conditions of life for long periods of time, all gene frequencies approach equilibrium at a certain peak (52:307-320). Under secular change in conditions the number, or peak itself, changes, and there is evolutionary change in the system of gene frequency. Here, evolution

may be said to be guided by intragroup selection.

In sufficiently small, completely isolated popula-
tions, the random divergencies of gene frequencies from
their equilibrium value becomes important, tending to bring
about approximate fixation of some random combinations of
genes which are not likely to be a peak condition. The
result is a largely non-adaptive differentiation. In
extreme cases there may be the deterioration which character-
istically follows excessive inbreeding. Isolation may here
be considered the dominating evolutionary factor (52:307-320).

In a large population subdivided into small, partially
isolated groups, the combination of genes associated with
intergroup selection gives a trial and error mechanism
under which the system of gene frequencies may pass from
lower to higher numbers and the species evolve continuously
even without secular changes in conditions (52:307-320).
Although this process itself tends to bring about secular
change, the combination of genotypes of partially isolated
subgroups with intergroup selection seems to provide the
most favorable conditions for evolutionary change.

A breeding population or gene pool may be defined as
a group of individuals which has received its genes from a
common pool established by reproductive communication and
mating among the antecedent members of the population (16:9).

Within the breeding population we find that certain
genes show a dominance over their recessive alleles. How-
ever, since the genes or gene loci have the same probability
of segregation, irrespective of dominance or recessiveness,
the dominant gene does not become segregated any more readily
than the recessive allele. Consequently the number of any
one gene reaches a stable numerical level within the same
population.

This independent segregation and particulate produc-
tion was used by Hardy in his formation of a law known as
the Hardy-Weinberg Law (20:49-50). This law states that
genes for any characteristic or its various phenotypes are
present in a population of random mating individuals in a
definite proportion. It further provides that the dominant
character or gene will not spread over the entire population
with resulting loss of the recessive alleles or genes (20:
49-50).

These facts can be seen if one takes a group of in-
dividuals that are homozygous for a given trait, with half
of the group homozygous dominant and the other half homo-
zygous recessive. Considering that this group makes up a
breeding population, we find according to mathematical
chance that the first generation (F_1) would have genotypes
half of which are heterozygous and the other half homozygous
genotypes corresponding to the parents. This ratio then

would be 1:2:1. One-fourth of the offspring would exhibit a homozygous dominant genotype, one-half would show a heterozygous dominant-recessive genotype, and one-fourth would show a homozygous recessive genotype.

Further random mating would result in generations which would show this same ratio of genotypes and in an equilibrium which would be reached after a period of time. A smaller population would reach this equilibrium more rapidly than a larger population. However, since this time is shorter, the smaller populations would be less stable over a long period of time. Each mutation that appears would be passed throughout the smaller population much more rapidly than a larger population.

Hardy's formula for the equilibrium reached by a random mating population of a given genotype would be:

$$n^2AA: 2n\ (1-n)\ Aa : (1-n)^2\ aa \quad (20:49-50)$$

(The initial number of individuals in the
population are represented by n and
1-n for the respective homozygous dom-
inant and recessive characteristics)

If random breeding does not occur and the organisms or individuals carrying the homozygous conditions show mating preference, the number of homozygous genotypes would be greater and the number of heterozygous genotypes would be less (44:149-173).

The differentiation or origin of species depends

upon the development of discontinuities or gaps in the
variation patterns of nature. The formation of these gaps
depends upon some isolating mechanism (42:150).

An isolating mechanism is any factor that keeps an
individual within a certain ecological area or separated
from individuals of species by physical or psychological
means. Some mechanisms are (1) geographic barriers, (2)
genetic barriers and (3) time.

Geographic barriers may be of a multitude of types.
Any restriction by a land form, mass or body of water would
tend to isolate many species in fairly definite regions.
However, the mere isolation of these species within given
areas does not cause species or genetic divergence.

Genetic barriers would include any physical features
that may enter its specific areas of the rassenkreis. These
genetic barriers include (1) individuals which do not meet;
(2) individuals which do not maturate at same time and
consequently do not have coincident breeding seasons;
(3) a mechanical failure in copulatory organs of different
individuals causing them not to breed successfully; (4)
the gametes produced by the two individuals are incompatible -
therefore fertilization is not accomplished; and (5) if
fertilization does take place, the hybrids produced die
during some phase of their development.

The importance of the isolation of the various

divergent forms found within a rassenkreis is to allow for
the evolution of discontinuities within the variation pat-
tern of the included species. The development of these
isolating systems occurs as evolution occurs, at a very
slow pace. The interaction of these isolating systems
with the variations that occur provide these small gaps in
the transitional forms that occur in nature. Without these
gaps the transition from one form to the next should be
considered as descent with modification and occurs in nature
over a very long period of time (42:150). Descent with mod-
ification takes place as a result of the interaction between
mutation, natural selection, and the random fixation of genes
in small populations. If these forces are relatively static,
the species will not evolve.

Discontinuities are developed when two parts of a
more or less rapidly evolving species are separated from
each other by any number of isolating mechanisms. These
mechanisms evolve slowly and are genetically independent
of the changes in outward form which produce visibly dif-
ferent species.

The evolution of new species of organisms is brought
about by the dynamic interaction of the divergent forms
that occur within a rassenkreis that are usually separated
from each other by any number of isolating mechanisms.
Between different forms there may be some intermingling,

but on the whole they will be separated so that smaller subgroups which are affected more rapidly by the forces of population evolution (36:333-343). The factor of time also must be taken into consideration. Over a long period of time a particular species may evolve by the action of the variations that occur and are selected by the slowly changing environment. If the environment does not change, the evolution will not occur and most mutations that occur will be deleterious to the organism.

CHAPTER VII

SUMMARY AND CONCLUSIONS

The formation of new species and their development
within the populations composing the plant and animal king-
doms is an extremely complex set of processes with many
diverse facets and problems. These processes can be grouped
into two areas. First, the process of variation that occurs
within the genetic material itself. Second, the inter-
action of the variation or mutant with its fellow members
of a population and the environment in which it finds itself.

The variation that occurs may be further divided into
two categories consisting of gene mutations or submicro-
scopic changes and chromosomal aberrations, where the vari-
ation is produced by change in position or relation of
chromosome parts to each other, the gain or loss of chro-
mosome materials, and the gaining or losing of entire
chromosome sets.

While the process of gene mutation and chromosome
aberrations are dissimilar in most respects, there may be
similar results from both processes. The variations that
are produced become the grist for the complex machinery at
the higher level of integration in the evolution of new
species.

Not all chromosome mutations and aberrations are

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useful or important in species formation. In the case of
deletions or loss of chromosome parts the usual effect is
lethal to the developing organism. An exception to this
rule is the Bar-eye condition in Drosophila. Bar-eye is
a condition that is produced by the interaction of multiple
genes but the relationship of this to lethality in all
deletions is not evident.

Inversions are important from the standpoint that
they may inhibit the process or incidence of crossing over
between chromosomes. Since crossing over brings about a
shuffling of maternal and paternal linkage systems, the
inversions may actually slow down the process of variation
within a population. Also the result of position effect
expresses itself in many instances of inversion, and the
development of the individual is affected to varying
degrees. The relationship of position between genes
affecting important structures or physiological functions
may be completely changed with a very profound effect on
the developing organism.

Translocations appear to be very similar to in-
versions in their effect on the developing organism. The
re-positioning of neighboring gene loci and the distance
between them in their new locations controls the position
effect greatly. The removal of chromosome segments and

Their subsequent implanting in another chromosome or chromosome arm would seriously affect the "normal" condition caused by the former positions of the genes.

Also any gross change in chromosome morphology or configuration would seriously affect the possibility of successful chromosome pairing or synapse during the meiotic processes. The usual consequence of this would be a very unviable condition and the subsequent death of the organism. If the individual developed successfully, its chances of reproducing would be extremely unlikely except where the organism is self-fertilizing.

Reduplications are important because they hold out the possibility of building larger, more complex genomes from smaller chromosome sets. The fact that reduplications appear to have less trouble in synapsis and chromosome pairing would tend to enhance their role as a factor in organic evolution.

The incidence of polyploid individuals and their subsequent development within populations that are normally self-fertilizing make this type of chromosome aberration extremely important. The occurrence of polyploid individuals in cross-fertilizing populations and their successful development and reproduction is extremely small. If they do occur, it would very likely be due to a malfunction of the meiotic processes or an inhibition of the spindle structure and its function.

The conclusions that can be drawn from this study are as follows:

(1) Chromosome mutations and aberrations are important in the processes of organic evolution. The importance varies in the different types of chromosome changes.

(2) Reduplications provide a means for developing more complex genomes from smaller linkage systems.

(3) Translocations may produce different genome configurations with consequent variation within a population. The failure of successful meiotic function in cross-breeding populations reduces the effect of translocation on organic evolution.

(4) Inversions may produce new genome configuration and subsequent new forms. However, the importance of the inversion appears to be more effective in the process of modification of descent than in total evolution.

(5) Since deletions appear to produce unfavorable effects, their importance in organic evolution may be less. However, if the material deleted is not critical to the development of the

organism, the overall change in position of
the remaining genes may give to a new form
within the population.

(6) Polyploidy is very important in populations
that are normally self-fertilizing. While it
is of little importance in cross-fertilizing
populations, the occurrence of ploidy is not
unknown. Mosaic areas in developing organisms
may be produced by polyploidy during the mitotic
process.

Some aspects of evolution and species formation are
easily understood, and as more information is compiled from
the related fields of science, the processes of organic
evolution will be more evident. The occurrence of chro-
mosome mutations and aberrations, their role in the evolu-
tion of new species, and their integration with the process
of gene mutation is of much more importance than is often
given in many genetics texts.

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