

R. Rieger A. Michaelis M. M. Green

# Glossary of Genetics and Cytogenetics

Classical and Molecular

Fourth Completely Revised Edition

## 遗传学和细胞遗传学词汇——《经典及分子的》第4版

这是一本遗传学和细胞遗传学专业的工具书。第1版及第2版是分别在1954年和1958年用德文出版的(原书名: Genetisches und Cytogenetisches Wörterbuch, 第2版曾编目于 K74/117)。从第3版(1968年)起改为英文版,现第4版又对前一版作了全面修订,并增加了许多近年来在遗传学领域的新词汇,如分子遗传学方面的。现共有词汇3000余条。每条词汇均有简明而通俗的文字解释,有些还有实验资料或图解和数据,全书共有100个插图,8个表。书后还附有大量的文献,详细说明了所引用的大多数词汇的出处。

R. Rieger A. Michaelis M. M. Green

# Glossary of Genetics and Cytogenetics

Classical and Molecular

Fourth Completely Revised Edition



R. Rieger A. Michaelis M. M. Green

# Glossary of Genetics and Cytogenetics

Classical and Molecular

Fourth Completely Revised Edition

## Authors

Professor Dr. Rigomar Rieger  
Zentralinstitut für Genetik und Kulturpflanzenforschung  
der Akademie der Wissenschaften der DDR, Gatersleben

Dr. Arnd Michaelis  
Zentralinstitut für Genetik und Kulturpflanzenforschung  
der Akademie der Wissenschaften der DDR, Gatersleben

Professor Dr. Melvin M. Green  
Department of Genetics, University of California,  
Davis/Calif., USA

(内部交流)

Springer-Verlag  
Berlin Heidelberg New York 1976



With 100 Figures and 8 Tables.

ISBN 3-540-07668-9 (4th edition) Springer-Verlag Berlin · Heidelberg · New York

ISBN 0-387-07668-9 (4th edition) Springer-Verlag New York · Heidelberg · Berlin

ISBN 3-540-04316-0 (3rd edition) Springer-Verlag Berlin · Heidelberg · New York

ISBN 0-387-04316-0 (3rd edition) Springer-Verlag New York · Heidelberg · Berlin

The first and second edition of this book were published in German in 1954 and 1958 by Springer-Verlag under the title:

„Genetisches und Cytogenetisches Wörterbuch“.

The third edition was published in English by Springer-Verlag in 1968.

Library of Congress Cataloging in Publication Data. Rieger, Rigomar. A glossary of genetics and cytogenetics.

“The first and second edition of this book were published in German ...

under the title: Genetisches und cytogenetisches Wörterbuch”. Bibliography:

p. Includes index. 1. Genetics—Dictionaries. 2. Cytogenetics—Dictionaries.

I. Michaelis, Arnd, joint author. II. Green, Melvin M., joint author. III.

Title.

QH427.R54 1976 575.1'03 76-16183

This work is subject to copyright. All rights are reserved, whether the whole or part of the material is concerned, specifically those of translation, reprinting, re-use of illustrations, broadcasting, reproduction by photocopying machine or similar means, and storage in data banks.

Under § 54 of the German Copyright Law where copies are made for other than private use, a fee is payable to the publisher, the amount of the fee to be determined by agreement with the publisher.

Copyright© by Springer-Verlag Berlin · Heidelberg 1954, 1958, 1968 and 1976  
Printed in the German Democratic Republic

The use of registered names, trademarks, etc. in this publication does not imply, even in the absence of a specific statement, that such names are exempt from the relevant protective laws and regulations and therefore free for general use.

Printing: VEB Druckhaus Köthen

Bookbinding: Konrad Triltsch, Graphischer Betrieb, FRG.





## Preface

In preparing the new completely revised edition of this glossary, which in the meantime has been translated into Russian and Polish, we have attempted to include the most important new terms and to revise the text in those cases where new data demanded it\*. As a result about fifty percent of the text is completely rewritten. Once more we have tried to provide material suitable and usable both for students and research workers. Accordingly, depending upon our evaluation, some terms have been simply defined, others have been described at some length even to the extent of providing experimental data. Wherever possible, synonymy and redundancy have been pointed out, and in the interest of historical accuracy the individual responsible for introducing a particular term or concept listed with the specific paper included in the literature citations. Cross references between related terms are designated by an arrow (→) before each relevant term.

To keep the book, as far as possible, to a reasonable size the terms carried over from the earlier edition have once more been critically selected and, where necessary, revised. In spite of these efforts a certain increase in volume was unavoidable.

We hope that the new edition will once more prove useful to a wide audience and enjoy the same cordial reception as the earlier ones. Comments and suggestions from the reviewers and users of the earlier editions have contributed significantly to the revision. We are grateful to all those colleagues who directed our attention to mistakes, omissions and ambiguities. Needless to say any comment of the users of the new edition will be much appreciated. Many colleagues and friends, too numerous to identify here, have once more aided in the compilation of the contents of the book. To all our sincere thanks. We are, however, especially indebted to Mrs. Erdmuthie Rieger who participated directly in the preparation of the manuscript; without her untiring and unstinting help the revised text would, in all probability, never have been typed and prepared for the printer.

Gatersleben and Davis  
June 1976

*Rigomar Rieger    Arnd Michaelis  
Melvin M. Green*

---

\* Some terms and references have been added in proof (see pages 634 to 647).



# A

**AI, AII** — abbreviations for the anaphase of the first and second meiotic division, resp. ( $\rightarrow$  meiosis).

**abbreviation** — the successive shortening of ontogenesis through cessation of individual stages.

**aberration rate** —  $\rightarrow$  chromosome mutation.

**abortive infection** (*Lwoff* 1953) — infection of prokaryotic (bacterial) or eukaryotic cells by bacteriophages or viruses, respectively, which does not result in the formation of infectious virus although one or more viral components are synthesized ( $\rightarrow$  productive infection; reductive infection; lysogenization).

**abortive transfer** — any DNA transfer from bacterial donor to recipient cells that fails to establish the incoming DNA as part of the hereditary material of the recipient. A. t. has been observed following  $\rightarrow$  transduction,  $\rightarrow$  transformation, and  $\rightarrow$  conjugation. In all cases the transferred fragment is diluted out as the culture grows. Failure of integration of transferred DNA into the hereditary material of the recipient cell may be due to: 1. the failure of incoming DNA to form circular molecules; 2. circularization takes place, but the circular molecule fails to take up its maintenance system. A. t. of extrachromosomal elements ( $\rightarrow$  plasmids), as opposed to chromosomal fragments, is relatively uncommon since plasmids are genetic elements of autonomous survival in a bacterial cell. It is only when a mutation in the recipient or a resident plasmid makes the host component of the plasmid maintenance system inactive that a. t. of a plasmid occurs. Genes carried on abortive pieces of DNA may be expressed in the recipient cells.

**accessory chromosome** (*McClung* 1900) —  $\rightarrow$  sex and  $\rightarrow$  B-chromosome.

**accessory DNA** — surplus DNA present in certain cells or cell stages due to, e.g.,  $\rightarrow$  gene amplification.

**accessory nucleus** — in the oocytes of some insects, any of the structures present in the peripheral cytoplasm during  $\rightarrow$  vitellogenesis and probably originating from the oocyte nucleus. The electron-dense a. nuclei contain RNA, possibly of nuclear origin. A. nuclei seem to be involved in the control of the synthesis of albuminous yolk and afterwards perhaps with the formation of the vitelline membrane.

**accessory plate** (*Darlington* 1936) — a supplementary metaphase plate which owes its origin to bivalents which, during the metaphase either remain outside the equatorial plate (because of a lack of  $\rightarrow$  centromere orientation) or have not yet attained this (noncongression) ( $\rightarrow$  congression).

**accommodation** (*Thach & Thach* 1971) — a GTP-dependent reaction in bacteria which occurs during  $\rightarrow$  genetic translation.  $\rightarrow$  Messenger RNA (mRNA) is moved a distance of about three nucleotides in the 5' direction relative to the  $\rightarrow$  ribosome during the translocation of peptidyl-tRNA from the A to the P site of the ribosome. This reaction is catalyzed by the  $\rightarrow$  G

## acentric

factor (→ translocation factor) and is dependent on the hydrolysis of GTP. In contrast, mRNA is not moved during the IF 2-catalyzed (→ initiation factor) hydrolysis of GTP which is involved in the activation of ribosome-bound fMet-tRNA (→ initiator tRNA). This second type of GTP-dependent reaction is called a. of fMet-tRNA.

**acentric** — ref. to → chromosomes or chromosome segments without a → centromere.

**achiasmate** — of a → meiosis without → crossing over and chiasmata.

Where a. meiosis occurs, it is usually confined to one of the two sexes. Generally, the other sex has a chiasmate type of meiosis. A common feature of a. meiosis is the absence of any opening-out of paired chromosomes (bivalents) at diplotene; the four chromatids remain parallel until the beginning of first metaphase. A. meiosis is a distinct and characteristic mechanism which has arisen independently in a large number of organisms. In higher plants it is rare and not yet observed in vertebrates (*White* 1974). (→ cryptochiasmate).

**achromatic** (*Flemming* 1879) — those parts of the → nucleus which may not be stained with dyes characteristic for chromosomes (→ chromatin).

**achromatic figure** — the → spindle during → mitosis and → meiosis (→ mitotic apparatus).

**achromatic lesion** — gap.

**A-chromosome** (*Randolph* 1928) — any of the standard chromosomes of the → chromosome complements of all eukaryotic organisms. A-chromosomes represent a delicately balanced system and each of them usually has to be present to secure normal viability. In many species, the standard complement of A-chromosomes may be supplemented by varying numbers of supernumerary or → B-chromosomes. These are derived from the A.-c. set and have become functionally subordinate.

**acquired character** — a → modification impressed on an organism by environmental influences during development.

**acrocentric** (*White* 1945) — of chromosomes where the → centromere is very close to one end so that one → chromosome arm is small or minute and the other very much longer (→ metacentric).

**acrosome** (*Lenhossek* 1897) — a cap-like structure which invests the front part of the sperm head. It is limited externally by an outer membrane that is reflected forwards at the posterior boundary of the a. to form an inner membrane contiguous with the nuclear membrane of the spermatozoon (*Hancock* 1966).

The details of a. formation vary but in general follow one of two paths (*Nath* 1956): either the Golgi elements (→ dictyosomes) are transformed directly into the a. or they "secrete" the a. and are then shed with the residual cytoplasm.

In function the a. is concerned with the enzymatic penetration of the protective cover of the egg cell after formation of a surface layer. When sperm draw near to recently ovulated eggs, the outer acrosomal membrane and overlying plasma membrane fragment, creating openings to release enzymes of the a. This process is called "acrosomal reaction" (*Bedford* 1970). Genetically controlled defects of the a. may impair zygote formation.

**acrosyndesis** (*Percival* 1932) — incomplete end-to-end pairing of two chromosomes during → meiosis.

**action system** (*Hamburger*) — in embryology, a system consisting of the → organizer and its organization field, which, in the → reaction system, brings about the realization of one or more developmental potencies (→ induction system).

**activation** — in egg cells, a chain of responses made by an unfertilized egg to fertilization or penetration by a pipette. These responses include the rupture of cortical granules, the lifting off of a vitelline membrane, and the free rotation of the egg nucleus by the influence of gravity (*Gurdon* 1974).

**activator** (*Huxley* 1935) — a gene-dependent substance which stimulates the development of a certain embryonic tissue or organ, i.e., is morphogenetically active.

1. **Local activator**: active only in the cell or in the tissue in which it is produced.

a) intracellular activator: active only in the cell;

b) chemodifferentiator: active on the tissue to bring about determination of embryonic parts.

2. **Distance activator** or **hormone**: active beyond the region of its formation. The transport in the body may proceed by

a) diffusion (diffusion hormone),

b) body fluids (circulation hormone).

**activator RNA** (*Britton & Davidson* 1969) — a regulator molecule capable of recognizing specific sites on DNA. A. RNA is assumed to play a role in the regulation of → gene expression in eukaryotes. According to the *Britton-Davidson* model of → genetic regulation in eukaryotes, the genetic material is in its normal state repressed. Particular control systems function specifically to overcome this repression and to switch on appropriate genes by the functioning of a. RNA. A. RNA is assumed to be coded for by "integrator" genes which are active only when an adjacent segment of DNA (= "sensor" gene) interacts with a specific protein.

**active transport** — passage of a substance across the → cell membrane against a concentration gradient; energy must be supplied for a. t.

**adaptation** — any change in an organism's structure or function that allows it to better cope with conditions in the environment. Harmonious adjustment to environmental conditions is the result of a. Adaptation as a process or the result of a process taking a different course in different individuals, signifies the build-up or the possession of → characters which prove advantageous for the individual or the population under the environmental conditions in which it lives and through which the organism acquires → adaptive value or fitness in a certain environment.

A. can be achieved in two different ways, as pure phenotypic a. or as genotypic a. In the first case, the → reaction norm of the genotype can be attuned to those environmental conditions prevalent under natural circumstances. In the second case, genotypic specialization leads to a. in such a way that a change of genotype results in the formation of a new reaction norm which makes it possible for the genotype to harmonize where the original form fails to do so.

## adaptedness

Adaptations consist of harmoniously working combinations of genes which are built up and preserved by the process of natural → selection. The adaptation presupposes in each case the possession of a genotype with a favorable reaction norm. The reaction is then favorable if the frequently recurrent environmental influences give rise to phenotypic modifications which permit the organism to remain viable and produce offspring (→ flexibility).

An adaptation process which furthers the group at the cost of the individual, i.e., the chance of the survival of the individual is lowered while the survival rate of the group increases, is designated as "**altruistic adaptation**" (Haldane 1932).

The possibility of certain genotypes adapting immediately to changed environmental conditions by means of prospective functions is so-called "**prospective adaptation**" (Simpson 1953) and means the formation of characters which are without adaptive value at the time of formation but which prove to be adaptive in a new environment (= **preadaptation**).

"Pseudoexogenous" (Waddington 1953) is an a. which appears to be occasioned directly by environmental influences but actually results without environmental stimulus or is independent thereof.

**adaptedness** — the state of being adapted. The a. of a genotype is a function of its → norm of reaction and of the range of environments in which it occurs.

**adaptability** — the potentiality for → adaptation. Physiological a. depends upon a → norm of reaction yielding a certain adaptedness in the environments which individuals or populations meet. Genetic a. (= evolutionary → plasticity) occurs by changing the norm of reaction to produce an improved adaptedness in some or all, old or new environments. A genotype that gives rise to adaptive traits in some or all of the environments it meets may be said to possess high a. which may depend upon physiological → homeostasis or upon developmental homeostasis (Dobzhansky 1968).

**adaptogenesis** — the formation of new → adaptations.

**adaptive** — of those changes of an organism which act to preserve life, i.e., tend to increase viability, survival rate, and reproductive rate. An a. trait or character is a structural or functional characteristic of the organism which enables or enhances the probability of survival and reproduction (Dobzhansky 1956).

**adaptive norm** (Schmalhausen 1949) — a well-adapted more or less stable complex of genetic diversity within the population.

**adaptive peak** (Wright 1932) — a symbolic representation (from an evolutionary point of view) of the relations between organism and environment in the form of a topographic map. Groups of related genotypes which make their carriers able to occupy certain ecological niches are said to occupy "adaptive peaks" situated in different parts of the map and separated from each other by "adaptive valleys" comprising unfit gene combinations. Any such peak represents a particular configuration of → gene (allele) frequencies and → genotype frequencies characteristic for a population equilibrium and (relatively) stabilized by a complex interaction of opposing



forces. If one of these interacting factors becomes modified in its action, three reactions may occur (Dobzhansky 1951, Lerner 1958):

1. compensating adjustments in the responses of the population to the other forces;
2. movement of the population from one such equilibrium across a "valley" to another new a. p. which may be represented by a completely different array of gene frequencies and may require a far reaching rebuilding of the  $\rightarrow$  gene pool. A shift from one to another a. p. is connected with the formation of stages intermediate between the two which may be more or less unbalanced;
3. disappearance of an original a. p. and extinction of the particular gene combinations in those cases in which no mutations occur creating new adaptive gene combinations or if the new combinations do not occur at the right time.

The construction of adaptive peaks is as follows: all genotypes are plotted as points on a plane — the more closely they lie the less they differ from each other — and as ordinate the prevailing  $\rightarrow$  adaptive value of these genotypes within the appropriate environment is used. In this way a "mountain range" is set up with "peaks" separated by "valleys" and "saddles". Each of the various genotypes is then represented by a point on this "mountain surface" and each population occupies a region on the same.

**adaptive radiation** — the evolutionary diversification of a group of organisms (of a single phyletic line) which leads, often within a relatively short period of time, to the formation by natural  $\rightarrow$  selection of a variety of types from a single ancestral species. These types are adapted to certain environmental conditions. A. r. results in a ramification of an adaptive type in a series of new adaptive zones (Simpson 1953).

**adaptive value** — the survival value and the reproductive capability of a  $\rightarrow$  genotype in comparison with other genotypes of the population in a particular environment. The a. v. (= fitness) represents a property of the genotype as a whole and is more than the sum of the values of its constituent genes, since, e.g., gene A may interact unfavorably in combination with B, neutrally with C, and favorably with D. A higher a. v. of a genotype means that the bearer, on average, will produce more surviving offspring than the bearer of another genotype in the same environment. This superiority can be the result of a higher resistance towards environmental influences and a greater longevity, or one genotype may be sexually more active or more fertile than the other (Dobzhansky 1951). The a. v. of a particular genotype in a given environment can be increased or detrimentally affected by the presence of other genotypes in the same environment (Weisbrot 1966).

**adaptive zone** — the "way of life" of a taxonomic group of organisms in a broad sense. An a. z. may be subdivided into adaptive subzones.

**adaptor hypothesis** (Crick 1958; Hoagland 1959) — an hypothesis (now experimentally proved) which states that the amino acid sequence of a protein is determined, during the course of  $\rightarrow$  genetic translation, by the alignment of aminoacyl-transfer RNA's at corresponding nucleotide  $\rightarrow$

## adaptor modification hypothesis

codons in  $\rightarrow$  messenger RNA. The specificity of the translation mechanism depends on base pairing between a nucleotide region of  $\rightarrow$  transfer RNA (the  $\rightarrow$  anticodon) and nucleotides in the  $\rightarrow$  codon.

**adaptor modification hypothesis** (Sueoka & Kano-Sueoka 1964) — an hypothesis proposed to explain the regulation of protein synthesis by modification of tRNA molecules at a site which affects recognition of either the mRNA codon, the enzyme ( $\rightarrow$  aminoacyl-tRNA-synthetase), or the ribosome. When multiple species of tRNA correspond to the same amino acid, modification of one tRNA species may prevent the  $\rightarrow$  genetic translation of mRNA with the corresponding codon(s).

**adaptor molecules** —  $\rightarrow$  genetic translation.

**additive genes** — genes interacting and showing no  $\rightarrow$  dominance if  $\rightarrow$  alleles or showing no  $\rightarrow$  epistasis if nonalleles ( $\rightarrow$  gene interaction).

**additive theorem** — the a. t. of  $\rightarrow$  exchange percentages states: the exchange percentage occurring on  $\rightarrow$  crossing-over between the loci A and C of a linkage group is equal to the sum of the values AB and BC, if the locus B lies between A and C, or equals the difference if locus B is localized outside the stretch AC (Fig. 1).

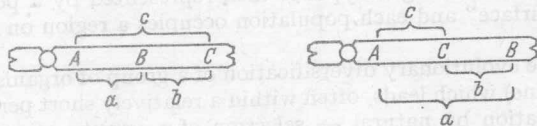


Fig. 1. Diagram showing the possible arrangements of three genes when only two of the distances (a and b) are known ("additive theorem of exchange percentages").

**adelphogamy** — sib pollination. Pollen and stigma belong to two different individuals which derive vegetatively from the same mother plant.

**adjacent distribution** (McClintock 1945) — the orientation and distribution of chromosomes lying adjacent in the ring or chain configuration of translocation heterozygotes ( $\rightarrow$  translocation) to the same pole in the first meiotic division ( $\rightarrow$  meiosis) in contrast to  $\rightarrow$  alternative distribution, in the course of which alternating chromosomes of the configuration are distributed to the same pole. It is a consequence of a. d. that either all or a part of the products of meiosis (gones or gametes) are genetically unbalanced and contain  $\rightarrow$  duplications or  $\rightarrow$  deletions. The proportion of unbalanced meiotic products is determined by the position and number of the chiasmata (in the  $\rightarrow$  pairing segments or  $\rightarrow$  interstitial segments). A. d. is responsible for partial sterility of translocation heterozygotes ( $\rightarrow$  semisterility). Two types of a. d. may be distinguished (Fig. 2a, b):

1. **adjacent-1 distribution** (= nonhomologous adjacent distribution; nondisjunctional distribution): chromosomes adjacent in the configuration with nonhomologous centromeres are distributed to the same pole in meiosis I. In such a case the translocated segments and the homologous segments of the structurally unchanged chromosomes are not separated from one another. For them it is a case of "non-disjunction".



**2. adjacent-2 distribution** (= homologous adjacent distribution; disjunctive distribution): chromosomes adjacent in the configuration with homologous centromeres are distributed to the same pole in meiosis I. The translocated segments and the homologous segments of the structurally unchanged chromosomes are separated from one another. For them it is a case of "disjunction".

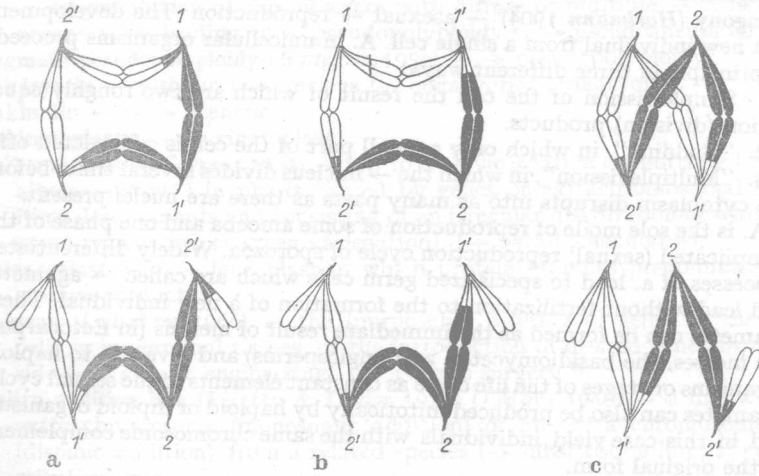


Fig. 2. The principal possible orientations in an individual heterozygous for a reciprocal translocation of a ring (upper row) or chain (lower row) of four chromosomes at metaphase I, assuming the spindle poles are towards the upper and lower margins of each row. The modes of distribution of the chromosomes resulting from these types of orientation are called adjacent - 1 distribution (a), adjacent - 2 distribution (b), and alternative distribution (c).

**adventitious embryony** (Strasburger 1878) — a form of → apomixis (agamosperry); the production of seeds without a sexual process.

**affinity** — 1. nonrandom → assortment of unlinked markers by some sort of a. between nonhomologous chromosomes causing them to pass preferentially to the same pole of the → spindle in anaphase of the first or second meiotic division. A. of this type has been inferred from genetic studies in mice and yeast (Michie & Wallace 1953).

2. In the case of selective → fertilization, the genetically controlled mutual attraction of male and female gamete types differing as to their genetic constitution. A. is a measure of strength of attraction, while the velocity with which this attraction proceeds, is called "reaction velocity" (Hausstein 1955).

3. → differential affinity.

4. → terminal affinity.

**agameon** (Camp & Gilly 1942) — a species reproducing exclusively by → apomixis.