HANDBOOK OF GENETICS

EDITED BY ROBERT C. KING

Volume 2

Plants, Plant Viruses, and Protists

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Volume 2
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PLENUM PRESS · NEW YORK AND LONDON

Library of Congress Cataloging in Publication Data

King, Robert C.
Plants, plant viruses, and protists.

(His Handbook of genetics; v. 2)
Includes bibliographies and index.
1. Plant genetics. 2. Plant viruses. 3. Unicellular organisms. I. Title.
[DNLM: 1. Genetics. QH431 K54h]
QH433.K56 581.1'5 74-23531
ISBN 0-306-37612-1

© 1974 Plenum Press, New York
A Division of Plenum Publishing Corporation
227 West 17th Street, New York, N.Y. 10011

United Kingdom edition published by Plenum Press, London
A Division of Plenum Publishing Company, Ltd.
4a Lower John Street, London, W1R 3PD, England

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Printed in the United States of America

Preface

The purpose of this and future volumes of the *Handbook of Genetics* is to bring together a collection of relatively short, authoritative essays or annotated compilations of data on topics of significance to geneticists. Many of the essays will deal with various aspects of the biology of certain species selected because they are favorite subjects for genetic investigation in nature or the laboratory. Often there will be an encyclopedic amount of information available on such a species, with new papers appearing daily. Most of these will be written for specialists in a jargon that is bewildering to a novice and sometimes even to a veteran geneticist working with evolutionarily distant organisms. For such readers what is needed is a written introduction to the morphology, life cycle, reproductive behavior, and culture methods for the species in question. What are its particular advantages (and disadvantages) for genetic study, and what have we learned from it? Where are the classic papers, the key bibliographies, and how does one get stocks of wild type or mutant strains? A list giving the symbolism for unknown mutations is helpful, but it need include only those mutants that have been retained and are thus available for future studies. Other data, such as up-to-date genetic and cytological maps, listings of break points for chromosomal aberrations, mitotic karyotypes, and haploid DNA values, will be included when available.

Genetics dates back to the work of the primitive agriculturalists who, thousands of years ago, in the ancient centers of civilization domesticated the various plants and animals we use to this day. However, modern genetics originated with the rediscovery in 1900 of a scientific article originally published in 1866 by the Augustinian monk, Gregor Mendel. About two thirds of this volume is made up of chapters covering plants that are favorites for genetic research, and, of course, Mendel's experimental organism, the garden pea, figures prominently among these.

In cases where a plant genus has been extensively studied there will be data presented for many related species, and here the nomenclature may become cumbersome and bewildering to geneticists working in other areas. In the chapter on cotton, for example, one sees reference to *Gossypium incanum* (Schwartz) Hillcoat and *G. stocksii* Masters ex Hooker. Lyle Phillips has explained to me that the name in parentheses is that of the original author of the specific epithet. The second authority changed the use of the epithet, i.e., moved the species from one genus to another or changed the rank of the taxon. In the *G. incanum* example, Schwartz described *incanum* as a species of *Cienfuegosia* and Hillcoat later transferred *incanum* to *Gossypium*. The "ex" is used when an author of a species name feels he should "share credit". In the *G. stocksii* example, Masters was the collector of the type specimen and had indicated on the herbarium sheet that he thought the specimen to be a representative of a new species. For unknown reasons he never published the species epithet, and when Hooker did subsequently, he gave Masters his due.

The plant chapters are followed by a chapter cataloguing the viruses attacking plants, and the volume ends with four chapters dealing with protists (as defined in the five kingdom classification described by Lynn Margulis in volume 1 of this series). Volume 3 will cover the invertebrates of genetic interest.

I am particularly grateful for the splendid assistance provided by Pamela Khipple and Karen Slusser during the preparation of this volume.

Robert C. King

Evanston
October, 1974

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PART D
THE PLANTS

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Corn (Maize)

MYRON G. NEUFFER AND EDWARD H. COE, JR.

Corn, *Zea mays* L., is a robust, monoecious summer annual of the grass family (Gramineae) with broad alternate leaves, an erect stalk terminated by a staminate inflorescence (tassel) composed of a main spike and several branches, and one to several pistillate inflorescences. The pistillate inflorescences are composed of 8–16 or more rows of kernel-bearing spikelets attached to a woody rachis (cob), and the whole (ear) is enclosed in several large foliaceous bracts (husks) and arises in the axils of the leaves at the mid-section of the plant. Long styles (silks) protrude from the tip of the ear through the husks as long silky threads.

Pollination is accomplished by wind dispersion, thus resulting in both self- and cross-fertilization. Cross-fertilization, wide distribution, and selection by man have brought about a high degree of variability. Corn grows only under cultivation, there being no truly wild variants known, although wild teosinte and corn show reciprocal introgression wherever they both occur (Galinat, 1971; Wilkes, 1972).

The international common name "maize" is used in most literature because the term "corn" is ambiguous internationally; however, some ambiguity exists for the term "maize" as there is a type of sorghum which is called "milo maize."

Corn exhibits several characteristics that make it a unique and useful organism for genetic and plant-breeding studies—these include high genetic variability; separate inflorescences, thus simplifying crossing techniques; free crossability; large ears with many kernels, thus providing large easily stored populations; kernels that express a wide array of easily

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observable phenotypes; adaptability to cultivation practices; and major economic usefulness.

As a result of easy recognition of segregating characteristics and the continuing investigations of many scientists, a significant number of special techniques and phenomena have surfaced involving corn as the investigated organism. These include: demonstration of multiple allelism (Emerson, 1911); discovery and utilization of hybrid vigor (heterosis) (Shull, 1911); genetic control of mutability (Emerson, 1914; Rhoades, 1941; McClintock, 1950); interactions in multiple-factor control of phenotypes (Emerson, 1918, 1921); maternal inheritance (Anderson, 1923); Mendelizing behavior in the gametophyte (Brink and MacGillivray, 1924; Demerec, 1924); inheritance of chromosome aberrations—translocations (Burnham, 1930, 1950), inversions (McClintock, 1933), rings (McClintock, 1932, 1938), deficiencies (McClintock, 1941); genic control of meiosis (Beadle, 1930, 1931, 1932*a,b*, 1933, 1937; Clark, 1940; Nelson and Clary, 1952; Rhoades and Dempsey 1966*b*; Sinha, 1962); association of cytological exchange with crossing over (Creighton and McClintock, 1931); pachytene chromosome morphology and its use in chromosome analysis (McClintock, 1931; Longley, 1938, 1939); cytoplasmic inheritance and its relationship to nuclear genotype (Rhoades, 1931, 1933; Josephson and Jenkins, 1948; Duvick, 1965); chromosome pairing, movement, and disjunction (Burnham, 1932, 1950; McClintock, 1933, Randolph, 1941; Roman, 1947; Laughnan, 1961; Rhoades and Dempsey, 1966*a,b*, 1972; Doyle, 1969; Burnham *et al.*, 1972); genetic effects of x rays and ultraviolet light (Stadler, 1932, 1939; Stadler and Roman, 1948; Nuffer, 1957); systematic linkage mapping (Emerson *et al.*, 1935); nucleolar inheritance and behavior (McClintock, 1934); variation in morphological features of chromosomes among populations (Longley, 1938, 1939; Longley and Kato, 1965); breakage-fusion-bridge-breakage behavior of broken chromosome ends (McClintock, 1939); behavior of accessory (B-type) chromosomes (Randolph, 1941) and the use of A–B translocations to locate genes on chromosomes and to control dosages (Roman, 1947; Beckett, 1972); relating DNA to genetic material by correlation of induced mutation with uv absorption spectrum (Stadler and Uber, 1942); genetic control of cytoplasmic inheritance of chloroplasts (Rhoades, 1943, 1947); cytological demonstration of pseudoallelism (McClintock, 1944); mutation analysis of selected loci (Stadler, 1946); discovery of transposable genetic elements and their control of chromosome breakage and gene expression (McClintock, 1950); compound loci (Stadler and Nuffer, 1953; Stadler and Emmerling, 1956; Laughnan, 1952, 1961); relationships among chlorophyll, carotenoid pigments, and seed dormancy (Robertson, 1955); allelic isoenzymes and the formation of hybrid enzymes (Schwartz, 1960); determination of a gene action se-

Chromosome	Unit Length	Arm Ratio
1	229	1.23
2	196	1.42
		1.14
3	179	2.0
4	175	1.63
		2.0
5	175	1.07
6	142	3.1
7	140	2.6
8	140	3.0
9	122	2.0
10	100	2.6

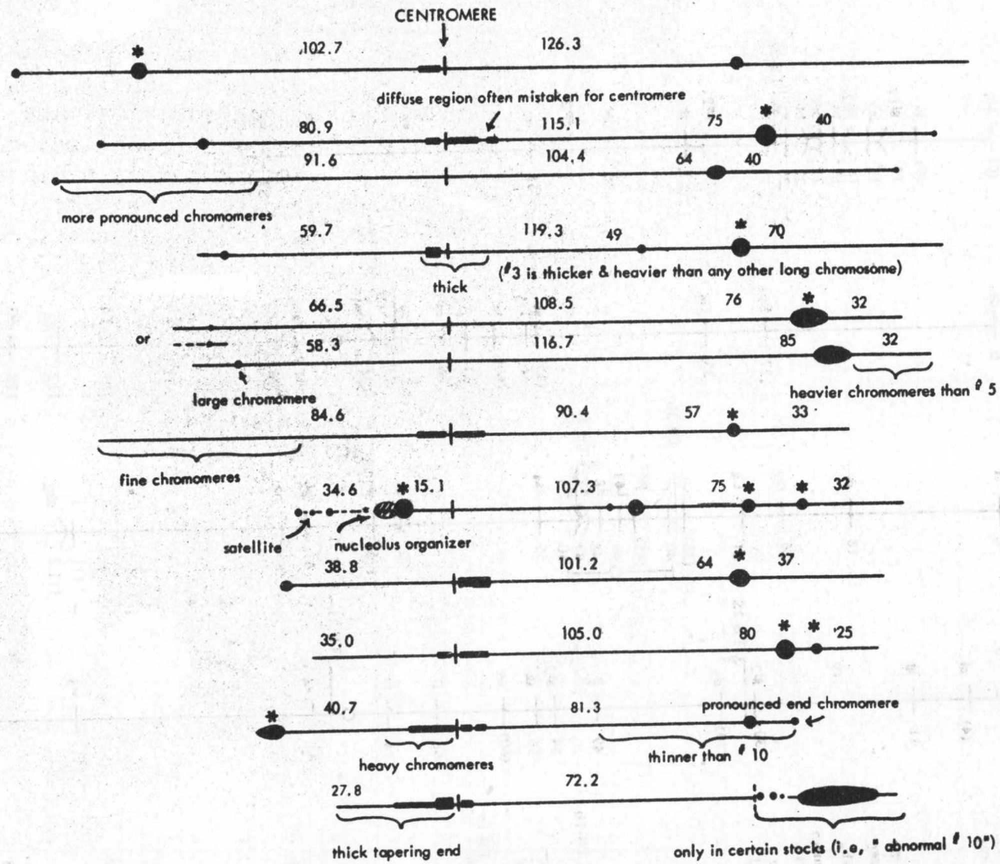
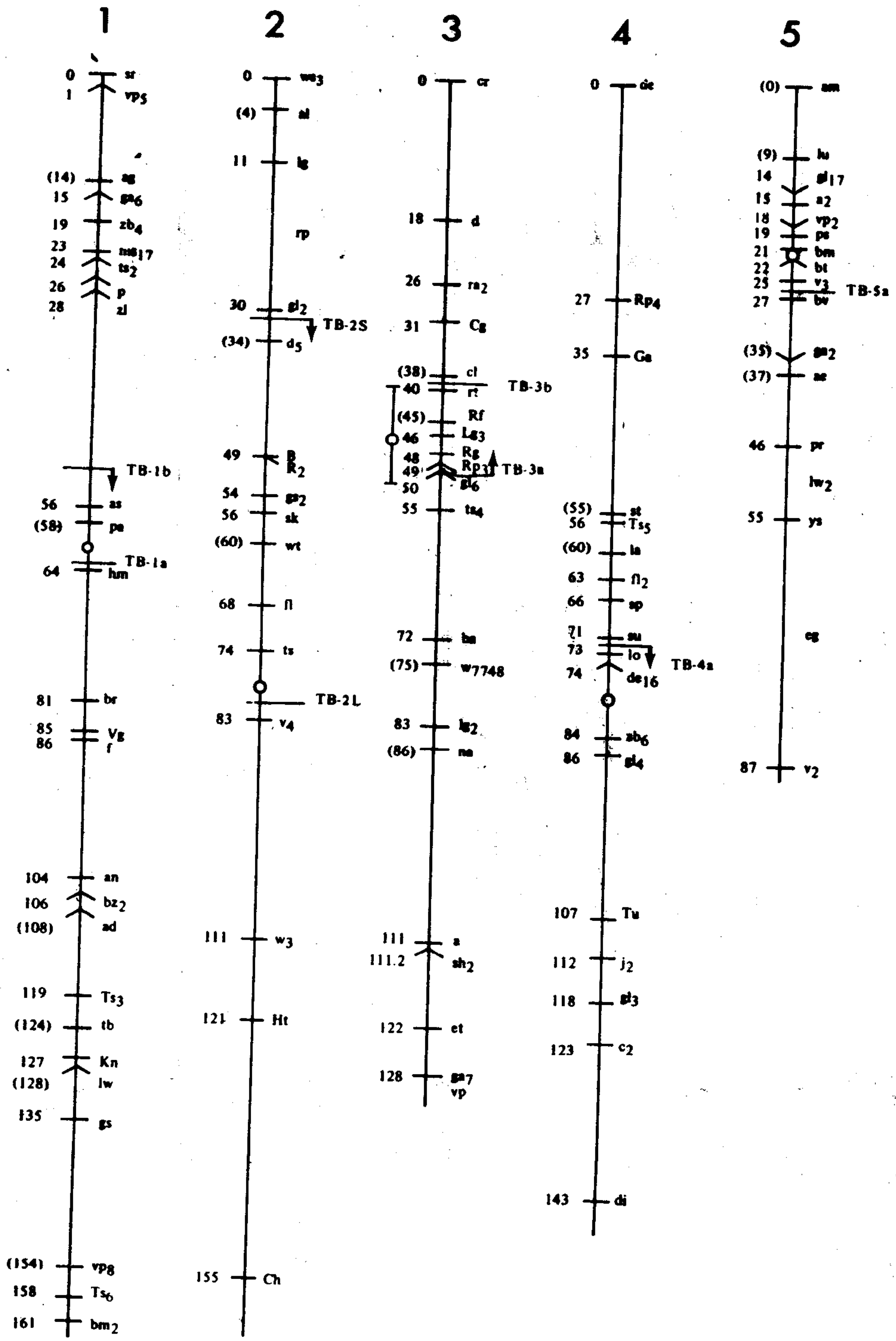


Figure 1. Cytological map of maize chromosomes. The smallest dots represent prominent chromomeres. An asterisk indicates that knobs are found in more than 50 percent of the races. The more common form of chromosomes 2 and 4 is given first. An error in the arm ratio for chromosome 6 printed in earlier versions of this map was called to our attention by Dr. B. G. S. Rao. Therefore, a correction has been made which conforms to the original data. The figure is drawn to scale and is based on published and unpublished data from Longley, McClintock, and Rhoades and Longley and Kato (1965).


1
2
3
4
5
TB-1b
TB-1a
TB-2S
TB-2L
TB-3b
TB-3a
TB-4a
TB-5a

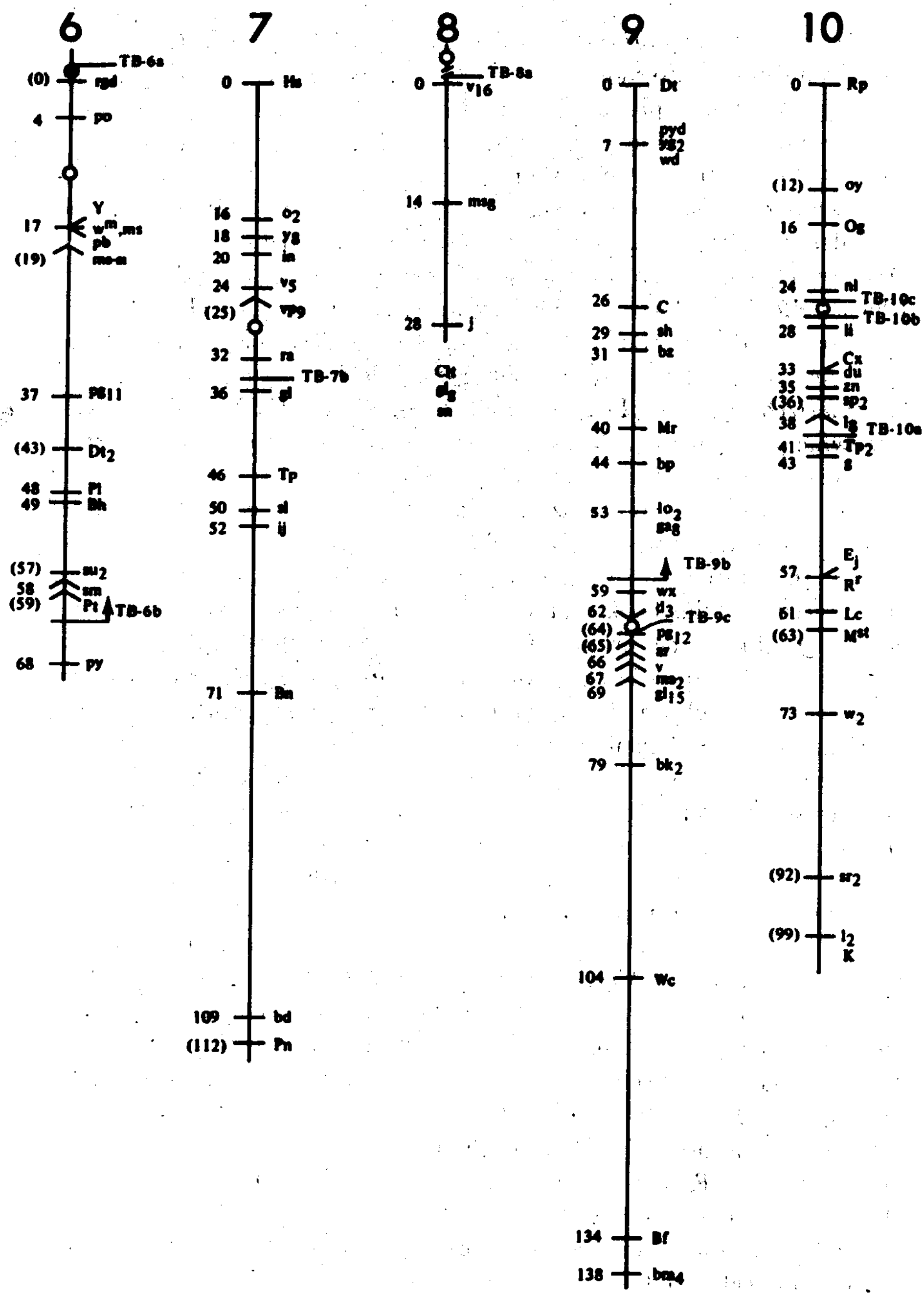


Figure 2. Linkage map of maize. Parentheses indicate probable position based on insufficient data, ○ indicates centromere position, and ● indicates organizer. Positions designated TB identify the genetic location of breakpoints of A-B translocations, which generate terminal deficiencies; ⟶ indicates that the TB breakpoint is in that position or is some distance in the direction indicated. Revised from Neuffer et al. (1968).

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