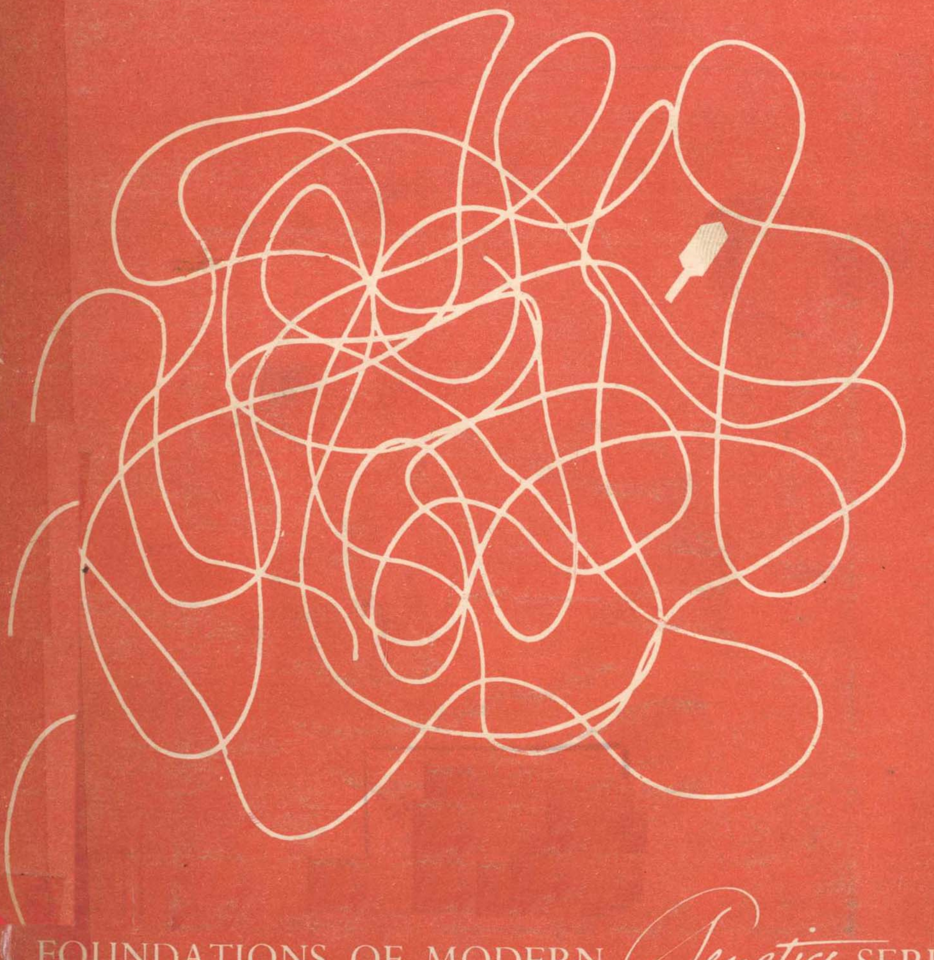
EXTRACHROMOSOMAL INHERITANCE

John L. Jinks



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EXTRACHROMOSOMAL INHERITANCE

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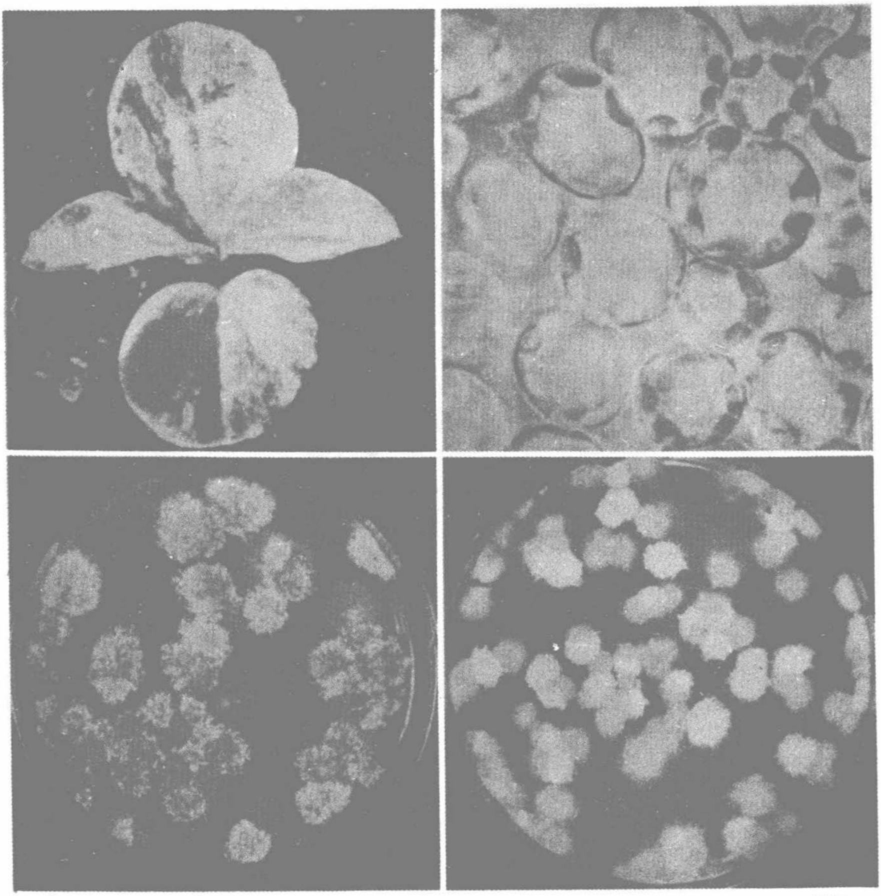

Frontispiece. Somatic segregation of extrachromosomal differences.

Top left. Somatic segregation of normal and mutant plastids in a seeding of privet.
Photograph courtesy of R.A.E. Tilney-Bassett,
Department of Botany, Oxford.

Top right. Somatic segregation of normal (dark) and mutant (light) plastids in the palisade cells of *Epilobium hirsutum*.
Photograph courtesy of Peter Michaelis,
Max-Planck-Institute, Köln-Vogelsang.

Bottom left. Somatic segregation of extrachromosomally inherited sexuality differences within a clone of *Aspergillus nidulans*.
Photograph courtesy of my colleagues
J. H. Croft and Morris Grindle.

Bottom right. Somatic segregation of the "red" extrachromosomal variant of *Aspergillus nidulans*.
Photograph courtesy of my colleagues
J. H. Croft and Morris Grindle.

Foundations of Modern Genetics

Genetic research is alive with excitement and revolutionary advances. Important to the development of science and to the evolution of social structure, genetic thought is widening its impact on many areas: immunology, protein chemistry, cellular physiology, developmental biology, medicine, agriculture, and industry.

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SIGMUND R. SUSKIND
PHILIP E. HARTMAN

McCollum-Pratt Institute
The Johns Hopkins University

Preface

The once widespread opinion that extrachromosomal inheritance is so rare a phenomenon that it must be regarded as an exception of minor importance is no longer tenable. From the earliest days of genetics the evidence for the existence of extrachromosomal inheritance has been firmly based on a few irrefutable examples in higher plants. Over the years these have been supplemented until today we have examples in representatives of almost every major group of organisms. In choosing illustrative examples I have tried to convey the breadth of the present-day support for extrachromosomal inheritance, but I have emphasized principles rather than examples. The examples set forth here by no means exhaust the list.

After two introductory chapters, the book falls into four main sections. The first, Chapters 3-6, deals with the criteria of extrachromosomal inheritance and presents the evidence that has been collected by their application; the second, Chapters 8 and 9, deals with the nature of the extrachromosomal system and as such is the most controversial section. The third section, Chapters 10 and 11, examines the relationships between the chromosomal and extrachromosomal systems and the fourth, Chapters 12 and 13, concerns the extrachromosomal role in development, variation, and evolution.

A knowledge of Mendelian genetics and the chromosome theory of heredity is assumed. Only brief reminders of relevant features are given. At the appropriate places novel properties of chromosomal genes are discussed in some detail because they often overlap with extrachromosomal phenomena.

Explicitly in the second section, and perhaps implicitly elsewhere, I have laid myself open to the criticism that alternative interpretations of particular instances of extrachromosomal inheritance in terms of "steady state" systems receive inadequate attention. The bias is deliberate. The determinants of extrachromosomal inheritance detected by our criteria share with chromosomal genes the properties of stability, mutability, segregation of alternative forms, maintenance of identity in the "heterozygous" state, and even the possibility of identity at the molecular level. Therefore, I can see no justification for a dichotomy in interpretation between the determinants of chromosomal heredity and those of extrachromosomal heredity.

I am indebted to my colleagues in the Department of Genetics, University of Birmingham, particularly Professor Kenneth Mather, Dr. Morris Grindle, and James H. Croft for innumerable discussions of the subject matter and for critically reading portions of the text.

J.L.J.

Contents

One

Cell Heredity

The chromosome theory of heredity has rightly become the cornerstone of genetics. The early identification of the chromosomal material of the cell as the bearer of the hereditary determinants, the genes, brought together the two most powerful tools for the experimental investigation of heredity, namely microscopic observations of chromosome behavior and precise breeding procedures for determining inherited characteristics in successive generations.

The immediate and continued success of this dual approach, however, led to the extensive study of chromosome heredity almost to the exclusion of study of the remainder of the cell. And yet, from the beginnings of genetics as a science, there have been constant reminders that the less easily defined extrachromosomal complement should not be ignored. No sooner had chromosomal heredity, with its Mendelian laws of inheritance, been defined and techniques for its recognition developed, than exceptions were described. As far back as 1909, C. Correns and E. Baur found instances of non-Mendelian inheritance for differences in the photosynthetic systems of strains of some flowering plants. Although correctly interpreted as examples of extrachromosomal heredity, these and the many similar examples that were described in the following years remained for a long time a miscellaneous collection of apparently unrelated oddities.

Indeed, these scattered exceptions to Mendelian inheritance aroused little interest in extrachromosomal heredity. But the natural extension of interests from the mechanism of the transmission of chromosomal genes to a consideration of their control of metabolism and development has led to continuing investigation of the extrachromosomal complement of the cell. The cell is now recognized as an integrated unit whose properties are more than a mere composite of its chromosomal and extrachromosomal contents.

Cell phenotype

The cooperation of the chromosomal and extrachromosomal components of the cell in producing the cell phenotype can be illustrated by an important attribute of plant cells, namely, their ability to carry out photosynthesis. This property depends on the presence in the cell of extrachromosomal structures, the plastids, and their associated pigments. The development and activity of the plastids are controlled both by heritable and by environmental factors. Light is the most important of the latter. Development of the plastids usually is not completed in the absence of light. Mutations at a number of chromosomal loci lead to a failure or upset in the development of the plastids and of the pigments they bear. These loci show strict Mendelian inheritance. Abnormal plastids may also occur in cells with a normal chromosomal gene complement, growing in an environment that is ideal for plastid development and activity. This condition is heritable, but the pattern of inheritance is non-Mendelian. At cell division, the cells with the abnormal plastids give rise to other cells that also possess the same kind of abnormal plastids, but only the maternal parent may regularly transmit this condition to the offspring of an outcross. Its determinants are extrachromosomal. Hence this important aspect of the cell phenotype is under the joint control of chromosomal, extrachromosomal, and environmental agencies.

The cell concept

The idea that the cell is an integrated unit and, indeed, the basic unit of life predates genetics itself. In its original form, the "Cell Theory" regarded an organism as a sum of vital units, each of which bore the complete characteristics of its life. The cell was not only equated to the vital unit, but was regarded as the ultimate unit of life. As in all useful generalizations in biology, there are exceptions in this instance—the viruses. The status of viruses is debatable. The only time a virus shows the characteristics of life is when it is exploiting the cellular organization of its host.

There are basic units of life smaller than the cell, for example, the gene or the chromosome. There are larger units, for example, tissues, whose properties may transcend those of its component cells. There are even more complex units, such as organs, individuals, and even collec-