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introduction to modern genetics

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introduction to modern genetics

john wiley & sons

New York

Chichester

Brisbane

Toronto

107
107

This book was printed and bound by Von Hoffman.
It was set in Palatino by Progressive Typographers.
The designer was Ben Kann.
The drawings were designed and executed by John Balbalis with the assistance
of the Wiley Illustration Department.
Claire Egielski supervised production.
Susan Giniger was the copy editor.

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Library of Congress Cataloging in Publication Data:

Main entry under title:

Introduction to modern genetics.

Includes indexes.

1. Genetics. I. Wagner, Robert P.
QH430.163 575.1 79-1414
ISBN 0-471-91430-4

Printed in the United States of America

10 9 8 7 6 5 4 3 2 1

preface

Information in the science of genetics has grown so greatly during recent years that covering its basic concepts in a one-semester course is a challenge bordering on the impossible. This book was written to help meet that challenge.

We present the basic principles of genetics and introduce the student to the analysis of genetic systems. The focus is primarily on the eukaryotic organisms but we discuss prokaryotes and viruses when necessary to illustrate a principle that also applies to eukaryotes. A balanced discussion of modern genetics should include the prokaryotes and viruses, but to give them the same amount of attention as the eukaryotes would involve a second volume and another semester's work.

To show how some of the concepts have been established we present and analyze experimental data. You are encouraged to apply this analytical approach to the solution of problems presented at the end of each chapter. We have included some history of how important principles have evolved, and we mention some of the people who helped establish them. However, we have been necessarily very selective with the examples used to illustrate particular points and, as a result, have had to omit or briefly treat many interesting and im-

portant experiments. We assume that the instructor will enrich the examples with his or her own favorites. We have tried to keep the book concise and dynamic rather than pack it with too many examples and details.

We believe the principles presented here form the core of genetics and can be applied to essentially all genetic systems. Furthermore, by analyzing genetic data, we can draw important inferences about the nature and functions of organisms that could not be done otherwise. Using genetic data to build models that can be tested through further experimentations is a powerful and exciting approach to understanding some of the central problems of biology.

We gratefully acknowledge those who read portions of the manuscript. The following provided constructive critiques and contributions of information and materials: Drs. C. S. Lee, M. Maguire, L. Powers, H. E. Sutton, J. R. Ellison, L. E. Hood, R. Teplitz, R. Perez, R. Diert, A. Templeton, J. K. Yoon and Ms. K. Kline. The preparation of the manuscript and the organization of the many details attendant to getting it into shape was made possible by the untiring efforts of E. Atherton, E. Eakin, L. Cooper, B. Judd, K. Kline and J. Wagner. Valuable aid in the reading of the proof was

vi rendered by M. Wagner. Appreciation is
preface also expressed for the critical persistence
and guidance of our Editor, Mr. Frederick
Corey and his associates at John Wiley,
and for the thoughtful critiques provided
by the anonymous reviewers selected by
Mr. Corey. We also express our thanks to
Mr. John Balbalis and his staff for their
fine work in the preparation of the illus-

trations, to Ms. Susan Giniger for copy-
editing, and to Ms. Claire Egielski for
guiding the manuscript through pro-
duction.

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contents

chapter 1	
• the scope and significance of modern genetics	1
part one	13
mechanics of inheritance in eukaryotes	
chapter 2	15
mendelism, chromosomes, and genes	
chapter 3	43
life cycles and genetic systems	
chapter 4	66
the action and interaction of genes	
chapter 5	84
genetic models and variation	
chapter 6	119
recombination of genetic information	
part two	149
nature and function of the genetic material	
chapter 7	151
DNA and RNA	
chapter 8	204
the genetic code, genes, proteins, and phenotype	
part three	237
variations in genomic constitution	
chapter 9	239
gene mutation	

chapter 10	271
chromosomal aberrations and their effects	
chapter 11	299
genic balance, ploidy, and sex determination	
part four	325
organization and regulation of genetic material	
chapter 12	327
molecular aspects of recombination and gene organization	
chapter 13	363
interspecific DNA recombination	
chapter 14	371
the regulation of gene activity	
chapter 15	414
immunogenetics	
chapter 16	444
somatic cell genetics	
part five	469
genetics of populations	
chapter 17	471
genetics of populations	
chapter 18	501
populations and evolution	
chapter 19	530
behavioral genetics	
credits	549
index	555

CHAPTER 1

the scope and significance
of modern genetics

GENETICS is concerned with the transmission of biological information and its utilization in the development and function of organisms. It has achieved a prominence among the biological sciences in recent years for laymen and scientists alike. Laymen are now more aware of the medical and sociological implications of human genetics; physicists and chemists continue to find fascinating problems in fundamental genetics that they can approach and in some cases solve with their different kinds of expertise; psychologists are finding that the study of the inheritance of behavioral patterns in animals is providing new insight into the understanding of behavior; medical scientists have become aware that a deeper understanding of many diseases will only be attained with further knowledge of their genetic bases; and ecologists, confronted with the enormous complexity of the environment-organism relationship, now appreciate that an important component of this interaction is a genetic one.

In this chapter we characterize genetics and give some information about its origins, its scope, and its significance, particularly as it relates to human affairs.

Modern genetics is a complex of inter-related subspecies that pervades all of biology and provides a major part of the conceptual framework of modern biology. This statement is not an exaggeration; one need only consider the questions that geneticists ask to recognize its validity: What is passed from parents to offspring that determines the characteristics of the offspring? What is the mechanism of this transmission? Why are the offspring of sexually reproducing parents somewhat different from the

parents? What factors guide and direct the development of a fertilized egg into a highly differentiated multicellular adult? What is the source of the variability in a population of a given species of organism? How is one species different from another species? What constitutes a species? How do organisms evolve? These are among the major problems of biology, and, although not all of them have been answered, it will be biologists using the tools of genetics who will provide many of the answers.

To deal with questions such as these the geneticist must resort to many different kinds of analytical methods ranging from the physical and chemical to mathematical. Thus there are geneticists who are biochemically oriented and work at the molecular level, those who work at the cellular level with chromosomes and other cellular organelles, and those who work with populations and are mathematicians or ecologists. Some even use the tools of paleontology to try to unravel what has happened in the past. Others are crystallographers who are unraveling the architecture of macromolecules that determine the structure of the organism and contain the information that is passed from one generation to the next. This heterogeneous assortment of methodologies and approaches constitutes genetics and makes it hard to delineate the scope of the field. However, there exists a "core" of knowledge drawn from this heterogeneity that forms the principles of genetics. In this book we attempt to make clear what this core is, principally for the eukaryotic organisms—those organisms with true nuclei in their cells as distinguished from the prokaryotes such as the bacteria that do not have nuclei.

1. the beginnings of genetics

The nineteenth century was an exciting period in the development of ideas in the Western world. Many concepts that form the framework of the physics, chemistry, geology, and biology of the present arose—and to a great extent were developed—during that century. Three events in the 1800s in the area of biology were to be important in dictating the course of its development up to the present. First, Charles Darwin published his *Origin of Species*; second, the cellular basis of plant and animal life began to be investigated and its significance appreciated; and third, Gregor Mendel published the results of his experiments with pea plants. Modern genetics owes its origins to all three of these events.

THE ORIGINS OF "CLASSICAL" GENETICS

Mendel's work, although published in 1866, was virtually ignored until 1900 when it was rediscovered. Let us start with what he did in the 1860s. Mendel interpreted the results obtained from crosses with pea plants as support for the idea that heredity has a particulate basis. Implicit in this hypothesis is the existence of physical elements in germ cells that pass unaltered from generation to generation through the intermediate adult forms. Mendel had no clear conception of what these elements were. At that time cytological knowledge was in a primitive state. Cells were recognized, but chromosomes were not, and the significance of nuclei was not realized until the 1880s.

How Mendel came to arrive at this conclusion will be made clear in Chapter 2. For the present it is only necessary to know that the significance of Mendel's discovery was not realized until 1900. In that year, Hugo de Vries and Carl Correns published papers in which they reported repeating the types of experi-

mental crosses made by Mendel. They came to the same conclusions he did. This time the full significance of the results and the conclusions to be drawn from them were recognized by most cell biologists and by many plant and animal breeders. Interest in genetics became intense, and the science developed, explosively.

One of the reasons for the rapid advancement of Mendelism was that by 1900 cell biology had reached a critical stage in its development. Chromosomes were by then recognized as the bearers of the hereditary material, the significance of mitosis was appreciated, and the nature of meiosis was beginning to be understood. By 1903 it was realized that meiosis with its separation of homologous chromosomes, and the formation of gametes followed by fertilization, provided an explanation for the results of Mendel's experiments.

This union of cell biology with Mendelism between 1900 and 1905 might be called the beginnings of "classical" genetics—the genetics of the first half of the twentieth century. This period saw the development of the *chromosome theory of heredity*, and the working out of the mechanics of inheritance in several eukaryotic organisms. Furthermore, during the latter half of this 50-year span, genetics began to provide the logical basis and experimental evidence for Darwin's theory of evolution by natural selection.

Darwin had no satisfactory explanation of heredity, and he did not understand the sources of natural variation. Hence the underpinnings of his theory of natural selection were absent. Genetics provided these underpinnings, and the result of this fusion of Darwinism and genetics was *population genetics* and a further development of evolutionary theory. This area of genetics is described and discussed in Chapters 17, 18, and 19.

4 THE RISE OF MOLECULAR GENETICS

the scope and
significance of
modern genetics

In 1869 Friedrich Miescher, a young Swiss physician, announced the isolation of nucleic acids from the nuclei of pus cells. Like Mendel's discovery, the significance of Miescher's work was also not immediately appreciated. At the turn of the century, the American cell biologist, E. B. Wilson, did observe that nuclein (as Miescher called his nucleic acid preparations) was probably the essential component of the chromosomes, and hence the hereditary material. However, this prescient observation aroused little interest, and it was not until 1944, 100 years after Miescher's birth in 1844, that experiments were reported which strongly indicated that deoxyribonucleic acid, the main component of Miescher's nuclein, was indeed the hereditary material of certain bacteria.

The recognition that something physical had to be passed from parent to offspring was firmly accepted in the last part of the last century, but what it was no one knew. The demonstration that this physical factor was a nucleic acid, the structure of which had already been partially worked out by the 1940s, ushered in a new era not only in genetics but in biology as a whole. This was the beginning of molecular genetics that is part of the broader field of molecular biology. The fusion of classical genetics with molecular genetics and the genetics of the lower organisms (prokaryotes) has evolved into modern genetics. In this book as stated previously we consider principally that part of modern genetics that is concerned with the eukaryotes.

2. the scope of genetics

Two aspects of genetics that were alluded to in the questions posed at the beginning of this chapter are of particular importance. The first is transmission: What is transmitted and how? Second, what does the transmitted material do to form a new individual and enable it to maintain itself so that it can in turn produce a new generation? These two questions address themselves to the same general property of living things—continuity. E. B. Wilson called this the "law of genetic continuity"—life is a continuous stream. *The scope of genetics is to study this stream.* When all the ramifications are considered, it is seen that such a study embraces a very large area with many facets ranging from predicting the outcome of a simple cross to the mechanisms involved in the evolution of new species.

Genetics involves the study of inheritance in many different kinds of organisms with different kinds of life cycles

and levels of organization. All of the living organisms on earth have been grouped into three categories. These taxonomic subgroups relate only to levels of organization at the organismal level as distinct from the population level. We consider two of these subgroups first.

PROKARYOTES AND EUKARYOTES

The *prokaryotes* include the bacteria and the blue-green algae. They are principally distinguishable by the absence of a nuclear envelope, the absence of highly organized cell organelles, and an apparent absence of a meiotic and mitotic apparatus.

The *eukaryotes*, on the other hand, have cells with "true nuclei" containing chromosomes made up of DNA closely associated with large amounts of protein as nucleoprotein. Eukaryotic cells also almost invariably contain highly organized organelles such as mitochondria

and chloroplasts, which possess DNA separate and distinct from the nuclear DNA (Fig. 1-1). The mechanisms of transmission of the genetic material from one generation to the next in eukaryotes are invariably by mitosis and meiosis—processes that are considered in detail in Chapter 2.

The eukaryotes include all those organisms we generally think of as plants and animals with the exception of the blue-green algae.

VIRUSES

Viruses may be thought of as “incomplete” organisms. They are incomplete in the sense that, although they pass a test of being alive since they can reproduce, they can do so only in a prokaryotic or eukaryotic cell. Their structure is relatively simple. They are composed principally of a core of nucleic acid

covered by a shell of protein (Fig. 1-1). The nucleic acid may be either DNA or RNA. Hence there are DNA viruses and RNA viruses.

Viruses “infect” their host cells by entering in toto or in part. If it is in part, it is the nucleic acid that enters. Generally the viruses of prokaryotes (usually called *bacteriophage* or simply *phage*) inject only their nucleic acid plus a small amount of protein. The animal viruses generally enter the host cell as whole particles.

Once having infected a host cell a virus may either attach itself in some way and replicate with the host cell, or it may reproduce itself in large numbers at the expense of the host cell, and in the process destroy it.

Viruses are, in a sense, parasites, but they are also more than that, since they appear to carry on important roles in the life cycles of prokaryotic organisms in particular. Their role in eukaryotic cells

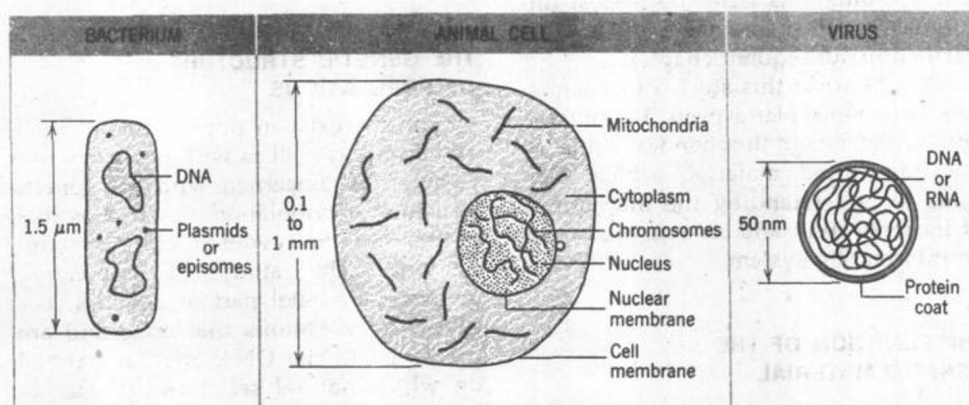


figure 1-1 Virus, prokaryote, and eukaryotes compared. The eukaryote cell represented here by a generalized animal cell has a nucleus separated from the cytoplasm by a nuclear membrane. In addition it contains organelles such as mitochondria, lysosomes, and Golgi apparatus not found in bacteria.

Prokaryotes represented here by a generalized bacterial cell do not have their chromosomal DNA included in a nucleus. They may contain plasmids, which are short pieces of DNA about 2 percent of the length of the bacterial chromosome or less. Viruses are essentially protein surrounding a core of nucleic acid.

The three forms are not drawn to the same relative scale. Viruses are in size about the order of plasmids in bacteria, and bacterial cells are about the size of the mitochondrial organelles in plant and animal cells. The sizes indicated are average values and do not indicate the extremes that may deviate greatly from the mean. For example the hen's egg (yolk) may be 3 cm in diameter while most eukaryotic cells are 20 to 40 μm in diameter.

is less clear. They do, of course, cause many kinds and numbers of diseases including some cancers.

THE TRANSMISSION OF GENETIC INFORMATION

The transmission of genetic information in all organisms appears to be basically the same: replicating a nucleic acid and passing the replicas on to the next generation. In viruses this nucleic acid may be either RNA or DNA. In prokaryotes and eukaryotes it appears always to be DNA. An important part of the study of genetics is the mechanisms of this transfer and their consequences. The mechanisms differ from one organism to the next. The viruses and prokaryotes may pass on all of their nucleic acid or only part of it; indeed, only fragments may be transmitted. The eukaryotes pass on whole chromosome sets through the processes of mitosis, meiosis, and fertilization. The transmission of the genetic material and its reassortment to form new combinations is of the utmost importance to all organisms. This will be clarified in subsequent chapters.

A vital part of this study of transmission is its molecular aspects. It is important to understand the chemical nature of the transmitted material, which then leads to understanding the mechanism of its replication and its functioning as an information system.

THE FUNCTION OF THE GENETIC MATERIAL

When it was recognized that the nuclei of cells must contain something inherited, presumably the chromosomes, which functioned to determine the characteristics of organisms, questions were raised about its structure and function. The answer to these questions did not begin to be realized until the development of molecular biology in its modern form in the 1950s and 1960s, an impor-

tant part of the study of genetics as a whole. It encompasses areas relating not only to the primary function of nucleic acid as the genetic material as discussed in Chapters 7 through 9, but to the mechanism of regulation of its functioning (since it does not all function at once at any given time). This then relates directly to the problems of differentiation and development, especially as seen in the eukaryotes as described in Chapter 14.

VARIATIONS IN THE GENETIC MATERIAL

The tremendous variety seen in the organic world has its sources in the differences in the genetic structure of the different organisms. The origins of these differences and their various affects on the characteristics of organisms is another important part of the study of genetics. This broad subject is considered in Chapters 9, 10 and 11, but is also involved in Chapters 2 through 6.

THE GENETIC STRUCTURE OF POPULATIONS

Organisms exist in populations of their own kind, as well as with other species. Genetics is concerned with the genetic structure of populations, as well as that of the individuals who make up the populations. The study of population genetics is a vital part of genetics, because the variations that arise and are preserved in the DNA are the material on which natural selection operates to bring about changes in populations over periods of time. Knowledge of the genetic structure of a particular population can lead to predictions about the genetic structure of future generations. This ability to make predictions about future generations is becoming more and more important in the area of medicine. The basic aspects of population genetics are described in Chapter 17 and 18.

THE UNITY OF GENETICS

In the first part of this section we have attempted to give the reader a feel for the broad scope of genetics as it relates to the more general but fundamental aspects of biology. Actually, if one were to make a list of the different fields of genetic research and application, only some of the terms used to describe the broad scope would be used. Terms such as bacterial genetics, wheat genetics, phage genetics, and the like, would be applied to indicate orientation toward a particular organism. But in each of these the

same concepts and approaches as have been described above would be used by workers with specific organisms. Fundamentally they all ask the same kinds of questions; this is what makes genetics a coherent science despite its great complexity. Other new fields of genetics are coming into existence—which instead of being organism oriented are specific problem oriented. Four examples of these are included in this book in Chapters 13 through 16. In these fields organisms are carefully chosen to answer specific problems.

7

the scope and
significance of
modern genetics

3. the significance of genetics: agriculture

One of the most important practical applications of genetics is in plant and animal breeding. Practical breeders draw on the immense store of basic genetic knowledge and use it to develop economically superior varieties and breeds of plants and animals to help feed the hungry of the world.

BREEDING

Although we may date the beginning of present-day genetics with the recognition of Gregor Mendel's work, an awareness of genetics must certainly go back far into the past. The continuity of life from generation to generation was certainly recognized for the various plant and animal forms, although hardly understood until the nineteenth century.

At some time in the past, humans began, perhaps first unconsciously and then consciously, to domesticate certain animals and selectively breed them to fit them to their needs. Our present-day cattle, sheep, goats, horses, cats, and dogs are descended from these early beginnings of breeding, started perhaps as long as 10,000 to 15,000 years ago in the Stone Age. The success of the selective breeding programs is amply illus-

trated by the wide variety of different breeds of dogs and horses adapted to carry out various kinds of functions. Most of these were developed long before the nineteenth century.

It was not until humans began to cultivate plants, however, and abandoned their nomadic existence, associated with the herding of herbivorous animals, that the really important applications of genetics began. About 6000 to 7000 years ago, the cultivation of plants that became our present-day staples began. Plants such as yams, rice, wheat, barley, oats, corn, and beans were derived from the wild forms and grown in fields. These became the mainstays of the human diet, more important even than the flesh of animals. Over the many-thousand-year period up to the last century, plant breeders produced many varieties of plants that served as food or as ornamentals. All this early breeding work had the status of an art. It was done empirically but was, in fact, highly successful, and it formed one of the bases for the development of cities and civilization.

With the rediscovery of Mendelism in 1900, there was an almost immediate application of Mendelian principles to

plant and animal breeding. For the first time breeding was put on a scientific basis. It can be stated unequivocally that production of food from every important food plant and animal has benefited and been increased by the application of genetics. Perhaps the best example is the development of hybrid corn.

HYBRID BREEDING IN PLANTS

In 1909, G. H. Shull, the geneticist, discovered that he could produce a superior strain of corn by hybridizing two *inbred* strains. By *inbred* we mean lines in which plants had been self-pollinated for many generations. From these early beginnings, and with the further work of many other corn geneticists, the present-day hybrid corn has been developed, and is now virtually the only kind of corn grown in the United States. Prior to the use of the hybrid strains of corn, production was on the order of 30 bushels per acre in the best corn-producing areas of the United States. Average yields are now 90 to 100 bushels per acre, a threefold increase! Significant increases in the yield and food quality of other staple food plants such as sorghum, sugar beets, onions, tomatoes, and carrots have also been achieved by the use of hybridizing techniques similar to those used in corn. Not all of this increase can be attributed to genetics alone, however. The use of fertilizers, insecticides, and herbicides has also been a large factor increasing the yield of all important food plants.

OTHER KINDS OF PLANT BREEDING

The increase in agricultural production is not only the result of producing strains that are able to grow faster and produce more by virtue of their efficiency in converting sun energy into food because of a superior metabolism. It is also the result of utilizing genetic techniques to produce strains of plants that are resist-

ant to animal pests such as insects and nematodes, and to various kinds of pathogenic microorganisms that can wreak havoc with crop plants, particularly in the breadbasket areas where many thousands of contiguous acres may be planted with the same kind of plant.

Plants can also be bred to be adaptable to mechanical harvesting. This has been done even with as dubious a candidate as the tomato. The ordinary tomato bought fresh in the vegetable market obviously would create a mess if picked mechanically, but varieties have been developed with tough skins that are easily picked by machines. When the skins are removed at processing plants, the remains constitute the present-day major source of canned tomatoes, tomato paste, and tomato juice.

In addition to producing hybrids with superior yields from *inbred* strains of the same species, plant geneticists have also been highly successful in developing new crop and ornamental plant varieties by crossing together two different species to produce a more desirable interspecific hybrid, or by merely introducing a small but desirable part of the chromosome complement of one species into an already established crop plant of another species. For example, the cultivated wheat plant, *Triticum aestivum*, is the Western world's major food staple, equalled in importance only by the rice plant, *Oryza sativa*, in the Orient. Like most plants, cultivated wheat has little or no resistance to certain diseases that can cause great reductions in crop yield. Other relatives of wheat do show resistance to these diseases; however, it is not feasible to make complete hybrids between the cultivated wheat and these resistant relatives, because the hybrids, although they may show some resistance, do not produce good wheat flour. Therefore, procedures have been worked out so that by "chromosome engineering" only those small parts of the chromosomes of the resistant plant that bear

the genetic material that confer resistance are transferred to cultivated wheat. This gives a resistant plant that is unimpaired in its ability to produce good flour.

The activities of plant geneticists described above have in part been responsible for what is called the "Green Revolution." There has been a dramatic increase in food production in the world during the last 20 years. This is not the result of increasing the acreage planted, but of using new varieties of plants and developing more efficient farming practices.

The breeding of new varieties of plants must be a continuing process; new resistant strains must be developed because old ones may no longer be able to cope with the newly acquired virulence of pests or new climatic conditions.

ANIMAL BREEDING

By the beginning of the twentieth century many hundreds of different varieties of domestic animals had been developed by the use of pre-Mendelian breeding. But since the application of genetic knowledge to the production of food from food animals, there have been enormous increases in total animal food produced per ton of plant food ingested by the animals. Cows now give more milk and tenderer beef; chickens produce more eggs, and the chicks grow faster to produce more meat per pound of grain eaten; turkeys have more white meat; bees produce more honey because they work harder; pigs produce more and leaner pork, and so on.

Much of the success in the breeding of better food animals has been the result of the widespread use of artificial insemination, particularly among mammals. You may have wondered why at stock shows prize bulls may go for prices up to and over several hundred thousand dollars. Surely no single animal has been worth that much! The fact is the bull is valuable

because of his sperm. His build and lineage make it highly probable that he will produce superior progeny (provided he is not sterile, which sometimes happens with these carefully bred animals). If his sperm are viable, they can be frozen and sent all over the world. A single bull can in this way be the father of thousands of offspring, and the sale of his sperm will more than pay for his original price and subsequent care.

BIOLOGICAL CONTROL

Various kinds of insects and other animals, and the fungi, bacteria, and protozoa have plagued agriculture as long as food plants and animals have been raised. Over the years various devices have been resorted to in order to combat these pests, including the development of resistant plant strains by selective breeding as already mentioned. While this application of genetics has been effective to a degree, it still has rather serious drawbacks because the predators and pathogens may change as fast as the geneticist can develop plants resistant to them. In addition, it is not always possible to find plant strains that are resistant to all the different kinds of pests. For this reason, it has continued to be necessary to use enormous quantities of insecticides, fungicides, and other pesticides to keep plant and animal production at profitable levels. As everyone knows, the use of these chemicals, most of which are not biodegradable, presents the serious problem of contamination of the environment. These chemicals are not specific; they can poison other forms of life—including humans.

A partial solution to this problem, aside from the development of resistant strains, is to use other biological means to control pests directly. One method has been used with moderate success to control the screwworm, the larva of the fly, *Callitroga hominivorax*, which is a serious pest to livestock in the southern part of

the United States and Mexico. These flies are raised in large numbers in special laboratories, and the adults are sterilized by use of X rays. The sterile males are then released in large numbers into the air. The screwworm fly normally maintains a low population density. Therefore screwworm populations are readily saturated with sterile males. The result is that only infertile eggs are produced. Other insects that are pests of both plants and animals can probably be similarly controlled without real damage to the environment.

Another possible means of controlling insects is to take advantage of the fact that they usually have complex mating

patterns that involve chemical attractants called *pheromones*. Mutant insect strains producing the wrong (ineffective) pheromones could theoretically be raised in large numbers and distributed in those areas where their nonmutant form is extant. This dilution of the wild population by the mutant forms might well cause a breakdown in the mating of males and females and a large reduction in the size of the next generation.

These are but examples of possibilities for the control of pests. None of them, however, can be brought to fruition without the application of genetic knowledge.

4. the significance of genetics: medicine and society

It has not been until relatively recently (since World War II) that medical researchers and practitioners have begun to pay much attention to genetics as an aspect of medicine. There are probably two reasons for this long neglect of genetics on the part of the medical profession. The first was a general abhorrence of the ideas of the eugenicists. The eugenics movement arose in a formal way in the latter part of the nineteenth century and persists in one form or another today. In general, the extreme form of eugenics maintains that human beings should be bred as are animals for the production, in future generations, of superior men and women. It has led to laws requiring the sterilization of individuals considered inferior. In its most extreme form, it led Adolf Hitler to order the murder of millions of Jews in Europe during World War II.

The second reason medicine tended to ignore genetics was the idea that, although there may exist diseases that are inherited, there was nothing medicine could do about them. A genetically determined disease followed an inevita-

ble course that could not be modified. We know now that this is not always true.

Today many members of the medical profession recognize that genetics can be a powerful ally, and nearly all medical schools have departments of genetics or at least geneticists on their faculties.

This change in attitude has, in large part, been due to the great advances made in the last 20 to 30 years in our understanding of human metabolism and the realization that it is under the control of genes. Also, the discoveries in human cytogenetics made in the last 15 to 20 years have opened the eyes of physicians to the importance of genes and chromosomes.

To give but a few examples, it may be pointed out first that of the half million or so spontaneous abortions occurring among pregnant women each year in the United States at least half are almost certainly caused by severe errors in the chromosome complements of the embryos. Second, a large fraction of the children born mentally retarded have genetic abnormalities. Third, probably