# GENETICS

GEORGE P. RÉDEI

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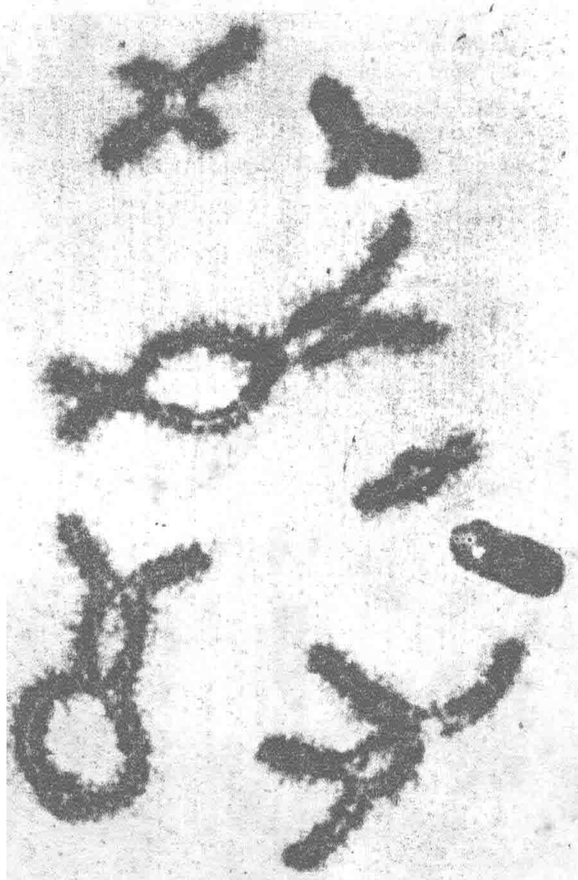

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All the errors in the text are the author's responsibility.

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The understanding of my family made it possible to spend uncounted thousands of hours on this project.

G. P. R.

# Preface

This introduction to genetics for undergraduate students is suitable for a range of one-semester courses. I have successfully used the evolving versions of this text during the last six years. In it I have attempted a balanced coverage of the three main areas of modern genetics: cytogenetics, molecular genetics, and population genetics—together with related topics. This material is more than needed for one semester but it provides the creative teacher an opportunity for selection and emphasis to meet the needs of her or his students.

The universal nature of genetic principles is stressed throughout, and a comparative approach is followed, with a balance among the various organisms and genetic mechanisms. This book assumes only a minimal knowledge for the beginning student. The most relevant elements of general biology are summarized in Chapter 3, to refresh memories, remedy deficiencies, and provide a handy reference during the course of study. For the coverage and organization of the material, the reader is referred to the table of contents. The 20 chapters are divided into parts, so the book contains 36 main sections. This format permits the discussion of concepts with gentle transitions from the simplest to the more advanced. Also, the student develops a historical sense without the burden of much historical data. With this sequence, genetics is easy to understand, and its study requires little memorization, because the principles form interlocking logical sets.

Under the chapter headings can be found the required background and a preview; this may facilitate studying the text in other sequences. Each chapter concludes with a summary of key points, generally followed by examples of practical applications of genetics to agriculture, medicine, and other human activities.

The many illustrations are integral parts of the text; their captions supplement, rather than repeat, the text. Some advanced or expanded information is boxed, without interrupting the thread of logic. Key terms are printed in boldface to facilitate reviewing the material. The literature cited is marked with Roman numerals in longer chapters, indicating the sections to which they particularly apply. Altogether, more than 1000 references are provided, directing the reader to the latest or most significant research reports and reviews. The questions allow students to gauge their comprehension of the principles; the problems introduce them to the logic of collecting and interpreting ever more sophisticated research data.

The appendixes provide various aides that broaden skills and/or present useful data. The modern glossary contains terms and definitions which may facilitate reading some of the more advanced references.

So, having our itinerary now at hand, let us embark on a journey together. I hope it will be as exciting for you as it is for me each time I revisit these monuments. I hope, too, that you will share your experiences with me. Good luck, and have a good time.

G.P.R.

# Contents

# 1 Development and Scope of Genetics

An optional broad outline of historical ideas.

The biological fact that offspring generally resemble their parents has been observed since the dawn of human history. This similarity between progenitors and progeny is due to **inheritance.** The nature and basic laws of inheritance have begun to unfold only since the second half of the last century. Several valid and interesting observations were made earlier, but interpretations of the facts were often metaphysical—lacking experimental verification—and inconsistent with natural laws known then or revealed subsequently (Fig. 1-1).

Early ideas on the mechanism of heredity can be classified into a few main groups. According to the theory of **pangenesis,** particles or fluids from various parts of the body accumulate in the germ cells, and are transmitted in some way to the offspring. This idea emerged in the ancient Greek schools and was entertained for more than two thousand years, up to the twentieth century. All adherents of this theory believed in the passing on of **characters acquired** during the lifetime of the individual. Individuals were expected to transmit to their progeny the heritage which they received from their predecessors, along with some of the qualities accumulated by exposure to the environment.

In the second half of the nineteenth century, the German August Weismann, in an experiment, cut off the tails of mice for 22 generations, yet the newborn displayed tails just as long as those of their ancestors. About the same time Francis Galton, an Englishman, performed blood transfusions among different breeds of rabbits, without any hereditary consequences. These two experiments clearly demonstrated that the pangenesis theory could not adequately account for the observed facts of heredity.

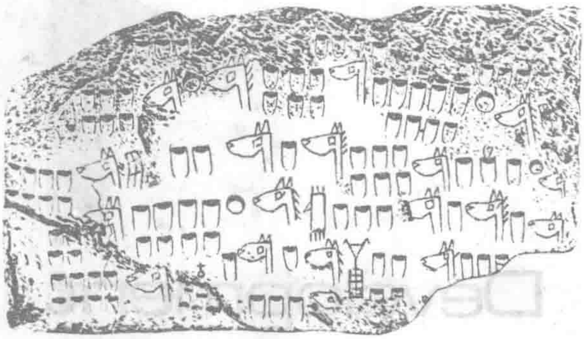

***Figure 1-1.*** *One of the oldest protocols of genetic research excavated in East Ur of Mesopotamia. The plate was engraved about 5000 years ago. Note that the horse heads are arranged in horizontal rows and that there are three types of manes (erect, pendant, and maneless) and three profiles (convex, concave, and straight). The meaning of the symbols is not known, except the ♀ sign in the lower left quadrant, which is today used to represent "female."* [*From W. Amschler, 1935.* J. Hered. ***26:****233.*] *Several Assyrian bas-reliefs in the museums of the world reveal that artificial pollination of dioecious palm trees was part of religious ceremonies performed about three millennia ago.*

During the seventeenth and eighteenth centuries, the **preformationist** idea of heredity was widely accepted. Henry Baker, the eighteenth-century microscopist and author of "serious and humorous" poems, summarized the essentials of this concept in 1754:

*Each Seed includes a Plant: that Plant again,*
*Has other Seeds, which other Plants contain:*
*Those other Plants have all their Seeds; and, Those,*
*More Plants again, successively inclose.*
*Thus, ev'ry single Berry that we find,*
*Has, really, in itself whole Forests of its kind.*
*Empire and Wealth one Acorn may dispense,*
*By Fleets to sail a thousand Ages hence:*
*Each Myrtle-Seed includes a thousand Groves.*
*Where future Bards may warble forth their Loves.*
*So Adam's Loins contain'd his large Posterity,*
*All People that have been, and all that e'er shall be.*
*Amazing Thought! what Mortal can conceive*
*Such wond'rous Smallness!—Yet we must believe*
*What Reason tells: for Reason's piercing Eye*
*Discerns those truths our Senses can't descry.*

In the late seventeenth century, the Dutchman A. Leeuwenhoek and his students believed they saw through their microscopes small encapsulated creatures (*animalcules*) within the sperms.

It is no wonder that Baker's senses could not confirm the physical existence of the preformed future generations within the organisms studied: a small *Arabidopsis* plant may contain not more than five million cells, and a seed is made up of about one thousandth as many. Vascular plants have a history of approximately a billion years, and an untold future. Thus neither observable facts nor simple logic can support the preformationist theory.

In the mid-eighteenth century the German K. F. Wolff suggested that organisms develop by **epigenesis.** According to this theory, development starts from an undifferentiated fertilized egg and proceeds through successive formation and addition of new parts which did not exist there preformed. This was a very important idea for the explanation of development and differentiation, yet inadequate by itself to account for the mechanisms of heredity. During this period speculation prevailed over experimental approaches. But the attitude toward biology underwent a dramatic change during the second part of the nineteenth century.

During a decade-long experimental study first reported in 1865, Gregor Mendel, an Augustinian monk in Brno, Czechoslovakia (then Brünn, Bohemia), discovered the basic laws of particulate inheritance. Mendel's principles have been greatly enriched during the twentieth century, after their fairly general acceptance beginning in 1900. The period (1900–date) is characterized by the use of statistical probability rather than natural philosophy.

In the early years of the twentieth century, the cellular and chromosomal basis of heredity (*cytogenetics*) was identified, primarily by the German Theodore Boveri, the Frenchman F. A. Janssens, and the Americans W. S. Sutton and, independently, T. H. Morgan and students.

The understanding of the biochemical basis of gene function (*biochemical genetics*) began essentially with the studies of the Americans George W. Beadle and Edward L. Tatum in 1941, who have shown that gene expression is mediated through enzymes.

A most important step in understanding the mechanism of inheritance was the discovery that **nucleic acids are the chemical carriers of hereditary information.** Recognition of the role of nucleic acids in heredity began at about the same time as Mendel's discovery, and led to the development of *molecular genetics* in the second half of the twentieth century. The biochemical studies on nuclein of the Swiss Friedrich Miescher were reported in print in 1871. In 1944 the Americans O. T. Avery, C. M. MacLeod, and M. McCarty demonstrated that genetic information in bacteria can be transferred by purified deoxyribonucleic acid (transformation). In 1953 James D. Watson, an American, and Francis Crick, an Englishman, presented a model of the structure of DNA that accounts for the storage, function, and evolution of the genetic information as it is known today. This genetic system is marvelous in its effectiveness and economy. A human gamete carries approximately 3 billion nucleotide pairs, while the fertilized egg has twice that many. This number of nucleotides determines all the potential of an individual from conception to death. The weight of the DNA (deoxyribonucleic acid) in a typical human cell is about 6.4 picograms. Thus the genetic material in the zygotes from which four billion humans developed (the estimated living population in 1975) weighed only 25.6 milligrams. This is a mass comparable to that of a grain of rice. The length of the total DNA in the body of an adult man is, however, about 50 times the distance from the earth to the sun.

Another major surge in the understanding of genetics began during the late 1960s. Chemical and physical progress made it possible to isolate the hereditary units (genes) and to reveal many of their ultimate structural and functional properties. This "new genetics" improved the analytical resolution in higher organisms by perhaps six orders of magnitude.

In 1906, the Englishman William Bateson suggested that the discipline concerned with heredity and its variation be called *genetics*. A Danish botanist, Wilhelm Johannsen, introduced the word "gene" in place of Mendel's "factor" in 1909. Modern genetics encompasses a broad spectrum of biology; it is often considered the core of biology. All morphological, physiological, biochemical, and behavioral properties of organisms are basically determined or controlled by the genes, the smallest integral functional units of heredity. The principles of genetics are basic to an understanding of evolutionary concepts as well as of the dynamic laws of populations within and among species. Genetics is also an indispensable tool in biochemistry. Plant and animal breeding, medicine, genetic counseling, and various demographic and social sciences use the information systematized by genetics. It is not surprising, therefore, that genetics has had a great impact on the economic and social systems of the twentieth century.

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# 2 Relevance of Genetics

**Genetics is important to agriculture, medicine, and society.**

The primary goal of genetics is understanding the fundamental processes of biological inheritance. Yet the great potential for applying genetic principles to practical problems can easily be illustrated with a few examples.

## The Search for Sugar Beets

Up to Napoleon's time (1811), all the sugar consumed in Europe came from tropical sugarcane plantations. In 1747 Andreas Marggraf, a German chemist, demonstrated that the sweetness of beets, eaten as a garden vegetable, was due to a sugar which he crystallized in alcohol extracts from the roots. When his student Franz Karl Achard began purposeful selection work, less than 2% sugar could be extracted from the beets. By the 1820s the sugar content had been increased to 5–7% by selecting the best progenies, and within the following decade it reached 9%. In 1858, plants of the cross *Beta vulgaris* × *B. maritima* were discovered which contained 11 to 14% sugar. Today some strains of beets contain over 20% sugar. In Germany sugar yields have increased from 1.85 metric tons per hectare in 1850–1859 to 4.32 metric tons by the mid-1950s.

Some presently grown varieties have been developed by more sophisticated genetic techniques, such as the use of triploid heterosis (see p. 282). The yield is not only higher, but also more certain, because genes conveying resistance to devastating diseases (Cercospora, virus) have been systematically incorporated into the commercial varieties. Even the taxonomical characteristics have been altered by transforming the original seedball, containing several seeds, to a "monogerm" form enclosing only single seeds. This new feature has greatly facilitated mechanized production. Before the beet was converted into a crop plant, the average sugar consumption in temperate climatic zones was negligible. During the last 50 years, per capita sugar consumption in developed countries increased four- or fivefold, to 30 to 50 kg/year.

## Hybrid Vigor in Corn

In about 1905, when George H. Shull, a botanist at the Carnegie Institution at Cold Spring Harbor, New York, began a project on self-pollination (inbreeding) and then crossing of maize, he expected to find out how the kernel-row number was inherited. Shull observed, however, that hybrids exhibited an unexpected vigorous growth, and by 1909 he recognized the potential of using crosses of inbred lines for agricultural purposes. By 1917 the major technical problems of producing hybrid corn were resolved through the joint endeavors of researchers at the Connecticut Agricultural Experiment Station (primarily E. M. East, H. K. Hayes, and D. F. Jones). Commercial production began in the early 1930s. At that time the average yield of corn per acre (0.4 hectare) in the United States was about 22 bushels (559 kg). By the late 1940s the yield per acre had increased to 33 bushels, and by the early 1980s it reached over 100 bushels. The best farmers of Iowa are now harvesting 13 to 14 metric tons of shelled grain per hectare (about 205 to 220 bushels/acre). This increase was not entirely the direct result of genetic improvement, but the improved yielding potential did stimulate more intensive agricultural practices, such as fertilization, plant protection, and mechanization. The increased production of commercial corn stimulated greater interest in the methodology and techniques of plant breeding, quantitative inheritance, and statistical analysis. The accumulated basic knowledge not only improved corn production further, but also led to progress in several basic and applied sciences.

In the 1960s biochemist Edwin T. Mertz and geneticist Oliver E. Nelson and their associates discovered that the *opaque* gene of corn improved the quality of kernel protein. Corn, the world's third largest grain crop, not only has a low total protein content (about 10% on the average) but also contains a type of protein which has very little nutritional value for monogastric animals (those having only one stomach) such as man, pig, and chicken. Furthermore, corn and other grain proteins are low in some of the essential amino acids, notably lysine and tryptophan. Nevertheless, approximately 70% of mankind's protein consumption relies on grains.

In opaque corn there is less of the undesirable protein zein than is found in commercial corn and more of the protein glutelin, which has a higher nutritional value. Furthermore, the total amount of the amino acid lysine is 50 to 60% higher. Piglets fed with this new high-lysine corn grew 3½ times faster in some experiments than did those receiving only normal corn. In addition, units of feed required per units of weight gained were only about half those of the commercial corn feed. In another experiment, weanling pigs on a high-lysine corn ration gained 73.2 pounds in five weeks, in contrast to those on a normal corn diet, which gained only 6.6 pounds under identical conditions. The potential benefits of substituting high-lysine corn in the diets of people suffering from kwashiorkor (malnutrition caused by protein-deficient food) are equally impressive. Currently, this new type of corn is limited in use, for various economic and social reasons. The yields of the best new varieties carrying the high-lysine genes seem to be comparable to those of normal corn.

## The Green Revolution

In the 1960s the short-straw wheat varieties developed by O. A. Vogel and N. E. Borlaug received great public attention. In some experiments in the northwestern United States the semi-dwarf soft white wheat varieties outyielded the best old ones by 170% on dry land, and showed an increase of 20 to 60% under irrigation. The wheat yield in Mexico between 1925 and 1970 shows a dramatic change (Fig. 2-1). The Mexican wheats imported to India and Pakistan repeated that superior performance. The incorporation of only a few genes into the standard wheat varieties provided a resistance to lodging[1] that, in turn, permitted the use of heavier doses of fertilizers, resulting in increased yield.

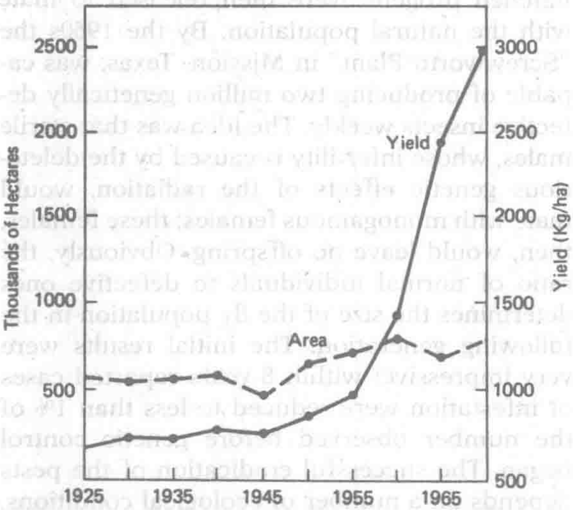


***Figure 2-1.*** *The wheat yields in Mexico before and after the introduction of the semidwarf varieties around 1960. (From K. J. Frey, 1971. In* Moving Off the Yield Plateau, *J. D. Eastin and R. D. Munson, eds., Am. Soc. Agron. Spec. Publ. 20, Madison, WI.)*

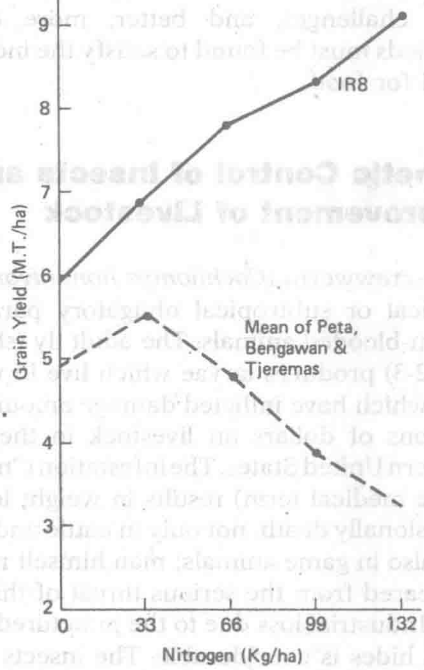


***Figure 2-2.*** *The yield of the lodging-resistant IR8 "miracle" rice under conditions of increasing nitrogen supply. (From K. J. Frey, 1971. In* Moving Off the Yield Plateau, *J. D. Eastin and R. D. Munson, eds., Am. Soc. Agron. Spec. Publ. 20, Madison, WI.)*

At about the same time similar results were obtained with paddy rice (Fig. 2-2). These examples demonstrate that improved varieties encourage or sometimes mandate the general improvement of agrotechnical practices. From a genetic point of view, Figure 2-2 demonstrates that genes provide only the potential for manifesting inherited abilities. Environmental conditions determine the degree of gene expression.

Genetics has made many other contributions to plant breeding and to human welfare, but the

[1]The term means falling down if beaten by rain and/or wind.

work is far from finished. New times present new challenges, and better, more efficient methods must be found to satisfy the increasing need for food.

## Genetic Control of Insects and Improvement of Livestock

The screwworm (*Cochliomya hominivorax*) is a tropical or subtropical obligatory parasite of warm-blooded animals. The adult fly (shown in Fig. 2-3) produces larvae which live in wounds and which have inflicted damage amounting to millions of dollars on livestock in the southwestern United States. The infestation ("myiasis" is the medical term) results in weight loss and occasionally death, not only in cattle and sheep, but also in game animals; man himself may not be spared from the serious threat of this parasite. Industrial loss due to the punctured, weakened hides is considerable. The insects can be controlled chemically, but only at a considerable cost, and the large-scale application of chemical pesticides results in undesirable pollution.

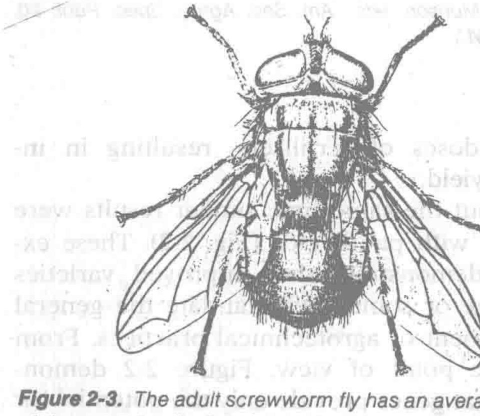

***Figure 2-3.*** *The adult screwworm fly has an average life span of three weeks. During that period it may travel 100 miles or more. It can survive only in warm winters, but because of its fast reproduction and travel it can spread from Mexico to the southern states and up to the Midwest. (From A. Stefferud, ed., 1952.* Insects, *Yearbook of Agriculture, USDA, Washington, DC.)*

In 1950, entomologists took notice of the basic genetic studies of H. J. Muller on the innocuous fruit fly Drosophila. When Muller irradiated Drosophila with X rays, he observed lethal genetic alterations (chromosomal breakage). Such alterations can cause the death of the individual or its offspring. In 1951, E. F. Knipling, R. C. Bushland, and D. E. Hopkins initiated experiments to control harmful insects by genetic sterilization and genetic death. They reared large populations of the screwworm flies in the laboratory and then treated their pupae (larvae) with 7500 R units[2] of X rays before eclosion (emergence from the pupal case). The hatched progeny were then released to mate with the natural population. By the 1960s the "Screwworm Plant" in Mission, Texas, was capable of producing two million genetically defective insects weekly. The idea was that sterile males, whose infertility is caused by the deleterious genetic effects of the radiation, would mate with monogamous females; these females, then, would leave no offspring. Obviously, the ratio of normal individuals to defective ones determines the size of the fly population in the following generation. The initial results were very impressive: within 8 years reported cases of infestation were reduced to less than 1% of the number observed before genetic control began. The successful eradication of the pests depends on a number of ecological conditions, the migration of the flies, and the size of the initial population.

Since the war on the screwworm began, newer and more sophisticated genetic methods have been contrived against a wide range of

[2]See p. 315 for definition.

pests (flies, mosquitoes, moths, etc.). Insects that have a very specific requirement for survival can be produced in the laboratory. When released, they may mate with the natural population, but all their offspring will die because nature cannot provide the special requirement (e.g., a certain temperature). Because of the special nature of the chromosomal structure in moths, radiation may not have immediate serious consequences on their mating behavior or vigor. In subsequent generations, however, a fraction of their offspring will suffer from fatal defects. This genetic time bomb which man is now able to implant in a pest population can either kill all of the offspring at one time or can, by delayed effect, keep thinning them out for several generations.

Numerous other examples could be cited from the field of applied animal genetics to demonstrate how a scientific approach to breeding has improved the quantity and/or quality of eggs, milk, meat, and wool (see Fig. 2-4 and Table 18-16).

## Genetics and Plant Disease

The actual yield of a crop depends not only on the plant, the fertility of the soil, and meteorological conditions, but also on the parasites and on the host–parasite interactions.

The old varieties of macaroni wheats performed reasonably well until 1953 and 1954, when a severe stem-rust epidemic swept over the Dakotas and Minnesota. In those two years the yield per acre was reduced to half or a third of that of the preceding years. In 1955 new varieties were introduced containing genes for resistance against the prevailing races of rust and the yield was restored or even increased.

In 1946 the cytoplasmically male-sterile lines (see Chapter 16) of maize with T (Texas) cytoplasm developed by P. C. Mangelsdorf and students and those of S (sterile) developed by D. F. Jones were released. These stocks made the production of hybrid corn much more economical and did not affect the disease susceptibility of the hybrids for many years. The T cytoplasm proved to be a reliable source of male sterility, and by 1969, 70 to 90% of the hybrid corn grown in the United States carried the T male-sterile cytoplasm. This could be considered a major triumph of scientific plant breeding.

In 1969 a frightening phenomenon appeared in several midwestern states. Hybrid corn containing the T cytoplasm was severely attacked by the blight fungus *Helminthosporium maydis*. In 1970 the epidemic spread over almost the entire corn belt. In some states 50% of the crop was lost, and nationally the loss was 15%.

Today the blight is under control because resistant cytoplasms have been substituted for the susceptible one. This ominous experience demonstrated on a very practical level the validity of some genetic principles. Apparently, new genetic changes occurred in the pathogen, making it more virulent on a particular host. Because the susceptible T-cytoplasm corn was prevalent, the new fungus strain spread rapidly. The practical lesson is that never again should 69 million acres be planted with a crop of genetically uniform constitution.

## Genetic Manipulation of Microorganisms

Several species of lower organisms (bacteria, yeast, fungi, algae) have important roles in man's economy. From the viewpoint of human health, the fungus *Penicillium notatum* and the actinomycete *Streptomyces griseus* are particularly important because of the production of the antibiotics penicillin and streptomycin, respectively. It has been estimated that the aver-

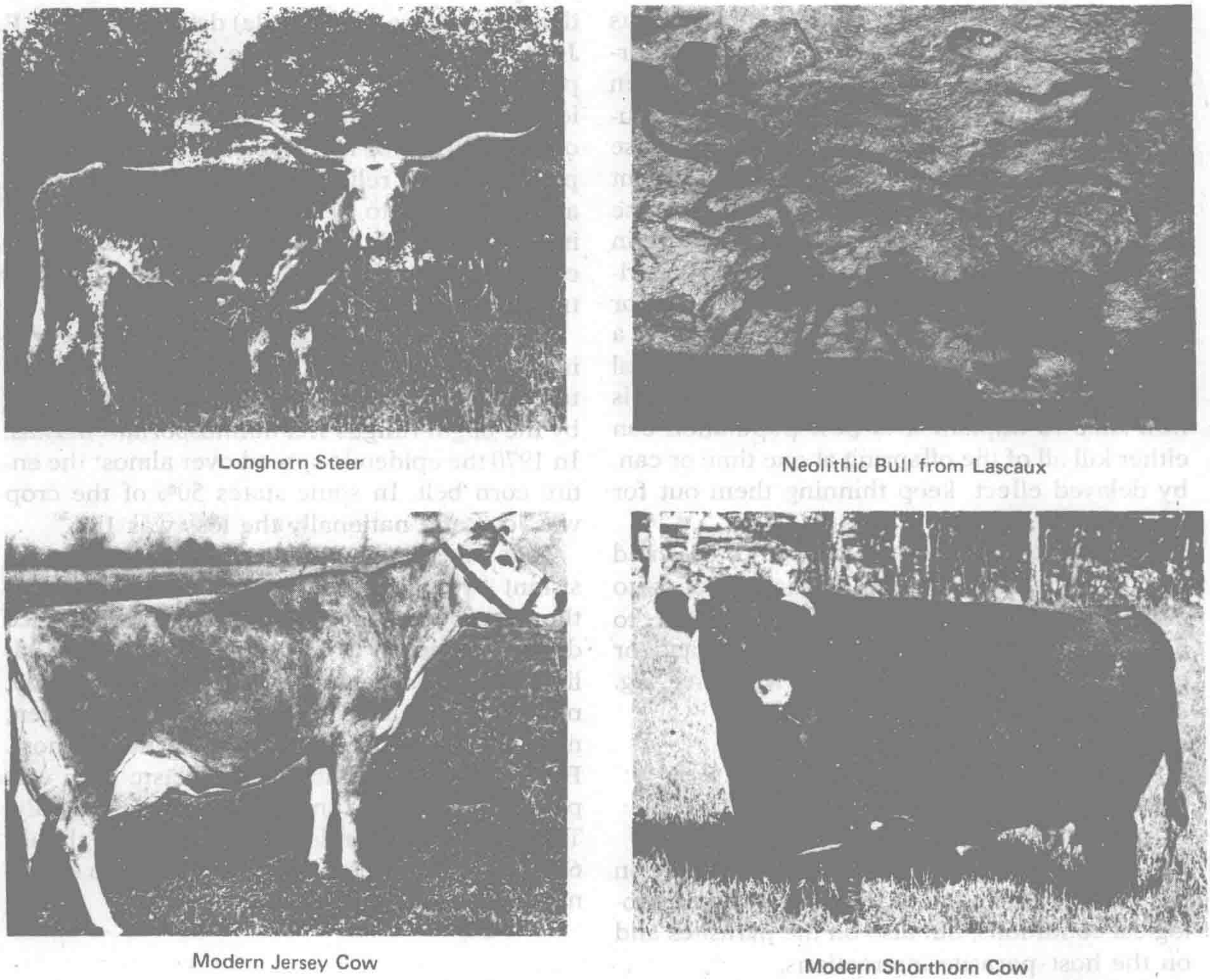


***Figure 2-4.*** *The primitive longhorn cattle still in existence are not much different from those seen on the painting in the Lascaux cave (France) executed by Neolithic man about 15,000 years ago. In sharp contrast, the Jersey cow systematically bred for dairy use, and the shorthorn cow developed for beef production, are much different from the ancient types of cattle and from each other because of 200 years of breeding work. (Cave bull by the courtesy of the Caisse Nat. Monum. Hist. Sites; others by the courtesy of Mr. R. C. Bjork, U.S. Dept. Agric.)*

age human life span has been prolonged by 10 to 20 years since antibiotics became available. Industry cultures these organisms under axenic (contamination-free) conditions. After harvesting, the drugs are collected and purified for human or animal medicinal use.

Penicillin was discovered in 1928 by A. Fleming, an Englishman, and streptomycin in 1940 by S. A. Waksman, an American. Purposeful cultivation of these organisms began only after these dates, making them relatively recent "crops." Prior to that, neither had been sub-