PRINCIPLES OF HUMAN GENETICS

Second Edition

by

CURT STERN

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by CURT STERN *University of California, Berkeley*

W. H. FREEMAN AND COMPANY
SAN FRANCISCO AND LONDON

Printed in the United States of America

Library of Congress Catalogue Card Number: 60–12098

PREFACE

ELEVEN YEARS AGO, when the first edition of this book appeared, the principles of human genetics seemed well established. These principles still stand, even though the past decade witnessed breath-taking changes and advances in the field of human genetics. As elementary a fact as the number of man's chromosomes was recognized and, based on this knowledge, human cytogenetics became a fruitful reality. "Classical" pedigrees of special traits were shown to have been unreliable. The sex-determining role of the Y-chromosome was discovered. Much information of value to geneticist, physiologist, and physician came from biochemical research on inborn errors of metabolism and on inborn differences among normal people. With the recognition of the universal existence of polymorphism and with the discovery of relationships between disease and blood group and hemoglobin constitution, the role of genetic selection in human populations acquired new meaning. And of crucial importance to all men living in the Nuclear Age was the demonstration that fewer mutations are produced in immature germ cells by exposure to a dose of radiation over a long period than by exposure to an equal dose over a short period.

Although the book has been extensively rewritten and expanded to take account of recent discoveries, the emphasis remains on principles rather than on detail. This edition, like the first one, is designed to serve many masters: students of genetics concerned primarily with man; students with special medical goals; students for whom the study of human genetics will be one of the foundations for their thinking as educators, psychologists, anthropologists, and social workers. The first ten chapters are intended for all readers; among the later chapters, however, are some that will be of more interest to certain groups of readers than to others. In spite of the wide variety of material covered, the book has a basic unity: the presentation of the principles of human genetics as a means of understanding some of the diversity, as well as the underlying community, of mankind.

This book is based on the work of many persons—some named in the text, but most uncited. Here I can acknowledge only a few who gave specific help. Dr. J. F. Crow commented on the whole manuscript, Dr. Gordon Walls on the sections on color blindness, Dr. J. H. Renwick on linkage, and Dr. W. L. Russell on radiation genetics. Mrs. Eva Sherwood was of constant support in the preparation of the new edition.

Many excellent drawings which Dr. Aloha Hannah-Alava prepared for the first edition have been used again, and many new drawings from the skillful

pen of Mrs. Emily Reid have been added. The investigators who generously made new, original photographs available and the publishers and authors who kindly granted permission for the use of copyright material are acknowledged in the figure and table legends. The system of acknowledging borrowed material is explained in the introduction to the references at the end of Chapter 1.

There were more errors in the first edition than I had anticipated. The asked-for corrections came from many sides, and a whole dossier of valuable comments was assembled by Dr. Norma Ford Walker's keen students at the University of Toronto. Most of the old errors have now been rectified, but how many new ones have slipped in?

In concluding this preface, I take pleasure in referring to the personal relations between Mr. William H. Freeman, his associates, and myself—relations in the distinguished tradition of the publishing craft.

July, 1960 CURT STERN

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CHAPTER 1

INTRODUCTION

The study of human inheritance is concerned with the existence of "inborn" characteristics of human beings: physical and mental, normal and abnormal. In its broadest sense, it deals with those qualities present in all human beings that distinguish them from nonhuman beings, as well as with those qualities which characterize only certain groups of man, certain families, or certain individuals. Thus, it is largely a study of hereditary similarities and differences among human beings. It is concerned with the causes of these similarities and differences and the way in which they are transmitted from generation to generation.

The science of inheritance is called *genetics,* a term derived from the Greek root *gen,* which means to become or to grow into something. It signifies that genetics deals not only with the transmission of hereditary factors but also with the ways in which they express themselves during the development and life of the individual.

The student of human genetics must draw on many sources of information. He obtains his material from studies of families or larger groups—from anthropological, psychological, medical, and sociological investigations. To evaluate the data, he needs the tools of the statistician. Human genetics is based on general principles derived originally from the study of plants and animals —principles which are as valid for man as they are for unicellular and other multicellular organisms. Since these general principles can often be demonstrated more clearly in organisms better adapted to experimental work than man, reference to such studies is often helpful in an analysis of human inheritance.

An understanding of simple inheritance in man was not possible before Mendel's work on peas. Elucidation of the genetics of body size, intelligence scores, and other "quantitative" characters in man was not even begun until Nilsson-Ehle's and East's studies on shades of color in wheat and size of Indian corn paved the way. The peculiar mode of transmission of color blind-

ness in man became clear only after similarly transmitted "sex-linked" traits were found in birds, moths, and flies. The riddle of sex determination was not solved until the cells of grasshoppers and plant bugs had been scrutinized. And no study contributed more toward the clarification of the heredity-environment problem than an investigation of the variability of size in beans. Work on nonhuman organisms will be cited, however, not only for historical reasons, but for the decisive experimental data that illustrate situations in man which are still obscure or that point out possibly significant factors known to play a role in animal or plant genetics but not yet recognized in human genetics.

Man as an Object of Genetic Study. At first sight, man appears to be an unfavorable object for genetic study. Ideally, the student of genetics works with groups of standardized organisms that are genetically identical or at least approach identity. He tries to breed and raise successive generations under similar environmental conditions. In man, however, the genetic diversity of individuals is great and uncontrolled, and biological and social environments vary greatly. The principal tool of the general geneticist is the experimental crossing of different genetic types. In man, on the other hand, parental unions are entered into with no intent to serve an experimental plan. Studies of inheritance are generally based on knowledge of a series of generations. Consequently, the preferred subjects for genetical study are organisms with rapid succession of parents and offspring. Annual plants and small mammals like mice and rats first served this purpose, with the still shorter-lived fruit flies, molds, and unicellular organisms gaining special favor later. More patience was required for work on fruit or forest trees or on horses and cattle —and relatively less scientific yield was expected. With man, the duration of a generation is alike in the observer and in the object of observation, and personal knowledge of successive generations is therefore restricted. Finally, many factors affecting transmission of hereditary traits obey statistical laws and are best studied when large numbers of offspring are available. In man, these numbers are always small; even large human families fall far short of the size desirable for statistical deductions.

Obstacles to the understanding of nature have always been challenging to the human mind. Even though genetic and environmental diversity in man is largely uncontrollable, the human geneticist can find groups that have similar heredity or similar environments. Even though he cannot arrange for matings in accordance with a research plan, he can collect data from those marriages which happen to fit into his schemes. Even though man's life cycle is longer than that of laboratory organisms, the scientist can devise special methods that enable him to get information from one or two generations, which normally only a longer series would provide. Even though the human family is small, pooling of data from many families may provide enough material for statistical analysis. The human population is large, and its millions of unions give the geneticist an immense amount of material from which to select what he needs.

The Principles of Human Genetics. This book will present the principles of human genetics, i.e., the general regularities of heredity in man that have been derived from the study of families, pedigrees, and large interrelated groups of individuals called populations. It will describe the various rules of transmission of hereditary traits and some of the methods which enable us to find out what kind of inheritance is involved in specific cases. It will also survey the effects of environment on the action and expression of human genes, the genetic aspects of sex, and the origin of new hereditary traits (mutation). Applications of these principles will be considered under such headings as Genetic Counseling (Chap. 8), Medicolegal Applications (Chap. 12), The Genetic Hazards of Radiation (Chap. 24), Selection in Civilization (Chap. 29), Medical Genetics (Chap. 30), and Genetic Aspects of Race and of Race Mixture (Chaps. 31 and 32).

No attempt will be made to treat systematically the genetics of the seemingly infinite range of normal and abnormal human traits, but many of these will be used as examples to illustrate principles. The reader who wishes to obtain more detailed information on various characters must go to the two-volume work of Gates on human genetics, to the treatise on clinical genetics edited by Sorsby, to von Verschuer's *Genetik des Menschen*, or to other works listed in the bibliography at the end of this chapter. When he consults these books, he will often find fragmentary or apparently conflicting information on the inheritance of specific traits. Only an understanding of the principles of human genetics will make it possible to evaluate such data.

The Scope of Human Genetics. Human genetics is a young science. When, in the early twentieth century, the modern study of heredity in plants and lower animals resulted in the discovery of the laws of biological inheritance, enthusiastic men drew far-reaching conclusions concerning the hereditary nature of differences among human individuals and of the consequences for mankind of the transmission of these differences to future generations. These conclusions were not just stated as theories, but included plans for "human engineering" involving legal prohibition of reproduction for certain large groups of humans and social incentives that would increase reproduction of other groups. It became evident later that the factual knowledge of man's inheritance was too narrow to justify such actions. The "eugenic movement" became discredited in the eyes of many, and a greater effort was made to accumulate specific information and devise specific methods applicable to human genetics. The work of the past three decades has greatly increased our knowledge, but the preliminary nature of much of it must still be emphasized. This book, accordingly, contains many such phrases as "it is not unlikely" or "it seems highly probable," and even positively worded statements should not be taken as final. Human genetics can claim significant achievements, but, as in any growing science, future discoveries will not only add new facts, but may also invalidate apparently established views.

Knowledge of human genetics does not only satisfy our desire to know about

ourselves; it must also form the basis of practical decisions. The physician and public health official need to understand the inheritance of diseases and abnormal characteristics. Every individual should know something about the genetic aspects of selecting a partner for marriage and about the kinds of children he may expect; he should also know that his prospects for physical and mental well-being and for a long or short life are genetically determined. Unavoidably, though often obscurely, social measures affect the type of men and women who will people a country and the earth. In order to gauge such influences, an understanding is needed of the causes of human differences, individual and racial; of the part heredity and environment play in the determination of such differences; and of the role of social organization and education in molding men. If it is proposed to change a population hereditarily, the prospects of successful selection of favored types must first be understood in order to reach rational conclusions; if such a change is feared, the same knowledge is required to evaluate the future.

As will be shown, human genetics has already made important contributions to these practical problems, and there is every reason to believe that its usefulness will increase greatly in years to come.

References

The references listed at the ends of chapters include important sources of the discussion as well as suggestions for further reading. Besides these references, other sources are also cited in the figure legends and table headings. If only the author's name is cited in a figure legend or table heading, the full bibliographical information will be found in the references at the end of the chapter. References in the figure legends or table headings which cite the author's name and, in abbreviated form, the time and place of publication are not given again at the ends of chapters; these are references which should be of further help in tracing the origins and ramifications of the topics treated.

In the figure legends and table headings, an attempt has also been made to indicate whether the illustrative and tabular material borrowed from other authors is unchanged or is in modified form. For both modified and unchanged material, credit is acknowledged in the figure legends and table headings; but for modified material, the author's name is preceded by the word "after."

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CHAPTER 2

THE BIOLOGICAL BASIS OF MAN'S INHERITANCE

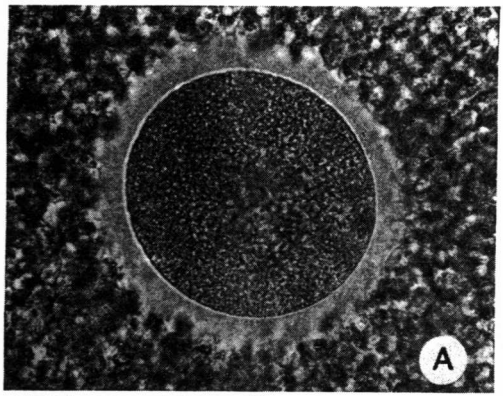
All the material a human being inherits from his two parents is contained in two cells, the egg and the sperm.

Egg and Sperm

The Human Egg. The human egg (Fig. 1) is a spherical cell about 1/7 of a millimeter, or about 1/175 of an inch, in diameter. Such small measurements are usually given in microns—a micron (μ) being one thousandth of a millimeter; thus the diameter of the human egg is about 130 or 140μ. In spite of its relatively minute size, the egg is one of the largest cells of the human body. Its cellular character is easily recognizable, since it possesses a typical nucleus enclosed in a mass of cytoplasm.

The weight of the human egg has been estimated to be 0.0015 milligram, or approximately one twenty-millionth of an ounce. In this tiny bit of matter is contained the genetic contribution of the mother to her child.

The eggs are produced in two ovaries, organs about the size of walnuts, which are attached to the dorsal wall of the female abdominal cavity. In the ovaries, immature germ cells are found in various stages of growth (Fig. 2). Each egg cell is surrounded by a wall of *follicle cells*. Concurrent with the growth of an egg cell, the follicle cells multiply. Fluid-filled gaps appear between the cells of the follicular wall and, by fusing together, split it into an external and an internal layer. Thus, a mature ovarian follicle originates. It consists of an outer layer of follicle cells, a large, fluid-filled center, and an egg cell located within an inner layer of follicle cells still connected on one side with the outer layer. As growth proceeds, the follicle bulges out on the surface of the ovary. The internal pressure of the follicular fluid stretches the thin sheets of tissue which separate the content of the follicle from the ab-



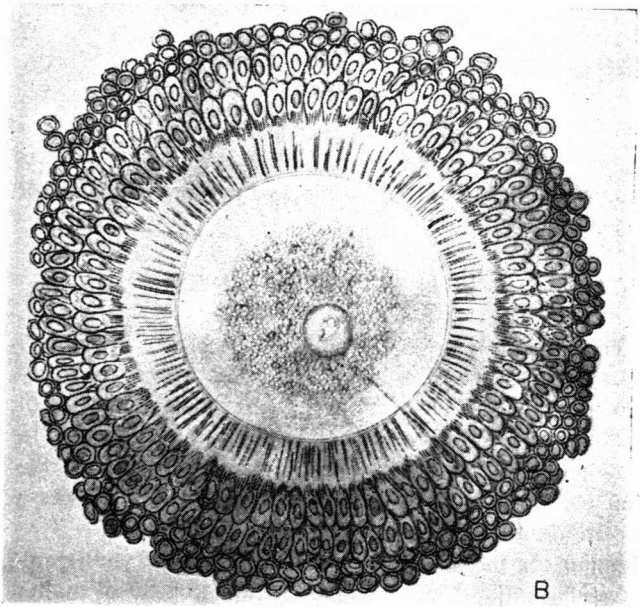


FIG. 1. The human egg. A. An egg, surrounded by a non-cellular layer, the zona pellucida, and corona cells, recovered from a large ovarian follicle. 250×. B. Drawing of an egg from a large ovarian follicle. The egg nucleus is visible. (A, original photomicrograph by Dr. Warren H. Lewis; B, Nagel, *Arch. Mikroskop. Anat.*, **31**, 1888.)

dominal cavity until both the follicle and the wall of the ovary burst. The egg, surrounded by its immediate cover of follicle cells, the *corona,* or *crown,* is released into the abdominal cavity, where it enters the funnel-like opening of the oviduct and starts its journey down the oviduct into the uterus.

If the oviduct is free of sperm, the egg cell disintegrates inside the uterus. If, however, as a result of a recent mating, live sperm are present, the egg may be fertilized in the oviduct and there begin its development. While undergoing the first steps of this process, it will move to the uterus, where it will become embedded in the uterine wall and remain for the nine months of embryonic development.

Normally, only one mature follicle develops during each monthly cycle. It may originate in either the right or left ovary: by and large, each has an

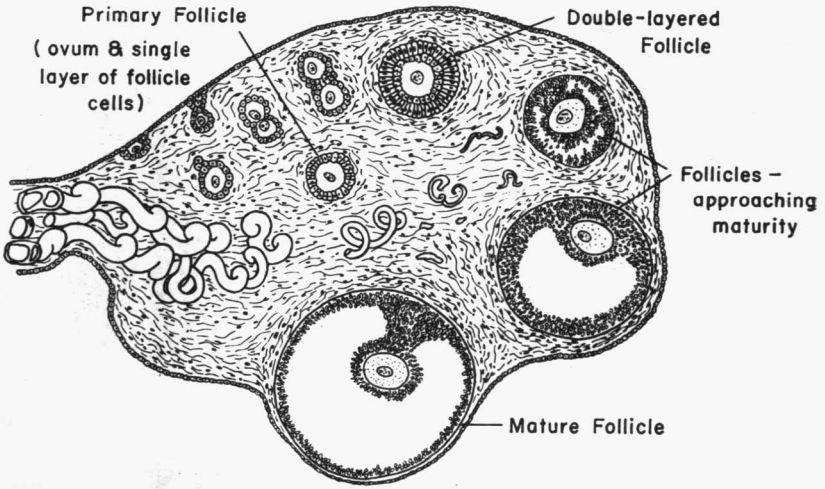


FIG. 2. Diagram of a human ovary with eggs and follicles at various stages of development. (Adapted from Patten, *Embryology of the Pig,* Blakiston, 1931.)

equal share, but one ovary often has several successive ovulations. Occasionally, more than one follicle matures at the same time, either in the same ovary or in both. Consequently, more than one ripe egg may be ready for fertilization at the same time, and a multiple birth may result. Occasionally, too, one follicle may contain more than one egg cell, again setting the stage for a possible multiple birth.

The human egg was discovered in 1827 by Karl Ernst von Bär (1792–1876), the founder of modern embryology. The basic research which led to this discovery was done with dogs. Von Bär obtained a series of female dogs in various stages of pregnancy and succeeded in tracing the embryos back to very small specks of matter—much smaller than the large ovarian follicles which had been thought to be the eggs. Finally, he found that the unbroken follicles contained minute bodies which were identical with the egg and its corona, which at a later stage were present in the oviduct. To confirm that what was true of dogs was also true of man was only a short step.

The Human Sperm. The father's genetic contribution to a child is contained in the *spermatozoon,* or *sperm* (Fig. 3), which is produced in the testes. Its cellular nature is less obvious than that of the egg. It consists of several parts, called *head, middlepiece,* and *tail.* Their dimensions are:

Head			*Middlepiece*		*Tail*	
	Width					
Length	(elliptical face view)	(side view anterior end)	Length	Width	Length	Width
3–5μ	2–3μ	1.8μ	3–6μ	1μ	30–50μ	less than 1μ

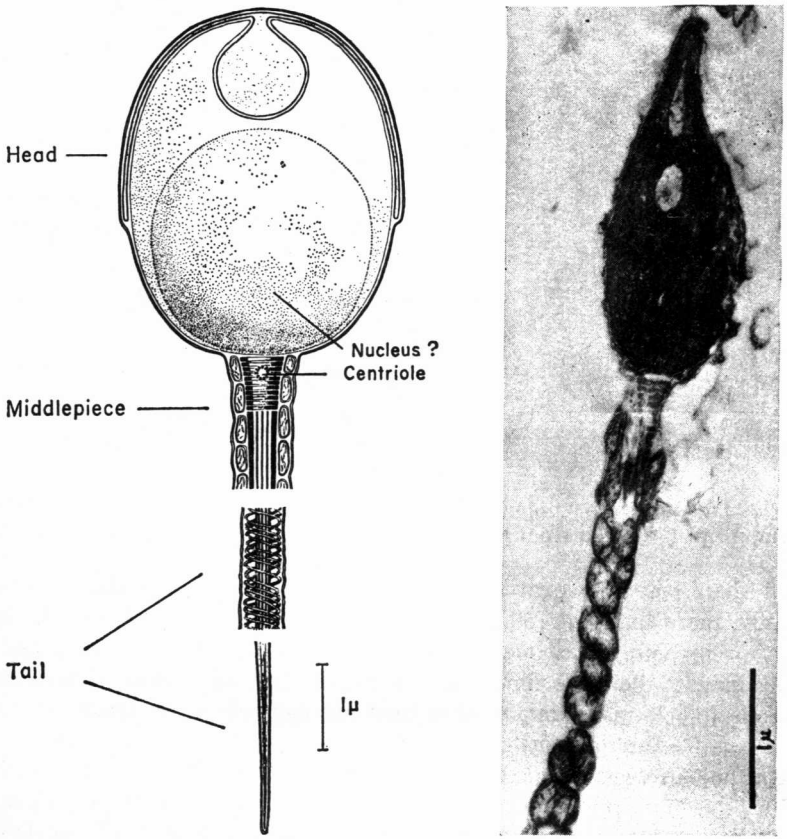


FIG. 3. Human sperm. *Left:* Diagram of a "frontal" section (based on electron-microscopic studies). *Right:* Electronmicrograph of a somewhat tangential "longitudinal" section through head and middlepiece, 19,640×. (Left, Schultz-Larsen; right, Lord Rothschild, *Brit. Med. J.*, **1**, 1958.)

The different types of immature germ cells, each representing a different stage in the development of mature spermatozoa, are called *spermatogonia, spermatocytes,* and *spermatids.* Each consists of a mass of cytoplasm and a nucleus, and is thus a typical cell. In the course of the transformation of a spermatid into a spermatozoon, striking changes take place (Fig. 4). The nucleus becomes smaller and more compact. It forms a large part of the head of the mature sperm, which is somewhat pear-shaped in side view and oval in face view. A minute body in the cytoplasm, the *centriole,* sends out a bundle of fibers, which, embedded in a thin cylinder of cytoplasm, become the tail. Most of the original cytoplasm of the immature cell is cast off and disintegrates inside the testes: a small part remains in the head, another develops into the conical middlepiece, and a third forms the outer covering of the tail.