EVOLUTION, GENETICS, and MAN

THEODOSIUS DOBZHANSKY

THEODOSIUS DOBZHANSKY

PROFESSOR OF ZOOLOGY AND MEMBER OF THE INSTITUTE FOR THE STUDY OF HUMAN VARIATION COLUMBIA UNIVERSITY

Evolution, Genetics, and Man

JOHN WILEY & SONS, INC. — NEW YORK CHAPMAN & HALL, LIMITED — LONDON

SECOND PRINTING, MARCH, 1957

Copyright © 1955 by John Wiley & Sons, Inc.

All Rights Reserved

This book or any part thereof must not be reproduced in any form without the written permission of the publisher.

Library of Congress Catalog Card Number: 55-10868 Printed in the United States of America

Preface

For almost a century the influence of the theory of evolution has been felt far beyond the limits of biology. In fact, this influence has been growing apace, and in our day the idea of evolution has become an integral part of the intellectual equipment of Western Civilization. In biology this idea is pivotal. To a beginning student no less than to a teacher and to a specialist, the idea of evolution makes sense of what would otherwise be wearisome descriptions of arid facts to be memorized, only to be forgotten as soon as the course is over. In the light of evolution the same facts and descriptions of creatures which we have seldom or never seen become fascinating. Learning them turns out to be an intellectual adventure.

Biological evolution is a part of the evolution of the cosmos. The rise and the development of mankind are a part of the story of biological evolution. Man cannot reach a valid understanding of his own nature without a knowledge of his own biological background. It may, then, be that the study of evolutionary biology is the most important practical endeavor open to the human mind. Accordingly, an effort is being made in this book to show to the student that biology is not only a craft which is interesting to technicians and devotees but also a part of the fabric of modern humanistic thought. I am quite conscious that this goal is too ambitious and that it has not been fully attained.

I hope that this book may be useful not only as a guide in courses devoted to the study of biological evolution but also as collateral reading in courses of general biology, general zoology, general botany, and anthropology. A sizable proportion of the space in this book is devoted to presentation of material which is usually given in elementary courses of genetics. Chapters 2, 3, 4, parts of 5 and 11, and smaller parts of other chapters deal with genetics. This emphasis is unavoidable, since modern evolutionism is incomprehensible except on the basis of familiarity with fundamentals of genetics. Therefore,

although it has not been my intention to turn this book into a brief textbook of genetics, a student who uses it will acquire an elementary knowledge of the subject. The book will probably fit the requirements of courses given in some institutions of higher learning, courses entitled "Genetics and Evolution" or "Evolution and Genetics."

An effort has been made to use, wherever possible, examples dealing with man and to point out the bearing of the topics discussed on human problems. The opinion once held fairly widely, that man is most unfavorable as material for biological and especially for genetic studies, is becoming less and less prevalent. Even though we cannot arrange many genetical experiments with man, there is an abundance of kinds of information bearing on the genetics and evolution of man which are not available for any other organism. And after all is said and done, the species *Homo sapiens* happens to be more interesting to most students than any other species, no matter how unserviceable it may be for some experiments. Being men, we understand many biological phenomena in man more easily and more clearly than we do the biology of much "simpler" organisms.

Although this book is meant to be comprehensible to a student with no more than an elementary previous knowledge of biology (at about high school level), some more "advanced" material and discussion of a number of unsettled and controversial problems have been included. As a result, the book contains more material than can be adequately covered in an average one-term course; but this superabundance of material is deliberate. The subdivision of the chapters into short sections with descriptive subheadings should make deletion of the unwanted material easy. On the other hand, what can be more challenging and inspiring to a student of average and above-average intelligence than to learn that science is not something all completed and finished, merely to be memorized from books, but a growing body of knowledge, in the development of which this same student may have a hand if he so chooses? Is finding this out not equally, or even more, valuable to a student than learning more "facts"?

In place of a conventional chapter on the history of evolutionary theories, the history of various ideas and concepts is discussed in this book in the same chapters which present the modern status of those ideas and concepts. This arrangement of material does not in any sense mean an underestimate of the importance of the history of science or of its interest to an intelligent student. But modern evolutionary thought is a result of confluence and integration of the work of many biological disciplines, which even in a recent past were de-

veloping more independently than they are now. The history of the evolutionary doctrine as a whole, from a modern standpoint, has never been written, and for the time being it seems more convenient to present the historical information piecemeal.

The "Suggestions for Further Reading" given at the end of most chapters are meant to assist the student who may wish to go beyond the limits of this book in exploring problems of evolutionary biology. These "Suggestions" are certainly not meant to serve as bibliographies in which a reference to an authority for every fact and name mentioned in the text may be located.

I am deeply indebted to several colleagues and friends who have read chapters of this book and suggested corrections and improvements. The greatest thanks go to Professors Ernst Mayr, of Harvard University, Charles Birch, of the University of Sydney, Australia, and A. B. da Cunha, of the University of São Paulo, Brazil, who have read the manuscript in its entirety. Chapters 1, 2, and 3 were read also by Drs. Alfred Mirsky and Stanley Gartler: Chapters 4 and 5 by Dr. M. Demerec; Chapters 6 and 7 by Dr. Phillip M. Sheppard: Chapters 6, 7, 8. and 10 by Professor H. L. Carson; Chapters 8, 10, and 12 by Professor John A. Moore; Chapter 9 by Professor P. C. Mangelsdorf; Chapter 11 by Professor Aubrey Gorbman; and Chapters 13 and 14 by Professor L. C. Dunn, Mr. Stephen Dunn, and Mr. M. D. Coe. Quite obviously, I remain solely responsible for all errors of commission and omission which doubtless will be found in the book. Mr. Stephen R. Peck has drawn many of the excellent illustrations which adorn the text. Several colleagues have contributed other illustrations and photographs, as acknowledged in the legends to these figures. Finally, thanks are due Miss Adelaide Richardson, who prepared the typescript.

TH. DOBZHANSKY

São Paulo, Brazil October, 1955

Contents

1. Nature and Origin of Life	.]
2. The Gene as the Basis of Evolution	28
3. Chromosomes as Gene Carriers	44
4. Heredity, Environment, and Mutation	72
5. Elementary Evolutionary Changes or Microevolution	91
6. Natural Selection and Adaptation	109
7. Individuals, Populations, and Races	134
8. Species	165
9 · Evolution under Domestication and Evolution by Polyploidy	191
$10 \cdot$ Evolution of the Organic Form and Function	222
11. Evolution of Sex	253
12. Historical Record of Organic Evolution	284
13. Human Evolution	319
14. Chance, Guidance, and Freedom in Evolution	357
Index	381

Nature and Origin of Life

The purpose of science is twofold. Science strives, in the first place, to understand man and the universe of which he is a part. In the second place, science endeavors to provide man with the means to control his environment. The quest for understanding is a function of theoretical, fundamental, or pure science. Knowledge and understanding are sources of satisfaction even when they do not yield any immediate material benefits. Control of the environment is a function of applied science or technology.

Understanding things, however, is the surest approach to controlling them; and the distinction between pure and applied science is, therefore, not always sharp. This distinction often describes the attitudes of mind of investigators and students rather than the subject matter of their investigations and studies. Some discoveries of greatest practical utility have been made by scientists engaged in exploration of the laws of nature without regard for their possible utilization. For instance, the germ theory of disease and much of the modern food technology are outgrowths of the studies of the great French biologist Pasteur (1822–1895) on the nature of life.

Cosmic Evolution. Discoveries made in various branches of science during the nineteenth and twentieth centuries have converged to establish an evolutionary approach to the understanding of nature. The universe has not always been as it is now. Nature as we observe it today is the outcome of a historical process of development, evolution. The human race with its social, intellectual, and artistic achievements, the world of living creatures, and inanimate nature, all evolved gradually and by stages from very different antecedents.

The classical atomist view of nature, which dominated physical sci-

ences up to the beginning of the current century, held that the basic physical and chemical properties of matter were always as they are today. Matter consists of atoms of several scores of chemical elements, and the atoms combine with each other according to certain rules which the chemists describe. All material objects in the universe consist of different combinations of atoms, but the atoms themselves were believed to be unchangeable and indivisible. The very word "atom" means indivisible in Greek.

Classical atomism was right as far as it went, but it oversimplified the actual situation. Physicists have shown that atoms consist of still smaller units-electrons, neutrons, protons. Atoms of chemical elements have been transformed in laboratory experiments into other elements. Moreover, modern cosmology, the study of the universe, assumes that the atoms which exist today have had a history. One of the theories is that the atoms were formed from a primordial substance, called the "ylem," and the inference is that they were formed in a tremendous explosion, which occurred supposedly more than 5 billion years ago. This stupendous event is, then, the first discernible date in the history of the universe and the beginning of cosmic evolution. After the formation of the atoms, cosmic evolution led to the concentration of the original cloud of atoms into galaxies. This process took a relatively "short" time, some 30 million years. The stars and planets were formed within the galaxies. Our earth came into existence presumably as one of these planets; it is, therefore, only a little "vounger" than the universe itself.

The work of geologists has shown that the earth underwent many transformations during its long history. Again and again mountain ranges rose above the plains, and were leveled back by erosion; portions of land sank beneath the seas, and sea bottoms rose to become land; the climates of many parts of the world changed from warm to cold, and vice versa.

Biological Evolution. Our earth is an insignificantly small particle of the universe, yet we cannot be sure that life exists anywhere except on this small particle. The evolution of life, biological evolution, has, to our knowledge, been enacted on earth alone. How long ago life appeared on earth, however, is a problem fraught with uncertainties. The most ancient indisputable and abundant fossil remains are estimated to be some 500 million years old. These ancient (Cambrian, see Chapter 12) fossils are remains of creatures which inhabited the seas. Because the principal types, or phyla, of the now-existing marine organisms are represented among Cambrian fossils we can sup-

pose that much evolution took place before these organisms could have appeared, and, therefore, that the origin of life took place long before then.

The extreme scarcity of the fossil record of the beginning stages of biological evolution is probably due to two causes. First, the most primitive organisms now living are too small and too delicate to be preserved as fossils, and this was most likely true in the early stages of organic evolution. Second, the geological strata older than 500 million years (and many of those younger than that) were altered by heat and by great pressures in such ways that whatever fossils had been present in them were destroyed. For all these reasons it is conjectured that life appeared on earth much earlier than 500 million vears ago. Unaltered pre-Cambrian rocks are rare, and they contain a few doubtful fossils, which some authorities interpret as seaweeds and algae but others regard as possibly formed without participation of life. Perhaps more hopeful are very ancient deposits of carbon apparently of organic origin. Holmes claimed in 1954 that one such deposit in Africa is between 2.6 and 2.7 billion years old. If confirmed, this claim will mean that organic evolution became superimposed on cosmic evolution very long ago (Table 1.1).

The first land-growing plants appeared, as shown by the fossil record, at least 400 million years ago. Land animals were added later—some 300 million years ago. The first known land-inhabiting vertebrate animals are still more recent—200 to 250 million years. Mammals, the class of animals to which man belongs, were evolved some 125 million years ago and became diversified and widespread at most 75 million years ago. Mankind is a newcomer even among mammals. The first traces of man's presence are less than one million years old, which is less than one per cent of the time span during which mammals are known to have lived.

Human Evolution and Evolution of Culture. With the appearance of man a third kind of evolution, that of the human spirit, became superimposed on the background of the biological and cosmic evolution. Of course the entry of man on the evolutionary stage did not mean that biological evolution had come to an end, no more than the origin of life meant the termination of cosmic evolution. The three kinds of evolution proceeded at the same time.

The Greek Anaximander (611–547 B.C.), the first evolutionist to leave a trace in the history of human thought, taught that life arose from mud warmed up by sun rays. Plants came first, then animals, and finally man. But, reasoned Anaximander, man could not have

TABLE 1.1

Some Approximate Dates of Cosmic, Biological, and Human Evolution

Year Ago (Approximate)	Events		
100 100–200	Publication of Darwin's Origin of Species Industrial Revolution		
300–400 1955	Life of Galileo and birth of modern science Birth of Christ		
3000	Beginning of Greek civilization		
3500 5400	Beginning of Chinese civilization Beginning of civilization in Mesopotamia		
5400 6200	Beginning of First Dynasty in Egypt Introduction of Calendar in Egypt		
15-25 thousand 20-50 thousand	Man in America Cro-Magnon man in Europe		
20-75 thousand	Old Stone Age in Europe		
500–800 thousand 75 million	First man-made tools Beginning of the Age of Mammals		
125 million 500 million	The first mammals appear Beginning of the fossil record		
2.5 billion 5 billion	Appearance of life on earth Appearance of atoms of the chemical ele-		
V PARAVAL	ments, followed by the formation of the galaxies, stars, and planets		

arisen directly from mud, since as a child he is unable to feed or to take care of himself. Hence he must have arisen from another animal. This, then, is the first statement of the view that man is biologically unique (see Chapter 13). At present we are confident that man is a product of biological evolution; his evolution was brought about by the same fundamental causes as the evolution of all other organisms. But in man the biological evolution has transcended itself. Man is able to use language symbols, to arrive at decisions by a process of abstraction and reasoning, and to distinguish between good and evil. Children inherit their biological heredity from their parents through the sex cells, but they inherit their culture by learning from other human beings, not necessarily related to them by descent. Biological heredity is set at fertilization, and it remains more or less constant thereafter (Chapter 6). Cultural heredity is acquired throughout life, but principally during childhood and youth (Chapters 13 and 14).

To develop culture, the human species had to evolve a human biological organization. No animal, not even the anthropoid apes, can

acquire the rudiments of human culture. The important thing, however, is that the biological organization which enabled man to acquire and develop culture has conferred on him, for that reason, an immense biological advantage (Chapter 13). Man adapts himself to his environment chiefly by using his technical skills, his knowledge of things, his science, art, religion, in brief his culture. Now, as indicated above, the process of transmission of culture is vastly more efficient than biological heredity, which comes only from our parents and other direct ancestors, and can be transmitted only to our offspring. By contrast, learning, art, belief, or wisdom can be transmitted by precept, by speech, or by writing, to any number of human beings, regardless of their being related by descent or not. Every one of us has "inherited" the wisdom of people whom we never met in the flesh. In many instances these people died centuries before we were born (see Chapter 13).

The rise of man from the animal level to truly human estate was slow at first. A few bone fragments of a creature which combined some human-like and some ape-like features were discovered in South Africa, together with charcoal remains. This discovery led the discoverer, Dart, to surmise that the creature was a user of fire, and to name it Australopithecus prometheus (pithecus, ape; Prometheus, the discoverer of fire). The dating of this fossil is, most unfortunately, quite uncertain; the creature may have lived half a million to more than a million years ago. Dart's interpretation of his find is regarded as doubtful.

There is, however, no doubt that at least 20,000 years ago there appeared in Europe a race of people who, judging by their bones, might have looked pretty much like ourselves. The drawings of animals which they made on the walls of the caves which they inhabited on the territory of the present France show that they possessed an exquisite artistic feeling (Figure 1.1).

The first light of recorded history dawned in the valley of the Nile, in Egypt, some sixty-two centuries ago. Within a few centuries a cultural awakening took place in several countries—in Egypt, in Mesopotamia (Iraq), in India, and somewhat later in China. Despite the numerous, and often grievous, setbacks, the development of human cultures has proceeded since then with, seemingly, accelerating tempo.

To a philosopher the cosmic, biological, and cultural evolutions are integral parts of the grand drama of Creation. A scientist, though he recognizes the unity of the evolutionary process, must perforce confine his studies within narrower bounds because the methods of in-

vestigation used by physicists, chemists, astronomers, geologists, biologists, anthropologists, sociologists, artists, and theologians are so diverse that no one person is able, at present, to use them all with equal competence. In this book our attention is focused on biological evolu-

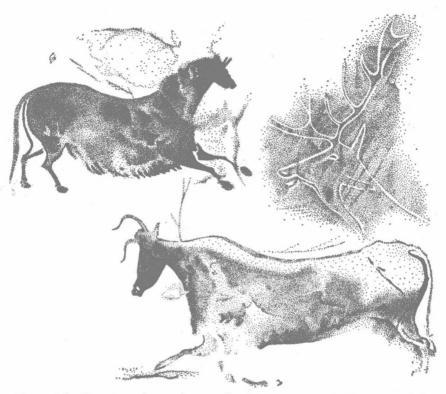


Figure 1.1. Drawings of animals on walls of Lascaux caves in France, made by man of the Old Stone Age.

tion. The relevance of the biological findings to human problems, as well as the importance of the environment in the midst of which the evolution of life is enacted, will, however, be pointed out whenever possible.

Characteristics of Living Matter. As yet nobody has offered a satisfactory formal definition of life, and we shall not attempt to produce one. For despite the lack of a definition there is usually no difficulty in deciding whether a given object is or is not living. Living beings usually possess the following combination of attributes:

A chemical composition including proteins and nucleic acids.

A definite organization.

Maintenance and growth through assimilation.

Reproduction and heredity.

Irritability and adaptation.

The living bodies consist very largely of oxygen, carbon, hydrogen, and nitrogen, that is, chemical elements which are quite common also in the inorganic nature. To those are added a number of other common elements, as shown in the following table, which indicates the percentages of the various elements in the human body:

Element	Per Cent	Element	Per Cent
Oxygen	65	Potassium	0.35
Carbon	18	Sulphur	0.25
Hydrogen	10	Sodium	0.15
Nitrogen	3	Chlorine	0.15
Calcium	2	Magnesium	0.05
Phosphorus	1	All others	0.05

Some organisms contain rather higher proportions of chemical elements which are present only as traces in the human frame. Thus the blood of many mollusks has a greenish color owing to the presence of copper, and the ascidians (a group of marine animals) contain some vanadium. But there is certainly no chemical element that would be confined to living protoplasm. Carbon comes nearest to deserving to be called "the stuff of life," because it is capable of forming innumerable complex compounds with other elements which occur in living matter. These "organic" compounds are far more characteristic of life than the elements which enter into the composition of living bodies. Proteins and nucleic acids are the two classes of such compounds which are important, because they are universally present in all life. But we cannot be entirely sure that some very different classes of chemical compounds could not produce life.

Proteins are large, and often huge, molecules, with molecular weights usually in tens or in hundreds of thousands, and often in millions. The proteins consist, in turn, of chemically linked building blocks known as amino acids. About twenty different amino acids are commonly found, all of them characterized by the presence of "amino groups" NH₂ and a carboxyl group, COOH, in their molecular makeup Their molecular weights are in hundreds. An important property of amino acids is their ability to combine in a great variety of complex

patterns such as are found in proteins. The specificity and constancy of the organization of living beings (see below) is presumed to rest on the specificity of the proteins. Enzymes, chemical substances which mediate many important chemical reactions taking place in living bodies, are among the proteins. The action of enzymes is as a rule highly specific since each enzyme mediates one and only one kind of reaction.

Nucleic acids are compounds of so-called nucleotides. A nucleotide, in turn, consists of a nitrogen-containing purine or pyrimidine base, a sugar, and a phosphoric acid. Depending on the kind of sugar involved, two types of nucleic acids can be distinguished, called, respectively, ribonucleic acids (RNA, for short) and desoxyribonucleic acids (or DNA). The DNA is invariably present in the chromosomes of the cell nucleus, whereas RNA is a characteristic constituent of the cell cytoplasm. The nucleotides are, in living cells, associated with each other to form compounds of, often, very high molecular weight. Furthermore, nucleic acids link up with proteins to form nucleoproteins. It appears that nucleoproteins are present in all existing living bodies, down to the simplest viruses.

Organization and Individuality. There is no question but that comprehension of the chemical processes which occur in living organisms is essential for an understanding of life, and that our knowledge of these processes is as yet insufficient. But we should not think of an organism as though it were simply a mixture of chemical substances. Life occurs always in discrete units, in individuals, which possess a fairly constant and usually highly complex structure or organization. From men, elephants, and whales to insects, polyps, and lowly amoebae, and from pine and oak trees to grasses, algae, and down to the simplest organisms, we can always discern the characteristic external structures (morphology), internal gross and microscopic anatomy, and the physiological properties of individuals of every species of organisms.

Inanimate objects do not usually possess definable individuality. Mountain ranges, rocks, rivers, or seas are not discrete individuals, since they do not have a cohesive structure that would be characteristic also of other individuals of a species. To be sure, crystals seem to foreshadow on the inorganic level the discreteness and the constant organization of living individuals. The shape of crystals is fixed by their chemical structure; the atoms inside a crystal are arranged in a definite pattern. Under proper conditions a crystal can grow and even restore missing parts, which makes us think of regeneration of

missing parts in lower organisms. Most crystals, however, consist of a single chemical compound, whereas organisms contain enormous numbers of substances arranged into strictly defined patterns.

Living individuals very seldom occur singly. Representatives of a species usually live in communities, members of which are related by mating and parentage bonds. Sometimes members of communities form colonies, and become so completely interdependent that it is no

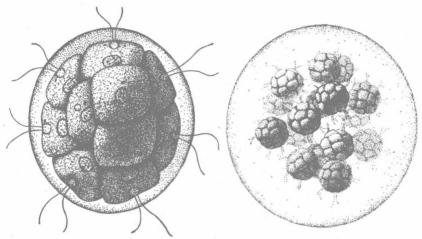


Figure 1.2. One individual or several? The microscopic alga Pandorina, several cells of which live together in a common gelatinous envelope. The drawing on the right shows each cell divided to form new groups which are about to become independent.

longer easy to delimit the constituent individuals. Thus some of the lower plants, algae, live in colonies composed of several or many cells (Figure 1.2). The whole colonies as well as the constituent cells may be referred to as "individuals." Cells are the fundamental building blocks of the bodies of all higher organisms, including man, but we have no doubt that it is the whole man, rather than each of his cells, that is the individual, since the cells of the body are incapable of independent existence (except in artificial tissue cultures). In some organisms, however, such as corals or the Portuguese man-o-war, multicellular individuals become again associated into colonies and lose their independence to such an extent that it becomes reasonable to regard the colonies as individual units (Figure 1.3). It is obvious that individuality is not an all-or-none affair but a matter of degree.

Self-reproduction. A human being begins his existence when a spermatozoon fertilizes an egg cell (Figure 1.4). A fertilized human egg cell is just large enough to be visible to a naked eye. Its weight is estimated as about one twenty-millionth of an ounce (slightly more

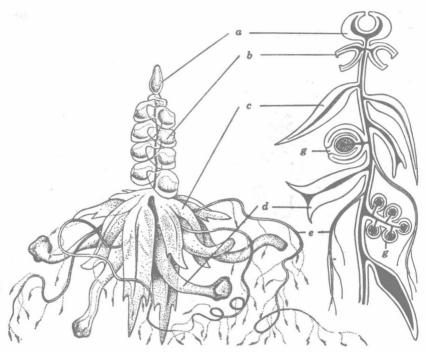


Figure 1.3. A siphonophore, a colonial marine animal consisting of several different kinds of individuals specialized to perform different functions. The appearance of the colony is shown on the left, and a scheme of its structure on the right. The individual which functions to make the colony float vertically in water is marked a; b, individuals which act as swimming bells; c, protective "leaves"; d, gasterozoids which ingest food; e, tentacle; g, gonophor or sexual individual.

than one millionth of a gram). Starting from this insignificant bit of matter, the body grows until it attains the adult size and weight of, say, 150 to 160 pounds. This is, then, an approximately fifty-billion-fold increase.

What is the source of material for this stupendous growth? Clearly, it is the food consumed—first by the mother in whose body the embryo coming from the fertilized egg develops, and then by the growing individual himself. Now food is derived ultimately from the