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Introduction to Evolution

Introduction to Evolution

THIRD EDITION

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INTRODUCTION TO EVOLUTION, THIRD EDITION

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To My Wife Judith
without whose cooperative silence
this book could not have been written

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Preface to the Third Edition

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ORGANIC EVOLUTION is the greatest general principle in biology. Its implications extend far beyond the confines of that science, ramifying into all phases of human life and activity. Accordingly, an understanding of evolution should be part of the intellectual equipment of all educated persons.

Like the first two editions of *Introduction to Evolution* this edition is intended to form an *introduction* to organic evolution for readers unacquainted with the subject. I have tried to make it understandable for students who have little or no background in biology, geology, and other cognate fields. At the same time, I have attempted to be sufficiently comprehensive in my discussions so that more advanced students will find the book useful, especially in aspects of evolution outside their own fields of specialization. To this end I have included in the bibliographies at the ends of the chapters references that will enable students to explore the subject matter of the chapter more extensively than beginning students may wish to do.

As with the first two editions, this edition stresses the *facts* of evolution—as revealed by anatomy, embryology, the geologic record, geographic distribution, and so on. These discussions have been brought up to date, with extensive rewriting to keep abreast of changing concepts and new research. Beyond revision of the older discussions, two of the principal changes in this edition are the addition of discussions of (1) evolutionary implications of modern research in the rapidly expanding field of molecular biology, particularly of comparative studies of DNA and of protein structure, and (2) modern theories of the origin of life on the earth, together with supporting evidence.

Several chapters are devoted to a discussion of theories of *how* evolution occurs—the operative forces and factors. These chapters also have been extensively rewritten. The contributions of genetics and population genetics are introduced in such a manner that readers with little background in genetics and mathematics can follow the thinking. In a book of this size, which emphasizes the facts of evolution, it is impossible to present these theories at full length, but the present discussion should prove sufficient for most needs of students using the book. Each instructor will supplement the text material in his lectures as he thinks best, of course. Frequent references to more extensive discussions will enable students to find additional details and points of view.

In a very real sense it is impossible to acknowledge adequately the assistance given by others in the preparation of this book. I am indebted to countless scientists both known and unknown to me. My gratitude continues to the many persons who made substantial contributions to the first two editions. In the preparation of the third edition I gratefully acknowledge the assistance of Henry S. Horn and Albert E. Wood, who read the entire manuscript; of Morris Goodman and Alexander S. Wiener, who read portions of it; and of Leigh Van Valen, who offered many helpful suggestions after critically reading the second edition. While these people have contributed greatly to the merits of the book, of course they are entirely without responsibility for any deficiencies it may have.

Many people have contributed to the illustrations in the book. It is a pleasure to acknowledge my continued indebtedness to Louise F. Bush, who made a large proportion of the drawings.

Authors and publishers have been most generous in permitting me to borrow illustrations. The legend for each borrowed figure credits the source, but I should like to list the individuals who responded to my request for original drawings and photographs: L. W. Erbe, Sidney W. Fox, Glenn L. Jepsen, H. B. D. Kettlewell, and Lyman S. Rowell.

Finally, it is a pleasure to express my gratitude to my efficient typists, Jeannette Brown and Jeanne O'Connor.

Paul A. Moody

Burlington, Vermont

Introduction to Evolution

1

Evolution as Seen in Perspective

ORGANIC EVOLUTION By the term "evolution" we mean the sort of change for which we commonly use the word "development." We speak of the evolution of the solar system, the evolution of the earth, the evolution of the airplane, and the evolution of the automobile. In such cases we are referring to the changes that have occurred in solar system, earth, airplane, or automobile.

The evolution with which this book is concerned involves a special form of the broader meaning of the term: ORGANIC EVOLUTION. This subdivision of evolution deals with changes undergone by living things, plants and animals. For our purposes we may define organic evolution as the theory that plants and animals now living are the modified descendants of somewhat different plants and animals that lived in times past. These ancestors, in their turn, are thought of as being the descendants of predecessors that differed from them, and so on, step by step, back to a beginning shrouded in mystery.

In the preceding statement the words "modified descendants" deserve special emphasis. The word "modified" refers to the element of change that we have just mentioned as inherent in the whole idea of evolution. The word "descendants" introduces an idea not present in the broader use of the term "evolution." When we speak of the evolution of the automobile we make reference to the changes occurring in the transition from the "horseless carriage" of a bygone era to the model currently advertised. We do not think of the older automobiles as being the parents or ancestors of the newer ones in any literal sense. Makers of automobiles learn from the experience gained with older models how to improve and modify their products so that later models are different from, and on the whole better than, earlier ones. But the later models are not literally the offspring of the earlier ones. Contrariwise, it is exactly this ancestor–descendant relationship that is visualized in the term "organic evolution." Later animals are thought of as the direct genetic descendants of somewhat differing ancestors that formerly lived on the earth.

The reader will have noted that the definition of organic evolution just given differs from the popular concept of the meaning of evolution. If the proverbial "man in the street" is asked the meaning of the word, he is likely to reply, "Man came from monkeys." This exclusive preoccupation with man is perhaps natural in a person little acquainted with, or interested in, the remainder of the living world. To a biologist the evolution of man is but one portion of the vast drama of evolutionary change including all living things. Each animal alive today is the product of long evolutionary history.

Another shortcoming of the man in the street's definition lies in the fact that he pictures one modern form as descended from another modern form. Man and monkey are contemporaries, both products of long evolution. It is as incongruous to speak of one as the descendant of the other as it would be to speak of one member of the sophomore class in college as the descendant of another member of that class. What, then, is the evolutionary interpretation of the relationship existing between monkey and man? Rather than being a father-to-son relationship, it is more comparable to a cousin-to-cousin relationship. You and your cousin have a pair of grandparents in common. Modern man and modern monkey are thought of as having shared a common ancestor in the distant past. From this common ancestor both inherited some characteristics in which they still resemble each other. Was this common ancestor a man or a monkey? He was neither. He was a form that had the potentiality to give rise to a monkey, on the one hand, or to give rise to a man, on the other. There is no evidence that any of the modern animals we know as monkeys have that potentiality.

BEGINNINGS OF THE EVOLUTION IDEA Many people seem to think that the whole idea of evolution started with a man named Darwin. This belief probably arose from the fact that Darwin's great book, *The Origin of Species*, published in 1859, was the first widely read book on evolution published in English. This classic in our field had two main objectives: to convince people that evolution is indeed a fact and to present evidence in support of Darwin's theory of the means by which evolutionary change occurs. This theory is called "natural selection"; it represents Darwin's special contribution to evolutionary thought. The fundamental concepts of natural selection are presented in Chapter 2 and are further elaborated in Chapters 19–21.

Ideas that by one means or another evolution does occur far antedated Darwin, however. In fact, such ideas are probably as old as human thought. As soon as man had attained sufficient intellect to observe the similarities and differences among the animals and plants surrounding him and to speculate about them, he undoubtedly began to form crude ideas of evolution. Certain it is that by the time he had learned to record his thoughts so that posterity might read them, concepts of evolution were present in his mind. Not that these early concepts correspond in detail with our modern ideas of evolution—far from it. They were highly speculative, frequently colored with mythology, and represented at their best what we might think of as "good guesses," since in part they were subsequently proved correct. But in them we see, though dimly, the outlines of the idea that the living world is one and that living things change, giving rise to new forms.

The ancient Greek philosophers afford evidence of these early gropings for an explanation of the earth and its inhabitants. Space forbids mention of more than a few of these pioneers in human thought. One was ANAXIMANDER, whose adult life spanned the first half of the sixth century B.C. According to Anaximander, men were first formed as fishes; eventually they cast off their fish skins and took up life on dry land. Here we have one of those "good guesses." As will be evident after perusal of Chapter 9, modern evidence supports the view that a distant ancestor of man was indeed a fish. How much credit should be accorded Anaximander for speculations which proved to contain this kernel of truth?

XENOPHANES was in part a contemporary of Anaximander, although he lived on into the fifth century B.C. Xenophanes is credited with being the first person to recognize that fossils, such as petrified shells embedded in rocks, represent the remains of animals that once lived. Today we take the idea for granted, but that fact should not lessen our appreciation of the insight shown by the first person to grasp it. Truth is "obvious" only after its discovery. Xenophanes also realized that the presence of fossils of marine animals on what is now dry land indicates that the ocean once covered the area.

The fifth century B.C. also saw the man who has been hailed by Osborn (1896) as "the father of the Evolution idea": EMPEDOCLES. According to this philosopher, plants arose out of the earth, as subsequently did animals. Animals arose as unattached organs and parts that joined together in haphazard fashion. Most of these conglomerations were freaks and monsters incapable of living, but occasionally a combination of organs appeared which could function as a successful living organism. Such successful combinations survived and populated the earth, while the incongruous assemblages died. It is possible to see in this account the first glimmerings of the idea of the survival of the fittest, an idea which formed such an important part of Darwin's theory of natural selection 23 centuries later. But the danger is great of "reading into" such ancient writings ideas that were not actually in the mind of the author. Empedocles included man among the beings formed in the manner described.

The fourth century B.C. is memorable for the life and work of ARISTOTLE, well termed by Locy (1925) "the greatest investigator of antiquity." Best known to us as a philosopher, Aristotle possessed far more of the spirit of scientific research than did his predecessors or most of his successors for centuries to come. Thus, within the limits of the materials and methods available to him he carried on investigations in such diverse fields as marine biology, anatomy, embryology, and the metamorphosis of insects. Although the accuracy of his scientific observation excites our admiration, we find less to admire in his speculations concerning evolution. There he failed to follow the ideal which he himself propounded: "We must not accept a general principle from logic only, but must prove its application to each fact; for it is in facts that we must seek principles, and these must always accord with facts." Yet our censure must be temperate, since the store of "facts" available to Aristotle was totally inadequate as a foundation for the activity of his towering intellect.

We shall confine our attention to one contribution made by Aristotle to evolutionary thinking: He maintained that there is complete gradation in nature. The lowest stage is the inorganic. Organic beings arose from the inorganic by direct metamorphosis. He conceived the organic world to consist of three states: (1) plants; (2) plant-animals, a transitional group in which he included sponges and sea anemones; and (3) animals, characterized by feeling or sensibility. Within the animal group he constructed a genetic series leading from the lowest forms up to man, placed at the apex. Hence, we may think of Aristotle as the father of those "family trees" that have been so conspicuous in writings on evolution ever since. It is to be noted, however, that his tree had no branches; it was a straight line from polyps to man. Nor did his tree contain any prehistoric animals. Unlike Xenophanes, Aristotle failed to appreciate the true significance of fossils. More accurate diagrams of relationship were far in the future. The first tree of life to possess branches and to be influenced by appreciation of the importance of fossils was published by Chevalier de Lamarck in 1809 (in his *Philosophie Zoologique*).

One is tempted to remark at this point that thinking on evolution stood still during the more than 2000 years that separated Aristotle from Lamarck. Such a statement would be extreme, yet true in the main. In this long interim what of real significance for evolution was occurring? During this time science, in the modern meaning of the term, came into existence and developed. Little by little that body of facts accumulated which, as we have seen, Aristotle recognized as the essential basis for the formulation of general principles. Without such a foundation thinking on evolution would have remained forever mere speculation. Accordingly, we can recognize the importance to evolution of developments occurring during these 20 centuries, while at the same time realizing that we lose but little when we omit a discussion of evolutionary ideas prevalent during that time. The foundations were not ready to receive the superstructure until the nineteenth century A.D.

No complete survey of the history of evolutionary thought is possible within the confines of this volume. Interested readers are referred to books listed at the end of this chapter. The present aim has been to demonstrate that thinking about evolution is as old as human thought and to mention a few of the first contributions to the subject. The theory proposed by Lamarck is discussed briefly in Chapter 17. Darwin's contributions are referred to repeatedly throughout the book (e.g., pp. 406–414).

EVOLUTION AND THE CHURCH The idea of evolution shares with various other scientific advances, such as the idea that the earth revolves, the distinction of having been opposed in times past by religious leaders. The latter were, of course, primarily interested in the application of evolution to man, or rather in making certain that evolution did not apply to man. It was felt that in some way man was degraded if one admitted any connection between him and the lower animals. Admittedly, also, the story of man's origin through evolution does not agree in detail with the story of his origin through special creation as contained in the first chapters of Genesis. Wise churchmen like St. Augustine and St. Thomas Aquinas early recognized that these chapters, while expressing important religious truths concerning the Creator, should not be regarded as literal history. Unfortunately, both for religion and for science, the leadership of these men was little followed.

The controversy that climaxed after the appearance of Darwin's *Origin of Species* has now largely subsided. For the most part the churches recognize evolution as the means by which the Creator works. Some portions of Protestant denominations, commonly called "fundamentalist," still deny the truth of evolution. There are fundamentalists in the Roman Catholic Church also, but that church does not officially oppose evolution, even of man, so long as no attempt is made to explain the origin of the human soul by this means. This is a restriction readily accepted by the present author since in his opinion the soul does not come within the province of science (p. 227). Readers interested in the relationship of evolutionary thinking to religion are referred to Chapter 22.

PLAN OF THE BOOK Evolution manifests itself in varied aspects of the living world—in structure, in chemical composition, in the nature of life processes (metabolism), in embryonic development, in the chemical nature of blood, in the manner in which animals are distributed over the earth and adapted to differing environments, in the classification of animals, and in the remains of prehistoric animals preserved to us as fossils. In the next chapter we shall summarize some ideas of the nature and causes of evolutionary change, ideas which will be of use to us in understanding the varied manifestations of evolution. Then the factual contributions to the study of evolution made by various fields of biology are considered. Finally, Chapters 17–21, we shall discuss in more detail the means by which evolutionary change occurs.

References and Suggested Readings

Darwin, C., *On The Origin of Species by Means of Natural Selection*, London, John Murray, 1859. (Facsimile of this 1st ed. published in paperback, No. 106, Atheneum, New York, 1967. The more commonly reprinted 6th ed. available in various reprints, e.g., Modern Library, Random House, New York; Mentor, No. MT294, New American Library, New York; Collier, No. HS34, Crowell-Collier, New York.)

Locy, W. A., *Biology and Its Makers,* New York, Holt, Rinehart & Winston, 1915.

Locy, W. A., *Growth of Biology,* New York, Holt, Rinehart & Winston, 1925.

Nordenskiöld, E., *The History of Biology,* New York, Alfred A. Knopf, 1928.

Osborn, H. F., *From the Greeks to Darwin,* 2nd ed., New York, Macmillan, 1896.

2

Changing Animals

THE FACT OF CHANGE We mentioned (p. 1) that organic evolution deals with changes undergone by living things, plants and animals. Some readers who are not used to thinking of these matters may feel that we are making an unwarranted assumption when we speak of animals *changing*. The fact that they do change has by no means always been recognized. Indeed, until quite recently in the history of human thought most people believed that the animals living today were created as they now are, once and for all, as recorded in the first chapters of Genesis. This belief was championed by many eminent scientists of former times. Among these was Carolus Linnaeus, the eighteenth-century Swedish naturalist who founded the system of classification still used (see Chap. 15). Linnaeus assigned scientific names to great numbers of plant and animal species and genera. He believed that these species were for the most part the ones created as described in Genesis. As his knowledge expanded, however, he modified this view to the extent of conceding that new species might arise through hybridization (cross mating) between the original species. In view of this widespread belief in the fixity of species, how is it that we now speak of animals as changing? In other words, what makes us think that the kinds of animals living today are not the kinds of animals that have "always" existed?

The direct evidence on the question just raised comes from the "record of the rocks"—from the remains of animals that formerly lived but are now known to us only as fossils. In fairness to Linnaeus we should recall that almost nothing was known about fossils in his day. As we shall see in Chapters 8–12, this geologic record demonstrates that hosts of animals not present in the modern world formerly lived. What became of them, and what was their relationship to modern animals? According to one point of view, formerly widely held, they became extinct, leaving no descendants. Perhaps widespread calamities (such as floods) effected the wholesale removal of these ancient animals. And perhaps they were then replaced either by new animals especially created for the purpose or by animals that migrated in from regions of the earth untouched by the catastrophe in question. This THEORY OF CATASTROPHISM was prevalent among biologists of past centuries. The eminent French biologist Baron Georges Cuvier, whose life spanned the close of the eighteenth century and the first part of the nineteenth, was one of its most powerful exponents.

We note that according to the theory of catastrophism the "new" animals inhabiting a given region after a catastrophe would not be the descendants of the "old" animals formerly found in the region. They would be fresh creations, created either in the region in question or elsewhere. This idea stands in direct contrast to the idea of organic evolution, which holds that the "new" animals are modified descendants of certain of the differing animals that formerly existed, in that region or some other. Not that *all* the old animals left modified descendants—far from it. Evidence indicates that only a small minority did; the rest became extinct without issue.

THE CHANGING WORLD Returning to our original question concerning the fact of changes in animals, we may note that we should expect such change even if the geologic record did not afford a direct testimony of it. It is a truism that change is the only unchanging aspect of our world. So far as we can judge this has always been true. The physical world has undergone great changes. Periods of glacial cold have alternated with periods of tropic heat. The floors of shallow seas have been elevated to form lofty mountain ranges, and the latter in turn have been worn down to low hills and plains and perhaps eventually covered by the sea once more. Aquatic environments, the home of great proportions of the animal kingdom, have undergone continual change. The oceans have changed the least, yet even here changes have occurred, for example, in temperature and in salinity. The oceans have also fluctuated greatly in depth, particularly along the margins of continents. Elevation and subsidence of areas of the earth's crust have been involved in this fluctuation as has, during glacial periods, the locking up of vast quantities of the earth's water supply in polar icecaps and their extensions equatorward. The environments of freshwater animals have been even more subject to change. Rivers and lakes are notably short-lived, changing features of the landscape. Terrestrial environments are most variable of all. As a rule terrestrial animals face great fluctuations in temperature, humidity, and other environmental factors, even changes between night and day or summer and winter.

What have such changes in the external world to do with changes in animals themselves? Simply this: If a species of animal is to succeed it must at all times be *adapted* to its environment. If the environment changes, as we have seen that it does repeatedly, the species must either adjust to that environmental change or die. The geologic record is full of examples of animals that did not adjust to changed conditions and hence became extinct.

We may well note at this point that change in one species will inevitably lead to changes in other species. Change in the organic environment of an animal may be at least as important as change in its physical environment. For example, an animal may become adapted to a diet consisting of a certain plant, as the koala (the marsupial "teddy bear") is dependent upon a diet of eucalyptus leaves. If the climate changes so that the plant can no longer exist in the region, the animal either must change its food habits or become extinct in that region. If it becomes extinct, that fact will affect the fate of flesh-eating animals (predators and parasites) that had been dependent upon the plant eater as part of their food supply. And changes in numbers of predators will affect the numbers of other species of plant eaters preyed upon. So one change sets off a whole series of other changes.

Thus we see that changes in the physical environment and changes in the organic environment make change in a species inevitable if it is to continue inhabiting this changing world. As we have intimated, these changes must *adapt* the species to live under the conditions in which it finds itself or, alternatively, to live under some conditions available to it, by migration perhaps. In the following chapters we shall see examples of such adaptations in modern animals. Despite changes necessitated by the requirements of life under particular conditions, species retain basic similarities of structure that can best be explained as indications of their ancestry. Both the adaptive changes and the basic similarities are important to the study of evolution.

CHANGING GENES We noted that the geologic record gives testimony that animals do change and that the demands of living in a changing world ensure that animals must change. We may now note that animals possess within themselves the seeds of their own changes. Nearly everyone has at least heard of the units of heredity called GENES. These submicroscopic structures are found in the nuclei of the myriads of cells composing our bodies and the bodies of other animals and plants. Genes are concerned in the determination of what an individual's characteristics shall be, and they form the principal hereditary link between one generation and the next. To a very large extent the characteristics of an offspring are determined by the genes he receives from his parents: from his mother through the egg or ovum and from his father through the sperm cell that fertilizes that ovum. The point we wish to emphasize here is that genes are not unchanging units; they undergo changes called MUTATIONS. When a gene mutates, the result is a gene that conditions production of a changed characteristic. For example, if the gene originally participated in production of brown eye color, the mutated gene might fail to play its role in formation of brown pigment; the eye would be a color other than brown. The matter of mutation will be referred to in other connections later (pp. 416–422); at present we merely wish to point out that it provides animals with a means by which change can occur and, indeed, inevitably will occur, since mutations arise spontaneously at a fairly constant, though slow, rate.

CHANGES IN ANIMALS AND THE MECHANISMS OF EVOLUTION We may appropriately inquire at this point: What happens to inheritable changes (mutations) after they appear? In later Chapters 15–21 we shall discuss the nature of mutations and of the forces that play upon them. In the present connection it is sufficient to state a few general principles that will be useful in the following discussion of the varied manifestations of evolution.

NATURAL SELECTION Much of our thinking on the causes of evolutionary change has its roots in Darwin's great book, *The Origin*

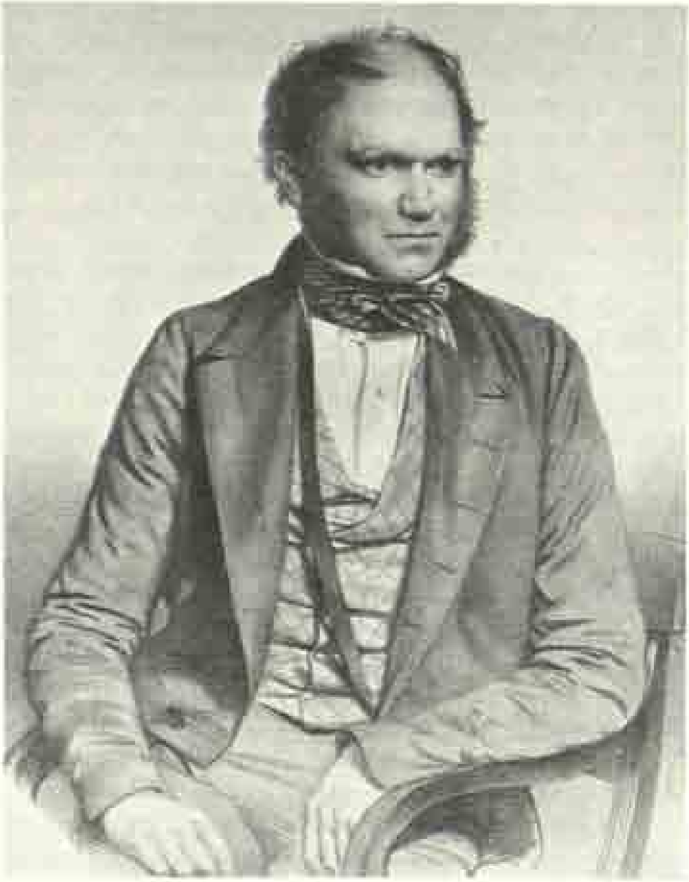


Fig. 2.1. Charles R. Darwin at the age of 40. (Courtesy of the Smithsonian Institution, and of *Science*, *130* (1959), No. 3387, p. 1451.)

of Species by Means of Natural Selection. Charles Darwin (Fig. 2.1) was born on the same day as was Abraham Lincoln, February 12, 1809. He developed his theory as a result of observations made on a five-year voyage around the world. Immediately after graduation from Cambridge University he was appointed naturalist on the sailing vessel *H.M.S. Beagle*, about to depart on a surveying voyage. Most of his time was spent along the coast of South America. Observations on this continent and on neighboring islands (e.g., Galapagos, pp. 299–310) profoundly influenced Darwin's thinking. We shall refer to some of his observations when in later chapters we discuss the manifestations of evolution. Many readers will be interested in Darwin's own account of the voyage (Darwin, 1845), as well as in biographies of Darwin (e.g., de Beer, 1963; Irvine, 1955).

Darwin introduced the term NATURAL SELECTION to convey the idea that nature exercises selection somewhat as an animal breeder does when he wishes to improve a stock of domestic animals. The breeder selects as parents of the next generation those individuals possessing qualities he wishes his stock to have. At the same time he prevents the reproduction of individuals that lack the desired qualities. Thus selection by breeders (artificial selection) has two aspects, one positive and the other negative. Similarly, natural selection is both positive and negative in its working.

Directing attention first to the negative aspect, we can readily understand that if a bodily change is harmful, so that possessors of it are not so well adapted to life as they would have been without it, the change will be a handicap. Possessors of such a handicap may not live to maturity or if they do live they may not reproduce or if they do reproduce they may not produce as large a proportion of the next generation as do their unhandicapped brethren. As a result the harmful change will tend to disappear in subsequent generations.

This negative aspect of natural selection is important to animals as a conservative or stabilizing force, ensuring that undesirable changes are weeded out and discarded from the species. Negative selection helps to keep the species always at its "adaptive peak" by preventing establishment of changes that would lessen perfection of adaptation to the environment in which the species lives. Negative selection is a preserver of the status quo; it is constructive insofar as deviations from the established norm would be detrimental to the species. But real progress is seldom achieved by enforcing conformity to established patterns. Accordingly we look to the positive aspect of natural selection for the means of progressive change.

If we say that a bodily change is beneficial to its possessors, we mean that the latter will have an advantage over their fellows who lack the change. If conditions are such that competition is keen, this advantage may be sufficient to make a difference in ability to survive or to produce offspring or both. If it is, possessors of the change will produce more than "their share" of offspring. If these offspring inherit the change, the result will be that among them will occur a greater proportion of individuals possessing the change than possessed it in the parental generation. Let us suppose, for example, that under a certain set of circumstances it is beneficial to an animal to have long legs, the better to run away from enemies. If some members of the species have longer legs (the result of mutation or recombination, p. 11) than do others, the longer-legged individuals may survive the ravages of their enemies better than do the shorter-legged members. There will be a tendency for the long-legged individuals to live long enough to become parents and hence to produce a larger proportion of the next generation than do their shorter-legged fellows. As a result, long legs will be possessed by larger numbers of the second generation than possessed them in the first. If this same trend continues for several or many generations, eventually the whole population may come to possess the beneficial change. This, in simplified, nontechnical terms, is the central idea of the positive aspect of natural selection. More complete statements, with a discussion of the forces operative, are found in the closing chapters of this book (pp. 406–488). The central idea, however, will be found most useful in interpreting the manifestations of evolution discussed in the chapters immediately following this one.

We note that positive natural selection resembles positive artificial selection in that in both instances individuals possessing some special attribute are favored to become parents of the next generation. In artificial selection the favored individuals are the ones possessing some quality desired by the breeder. In natural selection the favored individuals are the ones possessing some quality that renders them better adapted than their fellows for life under the circumstances in which they find themselves. In both instances the desirable quality or change will be likely to be of more frequent occurrence in the next generation than it was in the former.

POSTADAPTATION AND PREADAPTATION Our discussion so far has emphasized more and more perfect adaptation to a stable environment in which the species is already living. This type of adaptation is called POSTADAPTATION, since the species has already entered the environment, and additional adaptation merely perfects the animal for living under the conditions prevailing. Much evolutionary change is of this nature.

On the other hand, a bodily change may or may not be of value in the environment in which the species is living but would be beneficial in some other environment. If possessors of this change can reach that other environment, they may thrive there, with the result that the change may increase in frequency as generations pass in the new environment. Eventually the change may characterize all inhabitants of the new environment, becoming for this population "standard equipment." This phenomenon of a change that, though it may not be beneficial in the original environment, fits an animal to invade another environment is called PREADAPTATION or PROSPECTIVE ADAPTATION (Simpson, 1953).

Sometimes the change in question may be useful in the original environment and yet be of such a nature that it preadapts its possessor for life in another environment. Crossopterygian fishes (pp. 167–169), for example, had a fin adapted for locomotion in the water, yet the fin had within it a skeleton that could be made over to form a limb for locomotion on land. Thus we say that the skeleton of the crossopterygian fin (Fig. 9.18, p. 168) was preadaptive for life on land.

Apparently preadaptation has played an important role in progressive evolution, by which we mean the production of radical changes in animals, as contrasted with the perfecting of adaptation to the environment in which the animal is already living. To be sure, the perfecting of the adaptation of a species to its environment is in a sense progressive. Yet such a process, useful as it is, does not usually lead to radical change in structure. It is one thing for a fish to become more and more perfectly adapted for life in the water and quite another thing for it to climb out of the water and enter the new environment of air. Fishes (i.e., the Crossopterygii) possessing structures preadapted for life on land could make the change; other fishes did not.

MEETING ENVIRONMENTAL CHANGES Consideration of preadaptation has introduced a new factor into our discussion, that of change in the environment. In earlier pages of this chapter we noted that environmental change has occurred repeatedly throughout the history of the earth. How do species of animals meet such changes?

In the first place, species frequently meet changed conditions by succumbing to them—by becoming extinct. Such extinction of a species or type of animal may be worldwide or it may involve only certain regions of the earth. Thus, for example, at the close of the Mesozoic era the dinosaurs became extinct throughout the earth. On the other hand, in much later times the camels, formerly inhabitants of North America, became extinct on that continent while remaining existent in Asia, Africa, and South America (e.g., llama) (Fig. 13.5, p. 284).

Another manner in which animals may meet change in their environment is by being sufficiently adaptable or versatile so that they can live under a great variety of conditions. While this seems not to have been a very common solution of the problem, various examples come to mind. The rats and mice that dwell with us in our houses as unwelcome guests originated in Asia but are so adaptable to all manner of conditions that they have become practically worldwide in distribution. Apparently cockroaches, which have survived virtually unchanged all the vicissitudes of the earth since the days before the great coal deposits were formed, owe their vast lease on life to a similar ability to adapt to whatever may befall them. Other examples might be cited, but we may content ourselves by mentioning that man himself, thanks to employment of his intelligence, is the supreme example of ability to live under widely diverse conditions.

A third way in which animals may meet changes in environment is by undergoing changes themselves. This is the commonest method of solving the problem by species that do succeed in solving it. In Chapter 17 we shall discuss a theory that changes in the environment directly produce or call forth appropriate corresponding changes in animals—the theory of the inheritance of acquired characters. Since, as we shall see, there is little positive evidence that this phenomenon does occur, we shall concentrate attention here upon MUTATIONS as a source of bodily change in animals. As we shall see later, there are other sources of genetic variability than mutations. But in order to present the principles of natural selection as simply as possible we shall concentrate on mutations in our present discussion.

As noted before, mutations are changes in genes that result in changes in the bodies of animals possessing the changed genes in appropriate proportion (see pp. 371–378). Mutations occur at random, without regard to the needs of the individuals in which they occur. If the mutations are harmful in their effect, they will be eliminated by the negative action of natural selection discussed above. However, if the mutations are beneficial, they will be preserved, and the number of individuals possessing them will be increased in subsequent generations by the positive action of natural selection. Experiments showing that natural selection actually does operate as we postulate are briefly discussed in Chapter 20. Positive selection of beneficial mutations may lead to more perfect adaptation to an existing environment or, alternatively, to adaptation to new conditions when the environment changes.

We have seen that when the environment changes a species may become extinct. Sometimes, however, though most of the members of a species may fail to survive, a few members, usually the possessors of changes (mutations) adapting them to the new conditions, will survive. The surviving few then become the progenitors of future generations that inherit the changed condition, permitting life in the changed environent.

If a species becomes extinct, the result is an ENVIRONMENTAL NICHE—a possible place and means of livelihood—left vacant. There may be in the vicinity, however, some other species possessed of structures that preadapt it for life in the vacant niche. For such a species the disappearance of the former species would be the opening of a door to opportunity. Sometimes the environmental niche remains vacant for a long time before a species appears that is adapted to occupy it. Thus

Simpson (1953) has pointed out that the niche left vacant by the extinction of ichthyosaurs (reptiles, contemporaries of the dinosaurs having highly fishlike body form; Fig. 3.5, p. 30) was unoccupied until the advent of dolphins and porpoises 30 or more millions of years later.

Accordingly we see that possession of bodily changes, the result of fortunate mutations, may enable animals to meet changing environments in one of two ways: (1) In some cases possessors of changes among members of the species already present in the environment may be enabled to survive while their fellows cannot. (2) In other cases the species already present in the environment may become extinct, but other species possessing structures that preadapt them to life in the niche left vacant may be enabled to move in and occupy that niche.

A specific example may help to make clear the application of the general principles we have been discussing. We have already referred to the fact that the crossopterygian fishes gave rise to the first land vertebrates, the amphibians. This was one of the greatest changes to occur in the evolution of vertebrates. More information concerning it is found in Chapter 9. This change occurred near the end of the period of geologic time known as the Devonian (p. 146). Prior to that time all vertebrates had been water dwellers. Hence the dry land environment was an unoccupied environmental niche as far as vertebrates were concerned. As nearly as we can picture it from our great distance in time, the course of events ran somewhat as follows.

During the dry seasons some ponds probably dried up completely while others were reduced to stagnant pools of foul water, overcrowded with fishes. Under such conditions most fishes must have died, as they do when similar conditions arise today. But among the fishes in those Devonian ponds were some that were preadapted for invasion of the unoccupied environmental niche just across the water line. These were the crossopterygian fishes. Two of their most striking preadaptations were (1) the skeletal structure of the fins, providing raw material for a limb that could support the body and accomplish locomotion even when the body was no longer buoyed up by surrounding water (Fig. 2.2), and (2) an air bladder connected to the pharynx and capable of being used as a simple lung for respiration in the air.

We may picture some of these crossopterygian fishes as making use of their preadaptations to crawl from their fetid pools, probably at first in search of fresher and less crowded ones (Romer, 1959). Presumably the first overland excursions were brief. And probably very few of the crossopterygian fishes succeeded in making even this much departure from ancestral habits. Pioneering is seldom a mass phe-

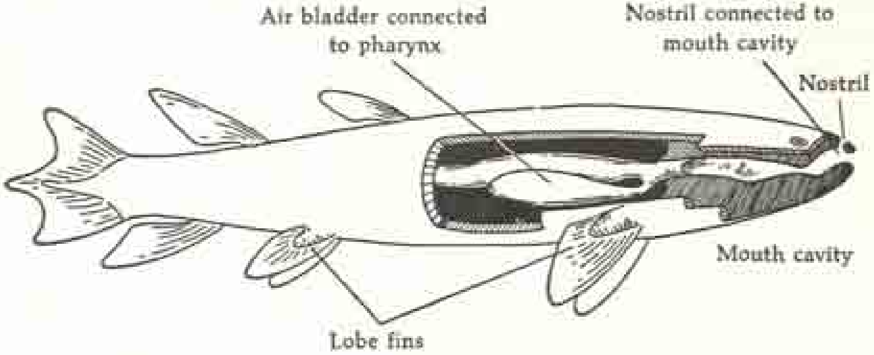

Air bladder connected to pharynx
Nostril connected to mouth cavity
Nostril
Mouth cavity
Lobe fins

Fig. 2.2. Diagram of crossopterygian fish dissected to show three ways in which it was preadapted for life on land.

nomenon. Eventually, however, there must have arisen small populations of crossopterygian descendants increasingly emancipated from life in the water and finally making use of it only as a place to spawn and lay their eggs, as most amphibians do to this day. The earliest descendants (labyrinthodonts, p. 169) seem to have been fish eaters. This increasing emancipation from life in the water would be accomplished by that postadaptation of which we have spoken. The principal mechanism involved in the change from water to air was doubtless the positive aspect of natural selection—the favoring of individuals possessing changes (arisen through mutation) that more adequately fitted them for life on land than their fellows.

"MANY ARE CALLED BUT FEW ARE CHOSEN" We have stressed the point that the numbers of individuals involved in making the dramatic change from water to air were probably small. The great bulk of fishes, even of the crossopyterygian fishes, stayed in the water, living and dying as might be determined by stringency of conditions confronting them. A few were the pioneers into the new environment outside the water.

As Simpson (1953) especially has pointed out, rates of evolutionary change vary greatly, from animal to animal and from time to time. We may be sure that the "chosen few" among crossopterygian descendants in the Devonian were in a highly unstable condition as regards adaptation. At first they must have been barely able to meet requirements of life in the new environment: life must have been a "nip and tuck" affair. Under such precarious conditions any slight improvement might have made an important contribution to survival and hence have been favored by natural selection. This fact, together with the small numbers of individuals involved, would have been conducive to rapid evolution.

(The influence of numbers upon rates of evolutionary change is discussed in Chapters 18, 19, and 21.) Consequently, the shift from water to land probably occurred quickly, in terms of geologic time, though millions of years were involved.

One reason for mentioning here the small numbers of transitional forms and the brief span of the world's history in which they lived is to point out that these facts may explain in some measure why we seldom find fossils of actual transitional forms between one major group of animals (such as fishes) and another major group (such as amphibians). Transitional forms are so seldom found, in fact, that one school of thought claims that they never existed and that one group arose from another by one sudden change ("systemic mutation" of Goldschmidt, 1940). This idea has been expressed by the striking statement: "The first bird hatched from a reptile's egg." It seems more likely, however, that Simpson is correct in postulating that transitional forms did occur but that they were so relatively few in number and occurred during such a brief interval of geologic time that chances of finding fossils of them are small. Moreover, in the following chapters we shall note examples of transitional forms whose fossils *have* been discovered. Chapter 8 presents additional information concerning reasons why the geologic record is incomplete.

POTENTIALITY PLUS OPPORTUNITY We may appropriately mention at this point an erroneous idea prevalent among many people who know little about evolution. This is the notion that if evolution is a fact all animals must be constantly tending to become "higher" animals or, in its most exaggerated form, that all animals must be tending to become man. One sometimes hears the argument that evolution cannot be a fact because if it were there would be no "lower" animals left—they would have all become men long since! Thoughtful consideration of the foregoing discussion will demonstrate the fallacy of such an idea. We have seen that animals are constantly tending to become *adapted* to the environment in which they live. Hence most fishes, either today or in Devonian times, may be thought of as tending to become "better" fishes; only a few, and that in one stage of the earth's history, became amphibians. Among the latter, in turn, only a few members of one group had the potentialities, and the opportunity, to become reptiles; the rest remained amphibians, becoming adapted to a variety of habitats. Thus it must have been always, and with all groups of animals. To only a minority of any group befell at once the potentiality and the opportunity for radical change into something different.

As we look about us today we see animals, each the product of long evolution, each occupying its own environmental niche in the world.

The modern amoeba in its drop of water is admirably adapted to the conditions of life as it finds them. It is not tending to become a "higher animal." There already are higher animals filling the available niches. But hundreds of millions of years ago there were no higher animals; then some one-celled animals having the necessary potentialities were presented with the opportunity to enter the vacant "higher-animal niches" and did so. But still the "one-celled-animal niches" remained and continued to be occupied by amoeba and its relatives to this day. Is not the modern amoeba as successful in being an amoeba as we are in being human beings?

In the following chapters we shall note many instances of preadaptation as well as of the perfecting of adaptation of new structures once they have appeared (postadaptation). In later chapters more complete discussions of the principles of evolutionary change, just sketched in the broadest possible strokes, will be discussed. The details of theory can best be understood and appreciated after we have acquired a background of fact.

References and Suggested Readings

Darwin, C., *The Voyage of the Beagle*, 2nd ed., 1845. (Available in various reprint editions, including Everyman's Library, No. 104, New York, E. P. Dutton; No. FC11, Bantam Books, New York; No. N16, Doubleday, Garden City, New York.)

Darwin, C., *On the Origin of Species by Means of Natural Selection*, London, John Murray, 1859. (See p. 6 for listing of reprint editions.)

de Beer, G., *Charles Darwin, A Scientific Biography*, Anchor, No. N41, Garden City, New York, Doubleday, 1965.

Goldschmidt, R., *The Material Basis of Evolution*, New Haven, Yale University Press, 1940.

Irvine, W., *Apes, Angels, and Victorians*, New York, McGraw-Hill, 1955.

Romer, A. S., *The Vertebrate Story*, Chicago, University of Chicago Press, 1959.

Schmalhausen, I. I., *Factors of Evolution. The Theory of Stabilizing Selection*, Philadelphia, Blakiston, 1949.

Simpson, G. G., *The Major Features of Evolution*, New York, Columbia University Press, 1953.

Simpson, G. G., *The Meaning of Evolution*, 2nd ed., New Haven, Yale University Press, 1967.

3

Evolution as Seen in the Structure of Modern Animals

MORPHOLOGY Structure is the easiest aspect of an animal to study. Perhaps it is for this reason that knowledge of animal structure dates from ancient times and was, indeed, the first aspect of biology to develop. The study of structure is called MORPHOLOGY, a word of slightly broader meaning than the more familiar term "anatomy," which is nearly synonymous. Biologists had not progressed far in the study of morphology before they were impressed by *similarities* among different animals and began to speculate on the reasons for these similarities.

ANALOGY Why are different animals similar in structure? In the first place, there is no cause for surprise in the fact that animals living in the same environment or having similar methods of locomotion, obtaining food, and so on resemble each other. Fishes and whales are both faced with the problem of moving rapidly through water. What could be more natural than that they both should have streamlined body forms and should be propelled by the thrust of powerful tails against the surrounding water? Or again, birds and bats utilize the

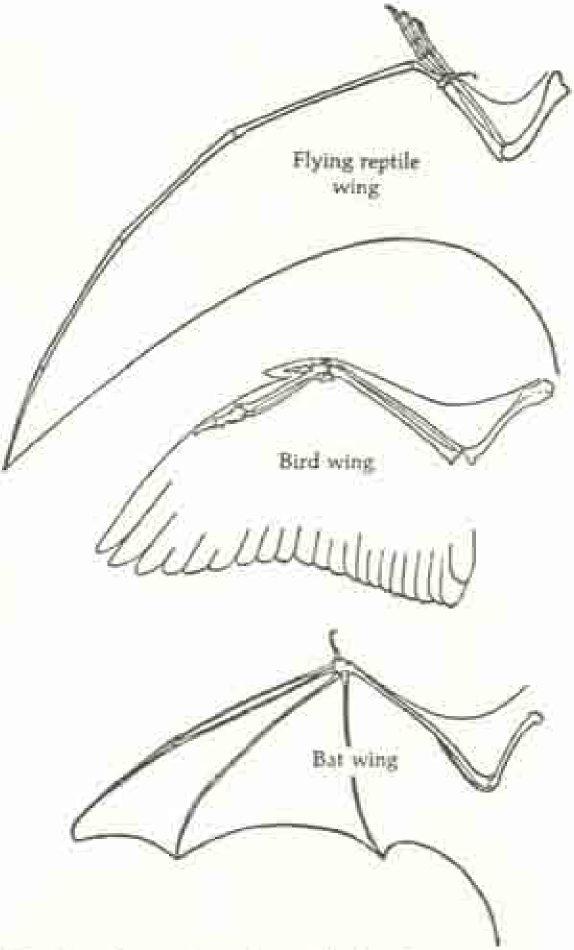


Fig. 3.1. Comparison of vertebrate wing structures. (From *The Dinosaur Book* by E. H. Colbert. Copyright 1945, 1951 by the American Museum of Natural History. Used with permission of the author and McGraw-Hill Book Company.)

air as a medium of locomotion. Both, therefore, possess wings which, like the wings of an airplane, support the body in the air and, unlike the wings of an airplane, serve as the means for forward propulsion. The reader can readily supply additional examples from his own observation. When animals live similar lives they usually resemble each other to some extent, the similarity being connected with the similar functions that their bodies serve. Similarity of structure connected solely with similarity of function is termed ANALOGY; structures exhibiting it are said to be analogous.

Insects resemble birds and bats in the possession of wings. The insect wing somewhat resembles a structure molded in plastic. Both the wing and the outer covering (exoskeleton) of the body contain a complex material (nitrogenous polysaccharide) called chitin. The wing is stiffened by a series of hollow tubes, the "veins" (Fig. 9.13, p. 165). The whole forms a lifeless structure operated by muscles attached to its base.

The wings of bird and bat are quite otherwise (Fig. 3.1). The supporting surface of the bird wing is composed of feathers; that of a bat wing, of a membrane formed of modified skin. The feathers, in the one case, and the membrane, in the other, are supported by an internal skeleton of bone, a very different material from the chitin of the insect. The skeleton of these wings forms a series of segments. The segment attached to the body is supported by a single bone (Fig. 3.1), the HUMERUS. To the free end of the humerus two bones attach, the RADIUS and ULNA. Next comes a group of little bones, the CARPALS (corresponding to man's wristbones), then the METACARPALS (corresponding to the bones in the palm of man's hand), and finally the PHALANGES (corresponding to the bones in man's fingers). In the bat the first "finger," corresponding to the human thumb, is short and tipped with a claw, while the other four fingers have long, slender metacarpals forming stiffening supports, like the ribs of an umbrella, for the wing membrane. In the bird the carpals, metacarpals, and phalanges are partly fused into an irregularly shaped bone serving to support the feathers of that part of the wing. We see, then, that the wings of insects are really very different from the wings of birds and bats. We may conclude that analogous similarities are on the whole superficial in nature.

HOMOLOGY In describing the skeleton of the wings of birds and bats in the preceding paragraph we repeatedly referred to the skeleton of the human arm to make our meaning clear. It is already evident, therefore, that considerable similarity exists between the skeletons of the arm of man and of the wings of bird and bat. The

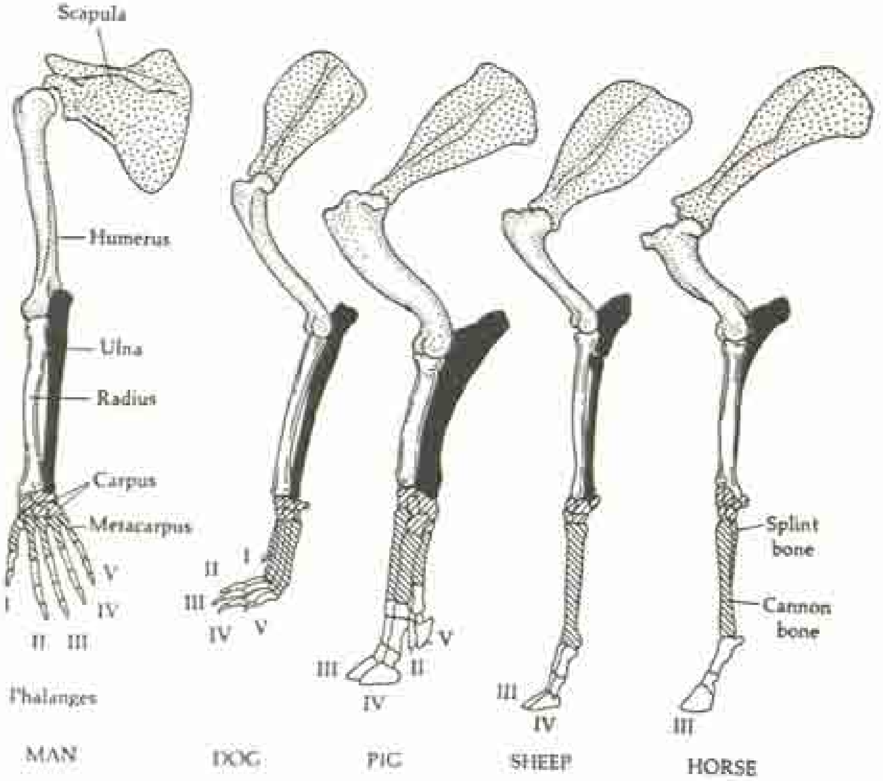


Fig. 3.2 Forelimbs of man and of several mammals adapted for walking and running. Roman numerals identify the five digits. (After Le Conte.)

similarity is particularly clear in the case of the bat. The similar segments found in arm and wings may be listed as follows, starting at the shoulder (Fig. 3.2): (1) humerus, (2) radius and ulna, (3) carpals, (4) metacarpals, and (5) phalanges. Here is similarity of structure not readily explained as connected with similar function.

Figure 3.2 presents, along with the forelimb of man, the limbs of four mammals adapted for more or less rapid movement over the surface of the earth. A glance at the figure suffices to reveal that dog, pig, sheep, and horse all have their forelimb skeletons constructed of bones arranged according to the same pattern. True, there are modifications. In the pig two of the "fingers" are much larger than the other two, whereas in the sheep only two are present, forming the support of the so-called "split hoof." The two remaining fingers are the third and fourth (in numbering, the human thumb is designated as I, the "index finger" as II, and so on). Digit III is the only one remaining intact in the horse; its enlarged fingernail forms the solid hoof. In the horse the radius and ulna are fused together, and the metacarpal of digit III is greatly enlarged and elongated, forming the so-called cannon bone. Closely attached to the rear surface of the cannon bone are two slender bones known as the splint bones; they represent reduced metacarpals of digits II and IV.

Directing our attention to animals living in the water we note that whales, seals, and sea lions have their forelimbs modified into paddle-like flippers. Dissection of one of these flippers reveals that its skeleton is composed of the same five segments we noted in the arm of man and in the limbs of terrestrial mammals (Fig. 3.3). The segments are shortened, but they are all there in the order listed above.

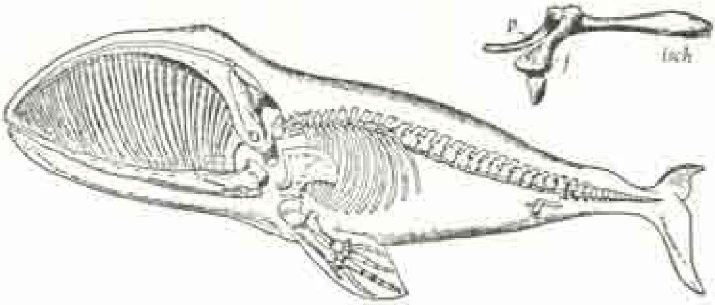


Fig. 3.3. Skeleton of a whalebone whale. The upper figure shows vestiges of the pelvic girdle and hind limb; *p*, pubis; *isch*, ischium; *f*, femur. (After Romanes; from Guyer, *Animal Biology*, Harper & Brothers, 1948.)

Thus we see that among birds and mammals limbs adapted for grasping, flying, running, and swimming are all constructed upon the same basic pattern. They share a fundamental similarity of structure that is evidently entirely unconnected with the uses to which they are put. How can we explain the origin of similarity of this kind, similarity that has no relation to function—which indeed exists in many cases despite dissimilar functions?

One way in which we might answer this question is that of the biologist who first called attention to the fact that a basic pattern underlies all these forelimbs. That was Baron Georges Cuvier, the eminent French comparative anatomist of the past century. Cuvier was not convinced of the truth of evolution. He believed that each species of animal has been created separately, an idea usually referred to as the theory of special creation. But if species were separately created, how could similarities among them arise? Obviously they would be similar if they were *created* to resemble one another. More specifically, we might assume that in shaping forelimbs the Creator used a certain pattern: When He created the hand of man He modified that pattern in a certain way; when He created the wing of a bat He modified the pattern in a different way; when He created legs adapted for rapid running He modified the pattern in still a different way; and so on. According to this theory there is no genetic relationship between man, bat, and horse; all they have in common is that they were made by the same Creator, using a common pattern.

Most modern biologists do not find this explanation satisfying. For one thing, it is really not an explanation at all; it amounts to saying, "Things are this way because they are this way." Furthermore, it removes the subject from scientific inquiry. One can do no more than speculate as to *why* the Creator chose to follow one pattern in creating diverse animals rather than to use differing patterns.

Hence most modern biologists explain the origin of similarities that have no relation to similar functions in a different manner. They are convinced that the similarity exists because the animals concerned *inherited* the structure from an ancestor that they shared in common. We have seen that the vertebrate forelimbs, for example, appear to be modifications of a five-fingered (PENTADACTYL) limb having one upper-arm bone (humerus), two lower-arm bones (radius and ulna), wrist-bones (carpals), and metacarpals and phalanges arranged to form five fingers (Fig. 3.2). Why are such diverse limbs as those of man, bat, bird, whale, horse, and so on all modifications of this pattern? The evolutionary explanation is that these animals all inherited the limb pattern from an ancestor that had the pentadactyl limb in more or less typical form. When the descendants of this ancestor took to life in the water, to locomotion through the air, or to running over hard ground they made over what they had in the way of limbs to serve the new functions. But despite the reconstruction necessary the indelible traces of the inherited pattern still remain. Thus, in contrast to the theory of special creation, the theory of creation by evolution maintains that different animals *are* related to each other in the sense of direct inheritance.

In our discussion we have noted two types of similarity. Similarity connected with similar functioning we have ascribed to analogy. We shall find useful a term for similarities not connected with similarities of function: the word HOMOLOGY. Two organs in different animals are analogous if they are used for the same function; two organs in different animals are homologous if they have the same fundamental structure, whether or not they are used for the same function.

These terms can be readily illustrated in connection with the forelimbs just discussed. We have seen that the wing of an insect is analogous to the wing of the bird; i.e., both wings are used for flight.

The insect wing is not homologous to the bird wing, however, since the structures of the two wings differ greatly. The wing of the bird is analogous to the wing of the bat since they are both used for flight. In this case, moreover, the two wings are also homologous, since they both have the same fundamental structure, both being modifications of the pentadactyl limb. For the same reason the leg of the horse is homologous to the wing of the bird, although the leg of the horse is not analogous to the wing of the bird, since the two limbs are used for different functions. Thus organs in different animals may be analogous but not homologous, analogous *and* homologous, or homologous but not analogous.

According to the most generally accepted interpretation, homologous structures owe their fundamental similarities to common ancestry. They are indications, remaining in modern animals, of what the ancestors of these animals were like. In a sense all modern animals are "made over" animals—the made over versions of their ancestors. And just as a made over garment if examined closely may reveal some indications of its former state, so modern animals reveal to a discerning eye what the characteristics of their ancestors must have been. For this reason the discovery and analysis of homologous structures forms one of the most powerful tools used in tracing the evolutionary histories and relationships of animals.

In this discussion we have illustrated homology with examples in which the fundamental similarities are easily seen. In all fairness we should mention that tracing homologies is frequently difficult. For example, there is convincing evidence that the "hammer" and "anvil" (malleus and incus) of the chain of three bones in our middle ear are homologous to two bones that formed the articulation of the lower jaw to the skull in our reptilian ancestors (articular and quadrate bones; see p. 198). In this case careful investigations of modern animals, of embryonic development, and of fossil forms were needed before the homology became evident.

ADAPTIVE RADIATION The concept of adaptive radiation may be illustrated by the limb structure of mammals. Mammalian limbs, like those of other vertebrates aside from fishes, are modifications of the pentadactyl limb. Primitive, ancestral mammals are believed to have been short-legged, five-fingered creatures living on the ground (or in trees?) but having limbs not strongly modified for any particular type of locomotion. Animals living on the ground are called TERRESTRIAL in Fig. 3.4; insect-eating (insectivorous) mammals such as the shrews form modern representatives of them. Mammals possessing this primitive limb structure are placed in the center of the diagram. Of the lines

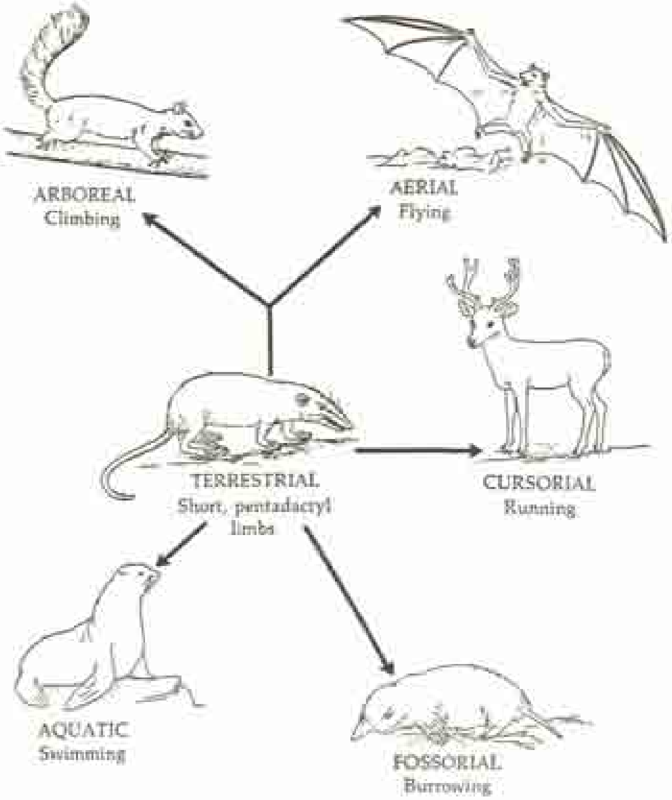

ARBOREAL
Climbing
AERIAL
Flying
CURSORIAL
Running
TERRESTRIAL
Short, pentadactyl limbs
AQUATIC
Swimming
FOSSORIAL
Burrowing

Fig. 3.4. Adaptive radiation in limb structure of mammals.

radiating from this central point one leads to ARBOREAL, a term for tree-dwelling forms, which in one way or another have adapted limbs for life in trees; squirrels, sloths, monkeys are among the examples. Another line leads to AERIAL, representing mammals adapted for flight. Only bats occupy the position at the terminus of this line, since they are the only truly flying mammals. Somewhere along the line we should place such gliding forms as the wrongly named "flying" squirrel. It will be noted that the diagram represents the lines leading to arboreal and to aerial as not entirely independent. A single line is shown emerging from terrestrial and then dividing into the two branches. This arrangement was made to suggest the probability that the ancestors of flying mammals lived in trees, i.e., that life in trees preceded flight. Perhaps gliding formed the transitional type of locomotion between climbing and true flight.

Continuing around the diagram in a clockwise direction we come to the line ending in CURSORIAL. This term refers to mammals, like horses and antelopes, that have developed limbs suitable to rapid movement over the surface of the ground. Part way along this line we should place animals with less strongly modified limbs, such as wolves, foxes, hyenas, and lions.

A line leading downward ends with the term FOSSORIAL, applying to burrowing mammals. Some of these, like the moles, have modified their forelimbs into such specialized and powerful digging organs that they are poorly adapted for locomotion on the surface of the ground. Others, like pocket gophers and badgers, are expert diggers but have retained limb structures enabling them to move about on the surface.

Finally, a line leads to the term AQUATIC. At the end of this line we find such mammals as whales and porpoises, with limbs so strongly modified for life in the water that they cannot move about on land. Part way along the line we should place seals, sea lions, and walruses, mammals with limbs strongly modified for life in the water yet retaining some ability to move about on land. Still nearer the center on this same line we should place such accomplished swimmers as otters and polar bears, mammals equally at home in water or on land.

All the mammals mentioned as belonging on one of the radiating lines have limbs more or less adapted for some particular mode of locomotion. All lines start from a common center representing the short, pentadactyl limbs of terrestrial mammals. From this center evolutionary lines radiate out in various directions. Hence ADAPTIVE RADIATION is evolution in several directions starting from a common ancestral type.

What is the relationship of adaptive radiation to homology and analogy? All the limbs mentioned are homologous to each other, since they are all variations of the pentadactyl limb. But for the most part a given limb is only analogous to others on the same radiating branch of the diagram. Thus the leg of the antelope is analogous to the leg of the horse, since they have the same function, but not to the leg of the mole.

What does the diagram of adaptive radiation indicate about the ancestry and evolutionary relationships of the animals included? In the first place we recall that, if the evolutionary interpretation is correct, possession of homologous structures is evidence of common ancestry. All the animals included in the diagram have modified pentadactyl limbs; hence they must be related to each other. Possession of this common limb pattern does not indicate *close* relationship, however, since the pattern is shared not only by all mammals but also by birds, reptiles, and amphibians—by all vertebrates except fishes, in other words.

What of the animals grouped together on one of the radiating lines? Are they related to each other? We have just noted that possession of the pentadactyl pattern indicates that they are distantly related, but does their position together on one of these lines indicate that they are closely related? The answer is evident if we recall that the groupings on the radiating lines are based upon possession of *analogous* similarities and that possession by two animals of analogous similarities is not in itself indicative of common ancestry.

PARALLEL EVOLUTION As examples of cursorial adaptation we have mentioned antelopes and horses. These two are placed on the same branch of the diagram because they have limbs serving the same function. But, as just mentioned, possession of analogous similarities does not indicate relationship. Both antelopes and horses are believed to have evolved from ancestors having short, pentadactyl limbs ("terrestrial," Fig. 3.4); both have achieved elongated, slender limbs adapted for rapid running. But the antelopes have developed two toes on each foot (after the manner of the sheep shown in Fig. 3.2), while the horses

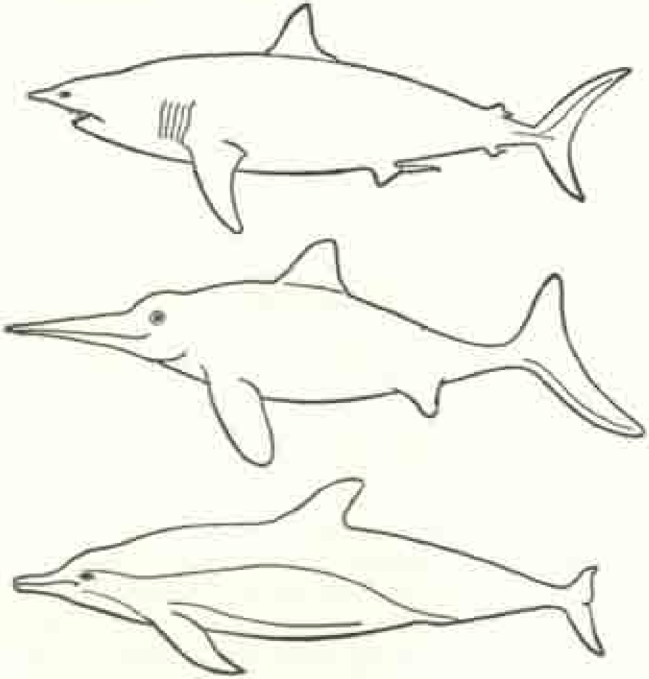


Fig. 3.5. Convergent evolution exhibited by a fish (shark), a reptile (*Ichthyosaurus*), and a mammal (dolphin), all strongly adapted for aquatic life. (From Lull, *The Ways of Life*, Harper & Brothers, 1947.)

have developed but one toe (Fig. 3.2). Both have achieved the same goal but have done so separately and in differing ways.

When we see two forms independently undergoing similar changes in the course of their respective evolutionary histories we say we have a case of PARALLEL EVOLUTION if the animals concerned are closely related or CONVERGENT EVOLUTION if the animals are more distantly related. The distinction between the two terms is not clear-cut. In the case of the horse and antelope we have two forms that are not closely related; they belong to different orders of mammals (p. 480). Therefore we might regard their evolution as a case of convergence. On the other hand, evolution of different two-toed mammals (e.g., the antelope and the deer) would form an example of parallel evolution, as would the development of flipperlike forelimbs by seals and walruses.

Sometimes convergent evolution involves organisms even less related to each other than are different orders of mammals. Thus the whales and their relatives such as porpoises evolved a fishlike body form, and so did the extinct reptile *Ichthyosaurus* (Fig. 3.5). The wings of the bee, bird, and bat afford another striking example of convergence.

In summary we may point out that parallel and convergent evolution lead to production of analogous similarities. On the other hand, homologous similarities are indications of the persistence of ancestral structure throughout all the vicissitudes of evolutionary change.

HOMOLOGY IN SKULL STRUCTURE Use of forelimbs for illustrative purposes in the preceding discussion was dictated by the clarity with which the several points could be shown and by the relative ease with which the structures could be understood by readers unacquainted with the details of vertebrate anatomy. Actually, however, our illustrative material might have been drawn from any portion of the body. All systems and parts of the bodies of vertebrates exhibit the fundamental similarities we have designated as homologous. For example, the skulls of vertebrates have received exhaustive investigation. Studies reveal that from fish to man a common pattern of bone arrangement is found; evolution has consisted of gradual reduction in numbers of bones, through loss and through fusion of one bone with another, and of changes in function and in relative size. Figure 3.6 illustrates the point that the skulls of amphibians, reptiles, and mammals are based upon this common pattern. The figure also demonstrates a progressive reduction in the number of bones and the corresponding increase in the importance of such bones as the frontals and parietals as the brain underlying them increases in size. Why do skulls of such diverse animals give evidence of having been constructed on a common pat-

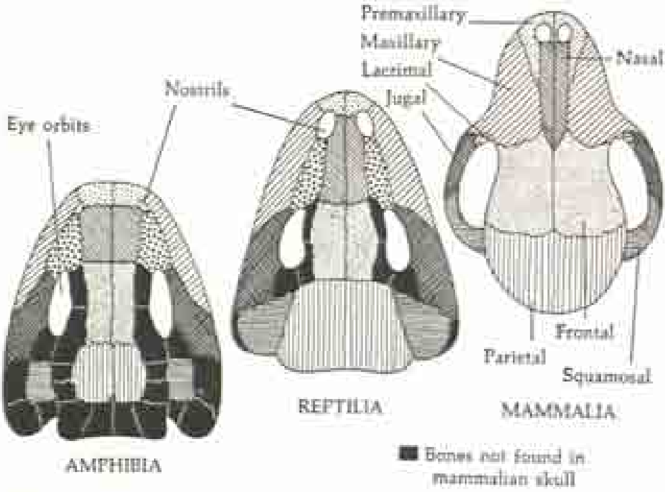


Fig. 3.6 Basic structural plan of the roof bones of the skull in amphibians, reptiles, and mammals. Bones present in mammals are named, others are shown in solid black. (See Zangerl, 1948.)

tern? Because if the evolutionary interpretation is correct, the diverse animals all inherited that pattern from a common ancestor.

We might continue to pile example upon example, but every reader who has taken a course in elementary zoology or in comparative anatomy can supply his own. Such courses are filled with examples of homology and, indeed, are constructed with the latter as a fundamental tenet. Why, for example, do students of comparative anatomy dissect the common cat? Not because they are particularly interested in cats as cats, but because the anatomy of the cat is to a considerable extent typical of the anatomies of all mammals, including man. By studying one mammal the student can learn much about all mammals, because of the fundamental similarities, homologies, found everywhere in mammalian structure.

HOMOLOGY IN BRAIN STRUCTURE Although we have stated that homology characterizes all bodily systems, our examples thus far have been confined to the skeletal system. Figure 3.7 illustrates the point that the "soft parts" of the body present common patterning as well as do the "hard parts." It is evident from the figure that brains of vertebrates, ranging from fishes to mammals, are constructed of similar series of parts: OLFACTORY LOBES, CEREBRAL HEMISPHERES, OPTIC LOBES, CEREBELLUM, MEDULLA, and other less prominent divisions and subdivisions. As we progress through the series some lobes become more

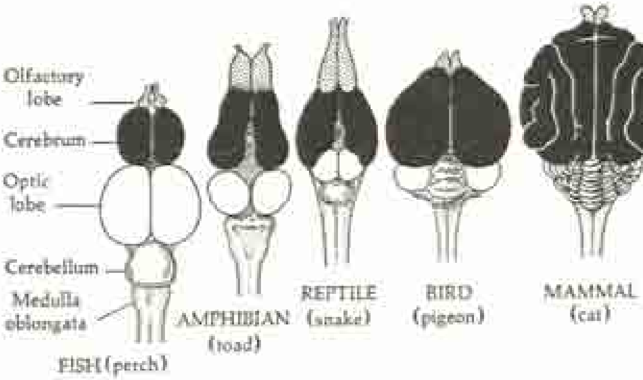
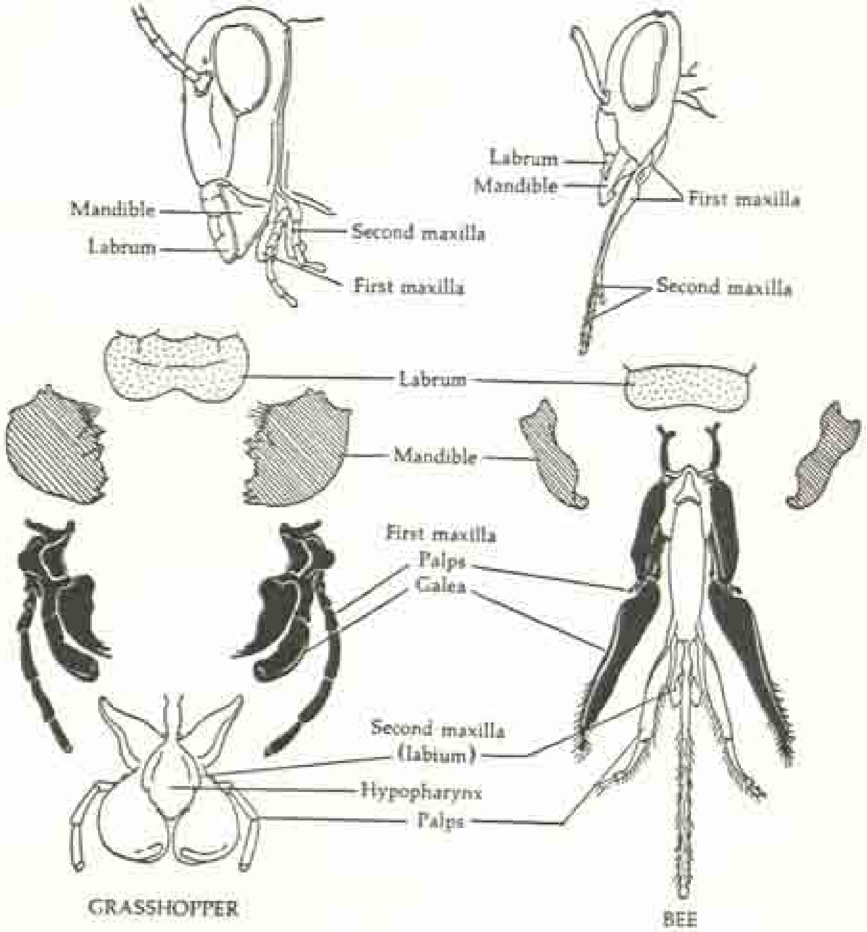


Fig. 3.7. Comparison of the brains of a series of vertebrates. Dorsal view. (After Guyer, *Animal Biology*, Harper & Brothers, 1948.)

prominent than others. In particular the cerebral hemispheres, much smaller than the optic lobes in fishes (Fig. 3.7), become in mammals the dominant portion of the brain, hiding the remains of the optic lobes beneath them so that the latter are not visible in the view of the mammalian brain shown in the figure. Despite the differences connected with differing functions, however, the common pattern of brain structure is clearly evident. The reader can now readily form his own conclusion as to the reason for this fact.

HOMOLOGY IN INVERTEBRATES Homology is by no means the exclusive attribute of vertebrates. We have concentrated attention upon vertebrates because the structure of vertebrates is better known to the average reader than is the structure of invertebrates. The latter, however, also show common patterns of structure upon which are superimposed modifications connected with differing functions. One of the most instructive examples of this phenomenon is derived from the mouthparts of insects. This example gains added interest from the fact that it was known to Darwin and cited in his *Origin of Species*.

Insects considered most primitive by entomologists have mouthparts adapted for cutting and shredding plant tissues. The common grasshopper is a typical example (Fig. 3.8). Its mouth is provided with a pair of MANDIBLES that act like jaws in cutting and biting. They move in a horizontal plane, in contrast to the vertical movement of the lower jaw of vertebrates. In the mouth there is a tonguelike structure called the HYPOPHARYNX. Accessory to the mandibles are two pairs of mouthparts unlike anything possessed by vertebrates. These are called, respectively, the FIRST and SECOND MAXILLAE; they aid in the process of



Mandible
Labrum
Second maxilla
First maxilla
Labrum
Mandible
First maxilla
Second maxilla
Labrum
Mandible
First maxilla
Palps
Galea
Second maxilla
(labium)
Hypopharynx
Palps
GRASSHOPPER
BEE

Fig. 3.8. Mouth parts of grasshopper and honeybee. Upper sketches show mouth parts in place in the head, lateral view. Lower sketches show mouth parts removed, front view.

conveying food into the mouth. They are provided with short, feelerlike processes called PALPS. In the grasshopper the pair of second maxillae enter into the formation of a LABIUM or "lower-lip." There also is present a LABRUM or "upper lip."

Starting with the cutting or mandibulate pattern of mouthparts just described we can trace an adaptive radiation comparable to the one illustrated by vertebrate forelimbs. For example, the honeybee has adapted the mouthparts for its particular means of food gathering (Fig. 3.8). The mandibles continue to function as jaws but are used principally not for cutting food but for "working" the beeswax until it is pliable and in condition to be utilized in construction of honeycomb. Food consists of the nectar of flowers drawn up into the mouth through a pumplike arrangement consisting of a tube with a plunger within. The tube is not a solid structure but is improvised by bringing together the pair of first maxillae and the labial palps. The plunger within the tube is a tonguelike structure formed from a portion of the labium. A muscular sac at the upper end of the tube acts in sucking up liquids much as does the rubber bulb of a medicine dropper (pipette).

Butterflies and moths also have a tube through which nectar from flowers is drawn into the mouth (Fig. 3.9). As in bees, suction is produced by a muscular sac connected to the tube; there is, however, no plunger (tongue) in the tube. In many butterflies and moths the tube is long and slender and when not in use is coiled like a tiny watchspring under the animal's head. This slender tube is composed of the pair of first maxillae elongated, hollowed out on their adjoining surfaces, and held together by interlocking grooves and ridges. Mandibles and second maxillae are rudimentary, except in one family of moths which have retained biting mouthparts, thereby adding evidence in support of the view that sucking mouthparts, possessed by other moths, are in reality "made over" from the biting and cutting type.

A third modification is possessed by the true bugs (order Hemiptera). They have a proboscis somewhat like a hypodermic needle which they thrust through the skin of plant or animal to withdraw underlying juices (Fig. 3.9). Though the most notorious member of the group is the bed bug, by far the larger number of true bugs suck the juices of plants and of other insects rather than the blood of vertebrate animals. Unlike a hypodermic needle the proboscis is not thrust through the skin by sheer force applied to it. The creature wielding it is too tiny for that. Rather, a hole is drilled for its insertion, the drilling being done by two pairs of sharp, piercing bristles (Fig. 3.9). The innermost pair of these is formed from the first maxillae, hollowed out on their adjoining faces to form the walls of two tubes. Plant and animal juices are sucked through the larger, dorsal tube; saliva may be forced outward into the puncture wound through the smaller, ventral tube (Fig. 3.9). On either side of the first maxillae are the mandibles, also modified to form piercing bristles. In drilling the hole the four bristles slide up and down independently, the mandibular pair being the more active in the process. This hypodermic arrangement is encased for a portion of its length in a rostrum or beak formed of the second maxillae (Fig. 3.9).

The two-winged flies, the housefly being the most familiar example, have a proboscis formed from labrum, hypopharynx, and labium (second maxillae; Fig. 3.9). In some flies the proboscis terminates in a pair of broad, soft pads (labella) pierced by many pores which function in "sponging up" liquids; in biting flies the proboscis is modified for piercing.

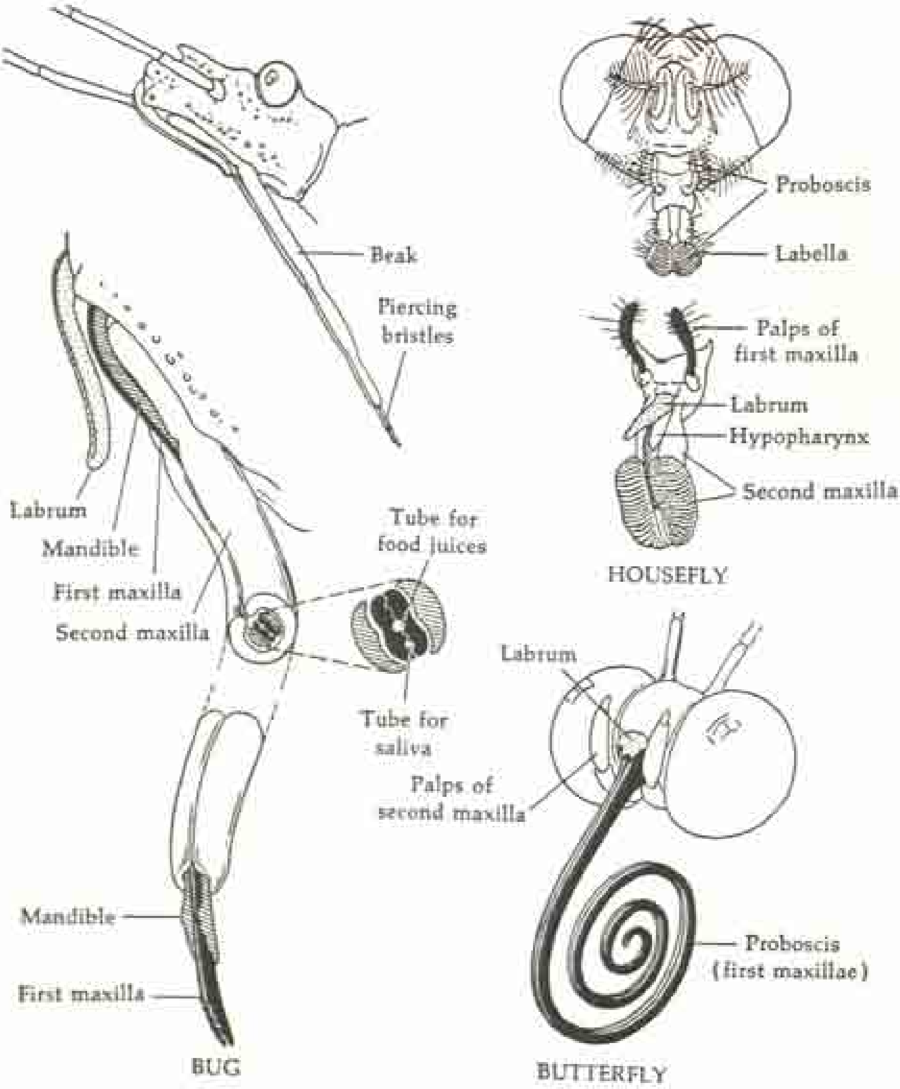

Beak
Piercing bristles
Labrum
Mandible
First maxilla
Second maxilla
Tube for food juices
Tube for saliva
Mandible
First maxilla
BUG
Proboscis
Labella
Palps of first maxilla
Labrum
Hypopharynx
Second maxilla
HOUSEFLY
Labrum
Palps of second maxilla
Proboscis (first maxillae)
BUTTERFLY

Fig. 3.9. Mouth parts of bug, housefly, and butterfly. Upper drawing of the bug shows the beak attached to the head; lower drawing shows a portion of the beak cut away to reveal the cross section, with an enlarged cross section of the bristles at the right. Mandibular bristles shown in diagonal shading; 1st maxillary bristles, solid black; 2nd maxillae, forming the beak, unshaded.

We see, then, how a set of "standard parts" (labrum, mandibles, hypopharynx, and first and second maxillae) have been modified to serve such diverse food habits as cutting and shredding plant tissues, sucking nectar from flowers (by two different types of mechanism), piercing the skin to suck juices of plants or animals, and gathering liquid from the surfaces of food particles. Why are such diverse mechanisms based upon the same underlying pattern? Evidently the basic pattern of mouthpart structure was inherited from an ancestor shared by all these modern insects. As noted above, the mandibulate or cutting mouthparts represent the type from which all the others are believed to have arisen through adaptive radiation.

SERIAL HOMOLOGY Thus far we have spoken of the homology of an organ in one animal with an organ in another animal. We have said, for example, that the wing of the bird is homologous to the arm of man. There is another type of homology in which two or more structures *in one individual* are compared. Fundamental similarity of structure between one part of an animal and another part of the same animal is called SERIAL HOMOLOGY.

An example of serial homology is seen in the arm and leg of man. The segment of each that is attached to the trunk has a single bone as skeletal support; in the arm this bone is called the humerus (Fig. 3.2), and in the leg it is called the FEMUR. In the succeeding segment of the arm and leg there are two bones, which are called radius and ulna in the arm and TIBIA and FIBULA in the leg. Then come a group of wrist and ankle bones, respectively, which are called carpals in the arm and TARSALS in the leg. Next are the bones of the palm of the hand and the sole of the foot, metacarpals and METATARSALS, respectively. Finally, the bones of fingers and toes are called PHALANGES in both cases. Evidently, then, our forelimbs and hind limbs are modifications of the same fundamental pattern, modified for grasping and handling in the one case and for locomotion in upright posture in the other.

Much more elaborate examples of serial homology are afforded by the jointed appendages of invertebrates. Examination of the numerous appendages of a lobster or crayfish reveals that those in different parts of the body have much resemblance despite the fact that they are modified for a variety of functions (Figs. 3.10 and 3.11). The most conspicuous pair are the "pinchers" or CHELAE, used by the animal in grasping food and in fighting. Just behind the chelae are the four pairs of WALKING LEGS, used in slow locomotion along the bottom of the stream in which the animal lives. Behind the walking legs and attached to the abdomen are several pairs of SWIMMERETS (XIV and XVI in Fig. 3.11; not shown in Fig. 3.10). These are small appendages; their name

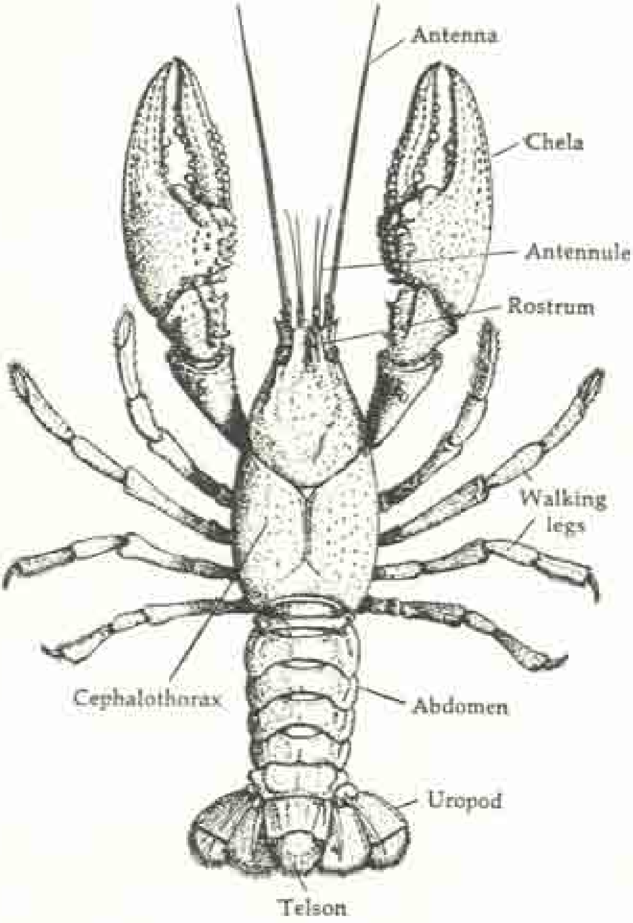


Fig. 3.10. Crayfish, dorsal view. (From Hagen, *Memoirs, Museum of Comparative Zoology*, Harvard University.)

gives a false impression of their importance in swimming. In females masses of eggs become attached to them, hanging like tiny bunches of grapes while embryonic development progresses. In males the first pair of swimmerets (XIV in Fig. 3.11) is modified for the transference of sperm cells to the female. A broadly expanded, somewhat paddlelike structure will be noted at the end of the abdomen (Fig. 3.10). When the animal wishes to move rapidly it flexes or bends its abdomen powerfully, this terminal structure offering resistance to the water much as does an oar. As a result the body shoots backward with great speed. The terminal structure employed in this maneuver is composed of a flap (telson, Fig. 3.10) attached to the last segment of the body,

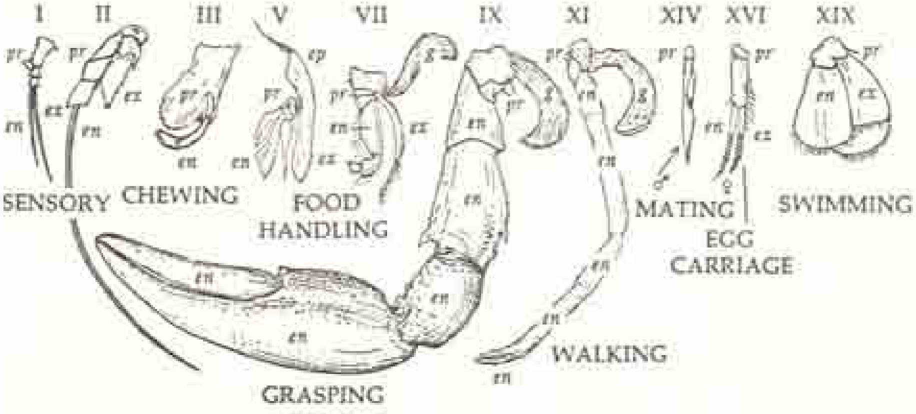


Fig. 3.11. Crayfish appendages; *pr*, protopodite; *en*, endopodite; *ex*, exopodite; *ep*, epipodite; *g*, gill. (From *General Zoology* by Storer & Usinger. 4th ed. Copyright © 1965 by McGraw-Hill, Inc. Used with permission of McGraw-Hill Book Co.)

augmented by flattened appendages on either side, the UROPODS (Fig. 3.10; XIX in Fig. 3.11).

Anterior to the chelae is found a succession of appendages modified for a variety of functions. Some of them, MAXILLIPEDS and MAXILLAE (VII and V in Fig. 3.11), aid in grasping food and conveying it to the mouth. One pair, the MANDIBLES (III in Fig. 3.11), crush the food. Two other pairs, the ANTENNAE and ANTENNULES (II and I in Fig. 3.11), form sensory "feelers."

The great variety of functions served by the appendages of the crayfish are evident from the foregoing summary. Careful study reveals that they are all modifications of a single pattern. We have spoken of a five-fingered (pentadactyl) pattern underlying vertebrate forelimb structure; similarly, we might say that a two-fingered pattern underlies the structure of crayfish appendages. This two-fingered structure is called a BIRAMOUS APPENDAGE and is well illustrated by the typical swimmeret of a crayfish (XVI in Fig. 3.11). The basal portion of the appendage, PROTOPODITE, is unpaired but may consist of more than one segment. Attached to the protopodite are the two "fingers," each composed of several or many segments. The "finger" nearest the midline of the body is called the ENDOPODITE and the lateral one the EXOPODITE. The labeling of Fig. 3.11 indicates clearly how, starting from this primitive arrangement, appendages adapted for the wide variety of functions have been derived by modification, and in some cases the loss, of one or another of the original parts.

What are the implications of serial homology for evolution? It will be noted that arthropods, such as the crayfish, have bodies composed of a series of METAMERES or somites (this segmentation is particularly clear in the abdomen of the crayfish, Fig. 3.10). Each metamere is provided with a pair of jointed appendages, modifications of the biramous pattern. It would seem that the common ancestor from which these arthropods inherited the arrangement described must have had a body composed of a series of metameres, somewhat like the earthworm's, and had each metamere equipped with a pair of biramous appendages in typical form. In descendants from this ancestor some of the metameres became fused together, to form a CEPHALOTHORAX as in the crayfish (Fig. 3.10) or to form a separate head and thorax as in an insect. At the same time appendages attached to different metameres of the body became modified to serve a variety of functions. Thus, like homology in general, serial homology finds its most reasonable explanation in a theory of descent with modification, i.e., of evolution.

Since the biramous pattern underlies the appendages of all members of phylum Arthropoda, the insect mouthparts discussed earlier are made over appendages of this type, connected to the metameres that fused to form the head.

VESTIGES Vestigial or rudimentary organs are parts of the body that are relatively small in size and have little, if any, ascertainable function. In every case of importance to the study of evolution they appear to represent useless remnants of structures or organs which are large and functional in some other animals.

The most familiar vestigial organ in man is the VERMIFORM APPENDIX (Fig. 3.12). "Vermiform" suggests its wormlike appearance. The appendix attaches to a short section of the large intestine called the CAECUM, and the latter is located at the point where the large intestine is joined by the small intestine. The caecum is a short pouch, ending blindly except for the small opening into its extension, the appendix.

If we study the digestive systems of other mammals we discover that carnivorous (flesh-eating) mammals have the caecum reduced to a short, blind pouch much like our own. Cats, for example, have a short caecum, with no appendix at all. On the other hand, if we study herbivorous (plant-eating) mammals having simple stomachs more or less like ours we find that the caecum is a large pouch, in some cases as capacious as all the rest of the digestive system put together. In some herbivorous mammals it is broad throughout its length. In others it tapers to a point at its free end. The combined length of caecum and appendix in a rabbit, for example, is about 18 in. (Fig. 3.12). For the first 12 in. or so it is a broad, thin-walled pouch containing a spiral

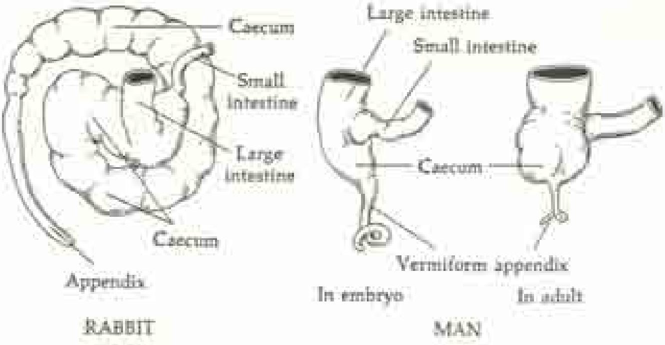


Fig. 3.12. Caecum and vermiform appendix in rabbit, in human embryo, and in adult man. (Rabbit, after Bensley, B. A., *Practical Anatomy of the Rabbit,* 7th ed. Copyright, Canada, 1945, by the University of Toronto Press. Man, redrawn from Walter, H. E., *Biology of the Vertebrates,* rev. ed. Copyrighted, 1939, by the Macmillan Company.)

fold or valve that increases the internal surface. The terminal five or six in. of it has thicker walls and no spiral valve and corresponds to our appendix.

The large caeca of herbivorous mammals form storage compartments in which partly digested food remains while bacterial action takes place upon it. One of the most abundant constituents of plant tissue is cellulose. The digestive fluids of mammals contain no enzymes that digest this substance. For this reason man, for example, could derive no appreciable nourishment from a diet of paper, a product consisting largely of cellulose. Certain bacteria, however, can break down cellulose into chemical compounds the body can utilize. In the caeca of herbivorous mammals such bacteria have time to act on the cellulose, thereby retrieving for the animal a portion of its diet that would otherwise be wasted. Accordingly the caecum is a valuable organ for many herbivorous animals.

How do we happen to have a caecum and associated appendix? Our diet consists of both plant and animal material, but in the preparation of plant material for human consumption we eliminate most of the cellulose (in the "woody" portions). We do not use our caecum and appendix as a container for food undergoing bacterial action. Then why do we have them? The most reasonable explanation seems to be that we inherited them from some remote ancestor having a diet that necessitated such adjuncts to the digestive system. When the descendants of this ancestor eventually changed their food habits the caecum and appendix, no longer useful, decreased in size until they became mere remnants of the functional organs they once had been.

It is difficult to explain the presence of useless vestiges upon a basis of special creation without imputing to the Creator some lack of skill in planning or construction. Accordingly, opponents of the idea of evolution commonly maintain that organs like the appendix are not useless at all, that they have functions that we have never been able to discover. Clearly, the burden of proof lies with the affirmative in the matter of proving the usefulness of vestiges for which no functions have ever been discovered. Many readers can testify from personal experience that if the appendix has a function at all it is so unimportant that the advantages of having the organ removed far outweigh the disadvantages.

Other vestiges are found in the human body. For example, in the inner angle of each of our eyes there is a little fold of flesh called the SEMILUNAR FOLD (plica semilunaris; Fig. 3.13). This corresponds to a structure that in many lower animals is a movable third eyelid, the NICTITATING MEMBRANE, lying under the other eyelids and sweeping across the eye from the inner angle outward. In many animals, for example, owls, the nictitating membrane is transparent, affording a means of cleaning and lubricating the surface of the eyeball without obstructing vision in the process, even for the fraction of a second necessary to wink the other two eyelids. In horses the membrane is well developed, containing cartilage. When the eye is strongly retracted the membrane extends across it for about an inch. The membrane is variably developed in other mammals and in lower vertebrates.

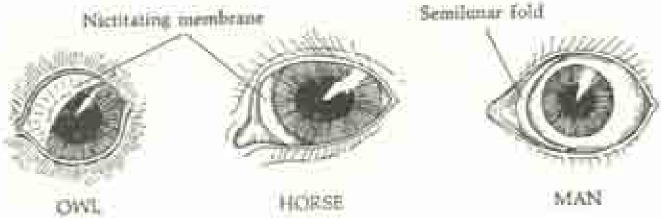


Fig. 3.13. Nictitating membrane (third eyelid) of owl and horse, and vestigial semilunar fold of man. (Mainly after Romanes, *Darwin and After Darwin*, 3rd ed., Open Court Publishing Company, 1901.)

The tails commonly possessed by both wild and domestic mammals are familiar to everyone. A chain of vertebrae continuous with those comprising the remainder of the vertebral column forms the skeletal axis of the tail, attaching just behind the pelvic girdle (the bones to which the hind limbs articulate). In man a much reduced string of vertebrae, partly fused together, arises at this same point and curves forward, instead of extending out into an external tail. This structure, called the COCCYX, clearly homologous to a group of reduced tail vertebrae (Fig. 12.7, p. 240).

Everyone who has watched a horse on days when biting flies were bothersome is familiar with the way in which this animal can twitch certain areas of the skin. All observers of horses also will recall the manner in which the animal can move and turn its ears the better to hear sounds coming from different directions. Although we do not have these capabilities we commonly have vestigial muscles connected with our skin and ears. Generally these muscles do not function, though some individuals can demonstrate the ability to move the scalp or "wiggle" the ears.

Although the list of vestigial organs in man is long, the above sample will suffice. We must not create the impression, however, that vestiges are the exclusive attribute of man. It may safely be stated that every specialized animal retains some vestigial structures in its anatomy. Snakes, for example, are noted for lack of limbs, yet a few, such as boas and pythons, possess in appropriate position in the body tiny bones which seem to represent the last vestiges of pelvic girdle and hind limbs. Similarly, whales have no hind limbs, yet in the position where hind limbs if present would occur small bones are found that seem to represent vestiges of pelvic girdle and hind limbs (Fig. 3.3).

Vestigial structures in the leg of the horse have already been mentioned (p. 25): the splint bones representing the metacarpals of digits II and IV. These vestiges are slender bones of variable development sometimes partly fused to the cannon bone (metacarpal of digit III) supporting the hoof. The lower end of each splint bone is bluntly pointed and without connection to other bones.

Birds are characteristically flying animals, yet a few are flightless. One of these, the kiwi of New Zealand, possesses useless vestiges of wings supported by tiny replicas of the usual bones of a bird wing (Fig. 3.1). Feathers covering the body conceal these vestigial wings from view.

How are we to explain the presence of useless structures such as those described above? Are we to suppose that creatures were "deliberately" made with structures that would never be of use to them? Or does it seem more reasonable to conclude that the kiwi, for example, inherited its wings from an ancestor which was a flying bird and hence had use for wings?

Occasional biologists doubt that structures usually classed as vestigial are in fact without function. It has been maintained, for example, that the small bones we have spoken of as vestigial hind limbs in whales are not such at all but are bones having the function of stiffening the walls of the anus, the posterior opening of the digestive tract. Most students of anatomy are not in accord with this view. Occasional mistakes may be made in labeling small organs as vestigial, but it seems entirely unlikely that the percentage of error is high. To most biologists, therefore, the presence of small organs that seem to have no function in themselves but correspond to functional organs possessed by other animals indicates inheritance from common ancestry. Descendants having use for the organ in question retained it as a functional organ; in descendants having no use for it the organ became reduced in size.

References and Suggested Readings

Darwin, C., *On the Origin of Species by Means of Natural Selection*, London, John Murray, 1859. (See p. 6 for listing of reprint editions.) Note especially chap. 13 of the 1st ed. or chap. 14 of the 6th ed.

Dewar, D., *Difficulties of the Evolution Theory*, London, Edward Arnold, 1931.

Guyer, M. F., *Animal Biology*, 4th ed., New York, Harper & Row, 1948.

Lull, R. S., *Organic Evolution*, rev. ed., New York, Macmillan, 1947.

Romer, A. S., *The Vertebrate Body*, 2nd ed., Philadelphia, W. B. Saunders, 1955.

Snodgrass, R. E., *Principles of Insect Morphology*, New York, McGraw-Hill, 1935.

Zangerl, R., "The methods of comparative anatomy and its contribution to the study of evolution," *Evolution*, 2, 351–374 (1948).

4

Evolution as Seen in Embryonic Development

HOMOLOGY IN EMBRYOS In the preceding chapter we saw that similarities of adult structure not connected with similar habits and adaptations are most reasonably explained as the result of inheritance from common ancestry. In the present chapter we shall consider similarities existing among embryos.

It is a striking fact that there are not only many evidences of common patterns in the adult structures of diverse animals but evidences of common patterns in embryonic development. Indeed, the two phenomena are related, since embryonic development is the process by which adult structure is attained. We might anticipate, therefore, that similar final results would usually be achieved by similar developmental processes.

Some of these embryonic similarities are displayed in Fig. 4.1, which represents six stages in the embryonic development of six different animals, ranging from fish to man. Each sequence begins with a single cell, the FERTILIZED EGG or OVUM, shown at the bottom of each of the six vertical columns. To facilitate comparison the ova are all drawn about the same size, although there are actually large size differences. Thus the human ovum measures only about $\frac{1}{250}$ in. in diameter while the ovum of a shark measures in the neighborhood of two ins. Each is a single cell, however, containing genetic contributions from both mother and father. Size differences depend mainly upon the amounts of food material—yolk—present.

Inspection of Fig. 4.1 reveals the great similarity of the early embryonic stages of all the forms shown. The embryos in the second and third horizontal rows from the bottom are so similar that only an expert could tell them apart if they were misplaced. By the stage represented in the fourth row, the fish and salamander have acquired more identifying characteristics, but even in the stage represented by the fifth row the similarities of embryonic lizard, opossum, monkey, and man are most striking. We see, then, that the embryos of these diverse animals all follow a common pattern at first but progressively diverge from this pattern as they approach their respective adult morphologies. As Karl E. von Baer, pioneer embryologist of the last century, expressed it, "During its development an animal departs more and more from the form of other animals" (as translated in de Beer, 1958).

Why do we find evidence of common pattern in embryonic development? This is the same question asked in the preceding chapter about common pattern in adult structure, and the answer is similar. The common pattern of embryonic development seems most reasonably explained as having been inherited from an ancestor common to all the animals possessing the similar embryonic developments. Explanations not involving common ancestry may take two forms. It may be maintained that the Creator created each species separately but saw fit to confer on different species similar processes of embryonic development. Or it may be maintained that mechanical and physiological necessities operating in development bring about the similarities—that there is, in effect, no other road that an ovum could follow in its development to the adult state. Similar physical forces undoubtedly have similar effects in producing basic similarities among embryos. Yet detailed similarities in development, like those to be considered presently, seem not to be completely explained as the result of such similar forces.

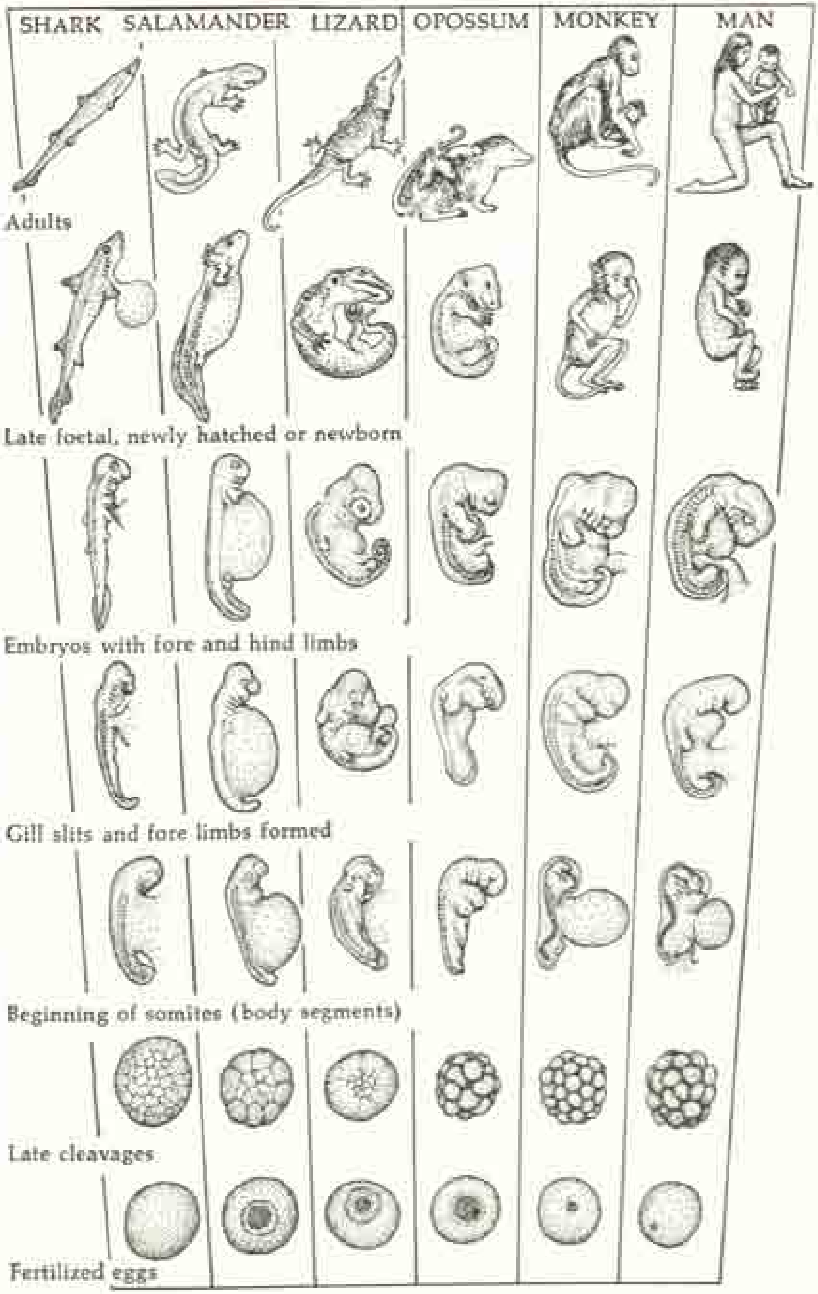

SHARK
SALAMANDER
LIZARD
OPOSSUM
MONKEY
MAN
Adults
Late foetal, newly hatched or newborn
Embryos with fore and hind limbs
Gill slits and fore limbs formed
Beginning of somites (body segments)
Late cleavages
Fertilized eggs

Fig. 4.1. Comparative embryology from fish to man. (Modified from Gregory, W. K., and M. Roigneau, *Introduction to Human Anatomy*, American Museum of Natural History, 1934. Courtesy of the American Museum of Natural History.)

HOMOLOGY IN EARLY DEVELOPMENT The earliest stages of embryonic development, even in much more diverse forms than those included in Fig. 4.1, which after all are all vertebrates, are remarkably similar—so much so that it is possible to design a "typical" diagram of early stages in development. Figure 4.2 shows typical development of an ovum containing little yolk, for example, starfish and sea urchin eggs among invertebrates or amphioxus eggs in phylum Chordata, the phylum to which vertebrates and a few other animals belong. In its essential features, however, the sequence of changes shown characterizes all animals. Figure 4.2 is related to Fig. 4.1 in the following manner. Stage *a* of Fig. 4.2 represents a fertilized ovum like those shown in the bottom row of Fig. 4.1. Stages *f* and *g* represent the stage shown in the second horizontal row of Fig. 4.1. Thus stages *b* through *e* stand in between the bottom and the second rows of Fig. 4.1, and

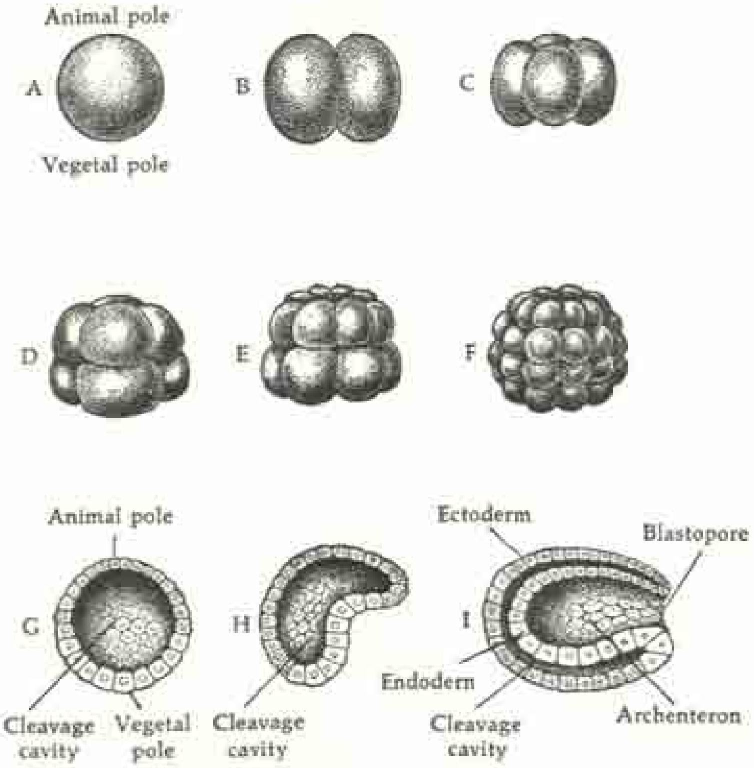

Animal pole
A
Vegetal pole
B
C
D
E
F
Animal pole
G
H
I
Ectoderm
Blastopore
Endoderm
Cleavage cavity
Vegetal pole
Cleavage cavity
Cleavage cavity
Archenteron

Fig. 4.2. Typical early embryonic development: *g*, *h*, and *i* are shown cut in half. (From Guyer, M. F., *Animal Biology*, 4th ed., Harper & Row, 1948.)

stages *h* and *i* are slightly later stages than the stage shown in the second row of that figure.

Figure 4.2 demonstrates that the fertilized ovum undergoes a series of cell divisions. The original single cell divides into two *(b)*, then each of these two divides into two in turn, the result being a four-celled stage *(c)*. The cells continue to divide, so that we have successively an eight-celled stage *(d)*, a 16-celled stage *(e)*, a 32-celled stage and so on. As the process continues there comes into existence a ball of cells, more or less hollow in the center, called a BLASTULA; *g* in Fig. 4.2 represents a blastula sliced open to reveal its internal cavity, the CLEAVAGE CAVITY. Essentially, a blastula is an embryo composed of a single layer of cells, as shown in the figure. This one-layered stage then proceeds to convert itself into a two-layered embryo, the GASTRULA *(i)*. Gastrula formation occurs in a variety of ways, various expedients being resorted to if the presence of yolk impedes the process. Figure 4.2 shows the relatively simple process possible when the cleavage cavity is not obstructed with yolk. One side of the blastula swings inward *(h)*; this in-bending, accompanied by continued cell division, suffices to produce the condition shown at *i*.

With attainment of the gastrula stage an embyro shows forecasts of things to come. The cells remaining on the outside constitute a layer called the ECTODERM, obviously in position to form the outer surface of the body. The cells that fold inward form a layer called the ENDODERM lining the newly formed cavity, the ARCHENTERON. The latter is the beginning of the digestive tract. The archenteron has but one opening to the exterior, the BLASTOPORE. In many invertebrates the blastopore becomes the mouth, at or near the anterior end of the body. In vertebrates, on the other hand, the region of the blastopore becomes the posterior or tail end of the body, though usually the blastopore itself does not remain as the posterior opening of the digestive tract, the anus.

Almost at once a third layer, the MESODERM, forms; although this is not shown in Fig. 4.2, it can be visualized as located in the remnant of the cleavage cavity, between the ectoderm on the outside and the endoderm on the inside.

The ectoderm gives rise to the external surface of the body, including such things as skin, scales, feathers and hair and to the nervous system and the sensory membranes of the sense organs. The endoderm lines the digestive tract and gives rise to glands associated with digestion, such as liver and pancreas. The lining of the lungs of land-dwelling vertebrates also arises from the endoderm. The mesoderm forms almost everything else: muscles, bones, kidneys, connective tissue, and so on.

The pattern of development illustrated above may be said to consist of the following sequence: (1) single cell; (2) successive cell divisions to form clusters of two, four, eight, 16, and so on, cells; (3) a one-layered stage; (4) a two-layered stage; (5) a three-layered stage. The uniformity of occurrence of this pattern of development throughout the animal kingdom, from worms to man, is remarkable.

At least two factors must be operative in the production of this uniformity: In the first place, the number of ways in which an organism consisting of multitudes of cells arranged in layers can arise from a single cell must be limited. In part, then, the uniformity is imposed by those mechanical and physiological necessities mentioned previously. Such necessities would operate to produce similarities in the broad outlines of development. Similarities in details of development, on the other hand, are more likely to have resulted from a second factor: inheritance from common ancestry.

VON BAER'S RULE Long before belief in evolution became prevalent, biologists arranged animals into a "scale of beings," starting with simpler organisms and advancing to more and more complex ones. It was noted that the embryos of the more complex, "higher," organisms somewhat resembled the organisms lower on the scale. Difference of opinion arose as to whether the resemblance was between embryos of higher organisms and *adults* of lower organisms or between embryos of higher organisms and *embryos* of lower ones. As the science of embryology advanced, this second interpretation was recognized as being correct. Early in the nineteenth century, von Baer, from whom we have already quoted, formulated this principle as follows: "The young stages in the development of an animal are not like the adult stages of other animals lower down on the scale, but are like the young stages of those animals" (de Beer's translation, 1958).

Later in the century, when belief in evolution became widespread, von Baer's rule was interpreted to mean that such similarities between embryos result from inheritance from common ancestry, as mentioned above. In other words, embryos exhibit homologous similarities just as adults do, and the evolutionary interpretation of these similarities is the same as it is for homologous similarities of adults.

THEORY OF RECAPITULATION Not everyone agreed with von Baer's principle. Later in the nineteenth century Ernst Haeckel strongly supported the theory that the embryos of higher animals repeat the *adult* stages of their ancestors (Haeckel, 1905). This was the theory of recapitulation or biogenetic law and is tersely summarized by the statement: "Ontogeny recapitulates phylogeny."

Ontogeny is the life history of the individual, starting with the ovum; phylogeny, as the term was used by Haeckel, is the series of adult ancestors of the individual in question. Haeckel maintained that in some way the adult condition of an ancestor is pushed back into embryonic development so that embryos of descendants pass through that ancestral adult stage. We shall see presently, for example, that in one stage the human embryo resembles a fish embryo. Haeckel would not have been satisfied with such a statement; he would have insisted that the human embryo at that stage resembles an adult fish. The recapitulation theory was a stimulus to research in embryology, but as investigation led to more complete knowledge of the subject it became evident that Haeckel was wrong and that von Baer had been right. The pros and cons of this intellectual conflict are ably set forth in de Beer's *Embryos and Ancestors* (1958).

HOMOLOGIES IN HUMAN EMBRYOLOGY

If the evolutionary interpretation of von Baer's rule is correct, we should be able to learn something of the evolutionary relationships of animals by comparing their embryologies (ontogenies), a point stressed by Darwin himself. Related organisms may be expected to show similarities in their patterns of development. Furthermore, as noted in our discussion of Fig. 4.1, the more closely related two animals are, usually the greater will be the proportion of their ontogenies exhibiting similarities. Thus the human embryo and the monkey embryo are similar throughout much more of their development than are the human embryo and the fish embryo (Fig. 4.1).

Turning to our own embryology, we recall that each human being begins life as a single cell, the fertilized ovum. This was formed by the union of a sperm cell produced by the father with an ovum produced by the mother. The first cell divisions with which the fertilized ovum begins its development are much like those diagramed in Fig. 4.2. As a result of repeated cell division a ball of cells is formed. This is similar to the blastula (Fig. 4.2) except that it is at first not hollow. As shown in Fig. 4.3, a cavity soon forms, following which an outer layer, the TROPHOBLAST, and an INNER CELL MASS can be distinguished. At about this stage the embryo digests its way into the wall of the uterus of its mother, where it comes in close contact with the latter's blood. This blood supplies the embryo with food and oxygen and removes waste products. The trophoblast forms the means of contact between the embryo and the maternal bloodstream and contributes to the formation of the embryonic membrane known as the CHORION. The embryo itself develops in the inner cell mass.

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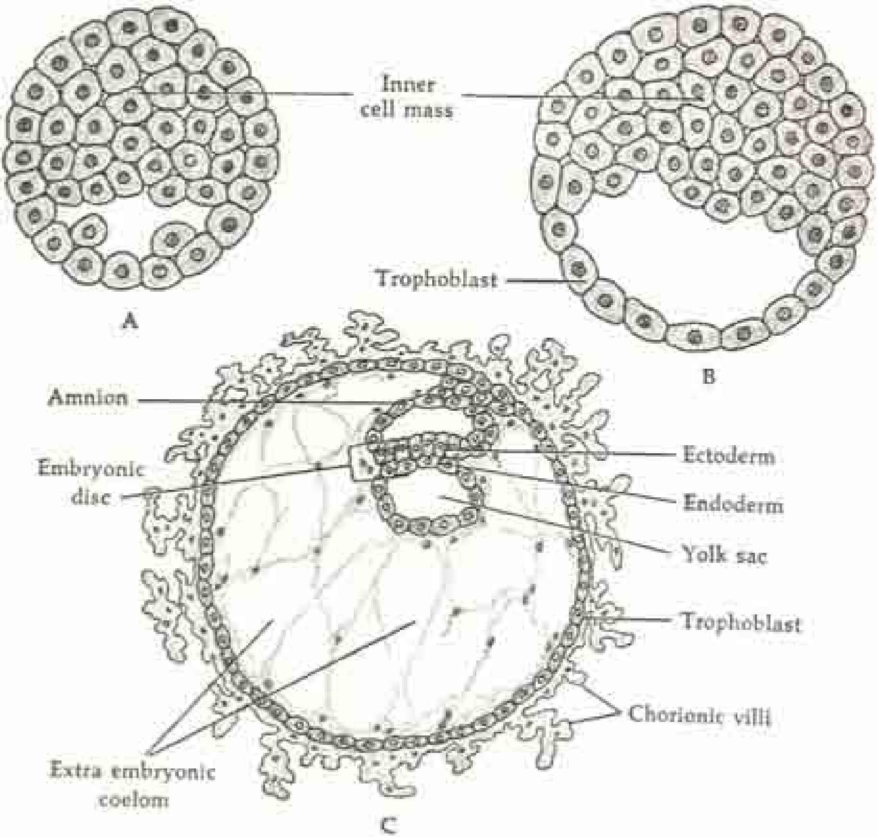

Inner cell mass
Trophoblast
A
B
Amnion
Embryonic disc
Ectoderm
Endoderm
Yolk sac
Trophoblast
Chorionic villi
Extra embryonic coelom
C

Fig. 4.3. Human embryonic development during the first 12 or 13 days following fertilization. (Based on several sources including Gilbert, M. S., *Biography of the Unborn*, Copyright 1938 The Williams & Wilkins Company.)

The inner cell mass soon becomes differentiated by the formation of two cavities separated by a double layer of cells (Fig. 4.3C). The upper cavity is called the AMNION, the lower one the YOLK SAC, and the double layer separating them is referred to as the EMBRYONIC DISC. The embryo itself forms from this embryonic disc, the two layers of which are the ectoderm and the endoderm. Hence this two-layered stage of the human embryo corresponds to the gastrula stage of typical development (Fig. 4.2), although it differs from the typical form in appearance and in method of formation. There is interest in the fact that gastrulation and mesoderm formation in the human embryo, as in the embryos of other mammals, are more like these processes in large-yolked eggs (e.g., reptiles and birds) than they are like the processes in small-yolked ones (e.g., Fig. 4.2). This is true despite the absence of yolk. The explanation of this fact will become evident from the discussion following.

AMNION, YOLK SAC, AND ALLANTOIS The amnion, yolk sac, and allantois are called extraembryonic membranes because they are attached to the embryo but are not part of it. As soon as the embryo passes beyond the embryonic disc stage, the AMNION surrounds the

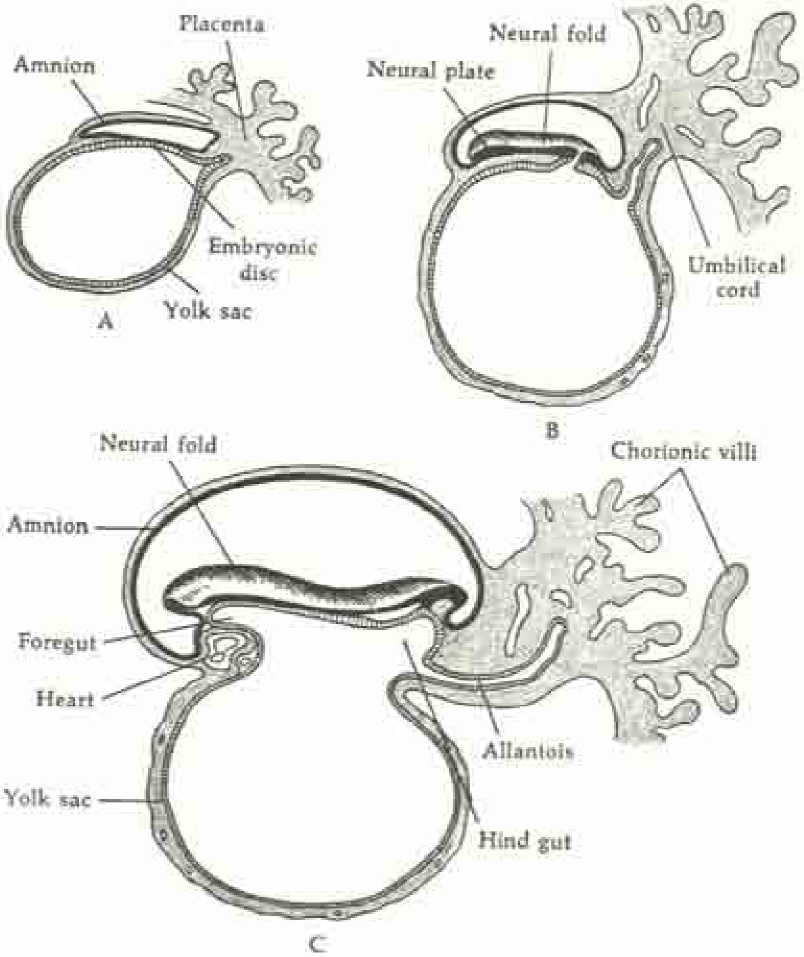

Placenta
Amnion
Embryonic disc
Yolk sac
A
Neural fold
Neural plate
Umbilical cord
B
Neural fold
Chorionic villi
Amnion
Foregut
Heart
Allantois
Yolk sac
Hind gut
C

Fig. 4.4. Human embryonic development during the third week. Longitudinal (sagittal) sections through the embryo and membranes. Ectoderm indicated with solid black, endoderm with cross lines, mesoderm with fine dots. (After Arey, L. B., *Developmental Anatomy*, 7th ed., W. B. Saunders Co., 1965.)

embryo, enclosing it in liquid and thus protecting it from mechanical and other injuries (Fig. 4.4C).

To understand the other two membranes we must examine the eggs of reptiles and birds (Fig. 9.23, p. 173). These animals lay eggs that are deposited in nests or buried in the soil and have an outer protective shell. Within those shells must be stored enough food (yolk) to nourish the embryo until it is ready to hatch and begin active foraging for its food. The large, yellow, globular yolk in a hen's egg is familiar to everyone. The embryo develops on top of this mass, and early in its development a large YOLK SAC grows out from the embryo and encloses the yolk. The lining of the yolk sac contains cells that digest the yolk, the products of digestion being carried to the embryo by blood vessels. Although most mammalian embryos obtain their nourishment in an entirely different manner, they nevertheless develop yolk sacs connected to the digestive tract just as do reptile and bird embryos (Figs. 4.4, 4.8, and 4.9).

The ALLANTOIS connected to reptile and bird embryos is also a large, useful membrane (Fig. 9.23, p. 173). It spreads around beneath the shell and shell membranes and serves in respiration and excretion (pp. 173–174). In most mammals, including man, the allantois is much reduced in size (Fig. 4.4C). Since the human embryo obtains its oxygen, as well as nourishment, from the mother's blood through the placenta (see below) and passes its waste products into the mother's blood, we may wonder why an allantois develops at all.

Considering the three extraembryonic membranes together, we see an example of a common embryonic pattern illustrative of von Baer's rule: Modern reptiles, birds, and mammals are similar in that they develop these membranes. We interpret this similarity as evidence that these three groups had a common ancestor. What was the nature of that ancestor? Embryology by itself cannot tell us, but as we shall see in Chapter 10, there is strong evidence that reptiles were ancestral to birds and to mammals. Accordingly, the membranes are thought to have originated when a group of prehistoric reptiles first developed the ability to produce eggs that no longer needed the protection of water (as frogs' eggs do; pp. 173–174).

We note that the three membranes differ in their importance to the human embryo and to most other mammalian embryos. The amnion continues to serve the same function it does for reptile and bird embryos. The yolk sac, on the other hand, has lost its function as a container of yolk. Why has it not disappeared completely? Does it still, perhaps, have some function? Embryologists have found that for some mammalian embryos, at least, it has a use, though one entirely unrelated to yolk. In these cases it contains the primordial germ cells—cells that later develop into sperms and ova. These primordial cells migrate into the reproductive organs when these organs form in the embryo.

As for the greatly reduced allantois, it contributes to the formation of the umbilical cord and placenta (Figs. 4.4 and 4.10; see below). In some mammals other than man (e.g., sheep) it retains one of the functions it has in reptiles and birds: that of a storage bag for urine produced by the embryo (see Ballard, 1964).

SOMITES Returning to the embryo itself, we note that during the first few days it grows rapidly. In Fig. 4.4 most of the trophoblast shown in Fig. 4.3 has been removed, with only that portion (the PLACENTA) most directly connecting the embryo to the wall of the uterus being shown. The embryonic disc becomes elongated, and the cavities above and below it become enlarged. Almost immediately the disc forms the beginning of the central nervous system. Two parallel NEURAL FOLDS are thrust up into the overlying amniotic cavity (Figs. 4.4 and 4.5B). These folds become more and more elevated above the surface of the embryonic disc. Eventually they bend toward each other and fuse to form a NEURAL TUBE. As shown in Fig. 4.5C, fusion of the folds occurs first in the middle of the "back" (really dorsal surface) of

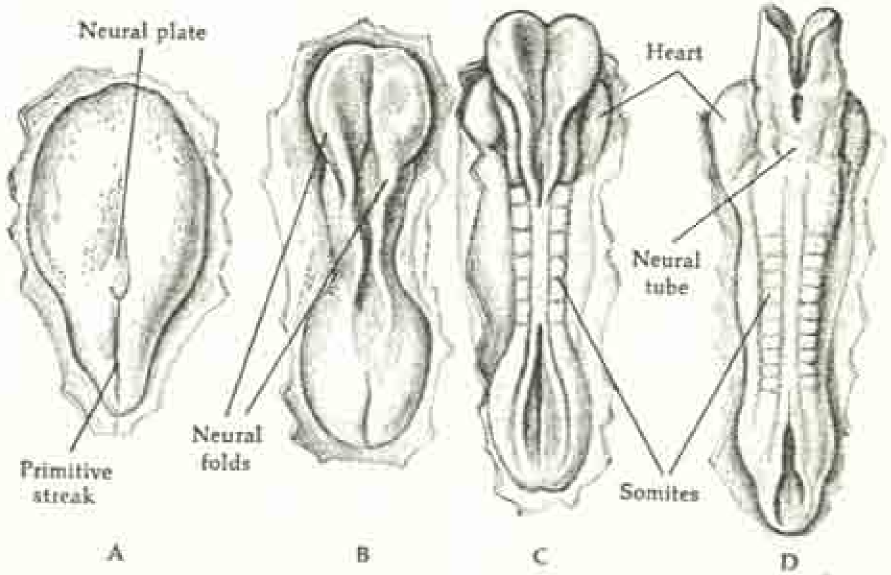


Fig. 4.5. Human embryonic development during the third and fourth weeks. Dorsal view, showing the "back" of the embryo. (After Arey, L. B., *Developmental Anatomy*, 7th ed., W. B. Saunders Co., 1965.)

the embryo, progressing from that point toward the head or anterior end and toward the tail or posterior end (Fig. 4.5D) as though being closed by zippers. The neural tube is wider at the anterior end than it is more posteriorly. The anterior portion will form the BRAIN; the rest the SPINAL CORD.

As we see in Fig. 4.5 and subsequent figures, rows of blocklike SOMITES form on both sides of the developing neural tube. These are more or less cubical blocks of mesodermal tissue forming between the ectoderm and the endoderm. The ectoderm is molded over them so that their outlines are visible externally. The first ones form just posterior to what will be the head, and later ones are added progressively, as shown. Somites form, among other things, the beginnings of the BODY MUSCULATURE.

We should now stress that mesoderm formation in this somite pattern is a very widespread embryonic pattern indeed, much more widespread than is the pattern of extraembryonic membranes discussed above. In fact it is a pattern that characterizes the embryos of *all vertebrates* (see Fig. 4.1, third row from the bottom). In line with von Baer's rule, therefore, we suspect that it forms one indication that all vertebrates had a common ancestor.

What was the nature of this ancestor? Again, embryology by itself cannot answer, but we learn from the fossil record that the first vertebrates were swimming animals of a type we may loosely characterize as "fish" (although the first ones did not have jaws of the sort possessed by most of the fishes with which we are familiar; see pp. 165–166). These first vertebrates had elongated bodies with muscles

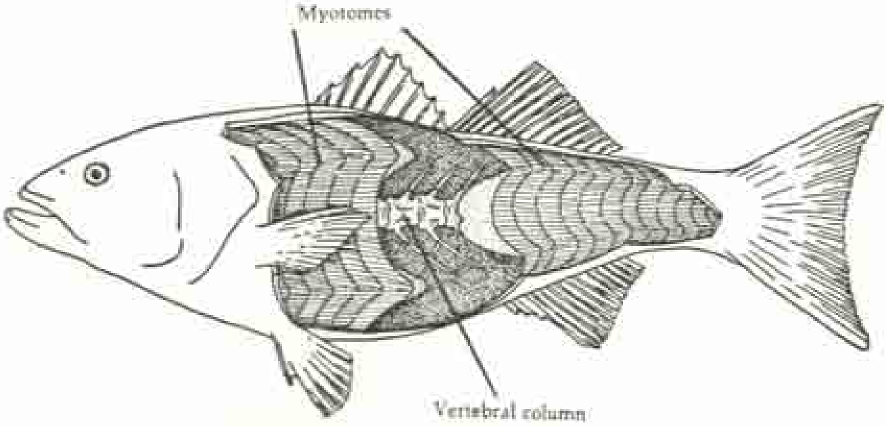


Fig. 4.6. Locomotor apparatus of a typical teleost fish. (After Gregory, W. K., and M. Roigneau, *Introduction to Human Anatomy*, American Museum of Natural History, 1934. Courtesy of the American Museum of Natural History.)

arranged in the form of segmental MYOTOMES, somewhat as does the modern perch (Fig. 4.6). Having the beginnings of the muscular system arranged in the form of a series of block-like somites would seem to be preparation for the formation of series of myotomes of the type possessed by fishes and other vertebrates that swim by undulations of the body (Fig. 4.7), or, for that matter, by elongated land animals such as salamanders, lizards and snakes that also move by undulations of the body.

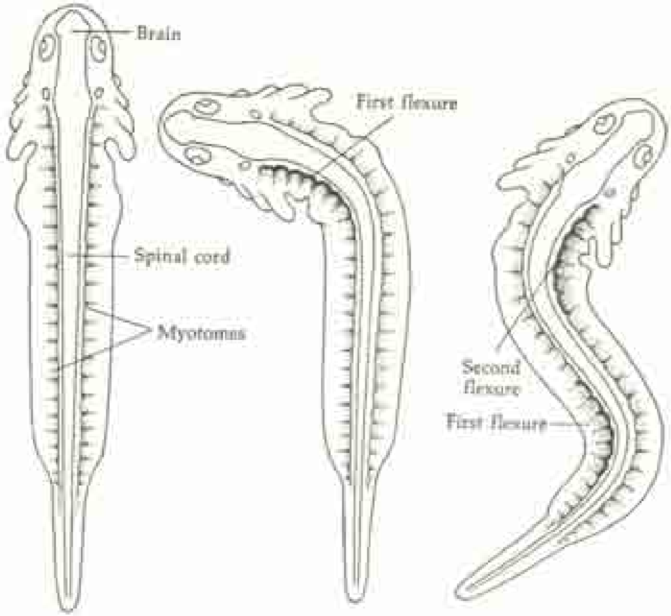


Fig. 4.7. Action of segmental body muscles in producing swimming movements in the aquatic larva of the salamander *Ambystoma*. The undulations result from alternate flexures on the right and left sides of the body, and these flexures are produced by contraction of a number of adjacent myotomes. Each flexure starts near the head and travels toward the tail by contraction of one myotome after another on the tail end of the flexure, accompanied by relaxation of one myotome after another on the head end of the flexure. As these bends in the body travel backward they press against the surrounding water, and give the tail a sculling motion. Thus the body is propelled forward. (After Coghill, G. E., *Anatomy and the Problem of Behaviour*, Cambridge University Press, 1929.)

But why do all other vertebrate embryos also begin their muscular systems with such a pattern of somites, even though, like birds and most mammals including man, the adults have entirely different methods of locomotion than do fishes? The most reasonable answer seems to be that this is an embryonic pattern inherited from aquatic ancestors.

BRANCHIAL GROOVES While the neural tube and somites have been forming, other changes have also taken place (Fig. 4.8). The heart has started to form, for example (Fig. 4.9). As the body increases in size, the embryo bulges up more and more into the amniotic cavity. Soon the embryo is free from underlying tissues, remaining attached to the wall of the uterus by the stalklike UMBILICAL CORD (Fig. 4.10; Fig. 10.12, p. 200). This cord contains blood vessels carrying the embryo's blood to and from the PLACENTA (Fig. 4.10), where it comes in close contact with the mother's blood, though the two bloods are separated by thin membranes. As shown in the figure, "buds" representing the beginnings of arms and legs have appeared, as also have the eyes.

Also noticeable in Figs. 4.9 and 4.10 are the BRANCHIAL GROOVES in the lower head and neck region. As indicated in Fig. 4.1, this is

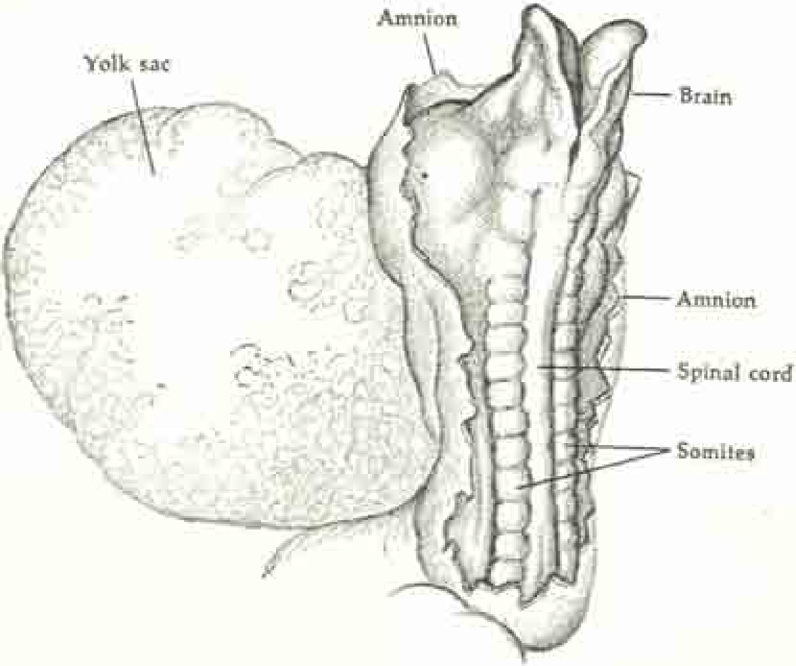


Fig. 4.8. Human embryo of about 20 days. Amnion partially cut away to reveal the embryo. (After Corner, G. W., in *Contributions to Embryology*, Carnegie Institution of Washington, Vol. 20, 1929.)

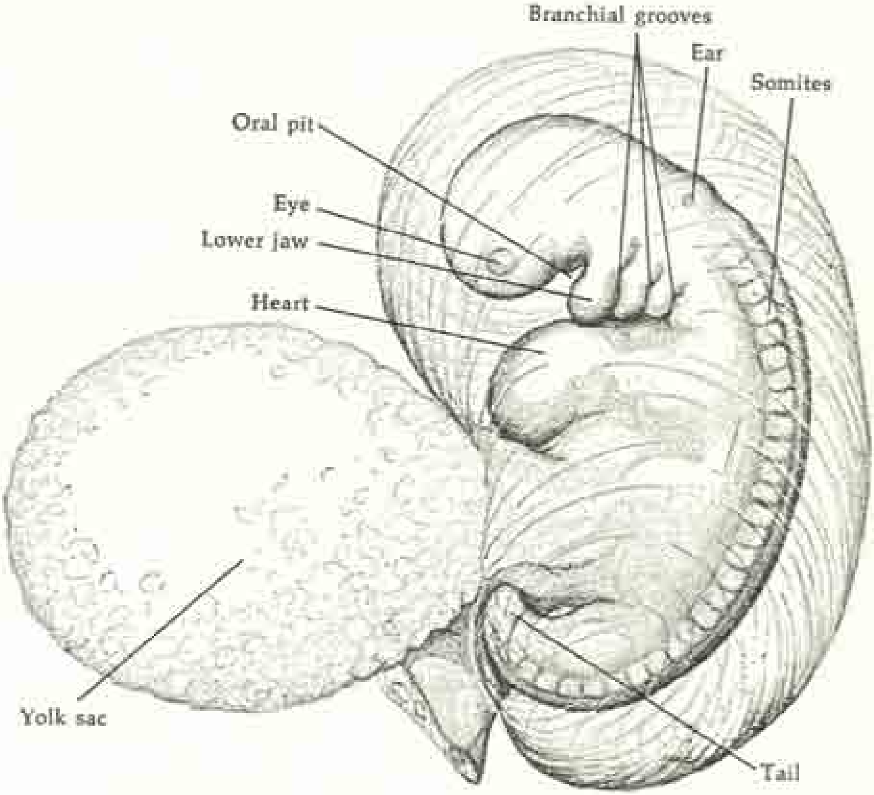


Fig. 4.9. Human embryo of the fourth week. (Based in part on an embryo in the collection of the Department of Embryology of the Carnegie Institution of Washington.)

also an extremely ancient embryonic pattern, shown by all vertebrate embryos. What is its significance?

Corresponding to the grooves on the outside of the body is a series of pharyngeal pouches in the wall of the digestive tract, in the region called the pharynx. In fish embryos the grooves on the outside finally meet the corresponding pouches from the inside. A perforation then occurs, converting the grooves into slits or clefts—openings directly from the pharynx to the exterior of the body. What is the function of these gill slits? Figure 4.11 presents diagrams of the head of a shark with portions of the surface cut away so that mouth, pharynx, and connected structures may be seen. As the fish swims, water is taken into the mouth and passes to the exterior through the gill clefts (note the arrows). As it passes through the clefts the water bathes the GILLS lining the walls of the clefts. The gills are soft,

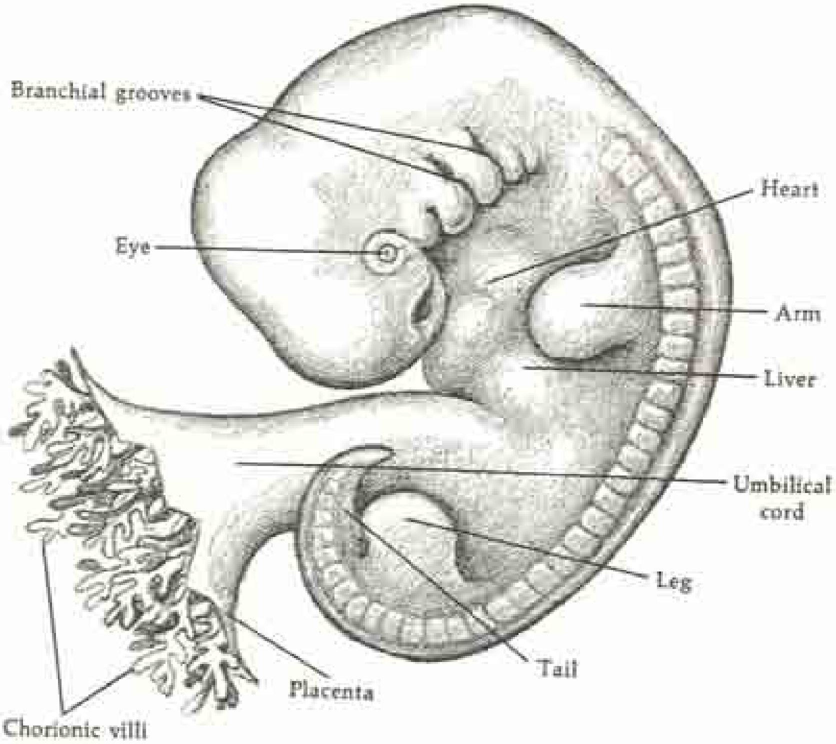


Fig. 4.10. Human embryo at the end of the first month (7 mm.). (Based on His, and on Gilbert, M. S., *Biography of the Unborn*, Copyright 1938 The Williams & Wilkins Company.)

fleshy structures with surfaces richly supplied with capillaries of the blood system. Since the blood in the capillaries is separated by only a thin membrane from the water passing through the clefts, means is provided for the taking on by the blood of oxygen dissolved in the water and for the giving up to the water of carbon dioxide carried by the blood. This is the mechanism by which the fish breathes.

Why do the embryos of other vertebrates, such as reptiles, birds, and mammals, which never breathe by means of gills, develop branchial grooves and pharyngeal pouches as though they *were* going to have gill slits? Evidently this is an embryonic pattern found in fish embryos and inherited by the descendants of the fishes, including the land-dwelling vertebrates.

It is probable that the ancestral fishes inherited the embryonic pattern from still more remote ancestors in which gill slits served more for food collecting than for respiration. This is in connection

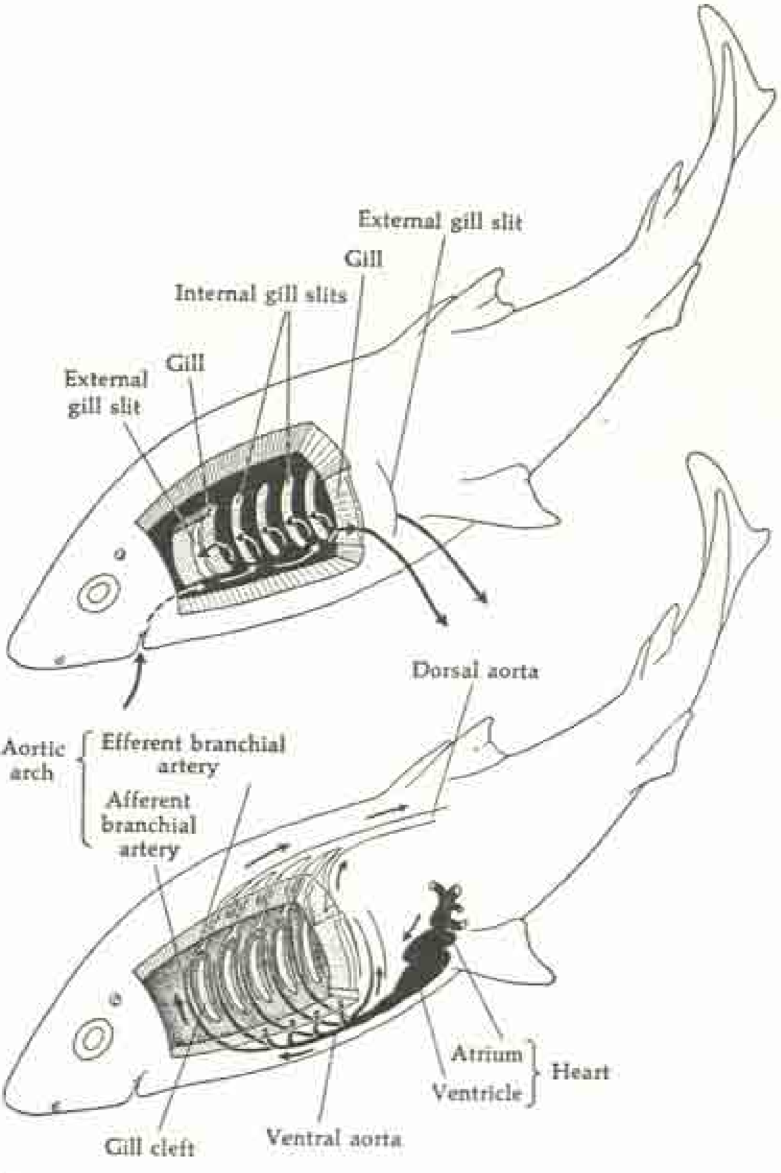

External gill slit
Gill
Internal gill slits
Gill
External gill slit
Dorsal aorta
Aortic arch
Efferent branchial artery
Afferent branchial artery
Atrium
Ventricle
Heart
Gill cleft
Ventral aorta

Fig. 4.11. Respiratory mechanism (upper diagram), and heart and aortic arches (lower diagram) of a fish (shark). A "window" has been cut into the pharynx. In the upper diagram arrows indicate paths of water currents. In the lower diagram arrows indicate direction of blood flow.

with the filter feeding referred to on p. 68, but a discussion of it would lead us too far afield (see Romer, 1962; Carter, 1967).

Although no gill slits develop in the human embryo or in the embryos of other mammals, birds, and reptiles, the pharyngeal pouches contribute to the developing organism. Thus the middle ear and its connection to the throat (pharynx), the eustachian tube, develop from the first pouch, and the thymus and parathyroid glands develop from other pouches.

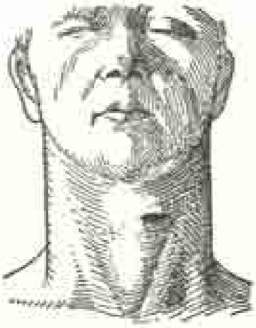


Fig. 4.12. Cervical fistula originating from the second pharyngeal pouch. (From Arey, L. B., *Developmental Anatomy*, 7th ed., W. B. Saunders Co., 1965.)

Occasionally a perforation will occur between a pharyngeal pouch and its corresponding branchial groove. The result is a CERVICAL FISTULA, an opening from the nasal cavity or throat to the surface of the head below the ear or to the surface of the neck, the exact location depending on which of the pouches forms the fistula (Fig. 4.12). A cervical fistula, then, results from return by one pharyngeal pouch to embryonic procedures normal to a fish embryo but abnormal for human embryos. Abnormal structures of this kind, reminiscent of normal embryonic structures of ancestors, are called REVERSIONS or ATAVISMS.

AORTIC ARCHES Although the human embryo does not develop gills, it forms a series of blood vessels in a pattern like that followed by fish embryos, which *do* develop gills. These blood vessels are the AORTIC ARCHES (Fig. 4.13). Typically, there is an aortic arch running through the tissue separating each pharyngeal pouch from its neighbor, as shown in the figure. Blood is propelled forward by the heart, enters

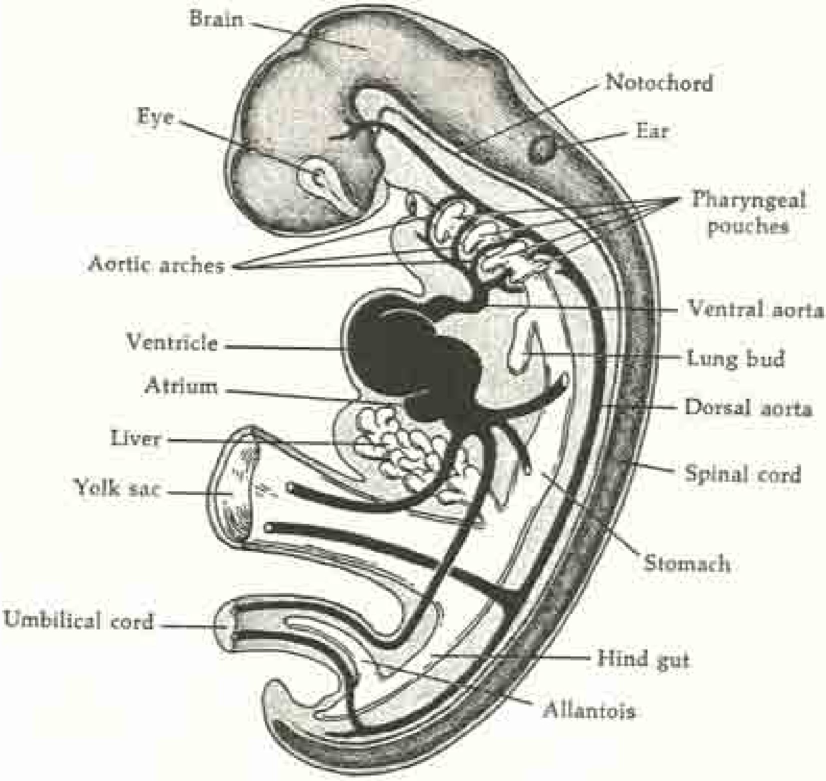

Brain
Notochord
Eye
Ear
Pharyngeal pouches
Aortic arches
Ventral aorta
Ventricle
Lung bud
Atrium
Dorsal aorta
Liver
Spinal cord
Yolk sac
Stomach
Umbilical cord
Hind gut
Allantois

Fig. 4.13. Human embryo of 4 mm. dissected to show digestive tract and aortic arches. (After Arey, L. B., *Developmental Anatomy*, 7th ed., W. B. Saunders Co., 1965.)

the ventral aorta, and then passes through the aortic arches into the dorsal aorta. In fishes a gill develops in the wall of each pharyngeal pouch, as noted above. The aortic arches supply blood to these gills (afferent branchial arteries, Fig. 4.11) and remove blood from the gills, conveying it to the dorsal aorta (efferent branchial arteries, Fig. 4.11).

Why do the embryos of terrestrial vertebrates that do not develop gills nevertheless develop a series of aortic arches as though preparing to supply gills? Evidently we see here inheritance of another embryonic pattern from remote ancestors that were fishes, in the broad sense of the term.

In the human embryo six pairs of aortic arches appear, although not all are fully developed at any one time. (They occur in pairs because the pharyngeal pouches are paired on the right and left sides, respectively, of the pharynx.) The six pairs of arches have a varied fate. Three of them disappear. Of the other three, one persists in connection with the system of arteries supplying blood to the head (carotid arteries), another persists on the left side as the connection between the heart and the dorsal aorta, and the third (actually arch number six) forms the pulmonary arteries conveying blood to the lungs. Thus we see how arteries "designed" for one purpose are made over to serve other functions when the original function is discarded or becomes obsolete.

HEART We have mentioned the heart as the organ propelling the blood forward into the ventral aorta, and so to the aortic arches.

The heart appears first in a form like that of the hearts of fish embryos. A typical fish heart has four chambers (Fig. 4.14). Blood from the veins is received by the SINUS VENOSUS, a collecting chamber that sends it on to the ATRIUM. The atrium sends the blood into the VENTRICLE, the most muscular chamber of the heart. The ventricle forces the blood into the fourth chamber, the CONUS ARTERIOSUS, which sends it into the ventral aorta. (The fourth chamber is sometimes called the bulbus cordis, based on a technical distinction that need not concern us.)

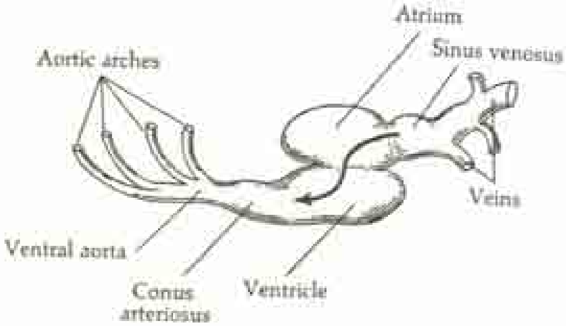


Fig. 4.14. Heart and aortic arches of a teleost fish. (See Fig. 4.11). Arrow indicates direction of blood flow.

Hence, in effect, the fish heart is a single pump composed of four parts arranged in tandem and having as its function the sending of blood to the gills. In man and other terrestrial vertebrates that have no gills the heart is a *double* pump, having two atria (plural of atrium) and two ventricles. One ventricle (typically the right one) sends blood to the lungs; the other ventricle, having received aeriated blood from the lungs (through the left atrium), propels the blood throughout the body through the arteries. Separation between right and left pumps is not complete in most reptiles, though it is in birds and mammals.

The point of interest at the moment is the fact that the fish embryo pattern of four chambers in tandem is found in the early embryos of these vertebrates that will develop the double-pump adult structure. By various means in different species the single-pump arrangement is converted by later embryos into the double structure characterizing the adult heart. Details of the processes will be found in discussions of comparative embryology and anatomy (e.g., Ballard, 1964).

PHARYNGULA In summary we may note that an early embryo in the stage we have been discussing is sometimes called a PHARYNGULA. The pharyngeal pouches, with their corresponding branchial grooves, the aortic arches, the heart of four chambers in tandem, and the somites all characterize this stage (although the somites first put in their appearance somewhat before it). The pharyngula is evidently a very ancient embryonic pattern. Indeed, as stated by Ballard (1964): "All vertebrate embryos at this stage have acquired a similar and nearly complete set of organs, similarly arranged, which constitutes the BASIC PATTERN OF VERTEBRATE ANATOMY" (emphasis in original).

We have concentrated upon only a small sample of the ways in which the human embryo resembles embryos of lower vertebrates. Many other traits might be cited. For example, there are bars of cartilage in the walls of the pharyngeal pouches. In fishes these cartilages stiffen the walls of the pharynx and support the gills. In embryos of higher vertebrates the cartilages appear in typical arrangement and then are made over to serve a variety of other functions, forming especially the jaws, the skeletal support for the tongue, and cartilages of the larynx. Other examples range all the way from kidneys to brains. But the examples given suffice to illustrate the general principle of embryonic homologies, though we might cite one additional example, that of the TAIL (Fig. 4.10). At this stage the human embryo seems prepared to provide us with as adequate a tail as that possessed by any lower mammal—our dog and cat companions, for example. The tail reaches its maximum relative length when the embryo is about six weeks old. At that time its length may be about one-sixth that of the embryo. But as the body grows, the tail fails to keep pace. Soon it is lost to view externally, persisting as the vestigial coccyx mentioned earlier (p. 43).

HUMAN FETUS So far our account of human embryology has brought us through only the first of the nine months of prenatal development (Fig. 4.10). At this time the embryo is only about ¼ in. long. It continues to grow and develop rapidly. By about the end of

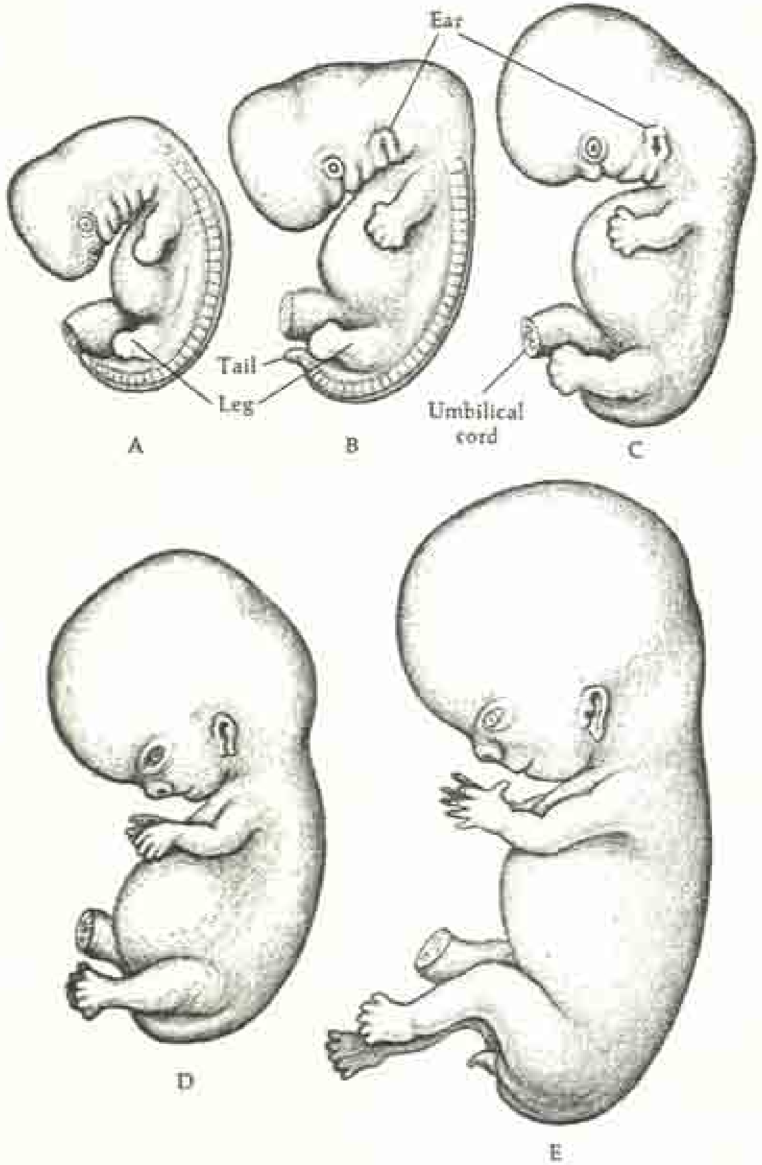

Ear
Tail
Leg
Umbilical cord
A
B
C
D
E

Fig. 4.15. Human embryos and fetuses. A, fifth week (10 mm.). B, sixth week (13 mm.). C, seventh week (15 mm.). D, seventh week (17 mm.). E, eighth week (23 mm.). (Based on His, and on Gilbert, M. S., *Biography of the Unborn*, Copyright 1938 The Williams & Wilkins Company.)

the second month the developing individual has a distinctly human appearance, and thenceforth by convention it is called a fetus rather than an embryo (Fig. 4.15).

EMBRYONIC SIMILARITIES AID IN CLASSIFICATION Earlier in the chapter we noted that embryos of diverse animals tend to resemble each other more than the adults do (p. 46). This being the case, we may anticipate that embryonic similarities will aid us in classifying animals when such classification is difficult on the basis of adult anatomy. Such an anticipation is justified in many cases, but there are cases in which the younger stages are more unlike than are the adults. This is particularly true among invertebrates having complex life histories in which the younger stages are free-living forms strikingly adapted to meet varied needs of larval existence (see de Beer, 1958). Nevertheless, embryonic similarities may be useful in helping us to classify organisms.

As an illustrative case we may consider the TUNICATES. One of the simpler members of the group is *Molgula* (Fig. 4.16). This is a small, soft-bodied creature living in the sea and attached to rocks, the pilings of wharves, and the like. Its outer surface is a tunic (hence the name "tunicate") of cellulose. It has a method of feeding that is very

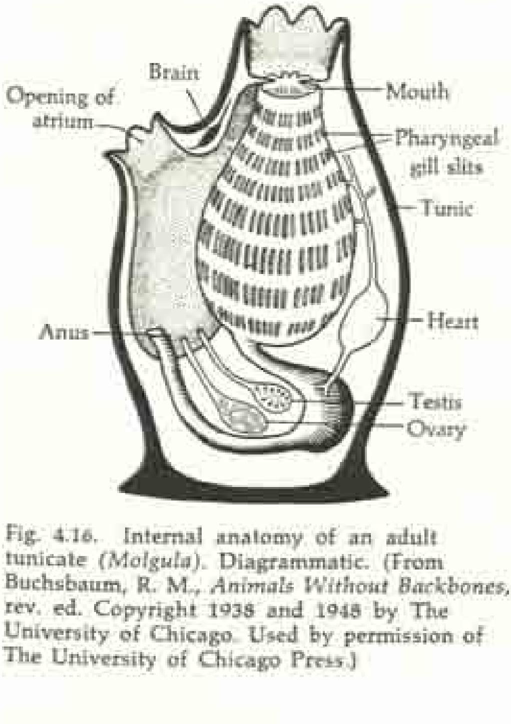


Fig. 4.16. Internal anatomy of an adult tunicate *(Molgula)*. Diagrammatic. (From Buchsbaum, R. M., *Animals Without Backbones*, rev. ed. Copyright 1938 and 1948 by The University of Chicago. Used by permission of The University of Chicago Press.)

common among aquatic invertebrates: filter feeding (p. 62). Clams and oysters, for example, obtain their food in much the same manner. The food consists of tiny plants and animals in the seawater, which is literally strained to obtain the organisms suspended in it. The water enters the mouth, propelled by the beating of countless, microscopic, hairlike structures called cilia. As shown in the figure, this water enters a pharynx having its walls perforated by large numbers of openings (gill clefts). In the sides of these openings other cilia aid in trapping food particles and in conveying them into the intestine. After having passed through the gill clefts, the strained water enters a cavity known as the atrium, from which it is propelled to the exterior.

Partly because of this similarity of feeding to that of such molluscs as clams and oysters, tunicates were at one time considered molluscs, or relatives of molluscs.

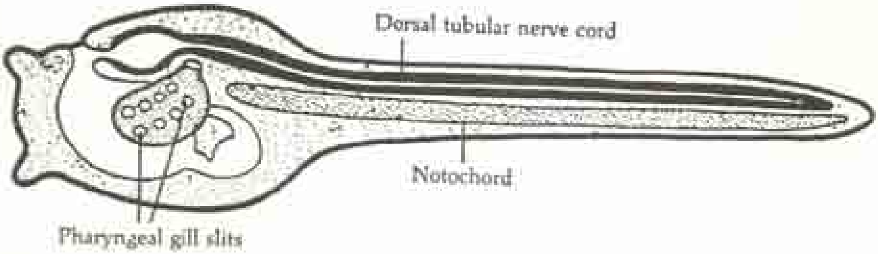


Fig. 4.17. Internal anatomy of a larval tunicate (*Molgula*). Diagrammatic. (From Buchsbaum, R. M., *Animals Without Backbones*, rev. ed. Copyright 1938 and 1948 by The University of Chicago. Used by permission of The University of Chicago Press.)

Later the young or larval stages of tunicates were discovered. Unlike the adults, these larvae are free-swimming tadpolelike creatures (Fig. 4.17). The swimming tail is stiffened by a NOTOCHORD. [The notochord is an unsegmented rod that is located in vertebrate embryos in the position later to be occupied by the vertebral column or backbone. In a few relatives of vertebrates, e.g., *Amphioxus*, and in a very few vertebrates, e.g., lampreys, it persists throughout life as an elastic, stiffening rod.]. The pharynx with its GILL CLEFTS is forming. And there is a small BRAIN and SPINAL CORD DORSAL in position. These are three of the most distinctive characteristics of phylum Chordata (the phylum to which all vertebrates belong) and are most unlike structures possessed by members of phylum Mollusca. Evidently, therefore, tunicates belong in phylum Chordata. [Filter feeding, incidentally, is found in some other members of this phylum, e.g., *Amphioxus*, and the ammocoete larva of the lamprey (see Carter, 1967).]

Was the ancestor of tunicates more like the larva or more like the present adult form? As in most cases where there is no definitive information, both points of view have been held. Those who consider that the ancestor was a free-swimming creature regard the sessile adult as a highly specialized descendant. On the other hand, perhaps the ancestor was a sessile, filter feeder. In view of the widespread occurrence of filter feeding among invertebrates, this seems a reasonable conclusion. According to this view, "The tail first appeared as an adaptation in the larva, rendering easier the search for a suitable place in which the animal could 'settle down'" (Romer, 1962). Such an interpretation would suggest that in the evolution of chordates the free-swimming habit arose by the elimination of a sessile adult stage, organisms that had previously been larvae becoming capable of reproduction (a phenomenon commonly known as neoteny; see de Beer, 1958).

ORIGIN OF THE METAZOA

We conclude our discussion of evolutionary aspects of embryology with an enigma of long standing. If, as is commonly believed, single-celled organisms preceded many-celled ones in the waters of this planet, by what sort of process did the many-celled descendants arise from their single-celled ancestors? Or, in terms of the animal kingdom, how did the Metazoa arise from the Protozoa?

It has long been thought that embryology may give us evidence on which to base an answer to this question. We return for a moment to our discussion of the very first stages in embryonic development (Fig. 4.2). In this figure we see how a single-celled *embryo* (the ovum) is transformed into a many-celled embryo by steps summarized on p. 50. Many people think that this series of steps shows us how, long ago, single-celled *adults* gave rise to many-celled descendants. In fact this point of view was strongly stressed by Haeckel in connection with his recapitulation theory (p. 50).

Now, even though we no longer agree that embryos of higher organisms repeat the adult structures of their ancestors, we may nevertheless regard this fundamental similarity in early embryonic pattern as significant evidence as to the probable nature of the embryonic pattern followed by the earliest many-celled organisms. According to this view, many-celled organisms arose by a process of division and subdivision of single-celled ones, forming at first clusters of similar cells.

Organisms composed of clusters of cells exist today. Three of them are shown in Fig. 4.18. The species of *Gonium* shown consists

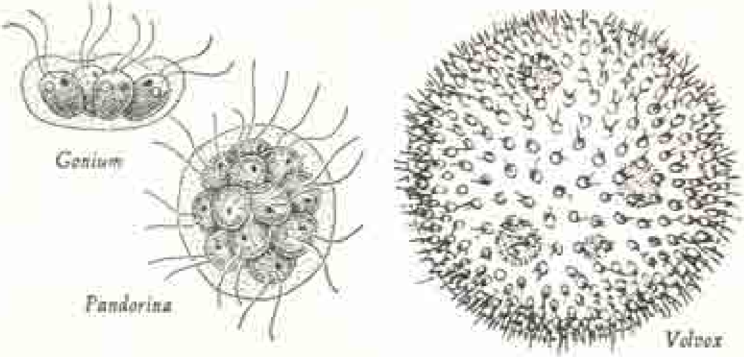


Fig. 4.18. Three organisms comprised of clusters or colonies of cells. See text.

of only four cells bound together by a gelatinous matrix. Each of the four cells is capable of reproduction, either singly (asexual reproduction) or by two cells fusing together to form a zygote (equivalent to a fertilized ovum). In either case the cell, be it single cell or zygote, divides into two cells, each of which divides into two again (as in Fig. 4.2 *a*, *b*, and *c*). In other species of *Gonium* there are more cell divisions and hence attainment of 16 or 32 cells (as in Fig. 4.2 *e* and *f*). A similar situation is found in *Pandorina*, successive cell divisions giving rise to clusters of eight, 16, or 32 cells, depending upon the species.

In organisms of this type we seem to see the embryonic pattern shown in Fig. 4.2 at its lowest level by creatures that progress only part way through the pattern. Other organisms progress further; *Volvox*, for example, consists of thousands of cells, though it is a hollow ball not unlike a blastula (Fig. 4.2*g*) in essential structure.

Do we find organisms that are like the gastrula (Fig. 4.2*i*) in essential structure? Members of phylum Coelenterata—including, among others, jellyfishes, sea anemones, and corals—resemble a gastrula in being composed of two layers, ectoderm and endoderm. No well-organized mesoderm is present, though between the ectoderm and endoderm there is a jellylike material (mesoglea) that may contain some cells. There are other similarities to a gastrula, including the presence of but a single opening into the central digestive cavity. This opening serves as a mouth and also for the ejection of undigested material. We should mention, however, that this gastrulalike adult structure is not attained by the embryonic process of infolding shown in Fig. 4.2*h*. Instead the blastula becomes completely filled with cells, elongates, and becomes a swimming larva known as a planula (swimming by means of cilia).

According to the hypothesis we have been explaining, coelenterates are the most primitive of the many-celled animals, and they arose from single-celled ones by a process essentially similar to that shown in Fig. 4.2, except that a planula would be substituted for stage *h*. Such a view is widely held (e.g., see Marcus, 1958). According to this view the coelenterates then gave rise to such other organisms as the flatworms (phylum Platyhelminthes).

Someone may ask, "Isn't one cell dividing to form two, the two dividing to form four, and so on about the only way in which a single cell *could* give rise to a many-celled organism, either in embryology or in evolution?" Other ways are possible; one has been seriously suggested for the origin of the metazoa: The hypothesized process is called CELLULARIZATION. Suppose we have a single-celled organism containing several or many nuclei instead of a single nucleus. Such organisms are known. If cell membranes should develop around each nucleus, walling it off from its neighbors, the multinucleated single-celled organism would be converted into a multicellular organism (Fig. 4.19).

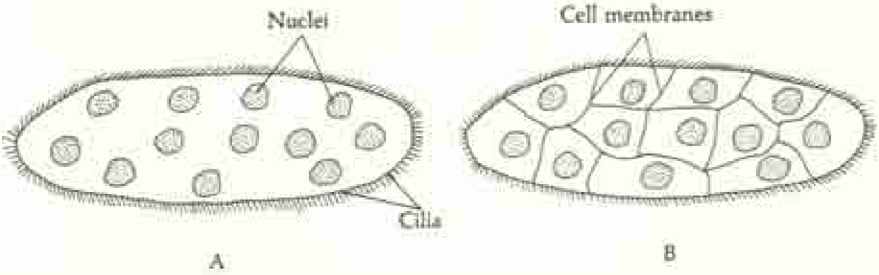


Fig. 4.19. Hypothetical diagram to illustrate the idea of cellularization. A, multinucleated single-celled organism. B, multicellular organism arising by development of cell membranes around each nucleus of A. See text.

Hadži (1963) hypothesized that ciliated protozoa with many nuclei gave rise by cellularization to very simple members of phylum Platyhelminthes, the Acoela of class Turbellaria. These minute flatworms are ciliated and have no digestive cavities. According to this view, then, protozoa gave rise to simple flatworms (Platyhelminthes), and the coelenterates are the somewhat simplified descendants of members of this phylum, not their ancestors (see de Beer, 1954).

What was the origin of the metazoa? We have presented two contrasting views. According to one view the earliest stages of embryonic development may afford a clue to the answer. According to the other view these earliest stages do not afford a clue to the answer. The answer is really not known and probably never will be. Only if there were a fossil record of the transitional forms would we actually know what transpired hundreds of millions of years ago. Why bother to ask the question, then? Man's desire to understand, even though he must be content with answers having varying degrees of *probability*, is a powerful stimulus to the development of human knowledge. Much knowledge is gained in pursuit of even elusive goals, as we shall see again when we discuss the origin of life itself in Chapter 7.

CONCLUSION

In this chapter similarities of embryonic development have been stressed. We have noted that all animals above single-celled protozoa are similar in the early stages of development and that in general there is a direct relationship between similarity of adult structure and the proportion of embryonic development that is similar in different animals. Thus, dissimilar animals are found to follow like paths of development for a time and then to diverge, each going its own way. The more dissimilar the animals the shorter the period of embryonic development that they share in common. Why do dissimilar animals share any similarity of embryonic development at all? The most reasonable explanation seems to be inheritance from common ancestry. In accordance with this view we may picture two species descended from a common ancestor. That ancestor had a certain pattern of embryonic development. Both species inherited the pattern. But each species proceeded to evolve in its own way; thus eventually each came to differ from the ancestor and from the other species. Consequently the later portions of the embryonic developments of the two species differ, even while both retain certain features of the pattern of early embryonic development inherited from the common ancestor.

Evidently, then, embryonic similarities are found in only those portions of development that two species share in common. The human embryo, for example, is never a fish or a fish embryo, yet it follows a course of development similar to that of a fish embryo up to a point representing the stage at which the line leading eventually to man diverged from the line leading eventually to modern fishes.

References and Suggested Readings

Arey, L. B., *Developmental Anatomy*, 7th ed., Philadelphia, W. B. Saunders, 1965.

Ballard, W. W., *Comparative Anatomy and Embryology*, New York, Ronald Press, 1964.

Barth, L. G., *Embryology,* rev. ed., New York, Holt, Rinehart & Winston, 1953.

Boyden, A. A., "Comparative evolution with special reference to primitive mechanisms," *Evolution, 7,* 21–30 (1953).

Carter, G. S., *Structure and Habit in Vertebrate Evolution,* Seattle, University of Washington Press, 1967.

Coghill, G. E., *Anatomy and the Problem of Behaviour,* Cambridge, Cambridge University Press, 1929.

Corner, G. W., *Ourselves Unborn,* New Haven, Yale University Press, 1944.

de Beer, G. R., "The evolution of the Metazoa," in J. Huxley, A. C. Hardy, and E. B. Ford (eds.), *Evolution as a Process,* London, Allen & Unwin, 1954, pp. 24–33.

de Beer, G. R., *Embryos and Ancestors,* 3rd ed., Oxford, Oxford University Press, 1958.

Gilbert, M. S., *Biography of the Unborn,* Baltimore, Williams & Wilkins, 1939. (2nd ed.: Hafner Publishing, New York, 1963.)

Hadži, J., *The Evolution of the Metazoa,* New York, Macmillan, 1963.

Haeckel, E., *The Evolution of Man,* 2 vols., 5th ed., New York, G. P. Putnam's Sons, 1905. (Of historical interest; sets forth the recapitulation theory.)

Marcus, E., "On the evolution of the animal phyla," *Quarterly Review of Biology, 33,* 24–58 (1958).

Romer, A. S., *Man and the Vertebrates,* 3rd ed., Chicago, University of Chicago Press, 1941. (Note particularly chap. 20.)

Romer, A. S., *The Vertebrate Story,* Chicago, University of Chicago Press, 1959.

Romer, A. S., *The Vertebrate Body,* 3rd ed., Philadelphia, W. B. Saunders, 1962.

Romer, A. S., "Major steps in vertebrate evolution," *Science, 158* 1629–1637 (1967).

5

Evolution as Seen in Chemical Composition, Genes, and Proteins

THE TWO PRECEDING chapters discussed the evolutionary significance of similarities in adult structure and in embryonic development. They dealt with structures that can be seen with the unaided eye or with a small amount of magnification. Now we turn our attention to fundamental similarities that in many cases cannot be seen but must be studied by the methods of the chemist, the biochemist, the serologist, and the physiologist.

CHEMICAL COMPOSITION

Perhaps basic to all other similarities is the fact that of the 100 or so known chemical elements, all living things are largely composed of four: carbon (C), hydrogen (H), oxygen (O), and nitrogen (N). Other elements—for example, phosphorus, potassium, and sulphur—are present in smaller amounts and play vital roles in the processes of living (metabolism). Why are the "big four" so predominant in all living things, be they bacteria, earthworms, or human beings? One reason undoubtedly is that these elements are abundant in the earth or its atmosphere. Yet silicon is also abundant, but it is of small importance in the composition of living things. The fact that carbon is quadrivalent—capable of combining simultaneously with four other atoms—and thus can form the basis for extremely complex compounds is no doubt the most important reason for its primacy in living things.

Could living things have been composed mainly of elements other than C, H, O, and N? This is an interesting question, but its discussion would take us too far afield. Briefly we may answer "probably not" in an atmosphere in which oxygen predominates, as it does on our earth, but "perhaps" on a planet having an atmosphere of a different type, for example, ammonia. (See Blum, 1955, chap. 6, for further discussion of the importance of the environment in determining the chemical composition of living things.)

What do C, H, O, and N form in living organisms? In these, from 70–90 or more percent by weight is comprised of WATER—H_2O. Water enters into all life processes; without it life as we know it could not exist.

Otherwise we may say that the "big four" characteristically form three classes of compounds and their derivatives in all living things: CARBOHYDRATES, FATS (lipids), and PROTEINS (including nucleoproteins). Here is another fundamental similarity. Carbohydrates (e.g., sugars, starches, and cellulose, the stiffening, fibrous material in plants) are composed of C, H, and O, with the latter two elements present in the same proportions that they are in water. Fats are also composed of these same three elements, but the oxygen comprises a smaller proportion of the fat molecule than it does of the carbohydrate molecule. Other elements, such as nitrogen and phosphorus, also may be present in fats (lipids). Proteins, familiar to us in "lean meat" (muscle), are the most complex substances known. They always contain carbon, hydrogen, oxygen, nitrogen, and sulfur. Other elements, such as phosphorus, may also be present and important to the functioning of the protein.

What are the functions of these compounds in the economy of the organism? Carbohydrates and fats are "fuel," supplying energy needed for living processes (metabolism). As mentioned above, the complex carbohydrate cellulose is important as a structural component in plants. But of the three classes of compounds we must accord primacy to proteins. They and their derivatives (1) form the basic structural components of living things, and (2) many of them serve as ENZYMES, without which living processes could not occur.

Nearly everyone knows that most organisms are composed of one or more CELLS. Cells are usually microscopic in size; they are the "building blocks" of which the tissues of plants and animals are composed. Although cells vary widely in shape and other properties, they are so similar in fundamental plan that we can draw a diagram of a "typical" cell stressing the points shared in common (Fig. 5.1). These complex structures in the cell are composed mainly of proteins and protein derivatives. In "higher" organisms the cells join together to form TISSUES, and these combine to form ORGANS (e.g., skin, liver, intestine, kidney, muscles, and brain). Hence we see the basic importance of proteins as components of structure.

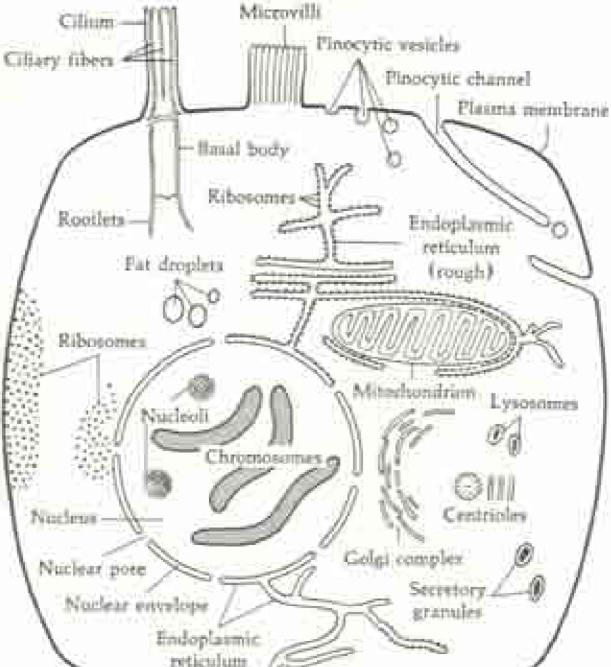

Cilium
Ciliary fibers
Microvilli
Pinocytic vesicles
Pinocytic channel
Plasma membrane
Basal body
Ribosomes
Rootlets
Endoplasmic reticulum (rough)
Fat droplets
Ribosomes
Mitochondrion
Lysosomes
Nucleoli
Chromosomes
Centrioles
Nucleus
Golgi complex
Nuclear pore
Secretory granules
Nuclear envelope
Endoplasmic reticulum (smooth)

Fig. 5.1. Diagram of a "typical" cell to indicate something of the complexity of structure revealed by the electron microscope. Most of the structures are commonly found in cells, though some types of cells lack some of the structures shown. (From *Cell Structure and Function* by Ariel G. Loewy and Philip Siekevitz. Copyright © 1963 by Holt, Rinehart and Winston, Inc. Reprinted by permission of Holt, Rinehart and Winston, Inc.)

But of perhaps even greater interest is the function of some proteins as *enzymes*. Enzymes are organic catalysts. A catalyst is a substance that accelerates a chemical reaction. In the case of the chemical reactions important to the processes of living, without enzymes the reactions would occur so slowly as to be totally ineffective. Thus it is no exaggeration to say that life as we know it would be impossible without enzymes, that is, without proteins.

Enzyme-controlled reactions are most familiar to the average person in the process of digestion—the breaking down of starches into sugars or of proteins into amino acids, for example. But enzymes also function in the reverse direction: in the building up of sugars into starches or of amino acids into proteins. In fact *nothing* occurs within the body without the appropriate enzyme control. We note from the foregoing that enzymes (proteins) themselves are only formed through the action of other enzymes (proteins). Since, as we stated earlier, proteins are the most complex compounds known, the formation of a protein molecule requires the cooperation of an amazingly complex array of enzymes.

Proteins are synthesized *within* the individual cells. Each cell requires many kinds of proteins (to serve as structural components and as enzymes). Hence the complexity and multiplicity of enzymes in a single cell stagger the imagination, and we ask: "What brings order out of chaos? Where are the *controls*?"

A huge body of evidence indicates that control rests with the GENES in the CHROMOSOMES (Fig. 5.1). The most characteristic components of chromosomes are NUCLEOPROTEINS. These are complexes consisting of proteins joined to NUCLEIC ACIDS. At the present time it seems that the nucleic acid is the more important portion of the molecule as the controlling mechanism in the cell.

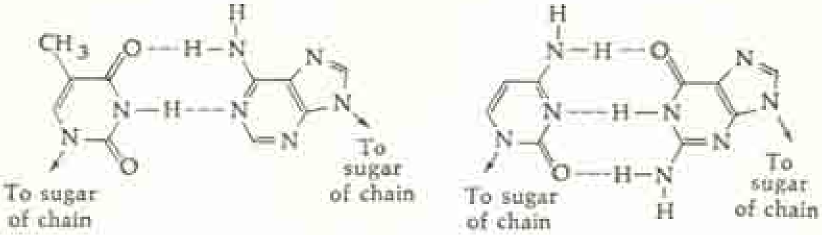
There are two kinds of nucleic acid: RIBONUCLEIC ACID (RNA) and DEOXYRIBONUCLEIC ACID (DNA). DNA is characteristic of the chromosomes, and in these days we usually think of DNA as composing the genes themselves. Both DNA and RNA consist of long chain molecules in which sugar and phosphate alternate regularly. A side group, organic base (purine or pyrimidine), is attached to each sugar. In RNA the sugar is ribose; in DNA it is deoxyribose.

DNA

The structure of DNA has been so widely publicized and so generally discussed wherever biology is mentioned that a brief summary will suffice us here.

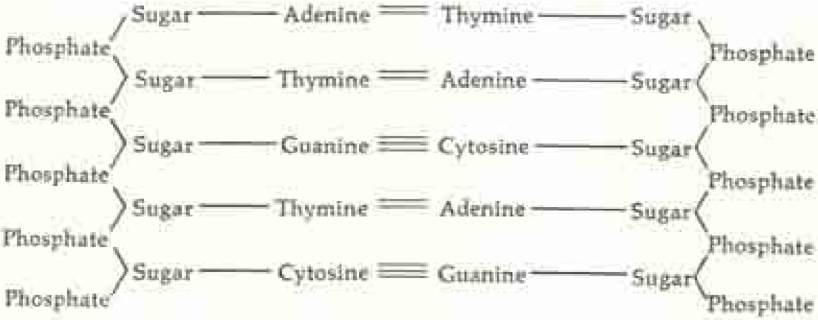
The chains of alternating sugar and phosphate molecules men-

[A] Hydrogen bonding between complementary base pairs



CH3
O
H
N
To sugar of chain
To sugar of chain

[B] Complementary sequences of bases in the 2 strands of DNA



Phosphate
Sugar
Adenine
Thymine
Guanine
Cytosine

[C] The arrangement of the 2 strands in the DNA double helix

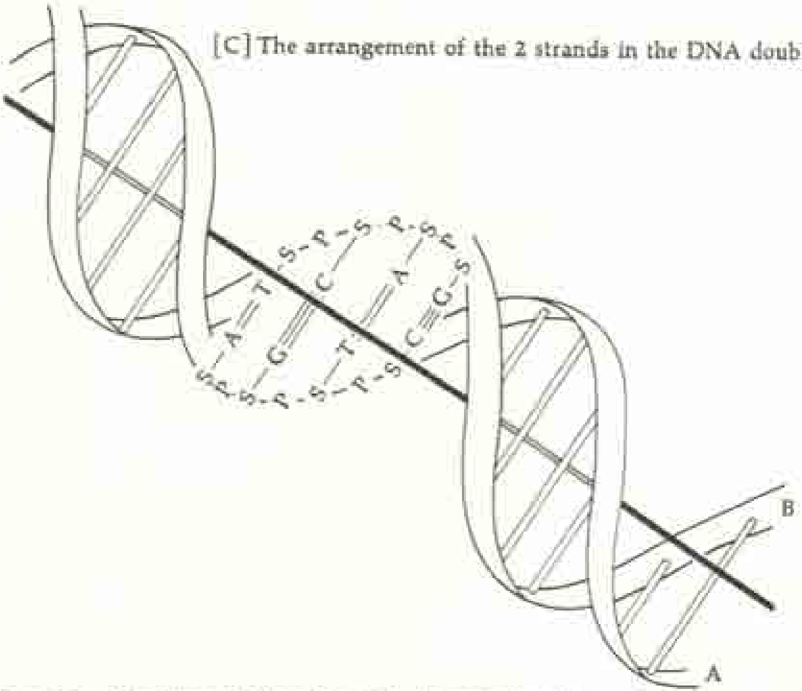


Fig. 5.2. Structure of DNA. See text. (Reprinted with permission of The Macmillan Company from *Cells and Energy* by Richard A. Goldsby. Copyright © Richard A. Goldsby, 1967.)

tioned above may be likened to the sides of a ladder (Fig. 5.2b). The rungs of the ladder are composed of a pair of organic bases joined together by hydrogen bonds in such a way that adenine (A) in one chain is bonded to thymine (T) in the other and that cytosine (C) in one chain is bonded to guanine (G) in the other (Fig. 5.2a and b). And the whole "ladder" is twisted to form a helix (the Watson–Crick model, Fig. 5.2c).

Each of the chains is composed of a unit of structure called a NUCLEOTIDE repeated over and over again. A nucleotide consists of a sugar compound joined to a phosphate compound and to an organic base (A, C, G, or T). When DNA duplicates itself the chains become separated by breaking of the hydrogen bonds between bases. Then each single strand serves as a template or pattern for formation of a new strand just like the one from which it separated. For example, a nucleotide containing the base thymine (T) fits into place so that the thymine binds to adenine (A) in the strand. Nucleotides containing C bind to G in the strand, and so on. Thus a new strand complementary to the one serving as template is built up nucleotide by nucleotide.

We focus attention primarily upon the arrangement of the base pairs: A–T (adenine–thymine), T–A, C–G (cystosine–guanine), and G–C. Seemingly these may be arranged in any sequence down the length of the DNA macromolecule and are in fact arranged so as to convey information, much as the letters in this sentence are arranged to convey information to the reader.

Since the pairing is always complementary (A with T and C with G) we customarily concentrate attention on the sequence formed by bases in one-half of the "ladder" only. Thus in Fig. 5.2b, we might attend to the sequence of the left side only: ATGTC, knowing that the corresponding right-hand portion must be TACAG. The thought is that ATGTC, for example, forms a *code* that contains information of importance to the cell. AGCTA would code for different information, just as the meanings of different words differ. A four-letter alphabet may seem small, yet if we imagine the almost infinite number of sequences possible with four "letters," singly and in multiples, we appreciate the true possibility of coding complex "messages" by this means. This is especially evident when we realize that the DNA in a single cell contains literally billions of these base pairs ("letters").

In one sense we may compare the DNA to the tape of a tape recorder. If we wished to we might record on tape the directions for making a pie or building a house or operating a piece of machinery. Similarly, the DNA contains the "directions" for operating the cell in which it is found. It exercises the *control* mentioned previously. If the cell needs a certain enzyme, the DNA sees to it that the enzyme is formed. This carries us beyond the analogy of our familiar tape recorder into the analogy of coded information supplied a computer that can respond by control of automated machinery. We begin to appreciate something of the remarkable properties of DNA.

This appreciation is heightened when we recall that the DNA can duplicate itself, leading to duplication of the chromosomes (mitosis) and eventually to duplication of the cell itself in the process that we customarily call cell division. It is a computer that can produce duplicates of itself and of the building in which it is housed!

Let us think now of a very special cell, the fertilized ovum. If this is a human fertilized ovum it normally contains 23 chromosomes from the mother and 23 chromosomes from the father. If current thinking is correct, the combined DNA from the two parents contains complete coded instructions for the making of a new human being. We must not forget, though, that environment plays a vital role in determining the nature of the "finished product." We customarily think of the importance of environment acting upon a child after birth, but environment within the uterus before birth is at least as important.

The fertilized ovum divides to form two cells. Preceding this division the DNA has duplicated itself so that one cell has exactly the same DNA as the other. Each of these cells, in turn, divides to form two, with DNA replication as before. Each of the resulting four cells divides, and so on until the billions of cells composing a human body are produced. The resulting cells become specialized into brain cells, liver cells, muscle cells, skin cells, and so on. But because of the manner in which each cell arises by division of a predecessor cell, each cell has in theory exactly the same coded information in its DNA that every other cell has or that the original fertilized ovum had. Obviously, a liver cell, for example, will not use much of this information—only those genes appropriate to liver function actually will be working. The manner in which genes (meaning sections of DNA) are turned on and off, as one operates a light switch, is a fascinating field of investigation, but its discussion would lead us far afield here.

Since each cell contains the coded information for production of an individual of its species, we might expect that the information would be similar in two species if the organisms themselves were similar. To return to our tape recorder analogy: Taped instructions for building a wooden house would be expected to resemble taped instructions for building another wooden house more than they would instructions for building a brick house. In a somewhat similar manner, the coded information in the DNA of a dog might be expected to resemble the coded information in the DNA of a wolf more than it would the information in the DNA of a cat. This suggests the possible value of a comparative study of DNA's to supplement comparative study of adult structures (Chap. 3).

For such a study we might wish to obtain a complete transcription of the coded message in the DNA of each species. The practical difficulties involved are enormous and at present are insurmountable for such complex organisms as cats and dogs, though good beginnings have been made with viruses and bacteria. As a substitute for such a complete analysis, however, we may employ a technique that rests on the ability of separated strands of DNA to "recognize" each other.

The double-stranded nature of DNA is indicated in Fig. 5.2. By suitable methods the DNA can be "melted," breaking the hydrogen bonds and permitting the single strands to separate into two independent sugar-phosphate chains, each sugar attached to its base (A, C, G, or T). Under suitable conditions the strands will rejoin to form the double strand again. In this rejoining A always joins to T and C to G as they did originally.

Making use of this property, Hoyer and co-workers (1964, 1965) have developed a method for estimating the amount of similarity between the DNAs of two species. The DNAs are "melted," as mentioned, into single strands. Then single-stranded DNA of one species (Species A) is broken into small fragments. These fragments are brought into contact with the single-stranded DNA of the other species (Species B). A Species A fragment containing a sequence of organic bases complementary to a sequence in some region of the Species B strand will combine with that region to form a double strand. Any Species A fragments that are complementary to *no* region of the Species B strand will remain uncombined (Fig. 5.3). Thus the greater the number of Species A fragments that "recognize" some portion of the Species B strand the closer the similarity between the genetic messages contained in the DNAs of the two species. The actual technique of the

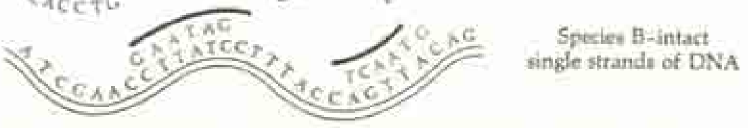

TCACCTG
CCAACG
GAATAG
TCAATG
ATCGAACCTTATCCTTTACCAGTTACAG
Species A-fragments of single strands of DNA
Species B-intact single strands of DNA

Fig. 5.3 Illustration of the idea forming the basis of tests of similarities between DNAs derived from different organisms. Species A fragments that have complementary sequences of nucleotides to sequences found in species B DNA become bonded to the latter. Species A fragments that do not have complementary sequences of nucleotides to sequences found in species B DNA remain unattached. See text.

tests is more complicated than this oversimplified account indicates, and there are variables and sources of uncertainty in interpretation. Nevertheless, in broad outline the picture is clear: Similarities of the genetic messages do correspond to structural similarities as these are expressed in accepted classification.

We might pause to ask, "Are these similarities in DNA structure homologous or analogous?" We noted on pp. 21–23 that analogous similarities arise when different organisms become adapted to live similar lives (e.g., bird and bat). Moreover, the similarities are of a general nature, not usually extending to details (e.g., bird wing composed of feathers and bat wing of skin). The DNA similarities, on the contrary, exist despite differing adaptations, and they are often tremendously detailed similarities.

Figure 5.4 shows the relative similarities to human DNA of a series of other DNAs. As would be expected (Chap. 12), the DNA of the chimpanzee was most similar. In fact the method used did not demonstrate differences between the two DNAs, but that must not lead us to conclude that differences do not exist—they will probably be demonstrated by future research. The gibbon, another of the great apes, also has DNA very much like that of man.

Less similarity was shown by the DNAs of monkeys, and still less similarity characterized the DNAs of tarsiers and lemurs (slow loris, galago, and lemur). As we shall see in Chapter 12, lemurs and tarsiers are classified in the order Primates with ourselves (and the monkeys and apes), but are quite unlike us in many ways.

The tree shrews occupy an interesting position since they are sometimes regarded as primitive members of the order Primates and sometimes as members of the order Insectivora (with shrews, moles, hedgehogs, and their relatives). This question is discussed further in Chapter 12; here we note with interest that these tests show that tree shrew DNA is less like human DNA than is lemur DNA but is more like human DNA than is hedgehog DNA.

The mouse is included as a representative of the mammalian order Rodentia. The chicken (class Aves) represents the only nonmammalian creature included in the figure, but in other tests fish DNA has been found to be less similar to mammalian DNA than is the DNA of birds.

However, any conclusions based on these results must be tentative only. This type of investigation is new, accompanied by many variables not all of which have been explored, and hence results are of a preliminary nature. In the paper presenting the data on which Fig. 5.4 is based, Hoyer and Roberts (1967) likened the situation to the early stages of the development of an oil field: "A small area has been worked, enough to have given returns on the effort invested. A much

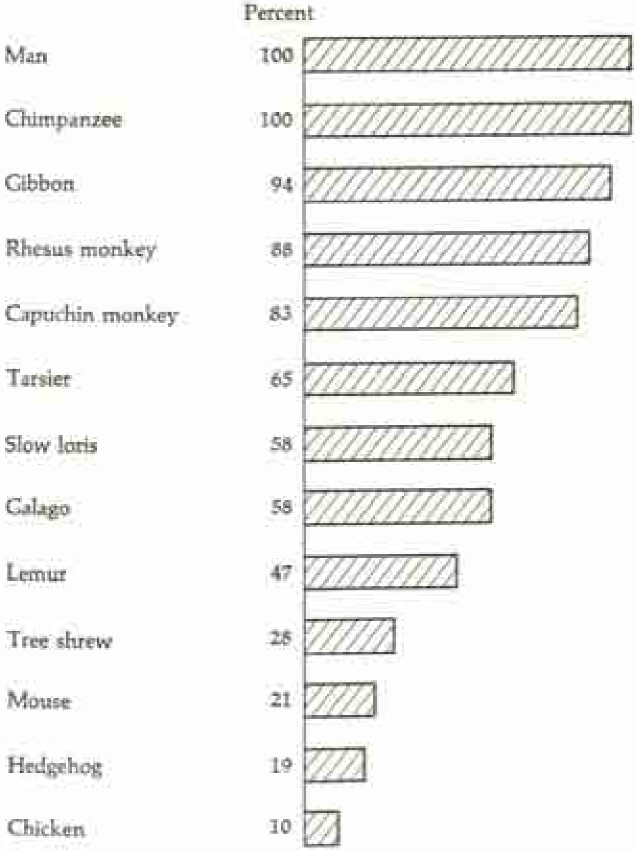


Fig. 5.4. Relative similarities to human DNA of DNAs from other vertebrates. The reaction of human DNA with itself under experimental conditions is arbitrarily set at 100%. (Data from Fig. 16, p. 460, of Hoyer, B. H., and R. B. Roberts, "Studies of nucleic acid interactions using DNA-agar," in Taylor, J. H. (ed.) *Molecular Genetics, Part II,* New York, Academic Press, 1967, pp. 425–479.)

larger area has had only wildcat drilling." But what has been done is enough to indicate that important oil reserves are there and that they "are bound to pay off when they are worked intensively."

Another word of caution is important at this point. Almost inevitably pioneer and exploratory experiments, like most of those described in this chapter and the next, are performed with material from only a small number of individual specimens—not infrequently from a single specimen. This situation arises from the complexity of most of the procedures and their expense in time and money. But equally important is the fact that specimens of unusual species cannot usually be obtained in quantity. If one wishes to study the DNA of the galago, for example, how many lemurs of this species can one obtain to work on? Ideally one should have a large sample of the species, representing the entire range of variation within it (a point of view strongly emphasized by Rasmussen, 1969). But suppose this is impossible. Perhaps only a single specimen is available or at best two or three specimens. Is it better to make use of this specimen or to do nothing? "It is better to light one candle than to curse the darkness."

Nevertheless, the number of specimens utilized does place a limitation upon conclusiveness of the interpretations drawn. In the investigation just discussed, for example, the comparison of galago DNA with human DNA is valid only insofar as the galago DNA used is typical of all galago DNAs and the human DNA is typical of all human DNAs. We are acquainted with the fact that every human individual differs somewhat in genetic structure (i.e., DNA) from every other individual (with the possible exception of identical twins). No doubt if the genetics of galagos were known, the same situation would be found among them. But in the type of experiment we are discussing here, we *assume* that the comparisons being made are between those portions of the DNA that all men share in common and those portions of DNA that all galagos share in common. Of course we can never *prove* that these portions of the DNA are what is being compared until we can do the experiments on many specimens in each species as mentioned in the preceding paragraph. But in the meantime useful tentative conclusions are possible. In the present instance there is reassurance in the fact that the three lemur DNAs (slow loris, galago, and lemur) agreed closely in the magnitude of their reaction with human DNA (Fig. 5.4).

If the DNA does contain the coded instructions for "building" an organism, we should expect that the DNAs of two organisms would be similar insofar as those organisms are similar. The DNA message of all vertebrates (aside from cyclostomes) must contain the instructions for building a backbone (vertebral column). This part of the message would be similar to a point but also dissimilar in some respects since there are many types of vertebral columns. The DNA of a fish contains instructions for forming scales of a certain type, that of a bird contains instructions for forming feathers, and that of a mammal contains instructions for forming hair. While all mammals have the genetic message for forming hair, some of them have the instructions for forming the forelimb into a wing, others for forming it into a hoof, and others into a flipper (Fig. 3.4, p. 28). Even closely related species must have some differences in their DNA instructions; otherwise they would not be separate species.

FROM DNA TO PROTEIN—THE GENETIC CODE

Precisely what does the DNA do? Earlier we stressed the importance of *proteins* as structural components of cells and as enzymes. A mounting body of evidence indicates that the principal function of DNA is to control the production of proteins and to determine their nature. Since nothing happens in an organism, either an adult or an embryo, without the action of enzymes (p. 77), control of enzyme production is the most fundamental function that DNA could have.

Before we consider how DNA accomplishes its task we must say a word about the structure of proteins. Although proteins are the most complex compounds known, they are composed of long chains of simpler molecules called AMINO ACIDS. Twenty amino acids are commonly found in the proteins of all living things—another fundamental similarity (Table 5.1). Apparently these amino acids may be arranged in all possible sequences in the chains composing a protein. A chain of amino acids is called a POLYPEPTIDE CHAIN. A protein may consist of one polypeptide chain, but it usually consists of two or more chains. Thus a molecule of hemoglobin in the red blood cells consists of four chains: a pair called α chains that is identical in amino acid sequence and a pair called β chains that is alike in sequence. The α chains contain 141 amino acid residues each; the β chains contain 146 amino acid residues each. Hence the entire macromolecule of hemoglobin contains 574 amino acid residues. (An amino acid residue is an amino acid joined to another one by a petide linkage, Fig. 7.1, p. 118.)

Table 5.1. THE 20 AMINO ACIDS COMMONLY FOUND IN ORGANISMS

Amino Acid	*Abbreviation*	*Amino Acid*	*Abbreviation*
Alanine	Ala	Leucine	Leu
Arginine	Arg	Lysine	Lys
Asparagine	Asn	Methionine	Met
Aspartic acid	Asp	Phenylalanine	Phe
Cysteine	Cys	Proline	Pro
Glutamine	Gln	Serine	Ser
Glutamic acid	Glu	Threonine	Thr
Glycine	Gly	Tryptophan	Trp
Histidine	His	Tyrosine	Tyr
Isoleucine	Ile	Valine	Val

The sequence in which the amino acids are arranged in the polypeptide chains is called the *primary structure* of the protein. The chains are coiled; this coiling is called the *secondary structure*. And the coiled chains are folded in intricate fashion: *tertiary structure*. This folding is important in the functioning of the protein as an enzyme. The pattern of the folding is determined by physical forces acting between amino acids. Hence the primary structure in large measure determines the tertiary structure. We now direct our attention to this primary structure.

As we have seen, DNA consists of a long chain of nucleotides. Proteins consist of one or more long chains of amino acids. It is "the central dogma" of molecular genetics that the linear sequence in the DNA *determines* the linear sequence in a polypeptide chain (Yanofsky, 1967). Much experimental evidence supports this theory.

If the theory is correct, how does the DNA accomplish its task? DNA is composed of only four kinds of nucleotides, those containing A, those containing C, those with G, and those with T. There are 20 kinds of amino acids to be arranged. Obviously the correspondence cannot be one-to-one between nucleotides and amino acids. An impressive body of evidence indicates that *three* adjacent nucleotides form a "code word" designating a particular amino acid. The letters A, C, G, and T can be arranged in 64 different combinations of three. This is more than enough to account for 20 amino acids. Apparently some amino acids are coded for by more than one nucleotide triplet. This is like the occurrence of synonyms in a human language.

If we grant that a series of nucleotide triplets in DNA determines a series of amino acids in a polypeptide chain, we still have the question: *How* is this accomplished?

Seemingly, in the first step of the process DNA serves as a template (pattern) for the formation of a molecule of RNA. As noted earlier, RNA differs from DNA in the sugar incorporated. Like DNA, it is composed of a long chain of nucleotides, and there are four types of these: one with adenine (A), one with cytosine (C), one with guanine (G), and one with uracil (U). Note that thymine in DNA is replaced by uracil in RNA. Uracil bonds with adenine.

At the top of Fig. 5.5 we represent a bit of DNA by two rows of letters standing for the two strands of the molecule. For clarity each row is divided by dashes into triplets, although no such divisions exist in the actual molecule. One of the strands serves as a template for formation of the RNA molecule. If this is the lower of the two strands, the first base in the strand is G; an RNA nucleotide containing C is fitted into place here. The second DNA base is A; this directs that an RNA nucleotide containing U shall join onto the first one. And so it goes, nucleotide by nucleotide, until the complete RNA chain is formed as "directed" by the DNA strand.

We recall that the DNA is part of a chromosome in the nucleus. The newly formed RNA strand detaches itself from the DNA and

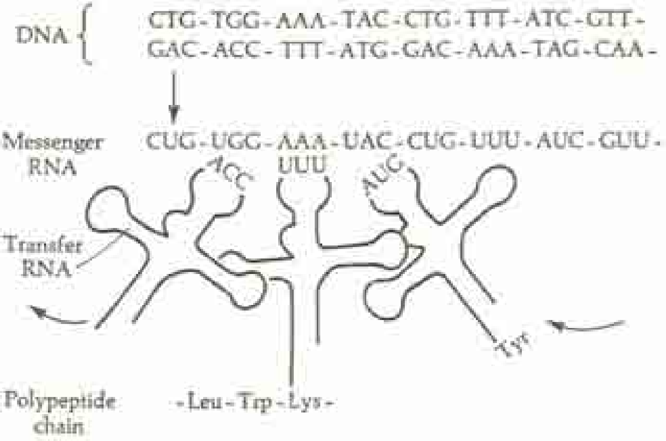

DNA
CTG-TGG-AAA-TAC-CTG-TTT-ATC-GTT-
GAC-ACC-TTT-ATG-GAC-AAA-TAG-CAA-
Messenger RNA
CUG-UGG-AAA-UAC-CUG-UUU-AUC-GUU-
ACC
UUU
AUG
Transfer RNA
Tyr
Polypeptide chain
-Leu-Trp-Lys-

Fig. 5.5. Simplified diagram of the highlights of the process by which the sequence of nucleotides in DNA is translated into a sequence of amino acids in a protein (polypeptide) by participation of messenger RNA and transfer RNA. See text.

moves out of the nucleus, into the cytoplasm of the cell. Here it does its work. Because it carries the "instructions" from the nuclear DNA into the cytoplasm it is called MESSENGER RNA (Fig. 5.5).

In the cytoplasm the messenger RNA in its turn serves as a template or pattern for the assembling of amino acids into polypeptide chains. How do the amino acids "find their way" into position? They do so through the agency of another type of RNA called TRANSFER or SOLUBLE RNA. A transfer RNA molecule consists of a chain of about 80 nucleotides folded and looped in a pattern that may resemble the diagrammatic representation of it in Fig. 5.5 (Holley *et al.*, 1965; Madison *et al.*, 1966). As the figure indicates, at one point the transfer RNA molecule is attached to an amino acid and at another point there is a so-called *coding site* that "recognizes" the appropriate triplet of bases in the messenger RNA strand. Such a triplet of bases in the messenger RNA constitutes a code word or CODON. The coding site in a transfer RNA molecule is called an ANTICODON. As indicated in the figure, an anticodon probably consists of three bases complementary to the three composing the corresponding codon.

Presumably, each of the 20 amino acids has its own specific type of transfer RNA, and in cases where synonyms occur each amino acid may be represented by two or more types of transfer RNA, each type with its appropriate anticodon to fit one of the synonymous codons.

In Fig. 5.5 three transfer RNA molecules are represented. The one on the left has the anticodon ACC and has just paired with the codon

UGG. As it did so, it added Trp (tryptophan) to the growing polypeptide chain. The second transfer RNA molecule, with the anticodon UUU, is even now pairing with its appropriate codon and adding Lys (lysine) to the polypeptide chain. As soon as this second transfer RNA molecule has become detached, the third molecule will move into position, adding Tyr (tyrosine) to the chain. Then a fourth transfer RNA molecule (not shown) will add another Trp (tryptophan), and so on to the end of the messenger RNA strand.

Thus, through the agency of messenger RNA and transfer RNA, the linear sequence of triplet bases in the DNA molecule has been translated into a linear sequence of amino acids in a polypeptide chain that will form part of a protein. Since this is the important point for our present purposes, we have omitted many of the details of the process. At each step enzymes are involved. Energy must be expended to accomplish all this; the energy is supplied by adenosine triphosphate (ATP). And small bodies in the cytoplasm, called ribosomes, have important functions in bringing the transfer RNA molecules into correct position on the messenger RNA strand. The process could not occur without the cooperation of all of these, but a description of their roles would lead us too far afield.

THE GENETIC CODE The messenger RNA codons are said to constitute a genetic code. Table 5.2 is a "dictionary" of this code, listing the 20 common amino acids and their corresponding codons. Since most of the amino acids may be coded for by more than one codon (i.e., synonyms occur) the code is sometimes said to be "degenerate." Seemingly, in many cases it is the first two bases that are important, the base found in third position being more or less irrelevant. Thus, having G and U in first and second position, respectively, seems to be important in coding for valine, but the third position may be occupied by U, G, C, or A. Such considerations have suggested that the code may have originated as a doublet code, the third base having been added later in evolution (Jukes, 1966; also pp. 128–129).

We are just at the dawn of knowledge about the evolution of the genetic code. Perhaps the most pertinent question we can ask at present is this: Do all organisms use the same code (is the code "universal")? This would be equivalent to all people speaking the same language. We might anticipate that all organisms using the same code have a common ancestry, however remote, from which the basic essentials of the code were inherited. Changing from one code to another would not be accomplished so easily as when people of differing ancestry learn to use the same language. The genetic code as we know it was worked out through the efforts of many people investigating viruses and microorganisms, especially bacteria. Our knowledge of the application of the code to other organisms is still fragmentary, though it increases steadily. One investigation indicates that the codon AAA codes for lysine in both the colon bacillus *(Escherichia coli)* and in the liver cells of a rat (Lengyel *et al.*, quoted by Abelson, 1963). In this we jump all the way from a bacterium to a mammal. The same jump was made when another investigation indicated that transfer RNA from *E. coli*, carrying leucine, participated normally in the synthesis of *rabbit* hemoglobin (Ingram, 1963).

Table 5.2. DICTIONARY OF THE MESSENGER RNA CODONS[a]

First Nucleotide	*Second Nucleotide*				*Third Nucleotide*
	U	C	A	G	
U	UUU Phe	UCU Ser	UAU Tyr	UGU Cys	U
	UUC Phe	UCC Ser	UAC Tyr	UGC Cys	C
	UUA Leu	UCA Ser	UAA Ochre	UGA Cys[b]	A
	UUG Leu	UCG Ser	UAG Amber	UGG Trp	G
C	CUU Leu	CCU Pro	CAU His	CGU Arg	U
	CUC Leu	CCC Pro	CAC His	CGC Arg	C
	CUA Leu	CCA Pro	CAA Gln	CGA Arg	A
	CUG Leu	CCG Pro	CAG Gln	CGG Arg	G
A	AUU Ile	ACU Thr	AAU Asn	AGU Ser	U
	AUC Ile	ACC Thr	AAC Asn	AGC Ser	C
	AUA Ile	ACA Thr	AAA Lys	AGA Arg	A
	AUG Met	ACG Thr	AAG Lys	AGG Arg	G
G	GUU Val	GCU Ala	GAU Asp	GGU Gly	U
	GUC Val	GCC Ala	GAC Asp	GGC Gly	C
	GUA Val	GCA Ala	GAA Glu	GGA Gly	A
	GUG Val	GCG Ala	GAG Glu	GGG Gly	G

[a] Abbreviations for names of amino acids are those given in Table 5.1. ("Ochre" and "amber" signal the termination of a polypeptide chain; they are somewhat like punctuation marks in a sentence.) Based on the researches of Nirenberg, Ochoa, Khorana, and many others.

[b] **UGA** codes for cysteine in some organisms but not in the bacterium *Escherichia coli*, where it is a chain terminator.

In an extensive investigation, Marshall, Caskey, and Nirenberg (1967) studied recognition of 50 codons by transfer RNA from three sources: (1) a bacterium *(E. coli)*, (2) an amphibian (*Xenopus*, the South African clawed toad), and (3) a mammal (guinea pig). All three types of transfer RNA responded to the same codons. "Thus an essentially universal genetic code is demonstrated." Yet there were differences in the extent to which the different transfer RNAs responded to synonymous codons. For example, transfer RNAs bearing alanine and derived from all three organisms responded to GCU, GCC, GCA, and GCG (Table 5.2). But the amphibian and mammalian transfer RNAs responded only slightly to GCG, whereas the bacterial transfer RNA responded best to GCG. Similar differences were observed with other transfer RNAs. When such differences occurred, the two vertebrate RNAs responded similarly; the difference lay in their response as compared to the response of bacterial RNA.

So we have the suggestion that each organism may have its own "preferred" codon for a given amino acid. In somewhat similar manner an American speaks of the "hood" of his automobile, while a Briton calls it a "bonnet." The same idea is also suggested by an investigation demonstrating that transfer RNA from *E. coli* does not respond well to messenger RNA from tobacco mosaic virus (Fraenkel-Conrat, 1964). Fraenkel-Conrat commented: "It is as if the genetic code, although universal in principle, contained varying dialects, the cells of different species using different versions of the general language."

So a small beginning has been made in what we may call a "comparative anatomy" of the genetic code. Only a few organisms have been studied to date. Further studies of the code in viruses, microorganisms, plants, and animals will yield results of the greatest interest for evolution.

COMPARATIVE ANATOMY OF PROTEINS

We have summarized the manner in which the DNA operates to determine the sequence of amino acids in a protein. We also have stressed the fundamental importance of proteins as structural components of all living things, and as enzymes. Since there could be no life without proteins, there could be no evolution without them. Hence they are of great interest for the student of evolution.

In their role as enzymes, proteins control all of the processes of living (metabolism) and, in embryos, the processes of development. Working hand in hand with environmental forces, enzymes control the destiny of the organism. The organism's ability to adapt to its environment is thus dependent on proteins. This means that they will be subject to natural selection.

As a consequence, proteins are acted upon by opposing forces: (1) a tendency to remain unchanged as, through the DNA, they are inherited from ancestor to descendant, and (2) a tendency to change in response to the requirements of differing environments. Some enzymes are needed to serve functions common to large groups of organisms; even in some cases common to almost all organisms. We might expect that such proteins would change but little throughout evolutionary history. A case in point is cytochrome *c*, a protein possessed by virtually all organisms that utilize oxygen for respiration. It is concerned with the oxidation of food, the process by which most organisms are supplied with energy.

CYTOCHROME *c* In its pure form cytochrome *c* is a pinkish compound. Its molecule is composed of approximately 100 amino acids, the number varying slightly in different species. Thus it is a relatively small protein and also a simple one since it is composed of a single polypeptide chain. The sequence of amino acids in cytochrome *c* from human heart tissue is shown in Figure 5.6. This is a typical example of what is called the "mammalian type" of cytochrome *c* found in such diverse organisms as baker's yeast, *Neurospora* (a bread mold), moth, tuna, rattlesnake, chicken, kangaroo, domestic rabbit, dog, pig, sheep, cow, horse, rhesus monkey, man, and doubtless many other forms not yet analyzed.

Acetyl-Gly-Asp-Val-Glu-Lys-Gly-Lys-Lys-Ile-Phe-Ile-Met-Lys-
1 10
Cys-Ser-Gln-Cys-His-Thr-Val-Glu-Lys-Gly-Gly-Lys-His-Lys-
└—Heme—┘ 20
Thr-Gly-Pro-Asn-Leu-His-Gly-Leu-Phe-Gly-Arg-Lys-Thr-Gly-
30 40
Gln-Ala-Pro-Gly-Tyr-Ser-Tyr-Thr-Ala-Ala-Asn-Lys-Asn-
50
Lys-Gly-Ile-Ile-Trp-Gly-Glu-Asp-Thr-Leu-Met-Glu-Tyr-Leu-Glu-
60
Asn-Pro-Lys-Lys-Tyr-Ile-Pro-Gly-Thr-Lys-Met-Ile-Phe-Val-
70 80
Gly-Ile-Lys-Lys-Lys-Glu-Glu-Arg-Ala-Asp-Leu-Ile-Ala-Tyr-
90
Leu-Lys-Lys-Ala-Thr-Asn-GluCOOH
100 104

Fig. 5.6. Amino acid sequence of human heart cytochrome *c*. See Table 5.1 for meanings of abbreviations. (Redrawn, with slight changes in abbreviations, from Fig. 1 of E. L. Smith, and E. Margoliash, "Evolution of cytochrome *c*," *Federation Proceedings*, *23* (1964), 1243–1247.)

All of these forms, from yeast to man, appear to have cytochromes *c* that are homologous—based on the same pattern. The situation seems directly comparable at the molecular level to the common pattern upon which vertebrate forelimbs are based, at the level of gross anatomy (Chap. 3). And just as we attributed the homology of limb structure to inheritance from common ancestry, we see in the homologous structure of all these cytochromes *c* evidence of inheritance from common ancestry. In this case, since the series runs from yeast to man and probably also includes the higher plants, we have evidence that most of the organic world descended from a remote common ancestor. This points to a single origin for most of the living things on earth.

In view of the fact that knowledge of the genetic code is based largely on research with a bacterium *(E. coli),* there is interest in the question of whether bacterial cytochrome *c* is based on the same pattern as are the cytochromes of other organisms. The evidence to date is conflicting. Some bacterial cytochromes seem to have an entirely different pattern (e.g., *Pseudomonas*). Yet one bacterium *(Rhodospirillum)* is found to possess a cytochrome-like protein that seems a variation of the pattern called mammalian-type (see Smith and Margoliash, 1964; Dayhoff, 1969a, 1969b). We await with anticipation results of further research.

Can the similarity of all these mammalian-type cytochromes *c* be explained on any other basis than that of common ancestry? To what extent *must* all cytochromes *c* be alike if they are to function normally in the cell? It has been found that in all of 20 species investigated 35 of the positions in the chain are invariant, each position always being occupied by the same amino acid. Most strikingly, the sequence numbered from 70–80, inclusive, in Fig. 5.6 is identical in all these widely diverse forms. On the basis of statistical analysis, Fitch and Margoliash (1967) concluded that substitution of other amino acids in from 27–29 of these 35 positions would be harmful. But conversely, the remainder of the positions can be occupied by various amino acids without impairing the function of the molecule. Similarities in most of the polypeptide chain, therefore, are not something imposed by functional necessity.

Someone may suggest that the similarities arose through convergent evolution from different ancestries (pp. 30–31). In our earlier discussions we noted that similarities ascribable to convergence tend to be superficial similarities arising by response to the same or similar environments. In the present instance the similarities involve minute details of molecular structure in organisms adapted to life in the widest diversity of environments. Hence it seems most probable that the similarities are truly homologous, rather than simply analogous.

The degrees of similarity in cytochromes *c* correlate well with the known relationships of the organisms and with the probable lengths of time since the postulated common ancestry occurred (Table 5.3). Thus the pig, cow, and sheep, all even-toed, hoofed mammals (order Artiodactyla), have identical cytochromes *c*. The horse (order Perissodactyla) differs from the cow at only three points in the chain of amino acids. Man differs from his fellow primate, the rhesus monkey, at only one point in the chain, but his cytochrome *c* differs from that of the dog and horse in 10 and 12 respects. Mammals differ from birds by about these same numbers and from fishes by a greater number, as would be expected.

Table 5.3. RELATIVE DIFFERENCES IN CYTOCHROMES *c* DERIVED FROM DIFFERENT ORGANISMS[a]

Species Compared	*Amino Acid Differences*	*Probable Time Since Divergence from Common Ancestry, in Millions of Years*[b]
Man—rhesus monkey	1	50–60
Man—horse	12	70–75
Man—dog	10	70–75
Pig—cow—sheep	0	—
Horse—cow	3	60–65
Mammals—chicken	10–15	280
Mammals—tuna	17–21	400
Vertebrates—yeast	43–48	1000–2000

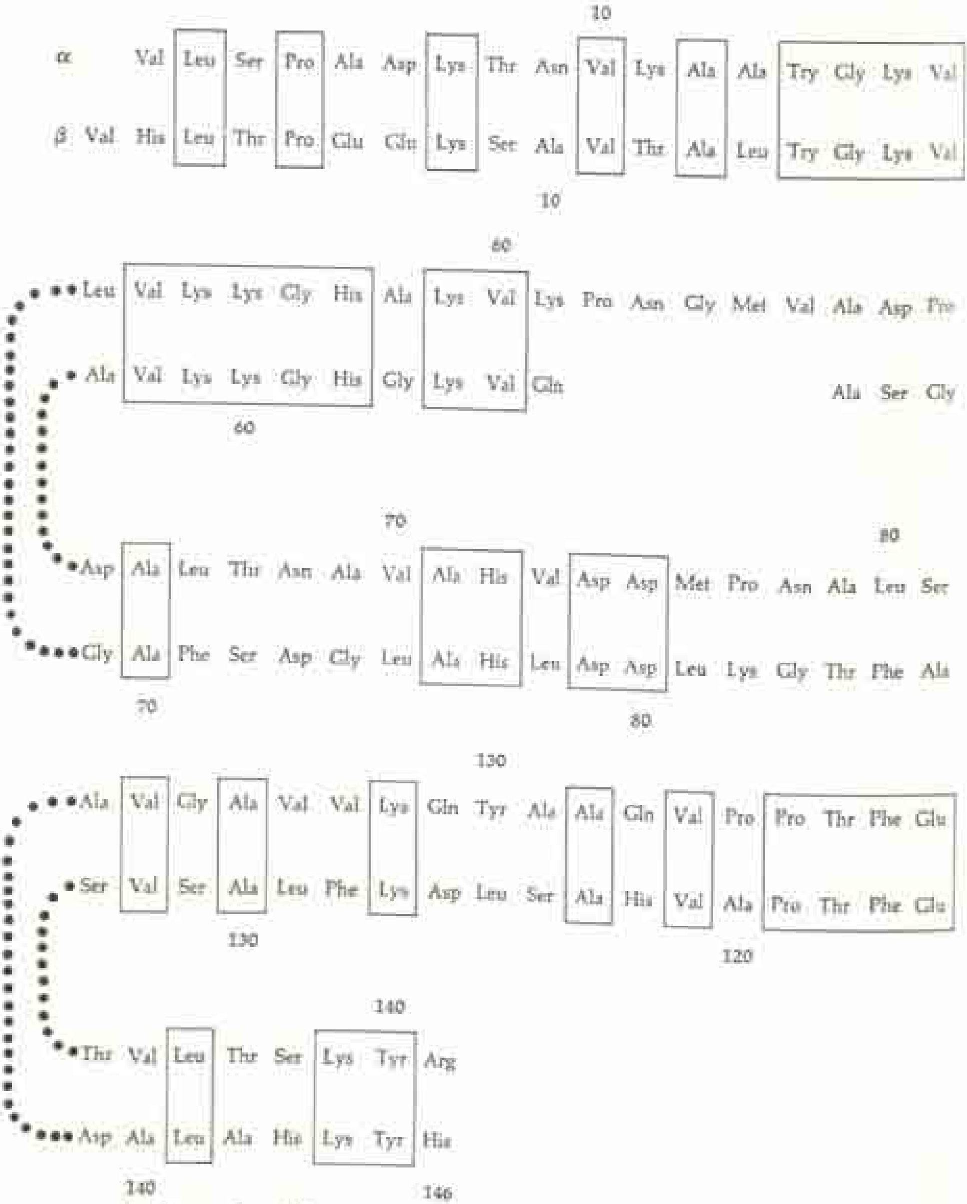
[a] Modified from Table 1 of Smith and Margoliash, 1964.

[b] Estimates supplied by G. G. Simpson and stated by him to be "subject to large errors."

The fact that vertebrate cytochrome *c* differs from that of yeast at only 43–48 points is eloquent testimony of the basic similarity of organisms far removed in the scale of life. Not included in Table 5.3 is the bread mold *(Neurospora),* which differs from vertebrates by at least 40 amino acids (Heller and Smith, 1965). Interestingly, it differs from yeast by 39 amino acids. Since yeast and *Neurospora* are related organisms, Heller and Smith suggested that evolutionary change may be much more rapid among microorganisms than among higher organisms.

Why did some portions of the cytochrome *c* molecule remain unchanged throughout evolutionary history, and why did other portions change? It is tempting to speculate that the invariant portions represent structures that could not change if cytochrome *c* were to continue to do its work in metabolism. Perhaps the portions that did vary were either (1) unimportant in the function of the molecule or (2) responding to differing requirements faced by differing organisms. The second alternative is in line with thought concerning natural selection as an evolutionary force. While it is interesting to speculate about these questions, a fuller discussion of them would be out of place in an elementary textbook. See Jukes (1966, Chap. 6), Margoliash and Smith (1965), and Simpson (1964) for further discussion.

The list of proteins for which the sequence of amino acids has been analyzed is steadily increasing. Space permits us to include but one


10
α Val Leu Ser Pro Ala Asp Lys Thr Asn Val Lys Ala Ala Try Gly Lys Val
β Val His Leu Thr Pro Glu Glu Lys Ser Ala Val Thr Ala Leu Try Gly Lys Val
10
60
Leu Val Lys Lys Gly His Ala Lys Val Lys Pro Asn Gly Met Val Ala Asp Pro
Ala Val Lys Lys Gly His Gly Lys Val Gln Ala Ser Gly
60
70
80
Asp Ala Leu Thr Asn Ala Val Ala His Val Asp Asp Met Pro Asn Ala Leu Ser
Gly Ala Phe Ser Asp Gly Leu Ala His Leu Asp Asp Leu Lys Gly Thr Phe Ala
70
80
130
Ala Val Gly Ala Val Val Lys Gln Tyr Ala Ala Gln Val Pro Pro Thr Phe Glu
Ser Val Ser Ala Leu Phe Lys Asp Leu Ser Ala His Val Ala Pro Thr Phe Glu
130
120
140
Thr Val Leu Thr Ser Lys Tyr Arg
Asp Ala Leu Ala His Lys Tyr His
140
146

more of them for illustrative purposes. Bryson and Vogel (1965), Jukes (1966) and Dayhoff (1969b) will provide good introductions to others.

HEMOGLOBIN As noted previously (p. 85), the molecule of human adult hemoglobin includes four polypeptide chains, two identical

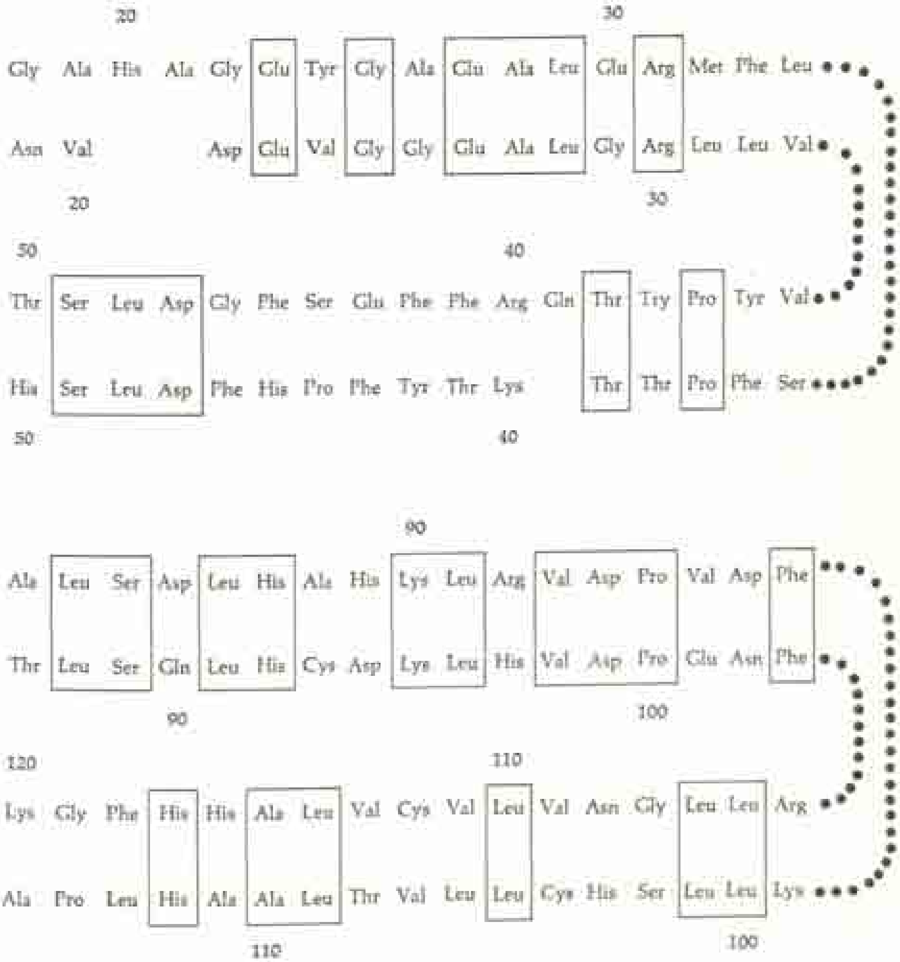

20
30
Gly Ala His Ala Gly Glu Tyr Gly Ala Glu Ala Leu Glu Arg Met Phe Leu
Asn Val Asp Glu Val Gly Gly Glu Ala Leu Gly Arg Leu Leu Val
20
30
50
40
Thr Ser Leu Asp Gly Phe Ser Glu Phe Phe Arg Gln Thr Try Pro Tyr Val
His Ser Leu Asp Phe His Pro Phe Tyr Thr Lys Thr Thr Pro Phe Ser
50
40
90
Ala Leu Ser Asp Leu His Ala His Lys Leu Arg Val Asp Pro Val Asp Phe
Thr Leu Ser Gln Leu His Cys Asp Lys Leu His Val Asp Pro Glu Asn Phe
90
100
120
110
Lys Gly Phe His His Ala Leu Val Cys Val Leu Val Asn Gly Leu Leu Arg
Ala Pro Leu His Ala Ala Leu Thr Val Leu Leu Cys His Ser Leu Leu Lys
110
100

Fig. 5.7. Normal human hemoglobin (hemoglobin A). "Sequence of amino acids in the normal human α and β peptide chains. The chains are arranged for maximum homology. Identical residues are enclosed by lines. The apparent 'gaps' exist only in the drawing. (Based on the work of Braunitzer, Konigsberg, and colleagues.)" (From Ingram, V. M., *The Hemoglobins in Genetics and Evolution*, New York, Columbia University Press, 1963.)

α chains and two identical β chains, with a total of 574 amino acids. As indicated in Fig. 5.7, the α and β chains agree at many points and may have had a common evolutionary origin (Ingram, 1963; Jukes, 1966). To each of the polypeptide chains is attached an iron-containing molecule called a heme group. Functionally the four heme groups are the most important part of hemoglobin since they serve for the temporary attachment of oxygen so that it may be transported to the tissues. But the polypeptide chains themselves are of most interest for evolutionary studies, since the heme group is the same in all hemoglobins.

We think of hemoglobin in connection with red blood, but actually hemoglobins are widely distributed throughout the organic world. For example, they are found in yeast, molds, the root nodules of leguminous plants, some ciliate protozoa (such as *Paramecium*), nematode worms, annelid worms, some crustaceans, many molluscs, a few insects, as well as in almost all vertebrates (Gratzer and Allison, 1960). These diverse hemoglobins have many features in common, but evolutionary studies to date have emphasized the hemoglobins of vertebrates.

Among the vertebrates, the four-chain structure already described is found in all forms except the jawless cyclostomes—the lamprey and the hagfish. As we shall see (p. 165), these lowly vertebrates may be modern remnants of the stock from which all vertebrates arose. The hemoglobin molecule of the lamprey consists of a single polypeptide chain with its heme group and hence is only about one-fourth as large as are the hemoglobin molecules of true fishes, amphibians, reptiles, birds, and mammals. This suggests that a single-stranded stage may have preceded the four-stranded one in the evolution of vertebrate hemoglobin.

The sequences of amino acids in the α and β chains have been most thoroughly analyzed for human hemoglobin, but enough is already known about the sequences in other mammals to make comparisons profitable. In general, as we should expect, the amount of difference is roughly proportional to the evolutionary "distance" between the mammals concerned. Thus there are 17 differences between the α chain of man and that of the horse (Zuckerkandl and Pauling, 1965) but only one difference between the α chains of man and gorilla (Zuckerkandl, 1963). The comparable numbers of differences in the β chains are 26 and one, respectively.

Turning to our own order, Primates, we find that the α chain varies but slightly from one extreme of the order to the other (with the interesting exception of the baboon). On the other hand, β-like chains vary considerably. Thus the α chain of one of the lemurs *(Lemur fulvus)* differs from the human chain by only six amino acid replacements while the β chains differ by 23 replacements (Buettner-Janusch and Hill, 1965). The hemoglobins of other lemurs differ from human hemoglobin even less.

Among the anthropoid apes (gibbon, orangutan, chimpanzee, and gorilla), both α and β chains are almost identical with the corresponding human chains. Thus the chemical structure of this protein reinforces the anatomical structure in emphasizing the closeness of the biological relationship between these apes and ourselves (see also pp. 107–112).

ABNORMAL HUMAN HEMOGLOBINS Occasionally a person may have hemoglobin that differs from the normal hemoglobin pictured in Fig. 5.7. Usually the abnormal hemoglobin differs from normal by only one amino acid replacement. The known number of abnormal hemoglobins is large, and new ones are constantly being found. Best known is the one that causes SICKLE-CELL ANEMIA. Normal hemoglobin is called HB A; sickle-cell hemoglobin is called HB S. Careful analysis has shown that the α chains of the two are alike and that there is only one difference in the β chains. In Fig. 5.7 we note that the sixth amino acid from the beginning of the β chain is glutamic acid. In HB S this position is occupied by valine (Ingram, 1963). Thus the change of one amino acid in this case is sufficient to cause hemoglobin to become so abnormal that persons who inherit the gene (altered DNA) for it from both parents (are homozygous, p. 358) suffer a severe, usually fatal disease.

Later we shall discuss the forces of natural selection acting upon the sickle-cell gene (pp. 430–431). We mention these hemoglobins here because they represent MUTATIONS and, as we noted in Chapter 2, mutations are given great importance in modern theories of evolution. Furthermore, this affords an example of the manner in which mutations can arise by a change in the DNA molecule.

From Table 5.2 we note that the RNA codons for glutamic acid are GAA and GAG (corresponding to DNA triplets of CTT and CTC, respectively). The RNA codons for valine are GUU, GUC, GUA, and GUG. Hence, if the human codon for glutamic acid were GAA, for example, substitution of U for A (uracil for adenine) in the middle would change the codon to one for valine (GUA). GAG would be changed to GUG by the same means. For our present purposes the significance of this lies in the fact that an important genetic change (mutation) *may* arise through no greater change in a DNA molecule than substitution of one nucleotide for another. Here we seem to see mutation reduced to its lowest common denominator.

In this chapter we have discussed briefly some pioneering studies on the comparative structures of (1) DNA and (2) proteins derived from diverse organisms. While we bear in mind the caution necessary in basing conclusions on preliminary studies using small numbers of individuals (pp. 83–84), we find that such studies supplement and complement studies on comparative morphology and embryology. Much of significance to the study of evolution is expected to emerge from future investigations of the structure of genes and proteins.

In the next chapter we shall continue our discussion of the "comparative anatomy" of proteins, briefly describing results obtained with the techniques of serology.

References and Suggested Readings

Abelson, J., "Transfer of genetic information," *Science, 139,* 774–776 (1963).

Blum, H. F., *Time's Arrow and Evolution,* 2nd ed., Princeton, Princeton University Press, 1955.

Bryson, V., and H. J. Vogel (eds.), *Evolving Genes and Proteins,* New York, Academic Press, 1965.

Buettner-Janusch, J., and R. L. Hill, "Evolution of hemoglobin in primates," in Bryson and Vogel (above), pp. 167–181.

Cold Spring Harbor Symposia on Quantitative Biology, vol. 31, *The Genetic Code,* Cold Spring Harbor, New York, Cold Spring Harbor Laboratory of Quantitative Biology, 1966.

Dayhoff, M. O., "Computer analysis of protein evolution," *Scientific American, 221,* 87–95 (1969a).

Dayhoff, M. O., *Atlas of Protein Sequence and Structure,* 1969, 4th ed., Silver Spring, Maryland, National Biomedical Research Foundation, 1969b.

Fitch, W. M., and E. Margoliash, "A method for estimating the number of invariant amino acid coding positions in a gene using cytochrome *c* as a model case," *Biochemical Genetics 1,* 65–71 (1967).

Fraenkel-Conrat, H., "The genetic code of a virus," *Scientific American, 211,* 46–54 (1964).

Gratzer, W. B., and A. C. Allison, "Multiple hemoglobins," *Cambridge Philosophical Society, Biological Reviews, 35,* 459–506 (1960).

Heller, J., and E. L. Smith, "The amino acid sequence of cytochrome *c* of *Neurospora crassa,*" *Proceedings of the National Academy of Sciences, 54,* 1621–1625 (1965).

Holley, R. W., J. Apgar, G. A. Everett, J. T. Madison, M. Marquisee, S. H. Merrill, J. R. Penswick, and A. Zamir, "*Structure of a ribonucleic acid,*" *Science, 147,* 1462–1465 (1965).

Hoyer, B. H., B. J. McCarthy, and E. T. Bolton, "A molecular approach in the systematics of higher organisms," *Science, 144,* 959–967 (1964).

Hoyer, B. H., E. T. Bolton, B. J. McCarthy, and R. B. Roberts, "The evolution of polynucleotides," in Bryson and Vogel (above), pp. 581–590.

Ingram, V. M., *The Hemoglobins in Genetics and Evolution,* New York, Columbia University Press, 1963.

Jukes, T. H., *Molecules and Evolution,* New York, Columbia University Press, 1966.

Madison, J. T., G. A. Everett, and H. K. Kung, "On the nucleotide sequence of yeast tyrosine transfer RNA," in *Cold Spring Harbor Symposia on Quantitative Biology* (above), pp. 409–416.

Margoliash, E., and E. L. Smith, "Structural and functional aspects of cytochrome *c* in relation to evolution," in Bryson and Vogel (above), pp. 221–242.

Marshall, R. E., C. T. Caskey, and M. Nirenberg, "Fine structure of RNA codewords recognized by bacterial, amphibian, and mammalian transfer RNA," *Science, 155,* 820–825 (1967).

Rasmussen, D. I., "Molecular taxonomy and typology," *BioScience, 19,* 418–420 (1969).

Simpson, G. G., "Organisms and molecules in evolution," *Science, 146,* 1535–1538 (1964).

Smith, E. L., and E. Margoliash, "Evolution of cytochrome *c*," *Federation Proceedings, 23,* 1243–1247 (1964).

Yanofsky, C., "Gene structure and protein structure," *Scientific American, 216,* 80–94 (1967).

Zuckerkandl, E., "Perspectives in molecular anthropology," in S. L. Washburn (ed.), *Classification and Human Evolution,* Chicago, Aldine Publishing, 1963, pp. 243–272.

Zuckerkandl, E., and L. Pauling, "Evolutionary divergence and convergence in proteins," in Bryson and Vogel (above), pp. 97–166.

6

Evolution as Seen in Serum Proteins and in Blood Groups

SERUM PROTEINS

THE BEST WAY to study similarities and differences among proteins is to compare their amino acid sequences. We have exemplified results of such studies in our discussions of cytochrome *c* and hemoglobin. Nothing in our discussion hinted at the complex testing procedures, the time consumed, and the cost of such studies, however. Investigations of this type are progressing steadily, but it will be a long time before amino acid maps such as Fig. 5.8 will be available for many of the proteins in which students of classification and evolution are interested. In the meantime, other actually older methods of comparing proteins are available and yield results of value.

The techniques we have particularly in mind depend upon the fact that an animal will form ANTIBODIES to complex compounds such as proteins if these compounds are *foreign* to that animal's body. Antibody formation is well known to everyone as one of the means by which our bodies protect themselves against bacteria and other disease organisms. Not so generally understood is the fact that the same antibody-forming mechanisms will be called into play if even harmless proteins are inoculated into the body, providing the protein is not a normal constituent of that body.

Antibodies formed by an animal against a foreign protein will react with that protein in ways that can be seen and measured. But these antibodies also will react with other proteins that are *similar* in chemical nature to the protein against which the antibodies were formed. Because of this fact antibodies can be used for testing the relative similarities of proteins even when maps of amino acid sequences are not available.

As an example let us suppose that we wish to test the degree of similarity of blood serum proteins in subhuman mammals to such proteins in man. We may proceed as illustrated in Fig. 6.1. We take

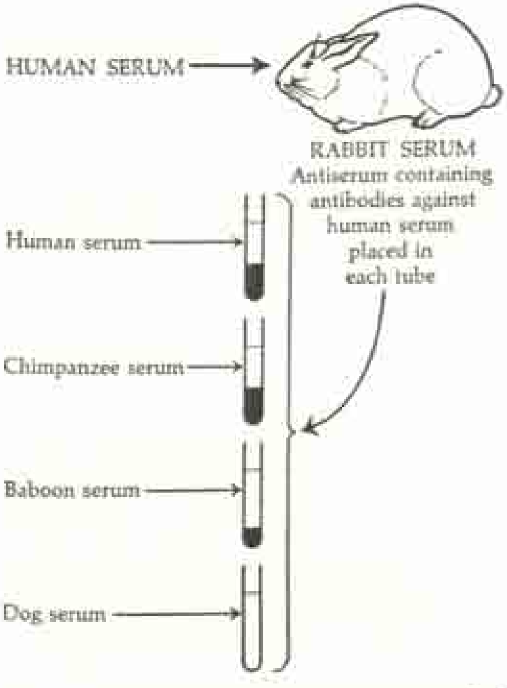

HUMAN SERUM
RABBIT SERUM
Antiserum containing antibodies against human serum placed in each tube
Human serum
Chimpanzee serum
Baboon serum
Dog serum

Fig. 6.1. Principle of the precipitin test applied to investigation of animal relationships.

some human serum and inject it into the body of an animal that will form antibodies against it. In the figure we have used a rabbit; various other creatures, e.g., domestic fowl, would serve as well. Any substance that will stimulate the formation of antibodies is called an ANTIGEN. The rabbit's body responds to the inoculated human antigen by forming antibodies. These are found in the blood serum of the rabbit; serum containing antibodies is called ANTISERUM.

Blood is removed from the rabbit, and the serum is separated from the blood cells. The rabbit serum with its antibodies against human serum now serves as a delicate test fluid. In the upper test tube shown in the figure some of it is mixed with human serum, thus bringing together antibodies and the type of antigen that caused the antibodies to be formed. Antigen–antibody reaction occurs, the visible result being the formation of a soft, white precipitate that settles to the bottom of the test tube. Antibodies that react with the antigen to form a precipitate are called PRECIPITINS, so the test we are describing is called the PRECIPITIN TEST.

When antibodies react with antigen of the type against which they formed a *homologous reaction* is said to have occurred. What will happen if the antibodies are mixed with an antigen other than the one against which they were formed *(heterologous reaction)?* The second test tube in Fig. 6.1 contains antibodies against human serum, but in this case this antiserum is mixed with chimpanzee serum. Will antibodies formed against human serum react with chimpanzee serum? As intimated above, they will do so if the proteins in human serum and the proteins in chimpanzee serum are the same or chemically similar. The fact that they are very similar indeed is demonstrated by finding that the second test tube contains as much precipitate as the first one. This result is typical of actual experiments.

The third test tube in the figure shows another heterologous test: antibodies formed against human serum reacting with baboon serum. Evidently baboon serum is less like human serum than is chimpanzee serum because we find a smaller volume of precipitate formed. This indicates that baboon serum is sufficiently like human serum so that antibodies formed against the latter "recognize" some of the proteins. Yet many of the proteins are different and so do not react with antihuman antibodies.

The fourth tube in the figure shows another heterologous test: antihuman antibodies mixed with dog serum. Here we have shown no precipitate, indicating that proteins in dog serum are so unlike proteins in human serum that antihuman antibodies will not react with them. With some powerful antiserums a small amount of precipitate may be formed. Probably all mammalian serums have some similarities in their proteins.

From our simple illustration we see that the precipitin test enables us to determine the relative similarities of antigens to the antigen that caused antibody formation. In this example relative amounts of precipitate demonstrate (1) that chimpanzee serum is more similar to human serum than are baboon serum and dog serum and (2) that baboon serum is more similar to human serum than is dog serum. Thus we have a means of testing similarities of proteins, even when the amino acid sequences in those proteins have not been analyzed.

So far we have spoken of *amount* of precipitate formed. Some means of measuring the precipitin reaction must be employed. Actually measuring the volume of precipitate, while most obvious, for technical reasons is the poorest type of measurement. Much better is the method in which the amount of nitrogen in the precipitate is determined. Antigen and antibody in this instance are both proteins. As we have seen, proteins are characteristically nitrogen-containing compounds. So if we measure the amount of nitrogen we have a measure of the amount of protein, since the two are proportional.

Before the precipitate settles to the bottom of a test tube there is a time when the particles are in suspension throughout the tube, giving the liquid a turbid or "milky" appearance. Thus the reaction may be measured by measuring this turbidity. Various photoelectric instruments are available for measuring turbidities of suspensions. Among them are spectrophotometers and the Libby Photronreflectometer.

RABBITS AND RODENTS My graduate students and I used the photronreflectometer in a study of the similarities of the serums of rabbits to those of other mammals (Moody, Cochran, and Drugg, 1949). The antiserum used in this case was formed by male domestic fowl that had been inoculated with domestic rabbit serum. The results are summarized diagrammatically in Figure 6.2. The numbers along the baseline represent successive dilutions of the antigens. These are doubling dilutions; each one has just half the antigen concentration of the one immediately preceding it. We might expect that the most concentrated solution of antigen (1) would produce the greatest turbidity when mixed with a constant quantity of antiserum. But too great a concentration of antigen inhibits precipitate formation (the so-called prozone effect). In this case the strongest reaction occurred in dilution 5, as indicated in the diagram.

By plotting the amount of turbidity obtained when a constant quantity of antiserum is added to each of the antigen dilutions and

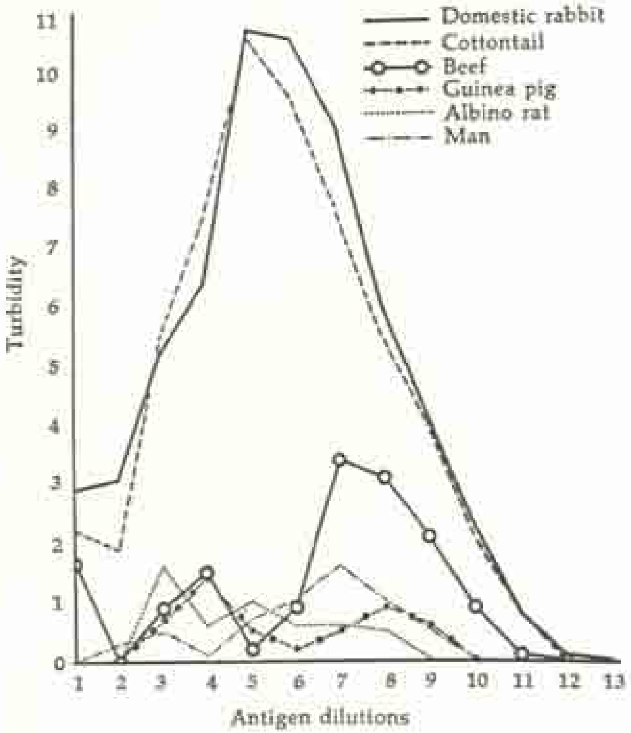


Fig. 6.2. Serological relationships of lagomorphs to several other mammals. Turbidity (photronreflectometer) test. (From Moody, P. A., V. A. Cochran, and H. Drugg, "Serological evidence on lagomorph relationships," *Evolution*, 3 (1949), 25–33.)

then connecting with a line the points plotted, we obtain a curve such as the curves shown in the figure. The total amount of turbidity obtained in the homologous reaction (that with domestic rabbit serum) is the greatest, as indicated by the size of the area under the curve (solid line). But the reaction of the antiserum (formed against domestic rabbit serum) with cottontail rabbit serum is almost as great. Thus these two have very similar serum proteins. The much smaller areas subtended by all the other curves indicate that these other mammals have but slight serological similarity to rabbits (Fig. 6.2). Thus protein structure demonstrated by serological methods indicates that the two rabbits are closely related but that all the other mammals tested are only distantly related to rabbits.

These results confirm the wisdom of placing hares and rabbits in a separate division in classification (order Lagomorpha). Sometimes they have been classed with rats, squirrels, woodchucks, and their kin as members of order Rodentia (all have gnawing teeth). But our results indicated that the serums of the two rodents tested (rat and guinea pig) are very unlike rabbit serum and hence suggested that rodents and hares and rabbits should not be combined in one order. Separation into the two orders mentioned is now common practice on the basis of anatomical differences; serology confirms the results of anatomical studies.

Our results suggest that order Lagomorpha and order Rodentia are not even closely related. Human serum (order Primates) reacted with antirabbit antibodies as strongly as did the rodent serums, and beef serum (order Artiodactyla) reacted more strongly than they did (Fig. 6.2).

We have stressed the point that protein structure, revealed by amino acid analysis or serological methods, supplements anatomical structure as a means of reaching conclusions concerning animal relationships and evolution. Indeed, from the pioneer investigations of Nuttall (1904) to the present, most serological results have served to confirm the generally accepted classification based on morphology. This would be expected if both morphological and serological similarities are attributable to inheritance from common ancestry. The fact that serological results confirm relationships as determined by morphology when these relationships are clear and firmly established promotes confidence in the validity of serological findings in cases where morphology does not by itself afford clear and unequivocal evidence as to relationships.

WHALES Whales afford a case in point. It is believed that they evolved from terrestrial mammals. Yet almost all aspects of their anatomy are so strongly modified for aquatic life that there remain few anatomical clues as to their relationships to other mammals. Serological tests indicate that their serum proteins are most like those of the even-toed hoofed (order Artiodactyla) mammals (Nuttall, 1904; Boyden and Gemeroy, 1950). This might mean that whales sprang from primitive artiodactyl stock or that both arose from the same ancestral Condylarthra (pp. 204–205). We shall not know the correct answer until the fossil record of whale evolution becomes more complete than it is at present.

PORCUPINES Another problem to which serology has contributed answers involves the question of the relationship between New World porcupines and African porcupines. Both have quills and some skeletal similarities concerning the attachments of the jaw muscles. Yet they differ in many respects. The quills of the African porcupine are much larger. African porcupines burrow in the ground; American porcupines live in trees. Fossil evidence indicates that porcupines appeared in the Old World and in South America in Oligocene times but that none lived in North America until the Pliocene (p. 146). If the porcupines had a common origin, how did some of them reach South America and others Africa without passing through North America? While it is possible, as suggested by Darlington (1957), that both they and monkeys may have passed through North America without leaving fossil evidence as yet discovered, the question remains a troublesome one. Land bridges from Africa to South America, rafting across the Atlantic Ocean, and island hopping via Antarctica have all been invoked to explain this peculiar distribution.

Perhaps the African and American porcupines are not closely related at all. They both may have evolved independently from rodents known to have been widely distributed before the first porcupines appeared (Wood, 1950). If so, we should expect their proteins to be quite unlike. This is indeed the case (Moody and Doniger, 1956). The serum proteins of the two are very different, no more alike than they are similar to the proteins of the guinea pig and the agouti, two rodents of South American origin. In passing we may note that quills are modified hairs and that various other relatively unrelated mammals have evolved quills and spines from hair (e.g., the European hedgehog and the spiny anteater of Australia, Fig. 13.2, p. 275).

MUSK OX One more enigma to the solution of which serology has contributed is the musk ox, a shaggy denizen of Arctic regions. It is obviously a member of the family of artiodactyls to which cattle, bison, buffalo, sheep, and goats belong: family Bovidae. But is it more closely related to cattle and bison or to sheep and goats? On the one hand it has sometimes been regarded as an arctic bison and hence closely related to cattle. On the other hand fossil evidence seems to indicate that its relationship is to goats rather than to cattle and their allies. Serological tests by the present author indicated that its relationship is to sheep and goats (Moody, 1958). Figure 6.3 indicates this and also demonstrates the value of *reciprocal* tests in serological studies. An antimusk ox antiserum gave a large reaction with sheep and goat serums. An antigoat antiserum gave a large reaction with musk ox serum, thus confirming the preceding test. Finally, an antibeef antiserum gave a small reaction with musk ox serum, thereby confirming the small reaction given by the antimusk ox antiserum when tested with beef serum. Incidentally, the tests also indicated the known close relationship to each other of sheep and goats as well as that of beef and bison.

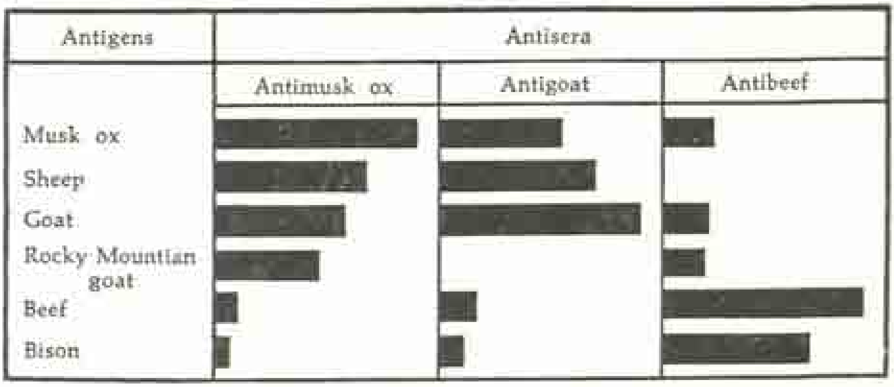


Fig. 6.3. Serological relationships of the musk ox to other members of Family Bovidae. Turbidity (photronreflectometer) tests. Abscissal scale is in precentage, the strength of the homologous reaction with each antiserum being designated as 100%. (Drawn by Melton M. Miller, Jr.; from Moody, P. A., "Serological evidence on the relationships of the musk ox," *Journal of Mammalogy, 39* (1958), 554–559.)

PRIMATES Space limitation forbids discussion of many other contributions of serology to the study of animal relationships (for example, see Wemyss, 1953; Leone and Wiens, 1956; Pauly and Wolfe, 1957; Leone, 1964; and the bibliographies of these papers). One additional program of investigation should be mentioned because it bears on the interesting question of the similarity of man's proteins to those of his fellow primates, especially the great apes. On preceding pages we mentioned the striking similarity of human DNA to chimpanzee DNA (p. 82), of human cytochrome *c* to that of the rhesus monkey (p. 93), and of human hemoglobin to that of the great apes, with the hemoglobin structure being almost identical (p. 96). Goodman (1962, 1963a, 1963b, 1967) investigated similarities of serum proteins. In doing this he separated serum proteins into their constituent parts, albumins and globulins, and employed a different serological technique from the techniques described previously. In this method (the Ouchterlony technique) two antigen solutions and an antiserum solution are brought into simultaneous contact with a block of agar-gel, as shown in Fig. 6.4. The solutions diffuse into the gel, and when antibodies come into contact with the corresponding antigen a band of white precipitate forms. When the two antigens are identical all components of both react with the antiserum where they come into contact (Fig. 6.4*A*). When the heterologous antigen differs from the homologous one, not all the antibodies react with the heterologous antigen; some diffuse on until they eventually come into contact with

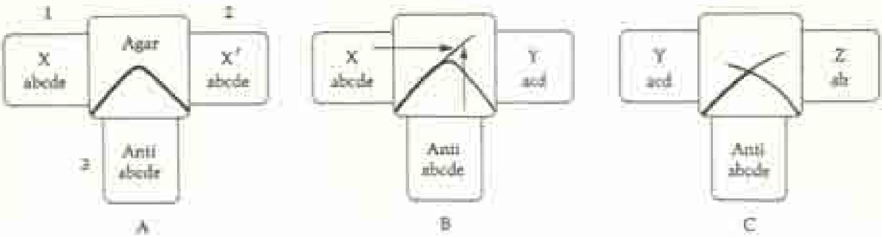


Fig. 6.4. Principle of the Ouchterlony test of serological relationships. 1, 2, and 3 are tiny wells or reservoirs on three sides of a block of agar-gel. 1 and 2 contain antigens; 3 contains an antiserum.
A. Reaction of identity. Reservoir 1 contains the homologous antigen, X, its parts or components being represented by the letters a, b, c, d, and e. Reservoir 2 contains an antigen, X^1, that has the same components. Reservoir 3 contains antibodies against these components. The antigens and antibodies diffuse into the block of agar until an antigen meets the corresponding antibody. When antibody anti-a meets antigen component a, the two react, forming a precipitate. The same happens when anti-b meets antigen component b, and so on. The result is the band of precipitate in the agar block. Since the homologous and heterologous antigens, X and X^1, have identical components all antibodies react with both, forming a band uniform in its right and left arms.
B. Reaction of partial identity, with single spur. Reservoir 3 contains the same antiserum as in the preceding case, and reservoir 1 the homologous antigen. Reservoir 2 contains antigen Y having components a, c, and d. Since antigen Y lacks components b and e, antibodies anti-b and anti-e find nothing in that antigen to react with, and so continue to diffuse through the agar until they meet components b and e diffusing inward from antigen X (horizontal arrow). At this point precipitation occurs, forming the spur indicated.
C. Reaction of partial identity, with bilateral spurs. The same antiserum is used again, but this time reservoirs 1 and 2 both contain heterologous antigens lacking some components of the antigen against which the antiserum had been formed. A spur is formed on the right side where anti-c and anti-d meet c and d diffusing in from antigen Y. A smaller spur is formed on the left side where anti-b meets b diffusing in from antigen Z. (Reprinted from Goodman, Morris, "Evolution of the immunologic species specificity of human serum proteins," *Human Biology*, *34* (1962), No. 2, 104–150, by permission of the author and Wayne State University Press. Copyright 1962 by Wayne State University Press.)

homologous antigen, when they then react to from a line of precipitate that appears as a "spur" (Fig. 6.4*B*).

Using this technique Goodman has demonstrated that the serum proteins of man and the chimpanzee are exactly alike so far as this test will indicate (reaction of identity, Fig. 6.4*A*). The proteins of man and the gorilla are almost exactly alike, though a very slight spur forms against the gorilla, indicating that gorilla protein differs from human protein in some small respect. Interestingly, some (but not all) of the proteins of these two African apes differ as much from each other as they differ from human proteins. On the other hand, the proteins of the Asiatic apes, orangutan, and gibbon, are less like human proteins than are the proteins of the African apes. On the basis of these findings and of the strong similarities in other respects just noted, Goodman has proposed that the chimpanzee and gorilla should no longer be considered members of the ape family [Pongidae (p. 231)] but should be classed along with humans in the family Hominidae. This is not the place to enter into a technical discussion of just how "human" a creature must be to be included in the family Hominidae, but the suggestion emphasizes another striking similarity between the African apes and ourselves.

Interestingly, this similarity also has been demonstrated by the use of a different type of serological test: complement fixation. The technique used employs minute amounts of the reagents and hence is called microcomplement fixation. Purified albumins from various species of primates have been the material tested. Among the findings is the fact that gorilla and chimpanzee albumins are no more similar to each other than either is to human albumin (Sarich and Wilson, 1967a, 1967b). The albumins of orangutan and gibbon are less similar to human albumin and the albumins of Old World monkeys are much less similar than are the albumins of the African apes.

There are other ways of analyzing proteins than those discussed so far. Mixtures of proteins, as found in blood serum, for example, may be separated into their component parts by subjecting the mixture to the influence of an electrical field (electrophoresis). The same technique may be applied to other mixtures of compounds from plant and animal tissues (see Sibley and Johnsgard, 1959). Mixtures also may be separated by the differential rate at which they diffuse through filter paper moistened with a suitable solvent or through other media (chromatography). These techniques, alone and combined, are being applied to problems of classification and evolution, but space forbids our discussion of them. Interested readers will find typical examples in Leone (1964).

BLOOD GROUPS

In connection with our discussion of serological tests we may appropriately mention some evolutionary aspects of the blood groups. So far we have been emphasizing similarities of proteins. The chemical substances that determine blood groups are compounds of high molecular weight found on the surface of red blood cells. They combine several kinds of sugars (carbohydrates) with fatty acids and are called glycolipids (Watkins, 1966). Since the synthesis of glycolipids involves enzymes (proteins), the blood group substances are not far removed from the primary gene action we have discussed.

Nearly everyone is acquainted with the fact that all human beings belong to one or another of four blood groups: O, A, B, and AB. The basis of this grouping is the presence or absence of two glycolipids called A and B. People belonging to group O have neither of these substances on their red blood cells. People of group A have substance A only. People of group B have substance B only. People of group AB have both substances. Since these substances are antigenic, their presence can be detected by the use of test fluids containing the corresponding antibodies.

The presence of substances A and B is determined by genes, as we have implied, and these genes are inherited according to the principles of Mendelian genetics (Chap. 17), though in the slightly complicated form known as multiple alleles. Space limitation prevents a description of the precise mode of inheritance; this is discussed in textbooks of genetics (e.g., Moody, 1967).

From the standpoint of evolution, substances A and B are of interest because of their distribution (1) among the human racial groups and (2) among the other primates, especially the great apes.

In all human races we find people who belong to each of the four blood groups. That is, no race is completely lacking either substance A or substance B, and no race is characterized by the possession of either substance by all members of the race. American Indians form the nearest exception to this statement; among most tribes the number belonging to group O is extremely high, reaching 100 percent in some South American groups. Nevertheless, Indians taken as a whole cannot be said to lack A and B completely.

Human races differ in the *proportions* of the population belonging to each of the four groups. For example, approximately 47 percent of white Americans or western Europeans belong to group O, 43 percent to group A, 7 percent to group B, and 3 percent to group AB. Thus about 46 percent of that population possesses A, alone or combined with B, while only about 10 percent possesses B, alone or combined with A. On the other hand, among Chinese the percentages are about as follows: group O, 30 percent; group A, 25 percent; group B, 35 percent; and group AB, 10 percent. In contrast to western Europeans, therefore, only about 35 percent of Chinese possess substance A, alone or combined with B, whereas about 45 percent possess B, alone or combined with A. Interestingly, geographically intermediate populations show intermediate percentages. Thus as one travels eastward across Eurasia one encounters decreasing percentages of substance A and increasing percentages of substance B. These gradients probably arose through past migrations of peoples, including wars of conquest, always potent means of distributing genes of the invaders among the invaded. But the reasons for the difference between the geographic extremes, Chinese and western Europeans, must still be sought.

Data concerning blood groups have been collected for great numbers of ethnic and national groups (see pp. 263–265; also Wiener, 1962; Boyd, 1950; Mourant, 1954; Mourant and Kopeć, 1958). In some cases the nature of the blood group proportions in a given population has aided anthropologists in determining the relationships of that population to others (see our discussion of human races, pp. 262–267; also Boyd, 1950 and 1964).

Table 6.1. ABO BLOOD GROUPS AMONG THE GREAT APES*

	O	*A*	*B*	*AB*
Chimpanzee	32	108	0	0
Gibbon	0	3	11	10
Orangutan	0	22	1	3
Gorilla				
Lowland	0	0	9	0
Mountain	0	2	0	0

* From Wiener and Moor-Jankowski, 1966, Table 1. Numbers given are actual number of individuals tested.

Turning to the anthropoid apes, we find the blood group distributions shown in Table 6.1. Here we note differences among the genera in the distribution of the antigens. Thus chimpanzees seem never to have developed substance B. The two kinds of gorillas seem to differ in which antigen is present, though in this case the numbers are too small to warrant firm conclusions. Interestingly, group O, a large group and frequently the predominant one in our own species, is poorly represented among the apes.

The gorilla presents a contrast to the other three apes: while in the latter, as in man, the antigens are found on the red blood cells, in the gorilla they are absent or nearly so from the red blood cells but present in the cells of organs and in secretions—as they may also be in man (Wiener and Moor-Jankowski, 1966). Studies of proteins discussed earlier have shown striking similarities between the two African apes; here we have an interesting difference between them. In this respect the chimpanzee resembles man more closely than does the gorilla.

Blood grouping tests have been performed on many Old World monkeys. Differences also are found among them. Thus all rhesus monkeys seem to belong to group B, while baboons may belong to any one of the four groups (only three group O baboons have been encountered to date; Wiener and Moor-Jankowski, 1969). For further details and for information on the presence in subhuman primates of such blood cell substances as M, N, H, Rh, and others see Wiener (1965), and Wiener and Moor-Jankowski (1966), and references given in these papers.

In summary we see in these cellular antigens another line of evidence pointing to the relationship of man to other primates. As we noted, the antigens are gene determined. The chemical difference between substances A and B is not great. We may anticipate, therefore, that a simple mutation in a gene concerned with production of one of them could result in production of the other one (or of no antigen at all, resulting in group O in individuals homozygous for the mutated gene). Because of the relatively simple genetic basis, the same mutation may have occurred more than once in the history of primate evolution. This being the case, we do not assume that all possessors of antigen A, for example, inherited that antigen from a common ancestor. Such a view might lead to the absurd conclusion that people who belong to group A are more closely related to chimpanzees than are people who belong to group B (Table 6.1)!

What, then, is the basic similarity between man and the other mammals that is expressed in the common possession of the blood group antigens? It is a basic similarity of germ plasm, demonstrated by the fact that genes possessed by man and at least his nearest relatives are so similar that when they undergo mutation the products of the latter are identical or closely similar. Here is another example of that parallel evolution already mentioned (p. 30). Doubtless such basic similarity of germ plasm underlies all the morphological, biochemical, and serological similarities we have called homologies and interpreted as indicative of common ancestry. But in the case of the blood groups the relationships between genes and their products (antigens A and B) appear to be more direct and clearly evident than are relationships between genes and many of the other characteristics of animals. Hence antigens A and B afford more distinct evidence of fundamental similarities existing between germ plasms than is supplied by characteristics whose genetic basis is not so thoroughly known. (Recall also our discussion of comparative studies of DNAs, pp. 81–84.)

This chapter discussed studies of serum proteins and red blood cell antigens using the varied techniques of serology. In some of the studies the number of individual specimens used was small, and we remember the caution needed in basing general conclusions on small numbers (pp. 83–84). Nevertheless, serological investigations have abetted other methods of analyzing proteins and studies of anatomy and embryology in indicating the relationships among organisms. Analysis of such relationships is basic to the study of evolution.

References and Suggested Readings

Boyd, W. C., *Genetics and the Races of Man,* Boston, Little, Brown, 1950.

Boyd, W. C., "Modern ideas on race, in the light of our knowledge of blood groups and other characters with known mode of inheritance," in Leone (below), 119–169 (1964).

Boyden, A., and D. Gemeroy, "The relative position of the Cetacea among the orders of Mammalia as indicated by precipitin tests," *Zoologica, 35,* 145–151 (1950).

Darlington, P. J., Jr., *Zoogeography: The Geographical Distribution of Animals,* New York, John Wiley, 1957.

Goodman, M., "Evolution of the immunologic species specificity of human serum proteins," *Human Biology, 34,* 104–150 (1962).

Goodman, M., "Serological analysis of the systematics of Recent hominoids," *Human Biology, 35,* 377–424 (1963a).

Goodman, M., "Man's place in the phylogeny of the primates as reflected in serum proteins," in S. L. Washburn (ed.), *Classification and Human Evolution,* Chicago, Aldine Publishing, 1963b, pp. 204–234.

Goodman, M., "Deciphering primate phylogeny from macromolecular specificities," *American Journal of Physical Anthropology, 26,* 255–275 (1967).

Leone, C. A. (ed.), *Taxonomic Biochemistry and Serology,* New York, Ronald Press, 1964.

Leone, C. A., and A. L. Wiens, "Comparative serology of carnivores," *Journal of Mammalogy, 37,* 11–23 (1956).

Moody, P. A., "Serological evidence on the relationships of the musk ox," *Journal of Mammalogy, 39,* 554–559 (1958).

Moody, P. A., *Genetics of Man,* New York, W. W. Norton, 1967.

Moody, P. A., V. A. Cochran, and H. Drugg, "Serological evidence on lagomorph relationships," *Evolution, 3,* 25–33 (1949).

Moody, P. A., and D. E. Doniger, "Serological light on porcupine relationships," *Evolution, 10,* 47–55 (1956).

Mourant, A. E., *The Distribution of the Human Blood Groups,* Oxford, Blackwell Scientific Publications, 1954.

Mourant, A. E., and A. C. Kopeć, *The ABO Blood Groups,* Oxford, Blackwell Scientific Publications, 1958.

Nuttall, G. H. F., *Blood Immunity and Blood Relationship,* Cambridge, Cambridge University Press, 1904.

Pauly, L. K., and H. R. Wolfe, "Serological relationships among members of the order Carnivora," *Zoologica, 42,* 159–166 (1957).

Sarich, V. M., and A. C. Wilson, "Rates of albumin evolution in primates," *Proceedings of the National Academy of Sciences, 58,* 142–148 (1967a).

Sarich, V. M., and A. C. Wilson, "Immunological time scale for hominid evolution," *Science, 158,* 1200–1203 (1967b).

Sibley, C. G., and P. A. Johnsgard, "An electrophoretic study of egg-white proteins in twenty-three breeds of the domestic fowl," *American Naturalist, 93,* 107–115 (1959).

Watkins, W., "Biochemical genetics of the A-B-O and Lewis blood group systems," in W. J. Kuhns (ed.), *John A. Hartford Foundation Conference on Blood Groups and Blood Transfusion,* vol. 1, New York, Better Bellevue Association, 1966, pp. 7–32.

Wemyss, Jr., C. T., "A preliminary study of marsupial relationships as indicated by the precipitin test," *Zoologica, 38,* 173–181 (1953).

Wiener, A. S., *Blood Groups and Transfusion,* 3rd ed., Springfield, Illinois, Charles C Thomas, 1943; New York, Hafner Publishing, 1962.

Wiener, A. S., "Blood groups of chimpanzees and other nonhuman primates: Their implications for the human blood groups," *Transactions of the New York Academy of Sciences, Series II, 27,* 488–504 (1965).

Wiener, A. S., and J. Moor-Jankowski, "Blood groups of nonhuman primates, and their implications for studies in man," in W. J. Kuhns (ed.), *John A. Hartford Foundation Conference on Blood Groups and Blood Transfusion,* vol. 1, New York, Better Bellevue Association, 1966, pp. 75–103.

Wiener, A. S., and J. Moor-Jankowski, "The A-B-O blood groups of baboons," *American Journal of Physical Anthropology, 30,* 117–122 (1969).

Wood, A. E., "Porcupines, paleogeography and parallelism," *Evolution, 4,* 87–98 (1950).

7

Life's Beginnings

HOW DID LIFE on earth begin? The answer is that we do not know and probably never will. The origin of life occurred more than three *billion* years ago and was not the type of happening to leave a clear indication of its course of events in the fossil record. Why, then, do we discuss the question at all? The best we can do is to point out what *might* have happened. As we shall see, attempts to do that have added greatly to our knowledge of biochemical events of a type that may have occurred under primitive conditions both before and after recognizable living organisms appeared. Gaining knowledge of this kind is intellectually satisfying. But it also contributes to two areas of great interest at present: (1) the question of life on other planets and

(2) the attempts to create life in the laboratory. The other planets differ from earth in many respects; may we expect that life in some form may be present? If so, what form may we expect life to have when atmospheric and other conditions are unlike those found on earth?

THE PROBLEM Our discussion will be based upon two assumptions:

1. We shall assume that life on earth originated on this planet. The postulate is sometimes made that life originated elsewhere in the universe and migrated to earth through space. Such an "explanation" raises as many problems as it solves and merely removes the problem to some distant, unknown point in space.

2. We shall assume that the living state arose from the nonliving state. This is called abiogenesis and is generally believed not to occur at the present time, though as Darwin pointed out long ago, if it did occur at the present time hordes of organisms already in existence would destroy the newly arising protoplasm. But some three billion years ago there were no organisms, not even bacteria. The earth was sterile, as surgeons use the word. Newly arising protoplasm would have had a chance for survival.

In preceding chapters we emphasized the importance in living things of (1) proteins and (2) nucleic acids. Proteins supply structural components for organisms, and they serve the absolutely essential role of enzymes. Among other things, enzymes are needed in the formation of nucleic acids. Nucleic acids provide the templates (patterns) for the formation of proteins and the means of inheritance. Thus we have a circle: Proteins depend upon nucleic acids; nucleic acids depend upon proteins. To a considerable extent the problem of the origin of life resolves itself into the problem of opening this circle—how did this mutual interdependence of proteins and nucleic acids *begin?* Which came first, proteins or nucleic acids? Or were both developed concurrently? How could the first proteins have been formed if there were no nucleic acids to serve as templates for them? How could the first nucleic acids have been formed if there were no proteins to serve as enzymes? Enzymes are organic catalysts. Various inorganic substances also have catalytic action—might some of them have served in place of enzymes in the formation of the first nucleic acids (and of proteins, too, since in modern cells enzymes are necessary to the production of proteins)?

Furthermore, we have the problem of *energy*. The living processes that we combine under the term "metabolism" require the expenditure of energy. Included among these energy-requiring processes is the manufacture of proteins and nucleic acids. What is the source of this energy? For most modern organisms the source is the *sun*. Through the process of photosynthesis green plants capture some of the sun's energy. Animals eat the plants and thereby obtain the energy they need (carnivores get their supply by eating animals that have eaten plants). Photosynthesis is a highly complex process involving many *enzymes*. It could hardly have been present on earth before there were any proteins to serve as enzymes. So we have another circular arrangement to be opened up. Before there were enzymes making possible modern photosynthesis, what sources of energy could have been utilized by the first organisms? What sources of energy could have made possible the synthesis of the first proteins and nucleic acids?

The questions we have asked are the fundamental ones. The discussion that follows consists largely of attempts to answer them.

THE PROTEINS-FIRST HYPOTHESIS

Which came first, proteins or nucleic acids? Not surprisingly, two schools of thought have developed on this question. We shall employ the term "proteins-first hypothesis" for the idea that proteins came first and that only later did the present dependence on a nucleic acid code develop. We shall use the term "gene-first hypothesis" for the opposite idea: that nucleic acids capable of self-replication came first and subsequently took upon themselves the task of organizing amino acids into polypeptide chains (proteins).

As we noted in Chapter 5, each polypeptide consists of a series of amino acid residues (amino acids joined together by peptide linkages, Fig. 7.1). It usually has been assumed that the amino acids first appeared and then were joined together into polypeptides. This idea has been challenged, as we shall see (p. 125).

What raw materials were present for manufacture into proteins? There was the ocean with its salts. The protoplasm of all living things is a salt solution. Then there was the atmosphere with its chemical compounds. There is general agreement that the primitive atmosphere did not contain free oxygen—in chemical terms it was a *reducing* atmosphere rather than an oxidizing one. What *did* it contain?

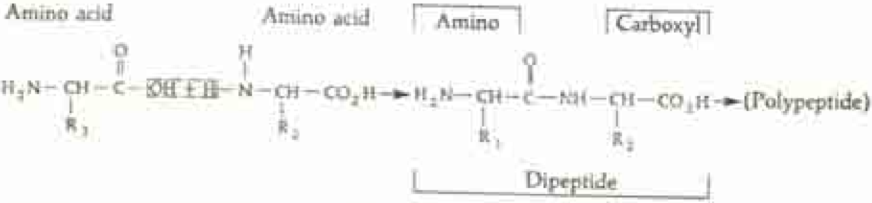
Here again we have two opinions: Most investigators have concluded that the primitive atmosphere contained large amounts of ammonia (NH_3) and methane (CH_4), as do the present atmospheres of Jupiter, Saturn, Uranus, and Neptune. (Arguments supporting this view will be found in Miller and Urey, 1959). Other investigators have concluded that the principal constituents were carbon monoxide (CO), carbon dioxide (CO_2), nitrogen (N_2), and hydrogen (H_2). (Arguments supporting this view, which seems to be favored by geologists, will be found in Abelson, 1966.) We shall not attempt to judge the relative merits of these two hypotheses. Rather, we shall ask: Could the substances mentioned in either hypothesis serve as ingredients for the formation of amino acids?

We must also ask: What sources of energy might have been present that could have been utilized in this energy-requiring process? We may mention four: (1) ultraviolet radiation from the sun, (2) ionizing radiation from the sun (e.g., protons, electrons, and x-rays), (3) electrical discharges (e.g., lightning), and (4) heat (e.g., from volcanoes; Ponnamperuma, 1965).

Starting with the pioneer experiments of Stanley Miller (1953), many experiments have been performed utilizing one or another of these energy sources applied, typically, to mixtures of methane, ammonia, and water (see Fox, 1965a). In Miller's experiment the mixture was boiled and the vapor subjected to an electrical spark. After a time the apparatus was found to contain amino acids and other substances of considerable complexity. Other experiments have employed varying methods and sources of energy, but the results have agreed in showing that in the absence of life amino acids can be generated by these means.

Would the same result follow if the atmosphere consisted of CO, CO_2, N_2, H_2? Under experimental conditions Abelson and his colleagues found that mixtures of CO, N_2, and H_2 would react to form HCN (hydrogen cyanide) and that when the latter was subjected to ultraviolet radiation the amino acids glycine, alanine, serine, aspartic acid, and glutamic acid were formed (Abelson, 1966). So we see that according to either hypothesis of the nature of the primitive atmosphere amino acids might have been obtained by nonbiological means.

Could amino acids have been joined into polypeptide chains under



$$H_2N-\underset{\underset{R_1}{|}}{CH}-\overset{\overset{O}{\|}}{C}-\boxed{OH + H}-\overset{\overset{H}{|}}{N}-\underset{\underset{R_2}{|}}{CH}-CO_2H \rightarrow H_2N-\underset{\underset{R_1}{|}}{CH}-\overset{\overset{O}{\|}}{C}-NH-\underset{\underset{R_2}{|}}{CH}-CO_2H \rightarrow \text{(Polypeptide)}$$

Fig. 7.1. Joining of two amino acids through dehydration condensation to form a dipeptide, the first step in the formation of a polypeptide chain. (The initials R_1 and R_2 indicate radicals or side chains, the portion of the amino acid molecule that gives it its distinctive attributes.) (Modified from Calvin, M., "Chemical evolution," *Proceedings of the Royal Society of London, Series A*, 288 (1965), 441–466. Used by permission of the author and The Royal Society.)

nonbiological conditions? In modern organisms this joining is accomplished through the action of enzymes. How could it have been accomplished before there were any proteins to serve as enzymes?

The combining of smaller molecules to form larger ones (macromolecules) is called *polymerization*. As Calvin (1965) has pointed out, the polymerizations in which we are interested here involve removal of molecules of water: dehydration condensation (Fig. 7.1). In the first line of the figure we see at the left abbreviated structural formulas of two amino acids side by side. A rectangle of dashed lines surrounds the elements composing a molecule of water. When this molecule is removed the amino acids are joined together (peptide linkage) to form a dipeptide. The same process occurs over and over again to form longer and longer chains of amino acid residues—polypeptides (polymers).

Calvin (1965) listed three possible conditions that might lead to such polymerization in the absence of enzymes: (1) Experiments by Fox and his colleagues indicate that if amino acids become dry (dehydrated) and are then subjected to heat, polymerization will ensue, with the formation of proteinlike substances called "protenoids" (pp. 121–123). (2) If amino acids became adsorbed on a clay or mineral surface the activity of the water might be reduced and polymerization might occur (Bernal, 1959). (3) The presence of certain substances might promote polymerization even in aqueous media. In Calvin's laboratory cyanide compounds have been found to cause formation of dipeptides and even of linkages of four amino acid residues (tetramers; Calvin, 1965). Since cyanide compounds are among the substances formed when ingredients believed to have been present in the primitive atmosphere are subjected to ultraviolet rays (or other sources of energy; see the preceding), the catalytic action of such compounds may well have been important in the formation of the first polypeptides.

Phosphate compounds also probably were present before the advent of life. Experiments reported by Young (1965) indicate that such compounds may catalyze amino acid polymerization to produce macromolecules of proteinlike complexity ("protenoids," p. 121).

These few examples will illustrate reasons for thinking that polypeptides could indeed have been formed by nonbiological processes. Importantly, even fairly simple polypeptides may have had some catalytic activity and thus have served as the first enzymes. With the advent of enzymes an important step would have been taken toward the origin of life. In this connection it is interesting that the modern enzyme ferredoxin consists of only 55 amino acid residues. It is an important enzyme in many organisms (Arnon, 1965). Furthermore, it lacks many of the 20 amino acids characteristic of most proteins. Eck and Dayhoff (1966) postulated that the original ferredoxin molecule was based on a repeating sequence of alanine, serine, aspartic acid, and glycine. Abelson (1966) pointed out that these amino acids are those produced most readily from hydrogen cyanide (p. 118).

So far we have followed the line of thinking that amino acids were formed at first and then were joined together into polypeptides. As noted previously, this idea has been challenged. Matthews and Moser (1967) found that with ammonia as a catalyst hydrogen cyanide and water are converted directly into polypeptides, seemingly without an intervening stage of free amino acids. The polypeptides formed were analyzed and found to contain 12 or more of the amino acids commonly found in proteins. This experiment may indicate that synthesis of the first polypeptides was more direct than we had supposed.

Could these first polypeptides (simple proteins) have reproduced themselves? Reproduction is an essential characteristic of living things. In modern organisms proteins do not usually duplicate themselves directly—production of new proteins is under the control of the elaborate DNA–RNA mechanism discussed previously. Do we have any evidence that in the absence of this mechanism proteins may produce replicas of themselves? Various investigators have suggested the possibility that some polypeptides may be at least weakly self-replicating (e.g., Sagan, 1965). Steinman and Cole (1967) presented experimental evidence that peptide production could be stimulated by peptides already present without the participation of nucleic acids. Evidence of a different type is perhaps furnished by the causative agent of a disease in sheep called scrapie. The agent seems to be a protein of low molecular weight capable of duplicating itself in the absence of DNA and RNA (Gibbons *et al.*, 1967). These may be straws in the wind indicating that future research will demonstrate that, under some conditions at least, proteins can reproduce without the nucleic acid mechanism commonly found in modern organisms.

Even if we grant that a protein molecule could arise under nonliving conditions, be capable of some degree of enzymatic activity, and be self-duplicating, we have not progressed very far toward formation of an "organism" as we usually think of it. Very early some separation of the proteins from the surrounding water must have arisen. The first means of separation might be no more than the surface membrane formed around droplets in a colloidal system: COACERVATE DROPLETS. Oparin (1957 and 1962), one of the pioneers in research on the origin of life, has stressed their importance and has done extensive research on coacervate droplets produced artificially. A simple example of coacervate formation is afforded by mixing together a solution of gelatin and a solution of gum arabic. The gelatin and gum arabic will combine to form droplets floating in the surrounding medium. The same thing may be done with many substances of high molecular weight, such as proteins. The droplets differ from the surrounding medium in properties. For example, coacervate drops were prepared containing gelatin, gum arabic, soluble starch, and the enzyme amylase (which converts starch to sugars). Starch was present in both the droplets and the surrounding aqueous medium, but as one might expect most of the reduction of starch to sugar occurred in the droplets, where the enzyme was concentrated (Oparin, 1959). The literature on coacervate droplets is extensive. We see in this tendency of molecules of high molecular weight to aggregate a means by which separation from the surrounding "soup" may have occurred in primeval oceans. Perhaps the first proteins may have aggregated to form coacervate droplets (Oparin, 1965). While such droplets have no permanent membrane surrounding them, and are easily fragmented into smaller droplets by mechanical forces (e.g., shaking), the presence of a surface layer does make possible selective absorption and accumulation of substances from the surrounding medium.

We mentioned previously (p. 119) the experiments of Fox and his colleagues in which proteinlike substances called PROTENOIDS were produced by heating together amino acids under anhydrous conditions. These protenoids have many of the properties of natural proteins (Fox, 1965c, Table I), though they lack antigenicity (the ability to stimulate formation of antibodies) and the helical molecular structure characteristic of proteins. When suitable chemicals are present they may be formed without the application of heat to the amino acid solution (Young, 1965).

When protenoids are dissolved in water by being heated to boiling and then are allowed to cool, they form tiny spheres suspended in the water. These are called MICROSPHERES (Fig. 7.2). While they vary in size, frequently they are of about the size of bacteria. They also may be formed without heating by simply cooling a saturated solution of protenoid from 25-O° C (Young, 1965). Young stated: "They offer certain advantages over the coacervate in that structurally they are much more stable, they are derived from material synthesized under primitive conditions, and thus are easier to imagine in a primitive sequence of events than the coacervate."

Microspheres exhibit some of the properties of cells (Fox, 1965b). They divide by fission. The electron microscope shows that the surface membrane is composed of two layers as in cells (though the membrane contains no lipids—fatty materials—characteristic of true cell membranes). When zinc is present the microspheres split ATP (adenosine triphosphate), a particularly significant reaction in view of the im-

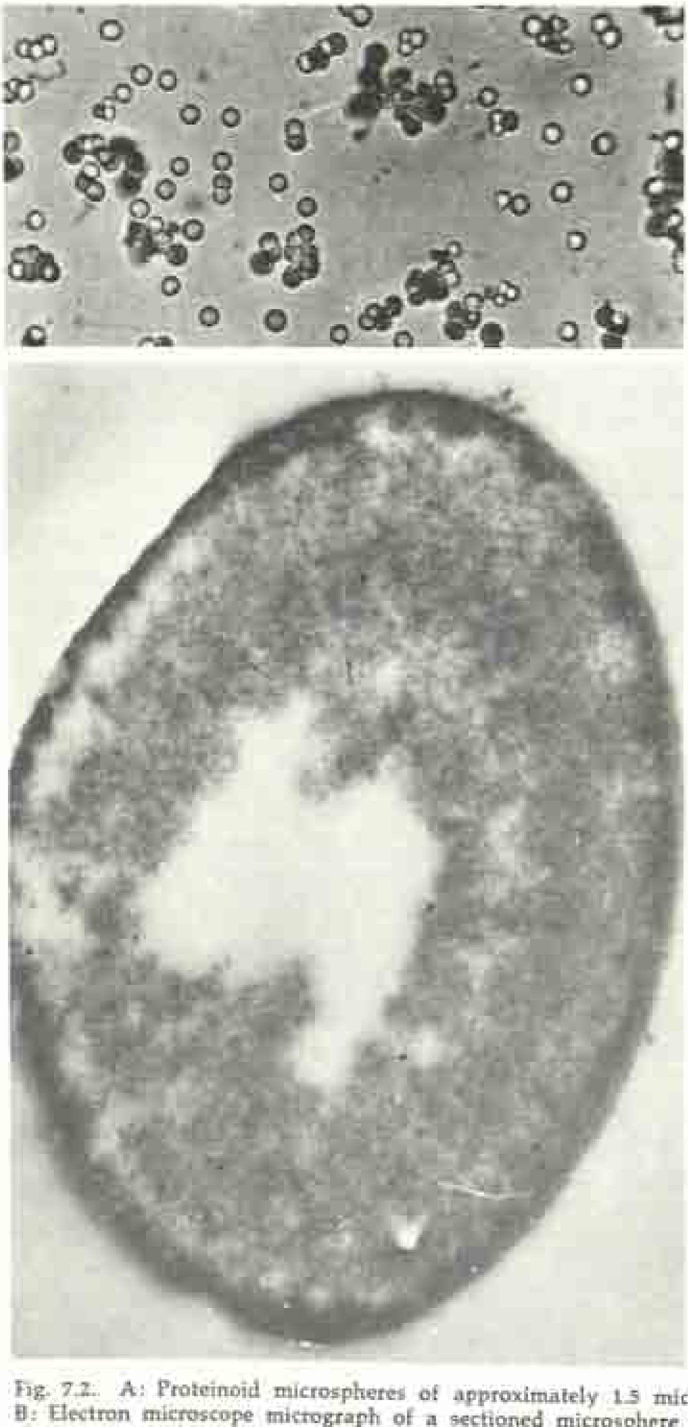


Fig. 7.2. A: Proteinoid microspheres of approximately 1.5 microns diameter. B: Electron microscope micrograph of a sectioned microsphere having a major-axis length of about 2.5 microns. Note the evidence of internal structure. (Courtesy of Sidney W. Fox.)

portance of ATP in providing energy for metabolic processes in living things (see the following).

The microspheres are not cells, and they are not living, but perhaps they indicate how precells may have formed in the primeval oceans. If heat was involved as in Fox's original experiments, it could have been provided by volcanoes. Indeed, in some experiments Fox (1965b) placed a mixture of dry amino acids in a depression in a block of lava. This was then heated in an oven at 170° C for several hours. A light, amber-colored liquid was formed. When this was diluted with hot salt solution or "artificial rain" microspheres were formed.

However, a cell consists of much more than proteins enclosed by a membrane. Could other essential cell constituents have been formed under nonliving conditions? We have mentioned adenosine triphosphate (ATP) as the important means by which energy is supplied for living processes. Could ATP have been formed under primitive earth conditions? One of the ingredients is adenine, the purine most readily formed from hydrogen cyanide. Experiments indicate that purines and pyrimidines (p. 77) could have been synthesized under nonbiological conditions (Oró, 1965). Phosphorus-containing compounds also were present. In the joining of adenosine to phosphate we have another dehydration reaction (Fig. 7.3). Experiments reported by Ponnamperuma (1965) indicate that ATP may be formed in this way by the action of ultraviolet radiation. In the figure one phosphate group is shown joined to adenosine (left-hand portion of Fig. 7.3). Adenosine diphosphate (ADP) contains two of these phosphate groups; ATP contains three. These compounds are said to be *energy rich* because one (in ADP) or two (in ATP) of the phosphate groups are joined to the molecule by *high energy phosphate bonds.* When fuel (e.g., glucose) is oxidized in modern organisms some of the energy released is trapped when ADP is converted to ATP by addition of that third phosphate group. The ATP then reacts with other components of the cell, passing on to them the energy contained in the high energy bond holding this group and reverting to ADP in the process. Energy thus supplied enables the cell to do its work (e.g., it enables a muscle cell to contract). Thus ATP is an essential intermediary between the oxidation of carbohydrates and cell mechanisms requiring energy for metabolic work.

In modern cells the process just summarized is very complex, involving participation of enzymes. It is of particular interest, therefore, that, in the absence of enzymes ATP with its high-energy phosphate bonds was probably formed under primordial conditions. In ATP the first organisms would have found a preformed source of energy. ATP was not the only energy rich compound formed, but it may well have been the most important one.

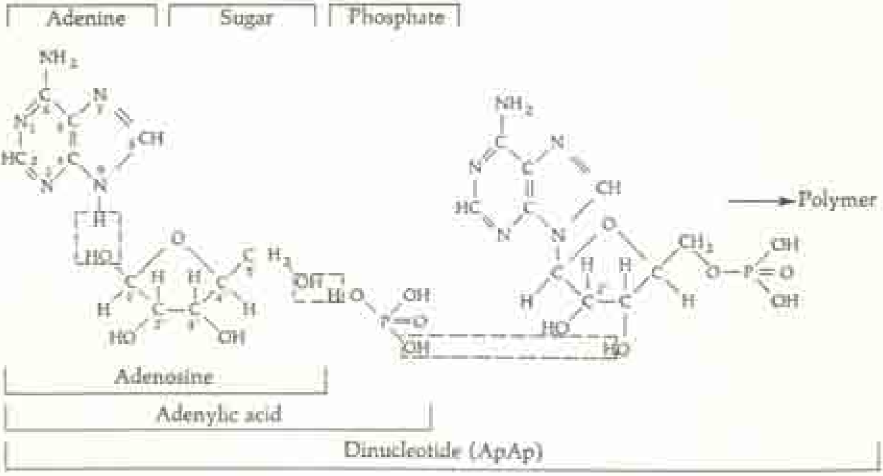


Fig. 7.3. Dehydration condensations in the formation of nucleic acid (RNA, in this case). Note removal of the elements of water (dashed-line rectangles) when adenine, sugar and phosphate join to form a nucleotide (adenylic acid), and when two nucleotides join to form a dinucleotide as a step in the formation of a chain of nucleotides (i. e., of a nucleic acid molecule). (Modified from Calvin, M., "Chemical evolution," *Proceedings of the Royal Society of London, Series A, 288* (1965), 441–466. Used by permission of the author and The Royal Society.)

Could nucleic acids such as DNA and RNA have been formed under nonliving conditions? We recall that these are formed of chains of nucleotides and that each nucleotide is composed of three constituent molecules: a purine or pyrimidine, a phosphate, and a sugar (ribose or deoxyribose; pp. 77–78). As noted above, purines, pyrimidines, and phosphorus-containing compounds were evidently formed under primitive earth conditions. How about the sugars? Here again we encounter a diversity of opinion. In general, supporters of the concept that the atmosphere consisted mainly of CO, CO_2, N_2, and H_2 conclude that sugars would not be formed or, if formed, would be rapidly degraded (Abelson, 1966). On the other hand, experiments in which mixtures of methane, ammonia, and water were irradiated yielded ribose and deoxyribose among the products produced (Ponnamperuma, 1965). Furthermore, it has long been known that formaldehyde (CH_2O) in aqueous solution, under suitable conditions, will condense to form simple sugars. This might have been a source of sugars in the primitive "soup." So while we await further evidence we may answer a cautious "perhaps" to the question of the nonbiological formation of sugars needed for RNA and DNA synthesis.

Given the needed ingredients, could energy sources available on the primitive earth bring about the necessary dehydration condensations (Fig. 7.3) to join them into nucleotides? Here the evidence is still much more fragmentary than it is for the nonbiological formation of amino acids and peptides. Schramm (1965) reports experiments indicating that nucleotides and even polynucleotides are formed when certain phosphorus-containing compounds are present under water-free conditions. So while we look forward to the results of further research, we may answer our question with "possibly."

The possibility that nucleic acids might have been formed by nonbiological processes brings us to the second hypothesis concerning the nature of the first "living thing": the gene-first hypothesis (p. 117).

THE GENE-FIRST HYPOTHESIS

Proponents of this hypothesis conclude that life began in the form of living molecules (sometimes called "naked genes") having the following essential properties: (1) the capability of *self-duplication* or reproduction, (2) the ability to undergo *mutation*, and (3) the "ability to *influence the environment* in such a way as to *insure a supply of the materials necessary for the perpetuation of the system*" (Horowitz, 1959).

The importance of reproduction needs no further emphasis. Mutation is important if evolution is to occur. If the "living molecules" mutated, then two or more forms of the molecule would be present and natural selection could operate upon them, assuming that one form was better adapted to existing conditions than was the other (Muller, 1966).

The importance of the ability to influence the environment to ensure a supply of needed materials is readily recognized if we realize that the supply of preformed purines, pyrimidines, phosphates, and sugars would soon be exhausted. Life could not progress very far without the ability to renew the supply of these raw materials. So living things must produce enzymes to promote the synthesis of needed materials (heterocatalysis).

Few investigators would challenge the three criteria of life just mentioned, though they would differ in the relative importance to be assigned each criterion. The main divergence of opinion comes on the question of whether or not a "naked gene" would really meet these criteria. For example, would a macromolecule of nucleic acid, a bit of DNA or RNA, floating freely in the primitive "soup" really be capable of self-duplication?

In modern organisms, when DNA duplicates, a single strand (e.g., a sequence of A–T–G–C–A–C) produces a complement of itself (e.g., T–A–C–G–T–G). Then this in turn may serve as a template for the formation of the original sequence, e.g., A–T–G–C–A–C. So the original strand has produced a replica of itself, not directly but in a two-stage process. Of great importance also is the fact that this joining of nucleotides to form polynucleotides occurs through the action of enzymes (e.g., DNA-polymerase). Under primitive conditions, could DNA have duplicated itself in the absence of enzymes? Only fragmentary experimental evidence is available to demonstrate that this might have occurred (see Schramm, 1965).

If we grant that a self-duplicating nucleic acid could arise in this manner, we are still faced with the question of whether or not it could influence its environment (heterocatalysis, our third criterion above). We recall that in modern organisms DNA contains the coded information for the production of proteins (enzymes) but that the actual production of the latter involves an elaborate apparatus of messenger-RNA, transfer-RNA, ribosomes, and enzymes. There is evidence, however, that under some conditions DNA may determine an amino acid sequence directly without the intermediacy of messenger-RNA (McCarthy and Holland, 1965). Perhaps, also, the first nucleic acid was RNA, with DNA as a storehouse of genetic information having evolved later (see Sagan, 1965). Some viruses have RNA only.

Under primitive conditions could a polynucleotide (a sort of pre-RNA) have controlled the formation of polypeptide chains before there were any enzymes? Proponents of the gene-first hypothesis have attempted to suggest ways in which this might have been accomplished (Muller, 1966). Perhaps there are polynucleotide chains that are weakly catalytic (enzymatic) in themselves (Sagan, 1965). Such a chain might have served as a template for the formation of a polypeptide that would have had *some enzymatic ability to promote replication of the nucleotide chain itself* (see Haldane, 1965; Schramm, 1965). Or perhaps this polypeptide might influence the environment in some other way favorable to the polynucleotide (stimulating the production of essential raw materials). In either case a polynucleotide able to do this would have an advantage over other polynucleotides, would replicate itself more rapidly than they, and hence would be favored by natural selection.

Despite the theoretical possibilities, the theoretical difficulties are so great that many investigators conclude that there was no such thing as a "living molecule"—that life is always the result of the combined activities of many molecules in a highly organized system. Thus Commoner (1964) concluded: "The simplest system capable of self-sufficient germinal activity and of actual self-duplication is the entire living cell" (see also Commoner, 1965, and Oparin, 1962).

FROM PRECELL TO CELL

We may picture a portion of the primitive ocean as containing coacervate droplets or microspheres (pp. 120–123) that incorporate such complex molecules as polypeptides—perhaps of even proteinlike proportions—polynucleotides, adenosine triphosphate (ATP), polysaccharides, and so on. What does such a structure lack of being a living cell? Its lacks are of staggering proportions if we compare it with modern cells. Its lacks are still formidable but not so overwhelming if we compare it to what we might regard as minimum requirements for a living cell. Even here the step is a large one, but it may be the sum of a myriad of small steps taken when cells first evolved.

Our precell would have to develop the ability to reproduce itself and to produce enzymes so that it could utilize raw materials available in its environment. A first consideration in this would be the obtaining of *energy*. As we have indicated previously, preformed ATP initially might serve as such a source of energy. But that source would soon become exhausted. This would place a premium upon the ability to utilize other sources—preformed polysaccharides (sugars) in the primeval "soup," perhaps. But such sources of energy could only be tapped if enzymes—at least simple and primitive ones—came into existence to facilitate their digestion. And so almost at once the precell would be faced with the necessity of producing enzymes. At first these may have been relatively simple polypeptide chains.

In the absence of the nucleic acid mechanism, what would determine the sequence of amino acids in a polypeptide chain? Would they join together at random? Experiments indicate that they would not. When mixtures of amino acids are treated so that peptide linkages are formed in the absence of nucleic acids and enzymes, these linkages are not formed at random (Steinman and Cole, 1967). For example, glycine joins to glycine much more frequently than it does to valine. The experimenters found that the relative frequencies of the different linkages depends both on the relative abundance of the different amino acids and on the differing chemical properties of them. Significantly, the relative frequencies of the different linkages found experimentally correspond in general to the relative frequencies of these linkages in natural proteins (Steinman and Cole, 1967). Thus in natural proteins glycine–glycine linkages are much more common than are glycine–valine linkages. This fact suggests that relative abundance and chemical properties of the amino acids played a role when proteins were first formed.

Despite the fact that peptide linkages are not formed at random, considerable variety would have characterized the polypeptide chains possessed by the precells we are discussing. Perhaps some of the precells chanced to contain polypeptides possessing more enzymatic activity than was possessed by polypeptides in other precells. If the latter were less successful in obtaining needed energy, natural selection would operate, favoring the precells with the more efficient polypeptides. But of course the surviving precells could only contribute to evolution if they were also capable of reproduction, passing on the useful polypeptides to "offspring."

Earlier in the chapter we discussed the possibility that reproduction of proteins might occur in the absence of the present DNA–RNA mechanism (pp. 120–121). At first this duplication of polypeptide chains may have been rather inexact as compared to the modern process. Exactitude may not have been so essential as it is now (see Commoner, 1965). Even modern enzymes may vary considerably in amino acid sequence and still retain enzymatic activity. Recall the varying cytochromes *c*, all with essentially the same function (pp. 91–93). This also is true of ferredoxin (p. 119).

Even if inexact duplication sufficed at first, we may be sure that exact duplication would be preferable in the probable event that some sequences of amino acids were more potent enzymes than were others. Thus natural selection would favor any precells capable of exact duplication. One is tempted to say at this point: "And so the nucleic acid mechanism arose." But *how* it arose is a difficult question. Did polynucleotides already present develop the capacity to determine the sequence of amino acids in polypeptide chains that previously had been self-replicating, even though inexactly? Or did polypeptides originally determine the sequence of nucleotides in the first nucleic acids—instead of vice versa as at present (Steinman and Cole, 1967)? Or was there some interrelationship between polynucleotides and polypeptides from the outset? Perhaps the present genetic code was preceded by some sort of chemical affinity or "recognition" between a given amino acid and a specific nucleotide (see Woese *et al.*, 1966). (Proponents of the gene-first hypothesis would say that the polynucleotides came first and determined the development of the first polypeptides.) All we really know is that self-replicating nucleic acids determining the sequence of amino acids in polypeptides did in fact arise. And we may be reasonably sure that the present elaborate genetic code has undergone an evolution from simpler beginnings.

As we noted when we first discussed the code (pp. 88–89), in the present triplet codons two of the three nucleotides may be more significant than the third nucleotide. Thus, the codon for valine has G in first position and U in second position, but the third position may be occupied by U, C, A, or G (Table 5.2, p. 89). Perhaps, therefore, the present triplet code was preceded by a doublet code (Jukes, 1966; Sagan, 1965). If there were no synonyms (no "degeneracy") a doublet code would provide for 16 amino acids. Very probably early proteins may have been composed of fewer than the 20 common today (recall ferredoxin with its reduced number as a modern example). The suggestion even has been made that the code originated as a singlet code (Sagan, 1965). In such a code A, C, G, and T or U would each code for one amino acid. As Sagan commented: "The catalytic properties of a protein composed of only four amino acids would be limited, but it would be a lot better than nothing."

An enclosed mixture of macromolecules containing polynucleotides that controlled production of enzymatic polypeptides (proteins) is still a long way from the modern cell, but it might have been a beginning. A cell membrane containing lipids (fats) must have been an early improvement, conferring greater selectivity in the matter of substances passing into and out of the cell. The cells of modern organisms, other than bacteria and blue-green algae, contain tiny bodies called mitochondria, and have the chromosomes enclosed within a nucleus. Mitochondria are regarded as the powerhouse of the cell since they are concerned with the formation of ATP mentioned earlier. They and nuclear membranes must have appeared early in the evolution of organisms other than bacteria and blue-green algae. Other structures characteristic of modern cells (Fig. 5.1, p. 76) doubtless had their evolutionary developments, though details of their histories are unknown to us.

AUTOTROPHY

So far we have pictured the development of an organism living in an environment devoid of free oxygen, i.e., it was *anaerobic*. It was also dependent upon preformed sources of energy, at first such energy rich substances as ATP and later perhaps preformed sugars. Such an organism is said to be *heterotrophic*. There is now general agreement that the first organisms were heterotrophic (Horowitz, 1945). As such primitive organisms multiplied, the supplies of these preformed substances must have become seriously depleted. If so, a premium would have been placed on the ability to obtain energy from other sources, especially from the greatest source of energy, the sun. Organisms that can do this are said to be *autotrophic*. "And so," we are tempted to say, "photosynthesis developed." Such a statement cloaks our almost complete ignorance of *how* it developed. We do have some idea of *when* it appeared. Algae living some 2.6 billion years ago testify to its presence.

Photosynthesis, the process by which plants containing the green substance chlorophyll manufacture carbohydrates, is so complex that its details did not become fully known until our own time. In principle it may be expressed very simply:

$$6CO_2 + 6H_2O + \text{energy} \longrightarrow C_6H_{12}O_6 + 6O_2$$

Utilizing energy from the sun, six molecules of carbon dioxide combine with six molecules of water to form one molecule of glucose and six molecules of oxygen. The oxygen is liberated into the air. A widely held theory maintains that all the oxygen in our present atmosphere arose as a result of this process.

Photosynthesis does not occur as a single step but by a series of steps. The $6CO_2 + 6H_2O$ forms the start for a series of intermediate substances, many of them of complex chemical composition; $C_6H_{12}O_6$ is the final product, the end of the series. All the numerous steps in the process are catalyzed by enzymes, usually with the collaboration of complex substances called coenzymes. Without going into detail, we sense something of the complexity of this wonderful process by which the sun's energy becomes "locked up" in carbohydrates, later to be released as the needs of the organism require.

Doubtless this efficient process did not arise in all its complexity all at once. We may anticipate that it arose by stages, the earlier stages being less efficient than the modern process. But all this happened at least 2.6 billion years ago!

Thus autotrophic organisms became independent of the diminishing supply of preformed sources of energy in the primeval "soup." As these substances became completely exhausted, most of the primitive heterotrophs may have become extinct. A few kinds of them probably survived because they evolved the ability to utilize the then newly developed autotrophs as *food*. One (or more?) of these survivors then became the ancestor(s) of the animal kingdom.

AEROBIC HETEROTROPHS

Animals are heterotrophs ultimately dependent on autotrophs (plants) for their energy. Even carnivorous animals are but a step away from this dependence, since the animals they eat are primarily herbivorous (plant eating). In the cells of animals, and of plants too for that matter, the chemical reaction given above for photosynthesis is reversed:

$$C_6H_{12}O_6 + 6O_2 \longrightarrow 6CO_2 + 6H_2O + \text{energy}$$

As we noted earlier (p. 123), the energy released is used to add an energy rich phosphate bond to adenosine diphosphate, changing it to adenosine triphosphate (ATP), which transfers the energy to metabolic processes of the cell.

As in the case of photosynthesis, the simple equation masks a series of at least 25 intermediate steps requiring enzymes and coenzymes before the energy is available to the cell in usable form. Doubtless this complex process also had its evolutionary development from simpler beginnings. And since oxygen is required for the process the latter could have developed only as oxygen became available in the atmosphere.

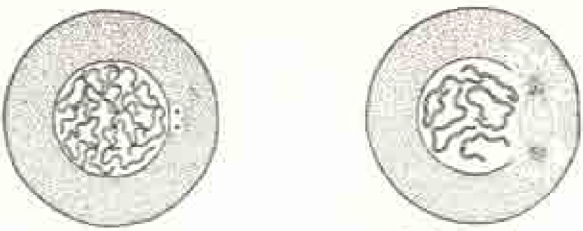
MORE THAN ONE ORIGIN OF LIFE?

Better stated, our question would be this: Are all present-day living things descended from a single group of organisms that arose from nonliving matter? We have no means of knowing how many "experiments" failed to succeed in making the transition from nonliving to living or gave rise to organisms inferior in some way so that they were later eliminated by natural selection. But by analogy with the later history of evolution we may presume that the number was large. Thus of the great panoply of reptiles dominating the Mesozoic era only one group, the therapsids, made the transition from reptiles to mammals and so became ancestral to the dominant animals of the Cenozoic (pp. 197–198).

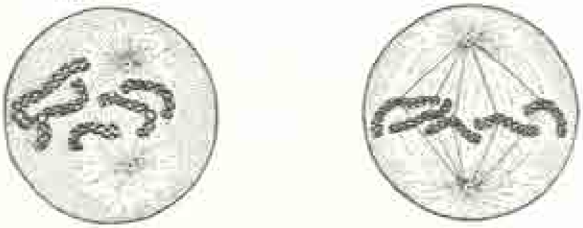
The question we have asked is another one for which we can give no definite answer. But many students of the subject suspect that all present-day organisms did share a common ancestor. The conclusion is based on fundamental similarities, the very phenomenon we have stressed all along as indicative of common ancestry. Could such detailed similarities, frequently in extremely complex structures and processes, have arisen more than once in evolution? We have space for only a few of many possible examples.

We have stressed the likelihood that the genetic code is essentially "universal" (pp. 88–90). If such a code had arisen twice, is it likely that both codes would have been alike, the same codons designating the same amino acids in both? This would be like two unrelated peoples developing the same language independently of each other.

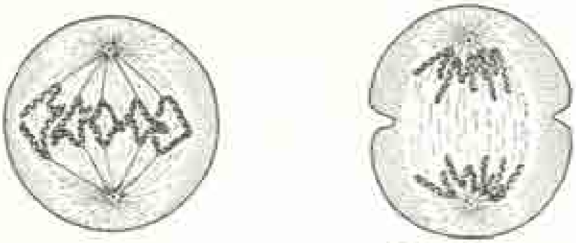
We have stressed, without describing, the complexity of photosynthesis. Is it likely that if photosynthesis arose independently in two evolutionary lines that the sequence of steps and the enzymes involved would have been the same each time? Many students think this unlikely and so conclude that all green plants are descended from a single ancestral group that developed the process.



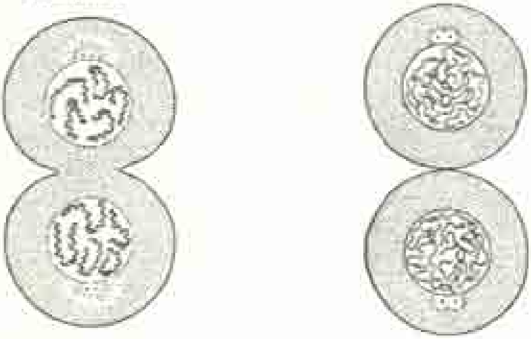
Interphase Early Prophase



Late Prophase Metaphase



Anaphase Early Telophase



Late Telophase Interphase

Fig. 7.4. Diagram of mitosis and cell division. Note the elaborate mechanisms insuring exact duplication of each chromosome, and exact distribution of the "daughter chromosomes" so that each cell receives one of each kind and thus has exactly the same number and kinds as the original cell had. In the first diagram (upper left) each chromosome is shown as having duplicated itself (indicated by the double lines representing parallel threads) to form chromatids. These shorten and thicken by coiling, and eventually separate, each one forming a daughter chromosome.

We also have stressed the complexity of the process by which all aerobic organisms, plant and animal, release the energy stored in carbohydrates. Is it likely that if more than one evolutionary line developed this capacity the steps and the enzymes would have been the same in detail in each line?

Biochemists sometimes state that biochemistry is "monotonous." By this they mean that wherever they turn they encounter the same organic compounds serving much the same functions, the same enzymes catalyzing the same metabolic reactions, and so on. Here we may recall the widespread occurrence of cytochrome *c*, with its underlying structural similarities in widely diverse organisms (pp. 91–93).

We have already stressed the fact that all cells seem to be based on a common pattern (Fig. 5.1, p. 76). As we have noted, cells of bacteria and blue-green algae differ from other cells in some respects, but resemblances are also evident, as in possession of cell membranes and DNA-RNA mechanisms.

As genes increased in number in the descendants of a primordial organism, the DNA strand increased in length and became, with its associated protein, a structure that we call a CHROMOSOME (composed essentially of nucleoprotein). (The chromosomes of bacteria may consist of nucleic acid only.) Since the chromosomes contain the information for cell function and reproduction, it is essential that when a cell divides (reproduces) each daughter cell contains exactly the same chromosomal material as the cell that divided. This exact partitioning of chromosomal material is accomplished by an elaborate process called MITOSIS (Fig. 7.4). The mitotic process is basically the same in most plants and animals. It must have arisen early in evolution. Many students see in this basic similarity of process another reason for suspecting that most, if not all, modern organisms arose from common ancestry in the remote past.

We might multiply examples of wide-ranging similarities in chemical structure and in living processes. While each example taken alone may be amenable to other explanations, we see why the similarities taken in their totality point to a unity in all living things. How did the unity arise? The evolutionary explanation is that it arose through inheritance from common ancestry.

SUMMARY

We may summarize with the following tentative statements:

1. The first organisms were preceded by a long period of chemical evolution in which there developed by nonbiological means such complex compounds as polypeptides (proteins), probably polynucleotides

(nucleic acids), and energy rich compounds such as ATP (adenosine triphosphate).

2. The first organisms were anaerobic and heterotrophic, dependent upon preformed energy rich compounds.

3. There are two schools of thought concerning the nature of the first living things: (a) They were "living molecules" (probably of nucleic acid) capable of self-replication, mutation, and heterocatalysis—the "gene-first hypothesis." (b) They were concentrations of proteins and other macromolecules separated from the surrounding water by some sort of surface membrane—the "proteins-first hypothesis." The proteins were enzymatic, and thus these precells were capable of metabolism. They also were capable of reproduction, though the division of precells may at first have been an inexact procedure.

4. As preformed sources of energy became exhausted, some organisms developed the ability to capture energy from the sun by photosynthesis—they became autotrophic.

5. Largely as a consequence of this photosynthesis, the atmosphere came to contain large amounts of free oxygen, making possible the evolution of aerobic organisms, both autotrophic (plants) and heterotrophic (animals).

6. Organisms living at the present time probably are remote descendants from one kind of original ancestor that made the transition from the nonliving to the living state—or at most from a very small number of kinds of such ancestors.

References and Suggested Readings

Abelson, P. H., "Chemical events on the primitive earth," *Proceedings of the National Academy of Sciences, 55,* 1365–1372 (1966).

Arnon, D. I., "Ferredoxin and photosynthesis," *Science, 149,* 1460–1470 (1965).

Bernal, J. D., "The problem of stages in biopoesis," in Oparin *et al.* (below), pp. 38–53.

Bernal, J. D., *The Origin of Life,* Cleveland, World Publishing, 1967.

Calvin, M., "Chemical evolution," *Proceedings of the Royal Society of London, Series A, 288,* 441–466 (1965).

Calvin, M., "Chemical evolution," in Th. Dobzhansky, M. K. Hecht, and W. C. Steere (eds.), *Evolutionary Biology,* vol. 1, New York, Appleton-Century-Crofts, 1967, pp. 1–25.

Commoner, B., "DNA and the chemistry of inheritance," *American Scientist, 52,* 365–388 (1964).

Commoner, B., "Biochemical, biological, and atmospheric evolution," *Proceedings of the National Academy of Sciences, 53,* 1183–1193 (1965).

Eck, R. V., and M. O. Dayhoff, "Evolution of the structure of ferredoxin based on living relics of primitive amino acid sequences," *Science, 152,* 363–366 (1966).

Fox, S. W. (ed.), *The Origins of Prebiological Systems and of Their Molecular Matrices,* New York, Academic Press, 1965a.

Fox, S. W., "Simulated natural experiments in spontaneous organization of morphological units from protenoid," in S. W. Fox (ed.) (above), 1965b, pp. 361–382.

Fox, S. W., "Experiments suggesting evolution to protein," in V. Bryson and H. J. Vogel (eds.), *Evolving Genes and Proteins,* New York, Academic Press, 1965c, pp. 359–369.

Gibbons, R. A., G. D. Hunter, and J. S. Griffith, "Nature of the scrapie agent," *Nature, 215,* 1041–1044 (1967).

Haldane, J. B. S., "Data needed for a blueprint of the first organism," in S. W. Fox (ed.), 1965a (above), pp. 11–18.

Horowitz, N. H., "On the evolution of biochemical syntheses," *Proceedings of the National Academy of Sciences, 31,* 153–157 (1945).

Horowitz, N. H., "On defining 'Life,'" in Oparin *et al.* (below), pp. 106–107.

Jukes, T. H., *Molecules and Evolution,* New York, Columbia University Press, 1966.

Keosian, J., *The Origin of Life,* 2nd ed., New York, Reinhold, 1968.

Matthews, C. N., and R. E. Moser, "Peptide synthesis from hydrogen cyanide and water," *Nature, 215,* 1230–1234 (1967).

McCarthy, B. J., and J. J. Holland, "Protein synthesis with single-stranded DNA as a template," *Science, 150,* 378 (1965).

Miller, S. L., "A production of amino acids under possible primitive earth conditions," *Science, 117,* 528–529 (1953).

Miller, S. L., and H. C. Urey, "Organic compound synthesis on the primitive earth," *Science, 130,* 245–251 (1959).

Muller, H. J., "The gene material as the initiator and the organizing basis of life," *The American Naturalist, 100,* 493–517 (1966).

Oparin, A. I., *The Origin of Life on the Earth,* 3rd ed., New York, Academic Press, 1957.

Oparin, A. I., "Biochemical processes in the simplest structures," in Orparin *et al.* (below), 1959, pp. 428–436.

Oparin, A. I., *Life: Its Nature, Origin, and Development,* Edinburgh, Oliver and Boyd, 1962; reprinted by Academic Press, New York, 1964.

Oparin, A. I., "The pathways of the primary development of metabolism and artificial modeling of this development in coacervate drops," in Fox, 1965a (above), pp. 331–346.

Oparin, A. I., A. G. Pasynskii, A. E. Braunshtein, and T. E. Pavlovskaya (eds.), *Proceedings of the First International Symposium on the Origin of Life on the Earth,* New York, Pergamon Press, 1959.

Oró, J., "Stages and mechanisms of prebiological organic synthesis," in Fox, 1965a (above), pp. 137–171.

Ponnamperuma, C., "Abiological synthesis of some nucleic acid constituents," in Fox, 1965a (above), pp. 221–242.

Sagan, C., "Primordial ultraviolet synthesis of nucleoside phosphates," in Fox, 1965a (above), pp. 207–219.

Schramm, G., "Synthesis of nucleosides and of polynucleotides with metaphosphate esters," in Fox, 1965a (above), pp. 299–315.

Steinman, G., and M. N. Cole, "Synthesis of biologically pertinent peptides under possible primordial conditions," *Proceedings of the National Academy of Sciences, 58,* 735–742 (1967).

Woese, C. R., D. H. Dugre, S. A. Dugre, M. Kondo, and W. C. Saxinger, "On the fundamental nature and evolution of the genetic code," in *Cold Spring Harbor Symposia on Quantitative Biology,* vol. 31, *The Genetic Code,* Cold Spring Harbor, New York, Cold Spring Harbor Laboratory of Quantitative Biology, 1966, pp. 723–736.

Young, R. S., "Morphology and chemistry of microspheres from protenoid," in Fox, 1965a (above), pp. 347–357.

8

Evolution as Seen in the Geologic Record: Nature of the Record

IN EARLIER CHAPTERS of this book we saw evolution manifested by similarities among living animals in chemical composition, structure, metabolic processes, embryonic development, and serological properties of the blood. If our conclusion based on what we might term circumstantial evidence is correct, in times past animals must have existed that were the common ancestors from which modern animals inherited these similarities. Can we find positive evidence that such animals actually did exist? If so our accumulated circumstantial evidence will be greatly strengthened by what we may regard as direct evidence. The nearest approach to direct evidence is supplied by the geologic record.

FOSSILS The geologic record, or "record of the rocks," is written in the language of FOSSILS. Any type of remains of a prehistoric animal may be considered a fossil. In the most frequently encountered fossils the harder parts of the animal's body—bones and teeth in the case of vertebrates, shells of molluscs, and exoskeletons ("shells") of arthropods (lobsters, crayfishes, spiders, insects, and their relatives)—are replaced by minerals: "turned to stone" in popular parlance. After an animal dies its flesh is destroyed by predatory animals, scavengers, insect larvae, bacteria, and so on. These destructive forces also act upon bones and shells, but more slowly. Occasionally such "hard parts" lie in surroundings that protect them from complete destruction, particularly if the animals lived in the water or, in the case of terrestrial animals, if the bones or shells were swept into a body of water or onto a flood plain by a river at a time of flood. The organic matter in bone gradually disintegrates, leaving the structure somewhat porous. Water seeps into the interior of the bone, and minerals dissolved in the water are slowly deposited there. Thus the porosities gradually become filled with deposits of such materials as lime and silica. The portions of the original structure composed of inorganic materials may remain substantially as they were in life, or they also may be dissolved away and replaced by minerals. The replacing material may preserve the details of the original structure with great fidelity or, on the other hand, it may preserve only the general form of the original. Yet fossils may contain some of the original materials found in the living organism; for example, amino acids have been found in fossils millions of years old. Under exceptionally favorable circumstances replacement of the type under discussion may even result in preservation of some of the internal organs ("soft parts") of an animal.

Natural preservatives sometimes have helped to save animal materials from destruction. Thus the bones of animals that became mired in the asphalt or tar pits at Rancho La Brea in California were preserved by the action of the crude asphaltic oil. In Poland two skeletons of the woolly rhinoceros, with some of the flesh and skin preserved, have been found buried in oil-soaked ground.

Not infrequently the buried body and skeleton of an animal disintegrate entirely. If the surrounding material is sufficiently firm a cavity may remain having the exact outlines of the structure that disappeared. Such a cavity is called a MOLD. It may be filled by natural deposits, forming a NATURAL CAST of the form of the original object. Such molds and casts reveal the shape but not the internal structure of the original object. Natural and artificial casts of the interior of the brain cavities of extinct animals form the only material available for study of the brains of these animals. Molds and casts of the burrows made by prehistoric animals frequently reveal something of the nature of the animals.

Similar to molds are IMPRESSIONS sometimes left by vanished objects or parts of the body upon the surrounding material. The impression is made while the latter is soft—like footprints in the snow. Thanks to such impressions we know something of the shapes and venations of prehistoric leaves, of the feathers of extinct birds, of the wing membranes of flying reptiles, of the skin surface of dinosaurs, and so on. Footprints of extinct animals are also impressions affording much valuable information about the animals that made them.

Occasionally the disintegrating soft parts of a body leave behind a thin FILM OF CARBON. Because of this we know, for example, the exact body outlines of the extinct swimming reptile *Ichthyosaurus* (Fig. 3.5, p. 30).

Among the most perfect fossils known are the insects preserved in AMBER. Millions of years ago insects became entangled and entombed in soft, sticky resin exuding from pine trees, just as their modern descendants may be observed to do today. The resin hardened and eventually changed to amber, preserving the minutest details of structure of the contained insects.

A few extinct animals are known from FROZEN SPECIMENS in which the flesh as well as the bones have been preserved in remarkably fresh condition for thousands of years. This type of specimen has occurred principally in northern Siberia where the ground remains permanently frozen. The woolly mammoth is the animal best known from such specimens.

There are other types of fossils, but the ones mentioned are most common and most generally useful. Frequently bones are more or less distorted or destroyed before fossilization begins or during the process.

"PAGES" IN THE GEOLOGIC RECORD If the history of life on earth is to be understood, the separate events comprising that history must be arranged in correct sequence and relationship. Printed records are firmly bound so that the pages follow one another in correct sequence to provide the reader with a coherent and connected account. But in the geologic record, how are we to tell which is "page 1," which "page 2," which "page 3," and so on?

The "leaves" comprising the geologic record "book" are layers of rock called STRATA. A stratum consists of more or less solidified material that was originally deposited by a carrying agent such as water or air. By far the larger proportion of the known strata was deposited on what was then the floor of shallow extensions of the sea. In such shallow seas multitudes of animals live, many of them species with calcareous shells or skeletons. As generation follows generation the shells and skeletons settle to the bottom in a layer of sediment of ever-increasing thickness. As time goes on the deeper portions of this deposit are subjected to the pressure of overlying portions. This pressure, and the cementing action of chemicals brought in by groundwater, solidify and consolidate the deposits into rock—limestone in the present example. If a river empties into this region of the shallow sea, deposits of material transported by the river mingle with the remains of marine animals. The river brings the products of erosion of the neighboring land, such as silt and clay, and mingled with them the remains of aquatic and terrestrial animals, particularly when the river is at flood stage. So through hundreds and thousands of years the sediment accumulates and gradually becomes consolidated into SEDIMENTARY ROCK. Sedimentary rocks may also be formed from material originally deposited by a river in its flood plain or delta. Rocks so formed are some of the richest sources of fossils of terrestrial animals.

Geologic changes in that region of the earth may eventually result in a change both in the animals inhabiting that section of shallow sea and in the materials being brought down by the river. The deposit following such a change naturally will be of somewhat different nature from the deposit formed before the change. Such changes account in part for the stratified or "layer cake" appearance of deposits, so evident in such places as the walls of the Grand Canyon of the Colorado River. The many strata visible there afford information concerning successive changes in that region of the earth for many millions of years.

As a general principle we may state that the oldest strata are the deepest ones and that as we proceed upward in such a series of layers as that displayed in the walls of the Grand Canyon the strata are successively younger and younger in age. This time sequence follows naturally from the manner in which the material is deposited, as just described.

DISTURBANCE OF THE RECORD Interpretation of the sequences of events in the geologic record would be relatively simple if confusing and destructive forces were not at work One destructive force is EROSION, which removes many "pages," even entire "chapters," from the record. For hundreds of thousands or millions of years a certain region is covered by shallow sea and receives successive deposits. If the earth's crust is sinking slowly, as portions of the Atlantic coastline of North America are known to be doing today, the deposits may eventually total thousands of feet in thickness. Finally geologic processes elevate the deposits, and eventually these are formed into a mountain range. In the process the deposits formed in the bottom of the sea are thrust up into the air—thousands of feet up perhaps. As soon as the strata are exposed to the air in this fashion the forces of erosion start to tear them down, and the rivers transport the products of their destruction to the neighboring sea, thereby initiating the formation of new deposits in that sea.

As erosion continues on a newly formed mountain range entire strata may be worn away, and eventually entire groups of strata. This process is going on in our present mountain ranges; since it is slow geologists have ample opportunity to study the strata before they disappear. But consider all the strata that were destroyed before there were any geologists—or any people at all for that matter. We are told that at one time the Appalachian chain, including the Green Mountains of Vermont, the White Mountains of New Hampshire, the Berkshires, the Alleghenies, the Blue Ridge, and so on was higher than the present Rocky Mountains. How many "chapters" of the geologic record were destroyed as these mountains were being worn down to their present height!

Fortunately strata lost by erosion in one part of the country may be preserved in another region. But it is not possible to fill in all the gaps in the record by comparing different regions of the earth's surface. Gaps are frequently left in the records of animal life, since a species of animal found in one part of the country at a certain time might not have been an inhabitant of another part of the country at that same time.

We may suppose that after millions of years of erosion our mountain range is reduced to a row of low hills. Finally another change in the earth's crust occurs and the region is dropped below sea level again, the hills being submerged. Then this newly formed sea floor will begin to collect deposits again, as did the floor of this region when we first began our story of it. The new deposits will be laid down immediately on top of whatever deposits were left by the preceding erosion. If eventually the region is again lifted into the air where geologists can study it they will find the old deposits, left from the preceding period of erosion, and immediately on top of them the new deposits. No remains will be left of the perhaps thousands of feet of deposits that were eroded away. The result is much like a book that has Chapter 15 immediately following Chapter 3. Fortunately geologists are astute in detecting such UNCONFORMITIES in series of strata, but detecting the presence of a gap does not necessarily enable one to fill in the lost history.

Another source of difficulty in interpreting the geologic record lies in the fact that at times older rocks may come to lie *above* younger

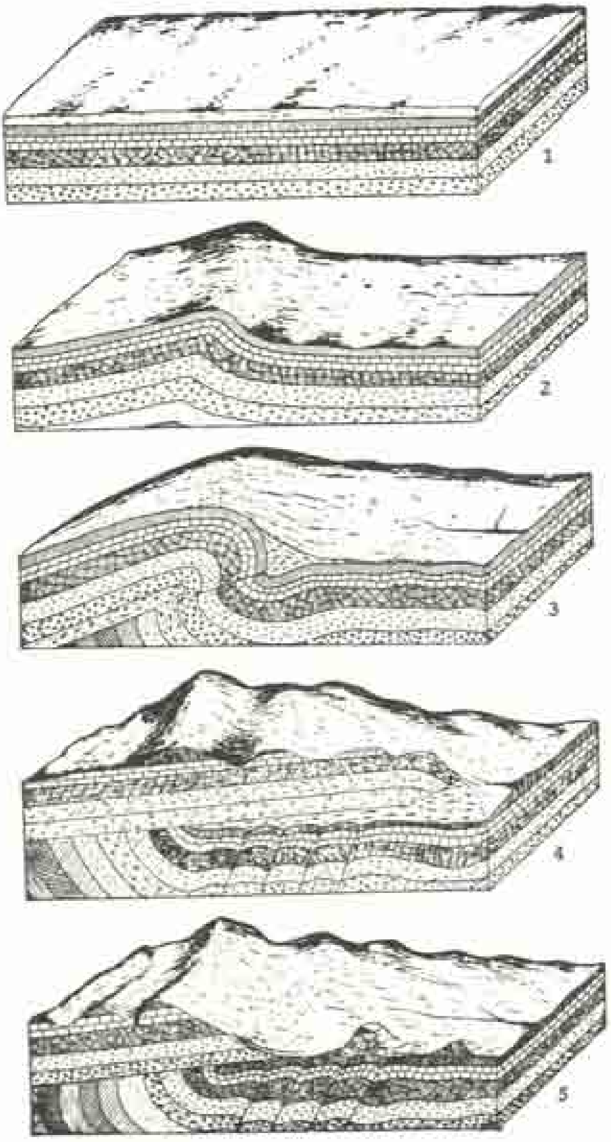


Fig. 8.1. Folding followed by overthrust, one way in which the time sequence of strata is disturbed. See text. (From *Historical Geology* by R. C. Hussey. Copyright 1944, 1947 by the McGraw-Hill Book Company, Inc. Used with permission of McGraw-Hill Book Company.)

ones. Figure 8.1 demonstrates graphically one way in which this comes about. The upper diagram shows a series of strata deposited smoothly, as described in our hypothetical example. Obviously the older layers are at the bottom of the series. Then a mountain range is formed by folding of the earth's crust. The fold is accompanied by a strong thrust, from the west in the example diagramed, which displaces a section of the crust toward the east, actually sliding it over the strata already present in that region, as shown in diagram 4 (Fig. 8.1). Such an OVERTHRUST may extend for many miles. The land surface is subsequently sculptured by erosion, many of the signs of the phenomena that produced the observed sequence of strata being obliterated. Prolonged study involving large areas suffices to reveal the true explanation, although the latter may not be evident if study is confined to a small area.

Over much of the earth the number of strata exposed on the surface in any one locality is usually strictly limited. In more level regions one or a few strata are more often found exposed for study.

The question may arise as to how geologists determine the age of, for example, a single stratum found exposed in a given region when the strata immediately older and younger are not available for study. To solve the problem requires the most painstaking comparison of the rock in this locality with rock in other localities where the relationships among neighboring strata are more evident. The comparison involves details of the rock structure itself, as well as distribution of "key fossils" that serve to distinguish rocks formed at one time from those formed at other times and characterized by other key fossils. When possible, reference always is made to a region where the stratum in question can be found in an undisturbed position relative to strata deposited before and after it (see Dating the Past, pp. 145–148).

INCOMPLETENESS OF THE GEOLOGIC RECORD Of the animals living at any one time in the history of the earth, how many will be known to geologists a million or more years later? In the first place we may subtract most of the animals having no "hard parts." This will include most of the protozoa, though some of them, notably the foraminiferans, produce calcerous shells. These shells, though individually of minute size, in the aggregate have produced thick deposits of limestone. Most of the coelenterates and worms also will fail to leave fossil remains. Among the coelenterates the corals are an exception to this statement since their calcareous skeletal supports form another important source of limestone.

Of the animals possessing hard parts, how many will be known to geologists a million or more years later? The chances of fossilization vary greatly. Evidently, from the foregoing account, animals living in the ocean have the best chance of being preserved as fossils. Animals inhabiting fresh water perhaps have the next best chance, while terrestrial animals have the least chance. In order to be preserved as a fossil the body of a horse, for example, must be prevented from destruction. Even the skeleton will disintegrate in a few years if exposed to the action of predatory animals, scavengers, insect larvae, and bacteria and the erosive forces of the weather. A dry climate favors preservation of bones, but even dry bones disintegrate in time. Hence it is necessary that the bones be protected by being covered. Windblown soil, such as that which produced the thick deposits of silt known as loess, may provide the protective covering. Or if the animal becomes mired in a bog or in quicksand the bones may gradually sink and be covered. The fossils in the Rancho La Brea asphalt pits are a special case of this procedure. Or if the bones happen to lie in the flood plain of a river they may be covered by a deposit of soil left by the river when it overflows its banks in time of flood. Or the river, in flood stage, may sweep the bones into a lake or into the sea, where they will be mingled with the remains of aquatic animals. Thus, one of the most productive sources of fossils of Tertiary mammals is the White River Bad Lands of South Dakota and Nebraska. The material of these beds was laid down as a flood plain by rivers flowing from the Black Hills, mountains formerly much higher than they now are. Mammalian remains were swept down by the rivers and became embedded in the flood plain.

We see, then, that the chances are against an animal's "hard parts" being fossilized, particularly if the animal is a land dweller. Of the animals that are fossilized, how many will be known to geologists a million or more years later? A first hazard facing these fossils consists of the physical, chemical, and geologic processes at work on the deposits in which the fossils are embedded. If later deposits are piled on the fossils in question, these may be crushed and distorted. The consummation of such destruction is reached if the deposit finally comes to lie deep in the earth's crust with thousands of feet of other deposits above it. As a result of the tremendous pressure and accompanying heat the deposit may be so altered that all fossils in it are destroyed. The various minerals will recrystallize. Rock that has undergone this process of internal alteration through heat, pressure, and recrystallization is called METAMORPHIC ROCK. We have mentioned limestone as a prominent sedimentary rock rich in fossils; when limestone is subjected to the process described, the product is marble. Metamorphism is a most efficient eraser of fossils.

Of the fossils that escape the destruction just described, how many will be known to geologists? It is evident that deposits that remain deeply buried under younger strata or under the sea will remain largely unknown. Some exception to this statement is afforded by mines, in the walls of which fossils may be found. Our knowledge of animals contemporaneous with the vegetation that entered into formation of coal depends to some extent upon fossils collected in connection with the mining of coal. Borings for artesian wells and oil wells reveal something of fossils in the strata through which they pass. But on the whole locating fossils depends largely upon their being exposed on the surface of the earth. Erosion acts on fossil-bearing rocks, wearing away the surrounding rock and exposing the fossil. If the latter happens to fall under the eye of a geologist, well and good, but if not erosion will eventually destroy it along with the enclosing rock. Erosion is continually exposing fossils in this way. Most of them are probably never seen by geologists. The earth is a big place, and geologists are few in number and strictly budgeted in time and funds.

The wonder is not that the geologic record is incomplete, but that it is as complete as it is.

THE GEOLOGIC TIME SCALE The "chapters" of the geologic record are arranged in chronological sequence, the result being the geologic time scale (Table 8.1). The time scale is arranged to agree with the fact that, when undisturbed, older strata lie beneath younger ones. Thus we begin to read the chart at the *bottom* instead of at the top.

The total span of geologic time is divided into five large divisions, called ERAS (first column of Table 8.1). The oldest era, Archeozoic, is placed at the bottom of the chart. The eras are subdivided into PERIODS (second column). The oldest period within an era is placed at the bottom of the sequence of periods comprising the era.

DATING THE PAST Table 8.1 includes estimates of the number of years that have elapsed since the beginning of each of the last three eras. These figures are rough approximations only. Estimates of the durations of the various portions of the time scale were originally based on the rates at which geologic processes are known to occur. Since many strata originated as deposits in the sea at the mouths of rivers, for example, we can gain some concept of the length of time required to produce a deposit of a given thickness if we measure the rate at which modern rivers are depositing sediments in the sea.

With the developing knowledge of radioactivity, more accurate dating of certain types of deposits has become possible. Many rocks have built-in "clocks" in the form of radioactive isotopes that change at a constant rate into the nonradioactive form. If this rate is constant and known to us, we can estimate the length of time since the rock was formed by measuring the quantities of the radioactive and non-

Table 8.1. GEOLOGIC TIME CHART

Eras	*Periods*	*Epochs*	
Cenozoic	Quaternary	Recent	Modern genera and species of animals. Dominance of man.
		Pleistocene	Many large mammals of types now extinct. Prehistoric men.
	Tertiary	Pliocene Miocene	Mammals increased in specialization, many groups attaining their maxima.
		Oligocene Eocene Paleocene	Ancestral representatives of most modern orders of mammals appeared. Archaic mammals attained their maximum in Eocene; most became extinct at its close.
			*63 million years ago**
Mesozoic	Cretaceous		First flowering plants (angiosperms); deciduous trees first abundant. Dominance of dinosaurs. Marsupial and placental mammals. First social insects (ants).
	Jurassic		Maximum of ammonites. Belemnites. Insects abundant. Dominance of dinosaurs. First birds: Archaeopteryx. Early mammals: Pantotheria.
	Triassic		Maximum of labyrinthodont amphibians. First dinosaurs. Mammal-like reptiles: Therapsida. First mammals.
			*230 million years ago**
Paleozoic	Permian		Expansion of ammonites. Last of trilobites. Expansion of reptiles: Cotylosauria and Therapsida.
	Pennsylvanian		Luxurious vegetation, forming coal. First insect fossils. Many labyrinthodont amphibians. First reptiles.
	Mississippian		Foraminiferans, spiny brachiopods, and crinoids abundant. Few corals and trilobites. Many shell-crushing sharks. Amphibians.
	Devonian		Brachiopods, corals, and crinoids abundant. Trilobites declining. First ammonites. Terrestrial plants and animals, spiders. Many kinds of fishes. First amphibians.
	Silurian		Corals, brachiopods, and crinoids abundant. Trilobites beginning to decline. Eurypterids prominent. Scorpions and millipedes. Ostracoderms and acanthodians.
	Ordovician		First corals, crinoids, nautiloid cephalopods, and ostracods. Graptolites, brachiopods, snails, and trilobites abundant. First vertebrates.
	Cambrian		Dominance of trilobites. Brachiopods. Calcareous sponges. Many other invertebrates; no vertebrates. Cephalopods appeared near its close.
			*600 million years ago**
Proterozoic			Few fossils: annelid worm burrows and calcareous deposits by algae. Graphite.
Archeozoic			Bacteria 3000 million years old. Calcareous deposits by algae 2600 million years old; graphite.

* See Kulp, 1961.

radioactive isotopes present in the rock. For example, uranium emits helium at a constant rate and is transformed into an isotope of lead. Thus the age of uranium-containing rocks can be determined by comparison of the proportions of undecayed uranium and of lead present in the rock. Somewhat similarly, potassium-40 undergoes radioactive decay to form argon-40 at a constant rate, thereby forming another "clock" usable for certain rocks. While the uranium and potassium–argon methods are the two best-known methods for measuring the age of older rocks, radioactivity of other elements also is being utilized with increasing frequency.

Somewhat different is the fission–track method. If a rock contains glass or crystals, the surface of these may be etched with hydrofluoric acid to reveal tracks caused by radiation damage as uranium-238 undergoes spontaneous fission. The tracks can be seen with a microscope and counted. From the count the age of the glass or rock can be computed.

The uranium and potassium–argon methods are most widely used for rocks that are millions of years old, though refinements of the potassium–argon method have made possible the dating of rocks no older than 400,000 years or under special conditions even as recent as 30,000 years. The fission–track method may be used for glass as young as 2000 years (Rainey and Ralph, 1966).

Most widely used for dating in terms of thousands, rather than millions, of years is the carbon-14 method, however. When nitrogen atoms in the atmosphere are bombarded with cosmic rays some of the atoms acquire radioactivity, being changed to an isotope of carbon, C^{14}. This radioactive carbon emits beta rays and becomes nonradioactive at a constant rate (its half-life is about 5720 years). Since the supply of carbon-14 atoms is constantly being replaced by the action of cosmic rays, an equilibrium is established in the atmosphere. The equilibrium point represents a concentration of radiocarbon atoms at which the disintegration of "old" ones is balanced by the formation of new ones. This equilibrium point is at about one radiocarbon atom for a trillion "normal" carbon atoms, C^{12}. Except as man of late has been upsetting the balance with his atomic explosions, this equilibrium remains constant over long periods of time.

Carbon-14 enters normally into the formation of carbon dioxide in the atmosphere. Plants utilize this carbon dioxide in manufacturing carbohydrates, and animals eat the plants. Hence the concentration of carbon-14 in the tissues of plants and animals is about the same as the concentration in the atmosphere. This is true so long as the plant or animal is living. But as soon as it dies, no more carbon enters the body (photosynthesis or food intake, respectively, have ceased). Following death the carbon-14 already present in the body decays steadily, as mentioned above. The smaller the number of carbon-14 atoms remaining, the smaller the amount of radioactivity still remaining. Thus if we take a piece of ancient wood or bone and measure the emission of beta rays from its remaining carbon-14 we can estimate the age of the material, since we know the rate at which these rays are emitted in living wood or bone. When this technique has been applied to materials of known age the demonstrated accuracy has been such as to give confidence in determinations made on materials of unknown age (see Libby, 1956).

The carbon-14 method is applicable only to organic materials still containing carbon; it cannot be used on fossils in which all organic matter has been replaced by minerals. Since the amount of radiocarbon present decreases steadily with time, the method can probably never be used on material older than about 70,000 years. Accurate dating within that time span will prove most valuable, however. Among the early inhabitants of North America, for example, were makers of a particular type of stone projectile point (probably used on darts), the so-called Folsom points. Pieces of burned bone found with some of these points give a carbon-14 date of 9883 years, indicating that these early Americans lived about 10,000 years ago (Sellards, 1952).

Some of the physicochemical methods of dating do not depend upon radioactivity. Thus the rate at which fluorine becomes incorporated into bones during fossilization has been utilized. Although variables in the process have yet to be explored, the test gives promise of usefulness. Utilization of this method contributed significantly to proof that the "fossils" called "Piltdown man" were a hoax (Weiner, Oakley, and Le Gros Clark, 1953).

VISUALIZING GEOLOGIC TIME Unavoidably our ideas of time are conditioned by the length of the human life span and its subdivision into periods (infancy, youth, and so on) and years. The term "a million years" is so far outside our experience as to be meaningless to most of us. Multiples of a million years are, if anything, even less meaningful. We may have the vague impression that a million years is "a very long time," and that a thousand million years is "a very, very long time." But in other connections a thousand years also seems "a very long time." Indeed, all periods longer than a human lifetime or two have a tendency to fade into vagueness for us. Such units of time as years, months, weeks, days, minutes, and seconds have meanings within the range of our experience. Since many readers look forward to the coming of the year A.D. 2000, let us condense our time scale so that 2000 years becomes the equivalent of 1 *minute* (min).

On such a speeded-up time scale Columbus discovered America about 14 *seconds* (sec). ago! The Age of Pericles, the culmination of "ancient" Greek civilization, began about 1 min and 14 sec ago (460 B.C.). The Shang Dynasty in China, the first one for which records exist, began about 1 min and 51 sec ago (1700 B.C.).

How long has man been present on earth? As we shall see in Chapter 12, our answer depends upon our definition of "man." There is still no consensus as to when our own species *(Homo sapiens)* first appeared. But about 4 hours (hr) and 10 min ago on our speeded-up time scale, a related species, *Homo erectus,* was living in Java (500,000 years ago; pp. 250–253); and about 14½ hr ago manlike creatures called the australopithecines (pp. 243–250) were living in Africa (1,750,000 years ago).

Turning our attention to the statements of years given in Table 8.1, we note that on our speeded-up time scale the dinosaurs became extinct and the Cenozoic began slightly under 22 *days* ago. (Note the sudden change in units from hours to days.) Similarly the Mesozoic, the Age of Dinosaurs, *began* about 80 days ago (2 months and 20 days). Taking a giant step backward we find that the Paleozoic began about *7 months* ago.

We now have records of fossil bacteria that lived about 3 billion years ago; on our time scale this would be about 35 months, or a little less than 3 years. The age of the earth is estimated to have been at least half again as great, perhaps 4½ years on our time scale.

In summary, life has existed on this planet for "3 years," but man (the upstart), even when we define "man" most broadly, has been around for only about half a *day* and his written history began less than *2 minutes* ago.

References and Suggested Readings

Dunbar, C. O., *Historical Geology,* 2nd ed., New York, John Wiley, 1960.

Hussey, R. C., *Historical Geology,* 2nd ed. New York, McGraw-Hill, 1947.

Knopf, A., "Time in earth history," in G. L. Jepsen, E. Mayr, and G. G. Simpson (eds.), *Genetics, Paleontology and Evolution,* Princeton, Princeton University Press, 1949, pp. 1–9.

Kulp, J. L., "Geologic time scale," *Science, 133,* 1105–1114 (1961).

Libby, W. F., "Radiocarbon dating," *American Scientist, 44,* 98–112 (1956).

Rainey, F., and E. K. Ralph, "Archeology and its new technology," *Science, 153* 1481–1491 (1966).

Sellards, E. H., "Age of Folsom man," *Science, 115,* 98 (1952).

Weiner, J. S., *The Piltdown Forgery,* New York, Oxford University Press, 1955.

Weiner, J. S., K. P. Oakley, and W. E. Le Gros Clark, "The solution of the Piltdown problem," *Bulletin of the British Museum (Natural History), Geology Series, 2,* 141–146 (1953).

Zeuner, F. E., *Dating the Past,* 4th ed., London, Methuen, 1958.

9

Evolution as Seen in the Geologic Record: Precambrian and Paleozoic Eras

SINCE SO LITTLE is known of Archeozoic and Proterozoic life, it is convenient to refer to these eras collectively as "Precambrian." Cambrian rocks are the oldest ones in which abundant fossils are found (Table 8.1, p. 146).

PRECAMBRIAN

Various methods of measurement and computation agree in estimating that the earth is at least 4500 million years old (see, for example, Tilton and Hart, 1963, and Ulrych, 1967). Doubtless at first the planet was unsuitable for the existence of living things. How soon did they appear? Fossils believed to be those of bacteria have been found in South African rocks dated as being slightly over 3000 million (3 billion) years old (Barghoorn and Schopf, 1966), and fossils that may be those of algae have been found in South African rocks older than 3200 million years (Engel *et al.*, 1968). In North America the Gunflint chert on the north shore of Lake Superior contains microfossils of bacteria and probable blue-green algae (Cloud, 1965; Schopf *et al.*, 1965). The potassium-argon method indicates that this rock is nearly 2000 million years old. Since it is probable that these early algae were autotrophic, photosynthesis evidently had a very ancient origin (pp. 129–130). Well-preserved microfossils interpreted as those of both green and blue-green algae have been found in Australian rocks estimated to be 700–900 million years old, though in this case radioisotope dating has not been made (Barghoorn and Schopf, 1965).

In addition to these fossils, indirect evidence that life was present in Archeozoic oceans is furnished by deposits of GRAPHITE in rocks of this era. Graphite, the "lead" of our pencils, is composed of carbon, as is coal. In later periods of earth history deposits of carbon in the form of graphite and coal represent the remains of vegetation. Accordingly, we may reasonably conclude that Archeozoic graphite also was derived from simple plant life, probably in the main from algae.

The presence of iron ore in Archeozoic rocks also is sometimes considered evidence of the existence of life, since iron ore frequently represents the result of bacterial action. Since, however, iron ore may be deposited by processes that do not involve the action of living things, the evidence here is not so conclusive as it is in the case of graphite.

Limestone in deposits of this era also may have been derived from living organisms. The fossils of algae, mentioned above, are of this nature. Some of the limestone deposits from later periods represent the massed shells of such protozoans as foraminiferans and the skeletons of such coelenterates as corals. Yet some limestone is of inorganic origin, and hence the mere presence of limestone does not prove that life existed at the time the deposit was formed.

Like rocks of the preceding era, many Proterozoic rocks were subjected to metamorphism, with consequent destruction of any fossils they may have contained. However, since there are large deposits of unmetamorphosed Proterozoic rocks, the scarcity of fossils in the latter is somewhat surprising. The most abundant fossils from this era consist of globular masses of limestone representing the remains of colonies of ALGAE. Many of these deposits are of large size, analogous in numerous ways to the coral reefs in our present oceans.

Animal fossils from this era are conspicuous by their rarity. Fossils of radiolarians and foraminiferans (protozoans that secrete shells of silica and calcium carbonate, respectively) have been reported, as also have fossils of brachiopods (see p. 155), the spicules of sponges, and even the impression of a jellyfish. Were there many-celled animals (Metazoa) living in the Proterozoic? There is no consensus on the answer. Some investigators have reported affirmative evidence, yet Cloud (1965) concluded that "there are yet no records of unequivocal Metazoa in rocks of undoubted Precambrian age." We await further investigations with interest.

The fossils most generally accepted as derived from a Proterozoic animal consist not of the remains of the animals themselves but of casts of the homes of the animals. In the bottoms of shallow portions of modern oceans ANNELID WORMS, marine relatives of our common earthworm, live in burrows. These burrows are not temporary affairs like the tunnels of earthworms but have definite walls secreted by their inhabitants. Casts that seem to have been formed in burrows of this type are found in Proterozoic deposits.

If we are correct in interpreting the Proterozoic worm burrows as evidence that annelid worms existed in this era, we must conclude that much evolution had occurred prior to and during the Proterozoic era. Unfortunately a fossil record of that history was for the most part never formed, has not been found yet, or was irrecoverably lost.

PALEOZOIC ERA

The beginning of the Paleozoic era is known to us from the earliest deposits bearing abundant fossils. This era is much the longest of the ones following the Proterozoic, and it is divided into seven periods, of which the Cambrian is the first or oldest (Table 8.1, p. 146).

CAMBRIAN PERIOD Between the rocks remaining to us from the Proterozoic era and the first ones representing the Cambrian period occurs a gap in the fossil record representing in all probability a lapse of many millions of years. In view of these lost chapters in the record we need not be surprised that the story of animal evolution does not commence in the Cambrian where it left off at the end of the Proterozoic era. In place of the paucity of fossils characteristic of Proterozoic rocks we find in Cambrian deposits abundant fossils, particularly in the later deposits of the period. Cambrian oceans teemed with a wide variety of invertebrates.

One reason for the increase in completeness of record may lie in the fact that in the interim between Proterozoic and Cambrian animals possessing hard parts (shells and exoskeletons) increased greatly in

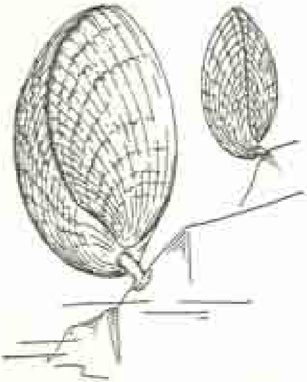


Fig. 9.1. Brachiopods, attached to rocks by their pedicles. Note the larger size and differing shape of the half-shell pierced by the pedicle.

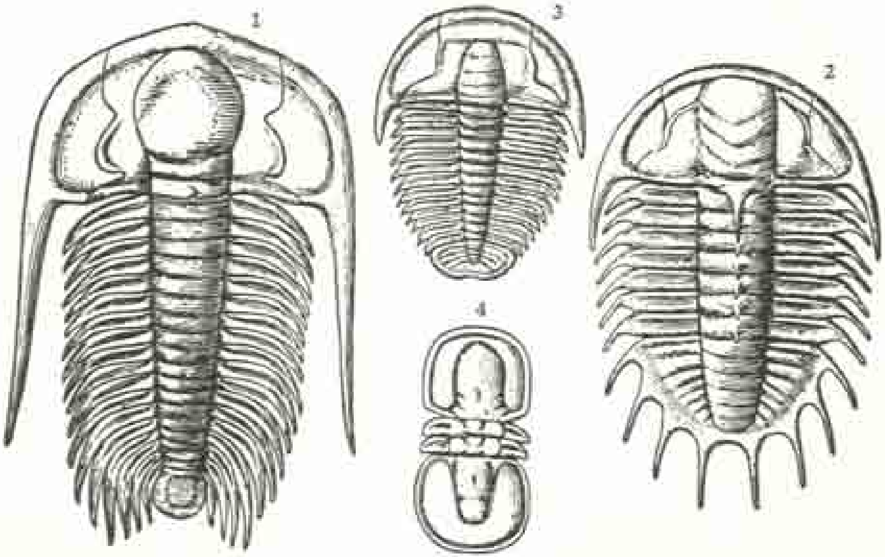


Fig. 9.2. Typical Cambrian trilobites. (Reprinted by permission from *Textbook of Geology, Part II, Historical Geology,* by L. V. Pirsson and C. Schuchert, published by John Wiley & Sons, Inc., 1915.)

numbers. BRACHIOPODS constituted an important portion of the Cambrian fauna. These animals are enclosed within shells consisting of two portions or valves. Unlike the shells of bivalve molluscs, such as clams, the two valves are unequal in size (Fig. 9.1), and they are dorsal and ventral shells rather than two lateral shells. Molluscs themselves are represented in Cambrian seas by a few SNAILS and, near the close of the period, rare CEPHALOPODS (p. 158). WORM BURROWS, recalling those of the Proterozoic, are abundant in some Cambrian deposits.

The dominant animals in the Cambrian seas were the TRILOBITES, constituting some 60 percent of the known inhabitants of those seas. They were small animals for the most part, ranging between one and four inches in length, the giant among them being 18 in. long. The examples presented in Fig. 9.2 are typical. Figure. 9.3 shows a trilobite with such structures as antennae and appendages restored to the appearance presented in life.

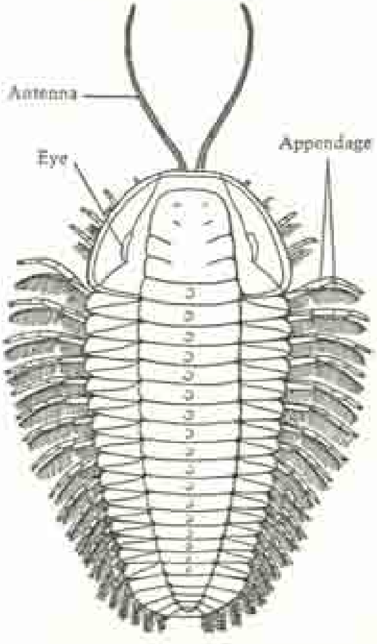


Fig. 9.3. Trilobite anatomy. (After Beecher.)

The first thing to note about trilobites is that they are members of the phylum Arthropoda, to which such creatures as lobsters, crayfishes, spiders, and insects also belong. The general similarity to a lobster, for instance, is evident in the shell-like exoskeleton, the segmented body, and the jointed appendages. Arthropods form the "highest" (most complex and specialized) phylum of invertebrates. Thus in the first geologic period that we know from adequate fossil material the highest invertebrate group of animals is represented. This fact indicates that a great proportion of the evolution of invertebrates had already occurred, although our records of its history are almost entirely lacking. Since trilobites appeared on the scene with such apparent abruptness their origin is uncertain. It seems reasonable to believe that they evolved from annelid worms, the other great group of invertebrates having segmented bodies. Evidence that annelid worms were present in the Proterozoic will be recalled.

Our knowledge of life in Cambrian seas would be confined almost exlusively to shells and exoskeletons were it not for a most fortunate and unusual fossil discovery in the Burgess shale of British Columbia. The fossils consist of thin carbon films (see p. 139) showing in amazing detail the structures of the animals from which they were formed. Both hard and soft parts are shown by these carbonaceous films. Among the remains are trilobites preserved with their limbs and antennae, delicate arthropods like the modern brine shrimp, annelid worms complete with setae (bristles), and details of the internal organs, sponges, and such soft-bodied creatures as jellyfish. One of the most interesting members of the assemblage is an onychophoran. The onychophorans are peculiar, wormlike arthropods exemplified by the modern *Peripatus* (Fig. 9.4). Their particular interest lies in the fact that they combine characteristics of arthropods with those of annelid worms. Thus they strengthen the evidence that arthropods evolved from annelids.

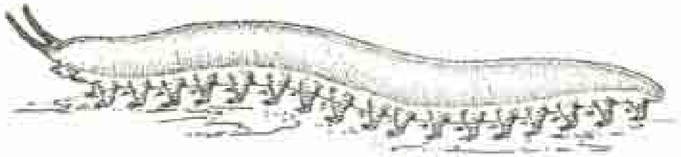


Fig. 9.4. *Peripatus,* an onychophoran.

Thanks to the rare fortune of the Burgess shale fossils we know that the Cambrian seas supported a wealth of invertebrate life of kinds not ordinarily preserved as fossils. Perhaps we should have inferred that this world of soft-bodied marine animals existed, but certainty is more satisfying than inference.

In conclusion we note two general facts about Cambrian animals. They all lived in the ocean; none were land dwellers. They were all invertebrates; no representatives of phylum Chordata, comprised of the vertebrates and their kin, are known from this stage in the world's history.

The Cambrian was a very long period. It was probably some 100 million years in duration. Comparison of earlier Cambrian fossils with those from later portions of the period reveals that much evolutionary change occurred during the course of this long period.

INVERTEBRATE EVOLUTION FOLLOWING THE CAMBRIAN

TRILOBITES As we have seen, trilobites were the dominant animals in Cambrian seas. Following that period they gradually declined in numbers and relative prominence. During the Silurian period trilobites with bizarre shapes and spines appeared (Fig. 9.5). This type of specialization apparently forms one indication that a group has become highly specialized for a particular mode of life and has correspondingly lost the plasticity that would enable it to adapt to other modes of life should conditions change. The spines in this instance may have served for protection from predators, if there were any present capable of preying on trilobites (cephalopods or early fishes perhaps?).

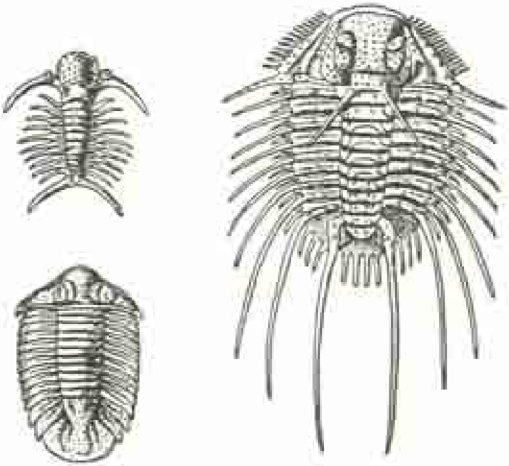


Fig. 9.5. Silurian trilobites. (Reprinted by permission from *Textbook of Geology, Part II, Historical Geology,* by L. V. Pirsson and C. Schuchert, published by John Wiley & Sons, Inc., 1915.)

By Mississippian times trilobites were rare. Many species of sharks with flat, "pavement" teeth adapted for crushing shells of molluscs and arthropods doubtless contributed to the decline in numbers.

No trilobites survived the end of the Paleozoic era. When the curtain rose on that era more than 300 millions years previously they had occupied the center of the stage. It is perhaps fitting that their extinction marked the closing act of the Paleozoic drama.

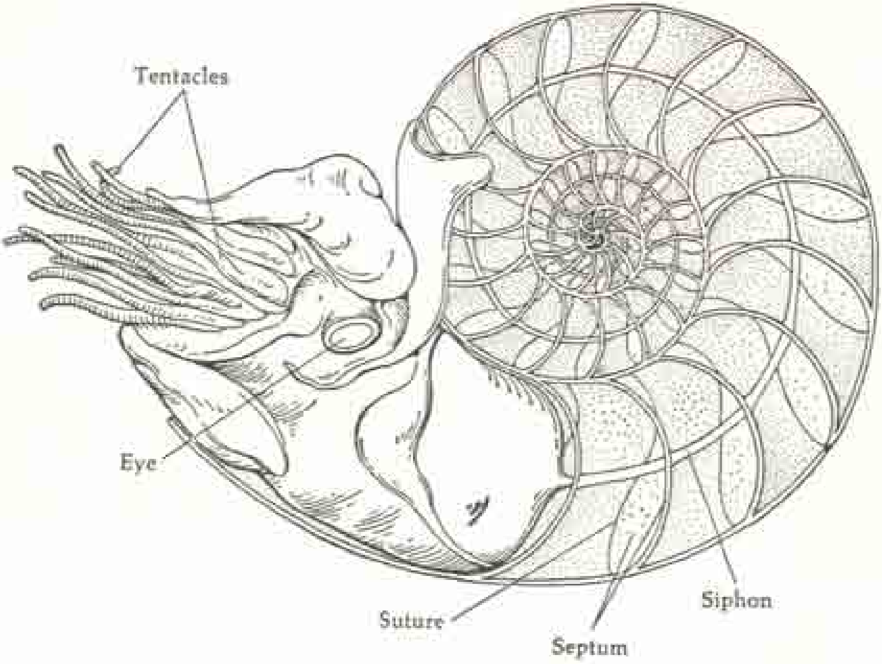


Fig. 9.6. Chambered nautilus, with shell cut longitudinally to show the chambers. (After Hancock.)

CEPHALOPODS Cephalopods became prominent in the Ordovician period. This group of molluscs includes squids, octopi, and nautili. The chambered nautilus (Fig. 9.6) of our modern oceans presents a structure not unlike that of its Ordovician ancestors. The animal itself is soft-bodied and unsegmented; it possesses a pair of eyes and a cluster of extensible, sucker-bearing arms or tentacles around the mouth. As shown in the figure, the animal lives in the outermost compartment of its tapered shell. When it grows it moves outward, adding to its shell and secreting behind it a wall or SEPTUM. Thus the shell eventually consists of a series of chambers or compartments, evidence of successive stages in the growth of the animal (Fig. 9.6). Where each septum joins the side wall of the shell a line of attachment, called a SUTURE, is formed. In the earliest cephalopods the suture lines were smooth curves (Fig. 9.7). In later periods cephalopods having suture lines following complex configurations were found, as noted in the following. Cephalopods having smoothly curved suture lines are called NAUTILOIDS. Interestingly enough, both our modern nautili and these earliest cephalopods were of this type. The principal difference between the shells of Ordovician nautiloids and those of their modern

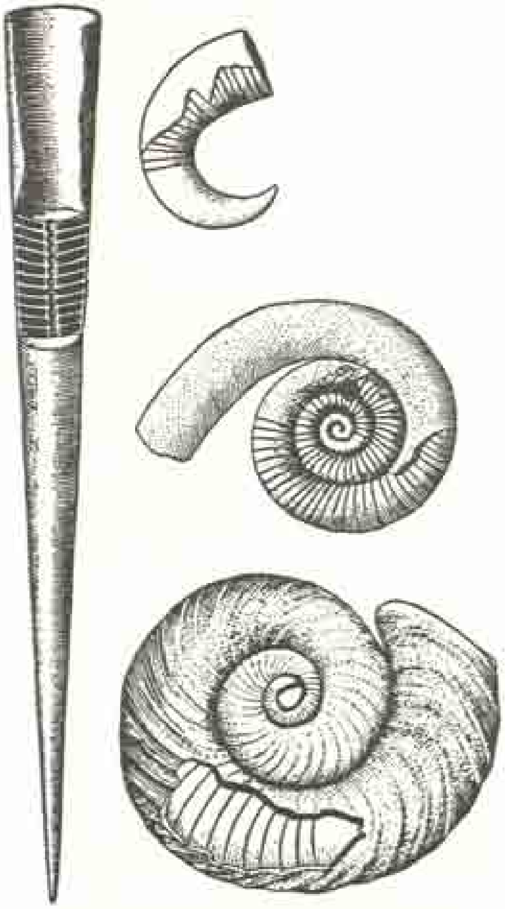


Fig. 9.7. Ordovician nautiloid cephalopods. (Reprinted by permission from *Textbook of Geology, Part II, Historical Geology*, by L. V. Pirsson and C. Schuchert, published by John Wiley & Sons, Inc., 1915.)

descendants relates to the coiling of the shell. Some of the Ordovician cephalopods had straight shells (Fig. 9.7), others were loosely coiled, while still others were closely coiled like those of modern nautili. In Fig. 9.7 the smooth sutures are visible in places where the outer surface of the shell has been chipped away. Cephalopods included the largest animals living in Ordovician seas; some of the straight-shelled forms reached a length of nearly 30 ft.

With the advent of Devonian times a new group of cephalopods appeared. These were the AMMONITES, in the first of which the suture

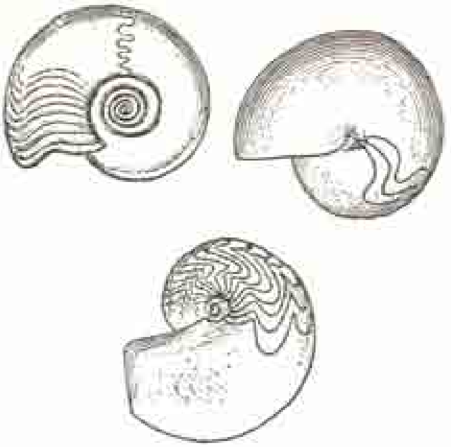


Fig. 9.8. Devonian ammonites (goniatites) showing wavy suture lines. (Reprinted by permission from *Textbook of Geology, Part II, Historical Geology,* by L. V. Pirsson and C. Schuchert, published by John Wiley & Sons, Inc., 1915.)

lines presented a wavy or "loop-and-saddle" appearance (Fig. 9.8). With the passage of time ammonites increased in relative abundance and variety, their progressive evolution being especially marked during the Permian. This foreshadowed their great expansion during the Mesozoic era (pp. 182–183).

CORALS, CRINOIDS, AND BRACHIOPODS The first CORALS appeared among the coelenterates in the Ordovician period. We noted above evidence that jellyfishes were present in the Cambrian period. Apparently, however, no coelenterates in that period developed the ability to secrete calcium carbonate, thereby forming what is for the coral animal at once its skeleton, its apartment house, and its memorial monument. Each of the pits or hollows on the surface of a piece of coral represents the point of attachment of a tiny sea anemone-like coral animal (Fig. 9.9). One generation builds upon the foundations laid down by its predecessors. Hence coral rock, built up at times into great reefs in the ocean, is the result of cooperative action of countless hordes of coelenterates over great periods of time. Much limestone originated in this way.

During the course of geologic time corals have waxed and waned in abundance. Their profusion in warm oceans of the present day is well known to all visitors to these regions.

CRINOIDS are members of the phylum Echinodermata, along with such spiny-skinned creatures as starfishes and sea urchins. Crinoids

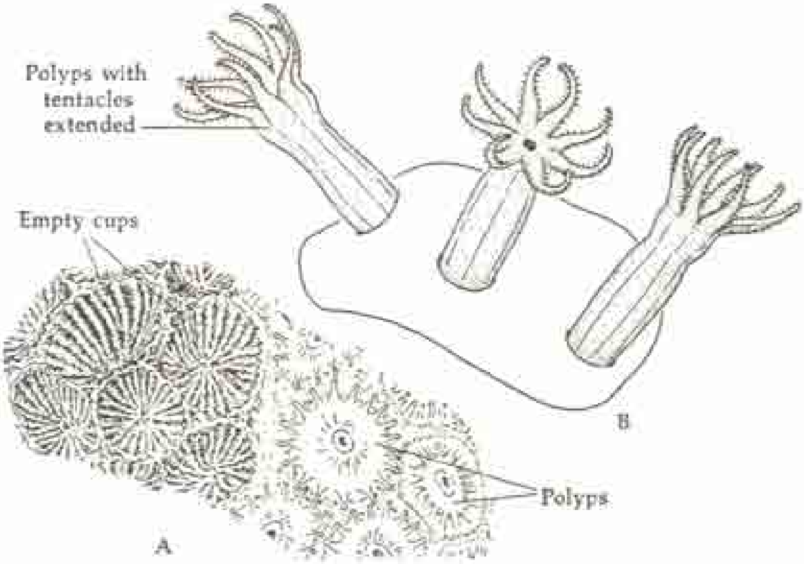


Fig. 9.9. Coral. A, coral animals (polyps) seen from above, and, at left, the empty cups remaining after their death. B, coral polyps of a species suggestive of *Hydra*, a free-living coelenterate.

first appeared in the Ordovician. Sometimes called sea lilies, they look like flowers growing in the ocean (Fig. 9.10). The stem or stalk attaching the creature to the ocean floor is composed of piled rings fastened together. Those rings, freed by disintegration of crinoid stems, are immensely abundant in many Ordovician, and later, rocks. Crinoids reached the peak of their development in Mississippian times and then declined, becoming relatively rare by the Permian period. But they still exist in modern oceans. Incidentally, starfishes themselves first appeared, though as rarities, in Ordovician seas.

The history of BRACHIOPODS (p. 155) parallels that of crinoids in some respects. They reached their evolutionary zenith in Devonian times and continued prominent throughout the Mississippian, when forms having long spines radiating from their shells occurred. They were abundant in the Permian but declined markedly by the end of that period. Their importance in prehistoric oceans far outweighed their prominence today.

Space forbids a discussion of many other invertebrates prominent in Paleozoic seas, such as graptolites and bryozoans. Interested readers will find discussions of them in books on historical geology such as those listed at the end of this chapter.

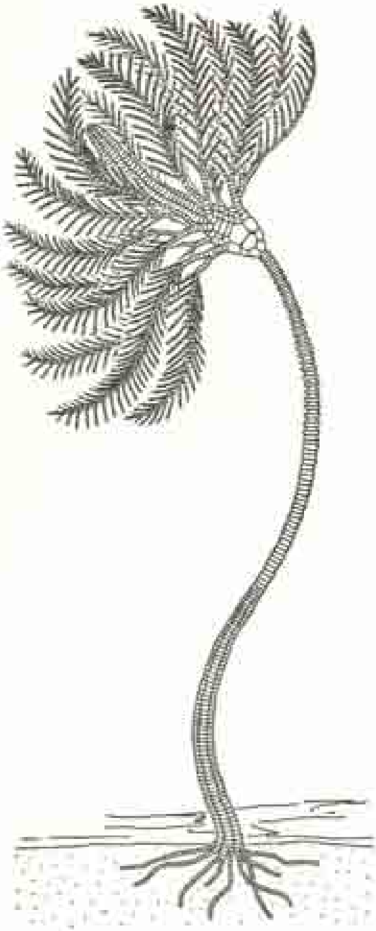


Fig. 9.10. A simple crinoid.

EURPYTERIDS AND SCORPIONS Among the interesting invertebrates of Silurian times were the EURYPTERIDS or "sea scorpions" (Fig. 9.11). They were a group of arthropods that had made a small beginning in the Cambrian but did not constitute an important feature of the fauna until the Silurian. These remarkable arthropods were small for the most part, though one had a body length of seven feet and was probably the largest arthropod that ever lived.

Closely similar to eurypterids in many ways, and probably descended from them, were SCORPIONS not unlike those of the present day (Fig. 9.12). These and MILLIPEDES existing at the time may have been

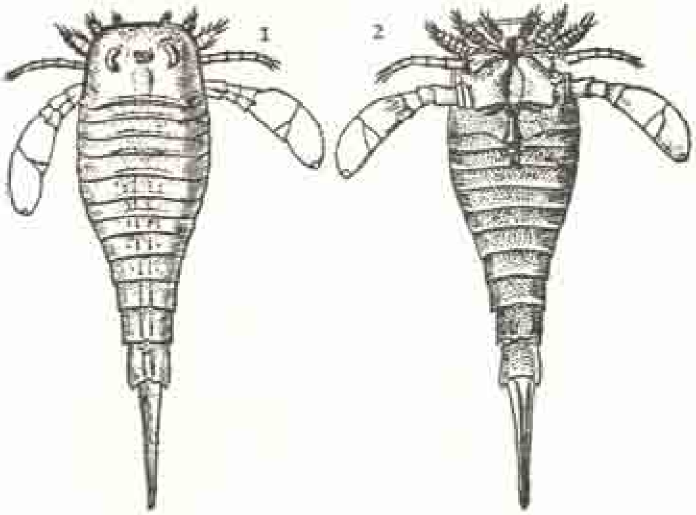


Fig. 9.11. Silurian eurypterid. 1, dorsal view. 2, ventral view. (Reprinted by permission from *Textbook of Geology, Part II, Historical Geology,* by L. V. Pirsson and C. Schuchert, published by John Wiley & Sons, Inc. 1915.)

terrestrial, thereby earning the distinction of being the first known animals to live on land. The evidence is inconclusive, however.

INSECTS The earliest known winged insects lived during the Pennsylvanian period, the time of the luxuriant plant growth that later became some of our largest deposits of coal. Remains identified as those of wingless insects such as springtails and silverfish have been found in Devonian deposits. From what ancestors did the insects arise? Various previously existing arthropods have been suggested, but at present the answer to the question is uncertain.

Most of the Pennsylvanian insects were of archaic types not now living, though one struck a distinctly modern note: the cockroach (Fig. 9.13). Although cockroaches constitute only about 1 percent of modern insect faunas, they formed about 60 percent of insects living in Pennsylvanian times. Some reached a length of four inches. They were strikingly similar to their modern descendants in structure. It is a remarkable fact that while some animals are undergoing great evolutionary changes others continue virtually unchanged for millions of years. Dynasties of animals wax and wane, but the cockroach goes on forever.

Aside from cockroaches the most numerous insects were of a group now extinct, the PALEODICTYOPTERA (Fig. 9.13). These insects are of interest as the probable ancestors of all other winged insects. Large

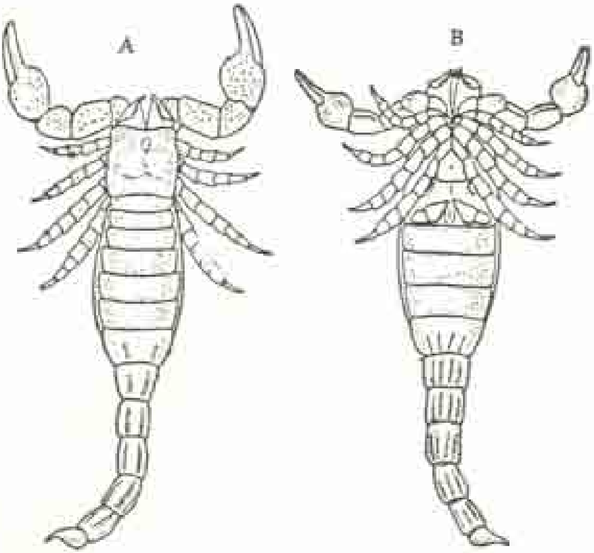


Fig. 9.12. Scorpions of Silurian age. A, dorsal view of one species. B, ventral view of a different species. (After Pocock; reprinted by permission from *Textbook of Geology, Part II, Historical Geology*, by L. V. Pirsson and C. Schuchert, published by John Wiley & Sons, Inc., 1915.)

size characterized many Pennsylvanian insects. Thus one of a group of insects closely resembling modern dragonflies had a wingspread of about 34 in., making it the largest insect ever recorded.

Interestingly, those first insects had mandibulate mouthparts of the general type we used as a starting point in our discussion of the adaptive radiation of insect mouthparts (pp. 33–37).

Carpenter (1952) listed the three main steps in insect evolution as (1) development of wings, (2) development of ability to fold the wings over the abdomen—in contrast to the stiffly protruding wings of dragonflies and Paleodictyoptera (Fig. 9.13)—and (3) development of complete metamorphosis with larval and pupal stages. The fossil record indicates that these major steps had all been taken by the end of the Pennsylvanian period.

Permian insects were quite unlike those of the preceding period. They averaged smaller in size; cockroaches formed a decreased proportion of them. Many varieties were of types not now living, but early in the Permian such modern orders as dragonflies, mayflies, true bugs (Fig. 3.9, p. 36), lacewings, and scorpionflies appeared. Beetles and stoneflies are found in late Permian deposits (Carpenter, 1952).

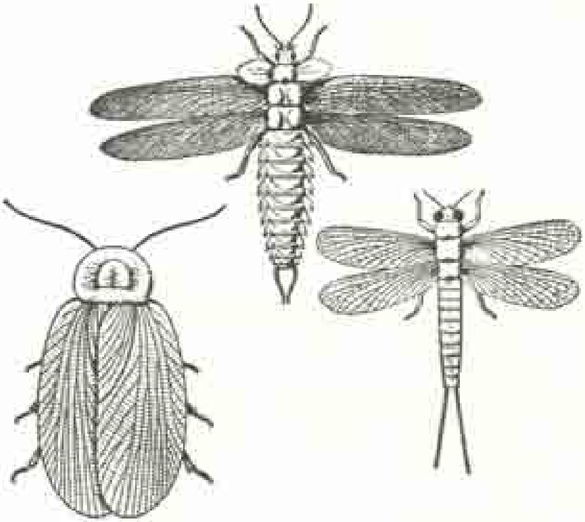


Fig. 9.13. Pennsylvanian insects: Paleodictyoptera (upper, and lower right). Cockroach (lower left). (Reprinted by permission from *Textbook of Geology, Part II, Historical Geology*, by L. V. Pirsson and C. Schuchert, published by John Wiley & Sons, Inc., 1915.)

VERTEBRATES IN THE PALEOZOIC

As noted earlier, no representatives of phylum Chordata have been found among fossils of Cambrian age (p. 156). Ancestral forms were doubtless in existence, but they may not have attained the traits we regard as characterizing the phylum Chordata (p. 68). Romer (1959 and 1967) has suggested that invertebrates that were filter feeders (pp. 67–68) may have been ancestral to both echinoderms and chordates. Such forms would not have had hard parts and hence would have been unlikely to have been preserved as fossils. Thus the first chordate fossils known are bony scales in deposits of Ordovician age —tantalizing evidence that armored vertebrates, perhaps ostracoderms, were living at that time.

OSTRACODERMS AND FISHES The first known vertebrates were the OSTRACODERMS. They lived in the Silurian period and much more abundantly in the Devonian. Like modern cyclostomes (lampreys and hagfishes) they had mouths without jaws, and they had no paired pectoral and pelvic fins. Fossils suggest that the early ones, at least, were filter feeders (Romer, 1967). They are commonly called "armored

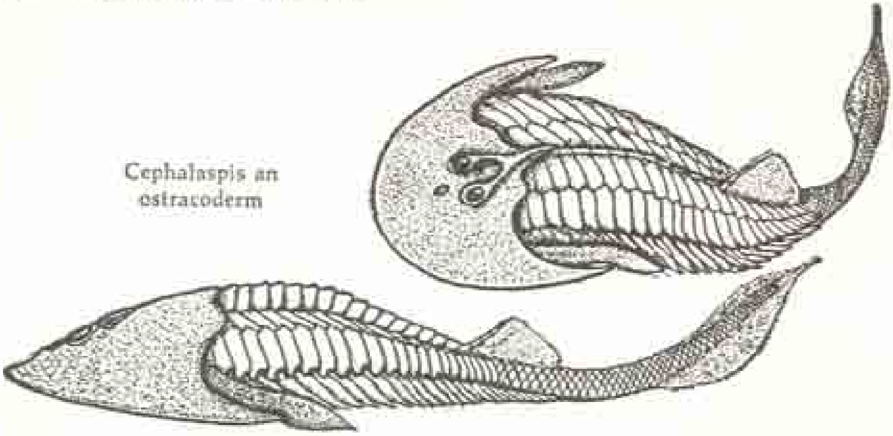


Fig. 9.14. An ostracoderm (armored fish), *Cephalaspis;* length one foot or less. (From *Comparative Anatomy,* by H. V. Neal and H. W. Rand. Copyright 1936 by McGraw-Hill Book Company, Inc. Used with permission of the McGraw-Hill Book Company.)

fishes" because many of them had armor plate covering the head (Fig. 9.14) and, in some species, part of the body. The armor of these little creatures may well have served as protection from predatory eurypterids (Romer, 1959 and 1967). The suggestion also has been made that it served to reduce the amount of body surface exposed to unfavorable osmotic action (pp. 338–344).

Ostracoderms were probably the ancestors of the first fishes to possess jaws. Here again the fossil record is incomplete. The jaws are believed to have originated from a gill arch (bones supporting a gill), but fossils showing this important change are still unknown.

The first fishes with jaws are called ACANTHODIANS (Fig. 9.15). Fragmentary fossils indicate their presence in Silurian times, but they

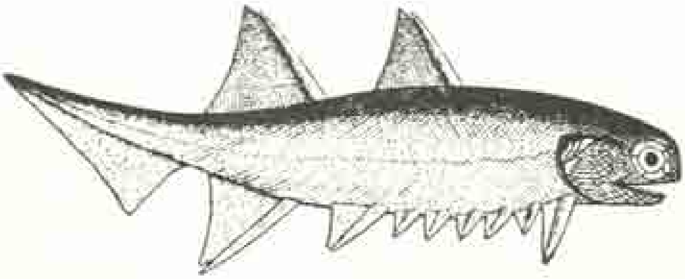


Fig. 9.15. An acanthodian fish (*Climatius*) from the Devonian; length about 3 inches. (After Romer, A. S., *Vertebrate Paleontology.* Copyright © 1933, 1945, and 1966 by The University of Chicago. Used by permission of The University of Chicago Press.)

are best known from Devonian deposits. Almost as ancient (early Devonian) were a varied assemblage of fishes known as the PLACODERMS. Fishes having jaws are conveniently divided into two main classes: (1) CHONDRICHTHYES, fishes with cartilaginous skeletons, such as dogfishes and sharks, and (2) OSTEICHTHYES, fishes with skeletons composed mainly of bone, such as sturgeon, gar pike, trout, salmon, bass, perch, and tuna. Placoderms are regarded as ancestral to the Chondrichthyes and acanthodians as ancestral to the Osteichthyes, though the possibility remains that acanthodians may have been ancestral to both (Romer, 1966).

Since Chondrichthyes have skeletons of cartilage, prehistoric representatives are known mostly from such hard parts as teeth, spines, and scales. In the case of *Cladoselache* (Fig. 9.16), however, we are more fortunate: the outline of the body and some details of skin and muscles were preserved in the fossilization.

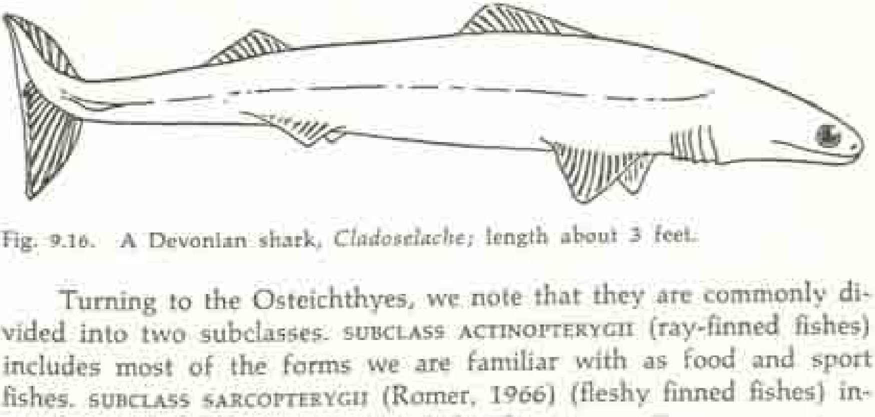


Fig. 9.16. A Devonian shark, *Cladoselache*; length about 3 feet.

Turning to the Osteichthyes, we note that they are commonly divided into two subclasses. SUBCLASS ACTINOPTERYGII (ray-finned fishes) includes most of the forms we are familiar with as food and sport fishes. SUBCLASS SARCOPTERYGII (Romer, 1966) (fleshy finned fishes) includes the lungfishes (Dipnoi) and the Crossopterygii, a group represented by the ancestors of the first amphibians and by the coelacanth fishes. Because of their ancestral position, the CROSSOPTERYGII (lobe-

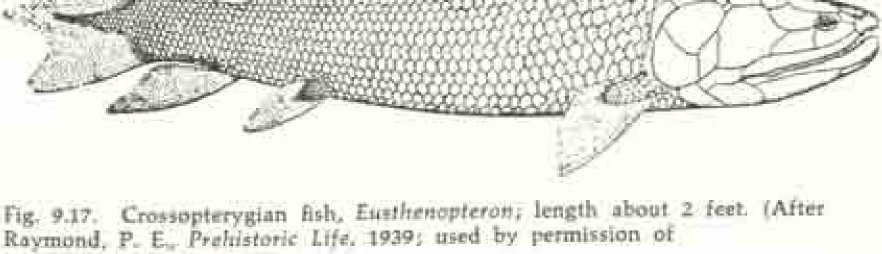


Fig. 9.17. Crossopterygian fish, *Eusthenopteron*; length about 2 feet. (After Raymond, P. E., *Prehistoric Life*, 1939; used by permission of Harvard University Press.)

finned fishes) are of particular interest to us. Each pectoral and pelvic fin had a thickened, fleshy base (Fig. 9.17). Within these fleshy bases in such a species as *Eusthenopteron* were skeletal elements capable of developing into the stiffening supports for limbs of terrestrial vertebrates (Fig. 9.18).

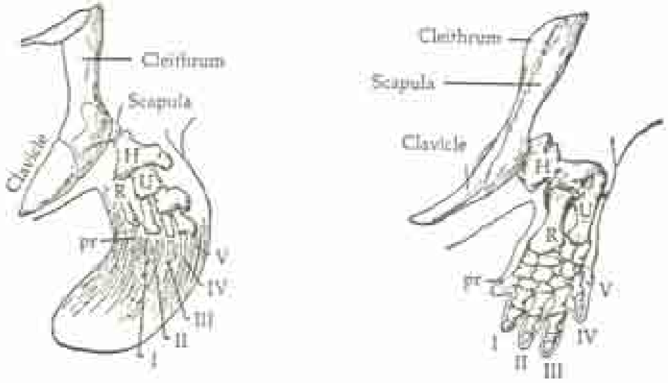


Fig. 9.18. Skeletal elements in the fin of the crossopterygian fish, *Eusthenopteron* (left), and in the limb of the Paleozoic amphibian *Eryops*, (right). H, humerus. R, radius. U, ulna. (After Gregory; from *General Zoology* by Storer and Usinger, 4th ed. Copyright © 1965 by McGraw-Hill, Inc. Used with permission of McGraw-Hill Book Co.)

Crossopterygians, like lungfishes and like some modern actinopterygians such as the gar pike, had air bladders connected to the pharynx. Such a connection makes possible filling of the bladder with air from the exterior. Thus gar pikes and some modern lungfishes, when the surrounding water becomes stagnant and unfitted for respiration by means of gills, rise to the surface and gulp in air. Their air bladders function as lungs. Accordingly we see that Crossopterygii of Devonian times possessed a mechanism capable of developing into the respiratory system needed by terrestrial vertebrates—an example of preadaptation (pp. 17–18). In many of the modern bony fishes, on the other hand, the air bladder has no opening to the pharynx; gas pressure in the bladder is regulated through action of the blood system. Thus the bladder serves as a swim bladder, a hydrostatic organ enabling the fish to adjust to varying pressures at different depths.

Ancestral crossopterygians also shared with lungfishes another feature useful for respiration in air. The external nostrils, instead of opening into blind pouches as they do in most fishes, connected to openings in the roof of the mouth. Thus terrestrial descendants of the Crossopterygii could breathe through the nose, with the mouth closed.

The nearest living relative of these ancestral crossopterygians is the coelacanth fish *(Latimeria)*, discovered in 1938. Previously the coelacanths were known only from fossils; they were thought to have become extinct at the close of the Cretaceous period. Then in the winter of 1938–1939 a specimen was caught off the coast of South Africa. Intensive search for other specimens was fruitless at first, but since 1952 several specimens have been obtained near the Comoro Islands off Madagascar. The drama of discovery connected with the first and second specimens makes a fascinating story as told by the scientist most concerned, J. L. B. Smith (1956). The modern coelacanth differs from ancestral lobe-finned fishes by having only a remnant of an air bladder (Millot, 1954), used for fat storage, and no internal nostrils. Yet the creature is of great interest because of the strong possibility that it has retained many primitive characteristics of tissues and internal organs and hence may give us clues as to the nature of these features in the ancestral Crossopterygii. The lobe fins are of especial interest; they have complex musculature, and observation of living specimens indicates that the fins are capable of a great variety of movements (Millot, 1955). "It is plain that the fish can crawl about, in the water at least" (Smith, 1956).

LABYRINTHODONT AMPHIBIANS The Crossopterygii gave rise to the first amphibians, the LABYRINTHODONTS. A few remains indicate that the transition occurred in the Devonian. These first amphibians were long-bodied, weak-limbed creatures, somewhat "lizardlike" in appearance (Fig. 9.19). The lobe fins inherited from their crossopterygian ancestors had been transformed to serve as supports for the body in a

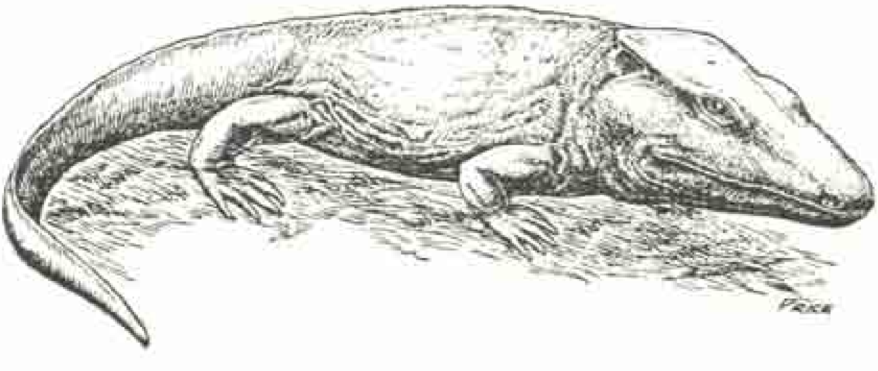


Fig. 9.19. A labyrinthodont amphibian, *Diplovertebron;* about 2 feet long. (After Raymond, P. E., *Prehistoric Life*, 1939; used by permission of Harvard University Press.)

medium, air, which did not buoy up the body as had the water of the old environment. Figure 9.18 shows the skeletal elements in a typical crossopterygian fin and in the limb of an early amphibian.

We may note in passing that the idea that Devonian Crossopterygii used their fins to crawl out on land does not seem improbable in view of the nature of the coelacanth fins and the fact that in certain parts of the world today even some actinopterygian fishes (e.g., "climbing perch") use their fins in just this manner, climbing trees in search of insects. The "walking catfish" introduced into Florida, is another example. The air bladder, inherited by amphibians from crossopterygian ancestors, served as simple lungs and, as we have seen, the nostrils were arranged to permit breathing with the mouth closed.

The labyrinthodonts retained many features of their crossopterygian ancestors. Their name refers to a complicated pattern of infolding that characterized the arrangement of the enamel of the teeth. A similar arrangement characterized the enamel patterns of crossopterygian teeth. The dorsal surface of the skull of labyrinthodonts was composed of a mosaic of small bones fitted together edge to edge. The first diagram in Fig. 3.6 (p. 32) represents this mosaic pattern. These bones correspond in detail to the bony plates covering the heads of the Crossopterygii (Fig. 9.17). These and other similarities cannot be mere coincidence; they leave no doubt that amphibians arose from Crossopterygii.

Although these first amphibians possessed many preadaptations for life in the air, it is likely that most of them spent the greater portion of their lives in the water, as many amphibians do to this day (Romer, 1959 and 1967). They had one great advantage over most fishes, however; they *could* leave the water when necessity arose. Under what conditions would it have been desirable to do so? Apparently they did not leave to escape predatory animals. In their freshwater environment the ancestors of amphibians were the largest animals present. Abundant food supply on land can hardly have been the explanation since these animals were carnivorous, and prospective prey in the form of animals living on land, it would seem, was much less abundant than was prey living in the water. The most generally accepted answer to the question is based on the idea that the ancestors of amphibians lived in pools that dried up periodically, as do the pools in which some lungfishes live today. Under conditions of overcrowding in stagnant water, followed perhaps by complete evaporation of that water, a premium would be placed on being able to breathe air directly and to move about on land, perhaps at first in search of a neighboring pool having better living conditions. Animals able to survive such stringent conditions were on their way to becoming true land dwellers.

Thus, as so often happens, progress occurred under the lash of adversity.

We may note that amphibians—exemplified today by salamanders, frogs, and toads—have never completely conquered the terrestrial environment. Their method of locomotion on land is relatively inefficient. Their skins do not prevent undue loss of water from the body by evaporation. And perhaps most important of all, many of them must return to the water to lay their eggs. Some have developed a variety of expedients to avoid returning eggs to the water, but none of these expedients hold promise of general usefulness as did the method developed by the first reptiles (pp. 173–174).

In the water amphibian eggs develop much as do fish eggs, and the aquatic larvae (tadpoles) have many of the characteristics of fishes. Interestingly enough, the "external gill stage" of an amphibian larva (Fig. 9.20)—the stage in which branching, frondlike gills project laterally from the surface of the head—is similar to stages in the development of some modern remnants of ancient groups of fishes: *Polypterus*, and some of the Dipnoi (lungfishes). If we ever learn of the larval development of the Crossopterygii we shall probably find that the latter had an "external gill stage" too. We recall our discussion of the value of embryonic and larval similarities to evolutionary studies (Chap. 4).

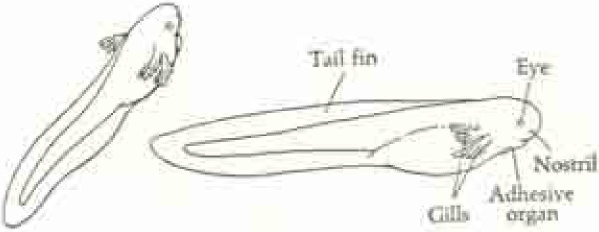


Fig. 9.20. Amphibian tadpole exhibiting external gills.

The labyrinthodonts themselves were abundant during the latter part of the Paleozoic, and continued on, though with reduced numbers, into the early Mesozoic. Their limbs were short, extending laterally from the body (Fig. 9.19) and forming a rather inefficient locomotor apparatus wherein an undue proportion of muscular energy was expended in raising the body off the ground. This inefficiency was probably mitigated by the fact that labyrinthodonts spent a great portion of their lives in swamps and streams where water supported much of the weight of the body. Many of these amphibians were small—only a few inches long. At the other extreme were animals about ten feet long and one, known only from its footprints, that probably weighed at least 500 lbs.

Most appropriate at this point is mention of a Permian vertebrate whose anatomical traits were almost equally divided between those of amphibians and those of reptiles: *Seymouria* (Fig. 9.21). Probably to be regarded as an amphibian, it was so like a reptile in many respects that it has sometimes been classed as a reptile (see Romer, 1966, pp. 94–95, for a summary of its amphibian and reptilian characteristics). If we knew what kind of egg it laid (see the following) we could be more certain as to where to place it in classification. But for us *Seymouria* is chiefly of interest because it shows how small the evolutionary step was between labyrinthodonts and their descendants the reptiles.

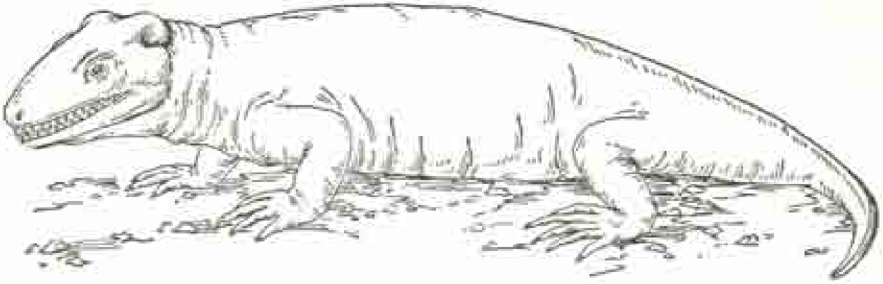


Fig. 9.21. A Permian vertebrate, *Seymouria*, combining characteristics of both amphibians and reptiles; length about 20 inches. (Mainly after Case.)

COTYLOSAUR REPTILES The first reptiles were the COTYLOSAURS. Fragmentary fossils indicate that they first occurred in Pennsylvanian times, but cotylosaurs of Permian age are much better known. All evidence indicates that they evolved from labyrinthodont amphibians. Indeed, as noted above in the case of *Seymouria*, anatomical changes

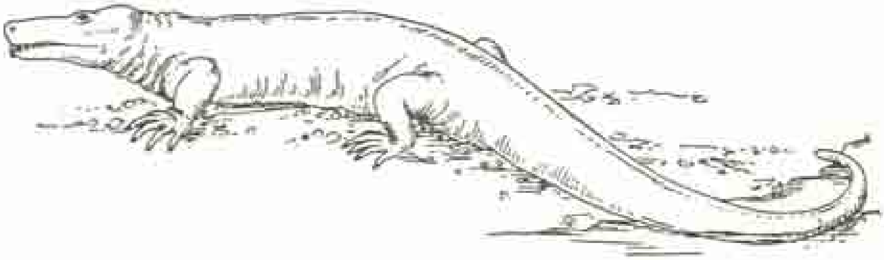


Fig. 9.22. A Permian cotylosaur reptile, *Limnoscelis*; length about 5 feet. (Romer, 1959, considered that this creature was amphibious and had webbed feet.) (After Case, *Publication No. 207*, Carnegie Institution of Washington, 1915.)

involved were small. In shape and bodily characteristics cotylosaurs closely resembled their labyrinthodont ancestors (Fig. 9.22).

Did the first reptiles live in the water or on land? Romer (1959 and 1967) has concluded that they spent most of their lives in the water, as their amphibian ancestors had done, but that unlike the latter they laid eggs on land, as aquatic turtles do today. He pointed out the advantages of laying eggs on land, especially the lessened danger of having the eggs and young eaten by predatory fishes, insect larvae, and the like.

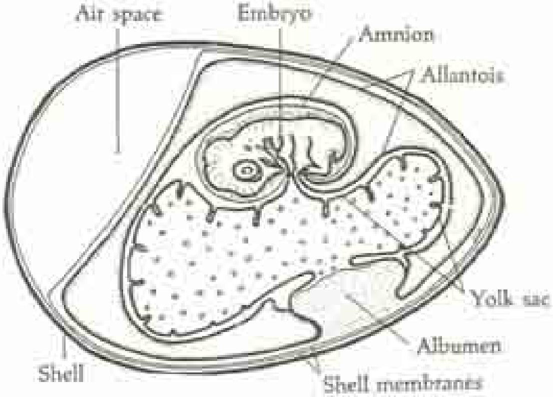


Fig. 9.23. Embryo of a bird, together with shell, shell membranes, and extra-embryonic membranes. (Drawn by Lyman S. Rowell.)

This important change was made possible by the enclosure of each egg within a protective capsule containing enough nourishment to last the embryo until it had reached a stage when, as a newly hatched young, it could move about on land and secure its own food. Figure 9.23 shows the arrangements by which this result is achieved for bird embryos; the reptilian egg is identical in its main features. The capsule mentioned is composed of a SHELL and SHELL MEMBRANES; the shell of reptilian eggs is pliable, in contrast to the brittleness of birds' eggshells. The embryo itself is enclosed within a bladderlike membrane called the AMNION. This serves as a container for the AMNIOTIC FLUID in which the embryo floats. The fluid protects the embryo from mechanical injury and from drying. Thus the embryos of reptiles and birds resemble those of fishes and amphibians in that all develop while submerged in liquid. In the case of fishes and amphibians the liquid is the water of streams and ponds; in the case of reptiles and birds the liquid is the fluid bottled up within the amnion. One may speculate that since the embryos of ancestors had "formed the habit of" developing in liquid, if descendants were to avoid laying their eggs in water they would be under the necessity of providing a substitute liquid in which embryonic development could occur. Incidentally, we may appropriately recall the many respects in which the embryos of higher vertebrates resemble the embryos of fishes (see Chap. 4).

The YOLK of the reptilian or avian egg constitutes the store of food mentioned above. Water for the needs of the embryo is present in the yolk and also in the ALBUMEN (white) of the egg. Early in development an outgrowth from the body of the embryo surrounds the yolk with a YOLK SAC. This, like the digestive system of which it is an outgrowth, is lined with endoderm. The endoderm cells digest the yolk. The products of this digestion are picked up by the blood, flowing in the network of blood vessels that permeate the walls of the yolk sac, and transported to the embryo as nourishment is needed.

Oxygen is another necessity for the embryo. Oxygen is abundant in the air surrounding the egg, but a means must be provided for securing it and transporting it to the embryo. The shell and shell membranes are sufficiently porous to permit air to enter. The blood serves as an agent of transportation, in this instance through a network of blood vessels in the walls of an embryonic membrane called the ALLANTOIS (Fig. 9.23). Like the yolk sac, the allantois grows out from the embryo; it spreads around underneath the shell membranes, where blood in its blood vessels can pick up oxygen from air diffusing through. Waste products of embryonic metabolism, principally uric acid (p. 344), are stored in a portion of the allantois to be discarded when hatching times arrives.

Thus we see that by means of elaborate arrangements of shell, shell membranes, yolk sac, amnion, and allantois, reptiles and their descendants the birds avoided the necessity of laying eggs in the water as their ancestors had always done. This was one of the greatest achievements in the entire history of vertebrate evolution.

What other advances over their amphibian ancestors did the reptiles achieve? Like amphibians, reptiles are "cold blooded," meaning that they have but little ability to regulate their body temperature. Reptiles achieve more of such regulation than do amphibians, but to a considerable extent body temperature fluctuates with fluctuations of the surrounding temperature.

Most modern amphibians lack scales on their skin, while reptiles have coverings of horny scales. This difference in body covering aids reptiles in living in drier habitats than are possible for amphibians, since the scaly covering decreases water loss by evaporation from the surface of the body. It is noteworthy that when scales are present in amphibians, as they were in labyrinthodonts and are in reduced form in the modern limbless caecilians, they are of the bony type characteristic of fishes. Apparently such scales were inherited from the crossopterygian ancestors of amphibians but have been lost by most modern representatives of the latter. Horny scales of the type characterizing the surface of reptilian skin formed a "new" evolutionary development.

Reptiles have larger brains than have amphibians, the enlargement of the cerebral hemispheres in particular being a portent of better things to come.

Reptiles differ from modern amphibians by having one occipital condyle, the bony knob by which the skull is articulated to the first vertebra of the backbone. Modern amphibians have two occipital condyles, but most labyrinthodonts had only one.

The cotylosaur reptiles are of greatest interest to us because they were the ancestors of higher reptiles and, indeed, the distant ancestors of birds and mammals. During the Permian and the early part of the Triassic (Table 8.1, p. 146) the cotylosaurs and their immediate descendants formed a diversified group of reptiles. A few Permian reptiles were surprisingly specialized. One of the commonest, *Dimetrodon*, is sometimes called a "finback" because of the enormous elongation of the neural spines projecting up from its backbone (Fig. 10.3, pelycosaurs, p. 186). Too slender to serve for protection, these spines apparently supported a membrane that stretched down the back like an enormous fin. But of what use to a land animal is a fin? Speculations are as varied as they are ingenious; perhaps the best idea is that the membrane served in connection with control of body temperature, since it presented a considerable area of skin to the surrounding air (Colbert, 1955).

THERAPSID REPTILES *Dimetrodon*, the Permian reptile just mentioned, was one of the synapsid reptiles (p. 185), the group to which the THERAPSID or mammal-like reptiles belonged. These latter were abundant in the second half of the Permian, forming a diversified group and foreshadowing most of the distinguishing characteristics of the skeleton of mammals, their descendants. The limbs were better developed than those of previous reptiles—not so sprawled out at the sides of the body (Fig. 9.22) but rather brought more directly under the body for more efficient support and more rapid locomotion. While reptilian teeth are typically simple cones, therapsids developed teeth resembling the incisors, canines, premolars, and molars of mammals (Fig. 9.24). Like mammals, later ones (Triassic, p. 146) had two occipital condyles in place of the single condyle possessed by other

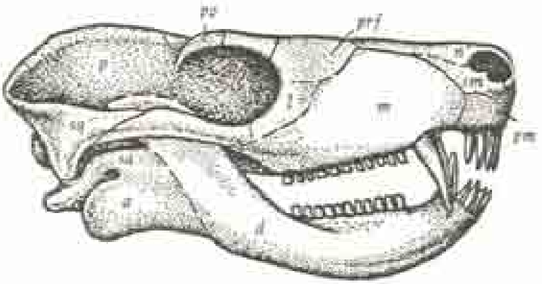


Fig. 9.24. Skull of a therapsid reptile from the Triassic, *Bauria*, lateral view. *a*, angular; *d*, dentary; *l*, lacrimal; *m*, maxilla; *n*, nasal; *pm*, premaxilla; *po*, postorbital; *prf*, prefrontal; *sa*, surangular; *sm*, septomaxillary; *sq*, squamosal. (After Broom and Boonstra; from Romer, A. S. *Vertebrate Paleontology*. Copyright © 1933, 1945, and 1966 by The University of Chicago. Used by permission of the University of Chicago Press.)

reptiles. Compared to other reptiles, they had a smaller number of bones in the skull, approaching the mammalian number. The pineal opening, the site of the third or pineal eye in many reptiles, eventually disappeared. The opening in the temporal region of the skull posterior to the eye (temporal fenestra) was arranged as it is in mammals.

The lower jaw of reptiles consists of several bones fastened together, whereas the mammalian lower jaw consists of a single pair of bones, the right and left DENTARIES. In therapsids of Triassic times the dentaries formed most of the jaw, the other bones being reduced in size (Fig. 9.24). The secondary or "hard" palate separating the mouth cavity from the nasal cavity above it was present in therapsids, as it is in mammals.

(In the next chapter we shall continue our account of the evolution of mammals from therapsids.)

PLANTS

Although this book is chiefly concerned with the evolution of animals, brief attention to the evolution of plants is appropriate. Our earlier discussion (Chap. 7) emphasized the dependence of animals on plants for food supply, either directly or indirectly when carnivores eat herbivores. Animal life as we know it would be impossible without plants.

Aside from bacteria, which are sometimes considered plants, the first plants were the blue-green algae. As we have seen (p. 152), they existed at least two billion years ago. They consist of single cells or of cell colonies; the cell structure is very simple. More complex cellular structure is seen in the green algae, which may have arisen from common ancestors with the blue–greens, probably in Precambrian times. The green algae have existed at least from early Paleozoic times. They are regarded as the ancestors of the higher plants.

Fragmentary fossils indicate that land plants were probably living in the Cambrian period, though the "earliest undisputed vascular plants are found in rocks of Silurian age" (Delevoryas, 1962). Vascular plants have a conducting system for transporting fluids throughout the plant. Clearly such a system is essential if a plant is to live out of the water and rise above the ground. The first vascular plants were very simple, consisting of little more than a system of branching stems, without roots and with no true leaves (e.g., *Psilophyton*, Fig. 9.25). Plants with true leaves and roots also are known from the Silurian (the Lycopsida); probably they evolved from the simpler plants just mentioned. Evidently plant evolution was relatively rapid at this time, for at least in the later part of the Devonian period plants were large and abundant enough to form actual forests.

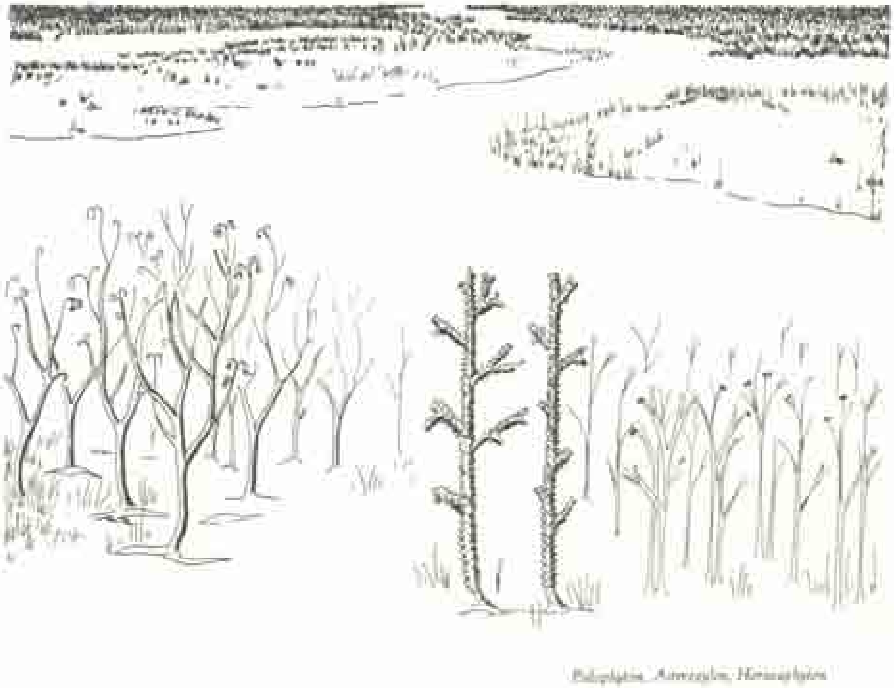


Fig. 9.25. Some of the first land plants. (From Stirton, R. A., *Time, Life, and Man*, New York, John Wiley & Sons, 1959; reprinted with permission.)

A Devonian forest differed greatly from a modern one, however. Ferns and fernlike plants were abundant, some of them growing to the size of trees. Plants considered seed ferns were also present, although no actual seeds have been found. A seed is an undeveloped plant consisting essentially of an embryo together with its food supply (endosperm) enclosed within a seed coat. Seeds enable a plant species to survive unfavorable climatic conditions, such as winter temperatures, and form a ready means of plant dispersal. So the development of the seed habit was an important milestone in plant evolution. Some of the seed ferns reached a height of more than 40 ft. and had a trunk diameter of three feet.

The Mississippian and Pennsylvanian periods are frequently grouped together under the name Carboniferous. The name refers to the great deposits of coal found in Pennsylvanian strata. In Pennsylvanian times vast expanses of lowland were but slightly elevated above sea level and hence were perennial swamps. In these swamps, encouraged by a mild climate, luxuriant plant growth flourished whose carbon later became preserved as coal. If a human observer had been present he would have missed our deciduous trees (such as maple, beech, and poplar). He would have seen varied conifers and coniferlike trees, although our familiar pines and firs had not yet appeared. Ferns would have looked familiar to him, though he might have been surprised by the sight of ferns with fronds five or six feet long and trunks 50 ft. high. Tree ferns still live in tropical rain forests, however. The largest trees, and among the most common ones, were the scale trees, so-called because the surface of the bark had a pattern resembling the pattern of scales on a snake's skin. The patterning was produced by scars left by the bases of closely set leaves. In one of the commonest genera, *Lepidodendron,* heights of 100 ft. and trunk diameters of six feet were attained. Relatives of our modern *Equisetum* (horsetails), some of them giant tree-like forms, added to the luxuriant plant growth destined for conversion into coal.

The Permian period saw marked changes in vegetation, connected with the creation of upland conditions through elevation of the land. Swamps became restricted in area, and much of the luxuriant vegetation of the Carboniferous disappeared, for example, the giant scale trees and the tree-like relatives of *Equisetum.* Smaller herbaceous relatives survived. Conifers became more abundant. Ginkgo trees were present, much as they are today.

In our brief account we have not attempted to trace evolutionary sequences among the land plants. It might be tempting to say that the earliest ones (such as *Psilophyton,* Fig. 9.25) gave rise to the ferns, which in turn gave rise to the seed ferns, which were ancestral to more advanced seed-forming plants, including the angiosperms (flowering plants) themselves. But such a statement would be an oversimplification, mainly unsupported by fossil evidence and posing technical difficulties at every point. Plant life presents such a profusion of variety that tracing ancestral lines is most difficult. But as the Paleozoic advanced there occurred plants representing *levels* of structure and organization that must have characterized ancestral forms. For example, the seed ferns had some of the characteristics of ferns and some of the characteristics of gymnosperms (such as cycads and conifers). Seed ferns tell us something of how seed formation began even though they may not have been the actual ancestors of more advanced types of seed plants.

Very much as with land animals, the evolution of land plants has been a story of increasing emancipation from life in the water. We have noted the appearance of a vascular system for conveying fluids to all parts of tall plants. Increasing adaptation to life on land brought other changes—none more striking than those connected with reproduction. At first sperm cells had to reach ova by swimming through a film of water. Eventually the male sexual form (male gametophyte) became a pollen grain, enclosed, protected, and capable of wide dispersal, as by wind and insects. The female gametophyte became a seed, at first not enclosed within an ovary (gymnosperms) and later protected in this manner, as in angiosperms (see Cronquist, 1961, p. 778). Angiosperms themselves seem not to have appeared until Mesozoic times.

References and Suggested Readings

Barghoorn, E. S., and J. W. Schopf, "Microorganisms from the late Precambrian of central Australia," *Science, 150,* 337–339 (1965).

Barghoorn, E. S., and J. W. Schopf, "Microorganisms three billion years old from the Precambrian of South Africa," *Science, 152,* 758–763 (1966).

Carpenter, F. M., "Fossil insects," in *Insects. The Yearbook of Agriculture 1952,* Washington, D.C., United States Department of Agriculture, pp. 14–19.

Cloud, Jr., P. E., "Significance of the Gunflint (Precambrian) microflora," *Science, 148,* 27–35 (1965).

Colbert, E. H., *Evolution of the Vertebrates,* New York, John Wiley, 1955.

Cronquist, A., *Introductory Botany,* New York, Harper & Row, 1961.

Delevoryas, T., *Morphology and Evolution of Fossil Plants,* New York, Holt, Rinehart & Winston, 1962.

Delevoryas, T., *Plant Diversification,* New York, Holt, Rinehart & Winston, 1966.

Dunbar, C. O., *Historical Geology,* 2nd ed. New York, John Wiley, 1960.

Engel, A. E. J., B. Nagy, L. A. Nagy, C. G. Engel, G. O. W. Kremp, and C. M. Drew, "Alga-like forms in Onverwacht Series, South Africa: Oldest recognized lifelike forms on earth," *Science, 161,* 1005–1008 (1968).

Hussey, R. C., *Historical Geology,* 2nd ed. New York, McGraw-Hill, 1947.

Millot, J., "New facts about coelacanths," *Nature, 174,* 426–427 (1954).

Millot, J., "First observations on a living coelacanth," *Nature, 175,* 362–363 (1955).

Moore, R. C., *Introduction to Historical Geology,* 2nd ed. New York, McGraw-Hill, 1958.

Raymond, P. E., *Prehistoric Life,* Cambridge, Massachusetts, Harvard University Press, 1939.

Romer, A. S., *The Vertebrate Story,* Chicago, University of Chicago Press, 1959.

Romer, A. S., *Vertebrate Paleontology,* 3rd ed. Chicago, University of Chicago Press, 1966.

Romer, A. S., "Major steps in vertebrate evolution," *Science, 158,* 1629–1637 (1967).

Schopf, J. W., E. S. Barghoorn, M. D. Maser, and R. O. Gordon, "Electron microscopy of fossil bacteria two billion years old," *Science, 149,* 1365–1367 (1965).

Simpson, G. G., *The Meaning of Evolution,* 2nd ed. New Haven, Yale University Press, 1967.

Smith, J. L. B., *The Search Beneath the Sea. The Story of the Coelacanth,* New York, Holt, Rinehart & Winston, 1956.

Stirton, R. A., *Time, Life, and Man,* New York, John Wiley, 1959.

Tilton, G. R., and S. R. Hart, "Geochronology," *Science, 140,* 357–366 (1963).

Ulrych, T. J., "Oceanic basalt leads: a new interpretation and an independent age for the earth," *Science, 158,* 252–256 (1967).

10

Evolution as Seen in the Geologic Record: Mesozoic Era

THE 160 MILLION years or more comprising the Mesozoic era are sometimes called the "age of reptiles," since during much of this time the group of reptiles called dinosaurs held undisputed sway over living things on the surface of the earth while other reptiles dominated the sea and still others the air.

PLANTS

The Mesozoic also sometimes is called the "age of cycads" because of the prominence of cycadlike plants throughout most of the era. Modern cycads, relatively few in number of kinds, resemble small tree ferns and are sometimes mistaken for small palms by people who are not botanists. Cycadlike plants existed during the latter part of the Paleozoic, probably having arisen from seed ferns, but became much more abundant in Mesozoic forests.

In the earlier portions of the Mesozoic cycadlike plants, gingkos and conifers were most prominent. The presence of flowering plants (angiosperms, p. 179) is suggested by fossil impressions of palmlike leaves, but the fossils have not yet revealed the presence of flowers. During Lower Cretaceous times the angiosperms became well established and thereafter spread rapidly over the earth to become the dominant group they have remained to this day.

CULMINATION OF CEPHALOPODS

AMMONITES Ammonites were the dominant invertebrates of Mesozoic seas. We recall that they first appeared in the Devonian (p. 159), probably as descendants of the nautiloids, which had existed from Ordovician times (p. 158). The nautiloids were characterized by straight or smoothly curved suture lines formed by junctures of the septa with the side wall of the shell (Fig. 9.7, p. 159). Ammonites, on the other hand, had suture lines of some complexity. The Devonian ammonites (goniatites) had suture lines with a "loop-and-saddle" configuration (Fig. 9.8, p. 160). Their descendants in later periods of the Paleozoic retained suture lines of comparable complexity. The Mesozoic, however, saw an "outburst" of ammonite evolution, accompanied by great increase in complexity of suture lines. More than 6000 species of ammonites have been described from Mesozoic deposits. Most of these were relatively small, with shell diameters averaging not more than four inches. Yet some Mesozoic ammonites attained large size; shell diameters of five feet were not uncommon, and some species were ten feet in diameter.

For the most part each individual turn or volution of the coiled shell was high and narrow in cross section. Lightness of structure characterizing many ammonite shells suggests that their inhabitants were active animals, perhaps good swimmers. A variety of knobs, spines, and ridges ornamented shells of a number of species. Many had a trapdoor-like arrangement (operculum) by which the opening of the shell could be closed when the body and tentacles were completely withdrawn into the shell. But in numerous ways the most remarkable feature of Mesozoic ammonites was the complexity of fluting of the margins of the septa. The intricacy of these lines suggests the tracery of frost patterns on a windowpane or the outlines of a fern frond (Fig. 10.1).

The Jurassic period (Table 8.1, p. 146) saw the culmination of the

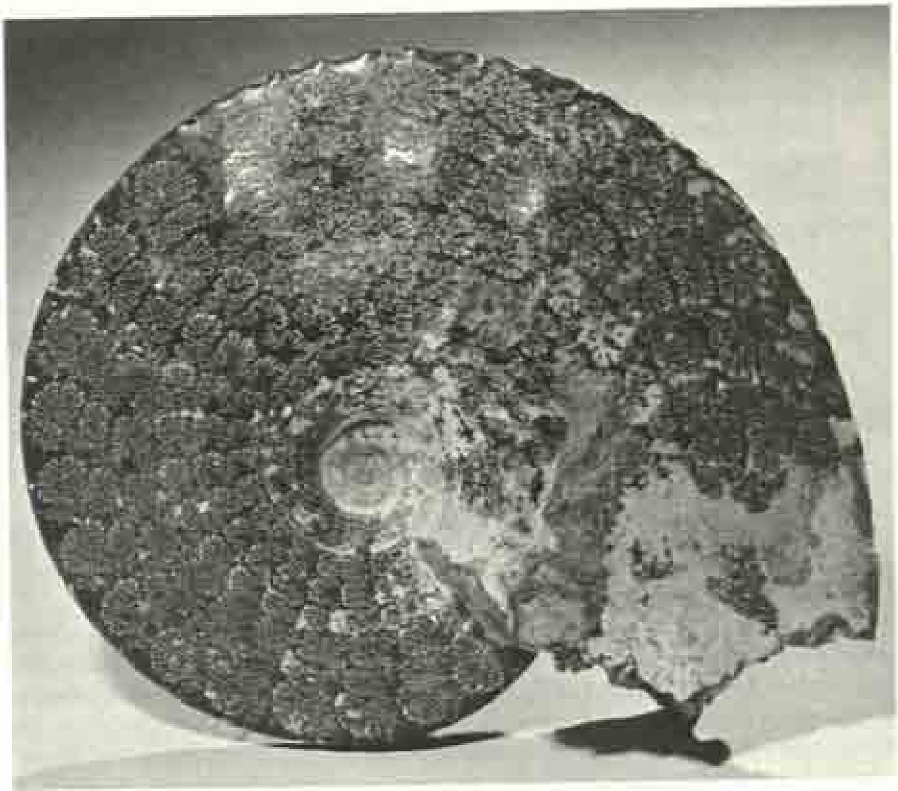


Fig. 10.1. Ammonite shell, showing complex suture lines. (Courtesy of Ward's Natural Science Establishment, Inc., Rochester, N. Y.)

ammonites. They continued into the Cretaceous in diminished numbers. During the later stages of their evolution bizarre shell forms occurred. Some shells showed a partial or complete tendency not to coil. Depending upon the degree of this tendency, loosely coiled, bent, or straight shells resulted. Some shells showed coiling of the first portion to be formed, followed by subsequent formation of a straight shell section. No ammonites survived the close of the Mesozoic.

We should note that the more conservative group of cephalopods, the nautiloids, did not share the extinction of their relatives the ammonites. We recall that the nautiloids were the first cephalopods to appear (p. 158); they are still represented by a few species dwelling in modern seas, including the nautilus commonly known as the pearly nautilus (Fig. 9.6, p. 158).

BELEMNITES The modern squids and octopi had a host of Mesozoic relatives, the belemnites. In general appearance they resembled the

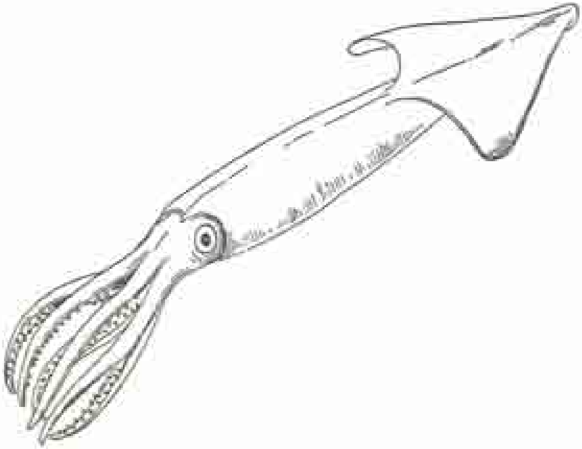


Fig. 10.2. Belemnite, restored; length 5 or 6 feet. (After *Historical Geology* by R. C. Hussey. Copyright 1944, 1947 by the McGraw-Hill Book Company, Inc. Used with permission of McGraw-Hill Book Company.)

modern squid (Fig. 10.2). Their cigar-shaped internal skeletons are extremely abundant in Mesozoic deposits. They ranged in length from a few inches to five or six feet. Fortunate occurrence of fossils having the outlines of the body indicated by a carbonized film informs us that there were six tentacles and that the latter were provided with hooks, in place of the sucking disks possessed by modern squids. Remnants of the "ink" by means of which belemnites, like modern squids, formed a "smoke screen" to facilitate escape are preserved with rare fossils.

The internal skeletons of belemnites were divided into chambers suggestive of those of the uncoiled nautiloids (Fig. 9.7, p. 159) that were probably their ancestors. There are indications that the internal skeleton was a remnant of an external, chambered shell possessed by nautiloid, or possibly ammonoid, ancestors.

INSECTS

By the beginning of the Mesozoic the insect fauna had changed markedly from that found in the Permian (pp. 163–164). Most of the orders not now found had already become extinct. By Jurassic times the insects were "so modern that if we had a collection of Jurassic species pinned in the usual way, it would not look very different from our present-day collections, except that there would probably be no flower insects, such as the bees and syrphid flies" (Carpenter, 1952). It is probable that with the appearance of flowering plants in Cretaceous times such flower-visiting insects developed. The finding of two worker ants in amber of Upper Cretaceous age indicates that social insects were then in existence (Wilson *et al.*, 1967). Interestingly, these specimens indicate the probability that ants evolved from nonsocial wasps.

Looking ahead into the Cenozoic, we note that the insects were all of modern types. In some groups even the *species* seem to have been the same as those existing today. Other groups have undergone greater evolutionary change during these last 63 million years.

EVOLUTION OF DINOSAURS AND THEIR RELATIVES

On preceding pages we traced the rise of land-dwelling vertebrates from crossopterygian fishes. We noted that the immediate descendants of the latter were the labyrinthodont amphibians that, in turn, gave rise to the cotylosaur reptiles. All this occurred before the beginning of the Mesozoic. As noted on page 175, cotylosaurs are important as the ancestors of higher reptiles (Fig. 10.3).

The cotylosaurs had skulls solidly roofed in the region back of the eyes, the temporal region. From the cotylosaurs arose several lines of descendants. The THERAPSIDA or mammal-like reptiles have already been mentioned (p. 175); they had a single temporal fenestra—an opening on each side, placed posterior to the eye and rather widely spaced from the midline of the skull. Therapsid and other reptiles so characterized are classed together as SYNAPSIDA (Fig. 10.4).

Some other lines of reptiles have two temporal fenestrae on each side of the skull—one near the midline, the other more lateral in position (Fig. 10.4). This condition is called diapsid. Among the diapsids the ARCHOSAURIA are of greatest interest to us. This group includes, among others, thecodonts, dinosaurs, flying reptiles, and crocodiles.

THECODONTS

Triassic THECODONTS were the direct ancestors of the dinosaurs (Fig. 10.3). Most of the thecodonts were small reptiles. They had narrow skulls that lacked a pineal opening but had the diapsid characteristic of two temporal openings on each side. The most distinctive characteristic of these reptiles, however, lay in their method of locomotion. Instead of walking or running on all four legs, as a dog does, many adopted a bipedal (two-footed) type of locomotion, running on the two hind legs as do many birds, e.g., the robin and the ostrich. The hind legs were elongated, forming a support upon which the body was balanced as on a fulcrum (Fig. 10.3). The body projected forward from this fulcrum, its weight counterbalanced by a long tail projecting backward. The forelimbs, freed from locomotor duties, were available for use in grasping and handling. Since all the weight of the body was

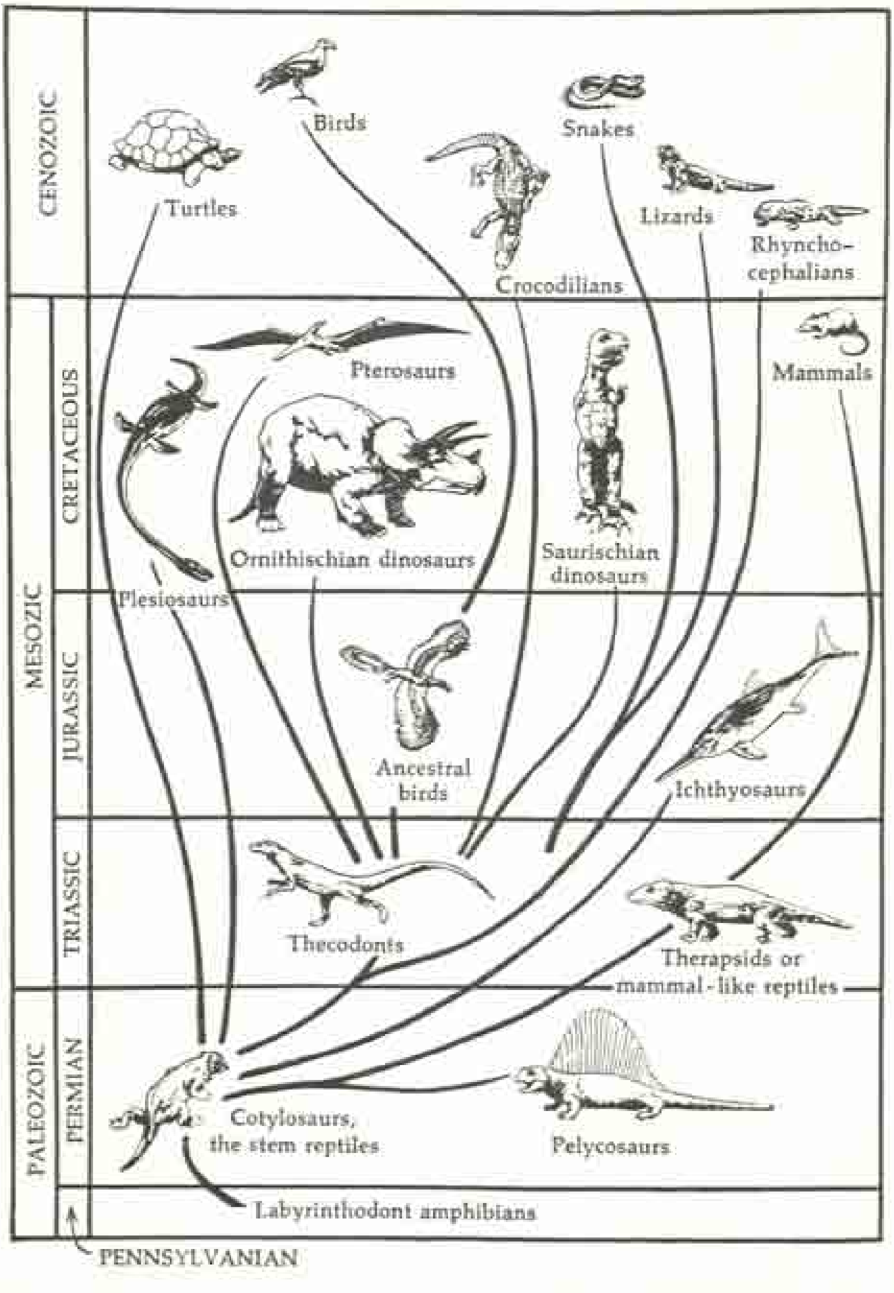

CENOZOIC
MESOZOIC
CRETACEOUS
JURASSIC
TRIASSIC
PALEOZOIC
PERMIAN
PENNSYLVANIAN
Birds
Snakes
Turtles
Lizards
Rhyncho-cephalians
Crocodilians
Pterosaurs
Mammals
Ornithischian dinosaurs
Saurischian dinosaurs
Plesiosaurs
Ancestral birds
Ichthyosaurs
Thecodonts
Therapsids or mammal-like reptiles
Cotylosaurs, the stem reptiles
Pelycosaurs
Labyrinthodont amphibians

Fig. 10.3. Family tree of reptiles. (From *The Dinosaur Book* by E. H. Colbert. Copyright 1945, 1951 by the American Museum of Natural History. Used with permission of the author and McGraw-Hill Book Company.)

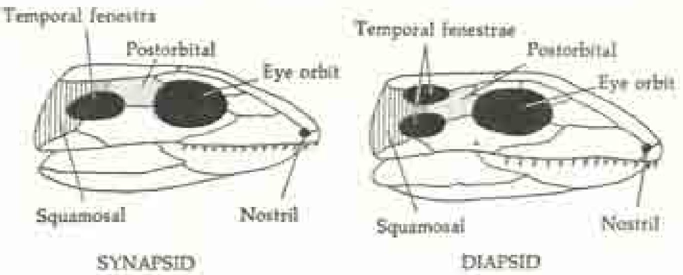


Fig. 10.4. Basic structural plans of the skulls of Synapsida and Archosauria, the latter having diaspid skulls. Note the single temporal fenestra in the synapsid skull, the two temporal fenestrae in the diapsid skull. (Redrawn from *The Dinosaur Book* by E. H. Colbert. Copyright 1945, 1951 by the American Museum of Natural History. Used with permission of the author and McGraw-Hill Book Company.)

concentrated on the hind legs, the attachment of the latter to the body was of necessity greatly strengthened. This involved strengthening of the pelvic girdle and of its attachment to the vertebral column, as well as the development of a more perfect ball-and-socket joint for attachment of the leg to the pelvic girdle. The legs no longer sprawled broadly at the sides of the animal, as they had in many earlier reptiles, but were placed well under the body, with knees turned forward, a position better calculated for efficient support of weight.

The body form resulting from this adaptation of the thecodonts for a bipedal gait provides the key to an understanding of dinosaur structure. The inheritance from thecodont ancestry was never completely obliterated, even in those dinosaurs which became huge in size and returned to a four-footed or quadrupedal locomotion. The thecodont body plan is, as Colbert (1951) has said, "the blueprint to dinosaurian body form."

ORDERS OF DINOSAURS The dinosaurs arose from thecodonts in the Triassic and continued as the dominant land animals throughout the remainder of the Mesozoic. In reality the dinosaurs did not constitute a single group; they were divided into two great orders, the SAURISCHIA and the ORNITHISCHIA. These names refer to the most clear-cut distinction between the two: the structure of the pelvic girdle. The Saurischia retained a triradiate arrangement of the pelvic bones similar to that of their thecodont ancestors (Fig. 10.5). The ILIUM was the bone attaching the girdle to the vertebral column. To the ilium attached two bones: the PUBIS, extending ventrally and anteriorly, and the ISCHIUM, extending ventrally and posteriorly (Fig. 10.5). The socket (acetabulum) for the head of the femur was located at the junction of these three bones. Since

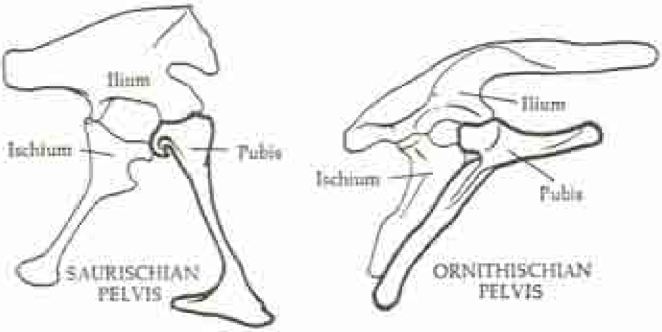


Fig. 10.5. Pelvic girdles of saurischian and ornithischian dinosaurs. (From *The Dinosaur Book* by E. H. Colbert. Copyright 1945, 1951 by the American Museum of Natural History. Used with permission of the author and McGraw-Hill Book Company.)

the ischium and pubis on one side of the body were usually attached to the corresponding bones of the other side, a firmly braced tripod for attachment of the legs to the body was achieved.

The pelvic girdle of the Ornithischia differed from that of the Saurischia mainly in the structure of the pubis. This bone possessed two prongs (Fig. 10.5), one extending anteriorly and the other posteriorly and ventrally, parallel to the ischium. The arrangement of the posterior prong resembled that of the pubis in birds, hence the name Ornithischia (bird hips).

SAURISCHIA The Saurischia include the dinosaurs most like their thecodont ancestors. These are the THEROPODA, which, like the thecodonts, were carnivorous and bipedal. They ranged in size from small animals to *Tyrannosaurus,* the largest carnivorous land animal we know (Fig. 10.6). This Mesozoic menace was about 47 ft long and 19 ft tall as he stood on his tremendous hind legs. The forelegs were tiny in proportion to the eight- to ten-ton bulk of the creature; each foreleg retained but two functional digits, armed with hooked claws. The lower jaw was hinged to the huge skull in a manner to give the animal a mouth of inordinate gape. The jaws were armed with rows of pointed teeth, some of them six in. long. This enormous engine of destruction was obviously well equipped to prey upon its giant herbivorous contemporaries.

The largest herbivorous dinosaurs belonged to a second division of the Saurischia, the SAUROPODA. These creatures departed from the characteristics of their thecodont ancestors by returning to a four-footed or quadrupedal locomotion and modifying the conical teeth of their carnivorous ancestors. Despite the return to quadrupedal locomotion, however, the forelegs of most of them remained shorter than the hind

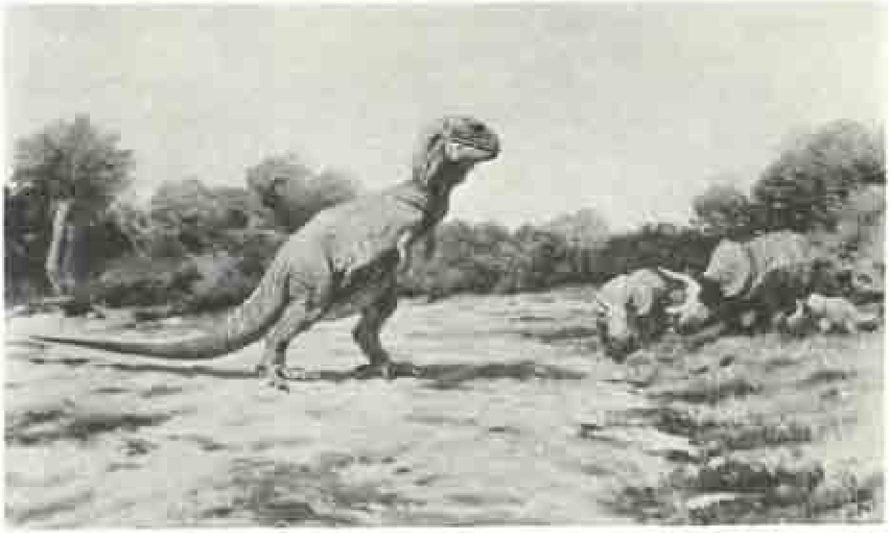


Fig. 10.6. *Tyrannosaurus* attacking the horned dinosaur, *Triceratops*. (Restorations by Charles R. Knight. Courtesy of the American Museum of Natural History.)

ones—a telltale trace of their thecodont ancestry. The heads of sauropods were absurdly small for animals of such great bulk. The teeth were reduced in size and number. This relatively ineffectual dental armament suggests dependence upon a soft type of water vegetation for food. Indeed, it is thought that these giants spent much of their lives in lagoons and swamps. The nostrils of some of them were located high up on the head, seemingly to make breathing possible while the mouth was engaged in underwater feeding. Also, the bulk was so great that it is difficult to see how the legs could have furnished adequate support, for protracted periods of time, without the aid of buoyancy provided by surrounding water. The weight of an animal varies in proportion to the cube of its length, while the strength of a pillarlike leg increases in proportion to its cross section, which increases only by squares. Thus, as Romer (1966) has pointed out, if a reptile doubles its length its weight is increased about eight times while the strength of its legs is increased but four times. The largest species of sauropods had weights ranging from 30–50 tons. It seems that much of the support for this weight must have been supplied by water in which the giants spent the greater portion of their lives.

Brontosaurus, one of the largest dinosaurs, reached a length of about 67 feet and weighed some 30 tons. Much of the length is attributable to the long neck and tail (Fig. 10.7). The small head contained a

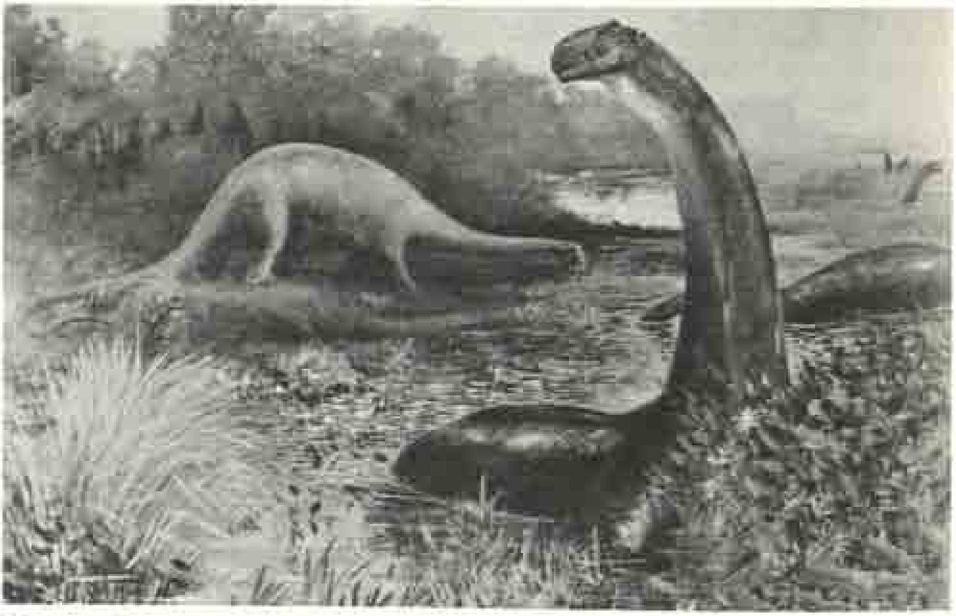


Fig. 10.7. *Brontosaurus,* one of the largest of the dinosaurs. (Restoration by Charles R. Knight. Courtesy of the American Museum of Natural History.)

brain disproportionately small even for a reptile, a class not noted for its brain development.

ORNITHISCHIA Whereas the Saurischia had their major period of expansive evolution during Jurassic times, living on into the Cretaceous as indicated in Fig. 10.3, the other great order of dinosaurs had their greatest period of development during the Cretaceous. The Ornithischia were on the whole more specialized than were the Saurischia. One indication is seen in the fact that the Ornithischia departed from the thecodont pattern of pelvic structure, while the Saurischia retained this pattern (Fig. 10.5).

All of the Ornithischia were herbivorous. Their teeth were somewhat leaf-shaped, with serrated edges. Most of the Ornithischia lacked teeth in the front of the mouth. Presumably this toothless region was covered with a horny beak somewhat like that possessed by turtles.

A majority of the Ornithischia forsook the bipedal gait of their thecodont ancestors, though in most of these secondarily quadrupedal forms the disproportionate length of the hind legs betrayed their ancestry. Among the bipedal ornithischians the forelegs were never so greatly reduced in size and function as they were among the saurischian bipeds.

The Ornithischia fall naturally into four groups or suborders:

1. The ORNITHOPODA include all the bipedal Ornithischia. Best known among them are the duckbilled dinosaurs. About 30 ft in length, these dinosaurs had long, powerful hind legs and somewhat reduced forelegs. The toothless beak was flattened and widened to form an oversized duckbill, probably used for underwater feeding much as a duck employs its bill. Mummies show us that the skin was covered with small scales and that there was webbing between the toes, indicative of life in swampy regions or along the margins of pools or lakes.

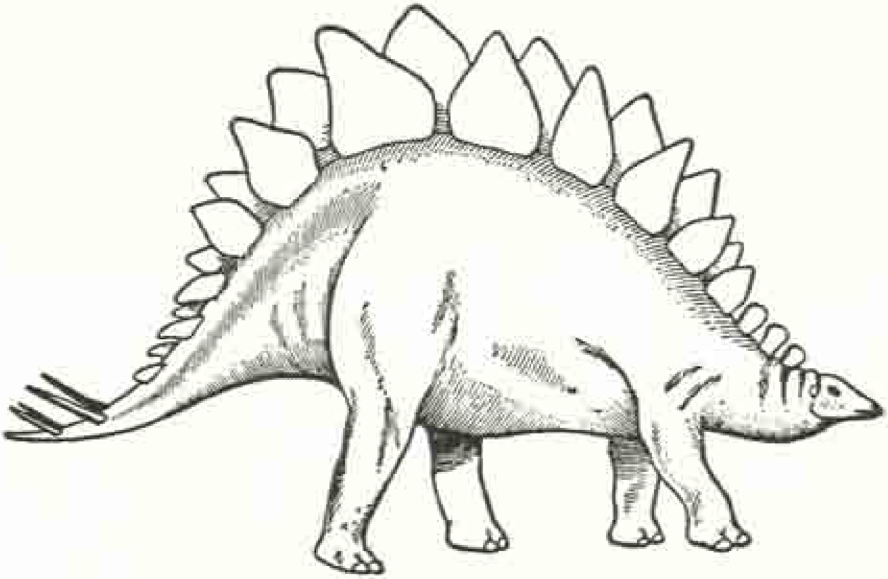


Fig. 10.8. *Stegosaurus*, the plated dinosaur; length about 20 feet. (From Lull, R. S., *Organic Evolution*, rev. ed. Copyright 1945 by Richard S. Lull. Used by permission of The Macmillan Company.)

2. The STEGOSAURIA or plated dinosaurs possessed a double row of projecting plates down the back and spikelike spines on the tail (Fig. 10.8). We may imagine that the thrashing about of that tail must have afforded persuasive discouragement to carnivorous dinosaurs in search of prey. Although *Stegosaurus* was quadrupedal, bipedal ancestry had left its mark in the disproportionately short forelegs (Fig. 10.8). The skull was inordinately small, housing a brain about the size of a walnut. This in an animal bigger than an elephant! In the region of the hind legs was found an enlargement of the spinal cord about 20 times as large as the brain. It would seem that the brain must have served principally in connection with the sense organs of the head and with the activities

of the small, weakly toothed mouth, leaving coordination of the remainder of the body to the spinal cord. Many other dinosaurs also had sacral enlargements of the cord greater than their brains. The Mesozoic era is not memorable for intellectual activity.

3. The ANKYLOSAURIA were heavily armored dinosaurs somewhat reminiscent of turtles or of armadillos in the completeness of their armor plate. They have been called the "tanks" of the Mesozoic battlefield.

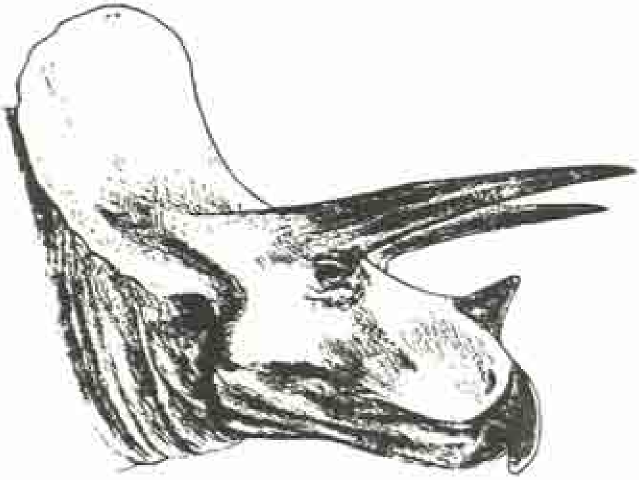


Fig. 10.9. Head of *Triceratops*, a giant horned dinosaur. Skull about 8 feet long. (Restoration by John C. Germann. From *The Dinosaur Book* by E. H. Colbert. Copyright 1945, 1951 by the American Museum of Natural History. Used with permission of the author and McGraw-Hill Book Company.)

4. The CERATOPSIA or horned dinosaurs owe their name to possession of a horn over each eye and a horn on the nose (Fig. 10.9). They possessed a parrotlike beak and a great frill of bone projecting backward over the neck. While this doubtless served to protect the neck, its principal function was probably to afford attachment for powerful muscles. The head in giant ceratopsians constituted an unusually large proportion of the body. The massive structure and armament of the "business end" of a horned dinosaur give us some conception of what was required for successful living in a world inhabited by such carnivores as *Tyrannosaurus* (Fig. 10.6).

The ceratopsians were the last dinosaurs to appear on the scene. Their entire evolution was confined to the second half of the Cretaceous period. We may note in passing that the famous dinosaur eggs that have received so much publicity were laid by a small, ancestral member of the group, *Protoceratops.*

EXTINCTION OF THE DINOSAURS For at least 140 million years the dinosaurs were "lords of all they surveyed." Then "suddenly," in the geologic sense, they all became extinct. Not one dinosaur fossil has ever been found in deposits more recent than those of Mesozoic age. Why this mass extinction of creatures that had been successful for so long?

This is one of the great unanswered questions of paleontology. As pointed out by Colbert (1965), the final disappearance was preceded by a long period during the late Cretaceous when the number of kinds of herbivorous dinosaurs was declining—perhaps a forewarning of things to come. But why did *no* dinosaurs (or ichthyosaurs or plesiosaurs or pterosaurs, see the following) survive into the Cenozoic? The climate was changing somewhat, but not very drastically—thus arguing against the opposed suggestions that either (1) high temperatures or (2) low temperatures, to which dinosaurs could not adapt, were at the basis of the extinction. Epidemics, the eating of dinosaur eggs by mammals, and harmful effects of radiation are among suggested reasons for the extinction. But none of the suggestions are adequate (see Colbert, 1965, Chap. 11, for a more complete discussion). Will we ever know the reasons? At present we can do no better than conclude with Colbert that this extinction "was complex in nature, the result of many subtle and interacting causes."

CONQUEST OF THE SEA Not all the reptiles of this golden age of reptilian life were dinosaurs. Several groups of reptiles returned to the sea for a home. Of these aquatic reptiles two are shown in Fig. 10.3: PLESIOSAURS and ICHTHYOSAURS. Both developed a somewhat fusiform body shape, but the plesiosaurs had long necks and tails while the ichthyosaurs had a fishlike absence of neck and a fishlike fin on the tail. The limbs of plesiosaurs were paddlelike; those of ichthyosaurs were more like the paired fins of fishes in external appearance. The ichthyosaurs even resembled fishes to the extent of developing a dorsal fin (Figs. 3.5, p. 30, and 10.3). Plesiosaurs probably swam rather slowly by an oarlike action of their limbs. Ichthyosaurs must have propelled themselves by undulation of the body, as does a fish (pp. 56–57), using the limbs as rudders. Thus the ichthyosaurs were much the more rapid and agile swimmers of the two, occupying the niche in Mesozoic marine life held by porpoises and dolphins in modern seas.

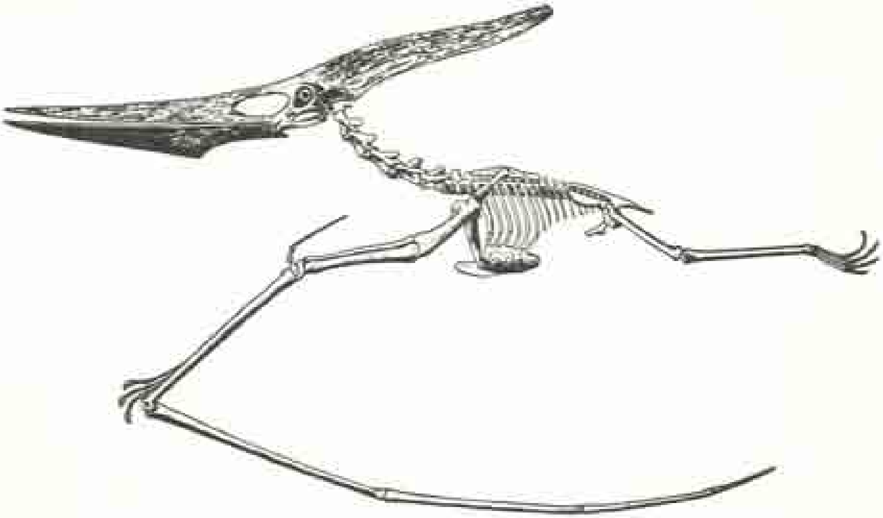


Fig. 10.10. The most specialized pterosaur, *Pteranodon*. (From Eaton, *Memoirs of the Connecticut Academy of Arts and Sciences*, 2 (1910), 1–38.)

CONQUEST OF THE AIR Another group of Mesozoic reptiles became adapted for flight. These were the PTEROSAURS (pterodactyls) descended like the dinosaurs from the thecodonts (Fig. 10.3). Pterosaurs developed membranous wings supported by a modification of the pentadactyl limb unlike that of either birds or bats (Fig. 3.1, p. 22). The fourth finger of the hand became greatly elongated, forming support for the front margin of the wing (Fig. 10.10). The first three fingers bore claws by which the creature could cling to rocks or to the limbs of trees. Pterosaurs had small bodies relative to wingspread (Fig. 10.10); this spread reached 27 ft in the largest species. The bones were hollow, and consequently light. The sternum or breastbone was relatively large, furnishing attachment for breast muscles connected to the wings. This motor mechanism was probably not of sufficiently great development to provide for strong and sustained flight. It is thought that pterosaurs used their wings largely in gliding and soaring, launching themselves, perhaps, from the tops of cliffs. The pterosaur brain was large for a reptile, the sense of sight being strongly developed, as in birds. Possibly pterosaurs were warm-blooded; it is difficult to see how a really cold-blooded animal could maintain the activity necessary for flight.

We may well note at this point that comparison of ichthyosaurs with fishes and dolphins (Fig. 3.5, p. 30), and of pterosaurs with birds and bats, presents some of the most beautiful examples available of that *convergent evolution* discussed in an earlier chapter (p. 31). It would be difficult to find a more fascinating aspect of evolution than that afforded by study of the variety of ways in which a given problem (e.g., flight) has been solved independently by differing groups of animals. Some solutions are better than others. Thus, it has been pointed out that the pterosaur wing, consisting of an unbroken expanse of membrane supported only along its outer edge, would not lend itself to agile maneuvering in flight. Also, a tear in it would be more disastrous than would a tear in a bat's wing, since the latter is supported by four elongated fingers instead of only one (Fig. 3.1, p. 22). As compared to the attainments of birds and bats, only partial success crowned pterosaur invasion of the air.

ORIGIN OF BIRDS

The thecodonts have claimed our attention as ancestors of the two orders of dinosaurs and of pterosaurs. Birds also arose during the Mesozoic from this same bipedal stock (Fig. 10.3). Indeed, the term "glorified reptiles" frequently applied to birds suggests the fact that they are similar to reptiles in many ways.

The principal distinguishing characteristic of birds is the possession of FEATHERS. But the structure and development of feathers reveal that they are modified reptilian scales. Birds are WARM-BLOODED, a condition, as mentioned above, that really is necessary if an animal is to be capable of sustained flight. Birds have an INSULATING BODY COVERING of feathers; this aids greatly in prevention of loss of heat from the body surface. Modern birds, like pterosaurs, have the light construction afforded by HOLLOW BONES. In flying birds the STERNUM or breastbone is greatly enlarged to provide anchorage for muscles operating the wings. We have seen that pterosaurs also showed development of this kind. Both birds and pterosaurs have, or had, "EYE BRAINS"—brains showing pronounced dominance of visual areas, with reduction of the portions connected with the sense of smell. Birds have a system of AIR SACS connected to the lungs. Mayr has suggested that these serve principally as an internal ventilating system, dissipating the heat generated by the vigorous metabolic activity necessary to flight. Birds have well-developed legs, with structure similar to that of the legs of some of the bipedal dinosaurs. Pterosaurs, on the other hand, had very weak legs. The wing surface composed of feathers is much more efficient, maneuverable, and readily repaired than was the flying mechanism of pterosaurs.

Discussions of evolution in former years frequently included mention of "missing links." The term was used in various senses but always included the idea of a form standing midway between two groups of

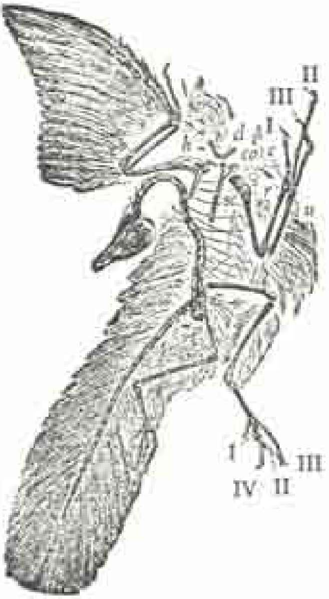


Fig. 10.11. *Archaeopteryx*, a Jurassic toothed bird. *cl*, clavicle; *h*, humerus; *sc*, scapula; *u*, ulna. (After Steinmann-Döderlein; from Guyer, M. F., *Animal Biology*, Harper & Row, 1948.)

animals now clearly separate from each other. In most cases such exactly intermediate forms have not been preserved to us, but the Jurassic bird *Archaeopteryx* forms a fortunate exception to this lack. This is clearly a bird, since the imprints of the feathers are preserved in the fossils (Fig. 10.11). Yet the skeleton was so reptilian that if the imprints of the feathers had not been preserved, the creature would probably have been classified as a small, bipedal dinosaur. Relative to body size the wings were small, and three of the digits of each hand persisted, armed with claws. Thus the forelimbs were probably used for climbing as well as for flight. Indeed, the small wingspread suggests that gliding from a height was a more probable activity than was sustained flight.

The tail was long, with a row of feathers along either side of the slender chain of vertebrae (Fig. 10.11), and clearly reminiscent of thecodont ancestry (Fig. 10.3). This tail is strikingly unlike that of modern birds. In them the bony portion of the tail is very short; the length of tail is due entirely to the length of feathers. Finally we may note that the jaws of these Jurassic birds, as well as the jaws of some Cretaceous birds, were equipped with teeth. In this respect again they resembled reptiles more than they did modern birds, since the latter are always characterized by toothless, horny beaks. It is interesting that the Jurassic birds did not possess the hollow bones characteristic of modern birds, on the one hand, and of pterosaurs, on the other. Apparently birds and pterosaurs, both descended from thecodonts, developed hollow bones independently and at widely differing times. Seemingly we have here another example of parallel evolution.

ORIGIN OF MAMMALS

It is fitting that our discussion of the Mesozoic conclude with the origin of the animals that were about to inherit the earth.

We noted (p. 175) the occurrence in the Permian period of therapsid or mammal-like reptiles. It will be recalled that these reptiles, especially the Triassic ones, approached mammalian structure in many ways (Fig. 9.24, p. 176), including the following: (1) teeth differentiated into incisors, canines, premolars, and molars; (2) two occipital condyles; (3) reduction in number of skull bones; (4) single temporal opening (fenestra) having boundaries similar to those of the mammalian temporal fenestra; (5) lower jaw in which the dentary bone was predominant; (6) presence of a secondary or "hard" palate; and (7) limbs arranged for more efficient locomotion than that characterizing most reptiles.

These therapsid reptiles are regarded as the ancestors of mammals (Fig. 10.3). The therapsids themselves were abundant in Triassic times but thereafter gradually declined in numbers. The earliest fossils regarded as mammalian are found in late Triassic deposits (Romer, 1967). Apparently, therefore, the transition from therapsids to mammals occurred at about that time.

Unfortunately the fossil record is most fragmentary at this point. Also, it is difficult to decide whether the remains that have been found are those of advanced therapsid reptiles or those of early mammals. This uncertainty is hardly surprising in view of the fact that the therapsids already had approached closely to mammalian structure. The problem arises as to where to draw the line between therapsid reptiles and mammals. The decision would be much easier if we knew more of these Triassic animals than is revealed by their skeletons. Did they have hair like a mammal? If so perhaps it was combined with scales—a condition still seen on the tail of a modern rat. Did they lay eggs, or were the young born as in a mammal? [The diagnostic value of this point is somewhat lessened by the fact that some other Mesozoic reptiles, e.g., ichthyosaurs, bore their young much as do mammals and by the fact that among presently living mammals, the monotremes (duckbilled platypus and spiny anteater) produce eggs much like those of reptiles.] Were they able to control the body temperature (warm blooded)? It is suspected that this ability developed gradually and may have been possessed by various Mesozoic reptiles. Were the young nourished with milk secreted by mammary glands of the mother? Since answers to these questions are denied us, or are largely inferential, we must rely mainly on conclusions based on the skeletons.

Special importance is placed upon the manner in which the lower jaw is hinged to the skull. We have seen that reptiles have several bones in each half of the lower jaw (p. 176). The dentary is the principal tooth-bearing bone, but the connection of the lower jaw to the skull is made by one of the other bones, the articular, which is hinged to the quadrate bone of the skull. In therapsid reptiles the bones other than the dentary became progressively reduced in size, while the dentary itself became progressively larger and extended back toward the squamosal bone of the skull [Fig. 9.24, p. 176; in this lateral view the quadrate is hidden by the squamosal (sq) and the articular bone of the lower jaw is posterior to the surangular (sa)]. Eventually the dentary became hinged to the squamosal, and the articular and quadrate bones, greatly reduced in size, lost their function of hinging the jaw and became the malleus and incus (hammer and anvil) of the chain of three little bones in the middle ear.

In summary, typical mammals have (1) the dentary hinging to the squamosal and (2) the articular and quadrate present in the ear but no longer taking part in jaw suspension. As Simpson (1959) has pointed out, these are related but somewhat separate criteria. Students of the subject differ in their emphasis upon one or the other criterion in deciding where to draw the line between therapsids and mammals. Interestingly, in some representatives of a group of Triassic animals, the tritylodonts, the articulation of the jaw was contributed to by all four bones: dentary, articular, quadrate, and squamosal. Thus these creatures were mammals by criterion one but not by criterion two. They were reptiles by criterion two but not by criterion one. (For further discussion see Simpson, 1959.)

This difficulty of distinguishing certain therapsid reptiles from mammals is highly significant. It arises from the existence of a series of transitional stages linking typical reptiles to typical mammals. People opposed to the idea of evolution sometimes maintain that the fossil record never shows transitional forms between one major group and another. Here we have a good example of just such a linking of two classes: Reptilia and Mammalia.

Evidence accumulates that several groups of therapsid reptiles gave rise to descendants that would be regarded as mammals by the criteria mentioned (Olson, 1959; Simpson, 1959). Some of the lines became extinct; one apparently led to modern monotremes and another to the PANTOTHERIA, the group usually regarded as ancestral to marsupials and placentals (see the following).

Undoubtedly mammals lived in the Jurassic, but they were not a prepossessing tribe compared to the ruling reptiles of the time. All of them were small, most of them of the sizes of mice and rats. One species approached the cat in size and apparently in carnivorous food habits, while one herbivorous species resembled a woodchuck in many ways. One hopeful portent for the future was presented by the brains of these early mammals. Although small and primitive, judged by modern standards, nevertheless the brains seem to have been a considerable improvement over the brains of reptiles.

Mammalian fossils of Cretaceous age are somewhat more abundant and complete than are those of Jurassic age. As we have noted, most of these Mesozoic mammals were small. They were potentially carnivorous, but the animals preyed upon were probably insects for the most part.

By the close of the Cretaceous the two main groups of mammals, the marsupials and the placentals, were in existence. These groups differ in many respects. The names suggest their differences in the reproductive process. The embryos of placental mammals undergo a relatively long period of development within the uterus of the mother, being nourished by the mother through the PLACENTA (Fig. 10.12). As noted previously (p. 58) blood vessels from the embryo pass through the umbilical cord to the wall of the uterus, where they come in close contact with the mother's blood. The embryonic blood vessels in this region give rise to a series of CHORIONIC VILLI; each of these villi is bathed in the blood of the mother, thereby providing a means for the ready interchange of oxygen, food, and waste products.

In marsupials, on the other hand, the placenta is absent or poorly developed. The young are born in an extremely immature, almost embryonic condition. They complete their development while housed in a pouch, or marsupium, on the abdomen of the mother. Marsupials also differ from placentals in a number of distinctive skeletal features.

The opossum is the only modern North American marsupial. Interestingly enough, marsupials similar to the opossum were living in the North America of Cretaceous times. Thus the opossum possesses a unique value in studies of mammalian evolution owing to its position as a "living fossil," giving us a glimpse of what Cretaceous mammals were like. In Australia, geographically isolated from the rest of the world from late Cretaceous times at least, marsupials were free from the com-

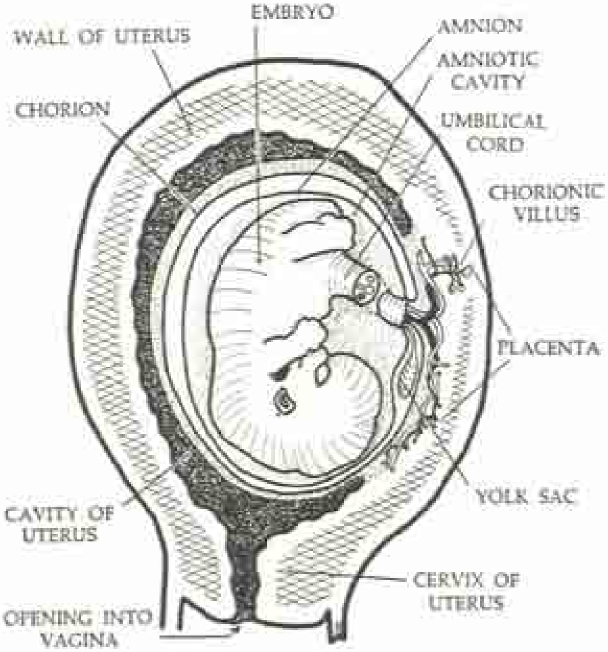

EMBRYO
WALL OF UTERUS
AMNION
AMNIOTIC CAVITY
CHORION
UMBILICAL CORD
CHORIONIC VILLUS
PLACENTA
YOLK SAC
CAVITY OF UTERUS
CERVIX OF UTERUS
OPENING INTO VAGINA

Fig. 10.12. Human embryo, with placenta and extra-embryonic membranes, in position in the uterus of the mother. (Drawn by Lyman S. Rowell.)

petition of placental mammals and evolved into a great variety of forms: kangaroos, wombats, bandicoots, koalas, and so on (see pp. 275–277).

Returning to the placentals, we note that development within the uterus increases the length of time available for embryonic development. This lengthened development may have been important in making possible the larger and more complex brains possessed by mammals, as compared to reptiles. With the larger brains came increased intelligence —the ability to learn and to modify behavior in the light of experience. Romer (1967) has suggested that the nursing of young mammals by their mothers provides a period for the training and teaching of the young. He stated: "In a sense, we can say that in the nursing habit we see the establishment of the world's first educational institution."

Like their ancestors, the first placentals were insect eaters. For that reason we classify them as members of the order INSECTIVORA. Moles and shrews are the most familiar modern members of this order. Early, relatively unspecialized insectivores are regarded as the ancestors from which other orders of placental mammals arose. We placed an insectivore in the center of our diagram of adaptive radiation among mammals (Fig. 3.4, p. 28).

While the majority of Cretaceous placentals were insect eaters, evidence is accumulating that evolutionary trends that were to lead during the Cenozoic to the evolution of the other orders were already beginning. Thus fossils regarded as those of a primitive primate and a very primitive ungulate (typical ungulates are hoofed mammals) of the type known as condylarths (p. 205) have been found in late Cretaceous deposits in Montana (Sloan and Van Valen, 1965; Van Valen and Sloan, 1965).

References and Suggested Readings

Carpenter, F. M., "Fossil insects," in *Insects. The Yearbook of Agriculture 1952*, Washington, D.C., United States Department of Agriculture, pp. 14–19.

Colbert, E. H., *The Dinosaur Book*, 2nd ed., New York, McGraw-Hill, 1951.

Colbert, E. H., *Evolution of the Vertebrates*, New York, John Wiley, 1955.

Colbert, E. H., *Dinosaurs. Their Discovery and Their World*, New York, E. P. Dutton, 1961.

Colbert, E. H., *The Age of Reptiles*, New York, W. W. Norton, 1965.

Lull, R. S., *Organic Evolution*, rev. ed., New York, Macmillan, 1945.

Olson, E. C., "The evolution of mammalian characters," *Evolution, 13* 344–353 (1959).

Romer, A. S., *The Vertebrate Story*, Chicago, University of Chicago Press, 1959.

Romer, A. S., *Vertebrate Paleontology*, 3rd ed., Chicago, University of Chicago Press, 1966.

Romer, A. S., "Major steps in vertebrate evolution," *Science, 158*, 1629–1637 (1967).

Simpson, G. G., "Mesozoic mammals and the polyphyletic origin of mammals," *Evolution, 13*, 405–414. (1959).

Sloan, R. E., and L. Van Valen, "Cretaceous mammals from Montana," *Science, 148*, 220–227 (1965).

Van Valen, L., and R. E. Sloan, "The earliest primates," *Science, 150*, 743–745 (1965).

Wilson, E. O., F. M. Carpenter, and W. L. Brown, Jr., "The first Mesozoic ants," *Science, 157*, 1038–1039 (1967).

11

Evolution as Seen in the Geologic Record: Cenozoic Era

ELEVATION OF THE Rocky Mountains, beginning in the Cretaceous, gradually changed the climate of North America and its topography. The continent attained nearly the outlines and general appearance it has today. Geologic changes during this era were largely connected with the wearing down of mountains, followed by their reelevation through regional uplift. These phenomena were particularly characteristic of western North America. Then, in the Pleistocene period, the face of the northern portions of the continent was altered by the action of great glaciers sweeping southward from arctic regions.

The Cenozoic era is commonly divided into two periods: TERTIARY and QUATERNARY. The Tertiary began some 63 million years ago. As shown in Table 8.1, (p. 146), it is divided into a series of epochs. These were of unequal length. The beginning of each is estimated to have occurred as follows (Kulp, 1961):

Pliocene: 13 million years ago
Miocene: 25 million years ago
Oligocene: 36 million years ago
Eocene: 58 million years ago
Paleocene: 63 million years ago

These epochs are represented by series of strata occurring in the order given and marked by progressive evolution of animals, particularly of mammals. Indeed, the Cenozoic is sometimes called "the age of mammals."

The Quaternary period includes two epochs: Pleistocene and Recent. The Pleistocene is sometimes called the "Ice Age" because of recurrent glaciations during it. It began two or three million years ago, estimates varying somewhat with the methods of measurement used (Ericson and Wollin, 1968; Fleischer *et al.*, 1965). The Recent epoch began with the retreat of the last glaciation, 10,000 years or more ago (see the following). The Quaternary is probably of greatest interest to us as the time during which man himself evolved.

CLIMATIC CHANGES AND PLANT DISTRIBUTION

During the first two epochs of the Cenozoic the climate of much of North America was mild. Much of the interior of the continent was a flat lowland enjoying a subtropical climate resembling that of Florida. Palm trees grew as far north as Minnesota and the Dakotas; crocodiles throve in these same regions. Figs and magnolias grew in Alaska. Temperate climates extended as far north as Greenland, where such trees as giant redwoods, beeches, and elms were found.

With the beginning of the Oligocene the climate became slowly cooler, particularly in the interior of the continent. Palms and large crocodiles disappeared from northern regions, though small alligators lived in Nebraska as late as Miocene times, along with plants similar to those found at present in our Gulf states. Local arid regions began to appear on the leeward side of newly elevated mountains. The moisture carried by westerly winds was condensed and precipitated as rain on the windward, western slopes of the mountains, as is the case today. The process culminated with the great regional uplift of the Cordilleran ranges in Pliocene and Pleistocene times. The widespread aridity of western North America followed that geologic occurrence.

Starting with Miocene times the aridity gave rise to the great plains, with their covering of grasses. As we shall see, the presence of this glassland played a decisive role in the evolution of horses, as well as of many other mammals.

The flora of the Miocene world was much like that of the world we see around us. In plant evolution the changes that have occurred since then are minor compared to the ones that occurred during earlier times (Cronquist, 1961).

The glaciation occurring in the Pleistocene has been mentioned. Actually there were four successive glaciations during this period. Four times glaciers centering around the Hudson Bay region swept down over the northern tiers of states, extending into Pennsylvania, southern Ohio, and Illinois. Such an Arctic animal as the musk ox ranged through Kentucky, Arkansas, and Texas. Each glaciation was followed by an interglacial period during which the climate in a given region was as mild as, if not milder than, it is today. The interglacial periods lasted for many thousands of years; the shortest is estimated to have been of 135,000 years' duration. Some 10,000 years are estimated to have elapsed since the last glaciation (Libby, 1956). Thus it may well be that we are at present living in an interglacial period, that the Recent period of our time chart (Table 8.1, p. 146) really forms part of the Pleistocene. The extensive ocean ice of the Arctic regions and the glaciers covering Greenland and the Antarctic continent remind us that glaciation is not far away. Indeed, it has been estimated that a lowering of average annual temperature by only 5° C would bring the ice sheets down upon us again. Will the glaciers return? Only our remote descendants will be able to answer that question with certainty.

MAMMALIAN EVOLUTION IN THE CENOZOIC ERA

Disappearance of the dinosaurs at the end of the Mesozoic left a clear field for mammalian expansion. We have noted the occurrence in Cretaceous times of both marsupial and placental mammals (p. 199). A few of the Cretaceous mammals persisted into the Paleocene, notably opposumlike marsupials and insectivores. We recall that the latter are the group of placental mammals from which the other orders of placental mammals are believed to have arisen. As we have seen (p. 201), evolution of some of these orders had already begun before the beginning of the Cenozoic. The carnivores (flesh eaters) and ungulates (hoofed animals) living at this time were quite unlike their modern relatives, however. Most of them belonged to groups that underwent a relatively rapid evolution during the Paleocene and Eocene and then disappeared. Thus they sometimes are called "archaic mammals" to distinguish them from the "progressive mammals," which were derived from some of the archaic forms and led to modern types of mammals. Some of the carnivores appear to have been ancestral to more progressive flesh eaters, but many of them, called CREODONTA, appear to have formed evolutionary sidelines (Romer, 1966). Many of the archaic herbivores are included in the order CONDYLARTHRA, "a truly basic stock from which many, at least, of the further ungulate orders may well have been derived" (Romer, 1966).

During the Paleocene and Eocene the archaic mammals had their brief period of ascendancy. Some of the archaic ungulates became quite large. *Uintatherium* (Fig. 11.1) with its curious horns was as large as a modern rhinoceros but was quite unlike the latter in structure. Among the archaic carnivores were some resembling modern wolves, weasels, cats, hyenas, and the like, but only superficially.

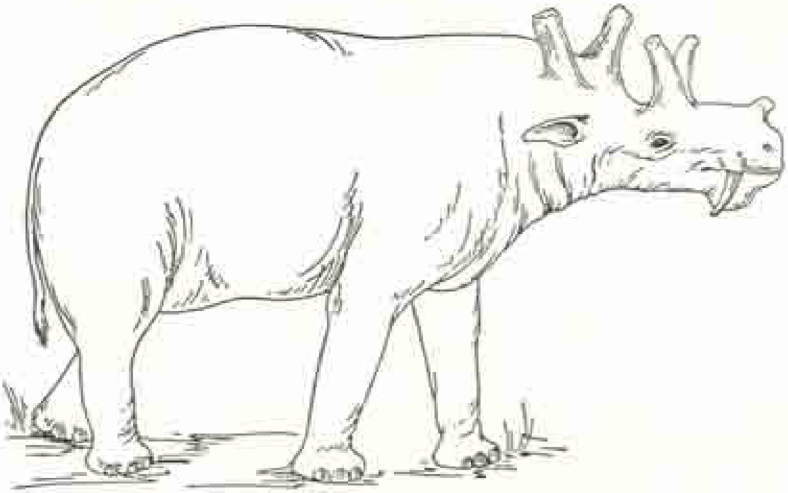


Fig. 11.1. *Uintatherium*, an archaic hoofed mammal. (After Osborn.)

The end of the Eocene saw the extinction of the archaic mammals. Apparently they were not able to compete successfully with the more progressive mammals developing around them—their own decendants in some cases.

Turning to the more progressive mammals, we find that the first rodents and first lagomorphs appeared late in the Paleocene. The beginning of the Eocene saw ungulates of the two orders existing today: Perissodactyla (odd toed) and Artiodactyla (even toed). Members of the Condylarthra were probably ancestral to these two orders. Indeed, representatives of most of the orders of mammals appeared in either the Paleocene or the Eocene, thus laying the foundations for evolution of these orders during succeeding periods of the Cenozoic. Within the orders evolutionary changes ran somewhat parallel courses. Ancestors in each were relatively small and were adapted for an insectivorous diet or a varied one containing both plant and animal material (omnivorous). Tooth structure was still simple as compared to the teeth of descendants that adopted specialized diets. On the whole, also, the structure of the limbs was more primitive than that of descendants, though the wings of bats were almost as highly specialized in the Eocene as they are today (pp. 485–487).

As samples of such evolutionary histories we shall summarize those of horses and elephants (proboscideans). We choose these in preference to others partly because of general interest in the end products of the evolution and partly because the fossil record is more complete for them than it is for many other familiar mammals.

EVOLUTION OF THE HORSE

ADAPTATIONS OF THE MODERN HORSE Horses belong to the order of odd-toed ungulates, Perissodactyla. In Chapter 3 we noted the limb adaptation of horses for rapid running on hard ground (pp. 24–25). We recall that digit III is greatly enlarged and elongated, its "fingernail" having become the hoof. The other digits have disappeared, except for the splint bones representing rudiments of metacarpals (or metatarsals) of digits II and IV. The metacarpal (or metatarsal) of digit III has become the powerful cannon bone of the slender lower leg of the horse. Since the muscles are concentrated in the proximal (attached) region of the limb, being connected to the bones they move by slender tendons, the entire structure forms a light, rapidly swinging pendulum, admirably adapted for swift movement.

One of the most striking adaptations of the horse's foot for rapid running consists of a set of spring ligaments on the posterior surface of the foot. Figure 11.2 shows the arrangement of some of the principal ligaments of the forefoot. A large, interosseous tendon (ligament) arises from the posterior surface of the cannon bone and ends in movable sesamoid bones that form a pulley arrangement back of the fetlock joint. As shown, various ligaments connect these sesamoid bones to the phalanges of the hoof (sesamoid ligaments). The whole arrangement is elastic and may be compared to a powerful rubber band. When the weight of the horse is placed upon the foot the toe is bent upward and the ligaments are stretched. The tension so developed tends to spring the foot back into its original position (to flex it) and so to propel the horse forward. Thus the impact of the foot upon hard ground is translated into upward and forward propulsion as from a springboard. Camp and Smith (1942), to whom we owe much of our knowledge in this matter, state that "the action resembles that of a boy jumping on a pogo-stick; the harder the impact, the higher the bounce—up to the capacity of the apparatus."

The automatic springing action of the ligaments is augmented by the contraction of the flexor muscles of the leg, the tendons of which are also attached to the phalanges (in the diagram these tendons are not shown, though the cut ends at the attachments of one of the principal ones, Flexor digitalis profundus, are indicated). Near the upper ends of these tendons check ligaments connect to adjacent bones. Thus when tension is placed on these tendons—for example, by impact of the foot on hard ground—these check ligaments may be stretched, reinforcing the action of the ligaments shown in Fig. 11.2 and preventing injury to the latter by overstretching (sprain).

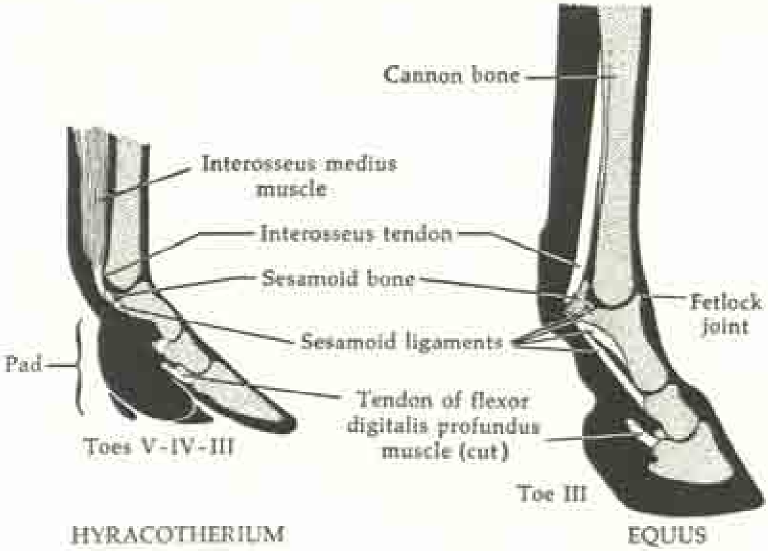

Cannon bone
Interosseus medius muscle
Interosseus tendon
Sesamoid bone
Fetlock joint
Sesamoid ligaments
Pad
Tendon of flexor digitalis profundus muscle (cut)
Toes V-IV-III
Toe III
HYRACOTHERIUM
EQUUS

Fig. 11.2. Pad-supported forefoot of *Hyracotherium* compared with the springing mechanism in the foot of the modern horse. The pad in *Hyracotherium* is shown in black, as are the tips of digits IV and V. Tendons and ligaments are shown in white; bones are dotted. (Modified from Camp and Smith, "Phylogeny and functions of the digital ligaments of the horse," *Memoirs*, University of California, *13* (1942).)

Horses obtain their food by grazing—feeding on such vegetation as grass covering the surface of the ground. If a long-legged animal is to do this, some means must be provided for getting the mouth down to the ground. Lengthening the neck would accomplish the result, and to a moderate degree the neck of the horse has been lengthened. But a horse has a large and heavy head; there would be obvious mechanical

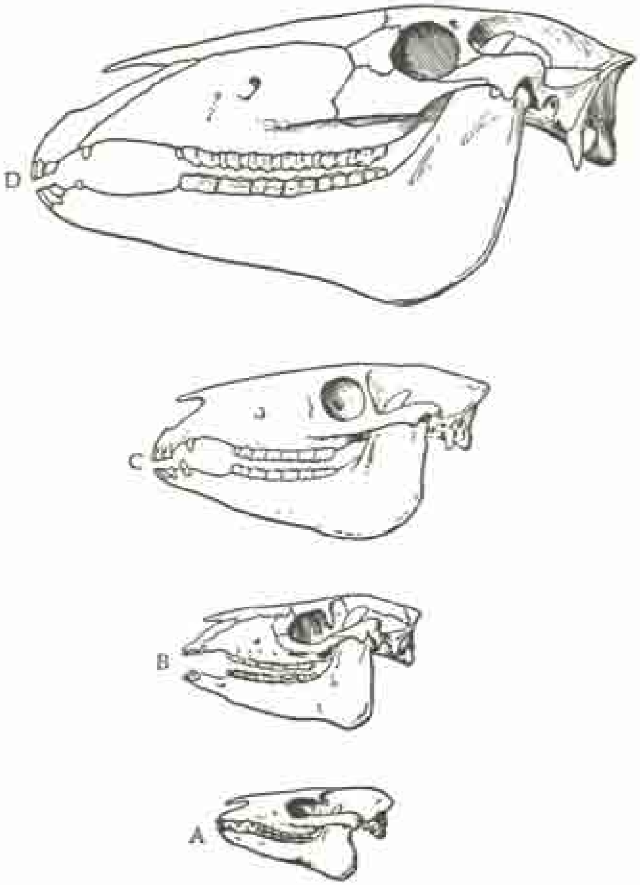


Fig. 11.3. Series of horse skulls in ascending geologic order. *A, Hyracotherium* (Eohippus). *B, Mesohippus. C, Merychippus (Protohippus). D, Equus.* (From Scott, W. B., *A History of Land Mammals in the Western Hemisphere.* Courtesy of the American Philosophical Society.)

disadvantage in perching it on the end of a really long neck. To a considerable extent the problem has been solved for the horse by lengthening the anterior part of the skull itself. The portion of the skull anterior to the eyes has been elongated into the well-known muzzle (Fig. 11.3*D*). One result of this elongation has been the production of a gap in the tooth row between the incisor (front) teeth and the grinding battery composed of premolars and molars. This toothless gap is called the diastema (Fig. 11.3*D*). It is utilized by man as a convenient location for the bit used to control the movements of the horse.

The grinding battery composed of premolar and molar teeth is an adaptation for the chewing of harsh grasses containing silica. The food material is so abrasive that it wears away teeth that chew it, and it must be eaten in large quantities to provide the required nourishment. The problem is solved by developing teeth that grow as they are worn away. As shown in Fig. 11.4, each individual grinding tooth is high-crowned (hypsodont). Such a tooth continues growing throughout a

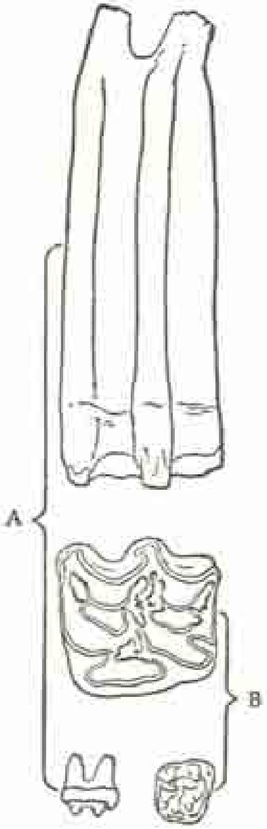


Fig. 11.4. Molar teeth of modern horse and of *Hyracotherium*. *A*, teeth in lateral view. *B*, crown of the teeth. (After Osborn. Reprinted by permission from *Textbook of Geology, Part II, Historical Geology*, by L. V. Pirsson and C. Schuchert, published by John Wiley & Sons, Inc., 1915.)

horse's reproductive lifetime. On the surface of such a tooth there is exposed a complicated pattern of lines of hard enamel (Fig. 11.4). The enamel pattern is set in a matrix of softer dentine and cement. The latter wear away more rapidly than does the enamel, with the result that the surface is continually maintained in a roughened condition reminiscent of the surface of a millstone, the ridges of hard enamel protruding above the dentine and cement. In this manner the horse is provided with a self-sharpening, self-renewing grinding mechanism for use on the harsh material comprising its diet.

If space permitted, other adaptations of the horse might be enumerated, but our purpose will be served by concentrating attention on those just discussed: (1) enlargement and elongation of digit III, with loss of other digits and development of a spring mechanism; (2) elongation of the preorbital portion of the skull; and (3) development of premolars and molars into high-crowned grinders that grow as they are worn away. To these should be added the large size characteristic of most varieties of horses.

HYRACOTHERIUM Having reviewed the characteristics of the modern horse we turn our attention to the characteristics of the first horse of which we have any knowledge: *Hyracotherium* (also called Eohippus). This animal lived in Europe and North America in Eocene times.

Hyracotherium differed greatly from our modern horse. In the

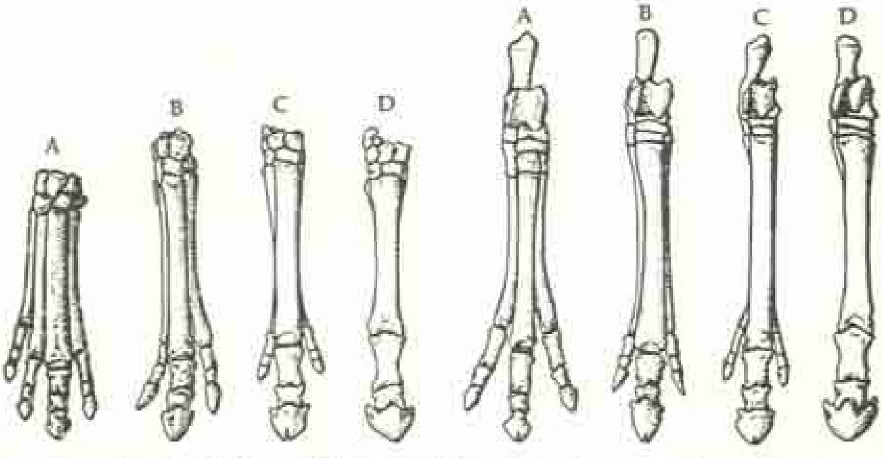


Fig. 11.5. Forefeet (left) and hind feet (right) of four horses. A, *Hyracotherium*. B, *Miohippus*. C, *Merychippus*. D, *Equus*. Not drawn to scale. (A, after Cope; B and C, after Osborn. From Romer, A. S., *Vertebrate Paleontology*. Copyright © 1933, 1945, and 1966 by The University of Chicago. Used by permission of The University of Chicago Press.)

first place it was small, about the size of a fox terrier. Its legs were short and had four toes on the front feet and three on the hind (Fig. 11.5A). We note, however, that digit III already showed incipient signs of predominating. Through study of the scars left on the foot bones by attachments of ligaments and tendons, Camp and Smith (1942) came to the conclusion that *Hyracotherium* did not have the springing mechanism characteristic of the modern horse (see preceding). Instead the foot must have been supported by a pad (Fig. 11.2) as in many forest-dwelling animals, including the tapir, a distant relative of the horse. The figure shows that the interosseous tendon arose from a muscle instead of attaching directly to the back of the cannon bone as it does in the modern horse. Most mammals including hoofed forms other than *Equus* have such a muscle. Indeed, occasional horses have muscle tissue in this tendon. Apparently reduction of fleshy fibers, virtually changing the tendon to a ligament, has been one of the evolutionary changes in the evolution of the springing mechanism. "Muscular tissue, by weakening the tendon, would tend to enfeeble this [springing] action" (Camp and Smith, 1942).

The preorbital portion of the skull was not elongated; the orbit of the eye was in the middle, measuring from front to rear (Fig. 11.3*A*). The molar teeth were not high-crowned grinders. In fact, they were somewhat like human molar teeth (Fig. 11.4). They had low crowns, developed pronged roots, and surfaces covered by rounded tubercles or cusps much as do our own molar teeth.

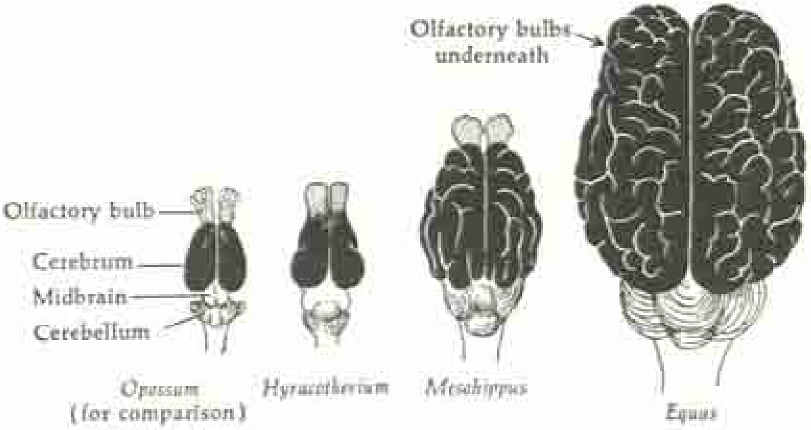


Fig. 11.6. Horse brain evolution. Comparison of the brain of *Hyracotherium* with that of the opossum and with the brains of *Mesohippus* and *Equus*. The horse brains, based on endocranial casts, are drawn to scale; *Hyracotherium* and opossum brains are of about the same size. (After Edinger, T., *Evolution of the Horse Brain, Memoir 25*, Geological Society of America, 1948.)

Another most unhorselike characteristic of *Hyracotherium* was its brain. Studies of casts of the interiors of skulls (endocranial casts) have revealed that the cerebral hemispheres were small and smooth; they did not cover the olfactory bulbs anteriorly or the midbrain posteriorly as did the cerebra of later horses (Edinger, 1948). In fact, as Fig. 11.6 shows, among brains of living mammals the one most similar to the *Hyracotherium* brain is that of the opossum, a relatively primitive marsupial. Evidently in the early stages of horse evolution brain development lagged behind evolution of the limbs. We shall see that this also appears to have been true of human evolution (Chap. 12).

Hyracotherium was a forest dweller, a browser subsisting on soft vegetation quite unlike the food of its plains-dwelling descendants. Its spreading toes formed better support on the soft forest floor than does the single hoof of its modern descendant. It probably escaped its enemies by hiding, as do most forest-dwelling, herbivorous animals, instead of by running away, as must inhabitants of treeless plains.

FROM HYRACOTHERIUM TO EQUUS We have sketched above the beginning and the ending of horse evolution. What occurred in the millions of years separating *Hyracotherium* from its modern descendant, *Equus?* Fortunately the intervening history is well documented by numerous fossils showing the transitional stages of the changes in body structure required to transform the ancestor into its modern descendant. Space limitations prevent more than a brief glance at a few of the main stages, but the interested reader may obtain more detailed information by consulting references at the end of the chapter.

Figure 11.7 summarizes some of the events in this evolutionary history. The diagram is designed to emphasize the point that at various times in the history of horses evolutionary radiations occurred, several or many forms arising from an ancestor. Thus *Hyracotherium* gave rise to several differing lines, one of which led to *Mesohippus*. This line included several intermediate forms that we shall not name.

Mesohippus was of about the size of a sheep, different species varying from 18–24 ins. high at the shoulder. The greatest change from *Hyracotherium* in foot structure was loss of one digit (Number V) from the forefoot, with only a functionless vestige remaining. Thus both forefeet and hind feet were three toed, with digit III predominant (as in *Miohippus*, Fig. 11.5B). The foot was still padded as it had been in *Hyracotherium*.

Various species of *Hyracotherium* showed a progressive tendency for the premolar teeth to become like the molars in structure (Simpson, 1951). This tendency was continued in *Mesohippus;* from this point on in the line leading to the modern horse premolars and molars combined to form the dental battery.

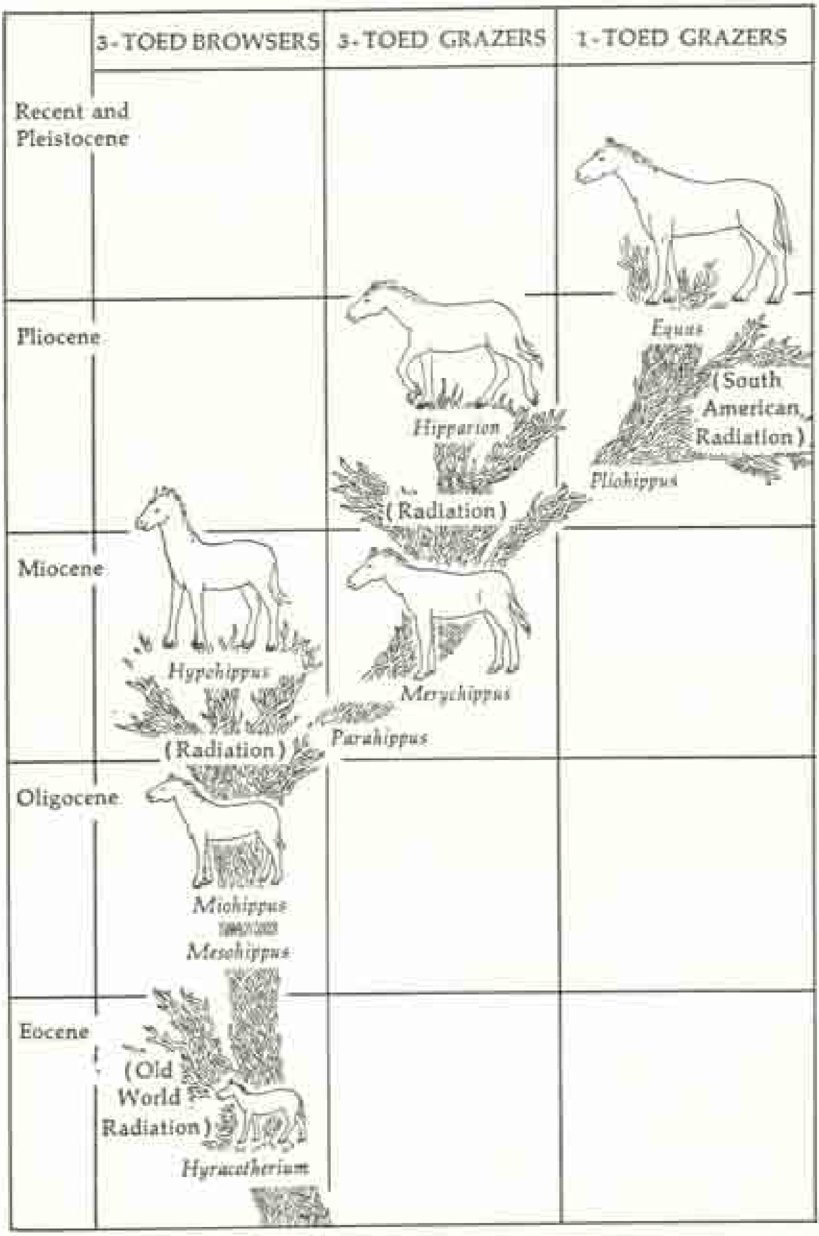

3-TOED BROWSERS
3-TOED GRAZERS
1-TOED GRAZERS
Recent and Pleistocene
Pliocene
Miocene
Oligocene
Eocene
Equus
(South American Radiation)
Hipparion
Pliohippus
(Radiation)
Hypohippus
Merychippus
Parahippus
(Radiation)
Miohippus
Mesohippus
(Old World Radiation)
Hyracotherium

Fig. 11.7. Evolution of the horse family. Only a few of the many evolutionary lines and of the known representatives in those lines are shown. (Modified from Simpson, G. G., *The Meaning of Evolution*, Yale University Press, 1967.)

The most remarkable change from *Hyracotherium* was in the structure of the brain. In *Mesohippus* the opossumlike configuration had been lost. The cerebral hemispheres had enlarged and become convoluted so that the brain assumed much the appearance of a small horse brain (Fig. 11.6). How interesting it would be to know what changes in behavior and intelligence accompanied these anatomical changes!

Miohippus was much like Mesohippus but of larger size. The low-crowned teeth and the spreading, three-toed feet indicate that these were forest horses living on soft vegetation—three-toed browsers like their ancestor *Hyracotherium*.

In Fig. 11.7 *Miohippus* is shown as an ancestor for several radiating lines. Of these, the line involving the least change led to *Hypohippus*, a "forest horse" living in Miocene and early Pliocene times. This three-toed browser was much like an enlarged version of *Miohippus*.

Parahippus, another descendant of *Miohippus*, presented in its various species a nearly complete spectrum of transitional stages between its ancestor and *Merychippus*, i.e., between "three-toed browsers" and "three-toed grazers" (Fig. 11.7). The teeth were becoming high-crowned grinders (hypsodont). The legs were becoming longer, and digit III was becoming more predominant than it had been in the forest-dwelling ancestors.

As indicated in Fig. 11.7, *Merychippus* was a three-toed grazer adapted for life on the western plains that arose in the Miocene as a result of widespread continental elevation. *Merychippus* carrier farther the development of high-crowned molar teeth capable of grinding the harsh grasses growing on those plains. Tooth structure became more complex, and cement filled what in ancestors had been valleys on the surface of the molars.

The legs of *Merychippus* were elongated, with still further predominance of digit III (Fig. 11.5C; the elongation is not shown in the figure, where all feet are shown reduced to the same absolute length instead of being drawn to scale). "There may still have been a vestige of the pad, but essentially the animal was now up permanently on extreme tiptoe, with the weight resting mainly or wholly on the hoof of the middle toe" (Simpson, 1951). As might be anticipated, *Merychippus* showed an increased development of the ligaments mentioned above as forming a spring mechanism in the foot of the modern horse. The relatively short side toes (II and IV) probably did not touch the ground most of the time, serving as support only "when the foot was under great pressure or sunk into sand or mud" (Camp and Smith, 1942).

It is also significant that during the course of the Miocene *Merychippus* underwent striking evolution of the cerebral hemispheres of the brain. Later specimens exhibited the fundamental pattern of fissures (convolutions) that was to characterize later horses, e.g., *Equus*, Fig. 11.6 (Edinger, 1948).

Merychippus is shown (Fig. 11.7) as the center of another radiation. Some descendants continued as three-toed grazers, e.g., *Hipparion*. On the other hand, *Merychippus* was ancestral to horses that reduced the number of digits on each foot to one—the line leading through *Pliohippus* to *Equus*. This loss of the side digits was a most striking evolutionary change. Why did it occur in the *Equus* line but not in the other lines? Did the side digits have a function in the three-toed forms, even the ones in which these digits were short relative to digit III? This question is usually answered in the negative, but Simpson (1951) has challenged such a conclusion. He pointed out that when a horse is galloping and lands on its middle toe, this toe is bent strongly upward. As noted above, under such great pressure the side toes of, for example, *Merychippus* would touch the ground. Simpson has suggested that the side toes may have had "an essential function to act as buffers to stop the bending of the middle toe at this point and to lessen the danger of spraining the elastic ligaments by stretching them too far." If this is correct, why did the side toes disappear in the line leading to *Equus*? Perhaps because other structures took over the function of preventing spraining of the spring mechanism. We have mentioned that in *Equus* the tendons of long flexor muscles are connected to adjacent bones by check ligaments. These assist the other elastic ligaments and form part of the spring mechanism, especially under powerful stress. Perhaps the safety factor provided by these check ligaments was not present in the three-toed horses. This is a point on which we do not have information, however. We may note in passing that the horse has paid a price for its highly specialized springing foot. Lameness connected with injury to the elastic ligaments is common.

Some species of *Pliohippus* had tiny side toes, though in other species these were represented only by splint bones, as in *Equus*. *Pliohippus* attained the size of a modern pony, some 40 in. (ten hands) high. The trends for increase in the preorbital length of the skull and for increase in size and complexity of the molar teeth continued.

The transition from *Pliohippus* to *Equus*—the genus to which modern horses, asses, and zebras belong—was a small one, involving further increase in size and some changes in anatomical details. The first representatives of *Equus* appeared in late Pliocene times; during the Pleistocene the genus achieved worldwide distribution, aside from Australia. Although North America has provided the stage for the greater part of their evolution, horses became extinct on this continent by the close of the Pleistocene. Why did they become extinct? As is true for the extinction of the dinosaurs (p. 192–193), we can only speculate on an answer. Was disease involved? Did early man play a role? We do not know, but we do know that by the time later men reintroduced horses into America conditions on our western plains were highly favorable for them.

In connection with a discussion of the fossil history, we find interest in the fact that occasionally a modern horse may develop vestigial toes connected to one of the splint bones (Fig. 11.8). We recall that the splint bones in the foreleg represent the reduced metacarpals of digits II and IV (p. 206). Here, then, we have another example of embryonic reversion (p. 62), reminiscent of such a prehistoric horse as *Merychippus* (Fig. 11.5C).

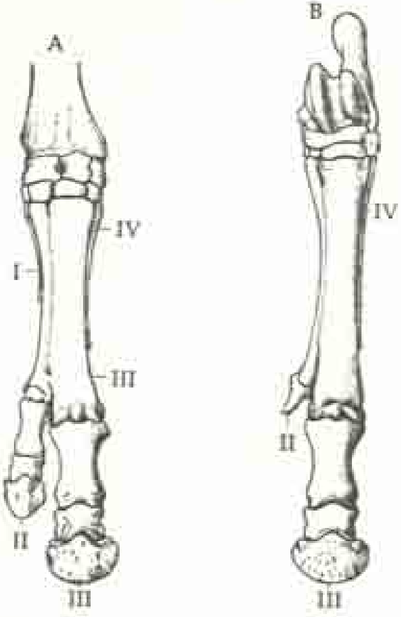


Fig. 11.8. Forefoot (*A*) and hind foot (*B*) of a multitoed modern horse. (From Lull, R. S., "The evolution of the horse family, as illustrated in the Yale collections," *American Journal of Science*, 23 (1907).)

EVOLUTION OF PROBOSCIDEANS

The living representatives of the order Proboscidea are the Asiatic and African elephants. The two differ somewhat in structure, the most

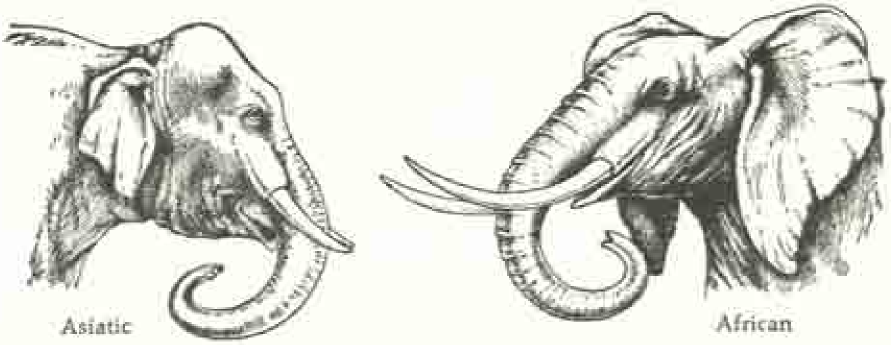


Fig. 11.9. Comparison of the heads of Asiatic and African elephants. (From Guyer, *Animal Biology*, Harper & Row, 1948.)

obvious difference to a casual observer being in the size of the ears (Fig. 11.9). The great palmleaflike ears of African elephants stand in marked contrast to the ears of Asiatic elephants. Asiatic elephants have long been domesticated and used as work animals; they are the species commonly seen in circuses.

ELEPHANTINE ADAPTATIONS Huge bulk is always brought to mind by the mention of elephants, and indeed many of the bodily adaptations of elephants are connected with their large size. To support the weight of the body the limbs have a strong, pillarlike construction. The feet have retained the full complement of five toes, but much of the weight is supported not by the toes but by a pad of elastic tissue that forms both the sole of the short, broad foot and a sort of functional "rubber heel."

Since the body is supported high above the ground on long legs, the elephant, like the horse, is faced with the problem of reaching the ground for feeding. We have seen how the problem was solved in the horse (p. 208). In the elephant the solution was entirely different. Here the head is so heavy that any lengthening of the neck would be a great mechanical disadvantage. Accordingly, elephants are characterized by short necks. Nor is the preorbital portion of the skull lengthened, as it is in the horse. Instead we find the development of the organ that gives the order its name: the proboscis or trunk. This versatile organ consists of the nose and upper lip greatly elongated. As everyone who has fed peanuts to elephants knows, the two nostril openings are at the tip of the trunk, along with a fingerlike projection (African elephants have two of them) by means of which small objects may be picked up.

The development of a proboscis has a peculiar effect upon the topography of the skull. In most mammals the external nares, bony openings in the skull at the base of the nostrils, are at or near the anterior tip of the skull. In mammals that develop a proboscis the nares recede from the tip; in elephants they have receded so far up the front of the skull that they appear to be located in the middle of the forehead (Fig. 11.10). Presumably this recession of the nares is connected with the necessity for firm anchorage for the powerful musculature of the proboscis. Owing to this effect of proboscis development upon skull topography it is possible to estimate from the structure of the skull the size of proboscis possessed by a prehistoric proboscidean.

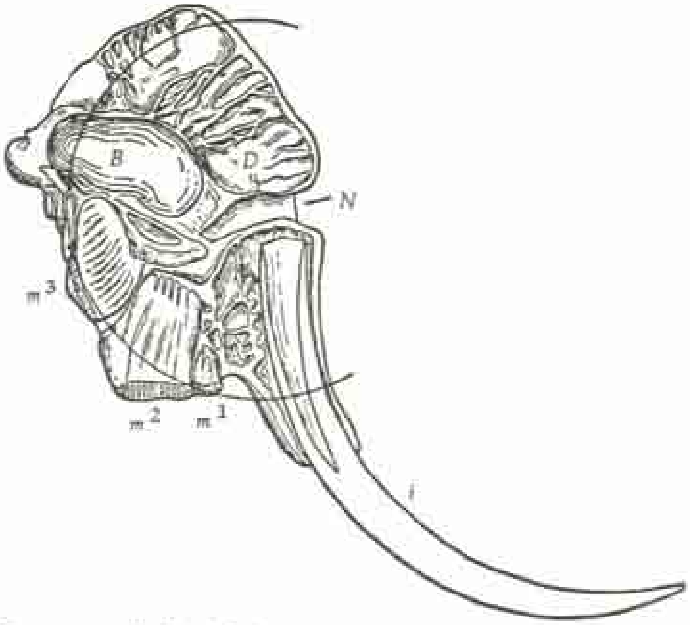


Fig. 11.10. Skull of elephant, sectioned longitudinally. *B*, brain cavity. *D*, diploe (air cells). *i*, incisor (tusk). m^1, m^2, m^3, molar teeth. *N*, nares. (From Lull, R. S., *Organic Evolution*, rev. ed. Copyright 1945 by Richard S. Lull. Used by permission of The Macmillan Company.)

Another characteristic of the elephant skull is development of extensive air cells or diploë (Fig. 11.10). While these serve to lighten the skull, their principal function is probably connected with support of the heavy head. It will be noted from the figure that an elephant's "high forehead" is not caused by brain development but by the presence of these diploë. The skull is hinged to the vertebral column by the occipital condyles, which thus constitute the fulcrum of a lever system.

Increasing the height of the head above these condyles increases the surface for, and the mechanical advantage of, the muscles and ligament that support the head. The importance of achieving such mechanical advantage is evident when we recall that the two tusks together may weigh more than 400 lb. and be nine to ten feet in length, though the average size is not so great as this.

The tusks are formed from the right and left second upper incisor teeth. The ivory composing them consists of the dentine material of the teeth, no enamel being present except for a small area on the end of the tusk when it first erupts. A large, open pulp cavity in the base of each tusk provides for continuous growth.

Nothing about an elephant is more unique than its molar tooth structure and system of molar replacement. Each individual molar is large and consists of flattened plates or lamellae side by side. In cross section each plate is a flattened oval, the outer surface being composed of enamel and the enclosed material being dentine. Cement fills the spaces between successive plates, so when the tooth has been worn down somewhat by use, the surface presents the appearance shown

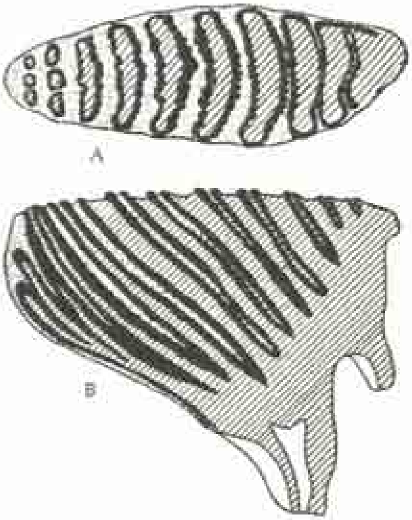


Fig. 11.11. Molar tooth of elephant. A, crown view. B, longitudinal section. Enamel shown in black, dentine by oblique lines, cement by dots. (From Lull, R. S., *Organic Evolution*, rev. ed. Copyright 1945 by Richard S. Lull. Used by permission of The Macmillan Company.)

in Fig. 11.11A. Thus, like the molar of the horse but on a much larger scale, the elephant molar has a grinding surface on which ridges of enamel protrude, owing to the more rapid wearing away of the softer dentine and cement.

As everyone knows, during the course of their lifetimes most mammals have two sets of teeth: the "milk teeth" or deciduous teeth and the permanent teeth. The permanent teeth replace the milk teeth *vertically;* a permanent premolar in the upper jaw, for example, develops above the corresponding premolar of the milk set and eventually replaces that tooth by moving down into the position formerly occupied by it. Thus, early in life a typical mammal has a complete set of milk teeth all in use at one time and later in life has a complete set of permanent teeth all in use at one time. Arrangements are quite otherwise in elephants. While some of the molars are identified as milk teeth and others as permanent teeth, the individual teeth succeed each other in series, one at a time, rather than as complete sets. Thus, typically, at any given time only four molars are in use, one in the upper jaw and one in the lower jaw on each side. As the molars wear out they are replaced by others, but replacement is *longitudinal* not vertical; the new molar is pushed forward from the rear of the jaw. Figure 11.10 shows this method of replacement in the upper jaw. In the figure the first molar (m^1) is present as a worn-out remnant; the second molar (m^2) is shown as the functional one, and the third molar (m^3) is shown forming above and behind the second one, as a reserve to replace the latter when it in turn wears out.

EVOLUTIONARY HISTORY

As in the evolution of the horse, proboscidean evolution seems to have started with a rather small animal living in the Eocene. *Moeritherium* (Fig. 11.12) lived in Africa in late Eocene and early Oligocene times. It was about the size of a tapir, some three feet in height, and probably had a short, tapirlike proboscis, as indicated by slight recession of the nasal openings of the skull (Fig. 11.13). The incisors were beginning to form tusks on both the upper and lower jaws. The molars were low crowned, possessed two transverse crests each, and occurred in rows as in most mammals. The longitudinal method of molar replacement came much later.

The relationships of the various later proboscideans to each other are not entirely certain. The arrangement shown in Fig. 11.12 is probably correct in broad outline. In the Oligocene we find the two closely similar genera *Phiomia* and *Paleomastodon*. These proboscideans were larger than *Moeritherium*, had a longer trunk, showed elongation of

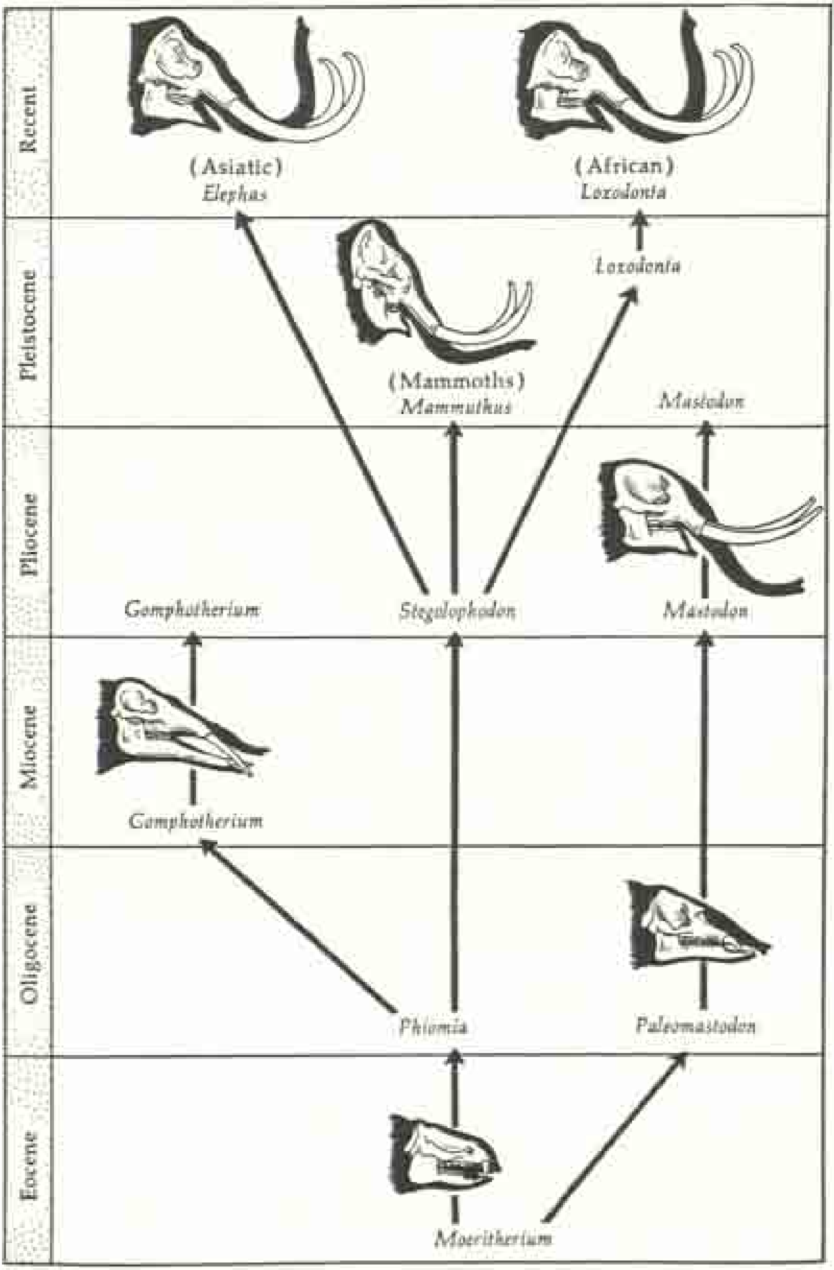

Recent
(Asiatic)
Elephas
(African)
Loxodonta
Pleistocene
Loxodonta
(Mammoths)
Mammuthus
Mastodon
Pliocene
Gomphotherium
Stegolophodon
Mastodon
Miocene
Gomphotherium
Oligocene
Phiomia
Paleomastodon
Eocene
Moeritherium

Fig. 11.12. Abbreviated chart of proboscidean evolution. (Sketches after Scott, W. B., *A History of Land Mammals in the Western Hemisphere.* Courtesy of the American Philosophical Society.)

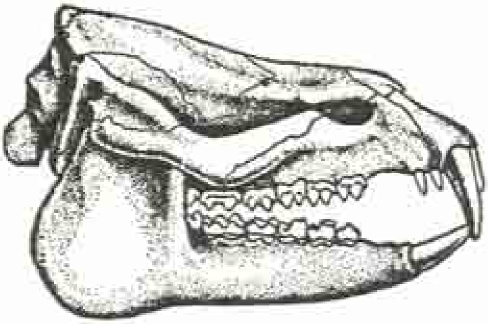


Fig. 11.13. Skull of *Moeritherium*. (After Andrews; from Romer, A. S., *Vertebrate Paleontology*. Copyright © 1933, 1945, and 1966 by The University of Chicago. Used by permission of The University of Chicago Press.)

both upper and lower jaws, and had already attained a limb structure quite like that of modern elephants.

Later epochs of the Cenozoic brought a variety of interesting proboscideans. One type ranging widely over Eurasia and Africa was *Deinotherium*. Oddly, this creature had no upper tusks but had large lower tusks curving downward and backward (Fig. 11.14). The molars were low crowned with two or three cross ridges, as shown in the figure. A diet of soft, succulent vegetation seems indicated. Some specimens exceeded modern elephants in size.

Another evolutionary line culminated in creatures of elephantine size having greatly elongated lower jaws: *Gomphotherium* (Fig. 11.12). The most extreme jaw recorded was six feet seven inches in length. *Gomphotherium* is of interest as the first proboscidean to reach North America, presumably as a migrant from Asia.

Mastodons formed the culmination of another evolutionary line. As large as elephants, they roamed North America until a few thousand years ago, as judged by the fact that their bones are found near the surface in bogs and swamps. The lower jaw was short and usually without tusks, although vestigial lower tusks are found in some specimens. The upper tusks were large, sometimes attaining a length of nine feet, and curved upward (Fig. 11.12). The molar teeth were low crowned and long-rooted and had on the surface three or four transverse crests without cement in the intervening valleys (Fig. 11.15). We note that this contrasts sharply with the molar structure of elephants (Fig. 11.11). Judging by stomach contents found with some specimens, mastodons were forest dwellers, including in their diet twigs of such coniferous trees as hemlock and spruce.

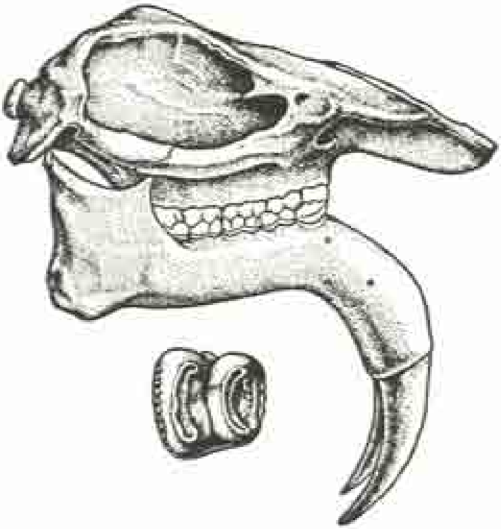


Fig. 11.14. *Deinotherium:* skull and surface of molar tooth. (After Gaudry and Andrews; from Romer, A. S., *Vertebrate Paleontology*. Copyright © 1933, 1945, and 1966 by The University of Chicago. Used by permission of The University of Chicago Press.)

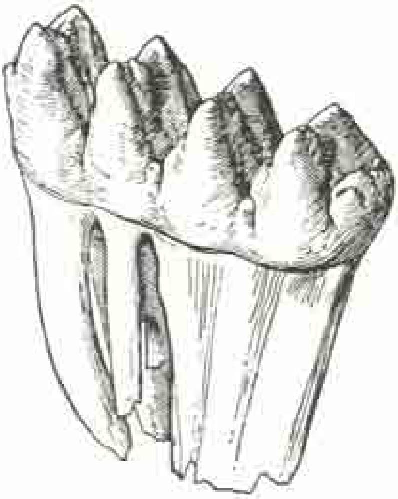


Fig. 11.15. Molar tooth of *Mastodon*. (From Scott, W. B., *A History of Land Mammals in the Western Hemisphere*. Courtesy of the American Philosophical Society.)

Turning to the true elephants we note that the two modern genera and the extinct genus (of mammoths) are believed to have had common ancestors in Pliocene times. These ancestors were probably several species of proboscideans that showed some resemblance to elephants in tooth structure and are classified as belonging to the genus *Stegolophodon* (Fig. 11.12; actually the ancestry of elephants is more complex than this simple diagram suggests; compare Fig. 8 in Aguirre, 1969). The mammoths were very similar to modern elephants in structure, though some were larger. Like modern elephants, they had a short lower jaw. Interestingly, the fetus of the African elephant has an elongated lower jaw, of somewhat the proportions shown by adult *Moeritherium*. As development continues the jaw becomes relatively shorter (de Beer, 1958). While of course we know nothing of the fetus of *Moeritherium*, we may safely surmise that this embryonic pattern in modern elephants was inherited from distant ancestry (Chap. 4).

During Pleistocene times a variety of mammoths ranged widely over the earth, including regions with climates unsuitable for the two modern elephants. Thus the woolly mammoth wandered into arctic regions. This mammoth is perhaps the most completely known of all prehistoric mammals, owing to the good fortune that complete carcasses have been found in the permanently frozen gravels of northern Siberia. Thus the "soft parts" usually unavailable for study in fossil animals have been preserved along with the bones. Thanks to this fortunate preservation, we know that this mammoth was covered with coarse, dark brown hair having a maximum length of 20 in. and with a dense undercoat of woolly hair about an inch long. The creature has added interest for us because of cave paintings and carvings of it made by prehistoric men. Mammoths doubtless formed a source of food for men of the time.

References and Suggested Readings

Aguirre, E., "Evolutionary history of the elephant," *Science, 164,* 1366–1376 (1969).

Camp, C. L., and N. Smith, "Phylogeny and functions of the digital ligaments of the horse," University of California, *Memoirs, 13,* 69–123 (1942).

Cronquist, A., *Introductory Botany,* New York, Harper & Row, 1961.

de Beer, G. R., *Embryos and Ancestors,* 3rd ed., Oxford, Oxford University Press, 1958.

Dunbar, C. O., *Historical Geology*, 2nd ed., New York, John Wiley, 1960.

Edinger, T., *Evolution of the Horse Brain*, Geological Society of America, *Memoir, 25*, 1948.

Ericson, D. B., and G. Wollin, "Pleistocene climates and chronology in deep-sea sediments," *Science, 162*, 1227–1234 (1968).

Fleischer, R. L., P. B. Price, and R. M. Walker, "Tracks of charged particles in solids," *Science, 149*, 383–393 (1965).

Hussey, R. C., *Historical Geology*, 2nd ed., New York, McGraw-Hill, 1947.

Kulp, J. L., "Geologic time scale," *Science, 133*, 1105–1114 (1961).

Libby, W. F., "Radiocarbon dating," *American Scientist, 44*, 98–112 (1956).

Lull, R. S., *Organic Evolution*, rev. ed., New York, Macmillan, 1945.

Osborn, H. F., *Equidae of the Oligocene, Miocene and Pliocene of North America*, iconographic type revision, New York, American Museum of Natural History, *Memoirs*, vol. II, pt. I, 1918. (Detailed descriptions and drawings of fossil horses.)

Romer, A. S., *The Vertebrate Story*, Chicago, University of Chicago Press, 1959.

Romer, A. S., *Vertebrate Paleontology*, 3rd ed., Chicago, University of Chicago Press, 1966.

Scott, W. B., *A History of Land Mammals in the Western Hemisphere*, rev. ed., New York, Macmillan, 1937.

Simpson, G. G., *Horses*, New York, Oxford University Press, 1951. (Authoritative account of horse evolution.)

12

Evolution as Seen in the Geologic Record: Evolution of Man

POPE'S DICTUM THAT "the proper study of mankind is Man" may be taken as symbolic of the enhanced interest most people feel in members of their own species as compared to their interest in other portions of the animal kingdom. Probably it is only natural that the subject of the evolution of man arouses more widespread interest than does, for example, that of the evolution of the horse. Yet it is unfortunate that the "man in the street" thinks of evolution only in terms of its bearing upon the question of man's ancestry, instead of recognizing that man's evolution is one scene in a much vaster drama. But perhaps our criticism of myopic vision should be mitigated by the realization that this restricted view is occasionally encouraged by those who should know better.

The foregoing is not intended to belittle man or the importance of his evolution but to suggest the perspective in which all evolution should be viewed. Many animals have arisen through evolution, among them man. The same principles at work in the production of other animals operated in the production of man. Man is the finest product yet arisen through the evolutionary process. But that is not to say that the evolutionary process was set in motion in the first place for the express purpose of producing man.

Why is man the finest fruit on the tree of life? The very fact that he can ask the question suggests the answer. Man is the only product of the evolutionary process to develop the mentality to wonder about himself and his origin and to acquire some measure of knowledge in the matter. The human mind, then, is the greatest achievement of the evolutionary process. His mind enables man to wonder and, within limits, to know and understand. To a considerable and increasing extent, also, man's mind enables him to control his environment instead of being controlled by it as other animals are. Nor should we forget the emotional and aesthetic attributes of mind that have underlain some of the noblest achievements of our species.

THE HUMAN BRAIN Because of the preeminent position accorded the human mind and because of the close association between mind and the functioning of the brain, we shall place emphasis on the development of the brain in our discussion of the evolution of man. Brain development affords some clue to mind development. It is noteworthy in this connection that the outstanding achievement of human evolution was the development of the brain. We have seen that birds specialized in developing wings, horses in developing legs for running, and elephants in developing tusks and trunk and giant molars. Man specialized in developing brain. Accordingly, the unique features of man's evolution are largely concerned with the evolution of this brain. It will occupy the center of the stage in the following discussion.

Before proceeding further a word is in order concerning an omission that might trouble some readers. We have accorded preeminence to the human mind but have said nothing about the human soul. The reason for the omission lies in the fact that the soul is outside the province of science. Science deals with phenomena that can be detected, studied, and measured by use of scientific instruments. The soul is not amenable to this approach. It cannot be seen or weighed or analyzed chemically; nor can it be studied by the methods of the psychologist. Thus discussion of the soul would be out of place in a book of science.

This may not always be true, but for the present we must look to religion and philosophy for knowledge of the soul.

PRE-PRIMATE ANCESTRY Man is clearly a mammal. Hence the evolutionary history that we have traced for mammals in general is also his evolutionary history. Briefly, we recall that the sequence subsequent to attainment of vertebrate status was as follows: crossopterygian fishes to labyrinthodont amphibians to cotylosaur reptiles to therapsid reptiles to primitive mammals of group Pantotheria to mammals of order Insectivora.

ORDER PRIMATES We have noted that the Insectivora constitute the group of mammals from which the other orders of placental mammals are believed to have arisen. Among these other orders is the order Primates, the order to which man belongs in company with lemurs, tarsiers, monkeys, and apes. These forms are grouped together in one order because they possess in common a number of anatomical features. Yet the order is not characterized by any one big specialization as are many other orders of mammals. Thus, members of the order Carnivora (e.g., cats and wolves) are specialized for flesh eating, members of the order Chiroptera (bats) for flying, members of the order Cetacea (e.g., whales and porpoises) for swimming, and so on. Members of the order Primates are an extremely varied group. In manner of locomotion, for example, some (such as lemurs) go on all fours, some (such as gibbons) swing through the trees by their forelimbs, and others climb in trees using both forelimbs and hind limbs. These tree-climbing and arm-swinging types of locomotion have been greatly facilitated by the development of opposable thumbs and, in many primates, opposable great toes, admirable adaptations for grasping branches.

Such arboreal primates hold the body at times in more or less of an upright posture. While sitting on branches they frequently use their forelimbs for nonlocomotor activities, such as grooming their fur and manipulating food. As we shall see, in the line leading to man such upright posture and nonlocomotor use of the hands became predominant. In most, though not all, primates flattened fingernails have largely replaced the claws possessed by other mammals.

In most primates the eyes are directed anteriorly instead of laterally. This makes possible stereoscopic vision and thus the accurate judgment of distances. Such an adaptation is obviously of great value to creatures that swing or jump from branch to branch. This overlapping of fields of vision also facilitates examination of objects held in the hands.

Clearly, from arboreal ancestors (though not of course from any of the present-day species) man inherited such traits as the tendency to upright posture (freeing the hands for nonlocomotor use) and stereoscopic (binocular) vision, without which he could hardly have become a tool-manufacturing and tool-using creature.

Primates also are characterized by many other features, such as a single pair of mammary glands, usually pectoral (on the chest) in position, and a complete bar of bone separating the orbit of the eye from the temporal fenestra (postorbital bar). The sample of traits given is sufficient to emphasize the many features shared by man with his fellow primates. In general primates are herbivorous and tree dwelling (arboreal herbivores).

BEGINNINGS OF PRIMATE EVOLUTION The order Primates is conveniently divided into two suborders: Prosimii and Anthropoidea (Simpson, 1945).

TREE SHREWS (Fig. 12.1) are frequently classed in suborder Prosimii, though they are sometimes regarded as members of the order Insectivora. Recent evidence is conflicting. From study of skull structure and of fossils Van Valen (1965) concluded that they are insectivores and may not even be closely related to the insectivores that gave rise to the primates. From studies of the nervous system, Campbell (1966) concluded that this system "contributes no evidence which establishes their proposed affinity with the primates." Study of reproductive mechanisms led Martin (1966) to conclude that tree shrews are not insectivores at all but should be placed in an order of their own; he found significant resemblances to marsupials! On the other hand, matching of DNA fragments (Fig. 5.4, p. 83—tree shrew vs hedgehog, an insectivore) and the precipitin test using serum albumins (Goodman, 1966) indicate closer relationship of tree shrews to primates than to insectivores. Suspended judgment pending results of future research seems wisest at this time.

The most typical prosimians are the LEMURS and TARSIERS, both represented by numerous forms in early periods of the Cenozoic era. Lemurs are small animals resembling monkeys in some ways, for example, in having hands tipped with flattened nails instead of claws. Even so, some lemurs have a specialized claw on one digit of each hand. The faces of lemurs project into unmonkeylike muzzles, however, suggesting the faces of little dogs (Fig. 12.1). Tarsiers are represented today by only one form, found in some islands of the East Indies. This animal is remarkable for its enormous eyes and concomitant development of the visual regions of the brain (Fig. 12.1).

That lemurs and tarsiers are related is indicated by the fact that

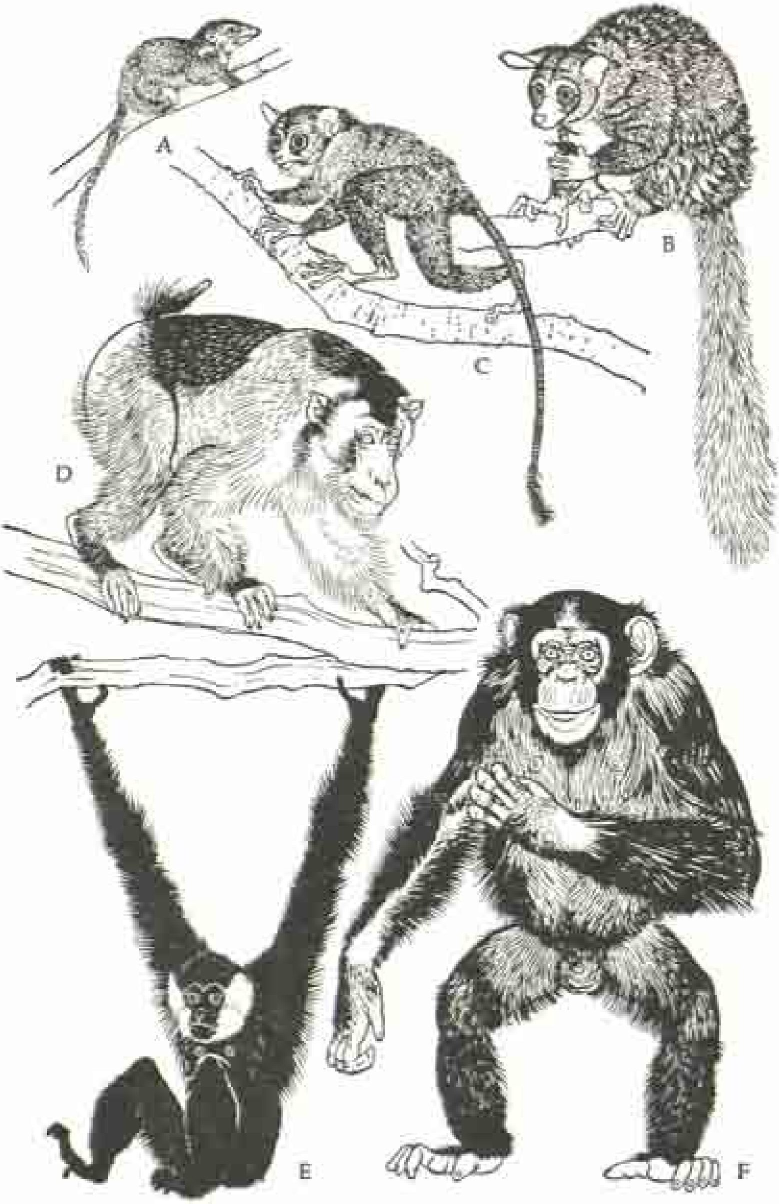


Fig. 12.1. A tree shrew and representative modern primates. A, tree shrew (*Tupaia*). B. lemur (*Galago*). C, tarsier (*Tarsius*). D, macaque monkey (*Macaca*). E, gibbon (*Hylobates*). F, chimpanzee (*Pan*). (From Le Gros Clark, W. E., *History of the Primates*, 1949; used by permission of the Trustees of the British Museum [Natural History].)

in the case of some of the early Eocene prosimians "it is a matter of great difficulty to decide whether they should be classified as lemurs or tarsiers" (Le Gros Clark, 1949–1957). These early prosimians had characteristics indicating that they were the ancestors of the primates that followed them in succeeding epochs.

MONKEYS, APES, AND MEN Suborder Anthropoidea may be conveniently divided into two groups: (1) New World monkeys (Platyrrhini—"broad noses"), and (2) Old World monkeys, apes, and men (Catarrhini—"narrow noses"). Man resembles Old World monkeys and apes, as contrasted with New World monkeys, in having a narrow nose with nostrils close together, in having two premolar teeth (instead of three) on each side of both jaws, in having a bony canal connecting his external ear with his middle ear, and in numerous other features. Man and ape lack an external tail; monkeys of the old World have tails, although the latter are frequently more or less shortened and in any event never develop the prehensile capabilities of the tails of some New World monkeys, which serve as fifth limbs.

In many ways man is similar in structure to the great apes, particularly to the chimpanzee and the gorilla. Clearly, none of these forms are the *ancestors* of any of the others because they are all contemporaries. The chimpanzee and gorilla are as completely "modern" in their own ways as man is in his. They may be our distant cousins; they are certainly not our grandparents.

Granted that modern monkeys, apes, and men are related, how close are the relationships among the several groups and when did the evolutionary line leading to each begin to diverge from the evolutionary lines leading to the others? Unfortunately the fossil record is still incomplete at many important points, though new fossils are being discovered with encouraging regularity.

Table 12.1. AN ABBREVIATED CLASSIFICATION OF OLD WORLD MONKEYS, APES, AND MAN (CATARRHINI)

- Superfamily Cercopithecoidea
  - Family Cercopithecidae—Old World monkeys
- Superfamily Hominoidea
  - Family Pongidae[a]
    - Subfamily Hylobatinae—gibbons
    - Subfamily Dryopithecinae—e.g., *Dryopithecus*
    - Subfamily Ponginae—orangutan, chimpanzee, gorilla
  - Family Hominidae—men, living and extinct

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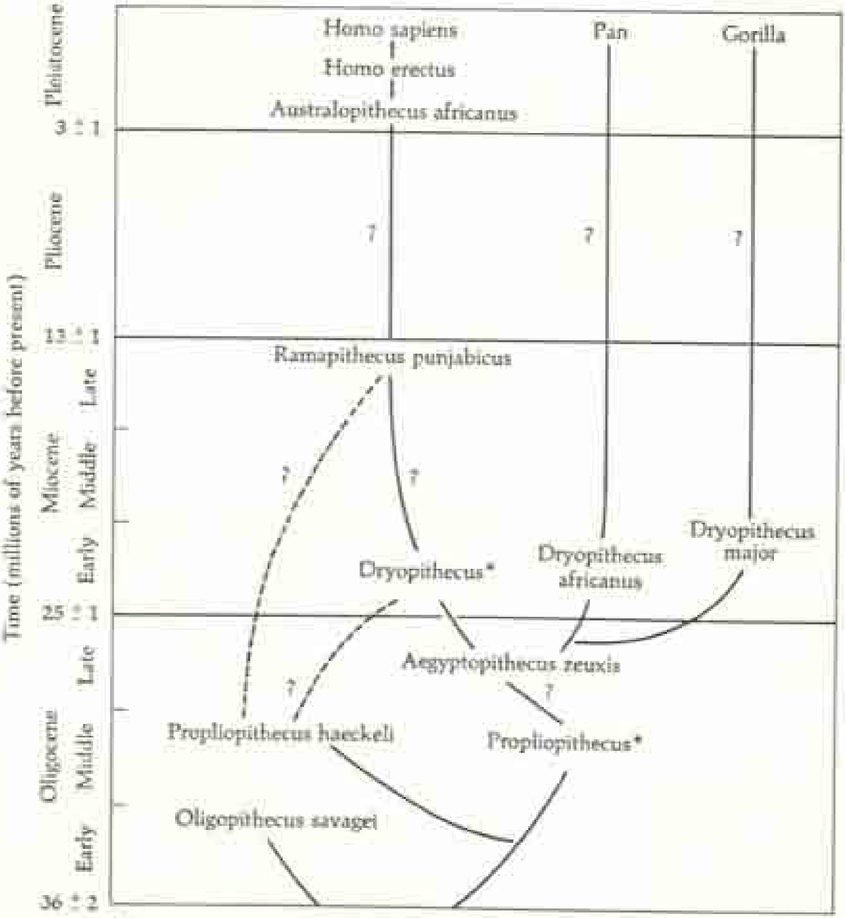
[a] In 1969 Van Valen published a classification placing family Pongidae in superfamily Cercopithecoidea; *American Journal of Physical Anthropology*, 30, 295–296 (1969).

At the present time very little is known about the evolutionary history of the New World monkeys. They have certainly gone their separate evolutionary way since Oligocene times and may not have shared a common ancestor with Old World forms more recently than the early Eocene or Paleocene.

There also is little doubt that the line leading to Old World monkeys (superfamily Cercopithecoidea, Table 12.1) diverged from that leading to apes and man as long ago as the Oligocene. A group of Oligocene primates (family Parapithecidae) known from fossils dis-


Time (millions of years before present)
Pleistocene
3 ± 1
Pliocene
13 ± 1
Miocene
Late
Middle
Early
25 ± 1
Oligocene
Late
Middle
Early
36 ± 2
Homo sapiens
Homo erectus
Australopithecus africanus
Pan
Gorilla
?
?
?
Ramapithecus punjabicus
?
?
Dryopithecus*
Dryopithecus africanus
Dryopithecus major
Aegyptopithecus zeuxis
?
?
Propliopithecus haeckeli
Propliopithecus*
Oligopithecus savagei

* The species have not yet been determined.

Fig. 12.2. Tentative family tree of primates. (Redrawn from Simons, E. L., "The earliest apes," *Scientific American*, 217 (1967), 28–35. Copyright © 1967 by Scientific American, Inc. All rights reserved.)

covered in the Fayum region of Egypt may have included the ancestors of Old World monkeys (Simons, 1967).

Turning to the apes, we find little information now available concerning the history of the Asiatic forms: gibbon and orangutan. The modern gibbon is strikingly adapted for the arm-swinging type of locomotion through the treetops (brachiation; Fig. 12.1E). Very like the gibbon, but not so long armed, was *Pliopithecus,* living in Miocene and Pliocene times. *Pliopithecus,* in turn, may well have descended from an Oligocene form known from the Fayum deposits of Egypt (*Aeolopithecus* or perhaps *Propliopithecus*). As for the orangutan, *Pongo:* "No unequivocal pre-Pleistocene ancestors of *Pongo* are known at present" (Simons and Pilbeam, 1965).

Thanks to extensive exploration of the Fayum deposits, our knowledge of Oligocene apes that probably numbered among them ancestors of the African apes, chimpanzee and gorilla, and even of man is steadily increasing (Simons, 1967). Figure 12.2 presents Simons' tentative family tree listing some of these forms and showing their possible relationships to later ones. We note the central position accorded *Propliopithecus* known largely from fossil jaws and teeth (Fig. 12.3). Some of the tooth characteristics of this little ape suggest those

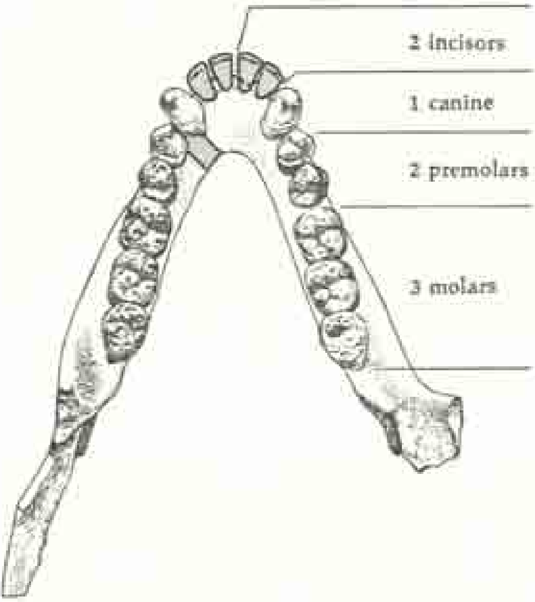


Fig. 12.3. Lower jaw of *Propliopithecus.* (Redrawn from Simons, E. L., "The earliest apes," *Scientific American,* 217 (1967), 28–35. Copyright © 1967 by Scientific American, Inc. All rights reserved.)

of man (e.g., incisor teeth vertical rather than jutting forward as in most apes; Simons, 1967). In 1966 a fairly complete skull of a similar though larger primate, *Aegyptopithecus*, was discovered—the earliest ape skull yet known. Somewhat more ape-like than *Propliopithecus*, *Aegyptopithecus* may have been ancestral to the Miocene apes of genus *Dryopithecus* and through them of the chimpanzee *(Pan)*, the gorilla, and even of man. Figure. 12.2 suggests other possible interpretations of man's Oligocene ancestry: (1) that *Pliopithecus* gave rise directly to *Ramapithecus* (see the following) and (2) that *Propliopithecus* gave rise to *Dryopithecus* but not through *Aegyptopithecus*. We await with interest further discoveries in Egypt and elsewhere. At present we can at least draw the general conclusion that apes, having the potentialities for giving rise to later apes and to man, lived in the Oligocene.

Going on to the Miocene, we find a group of apes known collectively as the DRYOPITHECINES (subfamily Dryopithecinae, Table 12.1). As indicated in Fig. 12.2, several species of these apes are known and among them are found the probable ancestors of the African apes and of man. Knowledge is most complete for *Dryopithecus africanus*, formerly known as *Proconsul* (Simons and Pilbeam, 1965). This ape had so many chimpanzee-like traits as to leave little doubt that it was ancestral to the chimpanzee *(Pan)*.

Figure 12.2 is drawn to indicate that the chimpanzee and gorilla descended from different species of *Dryopithecus*. These modern African apes are so alike in many ways that some investigators have concluded that they shared a common ancestry much later than shown in this diagram—until Pliocene or even early Pleistocene times. Again we await further evidence with anticipation.

ANCESTRY OF MAN Figure 12.2 presents the idea that some species of *Dryopithecus* was probably a distant ancestor of man. This seems the most widely held view at present, though a few investigators have concluded that man is not related to the apes but has followed a separate evolutionary line springing directly from Eocene tarsiers and lemurs.

The question of the ancestral position of *Dryopithecus* is of interest since it involves the whole question of man's relationship to the apes. Among living primates the chimpanzee and gorilla are man's closest relatives, as judged by many similarities of structure of both skeleton and "soft parts" and including such things as the type of placenta and the results of serological tests (see pp. 107–112). But there also are differences. Some of the most striking of the differences are connected with the manner in which apes travel through the trees. Modern apes are strongly specialized for arm swinging, BRACHIATION.

True, the massive gorillas no longer spend much time in the trees, but their anatomy bears incontestable evidence that their immediate forebears were brachiators. Among the specializations for brachiation are elongation of the forelimbs, reduction of the thumb so that the other fingers of the hand function as a sort of hook on the branches of trees, and shortening of the hind limbs (Figs. 12.1 and 12.4). Many correlated changes in muscles, muscle attachments, and joint structure also are entailed. If the body is heavy, great enlargement of the musculature of the shoulders and arms is necessitated.

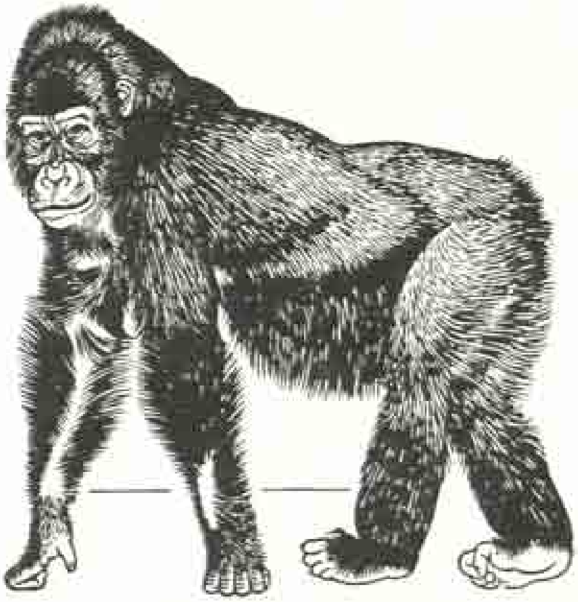


Fig. 12.4. Gorilla. (From Le Gros Clark, W. E., *History of the Primates*, 1949; used by permission of the Trustees of the British Museum [Natural History].)

Man is not a brachiator. Is he descended from ancestors who were? Relative to trunk height both modern apes and man have long arms (Washburn, 1950). Man differs from modern apes, however, in that his legs are longer than his arms; in this respect, as in some others, man resembles Old World monkeys more than he does the modern apes (Straus, 1949). In this connection it is of great interest that Miocene apes such as *Dryopithecus* also had forelimbs shorter than hind limbs (Simons, 1960). This fact suggests that elongation of the arms was a later acquisition in lines leading to modern apes specialized for brachiation and that in the lines leading to man the primitive relationship of shorter arms than legs was retained.

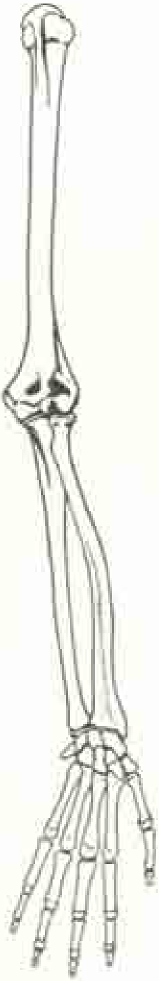


Fig. 12.5. Arm skeleton of *Dryopithecus africanus* (formerly called *Proconsul*). (Based on a reconstruction by Napier and Davis. From Le Gros Clark, W. E., *The Antecedents of Man*, Edinburgh University Press, 1959.)

Dryopithecus seems to have been a rather unspecialized brachiator. In fact, its arms possessed a sufficiently generalized structure (Fig. 12.5) so that both the arm structure of man and that of specialized brachiators among later apes might have been derived from it (see Napier and Davis, 1959; Le Gros Clark, 1960).

Great interest has been aroused recently by studies of a fossil primate known as *Oreopithecus,* living in late Miocene or early Pliocene times, some 10 to 12 million years ago. Many fossils of this form have been found in a lignite mine in Tuscany, Italy. At one time considered an Old World monkey, *Oreopithecus* has been shown by recent studies to be so unlike monkeys that it belongs in the same superfamily with apes and man—the Hominoidea (Table 12.1). Moreover, in many respects it resembles man more than it does apes, for example, in tooth structure (including small size of canine teeth), in shortness of the face, and in structure of the pelvis (Fig. 12.6). Should it therefore be regarded as a member of the family Hominidae? This has been suggested, but the suggestion also has been made that it should be placed in its own family (Oreopithecidae). In the latter case the interpretation would be that its manlike traits arose by parallel evolution and that it was not ancestral to man (Straus, 1963; Simpson, 1963).

Perhaps the most interesting trait of *Oreopithecus* is the broad, somewhat basinlike pelvic girdle, resembling that of man (Fig. 12.10C). The lumbar vertebrae (lower back) are unusually broad and robust. These characteristics together suggest that the animal walked in an erect position. The fact that the forelimbs were longer than the hind limbs suggests, however, that its principal mode of locomotion was brachiation (see the preceding; Straus, 1962).

Most students of *Oreopithecus* conclude that it was not in the direct line of evolution leading to man. Nevertheless, members of that line living in the Pliocene may have resembled *Oreopithecus* in many respects. (For a detailed account of its anatomy see Straus, 1963).

Knowledge is beginning to accumulate concerning other primates that were approximately contemporaneous with *Oreopithecus*—late Miocene and early Pliocene. Especially noteworthy are fossils named *Ramapithecus* from India and *Kenyapithecus* from East Africa. At present teeth and fragments of jaws are the only portions of the body known. But these dentitions are much more manlike than is the dentition of *Oreopithecus* (Simpson, 1963). The fossils of *Ramapithecus* and *Kenyapithecus* are so closely similar that investigators differ as to whether they should be placed in separate genera. It is hoped that more complete fossils of them soon will be found. At present they suggest that a geographically wide-ranging primate with many human traits lived in early Pliocene times and perhaps was directly ancestral to man

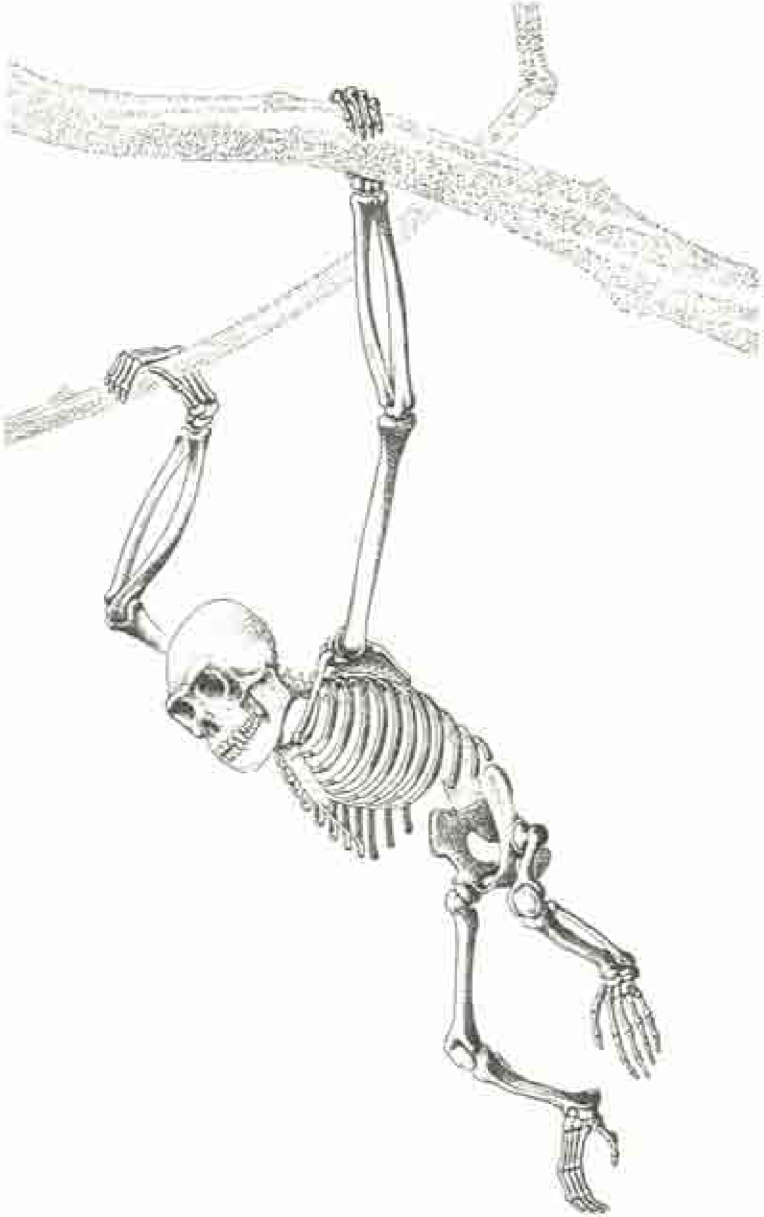


Fig. 12.6. Restoration of the skeleton of *Oreopithecus*. Height about 4 feet. (Redrawn from Simons, E. L., "The earliest representatives of man," *Scientific American*, *211* (1964), 50–62. Copyright © 1964 by Scientific American, Inc. All rights reserved.)

(Fig. 12.2). Potassium–argon dating indicates that *Kenyapithecus* lived some 14 or 15 million years ago (Leakey, 1967).

As we ascend the geologic time scale we encounter an unfortunate gap in the fossil record. We do not yet have fossils of possible human ancestors living in later portions of the Pliocene. At present we pass next to the early Pleistocene, recognizing that much of evolutionary interest must have occurred in the intervening millions of years.

CHARACTERISTICS OF *HOMO SAPIENS* Before we discuss the characteristics of Pleistocene hominids (members of the family Hominidae, Table 12.1), it will be useful to call attention to the characteristics of the species of man living at the present time, our own species. What are the characteristics of *Homo sapiens* for the evolution of which we should be watching as we study hominid fossils? For the most part we shall concentrate upon anatomical characteristics that affect the skeletal system and hence can be studied in fossils:

1. *Brain.* The large brain of *Homo sapiens* causes the brain case or cranium of the skull to have an average capacity of about 1350 cm^3. Normal human brains vary greatly in size, however, with the result that cranial capacities vary all the way from 900 to 2300 cm^3 (Le Gros Clark, 1959). Significantly, within this range there is no correlation between brain size and degree of intelligence. As extremes among notable men of letters we may cite Anatole France, with a brain volume of 1100 cm^3, and Jonathan Swift, with a brain volume of about 2000 cm^3.

The large size of brain, particularly of the frontal lobes of the cerebral hemispheres, has resulted in development of a relatively high forehead.

2. *Upright posture.* The upright posture of *Homo sapiens* entails a whole series of anatomical changes as compared to the structure of primates that do not have this posture. The skull is balanced on the upper end of the vertebral column instead of projecting anteriorly from it. This change, plus other factors such as expansion of the brain case, is accompanied by the shifting forward of the foramen magnum (the opening through which the spinal cord exits from the skull and enters the vertebral column), changing from the posterior position it occupies in forms that walk on all fours. Apes, with their partially upright posture, show an intermediate condition in this respect (Fig. 12.7). The upright posture in *Homo sapiens* is made possible by a lumbar curve in the vertebral column—a forward bending of that column in the "small" of the back. Apes lack such a curve (Fig. 12.7).

One of the greatest changes in the skeletal system connected with upright posture concerns the pelvic girdle. In *Homo sapiens* the ilium bones are expanded to form a sort of basin supporting the internal

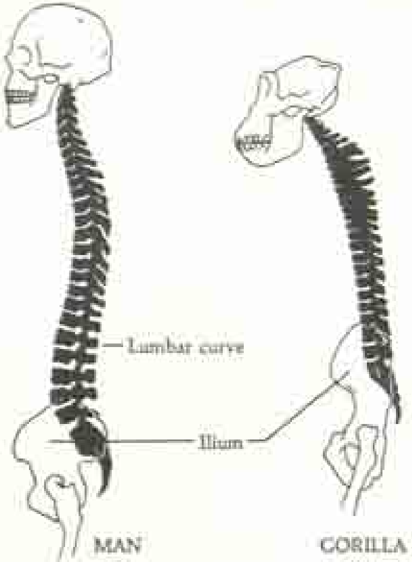


Fig. 12.7. Comparison of skull, vertebral column, and pelvis of man and gorilla. (Redrawn from Boule and Vallois, *Fossil Men*, The Dryden Press, 1957, by permission of Holt, Rinehart and Winston, Inc.)

organs of the body cavity. In forms that do not walk upright the ilia lack this supportive function and have a much more elongated shape (Fig. 12.7).

The legs of *Homo sapiens* are elongated, with relatively straight bones in upper and lower segments, and they terminate in a characteristic foot, most of the lower surface of which is in contact with the ground (plantigrade).

3. *Bipedal locomotion.* The upright posture in man is connected with the fact that he is bipedal—walking erect on two feet. Even arboreal primates may approximate upright posture more or less closely. We have seen that this posture was strongly evident in the brachiator, *Oreopithecus.* But by contrast, hominid ancestors forsook the trees and became terrestrial. The change to bipedal erectness may not have occurred all at once.

Straus (1962) has distinguished three types of bipedal erectness: (1) bipedal *running,* with knees bent (many primates do this); (2) bipedal *walking,* with knees bent (chimpanzees and gorillas do this); and (3) bipedal *standing* with knees straightened (Straus considers this characteristic of man alone).

Somewhat similarly, Le Gros Clark (1967) has distinguished between a *running* gait and a *striding* gait. The latter would involve straightening of the knee.

Readers may wonder how we can know anything about the gaits of the prehistoric hominids. From the shapes of the bones, especially the positions of attachments of ligaments and muscle tendons to those bones, a skilled anatomist versed in the action of muscles in modern animals can make many valid deductions about the movements that the long-vanished muscles of prehistoric creatures must have produced.

4. *Teeth and associated structures.* Of the numerous distinguishing characteristics possessed by the teeth of *Homo sapiens,* we shall list only a few outstanding ones, emphasizing those in which human teeth and jaws contrast with those of apes.

Homo sapiens differs from apes in the arrangement of the teeth. In apes the incisors are large and the front of the jaw is broad (Fig. 12.9). The canines are large, projecting tusks, and the premolars and molars extend backward from them in straight rows. The whole effect is that of a straightsided "U." By contrast the human tooth row resembles a smoothly rounded parabola without sharp bends (Fig. 12.8); the incisors are small, and the canines are not large and projecting as they are in apes. In apes there is characteristically a gap or diastema between the incisor teeth and the canine tooth on each side of the upper jaw; the canine tooth of the lower jaw fits into this space when the mouth is closed. *Homo sapiens,* lacking the projecting canines, also lacks this "simian gap" in the upper tooth row.

In apes the first premolar teeth in the lower jaw have a cutting

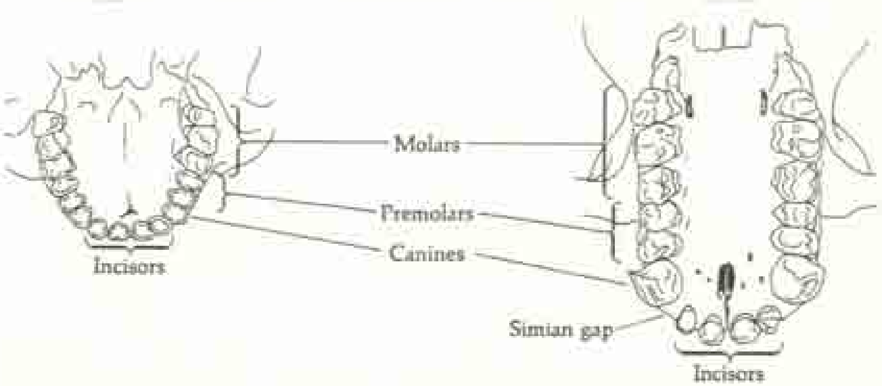


Fig. 12.8. Upper dental arches of man and gorilla. (Redrawn from Weidenreich, F., *Apes, Giants, and Man,* Copyright 1946 by The University of Chicago. Used by permission of The University of Chicago Press.)

edge (are sectorial). In *Homo sapiens* the first lower premolar does not have this character.

A characteristic of the jaw of modern apes related to the large incisor and canine teeth is the development of a reinforcing ledge of bone extending backward from the symphysis of the jaw (Fig. 12.9). This "simian shelf" is lacking in man, both *Homo sapiens* and his predecessors, and in many, at least, of the Dryopithecinae (e.g., *Dryopithecus africanus*, Fig. 12.9).

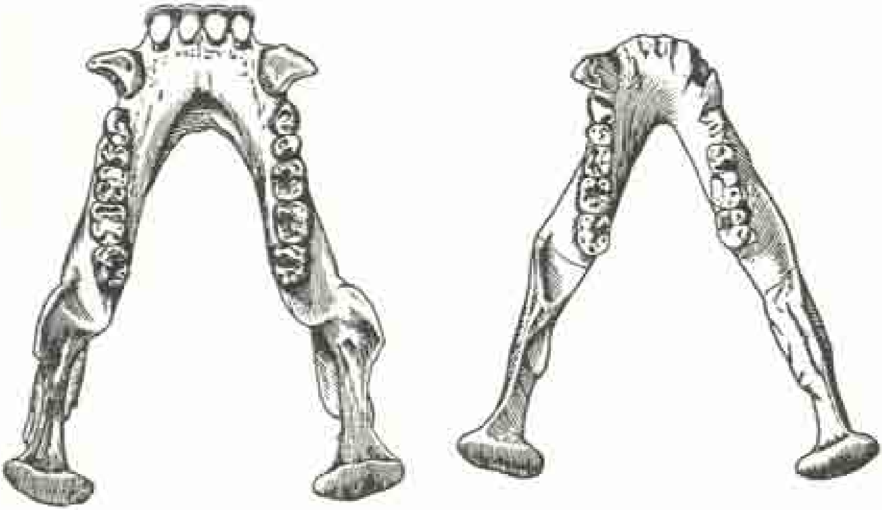


Fig. 12.9. Lower jaws of chimpanzee (left) and of *Dryopithecus africanus* (formerly called *Proconsul*). (From Le Gros Clark, W. E., *History of the Primates*, 1949; used by permission of the Trustees of the British Museum [Natural History].)

Another result of the small teeth in modern *Homo sapiens* is that the tooth row is short, as compared to that of apes and some of the earlier hominids. The longer tooth row possessed by these latter causes the face to protrude into a sort of muzzle—to be *prognathous*. The face of modern *Homo sapiens*, on the other hand, does not project in this fashion; the profile is more nearly vertical *(orthognathous)*.

In apes and earlier hominids with their long tooth rows, the upper edge of the lower jaw extends forward farther than does the lower—there is no projecting chin. In modern *Homo sapiens* with his shortened tooth row, the lower margin of the jaw extends forward as a chin (see Fig. 12.17). This chin may have evolved as an external buttress against the active stresses to which the broad human jaw is subjected in use (Du Brul and Sicher, 1954).

Modern *Homo sapiens* lacks heavy ridges of bone projecting over the eyes (supraorbital torus) possessed by apes and earlier hominids. In apes the eyebrow ridges are part of a series of ridges other portions of which provide attachment (origin) for powerful chewing muscles. In modern *Homo sapiens* the chewing apparatus is reduced and the skull is expanded, providing origin for the chewing muscles without development of ridges.

In summary we may characterize the striking features of the skeletal anatomy of modern *Homo sapiens* as follows: (1) cranial capacity varying from 900–2300 cm^3; (2) high forehead without projecting eyebrow ridges; (3) upright posture with bipedal locomotion, reflected in structure of skull, vertebral column, pelvis, and legs; (4) dental arch a smoothly rounded parabola; (5) canine teeth not projecting beyond the level of the other teeth; (6) no simian gap; (7) first lower premolar not sectorial; (8) lower jaw with a projecting chin; (9) no simian shelf; and (10) face orthognathous.

Having reviewed some of the skeletal features of the end product of human evolution we now turn our attention to earlier hominids.

HOMINID EVOLUTION IN THE PLEISTOCENE

It will be convenient to divide the Pleistocene history of hominid evolution into stages.

STAGE 1: UPRIGHT POSTURE, SMALL BRAIN

Steadily mounting evidence indicates that by early Pleistocene times hominids had attained an upright posture, though they retained ape-sized brains. These earliest hominids are conveniently called the australopithecines.

AUSTRALOPITHECINES The first-known fossil of these primates was the skull of a child discovered in South Africa in 1924 (for a fascinating account by the discoverer see Dart, 1959). Dart christened the owner of this skull *Australopithecus africanus*, a name that taken literally signifies that it belongs to a different genus and species from *Homo sapiens*. (The name written first and capitalized is that of the *genus*; the name written second and not capitalized is that of the *species*, see pp. 317.) "Australopithecus" means "southern ape"; this original child and fossils of adults subsequently discovered were grouped together into a subfamily, Australopithecinae, of the family Pongidae (apes, Table 12.1). Subsequent discoveries and thorough investigation revealed, however, that these South African forms have many characteristics of man combined with an ape-sized brain and some other apelike characteristics. Their resemblance to apes has been emphasized by some writers (e.g., Zuckerman, 1954) and their hominid characteristics by others. The controversy as to whether they are apes or men is in itself interesting. Suppose that remains of an actual "missing link" between apes and man were discovered: We may be sure that it would be like an ape in some respects that some investigators would classify it as such and so like man in other respects that other investigators would classify it as human. Here are the australopithecines in the midst of just such a controversy! Because, as we shall see, the characteristics they share with *Homo sapiens* are so fundamental and significant that there is at present almost a consensus among investigators that they should be included in our own taxonomic family, Hominidae. Consequently, we refer to them as hominids.

The australopithecines were of small stature, averaging in the neighborhood of four feet tall. One point of great significance about them is that they walked nearly or completely upright. The vertebral column had a distinct lumbar curve. As shown in Fig. 12.10, the pelvic girdle was strikingly like that of *Homo sapiens*, with its broadly expanded ilium, and unlike that of apes. Structure of the pelvic and leg bones indicates that bipedal locomotion was not as perfected as it is in modern man. Straus (1962) doubted that australopithecines were capable of prolonged standing with knees straightened, and Le Gros

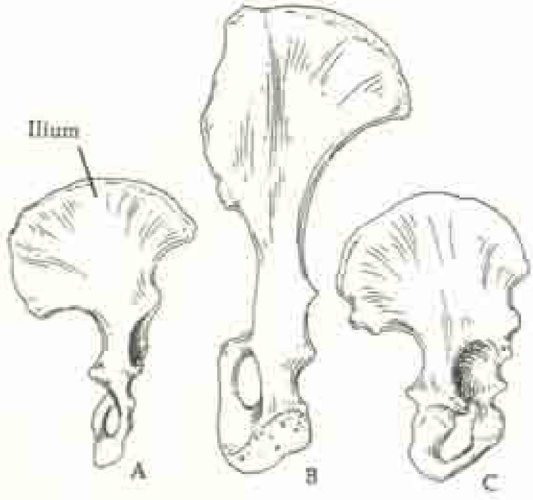


Fig. 12.10. The right pelvic bones of: A, *Australopithecus;* B, chimpanzee; C, *Homo sapiens.* (Redrawn from Broom and Robinson, "Further evidence of the structure of the Sterkfontein ape-man *Plesianthropus*," Transvaal Museum, *Memoir* 4.)

Clark (1967) concluded that they were capable of running but not of modern man's striding gait (see the preceding). The position of the foramen magnum forward under the base of the skull also may be indicative of upright posture.

The teeth were strikingly human. Australopithecines agreed with *Homo sapiens* (p. 241) in that (1) the dental arch was a smoothly rounded parabola (Fig. 12.8), (2) the canine teeth did not project beyond the level of the other teeth, (3) there was no simian gap, and (4) the first lower premolar was not sectorial.

What were their most striking differences from *Homo sapiens* himself? The skulls of these little people were notable for large jaws and teeth and small brain cases. The teeth were actually larger than those of modern man. As a result of the tooth and jaw development the face was prognathous and lacking a chin (Fig. 12.11). Eyebrow ridges projected over the eyes.

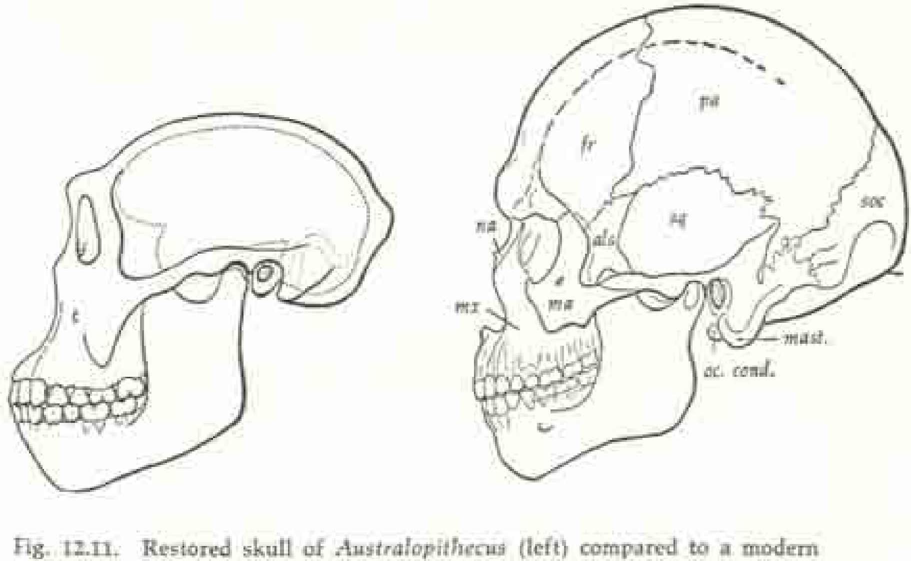


Fig. 12.11. Restored skull of *Australopithecus* (left) compared to a modern human skull (Tasmanian aboriginal). *als*, alisphenoid. *fr*, frontal. *ma*, malar. *mast.*, mastoid process. *mx*, maxilla. *na*, nasal. *oc. cond.*, occipital condyle. *pa*, parietal. *soc.*, supraoccipital. *sq*, squamosal. (From Gregory, W. K., *Evolution Emerging*. Copyright 1951 by the American Museum of Natural History. Courtesy of the American Museum of Natural History.)

The small, flat braincase stood in marked contrast to the large face. Casts of the interiors of the skulls reveal that the brain was of human form but was so small as to be outside the range for normal brains of *Homo sapiens*. Australopithecine brain capacity ranged from about 450 cm^3 up to 600 cm^3 or slightly above (Le Gros Clark, 1967). We have seen that the smallest normal capacity for *Homo sapiens* is about 900 cm^3. Indeed the australopithecine brain size is comparable to that of apes. The range for the gorilla is 340–752 cm^3 (Le Gros Clark, 1967). Yet a gorilla with a brain of 650 cm^3 weighs four or five times as much as did these early men. Evidently the lightly built australopithecines with their small brains represent an evolutionary trend quite unlike that which culminated in the bulky gorilla.

One of the principal advantages of bipedal locomotion lies in the fact that the hands are freed for nonlocomotor duties, such as the use of tools and weapons. Did these small-brained australopithecines make and use tools? Many mammals, and even occasional birds (e.g., the woodpecker finch of Galapagos, p. 307), at times *use* natural objects as tools. But man far surpasses other creatures in the ability to see a need and then to manufacture a tool to meet that need, though chimpanzees can fabricate simple tools. Crude stone implements have been found with australopithecine fossils. While some investigators have doubted that the australopithecines themselves made the tools, there seems little basis for such doubt (Le Gros Clark, 1967). Furthermore, Dart (1956 and 1959) has presented evidence that the australopithecines may have fashioned implements and weapons of *bone*. Interestingly, quantities of baboon skulls fractured in such a way as to suggest that the creatures were killed by skillful blows on the head have been found with australopithecine remains.

Actually, use of weapons by these little people would seem to have been essential to their survival. How else could they have protected themselves against the large predatory animals of Africa? Unlike baboons, their canine teeth were not fangs. Their hands were not armed with claws. They had no great physical strength. They lacked the antelope's swiftness in flight from a predator's attack. Weapons, however crude, would seem to be the answer. Furthermore, at least one type of autralopithecine seems to have been a hunter, an eater of meat.

There seem to have been two main types of australopithecines. (1) One type was lightly constructed, with a tooth structure indicating an omnivorous, though perhaps predominantly carnivorous, diet. Le Gros Clark (1967) called this the GRACILE TYPE. (2) The other type was of heavier body structure, with massive cheek teeth that suggested a more herbivorous diet. Le Gros Clark called this the ROBUST TYPE. Leg structure suggests that this was the more slow-moving of the two.

The first australopithecines discovered were of the gracile type and hence belong to the genus *Australopithecus*. When the robust type was discovered it was called *Paranthropus*, which indicates that it was regarded as belonging to a different genus (Robinson, 1956 and 1967a and b). The classifying of fossil hominids is filled with disagreements;

space forbids our discussion of pros and cons. Suffice it to say that most students of human evolution now regard both types as members of the genus *Australopithecus*, distinguishing the gracile type as *A. africanus* and the robust type as *A. robustus* (*e.g.*, Leakey, 1963; Le Gros Clark, 1967; Straus, 1967). Classifying them thus suggests that they were related species that probably did not interbreed with each other.

What were the relationships of the two types to each other? Here, as is so commonly the case, there are at least two points of view. Most investigators conclude that the gracile type was the original one and that the robust type arose from it as a side branch specialized for a more herbivorous diet. Robinson (1967a and b), however, has postulated that the robust type was the original one. Most primates are predominantly herbivorous; this suggests the likelihood that the ancestral australopithecines may have been plant eaters. There is evidence that during the time of australopithecine evolution prolonged drought afflicted large portions of Africa, causing the forest to be replaced by dry, grassy plains. Robinson has suggested that the robust type of australopithecine continued to inhabit the dwindling forests, with their accustomed supplies of plant food, but that australopithecines in less favored regions were forced to become carnivorous to survive. Even baboons will turn to flesh eating if their supply of plant food becomes scarce. In some such manner the gracile, hunter type may have arisen from the robust type. So we have the two hypotheses and await further evidence with interest (see also Le Gros Clark, 1967, Chap. 9).

That australopithecines were not confined to South Africa was indicated by the discovery of fossils of the robust type in Olduvai Gorge in East Africa (Tanzania; Leakey, 1959). This form was originally placed in the genus *Zinjanthropus* but is now regarded as another species in the genus *Australopithecus*, *A. boisei* (Leakey, 1963). The bones came from an early Pleistocene campsite and were accompanied by crude stone tools. Use of the potassium-argon method of dating has indicated that these East African australopithecines lived some 1.75 million years ago (Leakey *et al.*, 1961). Use of the fission-track method of dating has indicated an age of 2.03 ± 0.28 million years (Fleischer *et al.*, 1965). Considering the variables involved in these methods of dating, this is good agreement.

Did australopithecines live on continents other than Africa? Readers will not be surprised to learn that this question has been answered both "yes" and "no." Jaw fragments from Java have been given the name *Meganthropus* and are considered australopithecine by some investigators, but such a conclusion has been doubted by others. Again we await further evidence.

Were the australopithecines ancestral to later man, including ourselves? Again we find "yes" and "no" answers, but at present the "yes" seems to be more numerous. The point of view was succinctly stated by Mayr (1963): "Indeed, the Australopithecines do not have a single character or combination of characters that would clearly disqualify them from the main line of human evolution."

It is the gracile type of australopithecines that are regarded as ancestral to later men. Indeed, Robinson (1967b) has suggested that the gracile type was so like its presumed descendants that it should be placed in the same genus with them: *Homo*. In modified form this revives the suggestion made by Mayr in 1950 that australopithecines be considered to belong to genus *Homo* and be called *Homo transvaalensis* (Mayr, 1950). Mayr subsequently changed his mind and agreed that the great difference in brain size was sufficient to warrant recognition of two genera: *Australopithecus* and *Homo* (Mayr, 1963). Readers may consider that the disagreement involves a small and technical point, but it emphasizes the smallness of the differences, other than in brain size, separating australopithecines from later hominids.

We recall that the gracile type of australopithecines are believed to have been hunters and fighters. In his book *African Genesis*, Robert Ardrey (1961) has made much of the possible effect of our inheritance from them in shaping our own psychology and social attitudes.

In 1964 L. S. B. Leakey and his associates set up a new species in genus *Homo* to accommodate some hominid fossils found in Olduvai Gorge in East Africa: *Homo habilis* (Leakey *et al.*, 1964). The fossils came from two strata in the walls of the gorge, called Beds I and II, and so were of varying age (Bed I being the older). They were contemporaneous with the robust type of australopithecine called *Australopithecus boisei*. Leakey and his collaborators considered that they were more like later men than were the australopithecines, differing in many small respects and having "a mean cranial capacity greater than that of members of the genus *Australopithecus*, but smaller than that of *Homo erectus*" (the next stage in human evolution; see following).

At the time these words are written the fossils in question are the center of lively controversy (the normal state for investigations into human evolution!). We will not attempt to resolve the controversy; rather we will state the various positions being taken at this time. We note that almost every possible point of view is represented:

1. The fossils represent a new species in genus *Homo*, *H. habilis*, intermediate between australopithecines and *H. erectus* (Leakey *et al.*, 1964; Tobias, 1965).

2. The fossils belong to the genus *Australopithecus* (Le Gros Clark, 1967). The fragmentary nature of the fossils makes difficult accurate determination of cranial capacity. The number of australopithecine

skulls available is too small to give confidence that we know the *range* of brain sizes actually characterizing them. Recall that the size varies greatly in modern man (p. 239). Thus, if the estimated 680 cm^3 for "*H. habilis*" is accurate, that size may have been within the range of sizes found among australopithecines.

3. The Bed I fossils belong to *Australopithecus*, the Bed II fossils to *H. erectus* (Robinson, 1967a and b). This suggestion is based on the conclusion that there is an increase in brain size and in perfection of stone implements in Bed II fossils as compared to Bed I fossils (Robinson, 1967b).

4. The fossils represent an early form of *H. erectus* (Montagu, 1965).

Eventually a consensus will develop as to the status of "*H. habilis.*" In the meantime, what conclusion may we draw from the differing points of view? The fact that specialists can hold such a range of views indicates that the transition between australopithecines of the gracile type and *H. erectus* was indeed a small one, even in the matter of brain size. And the differences in structure of the teeth, subjects of the most intensive study, may be even less. Le Gros Clark (1967) stated: "Indeed, on the basis of the dental characters it is not always easy to draw a clear distinction in some individual specimens between the two" (*Australopithecus* and *H. erectus*). We should expect these things to be true if australopithecines were indeed ancestral to *H. erectus*.

In summary, we are indebted to our australopithecine ancestors for upright posture, freeing the hands for the manufacture and use of tools. We have seen that the primates as a whole are characterized by varying degrees of emancipation of the forelimbs from the duties of locomotion (p. 228). Different primates vary in the extent of this emancipation, and the brachiators among them have in a sense reversed the trend, although most of them have done so without serious loss of ability to use the hands in grasping objects. Man without tools would be a most undistinguished member of the animal kingdom. Tools, developed and employed by the human brain, have made possible the development of civilization. To a very considerable extent man's cultural attainments have been, and continue to be, measured by the tools employed, as implied in our designation of cultures as Old Stone Age (Paleolithic), New Stone Age, Bronze Age, Iron Age, Age of Steam, Age of Electricity, and so on. Accordingly, the importance of the changes that paved the way for development of the ability to use tools cannot be exaggerated. The primary change making this possible was attainment of upright posture which, as the australopithecines and perhaps even *Oreopithecus* show us, came at the dawn of human evolution and *preceded* the great development of brain that was later to characterize man. Hands free to make and use tools came first; brain development adequate for making the most effective use of those hands in devising, using, and perfecting tools came later. Probably the brain development never would have occurred had not the hands been available first. In this connection it is interesting to recall that in the evolution of the horse, brain development lagged behind adaptive changes in the limbs. *Hyracotherium* with its primitive brain nevertheless had begun the evolutionary changes in the limbs that were to characterize horse evolution (pp. 211–212; Fig. 11.6).

STAGE 2: BRAINS OF INTERMEDIATE SIZE

As we have seen, upright posture freed the hands from locomotor duties and made possible, at least potentially, the manufacture and use of tools. The brain, however, was still abnormally small for a primate that could be called human. In subsequent evolution to the *Homo sapiens* stage the brain increased in size and the jaws and teeth decreased. What fossil remains do we have indicating the steps in this process?

Long before the first australopithecines were discovered unusual human remains had been found on the Asiatic island of Java. Here, in 1891, Dubois collected a skullcap with a few associated teeth and bones, notably a femur. The original owner of these bones was named *Pithecanthropus erectus*, meaning "erect ape-man." For years a controversy as to whether the creature was ape or man raged around these meager fossils. Fortunately he and his fellows are now known from portions of four skulls and some additional bones. More recently similar fossils were found in a cave near Peking, China. Here remains of more than 40 individuals have been found (Chang, 1962). These fossils were named *Sinanthropus pekinensis*, but subsequent investigation revealed that they are so similar to the Javan fossils that they certainly should be included in the same genus. Accordingly they have been renamed *Pithecanthropus pekinensis*. But here, even more than in the case of the australopithecines, we are confronted with the question as to whether in reality these men should not be included in the genus of men, *Homo*. Mayr (1950) suggested that they be classified as *H. erectus*, and this name has been widely accepted. They are also sometimes called by the vernacular name "pithecanthropines."

H. erectus walked upright, as had the australopithecines, but was slightly taller than the latter, averaging in the neighborhood of five feet in height. The cranial capacity of three of the Javan skulls ranged from 775–900 cm^3, while the Peking specimens showed still greater capacity, ranging from 915–1225 cm^3 (Straus, 1967). Thus the known brain sizes nearly bridge the gap between australopithecines and modern man. Perhaps no australopithecine brain was quite as large as the smallest *H. erectus* brain, but the gap in sizes is small, and the controversial fossils known as "*H. habilis*" (p. 248) may fill it, or nearly so. At the other extreme we note that the largest cranial capacity known for *H. erectus* was not far below the 1350 cm^3 that constitutes the average of modern cranial capacities and was well above the lower limit of 900 cm^3 for normal brains of modern man (p. 239). The average of all known *Homo erectus* specimens was about 1000 cm^3. In part this small average size was probably a reflection of small body size, but it is to be noted that the modern Bushman, who has about the same body size, has a cranial capacity of around 1300 cm^3 (Le Gros Clark, 1949–1957). The evidence is that the Javan representatives with their smaller brains lived somewhat earlier than did the slightly larger-brained *H. erectus* from China—500,000 and 360,000 years ago, respectively (Straus, 1967).

The small brain was housed in a flattened skull with little or no forehead and with brow ridges projecting "to form a prominent and uninterrupted shelf of bone overhanging the eye sockets" (Le Gros Clark, 1959; Fig. 12.12). The braincase was broadest at the level of the ears and was pointed in back rather than broadly rounded.

As in the australopithecines, the teeth were large and the face prognathous and chinless. As noted previously, the molar teeth were so like those of australopithecines as to be almost indistinguishable.

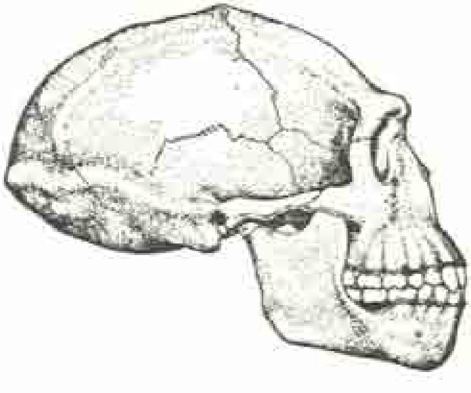


Fig. 12.12. Restored skull of *Homo erectus* from Java. (After McGregor and von Koenigswald; from Romer, A. S., *Vertebrate Paleontology*. Copyright © 1933, 1945, and 1966 by The University of Chicago. Used by permission of The University of Chicago Press.)

Was *H. erectus* confined to Asia? Three fossil jaws and a parietal bone almost indistinguishable from those of Asiatic *H. erectus* have been found in Algeria. The name *Atlanthropus* was given to these fossils, but they are now generally regarded as remains of a North African *H. erectus.* In South Africa fossils given the name *Telanthropus* were discovered. Further study convinced Robinson, one of the discoverers, that the hominid should be reclassified as *H. erectus* (Robinson, 1967a). But there is at present no consensus on this; Le Gros Clark considered "Telanthropus" to be an australopithecine of the gracile type (Le Gros Clark, 1967). So again we await further evidence. A cranium identified as *H. erectus* also has been found in Olduvai Gorge, Tanzania, East Africa. The potassium-argon dating indicates an age of 490,000 years (Le Gros Clark, 1967). We recall also that Robinson regarded the *"H. habilis"* specimen from Bed II in Olduvai Gorge as *H. erectus* (p. 249).

Did *H. erectus* live in Europe? The famous Heidelberg jaw (Fig. 12.13), long a bone of contention, is considered by some investigators as *H. erectus,* but as usual this is denied by others. In 1965 three teeth found in Hungary were identified as belonging to this species (Kretzoi and Vértes, 1965).

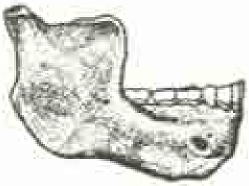


Fig. 12.13. The Heidelberg jaw. (From Romer, A. S., *Vertebrate Paleontology.* Copyright © 1933, 1945, and 1966 by The University of Chicago. Used by permission of The University of Chicago Press.)

Thus we see that in about the middle of the Pleistocene, some half-million years ago, there lived in Asia and probably other regions people who walked upright but who were larger in body and brain than were the South African australopithecines. Judged by modern human standards their brains were still small, however. Were these small brains indicative of markedly low intelligence? To answer this question we would wish more information about their culture than is available. Evidence from the caves in which the remains of the Peking men were found indicates that these people manufactured stone tools of quartz and that they used fire. They were hunters, and judging by the cracked bones and skulls found associated with their remains they regarded brains and bone marrow as especial delicacies. There is some evidence that human brains and marrow were as welcome articles of diet as were those portions of lower animals. Le Gros Clark (1949–1957) suggested that their habits may have been somewhat similar to those of headhunters of modern times in Borneo and elsewhere and that they may have been almost as advanced culturally as are some of the less civilized peoples of today. But they were back near the beginning of being human; as Gregory (1951) expressed it, "Whatever the inherent possibilities of the Javan and Peking people's brains may have been, their bank of learning and tradition was still in a relatively early stage of accumulating a favorable balance."

TRANSITIONAL FORMS We have now reached about the midpoint of the Pleistocene in time, and in human development we have reached a stage in which the brain averaged smaller than that of *Homo sapiens* though some individual brains were within the range of variation exhibited by the latter. Teeth were still large, and jaws were chinless. Skulls were flattened and had heavy eyebrow ridges. This brings us to a portion of the Pleistocene from which human remains now known are few and fragmentary. But such as they are, they exhibit trends from the *H. erectus* stage toward the two types of men found in later portions of the Pleistocene: Neanderthal man and *H. sapiens* of modern type.

The two oldest of these remains come from Steinheim in Germany and Swanscombe in England. The STEINHEIM SKULL is fairly complete. Its cranial capacity is estimated at about 1100 cm^3; it had heavy eyebrow ridges but a higher forehead than *H. erectus* (Fig. 12.14). In most respects it resembles the skull of *H. sapiens* (Le Gros Clark, 1955). The same is true for the SWANSCOMBE "SKULL," known only from three bones forming the roof and back of the braincase. The bones are unusually thick. The cranial capacity is estimated to have been about 1320 cm^3. Thus we see that living in the interval between the second and the third of the four glaciations in the Pleistocene (Second Interglacial) there were men resembling *H. sapiens* but of such unspecialized nature that they may well be representative of a varied population ancestral to both *H. sapiens* of modern type and to Neanderthal peoples.

Moving along in time to the interval between the third and fourth glaciations (Third Interglacial) we find the FONTECHEVADE SKULLS from

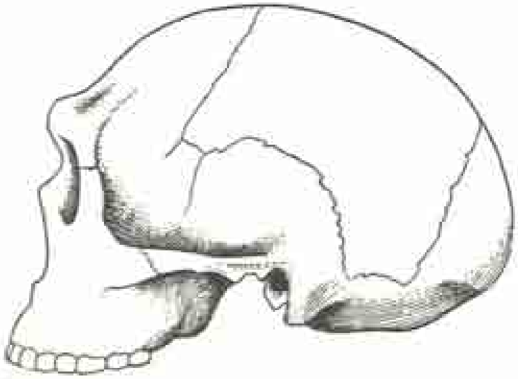


Fig. 12.14. The Steinheim skull (partly restored). (From Le Gros Clark, W. E., *The Fossil Evidence for Human Evolution*. Copyright 1955 by The University of Chicago. Used by permission of The University of Chicago Press.)

southern France. Parts of two skulls were found under a layer of stalagmite deposit in a cave. The bones, like those of the Swanscombe fossil, are unusually thick. The cranial capacity is estimated to have been greater than 1400 cm^3. The evidence is that, unlike the Steinheim (and perhaps Swanscombe) skull, these skulls lacked heavy eyebrow ridges. Interestingly enough, however, heavy eyebrow ridges did characterize another skull known from this period: the EHRINGSDORF SKULL from Germany (Fig. 12.15). This skull had a cranial capacity of about

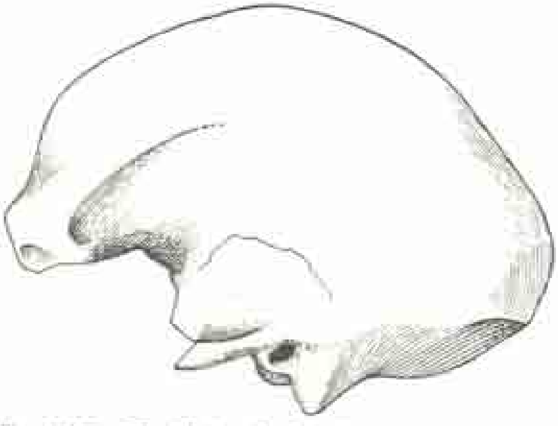


Fig. 12.15. The Ehringsdorf skull. (From Le Gros Clark, W. E., *The Fossil Evidence for Human Evolution*. Copyright 1955 by The University of Chicago. Used by permission of The University of Chicago Press.)

1450 cm^3 and a fairly high forehead. Thus it resembled Neanderthal man in brow ridges and *H. sapiens* in forehead.

We have mentioned only four of the fossils known from the second and third interglacial periods. Those we have mentioned suffice to indicate that during these periods there lived a varied assemblage of people capable in the aggregate of having been the ancestors of both Neanderthal man and *H. sapiens* of modern type. Classification of such transitional forms is difficult. Those most closely resembling *H. sapiens* are sometimes called "presapiens" (e.g., Vallois, 1954), but there is no clear indication that they constituted populations actually differentiated from their "pre-Neanderthal" contemporaries. In fact, as noted above, some *individuals* seem to have combined characteristics of both Neanderthal man and typical *H. sapiens*. Sometimes these early peoples not clearly differentiated as either Neanderthal or *H. sapiens* are called "early Neanderthals" and are represented as ancestral to both later or "classic" Neanderthals and to *H. sapiens* (Howell, 1957). But it would seem as logical to call them "early *Homo sapiens*" and to represent them as ancestral to classic Neanderthals and to later *H. sapiens* (essentially the view of Le Gros Clark, 1955).

Hominid fossils found in China form a relatively complete series of transitional forms between *H. erectus* and *H. sapiens* (Chang, 1962). Some of these Chinese fossils are Neanderthaloid in certain respects.

The transitional forms we have mentioned are now usually classified in our own species, *H. sapiens*, though sometimes they are regarded as being in different subspecies from ourselves (Campbell, 1963; Straus, 1967). Evidently, like modern man, prehistoric peoples at all stages have been a varied lot. From the varied assemblage of transitional forms of some 200,000 years ago (Oakley, 1964) two fairly distinct types emerged: Neanderthal man and *H. sapiens* of modern type.

STAGE 3: BRAINS OF LARGER SIZE

NEANDERTHAL MAN During the first portions of the fourth or last glaciation, distinctive groups of people collectively known as Neanderthal man lived in Europe. Known remains of these people are more numerous than are those of the men discussed above, some 90 individuals being representated by skeletal remains of varying completeness.

Typical Neanderthal men had brains at least as large as those of modern man. The adult cranial capacity ranged from about 1200 to more than 1600 cm^3, with an average of about 1450 cm^3 (Straus, 1967). The brain was somewhat differently proportioned than is ours, the lower and posterior portions being large and the upper and anterior portions being less well developed. It has been inferred that the difference indicates lower intelligence, but such a conclusion may not be warranted. Straus (1967) stated that "despite earlier claims to the contrary, the endocranial casts suggest a brain in no way inferior to that of modern man."

At any rate, the peculiarities of the brain affected the shape of the skull, which is called "bun-shaped" because of its protrusion at the back of the head (Fig. 12.16). The forehead was low and slanting, and heavy eyebrow ridges projected over the orbits of the eyes. As in *Homo erectus,* the greatest width of the skull was at the level of the ears, the skull tapering upward from that point. By contrast, the shape of the modern human brain causes the skull to bulge above the level of the ears, the greatest width occurring at this higher level. The teeth were large, and there was no chin.

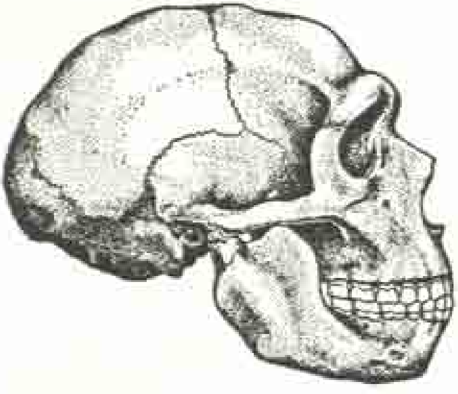


Fig. 12.16. Skull of Neanderthal man. (After McGregor; from Romer, A. S., *Vertebrate Paleontology.* Copyright © 1933, 1945, and 1966 by The University of Chicago. Used by permission of The University of Chicago Press.)

The Neanderthal peoples were shorter than are most modern groups; the men seem to have averaged a little more than five feet in height and the women somewhat shorter. This small stature was due in part to the short legs, in which the shortness of the lower leg (shin) was particularly marked. They were stout, powerfully built people. Early restorations seemed to indicate that these people did not have a fully upright posture, but later investigations have shown this interpretation to have been incorrect, having arisen from the fact that the first specimen restored was pathological, the skeleton of an individual suffering from severe arthritis (Straus and Cave, 1957). They had stocky chests, broad shoulders, and large hands, though the fingers were short.

The Neanderthal culture was of the Old Stone Age type known as Mousterian; chipped flint tools and crude carvings remain as evidence. The tools were made much more skillfully than were any of those found with remains of earlier men. Some of the skeletons give evidence of reverent burial and are accompanied by ornaments and flint tools; the implication would seem to be that these people had some form of belief in immortality of the spirit.

Typical or "classical" Neanderthal peoples are best known from Europe, but their remains "have been discovered at many localities in the eastern hemisphere north of the equator, i.e., in many countries of Europe and the Near East, thus extending from the Atlantic Ocean eastward to Iran and Uzbekistan (and possibly in the Far East and North Africa as well)" (Straus, 1967). Space forbids our mentioning all of these fossils by name. Suffice it to say that they show much variation, in some cases combining Neanderthaloid traits with characteristics of modern man. In this connection the skeletons found in caves on Mount Carmel in Palestine are interesting in that both Neanderthaloid and *H. sapiens* characteristics are represented. The various skeletons are sometimes regarded as having belonged to members of a single population. These people have been variously considered to be (1) hybrids between typical Neanderthals and typical *H. sapiens* or (2) intermediate forms in the ancestry of typical Neanderthals, representing stages by which the earlier transitional forms gave rise to the classic Neanderthals. It is possible, however, that the skeletons do not represent members of a single population but that "an early variety of modern man lived side by side, so to speak, with a Neanderthal variety" (Stewart, 1960).

This raises the question as to whether or not a distinct line can be drawn between Neanderthal man and *H. sapiens*. Because typical Neanderthal peoples are possessed of a set of distinctive characteristics, some investigations have concluded that while Neanderthal man should be placed in the same genus with ourselves he should be regarded as a separate species, i.e., he should be classified as *H. neanderthalensis*. However, in view of the varying combinations of characteristics noted above, as well as of the possibility that Neanderthal people and *H. sapiens* might have interbred if they came into contact, many investigators place Neanderthal man in our own species, *sapiens* (Campbell, 1963; Straus 1967). If desired he may be regarded as constituting a separate subspecies in that species and be called *H. sapiens neanderthalensis*.

As we might expect, dating of the various Neanderthal specimens yields varying ages (Oakley, 1964). It seems that Neanderthals were in existence at least as long ago as 70,000 years and that they may have continued up until some 30,000 years ago, becoming extinct before the end of the last glacial period. They were succeeded by *H. sapiens* of modern type. Among the first of these was Cro-Magnon man. What happened to the Neanderthal people? Were they conquered and exterminated? Or did they intermate with the Cro-Magnon people and thus disappear as a separate type? Both possibilities have been suggested, but actually our ignorance on the subject is complete because, as Howell (1957) stated, "There is no clear-cut evidence which would indicate that the classic Neanderthals either (1) lived contemporaneously with the earliest of the Cro-Magnon people . . . or (2) that they interbred with the latter people." While this is true of classic Neanderthals, there is interest in the fact that in late Pleistocene times individuals were still found who combined Neanderthaloid characteristics with those of typical *H. sapiens*. How shall we account for them?

SUCCESSORS TO NEANDERTHAL MAN During the last 30,000 years or more *Homo sapiens* of modern type has lived in Europe. While our knowledge of prehistoric men of this time is the most complete for Europe, the supplanting of Neanderthal man by *H. sapiens* was apparently a worldwide phenomenon. For example, evidence from North China indicates that there *H. erectus* was succeeded by Neanderthaloid peoples, who were succeeded in turn by *H. sapiens* of essentially modern type (Chang, 1962).

Of the European forms Cro-Magnon man is one of the best known, differing from modern Europeans no more than modern peoples differ among themselves. All the characteristics of *H. sapiens* listed previously (p. 243) apply to the Cro-Magnons. They differed from typical Neanderthals in that they were taller, with a long lower (shin) segment of the leg, a probable indication of swift footedness. The skull was of modern type, with a high forehead, no heavy eyebrow ridges, and a distinctly jutting chin (Fig. 12.17). Unlike the faces of all his predecessors, the face of Cro-Magnon man was orthognathous. Teeth and jaws were like those of modern man. Comparison of the skull of Neanderthal man (Fig. 12.16) with that of Cro-Magnon man (Fig. 12.17) will make these differences clear.

Cro-Magnon man was only one of many types living during the latter part of the last glaciation and differing from each other no more than do modern peoples. Evolution from this point on was an evolution of *culture* rather than of anatomy. Techniques of manufacturing stone weapons and tools improved as time went on. Stone Age cultures or industries are classified by the nature of these stone implements and of

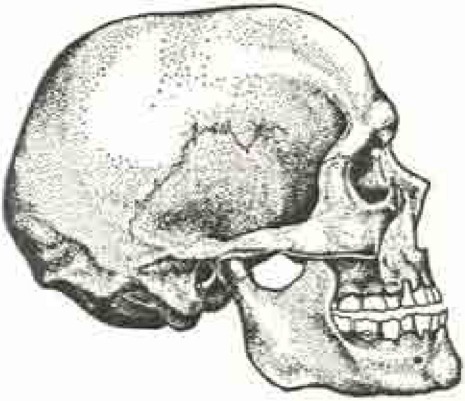


Fig. 12.17. Skull of Cro-Magnon man. (After McGregor; from Romer, A. S., *Vertebrate Paleontology*. Copyright © 1933, 1945, and 1966 by The University of Chicago. Used by permission of The University of Chicago Press.)

other indications of the manner of life of the makers of them, e.g., stone carvings of animals and of the human figure. Particularly noteworthy are the colored paintings on the walls of caves remaining to us from the Magdalenian culture.

With the retreat of the glaciers at the end of the last glaciation came a warmer climate, and this made possible the cultivation of plants and hence agriculture, including the domestication of animals. Whereas Paleolithic (Old Stone Age) peoples had been hunters and food gatherers, Neolithic (New Stone Age) peoples became farmers. Chipped stone implements were replaced by polished ones. Pottery was manufactured, and we have many other indications of developing civilization. Eventually the Stone Age was replaced by the Bronze Age and that by the Iron Age. *H. sapiens* was well on his way.

By 10,000 years ago, and probably before that date (perhaps as long ago as 37,000 years in the case of America; Krieger, 1957), *H. sapiens* had reached such out-of-the-way regions of the world as Australia and North America.

HUMAN EVOLUTION

How shall we picture the evolution of man? It is frequently diagramed as a tree with limbs, branches, and twigs. But such a picture makes no provision for the diversity of men living at any one time, with the complexities introduced by migrations and gene exchange between populations that intermate. A twig arises from one branch, not several branches, whereas a descendant may have drawn his genes from several ancestral groups. Figure 12.18 is an attempt to avoid these shortcomings by picturing human evolution in terms of a pattern of interlacing, interweaving lines. The intent is to convey the impression of many ancestral

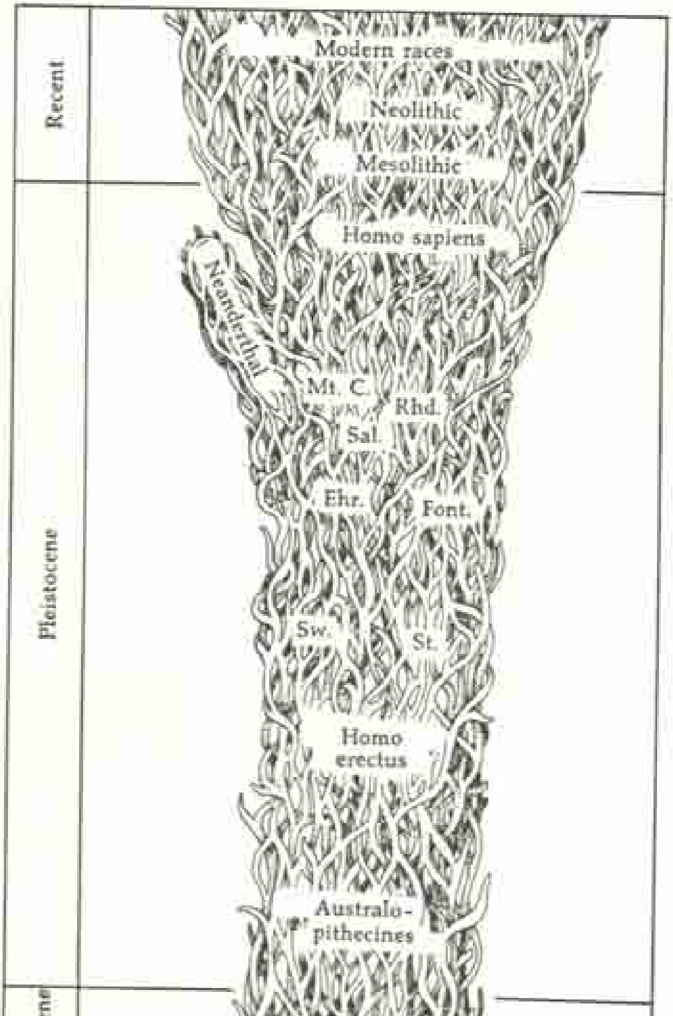

Recent
Pleistocene
Pliocene
Modern races
Neolithic
Mesolithic
Homo sapiens
Neanderthal
Mt. C.
Rhd.
Sal.
Ehr.
Font.
Sw.
St.
Homo erectus
Australopithecines

Fig. 12.18. Diagram of human evolution during the Pleistocene. Ehr., Ehringsdorf. Font., Fontéchevade. Mt. C., Mt. Carmel. Rhd., Rhodesian. Sal., Saldanha. St., Steinheim. Sw., Swanscombe.

lines crossing and recrossing as new forms arose, differentiated, combined characteristics by mating with other populations, and passed on their genes to descendants in varying proportion. As we have stressed repeatedly, the more we learn of hominids the more we appreciate that they have always been a variable lot. Like the time-honored tree, our diagram is hypothetical, but it seems to represent better than does the tree what we are learning both about the history of man's evolution and about the factors and forces operative in evolution in general.

At various points in the ascending pattern (Fig. 12.18) we have inserted the names of known fossil forms. These are placed to represent successive *stages* in human evolution. The diagram does not indicate the *extent* of time during which each form lived. The australopithecines, for example, may have arisen in the Pliocene, and they may have lived on as contemporaries of the earliest representatives of *H. erectus.* Similarly, the latter may have continued for a time as the contemporary of its descendant, *H. sapiens.*

THE HUMAN SPECIES

As mentioned earlier, we regard all modern peoples as belonging to one species, *H. sapiens.* What is a species? Chapter 15 discusses the attributes of this unit of classification. At present we shall confine ourselves to a definition generally acceptable in the light of modern biological knowledge, that of Mayr (1942 and 1950): "Species are groups of actually or potentially interbreeding natural populations, which are reproductively isolated from other such groups." Reproductive isolation is discussed in Chapter 20 (pp. 439–440). Briefly, two populations are said to be reproductively isolated from each other if they *do not* interbreed, and hence exchange genes, even when they have the opportunity to do so.

What is the situation of the modern races of man? Each race is certainly composed of actually or potentially interbreeding populations. Are the races reproductively isolated from each other? Clearly there are no anatomical or physiological incompatibilities separating them. As we shall note later, however, reproductive isolation may at times have a psychological basis. Observation seems to indicate some limited measure of psychological isolation among human races, since members of one race usually *prefer* to marry members of the same race than members of other races. Exceptions are common, however. In the absence of social taboos—for example, in Hawaii, Jamaica, and many other parts of the world—racial hybridization is frequent and biologically normal. It is upon this basis that we conclude that all living peoples belong to one species.

Different species usually differ *structurally* as well as in the matter of reproductive isolation. In the cases of the prehistoric men we have no direct evidence as to whether reproductive isolation was present or not. Thus students of the classification of man are forced to decide whether two fossil men differ *structurally* to sufficient extent to warrant placing them in separate species. In doing this they may have in mind the question of how much structural difference probably would lead to reproductive isolation. But the judgment is necessarily subjective; hence, differing opinions are inevitable. In the foregoing account we have attempted to present a consensus while recognizing that many authorities will disagree.

We recall that we have included in *H. sapiens* all modern peoples, Cro-Magnon man, Neanderthal men, and the preceding "transitional forms." Largely on the basis of difference in brain size, we have considered that *H. erectus* belongs to a separate species in genus *Homo*. The australopithecines we have regarded as a separate genus *(Australopithecus)* in the family Hominidae (Table 12.1). According to this view the genus is divided into two species: *A. africanus*, the gracile type, and *A. robustus*, the robust type. Robinson (1967a), however, would place the gracile type of australopithecine in genus *Homo* and the robust type in a separate genus, *Paranthopus*. This typifies the differing opinions one encounters. Wisely, we trust, we have suspended judgment as to the classification of "*H. habilis*" (pp. 248–249).

RACES OF HOMO SAPIENS

We have noted that modern men are usually considered to belong to one species, despite racial differences.

What is a race and how does it differ from a species? This question will receive further attention in our discussion of classification (pp. 328–330), where the point is made that race is equivalent to the subdivision of a species known as a *subspecies*. Here we may note that races or subspecies differ from species by the absence of that reproductive isolation forming an important hallmark of species. In addition to reproductive isolation, one species differs from another in some of its genes and thus usually in some visible traits. Similarly, one race differs from another in some of the genes present, but in this case the differences are usually less than they are between species. Indeed, the differences between races are more likely to take the form of variations in *frequencies* of occurrence of certain genes than they are to manifest themselves in the form of possession of certain genes by one race, with absence of those genes in another.

Thus races usually differ from species in two ways: (1) the absence of reproductive isolation and (2) a smaller amount of genetic difference. Both these attributes are complex variables, since there are degrees of reproductive isolation as well as degrees of genetic difference.

The next point is of great importance for the understanding of what races are and what they are not. *The differences between races are of the same kind as the differences between groups of people within races.* Much of our deplorable race prejudice would disappear if people generally could come to understand that fact, with all its implications. A great volume of evidence has been amassed on this point (see Boyd, 1950; *Cold Spring Harbor Symposia on Quantitative Biology*, 1950; Dunn, 1951; Dobzhansky, 1950 and 1962). A few brief examples must suffice us here.

The blood groups are the human characteristics most thoroughly analyzed as to genetic basis. As we saw earlier (pp. 110–111), racial groups differ in the *proportion* in which these blood groups occur (i.e., in the gene frequencies involved); so do populations *within* racial groups. Most American Indians, for example, exhibit a high percentage of individuals belonging to group O. Yet the Blackfoot and Blood tribes in Montana have an unusually high proportion of members belonging to group A. Contrariwise, groups of people usually considered to belong to different races may be quite similar in their blood group distributions. Thus, while a high proportion of group B characterizes Asiatic peoples it is also characteristic of Abyssinians and of Pygmies in the Congo. Eskimos, Portuguese, and Australian aborigines resemble one another in blood group distributions. We have picked a few examples at random; many others will be found in the references cited in the preceding paragraph. Similar differences and diversity exist in the distributions of the other blood cell substances (M, N, Rh, etc.). A point of great importance for us is the fact that there is no correlation between the distributions of these various substances—they vary in frequency independently of each other and of such characteristics as skin color.

Another genetically determined trait concerns the ability to taste the organic compound phenylthiocarbamide (PTC). Populations in different parts of the world differ in the proportion of persons able to taste this substance. Variability in this regard is independent of the variability in distribution of the several blood group substances.

Most persons think first of skin color when they think of racial differences. But here also there is great variability in the amount of skin pigment present in different members of a single racial group. There also is great similarity in this respect among members of some diverse racial groups. Some native inhabitants of India, for example, have darker skins than do some native inhabitants of Africa. And, again, variability in skin color occurs independently of variability in blood groups, tasting ability, and so on. Even hair form (straight, wavy, curly, or kinky) is independent of skin color in inheritance and, most important, there is no correlation between any of these characteristics and such attributes as mental ability.

In bodily proportions variability within racial groups resembles variability between racial groups, and there is no correlation with blood groups, skin color, hair form, tasting ability, and so on. Thus we think of Scandinavians as tall and long headed (dolichocephalic), although not all of them are by any means. Exceptionally tall and long-headed are the Watusi tribe in eastern Africa, while the African Pygmies form a marked contrast in both respects.

Space permitting, we might add to the list indefinitely. The point we wish to make will be evident from these few examples, however: In the matter of genetic difference a race is only a "constellation of characters," in Boyd's phrase (1950). Races present mosaics of characteristics varying independently in their distribution. A population is called a race if it differs from some other population in relative frequencies of blood group genes; in proportion of individuals possessing the "taster" gene; and in frequency of the genes controlling skin color, hair form, eye color, stature, head shape, and so on. Populations *within* a single race differ in these same ways. Thus races blend imperceptibly into each other and no sharp lines can be drawn between them. As Dobzhansky (1950) stated, "It is most important to realize that the differences between the 'major' human races are fundamentally of the same nature as the relatively minute differences between the inhabitants of adjacent towns and villages."

So we emphasize again that races are populations characterized by certain *frequencies* of the genes. Contrary to older ideas, there is no such thing as a racial "type" that all members of a race tend to approximate. The "typical Negro" or "typical Mongolian" has no more actual existence than does the "average man" about whom we sometimes read. No *individual* ever is "average"; each individual differs from every other in some respects ("identical" twins most closely approach an exception to this statement). We find the same situation when we attempt to classify *individuals* as belonging to one race or another. John Doe, for example, has dark brown skin and kinky hair; he belongs to blood group A, is Rh positive, round headed, and a "taster." Richard Roe has dark brown skin and wavy hair; he belongs to blood group B, is Rh negative, long headed, and a "nontaster." Despite all the differences between them people generally would classify them both as of the same race on the basis of their one point of similarity: dark brown skin (particularly if their ancestors came from the same continent). A third individual, George Goe, has little skin pigment, wavy hair, belongs to blood group B, is Rh negative, long headed, and a "nontaster." Despite the many similarities between George and Richard people generally would probably not classify them as belonging to the same race, their decision being based on the point that George has little skin pigment while Richard has much.

Of course our imaginary example is oversimplified; many more characteristics than these are involved in classifying people, and the matter of geographic origin also is considered important. Thus if some of the ancestors of John Doe and Richard Roe came from Africa, John and Richard would be called Negroes. On the other hand, if John's ancestors came from India and Richard's ancestors came from Africa, John and Richard would be considered to belong to different races. The artificiality of this whole system of classifying people is emphasized by the fact that individuals are not necessarily classified on the basis of the geographic origin of the *majority* of their ancestors. The extreme of absurdity is reached in the case of people most of whose ancestors were European, a minority having been African; such people by custom are classified as Negroes!

As indicated, our greatest lack of perspective concerns skin pigmentation inherited from African ancestors. Of all the genetic characteristics by which individuals differ from one another, why should skin color be the one about which we become emotional? It would be just as sensible for blood group A people to develop a "race prejudice" against blood group B people! The principal difference is that the one characteristic is exposed on the surface for everyone to see, while the other is hidden away, detectable only by serological tests. But the one difference is no more "important" than the other.

The idea that there once existed certain so-called "pure races" was formerly widely prevalent. A corollary was that the great human diversity observed today arose through intermating of these "pure races." From our discussion it will be evident that increasing knowledge of early and prehistoric people affords no evidence of "pure races." In fact, quite the opposite is the case: The more we learn of our predecessors on this planet the more we understand that they were always a highly diversified people. We have seen that "racial" differences in the Pleistocene period were at least as great as they are today. Furthermore, we have emphasized the fact that the genes possessed by modern races were undoubtedly derived from a mixed ancestry of Pleistocene peoples (pp. 259–261 and Fig. 12.18).

An attempt to visualize the processes at work may help to unify points included in the preceding discussions. When the ancestors of man first descended from the trees, assumed upright posture, and began to use tools they were probably few in number. As they succeeded in their new environmental niche they increased in numbers and migrated out into new territories. These first men were hunters, and their social organization was undoubtedly that of small, roving bands and nomadic tribes. As groups of people became separated from each other opportunity was presented for gradual development of genetic diversity. Certain mutations would have occurred in some isolated groups but not in others. By chance some mutations would have been lost in some of the groups in which they occurred and would have become established in some other isolated groups (genetic drift, pp. 394–401). Mutations that conferred some advantages on their possessors would have been favored by natural selection (pp. 13, 406–414). For example, if some groups entered regions characterized by high intensity of sunlight, mutations increasing the amount of pigment in the skin might have been of advantage (protection from harmful concentrations of ultraviolet rays) and hence might have been favored by natural selection. Thus in such a region the population might eventually have become quite dark in color. Conversely, if other groups entered environments having sunlight of low intensity, mutations decreasing pigmentation of the skin might have been favored by natural selection, since maintenance of a certain level of ultraviolet irradiation of the skin is important in providing the body with vitamin D (Loomis, 1967). Consequently, in this region a lightly pigmented population might have evolved.

Many of the differences between races are adaptive in this manner or were adaptive under the conditions in which the races originated. The exact nature of the adaptation, however, has not been analyzed in most instances. Such racial characteristics as are not adaptive may have become established in these isolated populations by chance, as noted above. The net result of these processes was development of diversity among geographically isolated peoples—the production of geographic races.

When these diverse peoples came into contact with each other (by migration or conquest) they exchanged genes, as discussed previously (pp. 259–261) and as diagramed in Fig. 12.18. Some of the combinations of characteristics thus arising may have proved superior to the characteristics of one or both of the parental populations. If so, natural selection would have favored the new combinations at the expense of the old. Particularly, natural selection seems to have favored the development of bigger and better brains, as we have noted. Such development was of first important in enabling man to devise tools and to improve them—in other words, in enabling him to become increasingly a civilized man.

If our interpretation is correct, then, modern races are descendants of ancient races, but probably no one modern race is the descendant of any one ancient race alone (see also Coon, 1962). Our inability to draw any clear-cut lines between races gives added confidence that such is the case. The genes have been continually "reshuffled" as time, in geologic copiousness, has gone by.

We have sketched in broadest outline the probable course of race formation and racial change, stressing (1) geographic isolation; (2) mutations and their fate as determined by chance and by natural selection; and (3) exchange of genes between populations. These are among the important factors operative in animal, including human, evolution. They receive further amplification and discussion in Chapters 17–21.

References and Suggested Readings

Ardrey, R., *African Genesis*, New York, Dell Publishing, 1961.(Delta paperback.)

Boule, M., and H. V. Vallois, *Fossil Men*, 4th ed., New York, Dryden Press, 1957.

Boyd, W. C., *Genetics and the Races of Man*, Boston, Little, Brown, 1950.

Campbell, B., "Quantitative taxonomy and human evolution," in S. L. Washburn (ed.), *Classification and Human Evolution*, Chicago, Aldine Publishing, 1963, pp. 50–74.

Campbell, C. B. G., "The relationships of the tree shrews: The evidence of the nervous system," *Evolution*, *20*, 276–281 (1966).

Chang, K., "New evidence on fossil man in China," *Science*, *136*, 749–760 (1962).

Cold Spring Harbor Symposia on Quantitative Biology, vol. 15, "Origin and Evolution of Man," Cold Spring Harbor, New York, The Biological Laboratory, 1950.

Coon, C. S., *The Origin of Races*, New York, Alfred A. Knopf, 1962.

Dart, R. A., "Cultural status of South African man-apes," *Annual Report for 1955, Smithsonian Institution*, Washington, D.C., 1956, pp. 317–338.

Dart, R. A., *Adventures with the Missing Link*, New York, Harper & Row, 1959.

Dobzhansky, Th., "The genetic nature of differences among men," in S. Persons (ed.), *Evolutionary Thought in America*, New Haven, Yale University Press, 1950, pp. 86–155.

Dobzhansky, Th., *Mankind Evolving*, New Haven, Yale University Press, 1962. (Yale paperbound Y–116.)

Du Brul, E. L., and H. Sicher, *The Adaptive Chin*, Springfield, Illinois, Charles C Thomas, 1954.

Dunn, L. C., *Race and Biology*, New York, United Nations Educational, Scientific, and Cultural Organization (UNESCO), Publ. 955, 1951.

Fleischer, R. L., P. B. Price, R. M. Walker, and L. S. B. Leakey, "Fission-track dating of Bed I, Olduvai Gorge," *Science, 148*, 72–74 (1965).

Goodman, M., "Phyletic position of tree shrews," *Science, 153*, 1550 (1966).

Gregory, W. K., *Evolution Emerging*, New York, Macmillan, 1951.

Howell, F. C., "The evolutionary significance of variation and varieties of 'Neanderthal' man," *Quarterly Review of Biology, 32*, 330–347 (1957).

Kretzoi, M., and L. Vértes, "Lower Paleolithic hominid and pebble-industry in Hungary," *Nature, 208*, 205 (1965).

Krieger, A., "Early man," *American Antiquity, 22*, 321–323 (1957).

Leakey, L. S. B., "A new fossil skull from Olduvai," *Nature, 184*, 491–493 (1959).

Leakey, L. S. B., "East African fossil Hominoidea and the classification within this super-family," in S. L. Washburn (ed.), *Classification and Human Evolution*, Chicago, Aldine Publishing, 1963, pp. 32–49.

Leakey, L. S. B., "An early Miocene member of Hominidae," *Nature, 213*, 155–163 (1967).

Leakey, L. S. B., J. F. Evernden, and G. H. Curtis, "Age of Bed I, Olduvai Gorge, Tanganyika," *Nature, 191*, 478–479 (1961).

Leakey, L. S. B., P. V. Tobias, and J. R. Napier, "A new species of genus *Homo* from Olduvai Gorge," *Nature, 202*, 5–7 (1964).

Le Gros Clark, W. E., *History of the Primates*, London, British Museum (Natural History); Chicago, University of Chicago Press, 1949–1957.

Le Gros Clark, W. E., *The Fossil Evidence for Human Evolution*, Chicago, University of Chicago Press, 1955.

Le Gros Clark, W. E., "The crucial evidence for human evolution," *Proceedings, American Philosophical Society, 103*, 159–172 (1959), condensation in *American Scientist, 47*, 299–313 (1959).

Le Gros Clark, W. E., *The Antecedents of Man*, Chicago, Quadrangle Books, 1960.

Le Gros Clark, W. E., *Man-apes or Ape-men?*, New York, Holt, Rinehart & Winston, 1967.

Loomis, W. F., "Skin-pigment regulation of vitamin-D biosynthesis in man," *Science, 157*, 501–506 (1967).

Martin, R. D., "Tree shrews: Unique reproductive mechanism of systematic importance," *Science, 152*, 1402–1404 (1966).

Mayr, E., *Systematics and the Origin of Species*, New York, Columbia University Press, 1942.

Mayr, E., "Taxonomic categories in fossil hominids," *Cold Spring Harbor Symposia on Quantitative Biology, 15*, 109–118 (1950).

Mayr, E., *Animal Species and Evolution*, Cambridge, Massachusetts, Harvard University Press, 1963.

Montagu, A., "*Homo habilis*," *Science, 149*, 918 (1965).

Napier, J. R., and P. R. Davis, "The fore-limb skeleton and associated remains of *Proconsul africanus*," *Fossil Mammals of Africa*, London, British Museum (Natural History), *16*, 1–69, 1959.

Oakley, K. P., *Frameworks for Dating Fossil Man*, Chicago, Aldine Publishing, 1964.

Robinson, J. T., *The Dentition of the Australopithecinae*, Transvaal Museum, *Memoir 9*, 1956.

Robinson, J. T., "Variation and the taxonomy of the early hominids," in Th. Dobzhansky, M. K. Hecht, and W. C. Steere (eds.), *Evolutionary Biology*, vol. 1, New York, Appleton-Century-Crofts, 1967a, pp. 69–100.

Robinson, J. T., "Relationships and trends in hominid evolution," in *Time and Stratigraphy in the Evolution of Man*, Washington, D.C., National Academy of Sciences–National Research Council, Publ. 1469, 1967b, pp. 22–29.

Simons, E. L., "New fossil primates: A review of the past decade," *American Scientist, 48*, 179–192 (1960).

Simons, E. L., "The early relatives of man," *Scientific American, 211*, 50–62 (1964).

Simons, E. L., "The earliest apes," *Scientific American, 217*, 28–35 (1967).

Simons, E. L., and D. R. Pilbeam, "Preliminary revision of the Dryopithecinae (Pongidae, Anthropoidea)," *Folia Primatologica, 3*, 81–152 (1965).

Simpson, G. G., "The principles of classification and a classification of mammals," *Bulletin, American Museum of Natural History, 85*, 1–350 (1945).

Simpson, G. G., "The meaning of taxonomic statements," in S. L. Washburn (ed.), *Classification and Human Evolution*, Chicago, Aldine Publishing, 1963, pp. 1–31.

Stewart, T. D., "Form of the pubic bone in Neanderthal man," *Science, 131*, 1437–1438 (1960).

Straus, W. L., Jr., "The riddle of man's ancestry," *Quarterly Review of Biology, 24*, 200–223 (1949).

Straus, W. L., Jr., "Fossil evidence of the evolution of the erect, bipedal posture," *Clinical Orthopaedics, 25*, 9–19 (1962).

Straus, W. L., Jr., "The classification of *Oreopithecus,*" in S. L. Washburn (ed.), *Classification and Human Evolution,* Chicago, Aldine Publishing, 1963, pp. 146–177.

Straus, W. L., Jr., "Nature of the problem and the evidence," in *Time and Stratigraphy in the Evolution of Man,* Washington, D.C., National Academy of Sciences–National Research Council, Publ. 1469, 1967, pp. 1–17.

Straus, W. L., Jr., and A. J. E. Cave, "Pathology and the posture of Neanderthal man," *Quarterly Review of Biology, 32,* 348–363 (1957).

Tobias, P. V., "Early man in East Africa," *Science, 149,* 22–33 (1965).

Vallois, H. V., "Neanderthals and Praesapiens," *Journal of the Royal Anthropological Institute of Great Britain and Ireland, 84,* 111–130 (1954).

Van Valen, L., "Tree shrews, primates, and fossils," *Evolution, 19,* 137–151 (1965).

Washburn, S. L., "The analysis of primate evolution with particular reference to the origin of man," *Cold Spring Harbor Symposia on Quantitative Biology, 15,* 67–78 (1950).

Weidenreich, F., "The skull of *Sinanthropus pekinensis;* A comparative study on a primitive hominid skull," *Paleontologia Sinica,* N. S. No. 10, 1943; whole series No. 127, pp. 1–484.

Zuckerman, S., "Correlation of change in the evolution of higher primates," in J. Huxley, A. C. Hardy, and E. B. Ford (eds.), *Evolution as a Process,* London, Allen & Unwin, 1954, pp. 300–352.

13

Evolution as Seen in the Geographic Distribution of Animals: Continents

ALMOST EVERYONE KNOWS that if he wishes to hunt lions he should go to Africa, and if tigers are his objective he must travel to India. But of those who know this, how many ever stop to wonder *why* lions are more common in Africa than they are in India and why tigers are not found in Africa? As a result of studies by persons who have wondered about such things, a subdivision of biology known as geographic distribution or zoogeography has developed.

Zoogeography is concerned with the manner in which animals are distributed over our planet and attempts to explain the observed distributions. We shall commence our discussion of the subject by considering some of the peculiarities encountered in the distribution of animals on the larger land masses of the earth, the continents.

AFRICA AND SOUTH AMERICA The two large continents crossed by the equator are South America and Africa. Both have extensive tropical regions. Both extend southward into the Temperate Zone. Both have lowland jungles; extensive river systems; broad, dry plains; and high mountains. In short, both present much the same variety of habitats for living things. We might anticipate, therefore, that both continents would be populated with the same, or closely similar, animals. Such an expectation would differ widely from actuality, however.

In Africa we find LIONS, ELEPHANTS, RHINOCEROSES, HIPPOPOTAMI, many kinds of ANTELOPES, GIRAFFES, ZEBRAS, HYENAS, LEMURS, BABOONS, MONKEYS with narrow noses and nonprehensile tails, CHIMPANZEES, and GORILLAS, to enumerate only a random sample.

In South America we find not a single one of the animals just listed. South America has MONKEYS, to be sure, but they are quite unlike their African relatives; many have broad noses and other distinguishing features, including prehensile tails which serve as a fifth limb as they swing through trees. In South America are (Fig. 13.1) (1) TAPIRS, representing the odd-toed, hoofed mammals; (2) a group of rodents of which the CAPYBARA, AGOUTI, CHINCHILLA, and PACA are perhaps the best known (our guinea pig is a domesticated relative); (3) MOUNTAIN LIONS (panthers), OCELOTS, and JAGUARS as representatives of the cat family; and (4) LLAMAS, GUANACOS, VICUÑAS, and ALPACAS as representatives of the camel family. There are also DEER (absent from Africa except in the neighborhood of the Mediterranean Sea), ARMADILLOS, many species of OPOSSUMS, GIANT ANTEATERS, RACCOONS, SPECTACLED BEARS, PECCARIES, and SLOTHS, those slow-moving arboreal animals which hang beneath the branches of trees instead of traveling on their upper surfaces, and others (Fig. 13.1). Furthermore, before white men overran the earth the two continents differed as markedly in their human populations as they did in their lower animals. The greater part of Africa was inhabited by various types of Negroes, while South America was inhabited by various types of Indians.

While we have stressed the differences between the mammalian faunas of these two continents, we do not wish to convey the impression that no groups of animals have representatives in both. Such widely ranging animals as bats, rats, mice, squirrels, hares and rabbits, and members of the cat, dog, weasel, and swine families occur in both continents. Despite this fact, however, differences outweigh similarities.

Why do these geographically similar continents differ so markedly

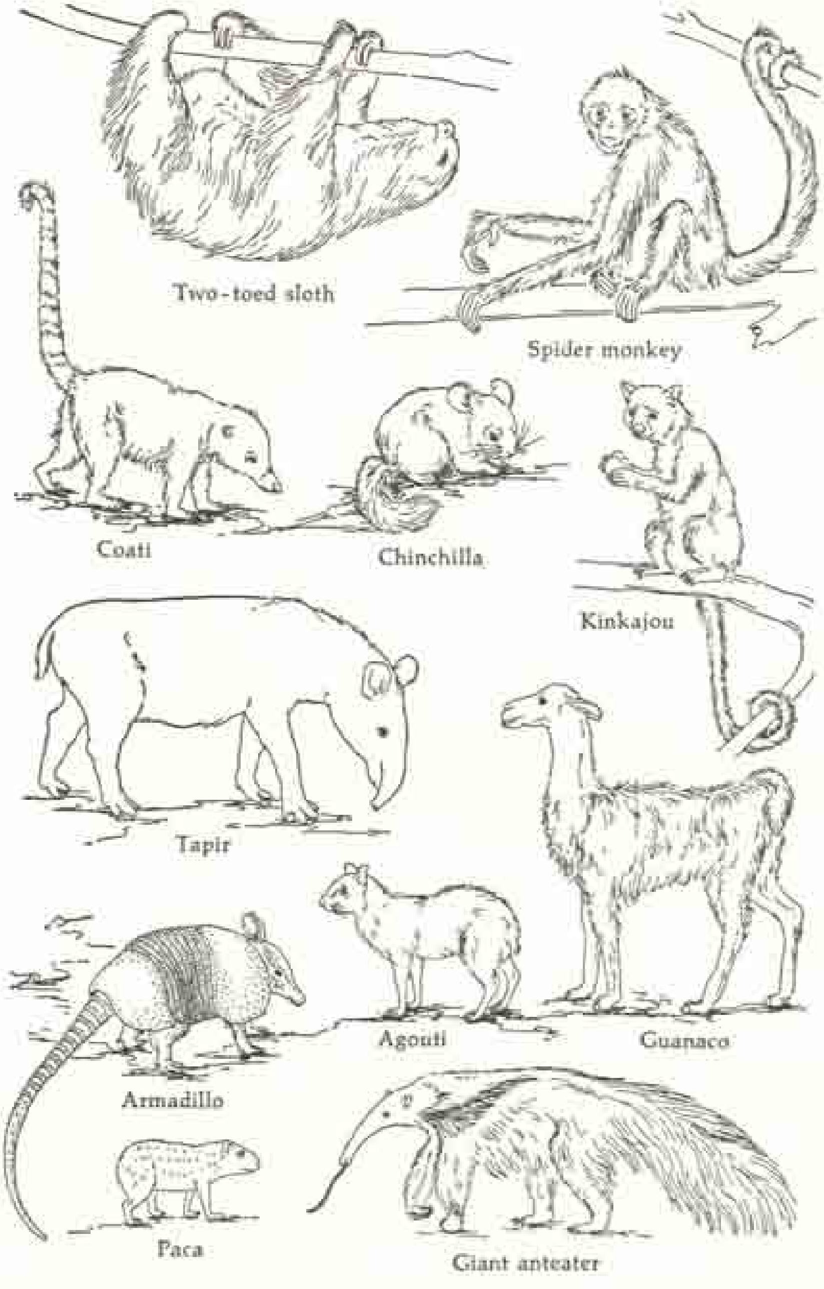

Two-toed sloth
Spider monkey
Coati
Chinchilla
Kinkajou
Tapir
Agouti
Guanaco
Armadillo
Paca
Giant anteater

Fig. 13.1. Typical South American placental mammals. Not drawn to scale.

in their animal populations? We shall defer the answer to this question until we have gained a more comprehensive view of animal distribution on other continents. We may note in passing, however, that for some people the answer is simple and clear. It is possible to be satisfied with the explanation that these continents have their present inhabitants because the latter were created in place, so to speak. Lions were created in Africa, not in South America; jaguars were created in South America, not in Africa, and so on. For people contented with this explanation the final answer has been given and there is nothing left to explain. Such an "explanation" removes the whole matter from the field of scientific inquiry.

In this connection we may note an interesting relationship between the distinctiveness of animals and the length of time they have occupied a given continent. This is particularly evident in South America, as pointed out by Simpson (1950), who called the relationship FAUNAL STRATIFICATION. The fossil record shows that armadillos and sloths, for example, occurred in South America as long ago as the earliest Cenozoic. There are no sloths anywhere else in the world and no armadillos either, except as they later spread northward in the Americas. These forms are representative of the oldest "stratum."

An intermediate stratum is exemplified by the New World monkeys which, as we have seen, are unlike the Old World forms in many respects. They have lived in South America since mid-Cenozoic.

As examples of a later stratum Simpson cited the field mice, which are closely allied to those of North America. They have formed part of the South American fauna since late Cenozoic times only.

Thus we see as a general trend a relationship between the length of time an animal has inhabited a given continent and the amount of differentiation that animal has undergone. Such a relationship is eloquent of evolution. If animals were created as they are and remained unchanging such a relationship would be meaningless or would have to be ascribed to mere coincidence. We shall return to this relationship between elapsed time and amount of differentiation when we discuss the organisms of oceanic islands (see especially pp. 304–305).

AUSTRALIA The Tropic of Capricorn crosses not only southern Africa and South America but also the continent of Australia. The animal inhabitants of that isolated continent are most unlike those of either of the other two continents crossed by the Tropic. Everyone knows of the Australian kangaroos, for the young of which a fur-lined pouch on the abdomen of the mother serves as nest and living perambulator. The kangaroos belong to the subdivision of the class Mammalia characterized by possession of such a pouch, or marsupium, and hence called MARSUPIALS (see p. 199). Africa has no marsupials; South America has opossums and some tiny creatures known as caenolestids. In passing we might note that marsupials also are absent from Asia and only one species, the so-called Virginia opossum, occurs in North America. How does it happen that marsupials are found only in such widely separated regions of the earth as America and Australia? The question suggests something of the complexity of problems confronting zoogeographers but belongs properly in a later portion of this discussion (pp. 280–286).

Before the coming of man, with his intentional and unintentional introduction of foreign species, Australia had only bats and rodents as representatives of PLACENTAL MAMMALS, the group that predominates in other regions of the globe (Simpson, 1961). A dog, the dingo, is also present but was probably introduced by early man.

The Australian realm is unique as the home of the only living representatives of the group of mammals which lay eggs, the MONOTREMES (p. 198). These representatives are the duckbilled platypus *(Ornithorhynchus)* and the spiny anteater *(Echidna;* Fig. 13.2).

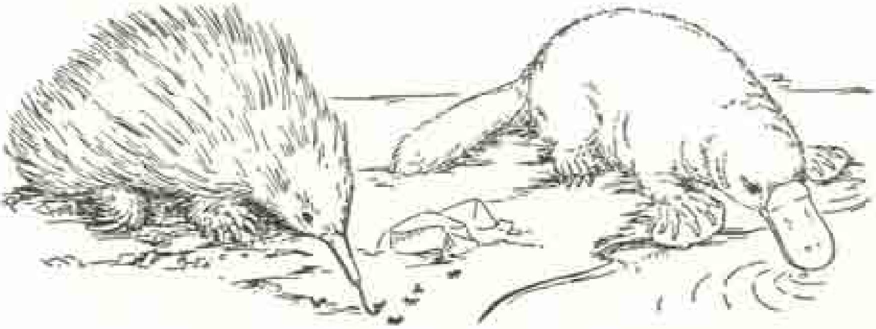


Fig. 13.2. Monotremes, *Echidna* (spiny anteater) (left), and *Ornithorhynchus* (duckbilled platypus).

Aside from this sparse representation of placental mammals and monotremes, Australia is populated by an odd assemblage of marsupials (Fig. 13.3). In many ways they parallel the adaptations of placental mammals in the rest of the world, affording striking examples of that parallel evolution we have stressed in other connections. Thus we find KANGAROOS of assorted sizes and means of livelihood. Most of them are terrestrial, though the TREE KANGAROO has forsaken life on the ground for life in trees. The GREAT RED KANGAROO is the closest Australian approach to the swift-moving, grazing animals of other continents (deer, antelope, horses, and so on).

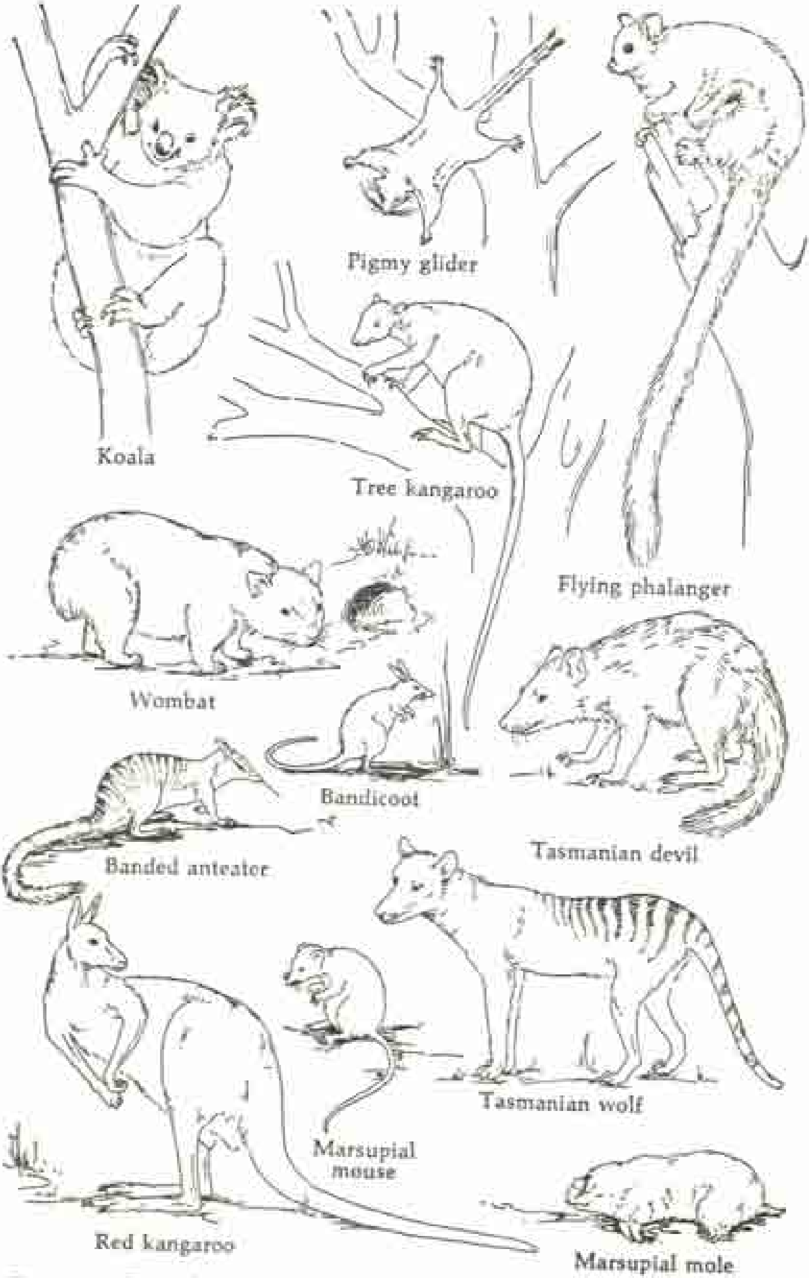

Koala
Pigmy glider
Tree kangaroo
Flying phalanger
Wombat
Bandicoot
Tasmanian devil
Banded anteater
Tasmanian wolf
Marsupial mouse
Red kangaroo
Marsupial mole

Fig. 13.3. Typical marsupials of the Australian region. Not drawn to scale. (Mainly after Troughton, *Furred Animals of Australia*, copyright 1947, Charles Scribner's Sons. Used by permission of Angus & Robertson Ltd, Publishers.)

The KOALA, a slow-moving, nocturnal marsupial that has captured the popular imagination as a living "teddy bear," lives in eucalyptus trees, feeding on the leaves. MARSUPIAL MOLES burrow in the ground just as do true moles in other parts of the world. WOMBATS are marsupials that have developed rodentlike teeth and habits much like those of our woodchucks. Some PHALANGERS resemble squirrels, while the FLYING PHALANGER resembles a flying squirrel in having membranes stretched between forelimbs and hind limbs to provide planes useful in gliding.

Of the other marsupials of Australia and neighboring Tasmania we may mention HARE WALLABIES, little kangaroolike creatures with habits much like those of our rabbits; the TASMANIAN WOLF, a carnivorous marsupial resembling true wolves in many respects; the TASMANIAN DEVIL, a carnivorous creature reminiscent of our badgers; and the BANDED ANTEATER, a small marsupial with a pointed snout and a long, sticky, extensible tongue, the hall marks of anteaters of whatever relationship the world over. In summary, the marsupials of the Australian region furnish a most striking example of *parallel evolution* and *adaptive radiation* discussed in an earlier chapter (pp. 27–31).

EURASIA AND NORTH AMERICA The foregoing discussion reveals that the three continents of the Southern Hemisphere present marked contrasts in animal inhabitants. In the Northern Hemisphere, however, we find the contrasts much less striking.

The faunas of Eurasia and North America abound in animals that are either identical or closely similar. Confining our discussion to mammals, we may mention such widely ranging groups as deer, cats, wolves, foxes, otters, weasels, badgers, moles, shrews, rats, and mice. Restricting our attention to mammals more distinctive of the two northern land masses, we may mention some of the hoofed animals common to both: (1) BISON, sometimes called buffalo in this country; (2) the large deer called MOOSE in this country and elk in Europe; (3) the WAPITI, frequently called elk in this country and closely similar to the stag of Europe; (4) REINDEER or caribou; (5) the North American MOUNTAIN GOAT, closely akin to the chamois of Europe; and (6) the MOUNTAIN SHEEP or bighorn.

BEARS afford another example of the similarity of mammalian life on the two northern continents. Aside from one species inhabiting the Atlas Mountains of North Africa and the peculiar spectacled bear living in the Andes of South America, bears are confined to these northern continents. Among the various species the POLAR BEAR is familiar to all as a denizen of circumpolar arctic regions.

Both northern continents have beavers, lynxes (bobcats), varying hares (brownish gray in summer and white in winter), and those odd little relatives of hares and rabbits, the pikas or conies. The list might be greatly extended, as well as expanded to include birds and other animals, but the examples cited will suffice to demonstrate the far-reaching similarities characterizing the faunas of these northern continents.

The preceding paragraphs presented evidence that the three continents in the Southern Hemisphere differ markedly in their animal inhabitants whereas the two great land masses in the Northern Hemisphere are closely similar in this respect. Can we now find some reasonable explanation for the contrasted situations in the two hemispheres?

ACCESSIBILITY As we examine a map, preferably a globe, we are struck by the fact that the three southern continents are widely separated from one another by expanses of ocean, whereas the northern land masses are nearly in contact, being separated from each other by only the 56 miles of the Bering Strait. Perhaps, then, accessibility forms the clue we are seeking. This seems all the more likely when we realize that the Bering Strait is shallow as well as narrow and that there is every reason to believe that in various past geologic periods the region lay above sea level to create a continuous bridge of land between North America and Asia. A similar bridge may have existed between Europe and North America, perhaps by way of Iceland and Greenland, but the evidence for it is less conclusive than is the evidence for the Alaska–Siberia connection. The latter must have made possible extensive migrations between Eurasia and North America, which would explain in large measure the great similarities of animal life observed to occur in these two great land masses.

Turning to the Southern Hemisphere, we note that *inaccessibility* characterizes the three southern continents. Widely separated from one another, such connections as they have are with northern continents.

Of the three, Australia is the most completely isolated. Perhaps it was at one time connected to the continent of Asia by a land bridge of which the East Indian islands to the northwest represent the unsubmerged remnants. But the connection, if it ever existed, must have been extremely ancient. While only shallow ocean separates many of these islands (e.g., Borneo, Sumatra, and Java) from Asia, there are deeper stretches between Australia and the islands mentioned. Evidence seems to indicate that Australia has been isolated from Asia since at least Cretaceous times (p. 146).

Did the ancestors of the monotremes and marsupials reach Australia by land before the present isolation of the continent occurred? Such an explanation is possible though, as Simpson (1943 and 1953) has pointed out, it may be more probable that these ancestors reached Australia by being transported from island to island across intervening ocean. Methods by which such transport might occur are discussed in the following chapter. "Island hopping" involves a large element of chance. The chances are against the dispersal of any terrestrial animal in this manner. As we have seen (p. 199), marsupial and placental mammals arose at about the same time. Why did the marsupials and not the placentals reach Australia originally? Simpson (1953) has suggested that this outcome was determined by chance. Once having chanced to arrive, the early marsupial immigrants were afforded opportunity for the remarkable adaptive radiation described above.

Until man began his introduction of placental mammals, among the latter only fliers, bats, and such accomplished stowaways as rodents had been able to reach the island continent. Even the rodents were few in number. Wood (1969) has concluded that their immigration occurred in Pliocene or Pleistocene times. At any rate, these rodent immigrations must have been unaided by any direct land connections.

Some reader may suspect that the reason higher mammals were not more abundant in Australia was because this continent was not suited to them. We should point out, therefore, the marked success some species of placental mammals have had following introduction by man. Rabbits, for example, introduced by man, have in some regions increased in numbers so prodigiously as to become a serious economic liability as well as to cause extinction in those regions of marsupials dependent upon the food supply the rabbits have successfully monopolized. A similar situation prevails in New Zealand, where animals introduced originally for sport have thrived so mightily that the forest is being destroyed. The worst offender is the European red deer. Clark (1949) estimated that in 1942 there were at least 90,000 of them on South Island, another 10,000 grazers being composed collectively of fallow deer, Virginia deer, thar (a beardless wild goat from the Himalayas), chamois, wapiti, and moose. Wild pigs, goats, and sheep add to the destruction. In some regions overpopulation is so great that the forest resembles a trampled cattle yard, all young growth being destroyed and even adult trees suffering devastation. Evidently, then, inaccessibility rather than unsuitability is the key to explanation of the original unique fauna in Australia and New Zealand.

To a considerable extent the same explanation applies to the peculiarities of the South American fauna. The connection of this continent to North America is the tenuous Isthmus of Panama. At various times in geologic history that isthmus has been submerged, leaving South America isolated from its northern neighbor. During most of the Tertiary, South America was cut off in this manner. We recall that this period saw the evolution of the placental mammals (Chap. 11). The fact that the evolution of South American mammals followed its own course, largely independently of that of the rest of the world, is doubtless attributable to the fact that during long periods South American forms had no contact with those on other continents. Occasional immigrants reached the continent by island hopping across the intervening sea. Once arrived, such invaders found ample opportunity for an adaptive radiation only slightly less striking than that of Australian marsupials. Thus there evolved the peculiar guinea piglike rodents (cavy, agouti, capybara, paca, porcupines, and their kin), the distinctive South American monkeys, the armadillos, the sloths, the anteaters, the opossums, and many other unique animals.

In Africa the Sahara and adjoining deserts have formed a most effective barrier to the dispersal of mammals adapted for life in forests or on open plains that are not deserts. So we find that the animals south of the Sahara differ greatly from those north of it. The northern animals resemble those of Europe. This is understandable on a basis of accessibility, since at various times the barrier presented by the Mediterranean Sea has been bridged—at the narrow Strait of Gibraltar, for example.

We have been developing the idea that accessibility and inaccessibility play major roles in the distribution of animals. If an animal is to live in a certain region, it must be able to reach that region and the region must be suitable for the existence of that animal. This latter point is self-evident and needs little elaboration. For example, since frogs and toads burrow into the soil to hibernate through the winter, they are not found in regions so far north that the subsoil remains frozen throughout the year. Examples of limitation of distribution by unsuitability of environments might be multiplied almost endlessly. But from the standpoint of the present discussion chief interest lies in the observed fact that animals do not inhabit all regions suitable to them. We cannot conclude that because an animal is not found in a given region the latter is necessarily unsuitable for it. If animals were separately and specially created, failure to find an animal in every region suited to it would be mysterious, to say the least. On the other hand, if animals have evolved from predecessors that differed in structure and frequently in place of origin, failure to find an animal in a region suited to it but inaccessible to it is exactly what we should expect.

CENTERS OF DISPERSAL There emerges from our discussion a picture of new forms arising from old ones in certain regions and then migrating out from the "old home" in search of new worlds to conquer.

We must hasten to add that this migration and "search" are not to any considerable extent voluntary activities of individual animals. Rather they represent slowly developing changes involving many generations and produced by many factors, including eventual overcrowding of what we have spoken of as the "old home" but what is more accurately termed the CENTER OF DISPERSAL.

As examples of dispersal from such a center we may cite the evolutionary history of placental mammals. We recall that the evolution and dispersal of placental mammals occupied the center of the stage during the Cenozoic era (Chap. 11).

If we look at the continents of Eurasia and North America on a map drawn with the North Pole as a center (Fig. 13.4), we note that these lands form the greater portion of a circle around the pole and if the Bering Strait were dry land would form one continuous land mass. Lowering the level of the ocean, or raising its floor, by only 150 ft. would provide a dry land connection across the strait. This land connection is believed to have arisen at various times in the past, most

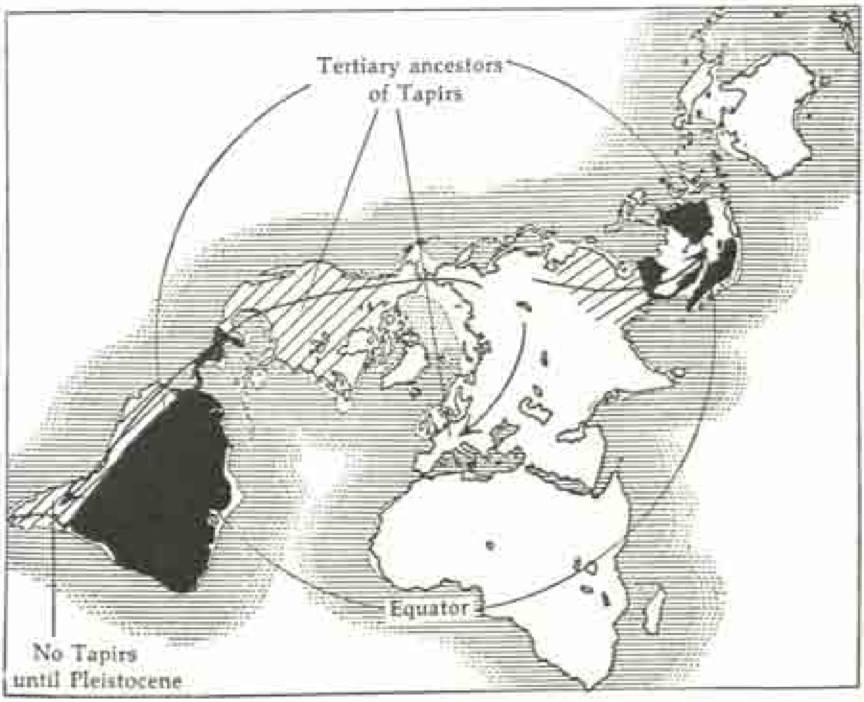


Fig. 13.4. Geographic distribution of tapirs. Present range shown in solid black; range during Pleistocene shown in diagonal lines. Arrows radiate from the center of dispersal. (From Matthew, W. D., *Climate and Evolution*. Copyright 1939 by The New York Academy of Sciences; reprinted by permission.)

recently during the Pleistocene period when much water was locked up in continental glaciers. Northern Alaska seems to have remained free of glaciers. Hence, during various periods of Pleistocene glaciation the land bridge could have afforded passage into the New World to such creatures as bison, musk oxen, goats, moose, woolly mammoths, and mastodons. Man himself probably also utilized this bridge, which was last open about 10,000 years ago. It had then been open for some 15,000–25,000 years and at least at times had been more than 1000 miles wide (Laughlin, 1963; Müller-Beck, 1966).

Most students of geographic distribution agree that this circumpolar land mass has provided the route by which animals have been distributed to the continents of the world. This land mass forms a hub from which three great spokes radiate southward to terminate, respectively, in South America, Africa, and southeastern Asia with its adjoining islands (Fig. 13.4). What was the point of origin and center of dispersal for modern orders of mammals? Matthew (1939) concluded that these orders originated in the North Temperate zone with its variable climate. Thus most of the evolution of the horse occurred in North America, as did that of the camels (see following). Other examples might be given. On the other hand, Darlington (1957) marshaled evidence that animals, including mammals, are on the whole more diverse and numerous in kinds in the tropics than they are in temperate zones. He concluded that "the main center of dispersal of mammals seems therefore to have been the main part of the Old World and especially the tropical part of it." He believed that the Old World tropics also was the center of dispersal of freshwater fishes, amphibians, reptiles, and birds.

During the early Cenozoic northern portions of the Old World enjoyed a mild, even tropical, climate. Since this was a time of great mammalian evolution, these mammals may have evolved in tropical conditions and yet have been in position for dispersal throughout the circumpolar land mass.

If dispersal from a center is an actuality we should expect to find evidence of it in the fossil record. Fortunately that expectation is realized, despite the imperfections of the known portions of the record. From many possible examples we shall cite only two. They are of particular interest since they involve striking examples of *discontinuity* in the ranges of living animals.

TAPIRS The first example is that of tapirs, animals with which most readers are not likely to be familiar. Tapirs are the least specialized of living odd-toed hoofed mammals (order Perissodactyla); they have four toes on each forefoot and three on each hind foot, being reminiscent of the Eocene perissodactyl *Hyracotherium* in that respect. In general appearance they somewhat resemble very large pigs. Their most unusual feature is a nose and upper lip drawn out into a short, flexible proboscis, a sort of incipient elephant's trunk (Fig. 13.1). But perhaps the most remarkable thing about them is their distribution. They live in only two regions: (1) Central and South America and (2) the Malay Peninsula and adjacent islands such as Sumatra and Borneo. Figure 13.4 reminds us that these areas, shown in solid black, are about as distant from each other as two points on this earth can be. How does it happen that tapirs are found in these two widely separated areas?

If we are not satisfied with the explanation that the tapirs were created in the two regions mentioned and not elsewhere, we find no clue to the answer to our question in the living animals themselves. When we turn to the fossil record, however, the explanation becomes clear. As indicated by the diagonally shaded portions of the map, during Pleistocene times tapirs ranged all over North and South America and through considerable portions of Asia. In preceding Cenozoic periods ancestral tapirs lived in Europe and North America, where they were found at least as long ago as the Oligocene. Interestingly enough, tapirs did not reach one of their two modern havens, South America, until the Pleistocene. This fact correlates well with the isolation of that continent from North America during long periods of the Tertiary. Tapirs apparently never reached Africa.

Evidently, then, the present widely separated regions inhabited by tapirs represent isolated portions of a once widespread range. For some reason tapirs disappeared from the intervening regions. Doubtless changing environmental conditions, coupled with competition from animals better fitted for them, were factors in causing this disappearance.

CAMELS Camels and their South American relatives supply another example of discontinuity in modern range, explicable by reference to the fossil record.

Of the camel-like inhabitants of South America, the llama and alpaca are domesticated animals derived originally from wild, camel-like forms inhabiting the continent before the coming of man. The llama (see guanaco, Fig. 13.1) is smaller than a camel and lacks the characteristic hump of the latter, but its undoubted relationship to camels is revealed by many anatomical features. The limbs of the camel family are characteristic, being elongated and having two equally developed toes. All traces of lateral digits have been lost; i.e., no "splint bones" are present as they are in the horse (p. 25). The digits of the one-humped Arabian camel spread widely, offering effective support on soft desert sands. The feet of the two-humped Bactrian camel of central

Asia, as well as those of the llama, are harder and less spreading, adapted for firmer and rockier terrain.

Camels and their South American relatives have a highly discontinuous distribution (Fig. 13.5). As shown by the solid black areas of the map, true camels inhabit Africa to the southern edge of the Sahara desert, Arabia, and the highlands of Asia. Llamas and their relatives inhabit the highlands of South America. The discontinuity between these ranges is almost as great as that between the two parts of the range of tapirs. As in the case of the latter, the explanation of the situation becomes evident when the fossil record is consulted. During Pleistocene times camels ranged over North and South America, Northern Africa, and most of Asia. Apparently they first reached the Old World in the Pliocene but did not reach South America until the Pleistocene. Again we note the effect of the isolation of the latter continent during the Tertiary.

Rather surprisingly, perhaps, for an animal we do not usually

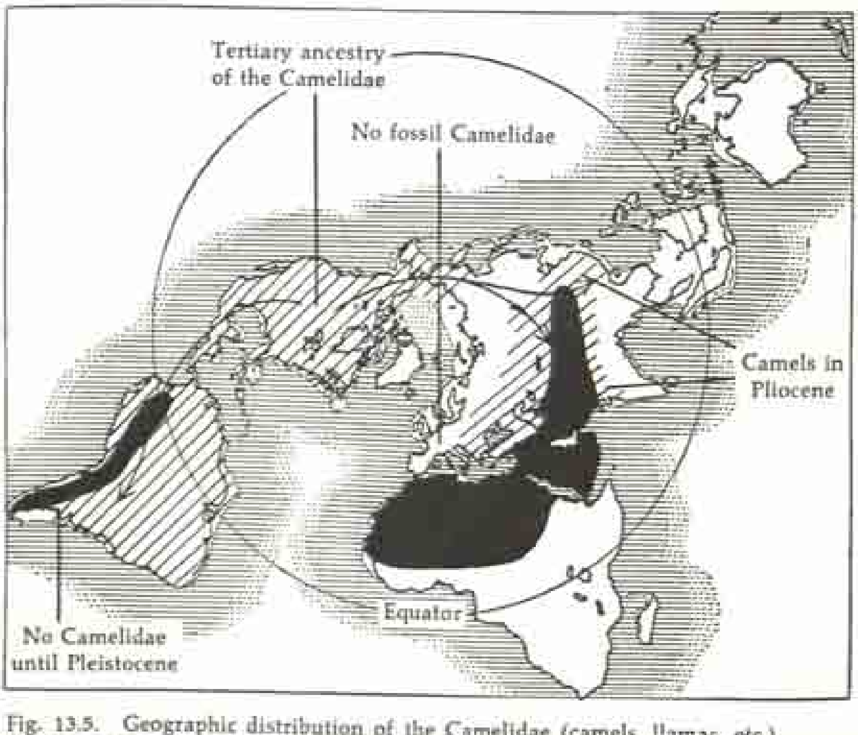

Tertiary ancestry of the Camelidae
No fossil Camelidae
Camels in Pliocene
Equator
No Camelidae until Pleistocene

Fig. 13.5. Geographic distribution of the Camelidae (camels, llamas, etc.). Present range shown in solid black; range during Pleistocene shown by diagonal lines. Arrows radiate from the center of dispersal. (From Matthew, W. D., *Climate and Evolution*. Copyright 1939 by The New York Academy of Sciences; reprinted by permission.)

associate with our own country, the major portion of camel evolution occurred in North America. Here the fossil record dates back to the Eocene, to a little animal, *Protylopus,* which was in a stage of evolution comparable to that of *Hyracotherium* in the horse line. The subsequent evolutionary history of camels is almost as completely documented by North American fossils as is the evolution of the horse.

Evidently, therefore, North America was the center of camel evolution and dispersal. Camels reached the Old World across the Bering Strait land bridge and South America across the Isthmus of Panama, when the latter was elevated above the sea in Pleistocene times (see arrows on the map, Fig. 13.5). Subsequently, camels became extinct in their center of dispersal, North America. As for the disappearance of the horses (p. 216), the reason is not known, although the same factor or factors may well have operated in both instances.

BARRIERS The examples cited above reveal a common pattern underlying much of evolution and dispersal. An animal arises by evolution in a certain region. Typically, it then attempts to expand its range, under the pressure of factors such as overpopulation in the original center. Whether it succeeds in expanding its range and also the extent of expansion depend upon many factors.

First among such factors we may mention PHYSICAL BARRIERS. Bodies of water are barriers to land-dwelling animals, the effectiveness of the barrier depending upon the attributes of the particular animal in question. Conversely, dry land is a barrier to the dispersal of aquatic animals. High mountain ranges, deserts, open plains (to forest dwellers), forest (to dwellers on open plains), as well as such climatic factors as intolerable extremes of temperature and many other physical factors serve as barriers to the dispersal of one animal or another.

No less effective are BIOLOGICAL BARRIERS. Among examples of these we may mention absence from a given region of food suitable to the species in question, presence in a given region of competitors for the same food supply or nesting site, presence in a region of predatory animals, and the like.

The action of barriers may be nearly or quite complete, as in the case of the barrier to amphibian dispersal presented by seawater, or the barrier may be only partially effective. The degree of effectiveness depends not only upon the nature of the barrier itself but also upon the nature of the animals concerned. In general, a species can surmount a barrier in one of two ways: (1) by being adaptable to a variety of living conditions or (2) by giving rise to new forms adapted to conditions unsuitable for the parent species itself.

Adaptability is a most valuable attribute. Animals possessing it can extend their ranges into regions that offer conditions of life differing from those in the center of dispersal. Animals possessed of a generous measure of this quality range widely and change but little in response to the varying habitats they enter. In this way the various species of Old World rats and mice, for example, have achieved a distribution as worldwide as that of man himself. And man is the star example of a form able to surmount all barriers to dispersal by virtue of adaptability.

Lack of adaptability, on the other hand, hinders (when it does not prevent) such dispersal. Furthermore, it may lead to extinction of a species in its home area if conditions in that area change sufficiently. The geologic record affords many examples of such extinctions. Between the extremes are found intermediate degrees of adaptability, contributing to the varying degrees of success with which animals meet changing conditions either "at home" or as the species attempts to extend its range into new areas.

Animals that do not possess adaptability enabling them to live in a wide variety of habitats may be able to solve the problem of invading new and differing regions in a different manner. They may be able to give rise to new forms capable of living under conditions the original species could not tolerate. This solution is a much more common occurrence than is the possession of the high degree of adaptability or versatility just discussed. Evidence that evolution of new forms has occurred is provided by the observation that *as animals have radiated out from their center of dispersal they have frequently become modified in various ways so that they are no longer identical with each other or with their ancestors.* The camels are a case in point. The llama, the Bactrian camel, and the Arabian camel differ somewhat from one another, and each differs somewhat from the camels that formerly inhabited North America, their center of dispersal (Fig. 13.5). Such differences, superimposed on fundamental similarities and correlated with the distribution of the forms concerned, offer eloquent testimony of evolution.

CONTINUOUS RANGES While tapirs and camels afford examples of marked discontinuity in geographic range, the distribution of many groups of animals is more or less continuous, related forms being found in regions between the center of dispersal and outlying areas. Such a situation is no less interesting for the study of evolution than is discontinuity of range. In fact, in his brief autobiography Darwin mentioned this fact of "the manner in which closely allied animals replace one another in proceeding southwards over the Continent" (South America) as one of the three observations that most strongly directed his thinking into evolutionary lines.

In his *Origin of Species* Darwin wrote, "The naturalist, in traveling, for instance, from north to south, never fails to be struck by the manner in which successive groups of beings, specifically distinct, though nearly related, replace each other. He hears from closely allied, yet distinct kinds of birds notes nearly similar, and sees their nests similarly constructed, but not quite alike, with eggs colored in nearly the same manner."

This observation of Darwin's suggests a frequently observed phenomenon: that related races or species may be observed to vary in a regular way as one progresses from one part of their geographic range to another. For example, in the common zebra inhabiting the southern half of Africa the black striping of the legs steadily decreases (and in a form now extinct eventually disappeared) in a progressive series from north to south (Fig. 13.6). Such a character gradient has been called by Julian Huxley a CLINE. Multitudes of examples might be cited (for comprehensive summaries see Goldschmidt, 1940, and Huxley, 1942). A typical example comes from the work of Alpatov, who investigated honeybees throughout European Russia. He found that from north to south the tongue increases in length, the abdomen becomes lighter in color, and the wax gland decreases in size (Goldschmidt, 1940). These changes were observed to occur in a regular gradient, intermediate localities having bees with intermediate characteristics. In this case at least some of the changes observed may be connected with adaptation of the bees to different conditions. The nectar-secreting flowers in southern Russia may differ from those in northern Russia sufficiently to necessitate the longer tongue observed, for instance. We might well expect that when over a wide territory the climate and other environmental factors change gradually, the nature of the organisms inhabiting the successive parts of the territory also would change gradually.

When clines are observed, the traits involved are usually, if not always, characteristics having adaptive value for the organism. This fact is reflected in what have come to be called the "zoogeographic rules." BERGMANN'S RULE states that in warm-blooded animals the body size increases with a decrease in average temperature. This means in the northern hemisphere that body size increases in the northern parts of the range, as compared to the size exhibited in the southern portions. Thus our common deer averages larger in the northern parts of its range than it does in the southern. The same is true of many other mammals and birds. Large size in a cold climate has adaptive value in preventing loss of body heat. Since the mass of a body (e.g., a sphere) increases as the cube of the diameter while the surface area increases only as the square, larger bodies have *relatively* less area through which

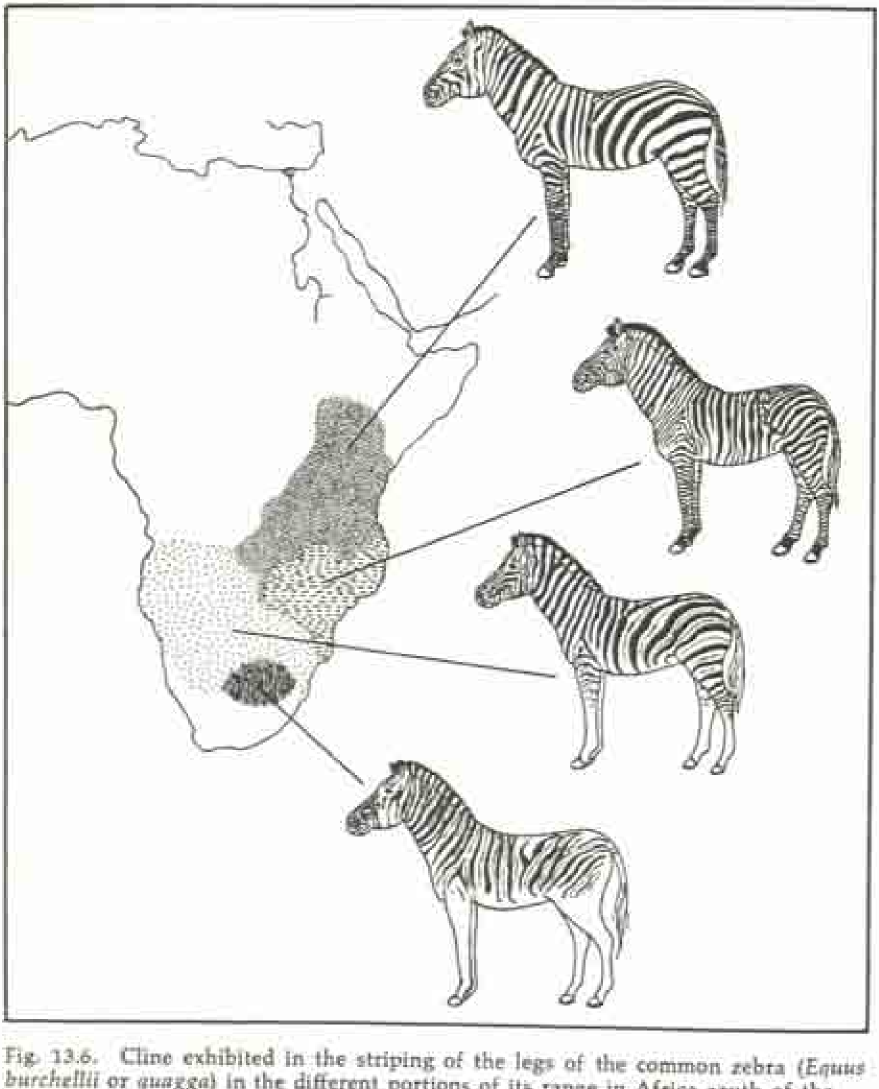


Fig. 13.6. Cline exhibited in the striping of the legs of the common zebra (*Equus burchellii* or *quagga*) in the different portions of its range in Africa south of the Sahara Desert. (Striping patterns redrawn from Cabrera, A., "Subspecific and individual variation in the Burchell zebras," *Journal of Mammalogy, 17* (1936), 89–112.)

to lose heat than do smaller ones. Hence it is of value to a warm-blooded animal in a cold climate to be large.

Loss of heat through exposed areas of limbs, tail, and ears also would be disadvantageous to an animal in a cold climate. ALLEN'S RULE states that such exposed portions of the body decrease in size with a decrease of average temperature. Comparison of the size of ears of an arctic fox, a fox of the temperate woodlands, and a desert fox illustrates the principle (Fig. 13.7). Of course the large ears of the desert fox also may have some positive adaptive value for that species.

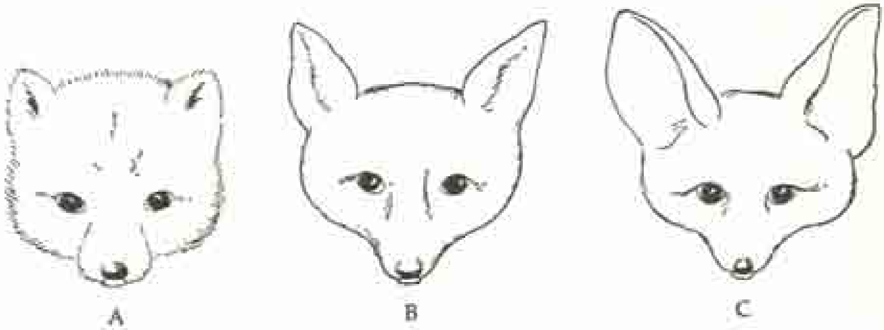


Fig. 13.7. Head of arctic fox (A), red fox (B), and desert fox (C). (From Guyer, M. F., *Animal Biology*, Harper & Row, 1948; redrawn from Hesse, Allee, and Schmidt, *Ecological Animal Geography*, John Wiley & Sons, 1937.)

GLOGER'S RULE states that "among warm-blooded animals those living in warmer and moister climates develop more melanin pigment [are darker than are animals in cold, dry climates], whereas forms in dry, hot climates have more yellow and red pigment" (Goldschmidt, 1940). There are other trends sometimes stated as "rules,"—e.g., within bird species in the Northern Hemisphere the number of eggs in a clutch increases from south to north. All of these rules are generalizations, and all have their exceptions. They describe tendencies exhibited in general by many clines.

The existence of clines themselves is perhaps the most interesting fact for our present purposes. They demonstrate a pattern of variability exhibited by species. This variability throughout a geographic region is most eloquent of evolution, as Darwin recognized. The phenomenon is exactly what we should expect if dispersal from a center, accompanied by evolutionary change, is a fact. On the other hand, if all these neighboring, slightly differing, forms were separately created, what a vast multitude of separate creations must have occurred!

The variability of species just mentioned forms the basis upon which species are commonly divided into geographic races or subspecies (see pp. 331–334 for additional discussion).

CONCLUSIONS

We have seen that similar continents are not necessarily populated with similar animals. Similarity among continents in animal inhabitants depends far more upon the accessibility of those continents to the same animals than it does upon mere similarity of living conditions.

As animals have attempted to expand their ranges, the attempts have met with greater or less success depending upon the barriers encountered and upon the versatility and adaptability of the organisms themselves. Success in invading new regions is frequently achieved by the adoption of bodily changes in structure and function. The changes may be great enough so that the resulting forms can no longer be considered to belong to the same species as the stock from which they arose. Such new species, however, will retain many points of similarity to each other and to the parent form. Since, at first at least, these kindred species occupy adjoining territories, the phenomenon of similar species replacing each other as one travels across the face of a continent arises. Eventually the original and derived species may become extinct throughout a considerable portion of their range, leaving remnants widely separated from each other, as in the cases of tapirs and camels. In such instances the original range frequently can be reconstructed by reference to the fossil record. All of these phenomena have significance if animals originate in separate regions (centers of dispersal) and then spread into those territories accessible to them, undergoing evolutionary change as their ranges expand into new environments.

References and Suggested Readings

Clark, A. H., *The Invasion of New Zealand by People, Plants and Animals. The South Island*, New Brunswick, New Jersey, Rutgers University Press, 1949.

Darlington, P. J., Jr., *Zoogeography: The Geographical Distribution of Animals*, New York, John Wiley, 1957.

Darwin, C., *On the Origin of Species by Means of Natural Selection*, London, John Murray, 1859. (See p. 6 for list of reprint editions.)

Darwin, C., *Autobiography*, in F. Darwin, *The Life and Letters of Charles Darwin*, vol. 1, Chap. 2, and *Charles Darwin, Autobiography and Letters*, Chap. 2, New York, Appleton-Century-Crofts, 1888 and 1892; also in F. Darwin, *Charles Darwin's Autobiography*, New York, Henry Schuman, 1950.

Goldschmidt, R., *The Material Basis of Evolution*, New Haven, Yale University Press, 1940.

Huxley, J. S., *Evolution—The Modern Synthesis*, New York, Harper & Row, 1942.

Laughlin, W. S., "Eskimos and Aleuts: Their origins and evolution," *Science, 142,* 633–645 (1963).

Matthew, W. D., *Climate and Evolution,* 2nd ed., New York, New York Academy of Sciences, 1939.

Müller-Beck, H., "Paleohunters in America: Origins and diffusion," *Science, 152,* 1191–1210 (1966).

Simpson, G. G., "Mammals and the nature of continents," *American Journal of Science, 241,* 1–31 (1943).

Simpson, G. G., "History of the fauna of Latin America," *American Scientist, 38* 361–389 (1950).

Simpson, G. G., *Evolution and Geography,* Eugene, Oregon State System of Higher Education, 1953.

Simpson, G. G., "Historical zoogeography of Australian mammals," *Evolution, 15,* 431–446 (1961),

Wallace, A. R., *The Geographical Distribution of Animals,* New York, Harper & Row, 1876; reprinted by Hafner Publishing, New York, 1962.

Wood, A. E., personal communication, 1969.

14

Evolution as Seen in the Geographic Distribution of Animals: Oceanic Islands

ANIMAL DISTRIBUTION on continents is highly complex. The situation observed at present is the result of a long series of changing events stretching back through the dim vistas of geologic time. Continents present a multiplicity of varied habitats open to animals capable of occupying them. Periods of isolation of continents, or portions of continents, resulting from submergence of intervening land, alternate with periods of connection, when the intervening land is again above sea level. Changing climates over great portions of the earth, extinction of previous inhabitants, appearance of new forms, and many other factors operating through the ages have rendered the continental zoogeographic record intricate and difficult to decipher. Accordingly, zoogeographers turn to oceanic islands as a means of studying factors operating in evolution and distribution under simpler conditions. Oceanic islands may be thought of as affording the zoogeographer an approach to laboratory experimentation. Unfortunately, biologists were not on hand to record the birth and subsequent population of the oceanic islands upon which we must depend at present for most of our knowledge of the subject. Consequently, inferences must be drawn as to the beginnings of most of the "experiments." Nevertheless, the inferences in many cases can be made with considerable confidence. Thus oceanic islands always have held particular fascination for students of geographic distribution.

CONTINENTAL ISLANDS Islands in the oceans of the world are frequently classified into two categories: continental islands and oceanic islands. CONTINENTAL ISLANDS are those that are part of a continent in the sense that they are located on a continental shelf. At times in the past such shelves have been dry land. Even now the ocean between a continental island and the adjacent continent is shallow, 100 fathoms (600 ft) or less in depth. In Figs. 13.4 and 13.5 (pp. 281 and 284) these stretches of shallow ocean have been left unshaded. Thus, if the land were raised or the sea level were lowered by 100 fathoms, the British Isles would be connected to Europe and Japan would be connected to Asia, to give only two examples. There is no doubt that the ocean level has in times past fluctuated by at least this amount.

In plant and animal life, continental islands are characterized by resemblance to the continent to which they were formerly joined. Naturally the resemblance is greatest if the connection to the continent was recent in geologic time and less if the connection was more remote in time, permitting the appearance meantime of new forms on the continent and perhaps also on the island. Of particular interest in comparison to the fauna of oceanic islands is the fact that continental islands possess amphibians and also the large mammals characteristic of the neighboring continent. Thus the mammals of the British Isles are in the main identical with those of Europe.

The reason amphibians and large mammals are mentioned is that such forms are relatively unlikely to engage in island hopping. Nevertheless, we must use caution in interpreting the presence of any single organism as evidence that the organism reached the island over dry land. We know so little of what is *possible* in the way of accidental transport. In general, if organisms reach an island over dry land we should expect that virtually entire faunas will reach the island, not merely a few members of a fauna. When only a few members reach an island we suspect island hopping or accidental transport of some kind.

The fact that at one time an island was connected to a continent does not prove that the present inhabitants of the island reached it during the period of land connection.

NATURE OF OCEANIC ISLANDS Typical OCEANIC ISLANDS are not located on continental shelves. Most of them are far from any continent, with hundreds or thousands of miles of deep ocean in between. Most of them are the summits of mountain peaks rising from the ocean floor through thousands of feet of water and thence on up into the air. Most of them are volcanic, many still actively so.

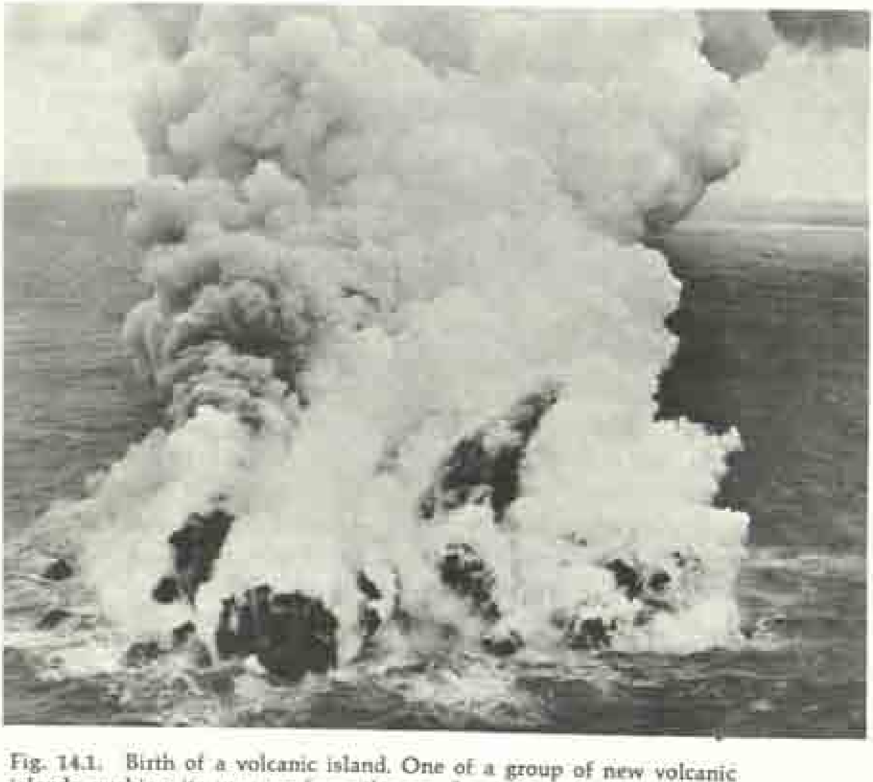


Fig. 14.1. Birth of a volcanic island. One of a group of new volcanic islands pushing its way up from the sea floor 200 miles south of Tokyo, Japan. Seen from the USS *Norton Sound* (AV-11), Lat. 31—57 N., Long. 140—01 E. (Official Department of Defense photograph.)

A dramatic view of the birth of such an island is shown in Fig. 14.1. Here the summit of a submerged volcanic mountain is caught in the act of breaking the surface of the Pacific, like a giant erupting tooth. From such beginnings oceanic islands are built. Perhaps the one shown in the picture may not develop into a large island; it may remain a small "bird rock," so-called because the principal inhabitants are sea birds which use the small island for nesting. On the other hand, it may continue to thrust itself upward until it becomes a towering mountain rivaling Mauna Kea in the Hawaiian group. Mauna Kea rises 31,750 ft above the ocean floor and hence is the world's highest mountain measured from base to summit.

HOW OCEANIC ISLANDS ARE POPULATED What animals and plants inhabit oceanic islands? The latter are populated by forms able to reach them by means other than passage across dry land. This statement follows from our definition of an oceanic island (p. 294). We must hasten to add, however, that there have been in the past, and are today, students of island life who believe that many of the islands usually considered oceanic nevertheless at one time or another were connected to continents, either by land bridges or by having actually constituted a portion of the continent. According to the latter view the island subsequently became detached from the continent and drifted away from it. This would be a very different method of oceanic island formation from the one described above. It forms part of the theory of "continental drift," according to which all the continents and islands at one time were gathered together into one continuous land mass. Eventually the parts of this mass separated from each other and drifted away, leaving the oceans in between. Within recent years evidence has increased that such continental drifting has in fact occurred. But most of the geologically young oceanic islands, of volcanic origin and separated from continents by long distances, cannot be accounted for in this way.

HARMONIC AND DISHARMONIC FAUNAS Faunas of oceanic islands usually present internal evidence of not having arisen by migration over land. The animals are usually a rather haphazard assemblage. Such a fauna is frequently spoken of as disharmonic, in contrast with the harmonic faunas of continents and continental islands. In HARMONIC FAUNAS the various habitats and means of livelihood (environmental niches) are uniformly filled by animals, each adapted for its particular niche. In DISHARMONIC FAUNAS many environmental niches remain unexploited or are filled by animals that in a harmonic fauna have different habits and means of livelihood. Under island conditions animals have sometimes "improvised" means of exploiting environmental niches foreign to them on continents. Examples are given later in the discussions of the Galápagos and Hawaiian faunas.

Disharmonic faunas seem, then, to indicate absence of land connection. Where land connections occur, to continental islands, harmonic faunas are transferred from continents to islands more or less intact, except as island conditions may be unsuitable for this or that species.

Not all faunas of oceanic islands are disharmonic. Some of the larger and older islands and archipelagos, like the Hawaiian Islands, have faunas that are quite harmonic. In such cases, however, it is evident that the harmonic fauna is not like that of any continent but is an evolutionary achievement that occurred on the islands themselves. It occurs on islands and archipelagos large enough to provide considerable diversity of habitat and ancient enough so that time has been provided for evolutionary change.

Absence of amphibians is particularly characteristic of most oceanic islands. Neither amphibian eggs nor adults can survive immersion in seawater. Transportation on rafts or by other means that avoid contact with seawater is possible and doubtless accounts for the presence of amphibians on those oceanic islands that do possess them.

Absence of mammals, particularly of larger species, also is characteristic of oceanic islands. Had land bridges existed, at any time subsequent to the Cretaceous period at least, such regularly observed absence would be inexplicable, since most of the islands prove to be entirely suitable to mammalian life once mammals are introduced by man or some other agency.

MEANS OF DISPERSAL TO OCEANIC ISLANDS If, then, we discount land connections as means by which animals reach oceanic islands, what other means are available?

Transportation by WIND may well be the most important means of populating oceanic islands. The efficacy of this means will be at once apparent in the cases of plants that produce microscopic seeds and spores. Dust from the explosive volcanic eruption that destroyed a large part of the island of Krakatoa in 1883 encircled the globe, remaining suspended in the atmosphere for many months. Hence there is no difficulty in accounting for the dispersal of seeds and spores that rival dust particles in minuteness.

Even larger seeds may be carried by winds and air currents. Thus Glick (1939) in connection with trapping insects in airplanes at high altitudes caught plant seeds at altitudes as great as 5000 ft. He concluded that transportation by prevailing winds in the upper air currents forms the most important means by which seeds reach oceanic islands. There seems no reason why this same method of transport may not be effective for animals and animal eggs that resemble seeds in diminutiveness, providing only that the animals or eggs can withstand conditions encountered in the upper atmosphere. Few people realize the vast multitude of minute land snails living all around us. Many of these snails are less than a millimeter in diameter and weigh less than one milligram. It should occasion no surprise that most oceanic islands possess such tiny snails and that in some cases snails found on these islands are hundreds, or even thousands, of miles distant from their nearest relatives.

The same situation applies to small insects. One investigator, Elton, has observed that aphids and flies are blown across the 800 miles between Europe and Spitzbergen (Zimmerman, 1948). In the investigation mentioned previously, Glick trapped thousands of specimens at heights up to 14,000 ft. Included were flightless larvae and nymphs, wingless adults, mites, and spiders. Significantly, the forms taken at greatest heights were weak fliers, while the stronger fliers, having heavier bodies, were found at lower altitudes. Thus for the most part transportation through the higher atmosphere was being accomplished with relatively little cooperation on the part of the insect.

Storms that reach hurricane intensity have great carrying power. Zimmerman states that a wind of 75 miles per hour has a lifting force of 16 pounds per square foot and that hurricane winds may exceed twice that velocity. The same author also records hurricane action that tore large sheets of iron roofing from a church on an island in Samoa and deposited it on another island six miles distant. We should not be surprised, therefore, that large insects and birds may be carried great distances by winds. Insects such as butterflies, grasshoppers, and beetles have been found as far as 1000 miles from their homes, and land birds are blown far out to sea. Zimmerman records that a pair of North American kingfishers flew ashore on Hawaii a few years ago. Many additional examples might be given, serving to support the view that windstorms transport small objects for long distances and blow flying animals far from the regions they normally inhabit and to which, if undisturbed, they would confine their flights.

A second means by which plants and flightless animals can reach oceanic islands is through TRANSPORTATION BY SOME ANIMAL CAPABLE OF FLIGHT. Examples have been observed occasionally for many years, and the matter was discussed by Darwin. Birds may carry mud and included small objects attached to their feet or feathers. Zimmerman records that a mallard duck shot in the Sahara was found to have snail eggs on its feet. The same author states that he picked a living bark beetle from the feathers of an owl. Seeds may pass undamaged through the digestive tract of a bird. Accordingly, migratory birds or birds blown by storms from their normal ranges may account for occasional introductions of plants and animals on oceanic islands.

But neither winds nor migrating birds can afford means of transportation for such creatures as land mammals and reptiles. Although land mammals are few on oceanic islands, such reptiles as lizards and geckos are common. For larger land animals, therefore, some means of transportation across the ocean itself must have been operative. Such means are afforded by NATURAL RAFTS AND "FLOATING ISLANDS." In times of flood large masses of earth and entwining vegetation, including trees, may be torn loose from the banks of rivers and swept out to sea. Sometimes such masses are encountered floating in the ocean out of sight of land, still lush and green, with palms 20–30 ft tall. It is entirely probable that land animals may be transported long distances in this manner. Mayr (1940) recorded that many tropical ocean currents have a speed of at least two knots; this would amount to 50 miles in a day and 1000 miles in three weeks. Heyerdahl's (1950) balsa raft, the *Kon-Tiki,* carried six men from South America to a South Sea island, a distance of 4300 nautical miles, in 101 days. This is an average of 42.5 miles per day. Since a sail was used, the steady trade winds augmented motive force provided by ocean currents.

Probably reptiles are more likely to withstand the vicissitudes of travel by natural rafts than are mammals, though the latter have occasionally been seen on rafts of this type. In this connection we may well recall that man, from prehistoric times, has traveled from island to island and from continent to island by boats and ships. He has intentionally transported some land animals in his boats, but in addition to these he has undoubtedly transported unintentionally an indeterminable number of stowaways. This fact adds difficulty to the problem of determining which mammals, for example, inhabited a given island before the coming of man. In the case of the Galápagos Islands there seems no doubt that rice rats, small rodents of South American relationship, were present before the advent of human visitors.

We note that all the means of dispersal just discussed are accidental, involving a large element of chance. It is significant that chance is just the factor that seems to have been operative in the production of the disharmonic floras and faunas characteristic of oceanic islands. The objection may be raised that the means postulated are too meager to have accounted for observed populations on oceanic islands. Yet the original number of immigrants may have been small and their arrivals widely spaced in time. In the long stretches of geologic time even very improbable events, if they are not impossible, may occur. Thus Zimmerman (1948) concluded with regard to the rich and varied insect population of Hawaii "that over a period of several millions of years, only about 250 overseas stragglers succeeded in becoming established in the several thousand square miles of the Hawaiian Islands—perhaps only one successful colonization per 20,000 years!"

Some of the smaller oceanic islands bear evidence of relatively recent formation. This fact precludes the possibility that they were ever connected to continents or other islands by land bridges. Thus they may be considered to provide test cases of the efficacy of the accidental means of dispersal described above. One such island in the Pacific is Henderson, located some 150 miles north and east of its nearest neighbor, Pitcairn. Henderson is about two and a half by five miles in extent; its greatest elevation is between 75 and 100 ft above sea level. It is certainly a young island, its age numbered in thousands of years rather than in hundreds of thousands. It appears to have risen sterile from the sea, like the island shown in Fig. 14.1. Zimmerman recorded that today it is densely covered with tangled tropical jungle. The Bishop Museum expedition of 1934 found more than 250 species of plants, mostly native, as well as an endemic genus or subgenus of rail, endemic insects, and endemic land snails. (Endemic species, genera, and so on, are those occurring nowhere else than in the region under discussion.) Zimmerman concluded, "Thus, all of the major elements of the Polynesian terrestrial biota have succeeded in being transported across the sea, colonizing this tiny bit of isolated land, and have not only established themselves there but have evolved into new forms quite distinct from their forebears."

Thus far in our discussion of oceanic islands we have summarized the general characteristics of their animal life and discussed the means by which animals reached them. With these facts in mind we shall now turn our attention to a particular group of islands that long have held special interest for biologists, partly no doubt because it was the peculiarities of the animals inhabiting these islands that gave impetus to Darwin's thinking on the subject of evolution. We refer to the Galápagos Islands, which Darwin visited in 1835 in connection with his circumnavigation of the globe as naturalist on *H.M.S Beagle.*

GALÁPAGOS ARCHIPELAGO

The Galápagos archipelago is located on the equator about 600 miles west of South America (Fig. 14.2). There are 5 large islands in the group, with 19 smaller ones and 47 rocks. The islands are of volcanic origin; some of the volcanoes are still active. The topography is rough and mountainous, the highest mountain rising more than 4000 ft above the sea. The lower regions of the islands are dry and barren, with a rough, inhospitable surface reminding visitors of an unfinished planet. Darwin (1845) wrote, "Nothing could be less inviting than the first appearance. A broken field of black basaltic lava, thrown into the most rugged waves, and crossed by great fissures, is every where covered by stunted, sunburnt brushwood, which shows little signs of life." Else-

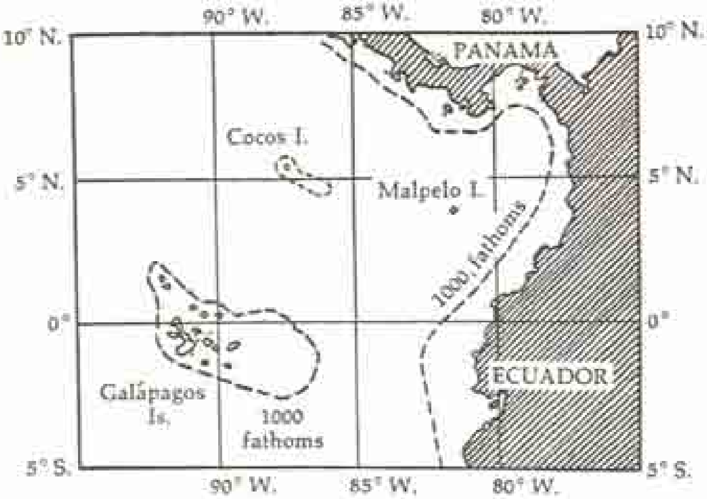


Fig. 14.2. Position of the Galápagos Islands. (From Lack, D., *Darwin's Finches*, Cambridge University Press, 1947.)

where he expressed himself still more feelingly: "The country was compared to what we might imagine the cultivated parts of the Infernal regions to be." To the hostility of the terrain to shoe leather is added the inhospitable nature of the vegetation: tree cactus, prickly pear cactus, and thornbushes.

As one progresses inland and upward from the coast on the three highest islands, extensive areas of open country are found. Humid forests occur in the interiors of the larger islands. Altogether, then, the archipelago exhibits a considerable variety of habitat.

Despite the fact that the islands are directly under the equator, the climate is not excessively hot. The ameliorating effect of the cold Peruvian current sweeping northward along the coast of South America accounts for this fact in large measure.

REPTILES The archipelago receives its name from the GIANT LAND TORTOISES that form some of the most distinctive inhabitants. These huge reptiles, weighing up to 500 lb, were formerly abundant but are now becoming scarce. Their tameness, coupled with their ability to stay alive for months in the holds of buccaneer and whaling vessels, furnishing a supply of fresh meat in prerefrigeration days, contributed to their downfall. Darwin recorded, "It is said that formerly single vessels have taken away as many as seven hundred, and that the ship's company of a frigate some years since brought down in one day two hundred tortoises to the beach." The size and strength of the creatures is indicated by the fact that people can ride on their backs, a pastime indulged in by Darwin, who wrote, "I frequently got on their backs, and then giving a few raps on the hinder part of their shells, they would rise up and walk away;—but I found it very difficult to keep my balance."

Two other distinctive reptiles of the Galápagos Islands are the LAND, AND THE MARINE IGUANAS. These big lizards are from three to four feet long. They contribute much to the feeling experienced by visitors of having stepped back into Mesozoic times. Formerly both varieties were extremely abundant. The marine iguanas are still found in large numbers, but the terrestrial iguanas are now nearly extinct. Yet of the latter Darwin wrote, "I cannot give a more forcible proof of their numbers, than by stating that when we were left at James Island, we could not for some time find a spot free from their burrows on which to pitch our single tent." That was in 1835.

The land iguanas are rather brightly colored: brownish red above, and yellow underneath. The marine iguanas, on the other hand, are black. Both species are vegetarians, the marine form living on green algae and the land form on a variety of plant material, such as cactus and the leaves of acacia trees.

The marine iguana is particularly remarkable in being the only known lizard to lead an aquatic existence. As adaptations for this mode of life it has partially webbed feet and a laterally flattened tail. It swims by serpentine movements of the body and tail, after the manner of the most accomplished swimmers in all classes of vertebrates, except birds. It seems reasonable to infer that when ancestral iguanas reached the islands they increased greatly in numbers until eventually the available food supply on land was inadequate to support further expansion. Under such conditions the pressure on the food supply would have been relieved if some of the iguanas proved capable of taking advantage of the algae abundant in neighboring shore waters. We may well imagine that the splitting of the iguana stock into the two forms found today occurred under such an impetus.

The roll of terrestrial reptiles on these islands is completed by mention of the fact that there is one genus each of snake, small lizard, and gecko.

MAMMALS The disharmonic nature of the fauna is still further attested by the mammals, or rather by the lack of them. There is one genus of BATS and one of RICE RATS. As noted before, the latter rodents were evidently the only terrestrial mammals to reach the archipelago prior to the coming of man. Intentionally and unintentionally man has introduced cattle, horses, donkeys, pigs, dogs, goats, and black rats. These have run wild over the islands. That they have found the new home congenial is affirmed by the statement of Lack (1947): "The characteristic music of the Galápagos forest is not the song of birds but the braying of donkeys."

It is particularly significant that before these introduced species arrived there were no large, herbivorous mammals on the islands. The environmental niches usually filled by grazing and browsing mammals (e.g., deer, moose, and antelope) were not filled by mammals. Probably it was owing to this fact that the reptiles were able to undergo the remarkable developments we have just noted. Darwin was impressed with this thought: "When we remember the well-beaten paths made by the thousands of huge tortoises—the many turtles—the great warrens of the terrestrial [iguana]—and the groups of the marine species basking on the coast-rocks of every island—we must admit that there is no other quarter of the world where this Order replaces the herbivorous mammalia in so extraordinary a manner." It was as though this isolated region, being free of mammalian competitors, afforded the reptiles one last chance for an adaptive radiation recalling, though dimly, the Mesozoic "golden age" of reptiles.

OTHER ANIMALS AND PLANTS The small number of land insects and of land molluscs as well as the great gaps in the expected types of plants also bear witness to the disharmonic nature of the fauna and flora. Many widespread plant groups are notably absent, among them conifers and palms as well as several important families characteristic of tropical America. The islands are old enough so that the environmental niches left vacant have been filled, at least partially, by plants that did succeed in reaching the islands. Thus, the typically low-growing prickly pear cactus on Galápagos has become a tree. We noted previously (p. 295) that the filling of environmental niches by forms other than those normally filling them on continents is characteristic of floras and faunas of oceanic islands.

HOW WERE THE ISLANDS POPULATED? How did plants and animals reach the Galápagos Islands? Were the latter ever connected to Central or South America? In the past this question has been answered affirmatively (e.g., Beebe, 1924), but the present consensus seems to be that they have not been so connected. The amount of vertical movement of the crust necessary to form a dry land connection to America seems unlikely during that portion of geologic time concerned in the distribution of immediate ancestors of the plants and animals inhabiting Galápagos. Also, as we have seen, the flora and fauna are notably disharmonic, a fact favoring the view that immigration across the ocean was the means of population. The affinity of the Galápagos fauna to that of Central America is attested by many investigations. C. T. Parsons (personal communication) is of the opinion that ancestral forms were carried by the Panamanian current, which swings south to include the archipelago every few years: "This current washes up many floating plants and brings much rain which would enable many plants and animals, thrown up on the usually barren shore, to gain a foothold."

Opponents of the view that plants and animals reached the archipelago by transportation across water have raised particular objection to the suggestion that land iguanas and land tortoises could have reached the islands in this way. Yet lizards, the group to which iguanas belong, have colonized most of Polynesia, including very isolated islands. Apparently they can be carried long distances on floating vegetation or perhaps even can float in the water themselves. Much remains to be learned about the means of dispersal possible to any particular animal. Tortoises have been observed to float and survive for long periods in seawater. Simpson (1943) has pointed out that the great land tortoises probably reached both South America and the Galápagos Islands in this manner, since they first appeared in South America in Miocene times, when that continent was not connected by land with North America. Some other islands (e.g., the Mascarene Islands in the Indian Ocean) also have giant land tortoises despite the fact that no evidence exists of a former land connection to a continent.

While the affinities of the Galápagos fauna are almost exclusively with the American fauna, one Polynesian form is included. This is a land mollusc, unrelated to those in America and apparently derived from islands at least 3000 miles to the west. It seems wiser to state that we do not know the means by which this creature reached the islands than to postulate a far-flung land bridge for its exclusive use.

GALÁPAGOS BIRDS No group of Galápagos animals is of more interest to students of evolution than are the birds, partly because of the role played by these birds in influencing the thinking of Darwin. He was particularly impressed by the varied adaptations exhibited by the unique finches of the archipelago. In commemoration of this fact, the Galápagos finches are now frequently called "Darwin's finches." To a book of that title by David Lack (1947) we are indebted for much of the following material on the Galápagos birds.

As is true of other animals, the affinities of the birds on the archipelago are with American forms. There is, however, great variation in the degree of similarity between the island forms and their continental relatives. Thus the cuckoo of the islands is identical with a South American species, and the single WARBLER is very similar to one living in Ecuador. The MARTIN is regarded as belonging to a separate subspecies of a species mainly inhabiting the continent. The TYRANT FLYCATCHER is a distinct species, but closely related to an American species. The MOCKINGBIRD differs so much from American mockingbirds that it is placed in a separate genus from the latter. Furthermore, the Galápagos mockingbird has become differentiated into nine island forms, "two of which are sufficiently distinctive to be treated as separate species, the other seven being treated as subspecies of a third species" (Lack, personal communication). Similarly, the VERMILION FLYCATCHER has differentiated into three island races. Finally, DARWIN'S FINCHES are so different from any existing American finch that, as stated by Lack, "there is considerable doubt as to their nearest mainland relative."

Thus we see all degrees of similarity between island and mainland species: from identity of characteristics to widely differing traits. How can these facts be explained?

In the first place, how does it happen that Galápagos birds resemble American ones at all? Surely this resemblance must mean that the Galápagos birds are the more or less modified descendants of American species. If the birds had been especially created to live on the Galápagos Islands it is difficult to see why they should have been created to resemble birds living on the neighboring continent rather than to resemble birds created to live on other islands, e.g., other islands in the Pacific or the Cape Verde Islands near the coast of Africa. The Cape Verde Islands resemble the Galápagos Islands in many respects yet, in the words of Darwin (1845), "the aboriginal inhabitants of the two groups are totally unlike; those of the Cape de Verd Islands bearing the impress of Africa, as the inhabitants of the Galápagos Archipelago are stamped with that of America." Such relationships of island faunas to those of neighboring continents are to be expected if evolution is a fact but are inexplicable upon any other basis.

In the second place, what is the significance of the fact that some Galápagos birds resemble American species more closely than do others? Lack is doubtless correct in explaining this fact upon a basis of the differing lengths of time during which the different species have been inhabiting the archipelago. Thus the cuckoo is probably a relative newcomer, so recently arrived that it has not had time to develop differences from its South American ancestors. The mockingbird, on the other hand, arrived much earlier, a fact evidenced by its greater degree of difference from mainland mockingbirds as well as by its differentiation into separate species and races on the various islands. Undoubtedly animals differ in rate of evolutionary change; conclusions correlating degree of difference with length of time during which isolation has been operative are probably valid in the main, however. (See the discussion of faunal stratification, p. 274.)

Following this line of thought we conclude that the ancestors of Darwin's finches were very early migrants to the archipelago, perhaps the first birds to reach it. These finches differ greatly from any other living finch and have developed many island forms.

Finches belong to the largest family of birds, the Fringillidae, which includes many of our most common birds—among them our captive songster the canary, the many species of sparrows, the goldfinch, the grosbeaks, and the cardinal. In the words of Chapman (1920), birds of this family "generally agree in possessing stout, conical bills, which are admirably adapted to crush seeds." With this fact in mind we direct our attention to Darwin's finches, characterized by Lack as follows: "Darwin's finches are dull to look at, not only in their orderly ranks in museum trays, but also when they hop about the ground or perch in the trees of the Galápagos, making dull unmusical noises. Only the variety of their beaks and the number of their species excite attention—small finch-like beaks, huge finch-like beaks, parrot-like beaks, straight wood-boring beaks, decurved flower-probing beaks, slender warbler-like beaks; species which look very different and species which look closely similar."

ADAPTIVE RADIATION OF FINCH BEAKS In the following series of sketches we present a few of the principal beak modifications connected with differing food habits.

The ground finches *(Geospiza)* have heavy, finchlike beaks (Fig. 14.3). Seeds form the chief item of food, although they occasionally eat

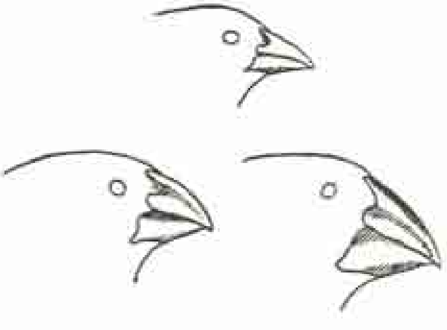


Fig. 14.3. Beaks of three species of ground finches (Subgenus *Geospiza*). (From Lack, D., *Darwin's Finches*, Cambridge University Press, 1947.)

insects. As the three sketches in the figure indicate, great differences in the size of the beak are found among these ground finches. To a considerable extent the large ground finches eat the same food as do the smaller ones, yet the larger ones can eat larger and harder seeds than can the smaller ones. In correlation with this fact the larger finches mainly ignore small seeds, such as those of grasses, which form the staple diet of the small ground finches. Thus the competition between the various ground finches is reduced and they are able to occupy the same habitat.

The cactus ground finch (Fig. 14.4) has a long, somewhat decurved beak and a split tongue. It probes the flowers of the prickly pear cactus tree for nectar. It also feeds on the soft pulp of this cactus and on various other food items.

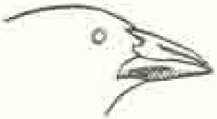


Fig. 14.4. Beak of the cactus ground finch (*Geospiza scandens*). (From Lack, D., *Darwin's Finches*, Cambridge University Press, 1947.)

The vegetarian tree finch (Fig. 14.5) has a short, thick, somewhat parrotlike beak. Leaves, buds, blossoms, and fruits form its main items of diet.

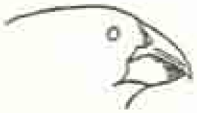


Fig. 14.5. Beak of the vegetarian tree finch (Subgenus *Platyspiza*). (From Lack, D., *Darwin's Finches*, Cambridge University Press, 1947.)

The insectivorous tree finches (Fig. 14.6) have beaks much like the beak of the vegetarian tree finch. They live chiefly on insects excavated from woody tissues, although they are not averse to eating young leaves, buds, and occasionally seeds.

Fig. 14.6. Beaks of two insectivorous tree finches (Subgenus *Camarhynchus*). (From Lack, D., *Darwin's Finches*, Cambridge University Press, 1947.)

One of the most remarkable of the finches is the so-called woodpecker finch. Its beak is stout and straight, similar to that of tree finches but longer (Fig. 14.7). Almost completely insectivorous, it searches bark and leaf clusters and bores into wood like a woodpecker. When a woodpecker has exposed an insect it uses its long tongue to extract the insect from the crack or hole. This finch, lacking the long tongue, picks up a small stick or cactus spine, holds the latter lengthwise in its beak, and probes out the insect, dropping the stick and seizing the insect as it emerges. This remarkable practice affords one of the few known examples of the use of a tool by a bird (Fig. 14.8). Clearly we have here an example of an animal that has "improvised" a means of entering an environmental niche foreign to it on the continents of the world (see p. 295).

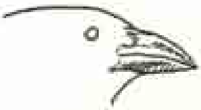


Fig. 14.7. Beak of the woodpecker finch (Subgenus *Cactospiza*). (From Lack, D., *Darwin's Finches*, Cambridge University Press, 1947.)

The warbler finch (Fig. 14.9) is so much like a warbler that its true relationship formerly was not recognized. Its beak is slender and warblerlike. It searches leaves and bushes for small insects and sometimes catches insects on the wing like a true warbler.

We have stressed differences in beaks because such differences seem to be the ones of most importance. Indeed, Lack (1947) presented evidence that the birds themselves depend upon the shape and size of the beak in distinguishing members of their own species from members of other species. The plumage of related species of these rather drab little birds is very similar. In some species the males are black and the females are a speckled brown. In other species the males resemble the females in plumage. The studies of Bowman (1961 and 1963) suggest that the colorations serve to some extent to camouflage the birds and thus protect them from predators. For example, black male plumage is found in species inhabiting regions where the soil is very dark (volcanic lava).

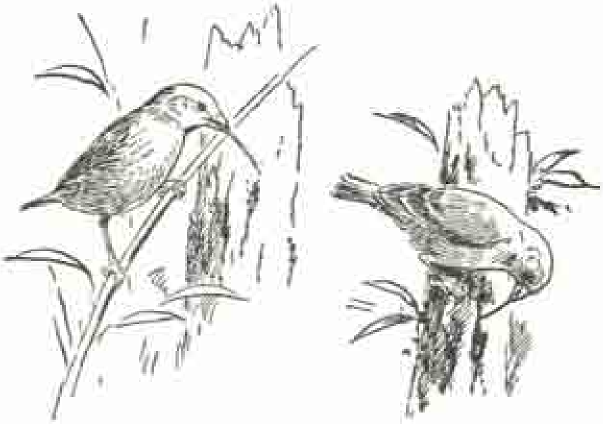


Fig. 14.8. The woodpecker finch and its stick. (Drawn from photographs; from Lack, D., *Darwin's Fnches*, Cambridge University Press, 1947.)

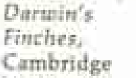


Fig. 14.9. Beak of the warbler finch (*Certhidea*). (From Lack, D., *Darwin's Finches*, Cambridge University Press, 1947.)

We have had space for only a few examples, briefly characterized. The literature on Darwin's finches is large. Aside from the book by Lack, interested readers are referred to Bowman (1961 and 1963) both for references and for thorough studies of the anatomy of the beaks and of the accompanying musculature as well as of many other anatomical adaptations of these fascinating birds.

ORIGIN OF THE DIVERSITY EXHIBITED BY DARWIN'S FINCHES

How did this adaptive radiation arise? Doubtless when the ancestors first reached the islands they found few, if any, competitors for the available food supply and also many "unfinchlike ecological niches" open to them. Perhaps at first they had few enemies, though Bowman (1961 and 1963) pointed out that we do not know that this was the case. At present the finches are preyed upon by at least one species of owl, by a hawk, and by a snake. Bowman concluded that such predation always may have been important in the operation of natural selection on the finches.

Undoubtedly the finches spread from island to island. Since the islands were sufficiently far apart so that little land birds would fly between them only infrequently, the population on each island was more or less isolated from the other populations and thus free to evolve separately. The islands differ in many features of the environment and in food plants available (Bowman, 1961), so we may readily imagine that each island population developed its own distinctive adaptations to its particular island conditions. These adaptive changes probably included behavioral and other genetic changes so that birds from different islands would no longer interbreed if and when they came into contact with each other (see reproductive isolation, pp. 439–440). If this occurred, each island population would be considered to have become a separate species (pp. 471–472). Eventually these species, evolved in isolation, spread to other islands. Thus there arose the condition observed today of several or many species on one island.

What happened when species, evolved as just described, came into contact on one island? Did they *compete* for the available food supply (especially seeds)? Such interspecies competition is frequently regarded as a factor making for further evolution. Lack (1969) saw in competition between species one means of explaining such observations as the following. On one island a certain species is adapted for eating seeds of varied size, including large ones. On another island this same species is not adapted for eating the larger seeds. On this second island there is the potential competition afforded by another finch, this one specialized for eating large seeds. On the first island no competitor for the large seeds is found; thus the species present there is free to eat the larger seeds as well as the smaller ones, and has become adapted accordingly. When several species were present on one island perhaps competition for seeds became so severe that some species were driven to seek other sources of food (e.g., insects, nectar, and plant tissues). Bowman (1961 and 1963), on the other hand, minimized the importance of such competition, concluding that adaptations to differing foods acquired while the species were still living on their separate islands *prevented* direct competition when these species eventually came into contact on one island. Perhaps both points of view present factors operating in the evolution of these birds.

Today we find Darwin's finches displaying a diversity of food habits that finches do not achieve on continents. Observing this diversity had great influence on the thinking of Darwin, who wrote in *The Voyage of the Beagle,* "Seeing this gradation and diversity of structure in one small, intimately related group of birds, one might really fancy that from an original paucity of birds in this archipelago, one species had been taken and modified for different ends."

DREPANID BIRDS OF HAWAII

In concluding our discussion of the light shed on evolution by the inhabitants of oceanic islands we shall cite another remarkable example of adaptive radiation among birds. The Hawaiian Islands are the home of a distinctive group of birds called "sicklebills," "honey creepers," or better, "drepanids," from the name of the family to which they belong: Drepaniidae (Drepanididae). The fact that they are thus placed in a separate family reflects their dissimilarity to all other birds. There is, indeed, considerable doubt as to their closest continental relatives. Present evidence suggests that their ancestors were allied to the honey creepers of tropical America (family Coerebidae).

The Hawaiian Islands occupy an isolated position in the mid-Pacific, far from any continent. North America is about 2000 miles away, and Japan is more than 3000 miles away. The archipelago is even remote from other large oceanic islands. The islands, of volcanic origin, rose directly from the ocean floor and were never connected to other bodies of land.

As would be expected in truly oceanic islands far from a continent, the number of land birds in the Hawaiian Islands is small. Also, this avian fauna would be disharmonic were it not for the fact that the archipelago is old enough so that a secondary harmony of its own has had time to develop The ancestors of the drepanids may have been the first land birds to reach the islands. These ancestors are believed to have fed upon nectar and to have had slender beaks and tubular tongues. Such tongues, possessed by many of the modern drepanids, end in a brushlike tip and, like a sort of built-in soda straw, are obviously adapted for sucking nectar from flowers.

The beak form believed to be most like that of the ancestral drepanids is possessed today by *Loxops virens*. Figure 14.10 shows a few of the forms that have arisen from this type. Note the position of *Loxops* near the base of the diagram. This relatively unspecialized little bird lives largely on nectar and insects obtained from blossoms of flowering trees; it also eats berries.

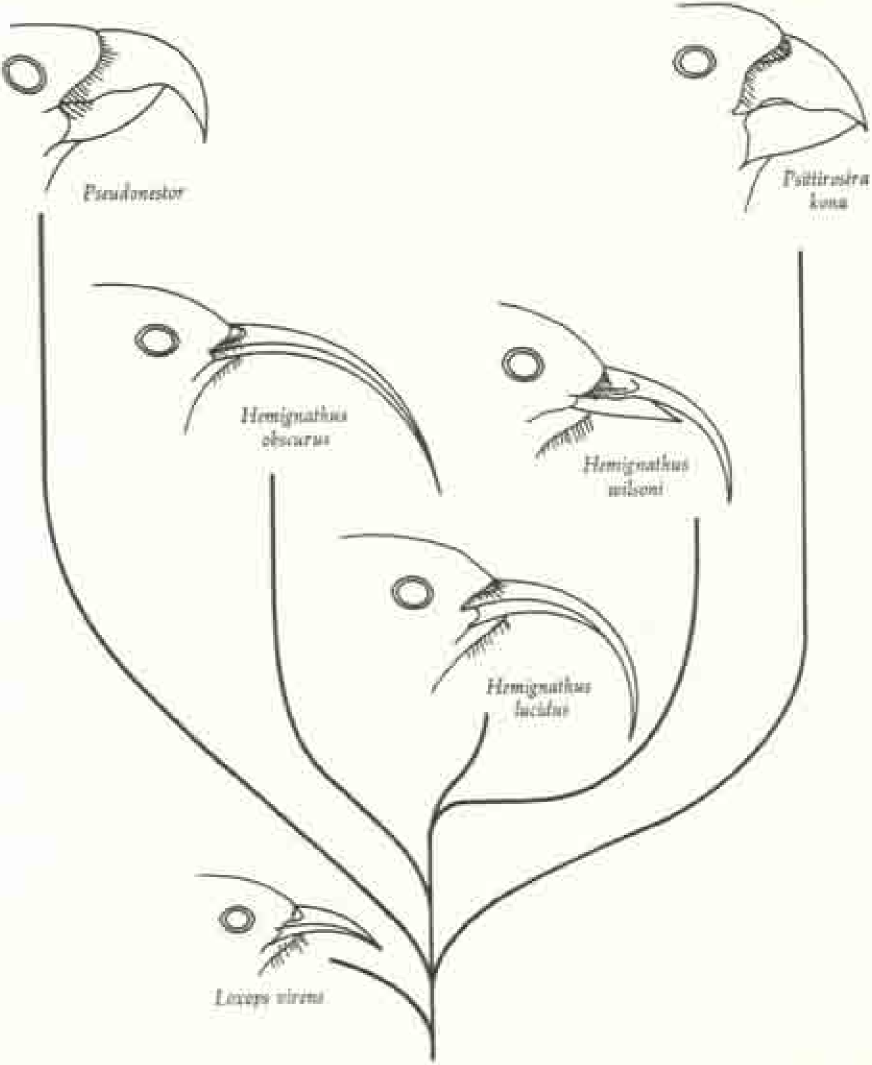

Pseudonestor
Psittirostra kona
Hemignathus obscurus
Hemignathus wilsoni
Hemignathus lucidus
Loxops virens

Fig. 14.10. Adaptive radiation of beaks in one subfamily of the drepanid birds of Hawaii. (Sketches after Rothschild, from Amadon, D., "Ecology and the evolution of some Hawaiian birds," *Evolution*, *1* (1947), 63–68.)

Three of the birds shown in Fig. 14.10 belong to the genus *Hemignathus* (subfamily Psittirostrinae). Of these, *H. obscurus* differs from *Loxops* principally by great elongation of both mandibles of the beak. This long beak was used mainly for probing bark cavities in search of insects. In another subfamily of drepanids (Drepaniinae) we find other species with similarly elongated "sicklebills." In this case the beak seems to be an adaptation for extracting nectar from the elongated, curved flowers of lobeliads (Fig. 14.11). Since the foreheads of these birds are frequently observed to be plastered with pollen, the visits of the birds aid in the reproduction of lobeliads.

Development of elongated, curved beaks from shorter ones in these two subfamilies may well be another example of parallel evolution (Amadon, 1950).

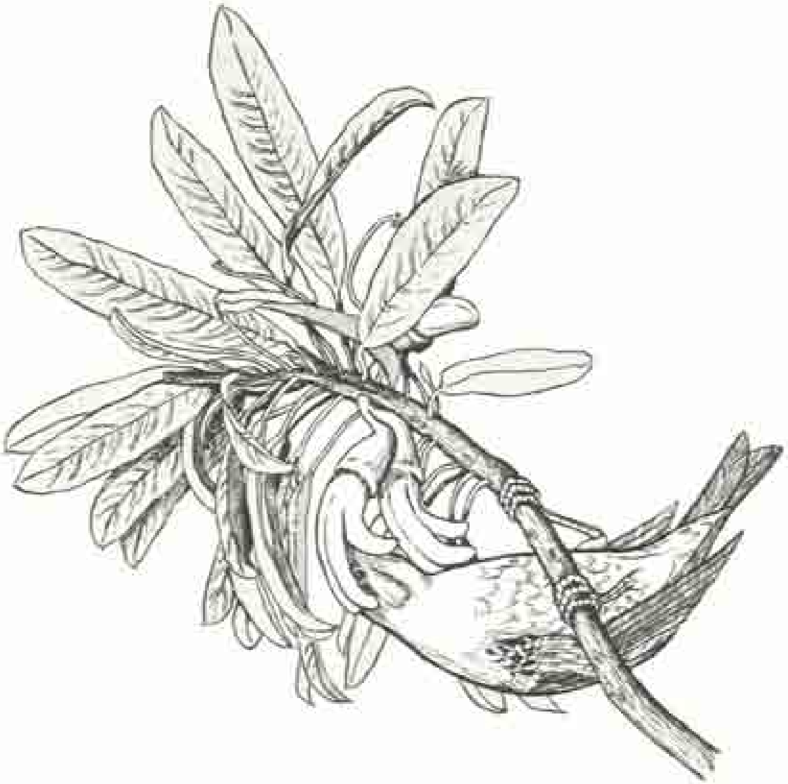


Fig. 14.11. A drepanid bird with curved beak feeding on a lobeliad flower. (Drawn by Herman T. Spieth, who commented, "Note the neat fit!" From Spieth, H. T., "Hawaiian honeycreeper, *Vestiaria coccinea* (Forster), feeding on lobeliad flowers, *Clermontia arborescens* (Mann) Hillebr.," *The American Naturalist*, *100* (1966), 470–473. Used by permission of The University of Chicago Press.)

In the other two species of *Hemignathus* (Fig. 14.10) the upper mandible is elongated but the lower mandible is shortened, more radically in *H. wilsoni* than in *H. lucidus*. *H. lucidus* (now extinct) used its lower mandible to chip and pry away bark in search of insects. *H. wilsoni*, still fairly common, is more efficient in securing insect larvae under bark and in wood. While holding the curved upper mandible to one side, the bird pounds vigorously with the chisel-like lower mandible, boring a hole and exposing the insect larva. Then the upper mandible, so slender that its tip is slightly flexible, is used as a probe to remove the insect. The slender tongue, which can be extended to the length of the upper mandible, aids in the process of extraction. We may say that this bird has found a means of entering the woodpeckerlike environmental niche but has done so in a manner quite unlike that by which the woodpecker finch of Galápagos did so (p. 307).

It is noteworthy that these three species of *Hemignathus*, all mainly insect eaters, have retained tubular tongues, thus betraying their nectar-feeding ancestry.

Some of the drepanids developed heavy beaks (Fig. 14.10). Of these, *Psittirostra kona* had a veritable nutcracker and lived primarily on a diet of nuts. The powerful, parrotlike beak of *Pseudonestor* is used to tear and wrench away pieces of bark and wood to expose wood-boring beetles.

We have mentioned only a few of the drepanids that are living, or did live, on the Hawaiian Islands. Alas, many, if not most, forms are extinct or rare today, known to us mainly from museum specimens. Many are the victims of man's activities in changing environments for his own purpose, thus creating conditions to which the native birds could not adapt. The examples we have chosen show some of the more extreme adaptations undergone by these birds in earlier times when enemies and competitors were few. Evolutionary forces at work were doubtless similar to those operative in the adaptive radiation of Darwin's finches on the Galápagos Islands (see the preceding).

CONCLUSIONS

We have dwelt at some length on the inhabitants of oceanic islands because they afford examples of evolutionary change occurring within relatively recent times and under conditions still largely observable. The islands themselves are geologically young; hence any observed evolution of their inhabitants must have occurred within a relatively short span of time. Thus, basing his conclusion on the opinion that the Hawaiian Islands are of Pliocene and later age, Amadon (1947) estimated that about five million years were available for the evolution of the drepanid birds. Although by human standards this is a very long time, it is but a small portion of geologic time, or even of that part of geologic time which has elapsed since the first birds appeared (p. 146). The Hawaiian Islands are among the older oceanic islands.

Owing to their isolation, oceanic islands develop disharmonic faunas and floras. Taking advantage of environmental niches left vacant in such disharmonic faunas, animals reaching larger and older archipelagos early in their history underwent adaptive radiation quite unlike that possible to their relatives on continents. Hence oceanic islands became the settings for some of the most vivid examples of evolution in action available to us.

References and Suggested Readings

Amadon, D., "Ecology and the evolution of some Hawaiian birds," *Evolution, 1,* 63–68 (1947).

Amadon, D., "The Hawaiian Honeycreepers (Aves, Drepaniidae)," *Bulletin of the American Museum of Natural History, 95,* 155–262 Art. 4 (1950).

Beebe, W., *Galapagos: World's End,* New York, G. P. Putnam's Sons, 1924.

Bowman, R. I., "Morphological differentiation and adaptation in the Galápagos finches," *University of California Publications in Zoology, 58,* 1–302 (1961).

Bowman, R. I., "Evolutionary patterns in Darwin's finches," *California Academy of Sciences, Occasional Papers, 44,* 107–140 (1963).

Bowman, R. I. (ed.), *The Galápagos,* Berkeley, University of California Press, 1966. (Emphasis is upon plants and on animals other than birds.)

Bryan, W. A., *Natural History of Hawaii,* Honolulu, privately published, 1915.

Chapman, F. M., *Handbook of Birds of Eastern North America,* rev. ed., New York, Appleton-Century-Crofts, 1920.

Darlington, P. J., Jr., *Zoogeography: The Geographical Distribution of Animals,* New York, John Wiley & Sons, 1957.

Darwin, C., *The Voyage of the Beagle,* 2nd ed., 1845. (See p. 6 for listing of reprint editions.)

Darwin, C., *On the Origin of Species by Means of Natural Selection,* London, John Murray, 1859. (See p. 6 for listing of reprint editions.)

Eibl-Eibesfeldt, I., *Galapagos,* New York, Doubleday, 1961.

Glick, P. A., "The distribution of insects, spiders and mites in the air," *United States Department of Agriculture, Technical Bulletin,* (673), 1939.

Gulick, A., "Biological peculiarities of oceanic islands," *Quarterly Review of Biology, 7,* 405–427 (1932).

Heyerdahl, T., *Kon-Tiki. Across the Pacific by Raft,* Chicago, Rand MacNally, 1950.

Lack, D., *Darwin's Finches,* Cambridge, Cambridge University Press, 1947. Available as Harper Torchbook TB544, New York, Harper & Row.

Lack, D., "Subspecies and sympatry in Darwin's finches," *Evolution, 23,* 252–263 (1969).

Mayr, E., "The origin and history of the bird fauna of Polynesia," *Proceedings of the Sixth Pacific Science Congress, 4,* 197–216 (1940).

Perkins, R. C. L., *Vertebrata,* in D. Sharp (ed.), *Fauna Hawaiiensis,* vol. I, pt. IV, Cambridge, Cambridge University Press, 1903, pp. 365–466.

Simpson, G. G., "Turtles and the origin of the fauna of Latin America," *American Journal of Science, 241,* 413–429 (1943).

Simpson, G. G., "History of the fauna of Latin America," *American Scientist, 38,* 361–389 (1950).

Spieth, H. T., "Hawaiian honeycreeper, *Vestiaria coccinea* (Forster), feeding on lobeliad flowers, *Clermontia*," *American Naturalist, 100,* 470–473 (1966).

Wallace, A. R., *Island Life,* New York, Harper & Row, 1881.

Zimmerman, E. C., *Insects of Hawaii,* vol. 1, *Introduction,* Honolulu, University of Hawaii Press, 1948.

15

Evolution as Seen in the Classification of Animals

MAN IS CHARACTERISTICALLY the collecting and classifying member of the animal kingdom. Whether it be stamps, antique automobiles, buttons, Chinese porcelain, coins, books, tapestries, or works of art, there seems to be an innate tendency in human nature leading to the acquisition of objects of interest. For some the acquisition is in itself sufficient satisfaction, but for most people, possessed of more tidy minds, accumulation must be accompanied by classification and cataloguing—the putting of everything "in its place." We are so constituted that we feel ill at ease when surrounded by chaos. We are not satisfied until we can introduce organization, can put things right, and can arrange things so that they "make sense." Much the same urge that leads one person to collect stamps leads another to collect animals. And for both, satisfaction is only complete when the items collected are properly filed and classified. Without this underlying human urge the great biological collections that are the pride of our museums and universities would never have come into existence.

BASIS OF CLASSIFICATION Biological classification doubtless had its inception in the desire of the human mind to put things in their place, as suggested above. A fundamental object of any system of classification—library books, stamps, or animals—is to arrange in orderly sequence, to place like with like. Thus in the library the books on photography are side by side in one place, books on ceramics in another, and biographies in still another. *Similarity*, then, of one kind or another is the basis of all classification. In the case of animals, similarity of *structure* (morphology) has traditionally been the basis upon which classifications have been built. More recently biochemical, physiological, and serological similarities have begun to contribute to classification, but it still remains true that most of the generally recognized classification is firmly grounded in morphological similarity. Morphologically similar animals are placed near together in classification; morphologically dissimilar animals are placed farther apart.

Classifications of one kind or another are probably as old as man's curiosity about his fellow inhabitants on this planet. During the centuries of the infancy of biology many classifications were suggested. Indeed, so many biologists created so many classifications that the resulting confusion finally became a stumbling block in the way of further scientific progress. It was the genius of the Swedish biologist CAROLUS LINNAEUS, born in 1707, that was able to devise a system of nomenclature that all biologists would agree to use and that was so logically developed that today, despite expanding horizons of biological knowledge, it still serves the needs of science.

BINOMIAL SYSTEM OF NOMENCLATURE The basis of the Linnaean system is the conferring of two names upon each species of animal. Hence this is a *binomial* system of nomenclature. Thus we say that the domestic dog belongs to the species *Canis familiaris*. The first name is that of the GENUS to which the domestic dog, along with other dogs, belongs. The second or specific name, as it is sometimes called, tells us which member of the genus is meant. An analogy lies in the practice of writing the name of an individual with the surname first, e.g., Smith, John. This tells us that the individual is one of the Smiths, the particular one of them being John. The prairie wolf or coyote is a member of genus *Canis* also, but not of the same species as the domestic dog. The name of his species is *C. latrans*. The jackal of Africa is *C. aureus*. Thus we see that the genus is a more inclusive unit of classification than is the species. Although some genera (plural of genus) may contain only one species, a genus is typically composed of a group of species having some morphological similarities. All members of genus *Canis* have some doglike attributes.

A few conventions will be noticed in the binomial system. The names are always in Latin or in Latinized form. While this practice strikes most American college students as needlessly cumbersome, it ensures uniformity of naming in writings of biologists of all nationalities. Although Latin is no longer regarded as the universal language of scholarship, knowledge of it is sufficiently widespread in all nations to render its use in forming names generally acceptable. With names agreed upon in this fashion, a biologist in one country, even though he may be writing in Russian or Chinese, can be sure that biologists in other countries will know exactly what animal he is discussing. Such understanding would probably not ensue if the Russian biologist were to employ the Russian name of the animal.

"Common" or vernacular names are notoriously variable even within the confines of one continent and one language. Consider, for example, the big American member of the cat family known to biologists as *Felis concolor*. According to Seton (1929) that mammal is called in various parts of America by the following "common" names: panther, puma, mountain lion, painter, cougar, catamount, brown tiger, varmint, sneak-cat, red tiger, silver lion, purple panther, deer-killer, Indian devil, mountain devil, mountain demon, mountain screamer, and king-cat. When we add to these the varied names for the animal in the Central and South American languages and dialects the confusion is truly appalling. We return to the simple appellation, *Felis concolor*, with a distinct sense of relief.

Another convention is that the scientific name of an animal is usually italicized (indicated in handwriting or typing by an underline). By convention, also, the name of the genus begins with a capital letter and the specific name with a "small" (lowercase) letter. Frequently a name or initial, not italicized, will follow the name of the species, for example, *Canis familiaris* L. This name or initial designates the name of the biologist who conferred the name in the first place. Since Linnaeus himself gave names to so many animals and plants, L. is sufficient to remind the reader that the name derives from the founder of the system.

FAMILY We have seen that the dog, the coyote, and the jackal are all grouped together in the genus *Canis* because they are all so very doglike in structure and characteristics. There are other mammals that are somewhat doglike but not sufficiently so to be included in genus *Canis*. For example, foxes are placed in the genus *Vulpes*. The common red fox is *Vulpes fulva*.

The more or less doglike animals comprising genus *Canis* and genus *Vulpes* and some others are grouped together into a higher category in our classification known as the FAMILY. The particular family concerned here is named Canidae. Another convention is evident at this point. The names of families always end with "-idae".

ORDER Another family somewhat related to the Canidae is that called Felidae, including all the catlike animals. This family, like the former, is composed of several genera, each of which is subdivided into species. The genus *Felis* already has been mentioned; in addition to *Felis concolor* we may mention the common house cat, *Felis domestica*. Other families include the Ursidae (bears), Procyonidae (raccoons), and Hyaenidae (hyenas).

All the animals mentioned in the preceding paragraph are alike in some respects, some of the most striking similarities being connected with the nature of their diet. They are all carnivorous—flesh eaters. This fact is recognized in classification by grouping these families together into a larger unit of classification, the ORDER. They all belong to the order Carnivora.

CLASS More than a dozen orders of living placental mammals rank along with the Carnivora. For example, the order Rodentia (gnawing animals) and the order Lagomorpha (hares and rabbits) were mentioned in connection with serological studies (pp. 103–105); elephants belong to the order Proboscidea (pp. 216–224), whales to the order Cetacea, even-toed hoofed animals to order Artiodactyla, odd-toed hoofed animals to the order Perissodactyla, and so on.

Members of all orders just mentioned, and of some not mentioned, have several characteristics in common. Mammals have hair; they are warm blooded; their teeth are differentiated into incisors, canines, premolars, and molars; the lower jaws are composed of right and left dentaries only, and they have other skeletal traits that we listed in our discussion of the therapsids (p. 197). Except in the case of monotremes (p. 275), the young develop in the uterus of the mother and then are born (as contrasted with being hatched from eggs). Following birth the young are nourished with milk secreted by mammary glands. Because of these and other similarities the orders are grouped together into a larger category of classification called the CLASS. The particular class with which we are concerned is the class Mammalia. Other classes are Aves (birds), Reptilia (lizards, snakes, crocodiles, etc.), Amphibia (salamanders, newts, frogs, and toads), and several classes of fishes.

SUBPHYLUM Members of all the classes mentioned above have a few fundamental similarities in common; for example, they all possess at least the beginnings of a backbone or vertebral column. Hence they are all grouped together into the subphylum Vertebrata. In members of this subphylum the vertebral column is preceded in embryonic development by an unsegmented, elastic rod called a *notochord* (p. 68). A few animals (e.g., *Amphioxus)* possess a notochord throughout life. Others (e.g., tunicates, p. 68) have a notochord only during larval life. Such protochordates, as they are called, are either grouped together into one subphylum or are placed each in a separate subphylum of its own.

PHYLUM The subphyla to which we have alluded combine to form the phylum Chordata. The name refers to the possession of a notochord at some time during life. Examples of other phyla are Arthropoda (insects, crustaceans, and so on), Mollusca (snails, clams, oysters, and all kinds of shellfish), and Protozoa (one-celled animals or small animals lacking cellular structure, depending upon one's point of view).

ASCENDING CATEGORIES Thus we see that classification consists of an ascending series of more and more inclusive categories (Fig. 15.1). In practice the categories we have listed are increased by such divisions as suborders, superfamilies, subfamilies, and so on. But such details need not concern us here. Presently we shall discuss one such subdivision, however, the subspecies.

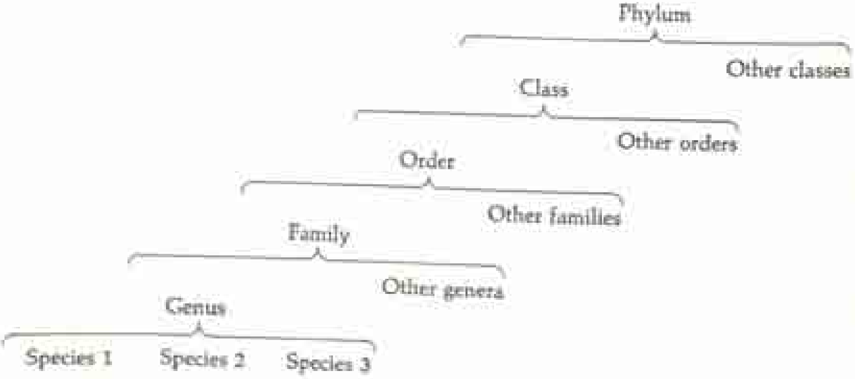


Fig. 15.1. Ascending series of more and more inclusive categories in classification.

We note that the higher or more inclusive categories are shared by large numbers of animals. Thus a dog and its master both belong to the phylum Chordata, the subphylum Vertebrata, and the class Mammalia. The parting of the ways comes at the level of orders. While the dog belongs to the order Carnivora, its master belongs to the order Primates. Within this order, man is classified as belonging to the family Hominidae. His genus within this family is *Homo*. His species within the genus is *Homo sapiens*.

CLASSIFICATION REFLECTS EVOLUTION Having reviewed the general principles followed in classifying animals, we may next ask: What has this classification to do with evolution? As already noted, the system was designed by Linnaeus as a logical method of classifying and cataloguing, a method to be adopted by biologists of all countries, thereby eliminating the confusion that had existed up to that time.

Linnaeus was not convinced of the truth of evolution. He originally believed that the species he named had been created as he found them. This view of the fixity of species was the one commonly held by biologists of his day although, as we saw in Chapter 1, ideas of evolution had existed long before the eighteenth century. Nevertheless, it was not until the nineteenth century, after the writings of Darwin, that belief in evolution became common. Before the end of his life, however, Linnaeus modified his views sufficiently to think it probable that some new species might have arisen by crossing or hybridization of the species originally created.

As we have seen, the Linnaean system is based on similarity. Animals similar in structure are classed together; animals dissimilar in structure are separated. Characteristics used in classifying are the fundamental similarities that we termed homologous in Chapter 3. Failure to distinguish homologous similarity from analogous similarity (i.e., that connected with similar function) results in errors of classification. Such an error was formerly made when whales were classified as fishes rather than as mammals.

To Linnaeus, two species that were similar in structure and therefore to be classed in the same genus were not *related* to each other in any sense of inheritance. In creating each separately the Creator had seen fit to make them similar to each other, just as a carpenter may see fit to build two houses that are much alike. The houses are not "related"; neither, to Linnaeus and most of his contemporaries, were the species.

Conceivably, then, fundamental similarities may be shared by two species because these species were created to resemble each other, no genetic relationship being present. On the other hand, fundamental similarities may be shared by two species because these species were derived from a common ancestor or because one species was the ancestor of the other. Common inheritance as the explanation for similarity accords with the evolutionary interpretation, a matter we discussed at some length in Chapter 3. According to this view, a classification based on fundamental similarities, as the Linnaean system is, becomes a classification reflecting the actual *relationships* of the animals classified. The species included in one genus are similar because they are related to each other; they inherited their similarities from a common ancestor. Two genera included in one family have many characteristics in common; these were inherited from a predecessor ancestral to both genera—and so on step by step through the classification. Creatures as diverse as a fish and a man are included in one phylum to pass to the "top" of our classification. Fish and man have some characteristics in common, notably the possession of a notochord during some stage of life. Why do they and all other members of the phylum Chordata have this notochord? If the evolutionary explanation is correct they have it because they inherited it from an ancient form that once lived on this planet and was the remote ancestor of all of them.

It is customary today to refer to the classification of animals as a "natural system of classification." By this is meant a system based on the true (i.e., genetic) relationships of the animals classified. A natural system may be contrasted with an "artificial system" of classification having as its sole objective the cataloging of plants and animals as a librarian classifies and catalogs books. The system as devised by Linnaeus was essentially an artificial system. But the similarities forming the basis for the cataloging are now regarded as indicative of genetic relationship—related animals being classified together and unrelated ones separated from each other. Hence the artificial system has become a natural system *if* we agree that fundamental similarities of structure derive from common ancestry—the evolutionary explanation.

WHAT IS A SPECIES?

Students of evolution lay particular emphasis upon the small unit of classification mentioned above, the species. This is reflected in the fact that Darwin named his great treatise on evolution *The Origin of Species*. It is felt that if the origin of separate species can be accounted for, the origin of genera, families, orders, and so on can be explained by the further application of the principles discovered or by extensions of those principles. To a considerable extent two new species arising from one original parent species would constitute the first step in evolutionary change. Two men walking down a road come to a fork in that road; one man follows the road to the right and the other man the road to the left. For a little while the two men are near together even though they eventually may have diverged so that they are thousands of miles apart. Similarly, two groups of animals starting on divergent courses of evolution would at the outset be very similar, enough so to be regarded as two species in the same genus, even though their remote descendants may be "poles apart" in structure. Accordingly, if we can account for the first step in developing diversity of structure, the step that produces enough diversity to separate groups into distinct (though related) species, we have gone far toward an understanding of the causes of evolution. The species, then, occupies a key position in thinking on evolution. It is important that we inquire into the nature of the species with a view to determining what is involved in the origin of species.

What is a species? We asked that question earlier, in our discussion of human evolution (pp. 261–262). There we noted two attributes of species: (1) some degree of structural difference and (2) reproductive isolation. From differences of opinion concerning the relative importance of these two attributes arises most of the controversy over the definition of the word. To focus attention upon the contrasting points of view we shall quote two proposed definitions. The first is that of Tate Regan, quoted with approval by various subsequent authors: "A species is a community, or a number of related communities, whose distinctive morphological characters are, in the opinion of a competent systematist, sufficiently definite to entitle it, or them, to a specific name." We note in this definition entire emphasis upon "distinctive morphological characters." We also note a point mentioned in our earlier discussion—the great amount of individual subjective judgment that enters into decisions as to what constitutes "sufficiently definite" morphological differences.

The second definition is that of Mayr (1942) quoted earlier: "Species are groups of actually or potentially interbreeding natural populations, which are reproductively isolated from other such groups." This definition places complete emphasis upon reproductive isolation, since the latter is felt to be primary. Given reproductive isolation, "distinctive morphological characters" usually will arise in due course (pp. 471–474).

These two definitions represent the extremes of a series. Many writers on the subject have proposed definitions of the word "species," most of them combining the two attributes of structural difference and reproductive isolation in various manners and degrees. Instead of proposing a definition of our own we shall discuss the various attributes that usually characterize species.

In the first place, a species is a group of animals all of which usually possess some *distinctive characteristic or characteristics*. The characteristic is usually morphological, a visible structure, although some species are known that are not visibly distinguishable from each other. In such cases the "distinctive characteristic" is chemical or physiological. When, as in most instances, the distinctive characteristics are structural, the difference in structure between two closely allied species need not be great. Indeed, the difference is frequently quite small. Sometimes the differing characteristics enable the different species to occupy different environmental niches, but frequently the differing traits have no known adaptive significance and so are commonly termed *nonadaptive,* although the existence of nonadaptive traits is disputed (see pp. 401–402).

In our discussion of continuous ranges we mentioned the cline in striping of the legs exhibited by the commonest species of African zebra (Fig. 13.6, p. 288). This species is usually named *Equus burchellii.*

What are the distinctive characteristics of *E. burchellii?* For illustrative purposes we shall mention only three of them: (1) The junction of the last vertical stripe on the back with the first diagonal stripe over the rump forms a saddle-like marking (well shown in the upper diagram of Fig. 13.6). (2) Except for the southernmost representatives of the species, there is a black stripe down the midventral line, joined by the vertical stripes on the sides. (3) The voice is like the barking of a dog (Rząśnicki, 1951). This reminds us that a distinctive characteristic need not be a morphological one.

Living in East Africa, at times on the same plains with the northern representatives of *E. burchellii,* is another species of zebra: *E. grevyi.* This species has a larger body size than does *E. burchellii,* and the striping is narrower and denser (Fig. 15.2). The vertical stripes do not reach the midventral line; the underparts are white. Instead of a saddle pattern on the rump there are white patches surrounded by a pattern of fine concentric lines. The voice is like the braying of a donkey "but is much more powerful" (Rząśnicki, 1951).

It is especially noteworthy that these two species are sometimes found together in the same herds yet do not interbreed with each other (Rząśnicki, 1951). Thus they exhibit the reproductive isolation we have stressed above. Do the distinctive characteristics we have mentioned serve any useful purpose? They may well be recognition characteristics by which males and females of the same species recognize each other and avoid mating with members of the "wrong" species. If so, they serve to promote reproductive isolation (see the following). Parenthetically, in view of the many instances of hybrids between zebra species, and even between zebras and donkeys, produced in captivity when the animals have no "choice," it is unlikely that crossbreeding between *E. burchellii* and *E. grevyi* is physiologically impossible.

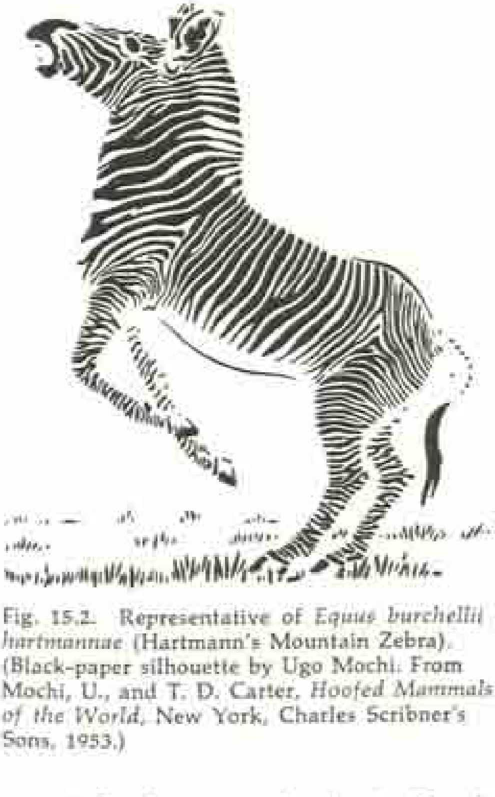


Fig. 15.2. Representative of *Equus burchellii hartmannae* (Hartmann's Mountain Zebra). (Black-paper silhouette by Ugo Mochi. From Mochi, U., and T. D. Carter, *Hoofed Mammals of the World*, New York, Charles Scribner's Sons, 1953.)

A third species of zebra is found in South Africa and adjoining regions: *E. zebra* (Fig. 15.3). It is primarily an inhabitant of mountainous regions. Comparing it to the other two species we may mention that *E. zebra* has among its distinguishing characteristics (1) a "gridiron pattern" on its rump (a pattern of transverse lines), (2) white underparts, and (3) a voice like the neighing of a horse.

As we have indicated, *reproductive isolation* is usually a hallmark of species. On later pages we shall discuss the means by which reproductive isolation is attained and maintained (pp. 439–440). In the present connection we note that the means run all the way from *inability* to mate successfully, through *preference* not to do so, and on to the production of *hybrids that are inviable or are infertile* like

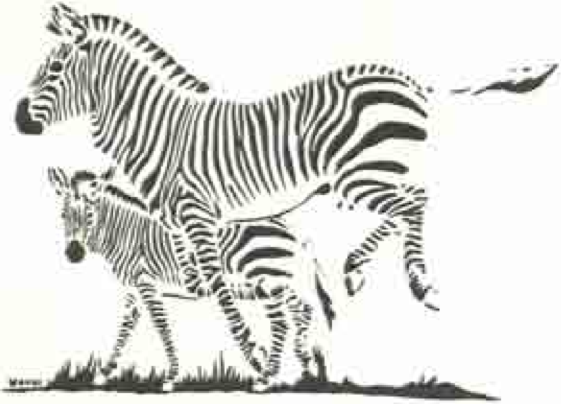


Fig. 15.3. Representative of *Equus grevyi* (Grevy's Zebra). (Black-paper silhouette by Ugo Mochi. From Mochi, U., and T. D. Carter, *Hoofed Mammals of the World*, New York, Charles Scribner's Sons, 1953.)

mules. Whatever the means, the point is that these means prevent the genes of one species from becoming mixed with the genes from another species. As a useful figure of speech we speak of a GENE POOL, meaning the total of all the genes possessed by a population. If, like *E. burchellii* and *E. grevyi*, two populations are in contact but do not interbreed, their respective gene pools remain intact. Such reproductive isolation is important for maintenance of species as discrete units. Without it two populations in contact would tend to combine into a varied hybrid population in which any original lines of distinction would be lost (pp. 471–474).

Reproductive isolation need not be absolute, however; frequently it is not. If hybridization between species is only occasional the respective gene pools do not lose their individualities, though each may be altered somewhat. Such a passage of genes between populations is called GENE FLOW. On a later page we shall discuss the role of hybridization in evolution (pp. 442–449).

One consequence of reproductive isolation is the fact that *forms intermediate in structure or transitional between two species are not usually found.* Exceptions occur, however.

We must mention the practical difficulty of applying the yardstick of reproductive isolation to populations that are separated geographically. Such populations are said to be *allopatric*, in contrast to populations that inhabit the same region (*sympatric*). *If* allopatric populations came into contact in nature, *would* they interbreed? One method of answering the question is to attempt artificial hybridization between them. But here the evidence is one sided. If the two populations will not interbreed in the laboratory (assuming that each population will breed within itself under such circumstances), that fact would be considered evidence that the populations are in fact separate species. Suppose, however, that the populations *do* interbreed in the laboratory: that fact is not in itself evidence that the populations should be considered to belong to one and the same species. In a state of nature they might not interbreed, and if they *did* not they would be as reproductively isolated as though they *could* not. For this reason, and because many animals will not breed in captivity anyway, the experimental approach to the question has limited usefulness. Hence frequently the question cannot be answered directly. Accordingly, systematists attempt to solve the dilemma by deciding whether the amount of morphological difference between the two populations is great enough so that they probably would not interbreed *if* they did come into contact naturally. But this brings us back to the variable of differences in judgment between individual biologists as to how much morphological difference is necessary if populations are to be regarded as separate species.

We should note, also, that the definition of "actually or potentially interbreeding populations, which are reproductively isolated from other such groups" has significance only for organisms that reproduce sexually. Plant and animal groups in which reproduction is asexual are not "interbreeding populations." In some cases a single individual may give rise to a whole line of descendants (a CLONE or BIOTYPE), all just like the original individual except as new mutations may from time to time introduce changes. Since interbreeding is absent, no test of reproductive isolation is possible. Classifying asexual organisms into species therefore must be based upon possession of distinctive characteristics as mentioned above. This is one reason why a species definition suitable for a majority of organisms is nevertheless not suitable for others (many plants and protozoans, for example).

Another attribute of species refers to the range or territory occupied. *Usually two closely allied species do not occupy the same territory, though frequently their territories will adjoin.* From the preceding discussion we can appreciate the fact that two closely allied species will usually be very similar to each other in appearance and habits. This implies that they will be likely to depend upon the same or similar food supply, seek the same home or nesting sites, and so on. Thus if they occupied the same territory they would usually be in direct competition. Such competition doubtless occurs and is important in promoting evolutionary change, yet in groups of species in a state of approximate equilibrium at a given stage in evolutionary history, direct competition is reduced when territories occupied by allied species are separate.

Referring again to the three species of zebras, we recall that *E. zebra* lives in mountainous regions while the other two species live on open plains. We mentioned that *E. burchellii* and *E. grevyi* may be found in the same herds, but even these two species are not completely sympatric. *E. grevyi* has greater preference for dry, semidesert regions than does *E. burchellii* (Mochi and Carter, 1953).

Frequently, when closely allied species are sympatric they differ in environmental (ecological) requirements. Thus we noted earlier (pp. 305–306) that three species of ground finches are able to live together on the Galápagos Islands because each species specializes in eating seeds of a certain size.

We may summarize our discussion of the species as a unit of classification and evolution by reviewing the attributes that *in general* characterize species: (1) possession of distinctive characteristics, (2) reproductive isolation, (3) absence of intermediate or transitional forms, and (4) possession by allied species of separate territories (or of differing ecological requirements if the species are sympatric).

It is safe to surmise that any population of animals having all four of these attributes would be considered a distinct species by all biologists. Disagreement enters when a group has some of the attributes but not all of them. Nature is enormously complex. We must not expect the classifying of organisms to be a simple matter—but in the complexity of problems lies challenge.

For a discussion of forces and factors operative in species formation see Chapter 21.

SUBSPECIES OR GEOGRAPHIC RACES

In Chapter 13 we called attention to the fact that *Equus burchellii* presents a cline in the striping of the legs. Four representatives of stages in this cline are shown in Fig. 13.6 (p. 288). We note that in this figure each drawing of a zebra is connected by a line to a certain area on a map of Africa. Each of these areas is commonly said to be occupied by a different SUBSPECIES of the species *E. burchellii*. Naming these subspecies in order from north to south we find (Cabrera, 1936):

1. *E. burchellii böhmi*
2. *E. burchellii selousii*
3. *E. burchellii antiquorum*
4. *E. burchellii burchellii*

We note here another convention: The binomial has become a trinomial; a *subspecific* name has been added to the other two. One of the most distinctive attributes of subspecies is emphasized by this map: Each subspecies occupies a territory of its own and hence is a GEOGRAPHIC RACE.

Subspecies usually differ from each other in one or more traits. Usually these differences are less than those found between two related species. Indeed, the visible differences may be so small that only an expert can see any difference at all, and frequently an expert must have a considerable number of specimens for comparison before he can be sure which of two subspecies is represented. Even then he may not be sure unless he knows the geographic area from which a specimen to be identified came. Difficulties are compounded by the fact that no two individuals are ever precisely alike. Thus, in the case of *E. burchellii* no two zebras are exactly alike in striping and other characteristics. The drawings in Fig. 13.6 show a *representative* of each subspecies, but there probably was never another zebra that looked exactly like that one.

Such difficulties in identification have led some investigators to question the reality of subspecies. Do they really exist, or are they the artificial creations of biologists' minds (Wilson and Brown, 1953)? In the case of *E. burchellii* the cline in striping of the legs is an observable fact. But what is the justification for segmenting the cline into subspecies? The difficulty encountered in delimiting these subspecies is reflected in the fact that no two investigators seem able to agree on how many subspecies there are or what shall be considered to constitute each one. We have followed Cabrera (1936) in the names used and the territories indicated. Rząśnicki (1951) differed in both respects. This may be an extreme case, but it is by no means an isolated one.

Despite the difficulties, however, most students of the subject conclude that the subspecies or geographic race is a useful concept as a means of distinguishing inhabitants of a certain region possessing, on the average, a certain set of characteristics. We noted in Chapter 12 that human races are comparable to subspecies. Subspecies differ from each other in the *frequencies* with which certain genes (and hence characters) occur rather than in the possession of certain genes by all members of one subspecies and the absence of those genes from all members of a second subspecies. This is the genetic basis for the observed similarities between neighboring subspecies. In most cases genetic analyses have not been made, but the varying distributions of the blood group genes in different human races furnish an example with a known genetic basis (pp. 109–111).

Among lower mammals we find an example in the race of deer mice inhabiting Santa Rosa Island off the coast of northern Florida.

This island is covered with exceptionally white sand and is inhabited by an extremely light-colored race of mice: *Peromyscus polionotus leucocephalus*. Presumably this is an example of protective coloration, the protection in this case being against predators that use their sense of sight in locating prey, especially owls (see pp. 345–346). From the results of breeding experiments Sumner (1932) concluded that *P. p. leucocephalus* differs from the fully pigmented subspecies inhabiting the mainland *(P. p. polionotus)* by a number of genes having additive effects (multiple genes or polygenes, pp. 368–370).

This example also illustrates the point that at times differences between subspecies may be adaptive, fitting the races to different environments. Frequently, however, the differences between subspecies seem to be more or less chance differences of no particular significance in the lives of the organisms (nonadaptive traits). At times we may consider differences nonadaptive merely through ignorance of their real significance, but evolutionary mechanisms are known by which traits that are actually nonadaptive may come to characterize populations (Chapter 18). There would seem to be little significance for the zebras in the slight average differences in markings characterizing neighboring subspecies of *E. burchellii* (Fig. 13.6).

As we mentioned in our discussion of human races, different subspecies within one species are usually interfertile and hybridize readily whenever they come into contact. Thus they lack the reproductive isolation that usually characterizes separate species. While this rule is not without its exceptions, the principal factor operating to keep subspecies separate is usually a geographic one. Different subspecies live in separate regions and hence come into contact with each other only at the borders of their territories.

Commonly, however, in areas between the ranges of neighboring subspecies intermediate forms are found. The usual interpretation is that these arose by hybridization between the neighboring subspecies. Biologists who doubt the reality of subspecies would consider this a cline—ordered variability of traits across a certain area of country but without any segmentation into units called subspecies.

NUMERICAL TAXONOMY

In comparing one subspecies with another or one species with another, how many traits and measurements should an investigator take into consideration? There is no rule concerning this. Sometimes only a few characteristics considered to be particularly significant are used. Sometimes many characteristics form the basis of diagnosis. Increasing the number of characteristics increases the complexity of the analysis, but within recent years the use of digital computers has made possible analyses so complex that they would not have been practicable otherwise.

Typically, many measurements are made on each individual specimen and then the degree of correlation between one specimen and another for *all* of these measurements is calculated. If the correlation is high the two specimens may be considered to belong to the same subspecies. If the correlation is slightly lower, the two specimens may be considered to belong to the same species but not to the same subspecies. If the correlation is still lower, the two specimens may be considered to belong to different species, and so on. While the aim of this NUMERICAL TAXONOMY, as it is called, is to make the classification of organisms completely quantitative and objective, subjective judgment enters in the decision as to the amount of correlation that should be considered to characterize each taxonomic level: subspecies, species, genus, and so on. For this reason some numerical taxonomists deny that subspecies and species exist in reality, affirming that the only unit of classification is the *individual*, with each individual differing to a greater or lesser extent from every other individual.

Whatever the interpretations drawn from the results, we shall doubtless see increasing use of computers by taxonomists in future years. In practice numerical taxonomy is quite complex; a relatively simple account of it is to be found in Ehrlich and Holm (1963).

SUBSPECIES AND MICROGEOGRAPHIC RACES Another difficulty in identifying subspecies or geographic races is the fact that they possess no clear-cut lower limit. They grade insensibly into MICROGEOGRAPHIC RACES, local races inhabiting small areas, e.g., one pond or one wood lot (Wilson and Brown, 1953). For example, Dice (1937) investigated populations of mice of genus *Peromyscus* inhabiting wood lots only 3 or 4 miles apart but separated by cultivated land. He found statistically significant differences between these various subpopulations in a variety of bodily and skeletal measurements and in hair color. I once made a serological study of three populations of *Peromyscus maniculatus* living a few miles apart in the Columbia River valley (Moody, 1948). I identified seven antigens in the red blood cells somewhat comparable to the A and B substances in human blood cells. As the profiles in Fig. 15.4 indicate, the three populations differed from one another in percentage of individuals possessing each of the seven antigens. This is the same sort of racial difference we noted in percentages of individuals belonging to the different human blood groups. Whenever genetic tests are made a genetic basis for cellular antigens is always disclosed. Hence we may feel confident that Fig. 15.4 repre-

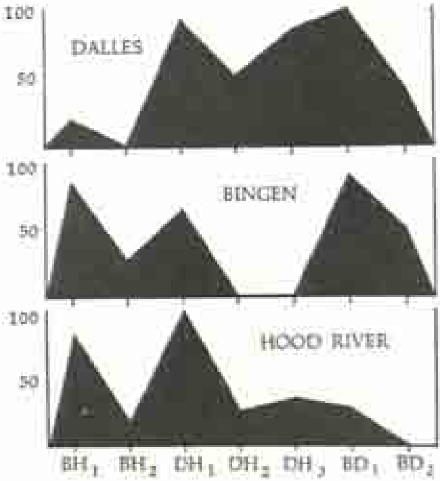


Fig. 15.4. "Profiles" representing the distribution of seven red-blood-cell antigens in three stocks of *Peromyscus.* Ordinate scale represents percentages of individuals possessing the respective antigens designated on the base line. (From Moody, P. A., "Cellular antigens in three stocks of *Peromyscus maniculatus* from the Columbia River valley," *Contributions from the Laboratory of Vertebrate Biology, University of Michigan,* No. 39, 1948.)

sents a genetic difference between populations of wild animals living only a few miles apart. The difficulty of distinguishing between geographic and microgeographic races is attested by the fact that these three populations of Columbia River mice may represent different subspecies, at least in part (Dice, 1949).

EVOLUTIONARY SIGNIFICANCE OF SUBSPECIES. We have presented several contrasts between species and subspecies: (1) Members of different species do not ordinarily interbreed when they come into contact; members of different subspecies within one species ordinarily do so. (2) Different species frequently occupy separate territories, but the territories may overlap, in which case intermediate forms usually are not found; different subspecies occupy separate territories that do not overlap, and if the territories come into contact intermediate or transitional forms are frequently found. (3) Structural differences between species are usually greater than those between subspecies.

We should note, however, that exceptions are found to every one of the above statements. In practice, then, it is frequently difficult to be sure whether two groups of animals should be classed as belonging to two subspecies in one species or whether they should be regarded as two distinct species in one genus. Thus, again, the judgment of the individual biologist comes into play—and with it the opportunity for much disagreement on the details of classification.

The principal interest in the subspecies or geographic race from the standpoint of evolution lies in the fact that it seems to represent a small step in the development of diversity. Most clusters of subspecies probably arose when descendants from some parental stock migrated out from a center of dispersal (pp. 280–282). As animals spread out over the country groups of them became separated from each other by distance and sometimes by geographic barriers. These separate groups, being out of contact with each other, gradually came to develop differences, so that each was no longer quite like the original parent stock or, on the other hand, quite like the other groups. (Recall our discussion of the processes involved in the evolution of the human races, pp. 262–267.) Each group would then rank as a separate subspecies or geographic race. Now if the groups became progressively different in structure and if, especially, these differences finally became sufficient to prevent interbreeding whenever members of different groups came in contact, the groups would be considered to have reached the rank of separate species. In brief, according to this view, the subspecies is a step in the development of the species.

We have referred to "clusters" of subspecies; sometimes these form more or less circular mosaics covering a certain geographic area. Such a mosaic or circle of races has been termed by Rensch (1960) as a RASSENKREIS. Suppose, for example, that a rough circle is formed by races *A*, *B*, *C*, and *D* (Fig. 15.5). Race *A* interbreeds with race *B* where their ranges come into contact. Race *B* interbreeds with race *C*, as does race *C* with race *D*. But race *D* does *not* interbreed with race *A* where their ranges come into contact (this situation is called circular overlap: Mayr, 1963). Are races *D* and *A* to be considered separate *species* because they are thus reproductively isolated from each other? Perhaps not so long as the circle of interbreeding forms (races *B* and *C*) connecting them exists. But if races *B* and *C* were not known (had become extinct before biologists investigated the situation), probably races *A* and *D* would be considered separate species. We mention this matter (1) to illustrate the fact that subspecies in some cases are not clearly distinguishable from species and (2) to indicate one way in which species may arise from subspecies. (For further examples and a discussion see Goldschmidt, 1940, p. 117 ff; Lack, 1947, Fig. 23, p. 127, and accompanying text; Rensch, 1960, p. 23 ff; Mayr, 1963, p. 507 ff.)

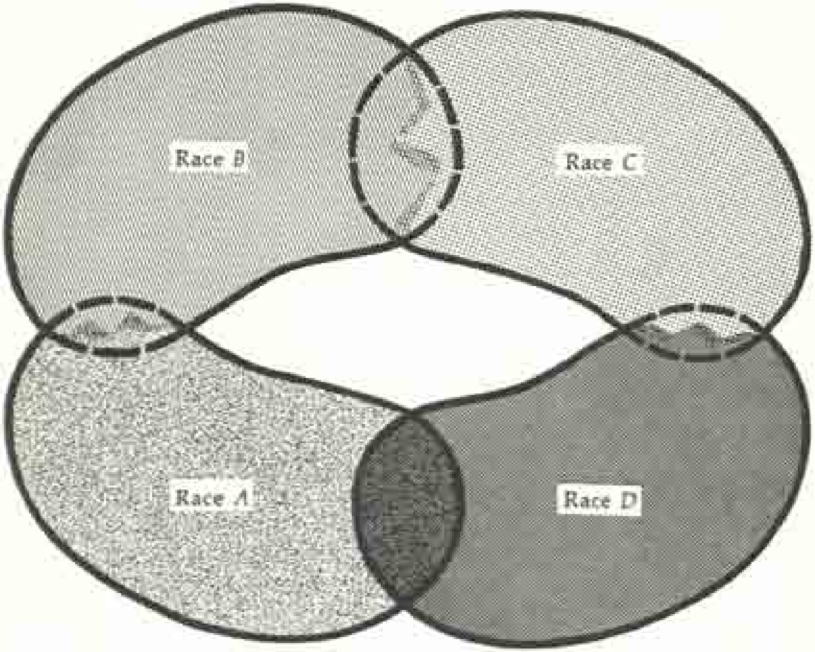


Fig. 15.5. The ranges of four geographic races forming a Rassenkreis. Where the ranges come into contact interbreeding occurs in three cases, but it does not occur in the area where Race D comes into contact with Race A—a region of circular overlap.

We do not wish to give the impression that all subspecies are on the way to becoming species. For most subspecies, conditions probably will never be favorable for further development. Opportunity will not knock on their doors. But for a minority, conditions will favor further evolution leading to the formation of new species and perhaps eventually to new genera, families, and so on.

In subsequent chapters we shall discuss in more detail the processes involved in subspecies and species formation as well as in the production of the major adaptive changes that usually distinguish members of different higher categories (e.g., different orders).

CONCLUSIONS

Let us return for a moment to the question of the manner in which classification supports the idea of creation by evolution as contrasted with the idea of special creation. We have seen that classification is based upon similarity, primarily morphological similarity. To most biologists it seems more reasonable to explain fundamental similarities as based upon inheritance from common ancestry than as resulting from the fact that separately created animals were created to be similar or created according to similar patterns. Again, the difficulty of defining a species, of separating one species from another, and of telling whether a certain group is a species or a subspecies seems to indicate a web of interrelationships in nature most readily explained as arising by divergence from common ancestry. If each species were separately created it should be much easier than it is to draw sharp lines between them and between species and subspecies.

References and Suggested Readings

Cabrera, A., "Subspecific and individual variation in the Burchell zebras," *Journal of Mammalogy, 17,* 89–112 (1936).

Dice, L. R., "Variation in the wood-mouse, *Peromyscus leucopus noveboracensis,* in the northeastern United States," *Occasional Papers, Museum of Zoology, University of Michigan,* No. 352, 1–32 (1937).

Dice, L. R., "Variation of *Peromyscus maniculatus* in parts of western Washington and adjacent Oregon," *Contributions, Laboratory of Vertebrate Biology, University of Michigan,* No. 44, 1–34 (1949).

Ehrlich, P. R., and R. W. Holm, *The Process of Evolution,* New York, McGraw-Hill, 1963.

Goldschmidt, R., *The Material Basis of Evolution,* New Haven, Yale University Press, 1940. (Includes a detailed discussion of subspecies formation.)

Huxley, J. (ed.), *The New Systematics,* Oxford, Oxford University Press, 1940.

Lack, D., *Darwin's Finches,* Cambridge, Cambridge University Press, 1947. Available as Harper Torchbook TB544, New York, Harper & Row.

Mayr, E., *Systematics and the Origin of Species,* New York, Columbia University Press, 1942.

Mayr, E., *Animal Species and Evolution,* Cambridge, Mass., Harvard University Press, 1963.

Mayr, E., *Principles of Systematic Zoology,* New York, McGraw-Hill, 1969.

Mochi, U., and T. D. Carter, *Hoofed Mammals of the World,* New York, Charles Scribner's Sons, 1953.

Moody, P. A., "Cellular antigens in three stocks of *Peromyscus maniculatus* from the Columbia River valley," *Contributions, Laboratory of Vertebrate Biology, University of Michigan,* No. 39, 1948, pp. 1–16.

Rensch, B., *Evolution Above the Species Level*, New York, Columbia University Press, 1960.

Rząśnicki, A., "Zebras and quaggas," *Annales Musei Zoologici Polonici, 14*, 203–252 (1951).

Seton, E. T., *Lives of Game Animals*, New York, Doubleday, 1929.

Simpson, G. G., "The principles of classification and a classification of mammals," *Bulletin of the American Museum of Natural History, 85*, 1–350 (1945).

Simpson, G. G., *Principles of Animal Taxonomy*, New York, Columbia University Press, 1961.

Sumner, F. B., "Genetic, distributional, and evolutionary studies of the subspecies of deer mice *(Peromyscus)*," *Bibliographia Genetica, 9*, 1–106 (1932).

Wilson, E. O., and W. L. Brown, Jr., "The subspecies concept and its taxonomic application," *Systematic Zoology, 2*, 97–111 (1953).

16

Adaptations

THE PROBLEM In preceding chapters we noted evolution manifested in many guises. We saw numerous examples of relatively unspecialized animals that gave rise to descendants specialized for some particular mode of life. We saw that frequently several lines of descendants arose from one ancestral group and termed this phenomenon "adaptive radiation."

We noted the independent occurrence of similar evolutionary trends and termed this "parallel evolution" when the independent evolution occurred in two related groups of animals and "convergent evolution" when it involved two relatively unrelated groups.

We observed the complexity of human evolution and suggested that isolated human populations developed differing characteristics while isolated and that these characteristics were variously combined and recombined when subsequently the populations came into contact through migrations and conquests.

We emphasized that the past and present geographic distribution of animals suggests that a form originates in a certain region (its "center of dispersal") and that as descendants spread out from this center they undergo modification, so that eventually they differ from one another and from the parent form.

We noted ways in which animals finding themselves on oceanic islands have been able to exploit environmental niches they would never have entered on continents.

We saw that the formation of geographic races (subspecies) represents one of the first steps in development of the diversity that is a hallmark of evolutionary change and that formation of the greater diversity characterizing species seems to be a later step in the same process.

All these evolutionary manifestations require explanation. In all of them two central themes are found: *adaptation* and *diversification*. At all stages in its evolution an organism must be adapted to its environment. And in order to explain evolution we must explain diversity—how it arises and how it is preserved and perpetuated. In this chapter we shall direct our attention to adaptation, discussing some examples of it. Then we shall consider genetic and evolutionary forces making for diversity. We shall see that those forces and the resulting diversity are potent in producing adaptation. Thus the two themes combine, even though it is convenient to consider them separately at the outset.

OSMOTIC REGULATION AND EXCRETION OF NITROGENOUS WASTES

In the preceding chapters we referred repeatedly to examples of organisms adapted to particular environments. Most of the adaptations we discussed have been morphological: e.g., the limb structures of mammals, mouthparts of insects, limbs and teeth of ancestral horses, and beaks of Darwin's finches and drepanid birds. Such adaptations are easily seen and in many cases well preserved in fossils. Of at least equal importance, however, are adaptations of a physiological and biochemical nature. As our principal example of this type of adaptation we select a major problem faced by vertebrates in their evolution—that of living in varied external media: salt water, fresh water, and air.

In earlier discussions we saw that cells contain a salt solution.

In complex animals like vertebrates these cells also are in close contact with another salt solution, the blood. Indeed, a widely held theory postulates that when early organisms attained a structure so complex that some parts were no longer bathed directly by seawater, some of this salt water became "bottled up" within the organism to form the blood. Originally the seawater transported foodstuffs, oxygen, and waste products to and from the cells. In complex organisms the cells still must be served in these ways, but now by the blood.

The osmotic problem arises when the salt concentration on the outside of an organism differs from the salt concentration of its internal fluids. Many of the living membranes of animals are DIFFERENTIALLY PERMEABLE (semipermeable); some substances pass through them more readily than do others. For example, if a differentially permeable membrane has salt solution on one side of it and pure water on the other, the pure water will pass through the membrane more readily than will the salt solution. Suppose we take a bag of differentially permeable membrane, fill it with salt solution, close it tightly, and then immerse it in pure water. We shall find that water passes *into* the bag through the membrane more rapidly than salt solution passes out of the bag through the membrane. The net result will be an increase in volume of the solution in the bag. If, as we have stipulated, the bag is tightly closed, an increase in volume of its constents will result in its becoming distended (Fig. 16.1). In other words, a pressure will develop inside

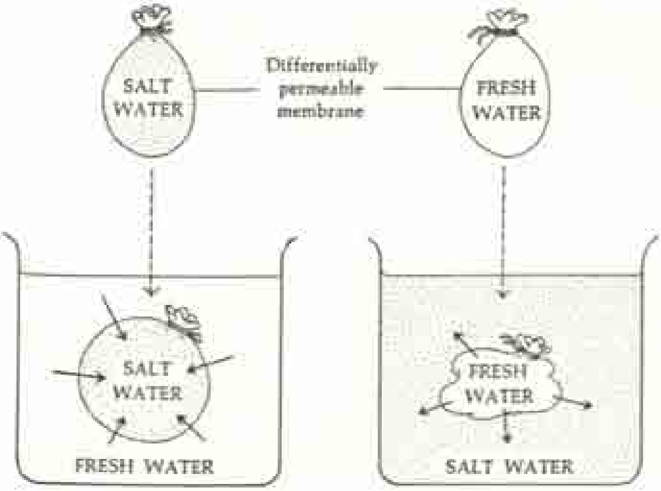


Fig. 16.1. Effects of osmotic pressure on two closed bags composed of differentially permeable membrane. Left: a bag containing salt water, immersed in fresh water. Right: a bag containing fresh water, immersed in salt water.

the bag. This is known as *osmotic pressure,* and under some circumstances it may develop considerable strength—sufficient to burst the bag, perhaps. If we reverse our experiment, placing pure water in the bag and immersing the bag in salt solution, we shall find the greater movement of material in the opposite direction: The contents of the bag will become less and less as it loses its water to the outer salt solution (Fig. 16.1). Note that in both cases water passes through the membrane *from* a region in which there is much water but little or no salt *to* a region in which there is less water in proportion to the concentration of salt. In other words, the water moves from a region in which *it* is present in relatively higher concentration to a region in which it is present in relatively lower concentration.

An organism such as a fish is in a real sense a salt solution enclosed within a bag of differentially permeable membrane. So long as the salt concentration on the outside is the same as the salt concentration on the inside there will be no osmotic effect of the kind just discussed. But suppose the fish lives in fresh water; then we have the situation described above of a differentially permeable membrane enclosing salt solution and immersed in water. The result will be movement of water *into* the fish through its exposed membranes. If this movement were unopposed, the fish would become distended and waterlogged and might even burst, like our hypothetical bag. Obviously, what is needed is a means of ridding the animal of excess water—a means of "bailing out." The kidneys of fishes provide such a means. The kidneys of freshwater fishes extract fluid from the blood, passing to the exterior quantities of dilute (hypotonic) urine (Fig. 16.2A).

We usually think of the kidney as an organ for ridding the body of nitrogenous wastes, since that is its function in ourselves. Proteins in our food are broken down by our digestive systems into the constituent amino acids. Some of these are utilized by our bodies for manufacturing needed proteins in our own bodies; others are further broken down by our bodies. We obtain energy from this process but also waste products, especially carbon dioxide, water, and ammonia (NH_3). Since ammonia is toxic to cells, the body must dispose of it quickly or convert it into a less harmful substance. In our own bodies the ammonia combines with carbon dioxide to form urea, and this is excreted by our kidneys. In fishes, on the other hand, the ammonia is passed from the blood to the surrounding water, primarily through the gills. Thus the kidney of fishes is not primarily an organ for ridding the body of nitrogenous wastes.

Freshwater fishes are faced with still another problem, that of conservation of the *salts* of blood and protoplasm (see the preceding). The urine contains salts. How can a freshwater fish excrete quantities of

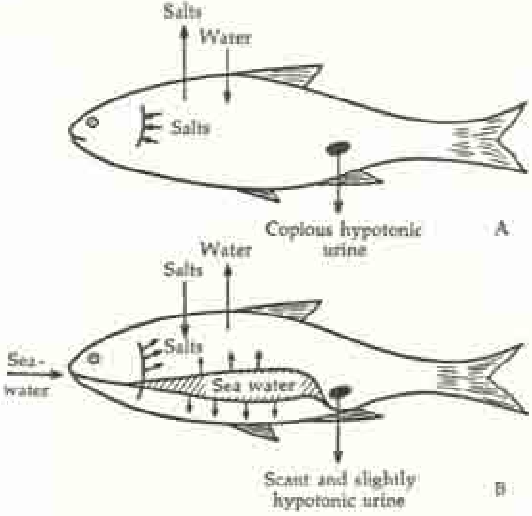


Fig. 16.2 Diagram of osmotic regulation in bony (teleost) fishes. A, fresh-water species. B, marine species. (After Baldwin, from Florkin, M., and S. Morgulis, *Biochemical Evolution*, New York, Academic Press, Inc., 1949.)

urine without seriously depleting the body's supply of salts? The problem is partially solved by the fact that the tubules of the kidney have developed sections where salts are reabsorbed from the urine back into the blood. Thus the urine reaching the exterior has a lower salt concentration than does the blood (that is what we mean when we say that the urine is "hypotonic"). But some salts are lost; the loss is made up by salts contained in food eaten by the fish and by special secretory cells located on the gills (Fig. 16.2). These cells have the power to extract salts from the surrounding water and to pass them into the blood; even "freshwater" contains some salts, though they are in low concentration.

The osmotic problem faced by fishes living in the ocean differs from that faced by freshwater fishes. The salt concentration of the blood plasma of bony fishes is only about one-quarter to one-third that of seawater (Robertson, 1957). This fact may be taken to indicate that ancestors of marine bony fishes lived in fresh water, where a salt concentration less than that of seawater (in which, as we have seen, life began) was acquired. When some of the descendants of these ancestral freshwater fishes returned to the ocean they were faced with the problem of living in a medium having greater salt concentration than did their own body fluids. They were in the position of bags of differentially permeable membrane enclosing a dilute salt solution and immersed in a more concentrated salt solution (Fig. 16.1). The contents of such a bag would decrease as water passed outward through the membrane. In other words, strange as it may seem, marine fishes have to fight desiccation or drying out, owing to loss of water through exposed membranes.

How could marine descendants of freshwater fishes meet the problem? From their freshwater ancestors they inherited kidneys that excreted quantities of water. But marine fishes need to conserve water! Such kidneys would prove a liability. So we find that in marine bony fishes the kidneys are greatly reduced in structure and excrete only small amounts of urine. But since even that amount of water loss must be compensated for, marine fishes swallow (drink) seawater, and the latter is absorbed, salts and all, into the blood (Fig. 16.2B). That practice restores the needed water, but it also gives the body a greater quantity of salts than is needed. Thus there is the further problem of ridding the body of excess salts. The kidney is of little help here, since its function has been much reduced in the interest of water conservation. The problem is solved by secretory cells in the gills that have the function of passing salts from the blood into the surrounding water (Fig. 16.2). Note that they function in just the opposite way from the secretory cells in the gills of freshwater fishes.

The method described above of solving the osmotic problems of marine life is that of bony (teleost) fishes. For cartilaginous fishes (sharks, dogfishes, and the like) the problem was solved in an entirely different manner. Their internal concentration was raised to meet the concentration of the surrounding seawater and this prevented unfavorable osmotic effects. This change was brought about in a most curious way: The salt concentration was not substantially increased; rather the *urea* concentration was increased. Whereas most fishes excrete their nitrogenous wastes as ammonia, sharks and their allies convert the ammonia to urea and then retain a high concentration of the latter within the body. This is a unique means of protecting these fishes from the desiccating effect of water loss to the surrounding seawater through exposed membranes.

Freshwater fishes also gave rise to amphibians, the first terrestrial vertebrates and the ancestors of reptiles, birds, and mammals. Water conservation is a primary problem of land dwellers. This being true, a kidney excreting large quantities of dilute urine would be as much a detriment to land dwellers as it is to marine teleost fishes. Accordingly, the amphibian kidney has some ability to absorb water from the urine back into the blood. Some of the salt supply also is salvaged in this way. In addition salt is obtained in the food. But amphibians are only incompletely terrestrial animals; many of them live their lives in fresh water and are much like freshwater fishes in matters of osmotic regulation. Other amphibians must stay in a moist environment, never having evolved skin coverings effective against desiccation. But these amphibians no longer excrete most of their nitrogenous wastes as ammonia, as did their freshwater fish ancestors. They convert the ammonia to urea and use the kidney as the principal means of ridding the body of the urea.

What was the *original* function of the vertebrate kidney? There are two opposite points of view:

1. Romer (1959) concluded that geological and other evidence indicates that the first vertebrates (jawless fishes called ostracoderms, Fig. 9.14, p. 166) lived in fresh water. If so, the vertebrate kidney functioned first as an organ for ridding the body of excess water and only later took on functions of excretion.

2. Robertson (1957) concluded that the geological and other evidence indicates that the first vertebrates were marine and that the kidney was primarily an excretory organ. Its microscopic structure resembles that of excretory tubules found in some invertebrates, in fact. According to this point of view the ridding of the body of excess water came as a later function of the organ. Robertson's opinion is that some marine vertebrates, notably cyclostomes (lamprey and hagfish) and cartilaginous fishes such as sharks, did not have freshwater ancestors; yet all have well-developed kidneys.

Both authors quoted agree, however, that evidence supports the view that bony fishes and amphibians had freshwater fishes in their ancestry. Hence an organ that functioned in connection with osmotic regulation in ancestors assumed (or resumed?) the function of excretion in descendants.

We should note, also, that some vertebrates can live in both salt water and fresh water. This is true, for example, of such fishes as the salmon that are hatched in fresh water, migrate to the sea, and later return to fresh water to spawn. Their systems are adaptable to the varying osmotic conditions.

Somewhat similarly, some amphibians live at times in the water and at other times in the air. Thus the tadpole of a frog lives a fishlike existence and during that time excretes most of its nitrogenous wastes into the surrounding water as ammonia, as do fishes. Later, upon metamorphosing into an adult living on land, it excretes its nitrogenous wastes as urea, as mentioned above. This reminds us that adaptation to environmental conditions is as necessary for larvae (and embryos) as for adults. The African clawed toad *(Xenopus)* normally lives in the water as an adult and excretes its nitrogenous wastes as ammonia. But if it is forced to live out of the water it transforms the ammonia to urea (see above) and stores it in the tissues (Bentley, 1966; McBean and Goldstein, 1967). This also occurs in African lungfish; these fishes live in the water during the wet season and then go into a dormant state (estivate) during the dry season. We may feel confident that the aquatic ancestors of amphibians had similar adaptability when they left the aquatic environment.

Unlike amphibians, reptiles, birds, and mammals developed skins relatively impermeable to loss of water by evaporation. Horny scales, feathers, and hair contribute to this end. Water loss through the kidneys in birds and mammals is reduced by the development of a special section of the kidney tubules (loop of Henle) that reabsorbs back into the blood much of the water in the urine (see Smith, 1953). Salts also are salvaged by regions of the tubules. Thus these truly terrestrial animals excrete a concentrated (hypertonic) urine, ridding the body of a maximum amount of waste dissolved in a relatively small amount of water.

Some turtles excrete nitrogenous wastes as urea (as well as in the form of uric acid; see the following), and all mammals excrete urea. This form of excretion was doubtless inherited from amphibian ancestors.

Modern reptiles and birds, on the other hand, convert ammonia to URIC ACID. (Most of the excretion of turtles is in this form.) Uric acid is a relatively insoluble compound that can be stored or, alternatively, passed from the body in the feces with very little water loss indeed. This is an obvious adaptation to life in dry environments. But in this case it also is an important *embryonic* adaptation. Locked away in their eggshells (Fig. 9.23, p. 173) reptilian and avian embryos must "live with" their waste products until hatching time. As we noted earlier (p. 54), the problem is solved by conversion of ammonia to uric acid, which is then stored in the allantois. This example serves to remind us that while we tend to think mostly of adult adaptations, to be successful an organism must be adapted at all stages in its life history.

Turning to the invertebrates for a moment, we note that insects differ from most other invertebrates in the high proportion of nitrogenous waste excreted as uric acid. Like terrestrial vertebrates, most insects are faced with the problem of conserving the body's water supply. Incidentally, this affords us another interesting case of convergent evolution.

PROTECTION FROM PREDATORS

As we noted in Chapter 2, one conspicuous aspect of natural selection is the predator-prey relationship. To survive a species must be successful in withstanding the onslaughts of its enemies, and these may range all the way from viruses and bacteria to birds and mammals, including man himself. Accordingly, many of our best examples of adaptation are derived from studies of the manner in which one species (the prey) succeeds in surviving predation.

Directing our attention to higher organisms, we note that some survive by flying (or running) away. Others survive by being inconspicuous: by camouflage or protective coloration.

DOES PROTECTIVE COLORATION REALLY PROTECT? By way of example we may cite the common observation that mammals (e.g., mice) living on light-colored soils are themselves light colored while inhabitants of dark-colored soils are dark colored. An example of a light-colored race of *Peromyscus* was described above (pp. 329–330). In this case an island of white sand is populated by an almost white race obviously descended from darker-colored mice inhabiting neighboring woodlands. How did the light-colored race arise? We may hypothesize that the light color protects the mice from attacks by predators, especially owls. If so, mice having mutations (or other genetic variability) making for light coat color would be expected to survive on the island in larger proportion than would mice having darker coloration. Thus the lighter-colored mice would contribute a larger proportion of genes to the next generation than would the darker-colored mice. If this trend continued for many generations, the present almost white race of mice could be accounted for. We note that in this explanation predators utilizing vision for hunting occupy a key position. Granted that light coat color causes the mouse to blend with the light background to our eyes, does it also do this in the eyes of predators?

In order to answer this question Dice (1947) performed a series of experiments with *Peromyscus* differing in shade, utilizing owls as predators. A darkroom was divided into halves by a low partition on one side of which light-colored soil covered the floor; on the other side was dark-colored soil. Both dark-colored and light-colored mice were placed in both halves of the room. The owl lived in a nest box near the ceiling in the middle of the room. Would the owl catch more dark-colored than light-colored mice on the light soil and more light-colored than dark-colored ones on the dark soil? At first there seemed to be no tendency of this kind. Gradually the experimenter reduced the dim light intensity used during the tests until finally there was no light at all. Still the owls caught mice. Evidently, then, they were not using the sense of sight in their hunting. Probably they located the mice by hearing their movements. Marks on the soil indicated that in the darkness they used their wings to sweep in mice located by hearing.

The problem was, then, to force the owls to rely on the sense of sight. The experimenter did this by covering the floor of the room with an artificial "jungle," a sort of latticework of light timber arranged so that owls could reach through the meshes and catch mice when the light intensity used during the tests was sufficiently high so that the mice could be seen. This "jungle" simulated the plants and bushes under which mice normally live. In a series of trials under these conditions 107 conspicuous mice (dark-colored on light soil and light-colored on dark soil) where captured but only 65 concealingly colored ones were. Dice found that "in every experiment in which the predator was evidently using sight to capture his prey, the concealingly colored individuals enjoyed more than a 20 percent advantage over the conspicuous animals in escaping capture." And he concluded: "Such a high rate of selection, should it be applied to a natural population, would undoubtedly result in a very rapid change in the frequencies of the genes producing the character under selection."

Previous experimenters, using different predator and prey organisms, had obtained similar results (Dice, 1947).

INDUSTRIAL MELANISM We see all around us plants and animals whose adaptations to the conditions of life we ascribe to natural selection. For the most part these adaptations were perfected long before there were human observers to record the process. Only seldom in the world around us will conditions have changed rapidly enough and recently enough so that biologists can obtain actual records of the changes and the forces effecting them. Usually it will be environmental changes produced by man that will lead to evolutionary change discernible within historic times. One of our best observed examples of natural selection in a state of nature concerns an effect of the Industrial Revolution upon the color of moths.

Most people are acquainted with the fact that albinos (individuals completely lacking pigment) occur from time to time in most kinds of animals including man himself. Fewer people are acquainted with *melanics,* individuals having heavier pigmentation than their fellows. Difference in a single pair of genes is commonly involved in the difference between normal pigmentation and melanism (pp. 358–359). Such melanism is found in animals, including many species of moths. Usually the proportion of melanic individuals is very low, but in certain regions the proportions have become high within historic times. These are predominantly regions in which pollution of the atmosphere by large industrial centers has altered the appearance and color of, for example, the tree trunks upon which the moths normally rest during their daytime period of inactivity. Kettlewell (1958) stated that in England some

70 species of moths are now in the process of increasing the proportion of darker individuals in their populations. Of these the peppered moth (*Biston betularia*) has been most intensively studied. Figure 16.3 shows the normal light and the melanic forms of this moth against a normally lichened tree trunk in a region free from pollution, while Figure 16.4 shows the same two forms on a blackened tree trunk, upon which no lichens grow, in an industrial region (near Birmingham, England). Evidently, to the human eye the light form is inconspicuous and the dark form conspicuous against the background of lichens, and the reverse is true against the blackened trunk. Does this difference in visibility also apply to visibility by birds, the principal predators of these moths?

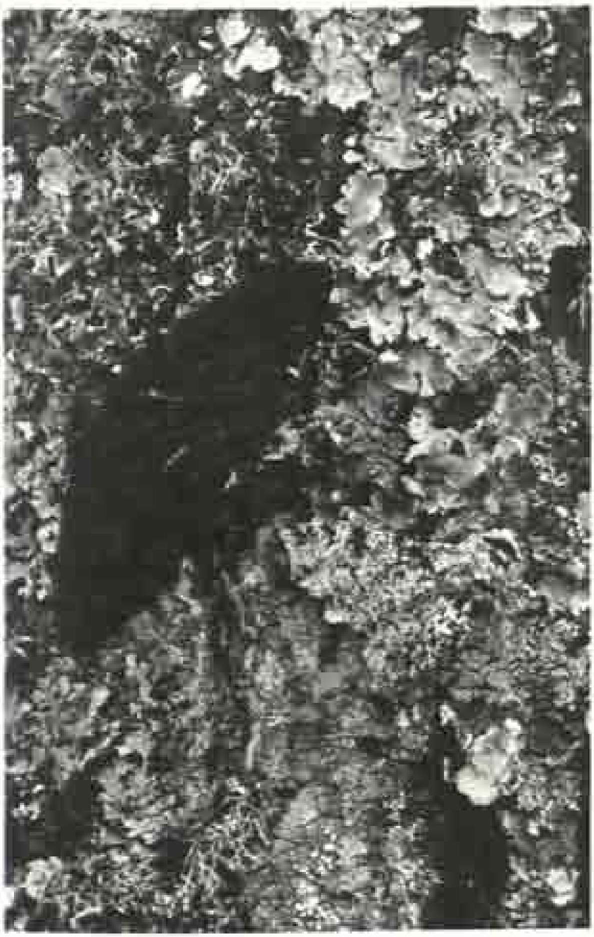


Fig. 16.3. Dark-colored (melanic) and light-colored ("typical") specimens of the peppered moth (*Biston betularia*) at rest upon a lichen-covered tree trunk. (Photograph by courtesy of H. B. D. Kettlewell.)

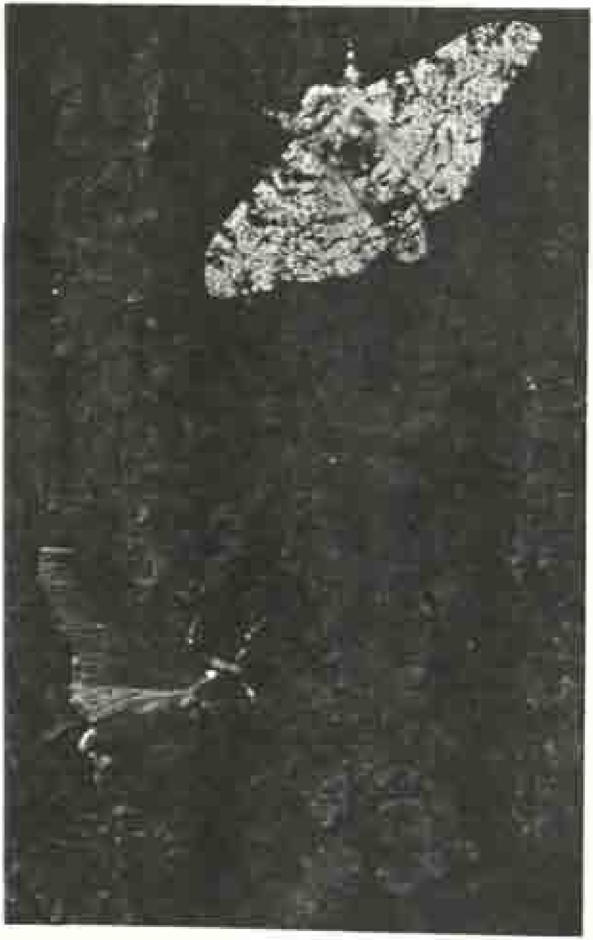


Fig. 16.4. Light-colored ("typical") and dark-colored (melanic) specimens of the peppered moth (*Biston betularia*) at rest upon a lichen-free, blackened tree trunk in an industrial region. (Photograph by courtesy of H. B. D. Kettlewell.)

Kettlewell has demonstrated by careful observation, recorded photographically, that birds do search out and eat motionless moths on tree trunks, a fact that had been doubted. This being true, does coloration that renders moths inconspicuous to our eyes also serve to protect them from being seen by birds? Careful observation indicates that the coloration is of protective value. Thus Kettlewell and his colleagues kept 18 moths under continuous observation. Nine were of the light form, nine of the dark, and they were all on blackened tree trunks. During the day of observation all nine of the light individuals were found and eaten by birds but only three of the dark individuals were.

On another occasion a pair of redstarts and their young were observed for two days in a polluted locality. Light and dark moths had been reared by the experimenters and were released in equal numbers. During the two days 43 of the light individuals were found and eaten but only 15 of the dark ones were. On the other hand, similar observations in unpolluted countryside yielded results that were just the reverse. Again the light and dark individuals were released in equal numbers, but in this case 164 dark individuals were observed to be eaten while only 26 of the light ones were. Thus it seems that coloration that renders the moths inconspicuous to our eyes has the same effect in the eyes of birds.

In addition to experiments in which predation by birds was directly observed, experiments were performed in which large numbers of light and of dark male moths were released into a countryside (Kettlewell, 1955 and 1956). These males were marked so that they could be identified if they were caught subsequently. After a time the males in the region were attracted to lights or to cages containing females and were trapped. In this way the investigator could determine whether more of the released males of one kind or the other had fallen victim to predators. During two different summers hundreds of marked males were released into the polluted countryside near Birmingham. The proportion of dark moths recaptured was twice as high as the proportion of light moths recaptured, demonstrating that more of the unconcealingly colored individuals had been killed by predators. The same conclusion, based on converse findings, was drawn from similar experiments in an unpolluted region. Here the light-colored males were protected: Three times as many of them as of dark-colored ones were recaptured. Kettlewell noted that to human eyes the light individuals were less easily visible on lichen-covered tree trunks than the dark individuals were on blackened trunks. But in both instances blending with the background afforded some protection to the moths.

The most common melanic form of the peppered moth differs from the normal light form by the possession of a dominant gene. The first melanic specimen on record was caught near Manchester in 1848. For many years following that date black specimens were rare; but by 1900 they had become common in many localities, forming as high as 83 percent of the population in some localities. At the present time black individuals constitute at least 85 percent of the population in all industrial areas of England; in some places the percentage reaches 98. Here, then, is an instance in which man's activities have altered an environment and a species has altered its characteristics in response to the changed conditions. Evidently what happened was this: Since, as we have seen, melanic individuals are in less danger of death from bird predation than are light-colored ones, they had a tendency to survive in greater numbers in the polluted regions and to pass on their genes to a greater proportion of offspring. Hence in polluted regions the dominant gene for melanism increased in frequency as the generations passed until the present high percentages were reached.

Not only have the melanics increased in numbers, they have apparently become blacker. A comparison of specimens caught many years ago with modern ones indicates that formerly the melanic specimens had more white markings than do modern melanics (Kettlewell, 1958). Probably this "improvement" in matching black backgrounds has been brought about by natural selection acting on genes that modify the effect of the main dominant gene.

It is of interest that in no populations do the melanics constitute 100 percent of the population. Why is this? Perhaps, as Kettlewell suggests, the *heterozygous* melanics have some advantage over both homozygous melanic and homozygous light individuals. Heterozygote superiority of this kind is discussed more fully later (pp. 422–431). In many cases it forms the basis for maintenance of a balanced polymorphism in a population.

Other forces also may be at work to maintain a balanced polymorphism of light and dark forms. Working with a different species of moth, Kettlewell (1957) found that in a certain unpolluted region the light individuals were inconspicuous when at rest but were much more visible when flying than were the dark individuals. Thus neither would be expected to completely supplant the other.

The example just given also is of interest in that it demonstrates that melanic forms may have an advantage in environments unaffected by industrialization. Nevertheless, most localities in which the percentage of melanism is high are either located near industrial centers or in portions of eastern England subject to "long continued smoke fall-out carried by the prevailing south-westerly winds from central England" (Kettlewell, 1958).

We have emphasized the importance of predation in the natural selection of melanic individuals. Other forces also may be at work. There are physiological differences between melanic and normally colored individuals. Thus Ford (1940) found that larvae of melanic moths withstand partial starvation better than do larvae of normally colored ones. Behavioral differences manifesting themselves in differences in success in mating also seem to be present (Kettlewell, 1957). Evidently, however, any advantages conferred by the gene for melanism were offset in normal countrysides by the added conspicuousness to birds. However, when man blackened the environment, then natural selection led to the establishment of the melanic form in the changed environment.

Additional evidence that coloration is, in part at least, controlled by predators using the sense of sight is afforded by the studies of Cain and Sheppard (1954; and Sheppard, 1955) on bright-colored, polymorphic European snails of the genus *Cepaea*. In this case the predator is a song thrush. The investigators found that the color patterns of snails most commonly found and eaten varied with the background. Interestingly enough, no such correlation existed in localities in which snails were preyed upon by rabbits rather than by birds. Apparently color as such was not involved in the locating of snails by rabbits.

MIMICRY Another situation in which natural selection can be seen at work in the predator–prey relationship is that in which organisms resemble not their backgrounds or surroundings but each other. The simplest example is that in which an edible species resembles an inedible one, a situation emphasized by Bates and hence called BATESIAN MIMICRY. If one species of butterfly is unpalatable to birds, another species which is palatable would find it of advantage to resemble the unpalatable one and thus be spared from predation by birds. This being so, natural selection would favor the acquisition by edible species of markings and behavioral traits that would cause them to resemble inedible species.

Sometimes two or more inedible or unpalatable species resemble each other; this is called MÜLLERIAN MIMICRY. Figure 16.5 presents a striking example; the insect has a remarkable resemblance to a wasp, yet it is a *moth*. Beebe and Kenedy (1957) reported that they found

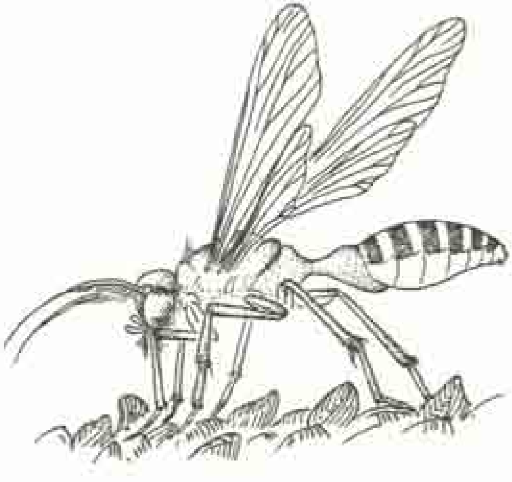


Fig. 16.5. Müllerian mimicry: a moth that mimics a wasp. (Drawn from a photograph in Beebe, W., and R. Kenedy, "Habits, palatability and mimicry in thirteen Ctenuchid moth species from Trinidad, B. W. I.," *Zoologica*, 42 (1957), 147–158.)

this moth unpalatable to a lizard, a bird, and three species of ants. Wasps also are highly inedible. Of what advantage is it for two inedible species to resemble one another? According to the theory of Müllerian mimicry the advantage stems from a reduction in the number of "lessons" required by a young predator in learning to avoid inedible species. Once a bird has learned not to eat wasps it automatically also has learned not to touch the Ctenuchid moth shown in Fig. 16.5. Thus moth individuals are not destroyed by the bird in learning that they are inedible. Conversely, if a bird learns that the moth is unpalatable it also will avoid wasps, and such avoidance will be of advantage to wasps. Thus Müllerian mimicry is of advantage to both or all species concerned, while Batesian mimicry is of advantage only to the edible species (the mimic) that resembles the inedible one (the model). In actuality the sharpness of distinction between Batesian and Müllerian mimicry is reduced by the fact that there are all degrees of edibility and palatability.

The most widely known example of mimicry in North America is that of the monarch and viceroy butterflies. The striking similarity of these actually unrelated species is evident in Fig. 16.6. This is usually cited as an example of Batesian mimicry, the monarch being said to be inedible and the viceroy edible. This conclusion has been challenged, however, on the ground that the viceroy is also edible. Brower (1958a), in an extensive series of experiments with captive jays, found that the monarch is indeed unpalatable to these birds and also that the birds do not distinguish between the monarch and the viceroy. Thus birds that had learned to avoid the monarch also avoided the viceroy. Brower found that birds that had not been given experience with monarchs ate viceroys but that on the whole viceroys seemed to be less palatable than were other species of butterflies tested (e.g., tiger swallowtails). Hence this example seems to fall somewhere between classical Batesian and classical Müllerian mimicry.

Brower (1958b) tested other cases of mimicry with her captive jays. She demonstrated one example of classical Batesian mimicry. The butterfly *Battus philenor* was unpalatable to the birds; having had experience with this model, the birds tended to avoid two other species that mimicked it in markings. These latter two species, however, were completely palatable to birds that had not had experience with the unpalatable model.

Mimicry is a widespread phenomenon among insects. In view of experiments such as those cited we may conclude that resemblances evident to human eyes also are effective in deceiving such predators as birds. Hence development of resemblances of this kind will be favored by natural selection. While, as we have seen, some mimicry is re-

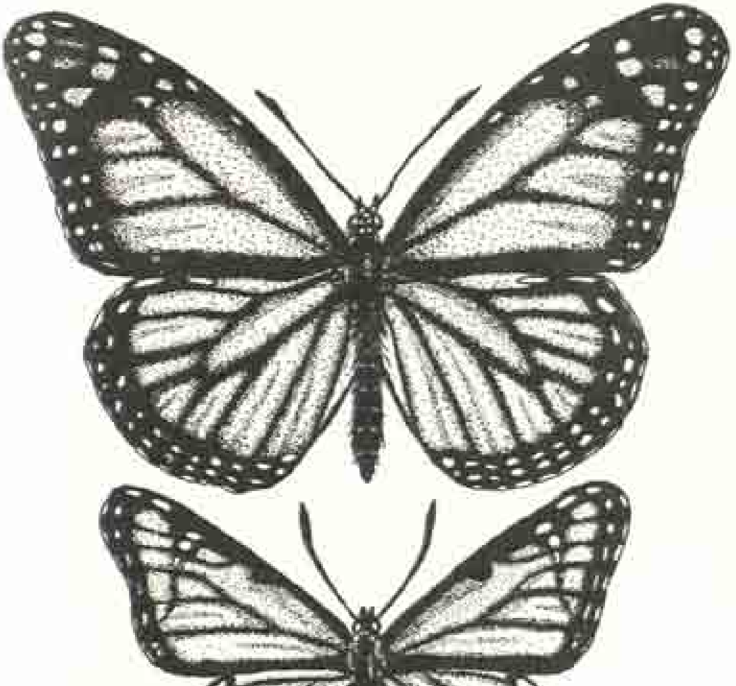


Fig. 16.6. Mimicry. Upper: monarch butterfly, the model. Middle: viceroy butterfly, the mimic. Lower: a relative of the viceroy showing a color pattern more usual for the group to which the viceroy belongs. Stippled areas of the monarch and viceroy are brown in color. (From Guyer, M. F., *Animal Biology*, New York, Harper & Row, 1948.)

markably detailed, more general resemblances and partial similarities also will have selective value insofar as they reduce the chance of attack by predators. There is experimental evidence (e.g., Brower, 1958c) that birds have some ability to generalize—once having learned to avoid an unpalatable model they will avoid other species that to our eyes have some, but not striking, resemblances to that model.

So far we have been discussing protective mimicry—mimicry that protects from predators. There also is the possibility that mimicry may be AGGRESSIVE. For example, if a predator resembles its prey, that predator may be able to approach its victim more easily than it could otherwise do. Some predatory flies lay their eggs in colonies of bees; when the larval flies emerge they feed upon the immature stages of the bees. If, as is sometimes the case, the fly resembles the bees, its entrance into the bee colony to lay its eggs may be facilitated. The bees may not be "suspicious" of the beelike fly. Brower, Brower, and Westcott (1960) have discussed this question, citing a probable example. In this case the adult fly attacks and feeds upon adult bumblebees. The authors concluded that the resemblance of the fly to the bee, extending even to the tone of its buzz, probably makes capture of the victim easier. The authors demonstrated that protective mimicry of the Batesian variety also is involved in this instance. Toads that had learned to avoid bumblebees (unpalatable because of their stings) also avoided the mimicking flies, whereas toads lacking experience with bumblebees usually ate the flies readily.

CONCLUSIONS

In this chapter we discussed selected examples of ways in which animals are adapted to their environments. Space permitting, the number of examples we might have included is legion. But the few we have discussed illustrate striking and important problems solved in the evolution of animals. Furthermore, in some of the examples we clearly saw how natural selection has operated to produce the adaptations.

References and Suggested Readings

Baldwin, E., *An Introduction to Comparative Biochemistry,* 3rd ed., Cambridge, Cambridge University Press, 1949.

Beebe, W., and R. Kenedy, "Habits, palatability and mimicry in thirteen Ctenuchid moth species from Trinidad, B. W. I." *Zoologica, 42,* 147–158 (1957).

Bentley, P. J., "Adaptations of amphibia to arid environments," *Science, 152,* 619–623 (1966).

Brower, J. VZ., "Experimental studies of mimicry in some North American butterflies. Part I. The Monarch, *Danaus plexippus,* and Viceroy, *Limenitis archippus archippus,*" *Evolution, 12,* 32–47 (1958a).

Brower, J. VZ., "Experimental studies of mimicry in some North American butterflies. Part II. *Battus philenor* and *Papilio troilus, P. polyxenes,* and *P. glaucus,*" *Evolution, 12,* 123–136 (1958b).

Brower, J. VZ., "Experimental studies of mimicry in some North American butterflies. Part III. *Danaus gilippus berenice* and *Limenitis archippus floridensis,*" *Evolution, 12,* 273–285 (1958c).

Brower, J. VZ., and L. P. Brower, "Experimental studies of mimicry. 6. The reaction of toads (*Bufo terrestris*) to honeybees (*Apis mellifera*) and their dronefly mimics (*Eristalis vinetorum*)," *American Naturalist, 96,* 297–307 (1962).

Brower, L. P., J. VZ. Brower, and P. W. Westcott, "Experimental studies of mimicry. 5. The reactions of toads (*Bufo terrestris*) to bumblebees *(Bombus americanorum)* and their robberfly mimics *(Mallophora bomboides*), with a discussion of aggressive mimicry," *American Naturalist, 94,* 343–355 (1960).

Cain, A. J., and P. M. Sheppard, "Natural selection in *Cepea,*" *Genetics, 39,* 89–116 (1954).

Dice, L. R., "Effectiveness of selection by owls of deer-mice (*Peromyscus maniculatus*) which contrast in color with their background," *Contributions, Laboratory of Vertebrate Biology, University of Michigan* (34), 1–20 (1947).

Fisher, R. A., *The Genetical Theory of Natural Selection,* 2nd ed., New York, Dover Publications, 1958. (Chap. 7 has a discussion of mimicry.)

Florkin, E., and S. Morgulis, *Biochemical Evolution,* New York, Academic Press, 1949.

Ford, E. B., "Genetical research in the Lepidoptera," *Annales of Eugenics, 10,* 227–252 (1940).

Kettlewell, H. B. D., "Selection experiments on industrial melanism in the Lepidoptera," *Heredity, 9,* 323–342 (1955).

Kettlewell, H. B. D., "Further selection experiments on industrial melanism in the Lepidoptera," *Heredity, 10,* 287–301 (1956).

Kettlewell, H. B. D., "The contribution of industrial melanism in the Lepidoptera to our knowledge of evolution," *British Association: The Advancement of Science,* No. 52, 245–252 (1957).

Kettlewell, H. B. D., "A survey of the frequencies of *Biston betulara* (L.) (Lep.) and its melanistic forms in Great Britain," *Heredity, 12,* 51–72 (1958).

McBean, R. L., and L. Goldstein, "Ornithine-urea cycle activity in *Xenopus laevis:* Adaptation in saline," *Science, 157,* 931–932 (1967).

Prosser, C. L., "Comparative physiology in relation to evolutionary theory," in S. Tax (ed.), *Evolution After Darwin,* vol. 1, *The Evolution of Life,* Chicago, University of Chicago Press, 1960, pp. 569–594.

Prosser, C. L., and F. A. Brown, Jr., *Comparative Animal Physiology,* 2d ed., Philadelphia, W. B. Saunders, 1961.

Robertson, J. D., "The habitat of the early vertebrates," *Cambridge Philosophical Society, Biological Reviews, 32,* 156–187 (1957).

Romer, A. S., *The Vertebrate Story,* Chicago, University of Chicago Press, 1959.

Sheppard, P. M., "Evolution in bisexually reproducing organisms," in J. Huxley, A. C. Hardy and E. B. Ford (eds.), *Evolution as a Process,* London, Allen & Unwin, 1955, pp. 201–218.

Sheppard, P. M., "The evolution of mimicry; A problem in ecology and genetics," *Cold Spring Harbor Symposia on Quantitative Biology, 24,* 131–140 (1959).

Sheppard, P. M., *Natural Selection and Heredity,* New York, Harper & Row, Harper Torchbook TB528, 1960. (Mimicry is dicussed in Chap. 10.)

Smith, H. W., *From Fish to Philosopher,* Boston, Little, Brown, 1953.

17

Origin of Diversity

EARLY IN THE last chapter we stressed the point that two central themes of evolutionary change are adaptation and diversification. We now turn our attention to diversity. In this chapter we shall discuss means by which differences between *individuals* arise. Later we shall discuss means by which differences between populations are produced.

RECOMBINATION OF GENES

It is a common observation that no two individuals are alike. Even so-called "identical twins," if observed closely enough, will be found to differ in some respects. And the extreme diversity among the population at large needs no emphasizing. The same diversity exists in the subhuman portions of the animal kingdom. If "every mouse looks like every other mouse" to us it is because we have not observed mice closely enough to be familiar with their distinguishing features.

What is the basis of this diversity among individuals? Insofar as it is hereditary in nature it arises in good part as the result of the operation of the mechanisms of Mendelian inheritance.

MENDELIAN INHERITANCE

SINGLE-GENE DIFFERENCES We take as our first example the European hamster, a larger relative of the golden hamster from Iran that is popular as a pet in the United States. In Russia, especially, the European hamster is trapped in great numbers for its fur, much as the muskrat is in this country.

"Normal" hamsters vary from gray to grizzly brown in appearance, but black individuals frequently occur. In some regions the black (melanistic) individuals are rare; in other regions they occur with varying frequencies, the extreme being reached in localities having populations in which nearly all individuals are black.

Genetic experimentation has demonstrated that the color difference between a normal and a black hamster depends upon a single gene. Melanism (blackness) is dominant to normal pigmentation (Gershenson, 1945). We may represent the gene for melanism by *M* and the gene for normal pigmentation by *m*. These genes are said to be the ALLELES of each other. That means that they are each other's "opposite numbers" or, more precisely: Either one may occupy a certain specific location (locus) on a certain one of the hamster's chromosomes. The chromosomes occur in pairs, one member of each pair having come from the mother, the other from the father (see the Appendix). Thus the genes (alleles) also occur in pairs. This means that hamsters may be of the following genetic constitutions (GENOTYPES): *MM*, *Mm*, or *mm*. Individuals having the genotypes *MM* or *mm* are said to be HOMOZYGOUS; the alleles constituting each pair are alike. Individuals having the genotype *Mm* are said to be HETEROZYGOUS; the alleles constituting the pair are unlike. Hamsters having the genotype *MM* are black, but so are hamsters having the genotype *Mm*. This is the reason the gene for melanism is said to be dominant. A DOMINANT gene is one that produces its visible effect (PHENOTYPE) in heterozygotes.

What will be the result of mating homozygous black hamsters to gray ones? The homozygous black individuals have the genotype *MM* and the gray individuals the genotype *mm*. Thus the cross becomes

MM × *mm*. Each germ cell (sperm or ovum) produced by the black parents will contain one of the *M* alleles; each germ cell produced by the gray parent will contain an *m* allele. This separation of members of pairs of alleles so that each germ cell receives but one member is sometimes called Mendel's "law of segregation." A little more than 100 years ago Gregor Mendel postulated this principle to explain results he obtained in breeding garden peas. Some 40 years later biologists realized that the basis for this separation was the fact that the chromosomes, containing the genes, separate in this manner when germ cells are produced from precursor cells by the process of MEIOSIS. (Most readers will probably be familiar with meiosis; for those who are not we describe it in the Appendix.)

Since the germ cells (GAMETES) of one parent contain gene *M* and those of the other parent gene *m*, when fertilization of an ovum by a sperm occurs each fertilized ovum (ZYGOTE) will produce an individual with the genotype *Mm*. In this case it makes no difference whether the black parent is the male or the female. All of the F_1 (first filial generation) offspring will be black and heterozygous (Fig. 17.1).

Suppose that the *Mm* females are now mated to the *Mm* males. What will be the result in the next, or F_2, generation? As in the preceding generation, the members of a pair of genes will separate from each other, each gamete receiving only one member of a pair. Hence these heterozygous individuals will produce *M*-containing and *m*-containing gametes in about equal numbers (Fig. 17.1). This will be true of both ova and sperm cells.

We may now ask: What are the chances that an *M*-containing ovum will be fertilized by an *M*-containing sperm cell? The question may be answered in three stages: (1) What are the chances that any given fertilization will involve an *M*-containing *ovum?* Since half the ova are *M*-containing this chance is 1 in 2 or $\frac{1}{2}$. (2) What are the chances that any given fertilization will involve an *M*-containing *sperm cell?* Again, since *M*-containing sperm cells and *m*-containing ones are equal in number, the chance that an *M*-containing one will be involved is $\frac{1}{2}$. (3) What, then, is the chance that both an *M*-containing ovum and an *M*-containing sperm cell will be involved? The probability that two independent events will occur together is the *product* of the probabilities of their occurring singly. Thus the chance that an *MM* fertilized ovum will occur is the chance that an *M*-containing ovum will be involved ($\frac{1}{2}$) multiplied by the chance that an *M*-containing sperm will be involved ($\frac{1}{2}$): $\frac{1}{2} \cdot \frac{1}{2} = \frac{1}{4}$. A similar situation arises when two coins are tossed together. What are the chances that both will come up "heads"? The chance that one coin will be heads is $\frac{1}{2}$; the chance that the other

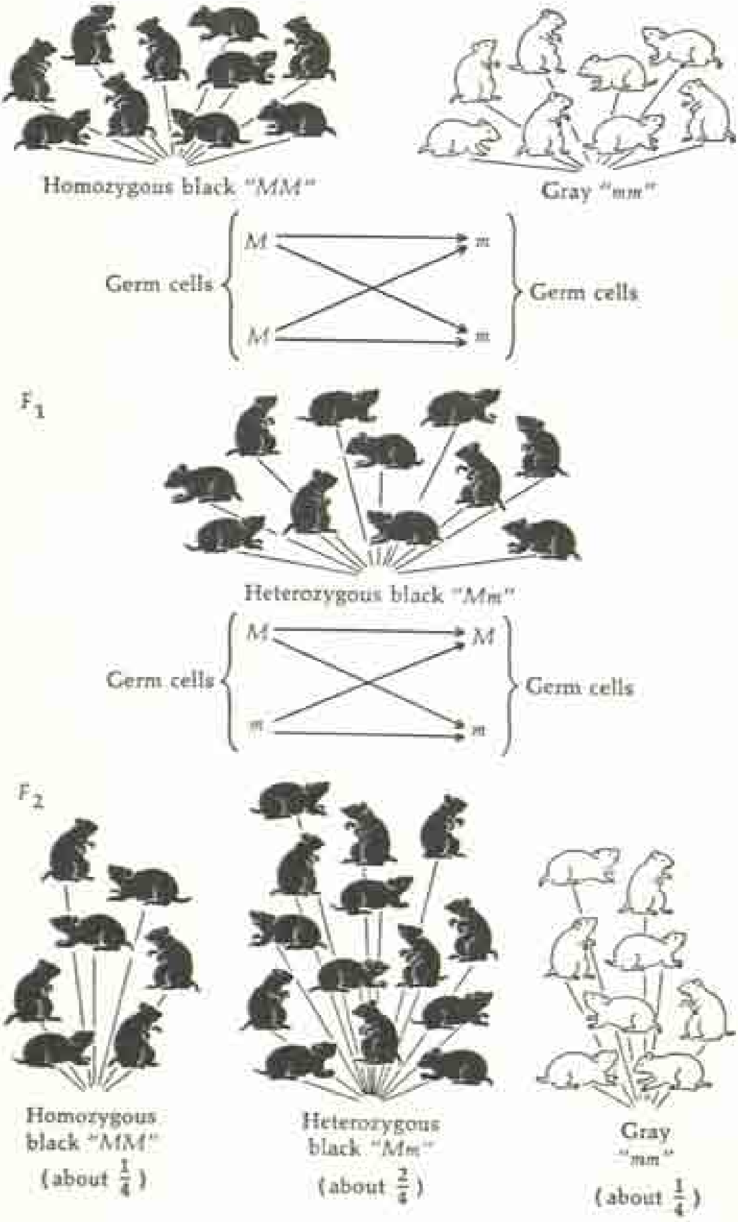
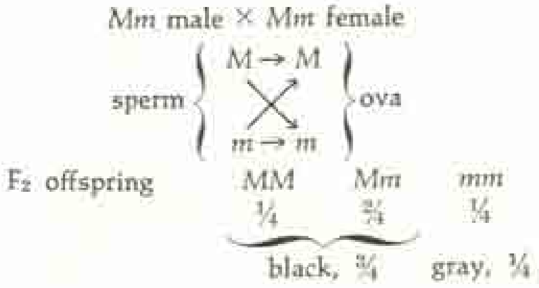

Homozygous black "MM"
Gray "mm"
Germ cells
M
M
m
m
Germ cells
F_1
Heterozygous black "Mm"
Germ cells
M
m
M
m
Germ cells
F_2
Homozygous black "MM" (about $\frac{1}{4}$)
Heterozygous black "Mm" (about $\frac{2}{4}$)
Gray "mm" (about $\frac{1}{4}$)

Fig. 17.1. Mendelian inheritance of melanism (black color) in the European hamster.

will be heads is ½. Thus the chance that both will be heads is ½ · ½ or ¼.

Similarly, what are the chances that an *m*-containing ovum will be fertilized by an *m*-containing sperm? The answer is exactly the same as in the case just described. The chance that an *m*-containing ovum will be involved is ½; the chance that an *m*-containing sperm will be involved is also ½. So the chance that an *mm* fertilized ovum will arise is ½ · ½ or ¼.

We have seen that the chances that offspring will be *MM* are ¼, and the chances that they will be *mm* are ¼. Thus on the average ¼ of the offspring may be expected to be homozygous black and ¼ to be homozygous gray. The remaining 2/4 will be expected to be heterozygous black: *Mm*. Such individuals can arise in two ways: (1) by an *M*-containing sperm cell's fertilizing an *m*-containing ovum (chances of this ½ · ½ = ¼) or (2) by an *m*-containing sperm's fertilizing an *M*-containing ovum (chances of this ½ · ½ = ¼). Since the chance that two mutually exclusive events will occur is the sum of the chances that either event will occur alone, the chance that *Mm* offspring will arise is ¼ + ¼ or 2/4:



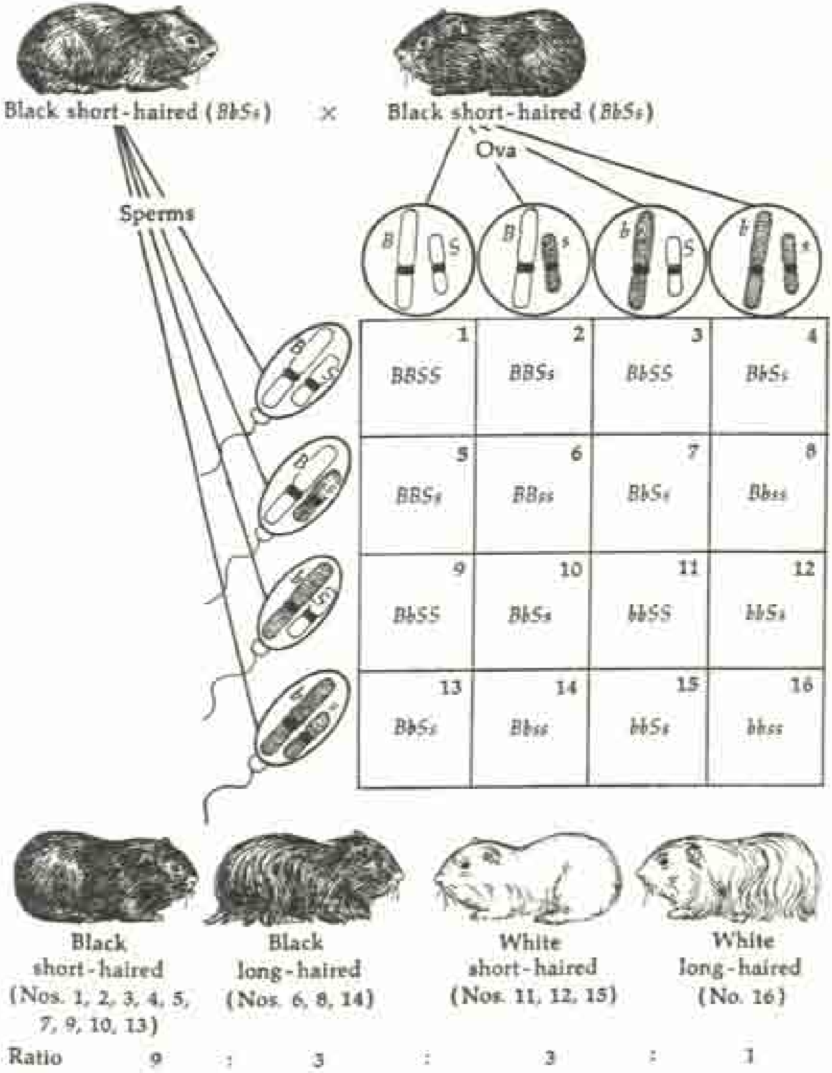
The above results are sometimes expressed as ratios. The fundamental ratio among offspring of parents both of whom are heterozygous is 1:2:1 (1 homozygous dominant to 2 heterozygotes to 1 homozygous recessive). When dominance is present, this fundamental ratio is masked, since homozygous dominants *(MM)* look like heterozygotes (*Mm*). Thus on the basis of phenotype (p. 358) the ratio becomes 3 black-colored offspring to 1 gray one (Fig. 17.1).

Sometimes dominance is not present. In such cases the 1:2:1 ratio is the ratio of phenotypes as well as the ratio of genotypes. We should emphasize that these 1:2:1 and 3:1 ratios, so prominent in writing concerning Mendelian inheritance, depend upon the operation of the laws of chance as set forth above. The ratio expresses the average outcome to be expected when two types of sperms fertilize two types of ova. Ratios obtained in actual experiments approach the ratio but seldom conform to it exactly. On the whole the larger the number of offspring produced, the more closely the ratio will be approached.

INDEPENDENT ASSORTMENT As an example we shall employ the guinea pig, a form whose genetics is more thoroughly known than is the genetics of hamsters. Two pairs of contrasting characteristics in guinea pigs are (1) black vs white and (2) short hair vs long. Individuals heterozygous for both pairs of characteristics are black and have short hair. This shows that the gene for black *(B)* is dominant to the gene for white *(b)* and that the gene for short hair *(S)* is dominant to the gene for long hair *(s)*. The genes concerned with color are in one pair of chromosomes; the genes concerned with hair length are in another pair. In Fig. 17.2 the genes for color are shown in long chromosomes and the genes for hair length in short chromosomes. As a result of meiosis (Appendix) each sperm and ovum contains one long chromosome and one short one. As shown in Fig. 17.2, each doubly heterozygous guinea pig produces gametes of four different kinds: *BS, Bs, bS,* and *bs*. The reason for this is that in meiosis a gamete with a *B*-containing long chromosome is equally likely to be combined with an *S*-containing or an *s*-containing short chromosome, and the same applies to a gamete with a *b*-containing long chromosome. In meiosis the pairs of chromosomes do not influence each other. As a result the members of different pairs of alleles are distributed independently to the germ cells. This is called Mendel's "law of independent assortment."

What offspring will be expected when doubly heterozygous males and females are mated to each other? In other words, what combinations of the four types of sperms with the four types of ova will occur? This is diagrammed in Fig. 17.2 in the form of a "checkerboard" having four squares on a side. Across the top are placed the four types of ova. Each square in the diagram represents a fertilized ovum; in each case the genotype is indicated without drawing the enclosing chromosomes. The squares are numbered. At the bottom of the diagram are shown the four expected types of offspring with the numbers of the squares corresponding to each. We note that 9 of the 16 fertilized ova contain at least one *B* and at least one *S* and so give rise to black, short-haired offspring; 3 of the 16 contain at least one *B* but are homozygous *ss*, and hence result in black, long-haired offspring. Similarly, three of the fertilized ova are homozygous *bb* but have at least one *S*; they have the phenotype white and short haired. Finally, 1 of the 16 fertilized ova is homozygous *bbss* and hence gives rise to a white, long-haired individual.

We may note that this 9:3:3:1 ratio is merely two 3:1 ratios multiplied together. Considered alone, the mating of heterozygous black females to heterozygous black males results in an expected $\frac{3}{4}$ black offspring and $\frac{1}{4}$ white. Similarly, considered alone, the mating of heterozygous short-haired females to heterozygous short-haired males results in an expected $\frac{3}{4}$ short-haired offspring and $\frac{1}{4}$ long haired. Combining these expectations:


Black short-haired (*BbSs*)
×
Black short-haired (*BbSs*)
Ova
Sperms
B
S
B
s
b
S
b
s
Black
short-haired
(Nos. 1, 2, 3, 4, 5, 7, 9, 10, 13)
Black
long-haired
(Nos. 6, 8, 14)
White
short-haired
(Nos. 11, 12, 15)
White
long-haired
(No. 16)
Ratio 9 : 3 : 3 : 1

1 *BBSS*	2 *BBSs*	3 *BbSS*	4 *BbSs*
5 *BBSs*	6 *BBss*	7 *BbSs*	8 *Bbss*
9 *BbSS*	10 *BbSs*	11 *bbSS*	12 *bbSs*
13 *BbSs*	14 *Bbss*	15 *bbSs*	16 *bbss*

Fig. 17.2. The effect of independent assortment of genes in determining the offspring to be expected when doubly heterozygous guinea pigs are mated to each other. The genes are in the chromosomes but for clarity the symbols for them are placed outside the latter.

$\frac{3}{4}$ (black) + $\frac{1}{4}$ (white)

× $\frac{3}{4}$ (short) + $\frac{1}{4}$ (long)

$\frac{9}{16}$ (black, short) + $\frac{3}{16}$ (white, short) + $\frac{3}{16}$ (black, long) + $\frac{1}{16}$ (white, long)

When additional pairs of contrasting characteristics are considered, still more complicated ratios are obtained. Another pair of characteristics in guinea pigs is rough hair vs smooth hair. The gene for rough *(R)* is dominant. Thus when heterozygous rough guinea pigs are mated together $\frac{3}{4}$ of the offspring are expected to be rough haired and $\frac{1}{4}$ smooth. What will be expected when *triply* heterozygous black, short, and rough *(BbSsRr)* guinea pigs are mated together? We may answer the question by the checkerboard method, noting that in this case *three* pairs of chromosomes are involved and that the females will produce *eight* types of ova and the males *eight* types of sperms; or we may answer the question by multiplying the 9:3:3:1 ratio already obtained by another 3:1 ratio:

$\frac{9}{16}$ (black, short) + $\frac{3}{16}$ (white, short) + $\frac{3}{16}$ (black, long) + $\frac{1}{16}$ (white, long)

× $\frac{3}{4}$ (rough) + $\frac{1}{4}$ (smooth)

The reader will find working this out completely an instructive exercise. We may note that the first and largest item will consist of offspring showing all three dominants (black, short, and rough) and that $\frac{9}{16} \cdot \frac{3}{4}$ or $\frac{27}{64}$ of the offspring will be expected to be of this type. There would be eight types altogether.

How many types of offspring will be produced when individuals heterozygous for *four* pairs of genes are mated together? We answer by noting a certain regularity in the above results. When parents are heterozygous for one pair of genes two types of offspring are produced. When parents are heterozygous for two pairs of genes four types of offspring are produced; this is 2^2. When parents are heterozygous for three pairs of genes eight types of offspring result: 2^3. So with independent assortment the general formula is 2^n, where n is the number of pairs of genes for which both parents are heterozygous. To answer our question concerning four pairs: $2^4 = 16$.

Since in actuality every individual in populations of free-living organisms is heterozygous for many pairs of genes (p. 432), the amount of genetic diversity produced by this "shuffling" of chromosomes, with their contained genes, is enormous. What is 2^{100}, for example? Actually this simple formula does not express all the genetic diversity produced by recombination of genes; it applies only to gene pairs in which one gene is dominant. When dominance is lacking the number of types of offspring is increased. Thus with one pair of genes, the genotypic 1:2:1 ratio becomes the phenotypic ratio also. Thus there are three types of offspring instead of only two. With dominance lacking in two or more pairs of genes the effect is compounded.

Some readers will be familiar with the fact that a given locus in a chromosome may be occupied by more than one or the other of a *pair* of alleles, as in our examples so far. Such series of alleles are called MULTIPLE ALLELES, and they may include several or many genes, e.g., A, a^1, a^2, a^3, and a^4. Each individual can have not more than two of the series, because he has only two chromosomes comprising the pair concerned. But that pair may contain any two of the series, e.g., Aa^3, a^1a^4, a^2a^3, and so on. Obviously this phenomenon of multiple allelism greatly increases the amount of genetic diversity.

LINKAGE AND RECOMBINATION So far we have discussed recombinations arising through independent assortment of genes located in different pairs of chromosomes. But in fact each chromosome contains many genes. Genes located in the same chromosome are said to be LINKED to each other (Fig. 17.3). At first thought it might seem that genes in the same chromosome would always "go together" in inheritance, thereby reducing the amount of recombination. But because of the occurrence of CROSSING-OVER during meiosis, recombination of linked genes also occurs. At one stage of meiosis the members of a pair of chromosomes lie side by side (synapsis; Appendix) and may exchange portions of themselves (Fig. 17.4). This is called crossing over. As a result of meiosis of the type shown in the figure most of the gametes will contain either chromosome *(AB)* or chromosome *(ab)*,

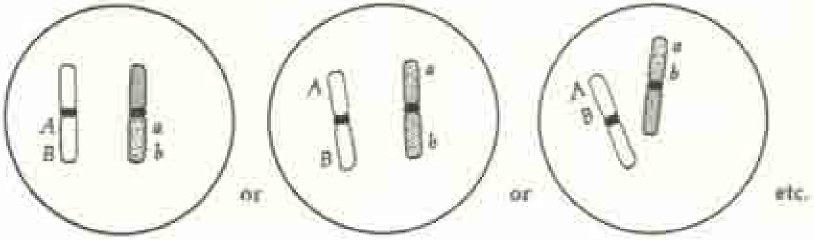


Fig. 17.3. Chromosomal basis of linkage. Genes may be linked in various ways, close together or far apart. The genes are in the chromosomes but for clarity the symbols for them are placed outside the latter.

as shown in part A of the diagram. (In writing it is convenient to represent a chromosome by a parenthesis.) But because of the occasional occurrence of crossing over (part B), a small proportion of the gametes will contain either chromosome *(Ab)* or chromosome *(aB)*. The exact proportion of crossover gametes depends upon various factors, including the distance the genes are apart in the chromosome. Crossing-over seldom occurs between genes very close together. But if the genes are far apart (as they are in Fig. 17.4) the chance that crossing-over will occur somewhere along the chromosome between them is much greater. And once *A* and *b*, for example, are combined in a chromosome they are no more likely to be separated by crossing-over than were *A* and *B*.

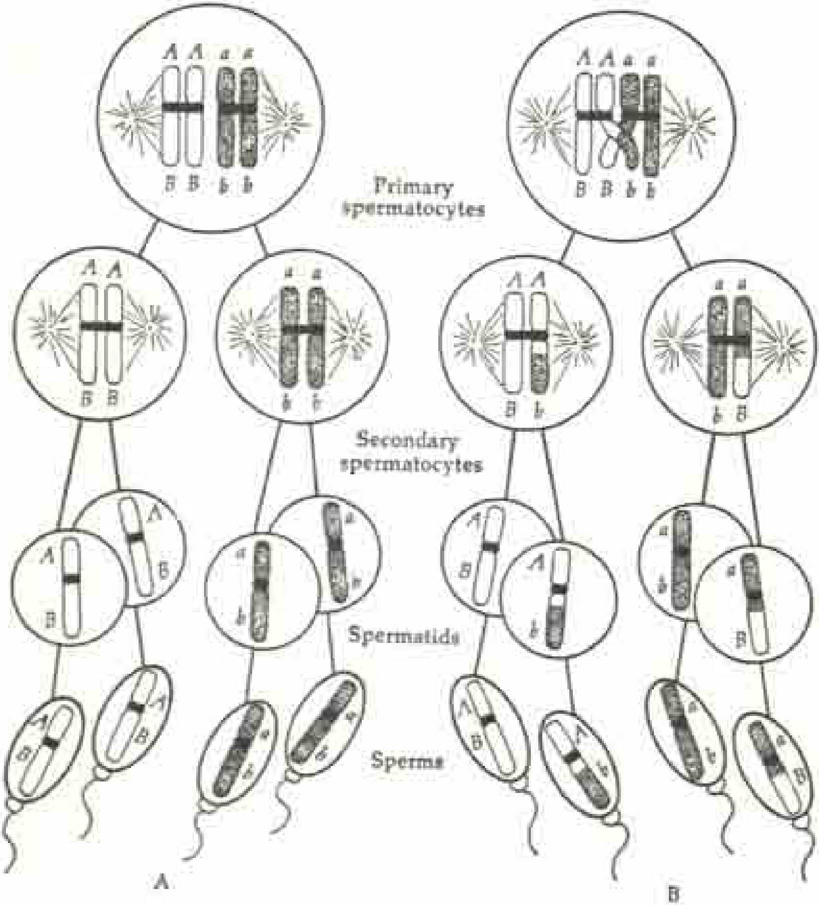

A A a a
B B b b
Primary spermatocytes
A A
B B
a a
b b
A A
B b
a a
b B
Secondary spermatocytes
A
B
A
B
a
b
a
b
A
B
A
b
a
b
a
B
Spermatids
Sperms
A
B

Fig. 17.4. Effect upon linkage of meiosis without crossing over (A), and of meiosis with crossing over (B). The genes are in the chromosomes but for clarity the symbols for them are placed outside the latter.

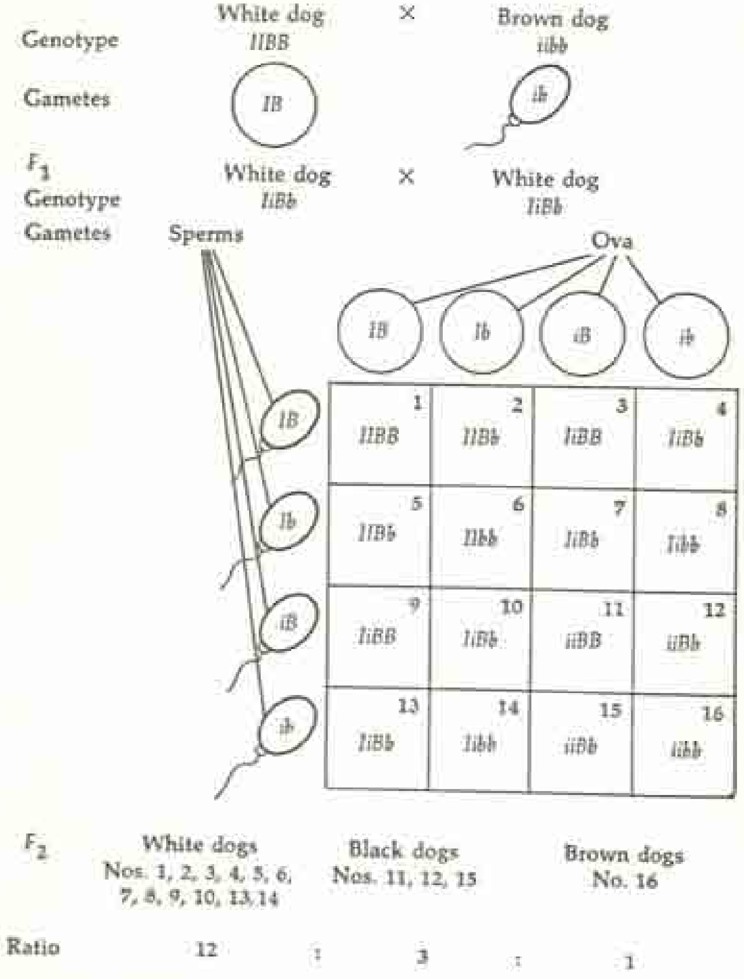
Chromosomes may be thought of as long chains of genes. Crossing-over leads to a regrouping of genes in the chain and hence is one of the forces making for genetic diversity. Since at times genes work together or interact in various ways, a certain grouping of genes in a chromosome occasionally may be of such value to the organism that breaking up the group through crossing-over would be disadvantageous. Suppressors of crossing-over are known; the chromosomal aberration known as inversion (p. 373) has this effect and hence may be of value to an organism. Groups of genes that cooperate in producing a phenotypic effect are sometimes called SUPERGENES.

INTERACTION OF GENES Genes that interact in producing a given phenotype need not be in the same chromosome. At times pairs of genes may be independent in inheritance *but not* be independent in their effect upon the phenotype. An example of such interaction of genes is afforded by EPISTASIS, a situation in which one pair of genes prevents or hides the expression of another pair of genes. This interaction of genes assumes various forms. We shall mention but one example.

In dogs there is a dominant gene *B* for black hair color; its recessive *b* results in brown color in homozygotes. Another dominant gene *I* inhibits the action of the genes just mentioned, causing the coat to remain unpigmented (white) despite the presence of genes *B* or *b*. Dogs having the genotype *ii* will be colored if the proper genes for color are present. Thus a brown dog has the genotype *iibb*. Some white dogs have the genotype *IIBB*. What would be expected from matings of dogs of these genotypes? As a result of meiosis the brown dog produces germ cells having the constitution *ib;* the white dog produces germ cells of *IB* constitution. The resulting fertilized ova have the genotype *IiBb* and give rise to white dogs because of the presence of *I*.

When these F_1 white dogs are bred together the offspring shown in Fig. 17.5 are expected. We note that 12 of the 16 combinations contain at least one *I* and hence result in white dogs. Of the four combinations that are homozygous *ii*, three contain at least one *B* and hence are black while one is homozygous *bb* and hence brown. Thus the 9:3:3:1 ratio (p. 362) has been modified to a 12:3:1 ratio.

Epistasis is not the only type of gene interaction. The expression of many genes is modified by the action of other genes. An example of such modifier genes is afforded by the genes affecting the size of the pigmented areas of hooded rats. Hooded rats are white with black heads and shoulders and a black stripe down the middle of the back and tail. They are homozygous for a recessive gene *h*. But in addition to this gene there are other genes that determine the size of the pigmented areas—whether, for example, the black stripes down the back


White dog
×
Brown dog
Genotype
IIBB
iibb
Gametes
IB
ib
F_1
White dog
×
White dog
Genotype
IiBb
IiBb
Gametes
Sperms
Ova
IB
Ib
iB
ib

	IB	Ib	iB	ib
IB	1 IIBB	2 IIBb	3 IiBB	4 IiBb
Ib	5 IIBb	6 IIbb	7 IiBb	8 Iibb
iB	9 IiBB	10 IiBb	11 iiBB	12 iiBb
ib	13 IiBb	14 Iibb	15 iiBb	16 iibb

F_2 White dogs Nos. 1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 13, 14 Black dogs Nos. 11, 12, 15 Brown dogs No. 16

Ratio 12 : 3 : 1

Fig. 17.5. Epistasis in coat-color inheritance in dogs.

shall be narrow or broad. Such interaction of genes is very common; in fact, it is probably the rule. When we speak of a gene "for" a certain characteristic we mean that without the gene the characteristic cannot develop, but we do not imply that the gene in question works alone in producing the characteristic.

A type of gene interaction that is very common is the *addition* of the effect of one gene to that of another. Genes that have cumulative effects of this kind are called MULTIPLE GENES OF POLYGENES. Many quantitative characteristics have polygenes as their genetic basis.

Suppose, for example, that a certain species of plant has a tall variety and a dwarf variety, the tall variety averaging 34 ins. in height and the dwarf variety 10 ins. Thus the difference between them is 24 ins. We also suppose that the dwarf variety has the genotype *aabb* and that the tall variety has the genotype *AABB*. In this case each "capital letter" gene contributes a certain increment in height. If the effect of each "capital letter" gene is the same, each one contributes a six-inch *increase* in height over the height of the dwarf variety having the *aabb* genotype. What will be expected from a cross between the two varieties?

As shown in Fig. 17.6, the F_1 offspring from the cross will have

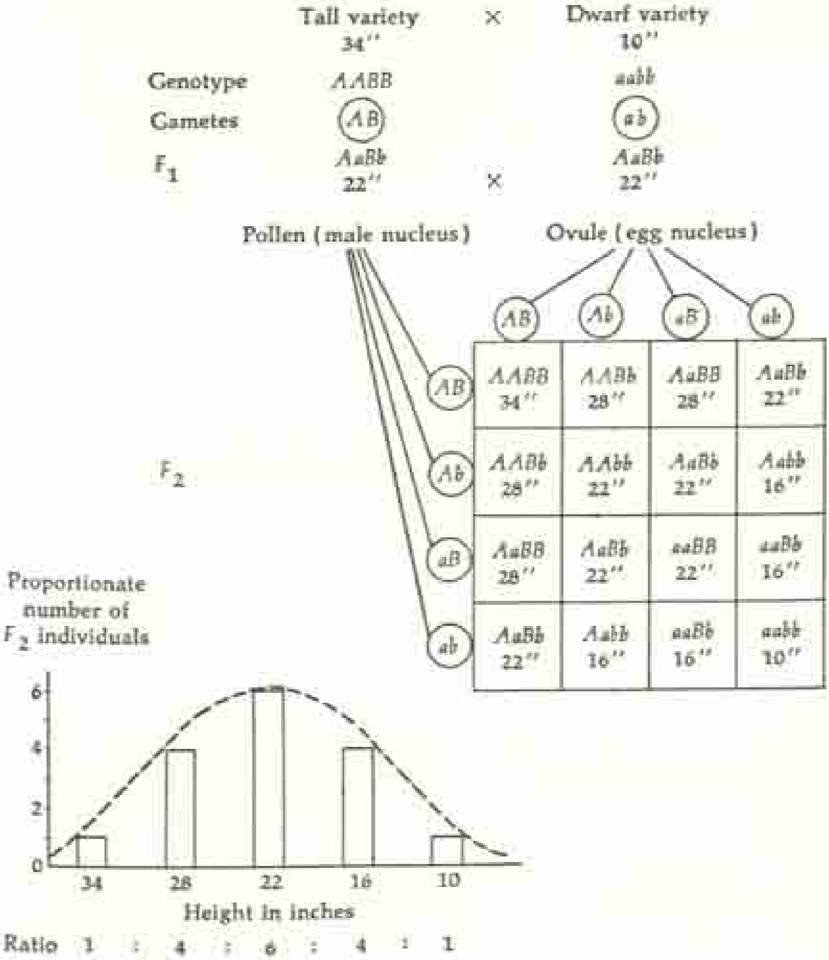

Tall variety
34''
×
Dwarf variety
10''
Genotype
AABB
aabb
Gametes
AB
ab
F1
AaBb
22''
×
AaBb
22''
Pollen (male nucleus)
Ovule (egg nucleus)
AB
Ab
aB
ab
AB
AABB 34''
AABb 28''
AaBB 28''
AaBb 22''
Ab
AABb 28''
AAbb 22''
AaBb 22''
Aabb 16''
aB
AaBB 28''
AaBb 22''
aaBB 22''
aaBb 16''
ab
AaBb 22''
Aabb 16''
aaBb 16''
aabb 10''
F2
Proportionate number of F2 individuals
0
2
4
6
34
28
22
16
10
Height in inches
Ratio 1 : 4 : 6 : 4 : 1

Fig. 17.6. Quantitative inheritance based upon multiple genes (polygenes). In this example the difference in height is assumed to depend upon two pairs of cumulative alleles with additive effect.

the genotype *AaBb*. Each "capital letter" gene adds six inches to the ten inches the *aabb* genotype would produce. Consequently, these F_1 plants are 10 + 6 (for the *A*) + 6 (for the *B*) or 22 ins. tall.

The F_2 offspring produced by these F_1 parents are shown in the "checker board" and summarized in the graph at the bottom of Fig. 17.6. We note that $\frac{1}{16}$ of the F_2 offspring are expected to be as tall as the original tall variety and $\frac{1}{16}$ as short as the original dwarf variety. The rest of the offspring are intermediate, the mean or average height being 22 ins. Connecting the tops of the columns in the graph results in an approximation to a normal frequency curve. Many of the quantitative characteristics determined by polygenes exhibit such a normal distribution. The greater the number of pairs of genes involved the closer the approximation to the typical bell-shaped curve.

For the sake of simplicity we have assumed that the difference in height between the two varieties depends upon only two pairs of genes; obviously such differences might be dependent on three or four or more pairs of genes. Also for the sake of simplicity we have assumed that the *A*'s and the *B*'s contribute equally to the increase in height. This need not be the case. The genes may interact in various ways and to different extents, the result being skewed or subdivided distribution curves among the offspring. Furthermore, not all individuals having the same genotype will have the same phenotype. Not all *AABB* individuals will have the same height, for example. In general, two factors operate to produce such differences: (1) the effect of other genes, commonly called modifiers, and (2) the effect of environmental differences to which individuals of the same genotype are exposed. Both these factors increase the diversity of phenotypes actually produced.

GENE FLOW We have seen that much diversity is possible as a result of recombination of genes possessed by the varied members of one population. Suppose that, in addition, members of two different populations having somewhat differing genes come into contact. The two populations may be living near each other, or if they are farther apart some individuals may migrate from one to the other. Interbreeding under such circumstances will greatly increase the possibilities for diversity. Examples spring to mind of individuals in such crossroads of the world as Hawaii who exhibit a combination of characteristics inherited from, for example, Polynesian, Japanese, and Irish ancestors. Indeed, earlier we surmised that interbreeding of originally separate human populations has occurred repeatedly during the course of human evolution and that the occurrence explains much concerning the origin of observed diversity of mankind past and present (pp. 259–261).

SIGNIFICANCE FOR EVOLUTION Of what significance for evolution is this recombining of genes? In Chapter 2 we noted that the positive aspect of natural selection consists of the favoring of animals possessed of hereditary characteristics that are beneficial, either in the environment in which the animal finds itself or in some other environment open to it. The cumulative result of this favoring is postadaptation in the former case and preadaptation in the latter. While our earlier discussions concentrated attention on single hereditary characteristics, we readily appreciate that the same principles apply to *combinations* of characteristics. Animals having beneficial *combinations* of characteristics will be favored by natural selection over those having less favorable combinations. Indeed, natural selection always operates on whole animals, never on separate parts of animals. Hence in a given environment the successful animal usually will be the one that combines the greatest number of qualities tending to adapt it to the environment in question. Accordingly, the shuffling of the genes is a means of producing a continuous supply of new combinations to be "tried out" by natural selection. Deleterious combinations are weeded out; beneficial combinations are favored.

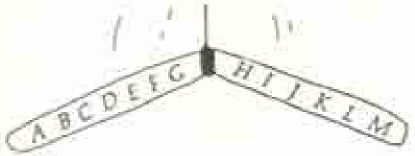
Thus we see in recombination a means whereby natural selection is provided with raw materials for the production of evolutionary change. Recombination involves the reassorting and recombining of genes already present, as when one deals hands of playing cards. How do differing genes (and chromosomal constitutions) arise in the first place? The answer lies in phenomena we group together under the term "mutation."

MUTATIONS

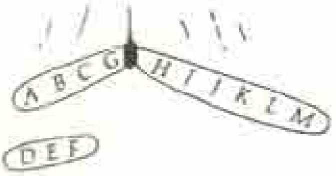
Changes in the genetic materials are known as mutations in the broad sense of that term. They may be conveniently divided into those that produce visible changes in the chromosomes and those that do not. Mutations involving visible changes in the chromosomes are called "chromosomal mutations" or perhaps better CHROMOSOMAL ABERRATIONS. Mutations that do not involve such visible changes and are presumably chemical changes in single genes are called gene mutations (pp. 376–378).

CHROMOSOMAL ABERRATIONS

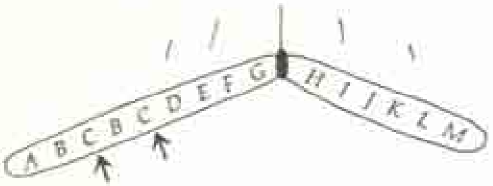
Chromosomal aberrations are of two main types: (1) changes in structure of individual chromosomes and (2) changes in number of chromosomes.



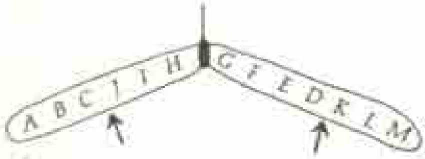
A. Normal chromosome



B. Deletion or deficiency



C. Duplication



D. Inversion

Fig. 17.7. Chromosomal aberrations—three structural types.

STRUCTURAL CHANGES Turning our attention to structural aberrations, we may note that a piece of a chromosome may become detached and lost. Such a loss is called a DELETION or DEFICIENCY. The diagram in Fig. 17.7A represents a normal chromosome. The dot near the center represents the centromere to which the spindle fiber seems to attach. The letters of the alphabet represent genes. The second diagram shows a deletion. The part of the chromosome containing genes *D, E,* and *F* has become detached. Since it has no centromere this fragment probably will be lost, though it might possibly become attached to another chromosome.

Deletions are harmful to their possessors. If an individual is heterozygous for a small deletion (i.e., has one normal chromosome and one deficient one, Fig. 17.7) that individual will probably be viable but is likely to be abnormal in some way. For example, the missing genes *D*, *E*, and *F* on one chromosome are likely to be compensated for, but usually not completely so, by the corresponding genes in the other chromosome. On the other hand, homozygosity for a deletion is likely to be lethal (e.g., both chromosomes of a pair like the one in Fig. 17.7B). Normal viability requires that the full complement of genes be present.

The opposite of a deletion is a DUPLICATION OR REPEAT. In Fig. 17.7C the section of chromosome containing the genes *B* and *C* is present twice. The repeated section may have come from another chromosome that suffered a deletion. Duplications do not necessarily lower the viability of their possessors, although they may result in abnormalities of structure or function. It is possible that repeats of this kind have been important in the evolution of chromosomes—that chromosomes were originally small and that in the course of evolutionary history they have increased in size by the formation of repeats, accompanied or followed by gene mutations of the contained genes.

Sometimes the number of genes in a chromosome is not changed but the order or sequence of genes is altered. Such an INVERSION is shown in Fig. 17.7D, where the middle section of the chromosome, involving genes *D* through *J*, has become reversed or inverted. Since all the genes are present in normal number, the effects of inversions are not so drastic as are the effects of deletions and duplications. Effects on the phenotype may be produced, however, because of what is known as POSITION EFFECT. A gene in one location on a chromosome does not necessarily have the same action it would have in another position. (Gene *D*, Fig. 17.7D, when located next to gene *K* may not have the same action it would have when located next to gene *C*.)

Inversions have another interesting genetic effect: They tend to suppress crossing-over (p. 367). In a heterozygote for an inversion (an individual having in a certain pair one "normal" and one inverted chromosome) normal pairing at synapis is difficult and hence the likelihood of crossing-over is reduced. Thus inversions tend to cause chromosomes to remain intact. This might have evolutionary significance since if a chromosome came to contain a superior arrangement of genes it might be of advantage *not* to have the arrangement destroyed through crossing-over, as we mentioned earlier. At times experimenters deliberately introduce inversions into their experimental stocks so that the chromosome in which they are interested may remain intact (pp. 425–429).

Crossing-over involves the exchange of parts of homologous chromosomes—chromosomes that constitute a pair. Sometimes part of a chromosome may become detached and then become attached to another chromosome that is not homologous to the first. This is known as TRANSLOCATION If nonhomologous chromosomes *exchange* parts the exchange is known as RECIPROCAL TRANSLOCATION. A case is illustrated in Fig. 17.8; two chromosomes (not homologous, as evidenced by the differing genes) are shown as exchanging their entire right "arms." Reciprocal translocation of this type seems to have been important in the formation of varieties within some species of plants.

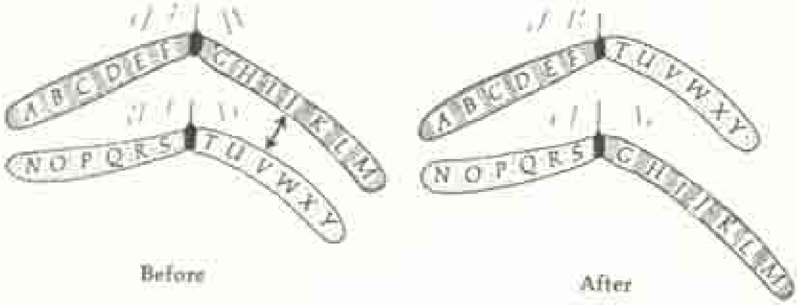


Fig. 17.8. Reciprocal translocation of entire right "arms" of two nonhomologous chromosomes.

NUMERICAL CHANGES The second class of chromosomal aberrations involves changes in number of chromosomes. Rarely a whole chromosome may be lost and the organism still survive. But loss of chromosomes is usually lethal, as we have noted that loss of pieces of chromosomes (deletion) is likely to be. An increase in number of chromosomes may occur at times and may have genetic and evolutionary significance.

A gamete may come to possess an extra chromosome by *an error* in meiosis. In a secondary oocyte, for example, each chromosome is represented by a pair of chromatids held together by the centromere (Fig. Ap. 2, Appendix). Normally the chromatids separate, the ovum and the second polar body receiving one of each pair, as shown in the figure. Suppose, however, that one pair of chromatids failed to separate and that both were retained in the ovum. Such failure of chromatids to separate and be distributed normally is called NONDISJUNCTION. For example, if the "short" chromatids (Fig. Ap. 2, Appendix) failed to separate, the result would be an ovum containing one "long" chromosome and two short ones. When fertilized by a normal sperm, the fertilized ovum would contain two long chromosomes and *three* short ones. Such an individual is called a TRISOMIC (Fig. 17.9). Increase in chromosome number by the addition of one or more single chromosomes is called ANEUPLOIDY; it seems to have been important in producing varieties of plants.

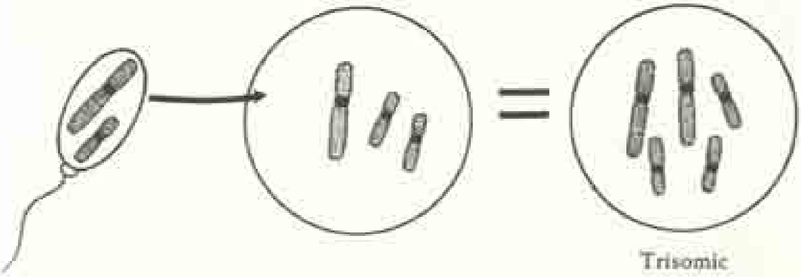


Fig. 17.9. Production of a trisomic fertilized ovum (zygote). Nondisjunction of the "short" chromosomes resulted in an ovum containing two of them. This ovum was fertilized by a normal sperm cell.

Suppose that both pairs of chromatids in the secondary oocyte failed to separate (Fig. Ap. 2, Appendix). As a result the second polar body might be empty of chromosomes, the ovum containing two long ones and two short ones. Such an ovum would contain twice as many chromosomes as normal and hence would be DIPLOID. The number of chromosomes normally present in a mature sperm or ovum is just half the number of chromosomes present in other cells of the body and is called the HAPLOID number. A cell that contains two haploid sets of chromosomes is said to be "diploid." Ordinarily these are body cells or germ cells prior to meiosis. But in the special circumstances just described, a diploid ovum is produced. When such a diploid ovum is fertilized by a normal haploid sperm the resulting fertilized ovum has three of each kind of chromosomes and is called a TRIPLOID (Fig. 17.10).

Diploid sperm cells also may arise by suppression of meiosis. When a diploid ovum is fertilized by a diploid sperm cell a TETRAPLOID is the result (Fig. 17.10). An increase in chromosome number by addition of complete haploid sets is called POLYPLOIDY.

For simplicity's sake we have pictured aneuploidy and polyploidy as occurring through abnormal behavior of chromosomes in the secondary oocyte. Nondisjunction and suppression of reduction in number of chromosomes is at least as likely to occur in the *primary* oocyte (or spermatocyte). Our diagrams also have shown a haploid set as composed of two chromosomes. The actual number varies from species to species. Each somatic (body) cell of man contains 46 chromosomes, for example. This is the diploid number and is composed of 23 pairs. Following meiosis each sperm and ovum normally contains 23 single chromosomes. Thus in man a haploid set (sometimes called a "genome")

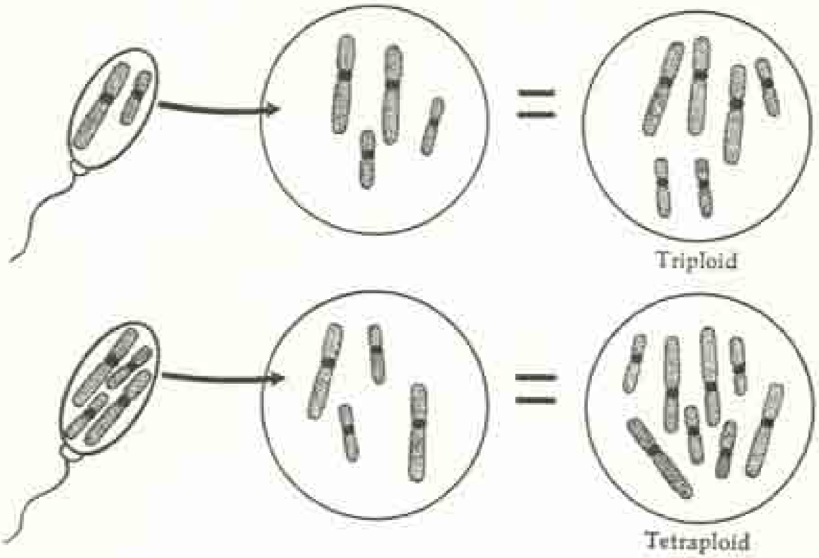


Fig. 17.10. Polyploidy. Formation of a triploid fertilized ovum when a haploid sperm cell fertilizes a diploid ovum (upper diagrams). Formation of a tetraploid fertilized ovum when a diploid sperm cell fertilizes a diploid ovum (lower diagrams).

numbers 23. In that favorite fly of geneticists, *Drosophila melanogaster*, a haploid set numbers 4.

Polyploidy seems to have been important in the evolution of plants (pp. 449–451).

GENE MUTATIONS

Evidence accumulates that genes consist of molecules of DNA (Chap. 5). This is not to imply that the protein portion of nucleoproteins is without genetic significance, but at the present time we know much more about the genetic code formed by the nucleic acid portion. In our discussion of the abnormal hemoglobins (pp. 96–97) we described how substitution of one nucleotide for another in the DNA molecule could result in the production of an altered protein (hemoglobin in this case). Alterations in the DNA molecule may occur in various ways, but the evolutionary significance of all of them lies in the production of altered proteins. As we saw earlier, proteins serving as enzymes catalyze all living processes. Since this is true in embryos as well as in adults, the developmental processes depend upon enzymes and hence upon genes. (This is not to minimize the importance of the environment in which the embryo develops, but in the last analysis the capability of an embryo to respond to environmental stimuli is determined by genetic constitution.) Changes in genes result in changed enzymes which, in turn, result in changes in metabolism and developmental processes. Hence mutations may affect any aspect of metabolism and development.

Because they are most easily observed, we think most frequently of *structural changes* resulting from mutation. An insect's eye is changed in color or a wing is changed in shape, for example. Changed enzymes during embryonic development have resulted in these changes in morphology.

At least as important as changes in structure, however, are changes in function—*physiological changes.* These are usually less easily observed and measured than are structural changes, but they may be of even greater significance to their possessors. Mutations, for example, have given rise to strains of the bread mold *Neurospora* that are unable to utilize the sugar lactose as a source of food (Bonner, 1948) or to manufacture various vitamins and amino acids as normal strains do (Beadle, 1946 and 1959). The "temperature races" of *Drosophila funebris* have no structural differences distinguishing them but are characterized by different tolerances to external temperatures (pp. 418–419). These races doubtless arose by mutation.

A special case of physiological effects of mutation is afforded by the development of resistance to disease or to antibiotics. The colon bacillus *Escherichia coli* is susceptible to streptomycin. Demerec (1950) has found that on the average one in many millions of cells undergoes a mutation to streptomycin resistance. Such individual cells can live and multiply in a medium containing streptomycin. Indeed, some of these strains must have streptomycin in order to live—they become "streptomycin addicts." Doubtless the development of strains of houseflies resistant to the insecticide DDT also has occurred through processes utilizing mutations.

Many other examples of physiological effects of mutations might be given. Probably there is no aspect of metabolism that cannot be altered, for better or worse, by mutation. Of great importance for evolution are the *viability and fertility aspects* of mutation. Viability, the ability to live, may vary from fully normal to zero. A mutant gene that confers zero viability is said to be LETHAL. Most of the lethal genes that exist long enough to be studied are lethal only to homozygotes and hence may be carried by viable heterozygotes. Death results from some lack, in most cases a physiological or metabolic lack, dependent upon abnormal enzymes. Other mutations reduce viability less drastically than do lethal mutations. In our discussion of natural selection (pp. 416–422) we shall enlarge upon the viability relationships of mutations. Mutations also may affect fertility. Since success in natural selection is measured by relative numbers of offspring produced fertility effects of mutations are of great importance to evolution.

Since structure and function are so intimately related, a single mutation frequently may affect both, or it may affect more than one structure or more than one physiological process. Genes producing more than one phenotypic effect are said to be PLEIOTROPIC GENES. For example, the first mutation observed in *Drosophila* goes by the name of "white eye." It changes the color of the eye from red to white, but it also changes the color of the testicular membrane, the shape of the spermatheca, and the length of life. So while it may be a matter of indifference to a fly whether its eyes are red or white, some of these other changes may well be of importance to the individual. Another example is Keeler's (1942) discovery that in rats genes that change the color of the hair change the animals' disposition, increasing or decreasing tameness. Castle (1941) has shown that the gene that produces brown pigmentation in rats, mice, and rabbits accelerates growth and thus results in the attainment of increased body size. Hence, although brown color might be of no consequence to a mouse, the gene in question might be favored if it were of advantage to the mouse to be large. Examples might be added indefinitely. The more we learn about genes the more of them we discover to have effects in addition to the one that originally attracted our attention. Although the point is not established as yet, it may be that all genes have several effects, some of them indifferent or unimportant and some important, at least under some circumstances.

Evidence accumulates that it is the genotype as a whole, all the genes working together, that determines the phenotype. Thus alteration of one gene may have far-reaching effects upon developmental and metabolic processes and hence upon evolution.

WHAT CAUSES MUTATIONS?

We sometimes speak of the mutation process as being "spontaneous," but such a term serves to cloak ignorance since we do not wish to imply that mutations arise without causation. Doubtless such forces as thermal agitation at the molecular level may operate to induce changes in the DNA molecule. That other forces also operate is attested to by experiments that *increase* the rate of mutation. In forms investigated intensively, mutations have been observed to occur at an extremely low but relatively constant rate. For example, a given mutation will occur spontaneously in one of a million individuals of the fruit fly *Drosophila*. Muller (1927) inaugurated the science of radiation genetics by discovering that this rate can be greatly increased by bombarding the parents with x-rays. The radiations penetrate the germ cells and alter the DNA molecule, either directly or probably more usually by altering chemical compounds in the cellular environment of the DNA molecule. The altered compounds then alter the DNA. Both gene mutations and chromosomal aberrations are induced by radiation. Aside from x-rays, other radiations, including ultraviolet light, have been found to have mutagenic (mutation-inducing) effects. Similarly, many chemicals have been found to be mutagenic. Mustard gas was one of the first to be discovered. As investigation continues, the list of known mutagenic chemicals increases steadily.

Thus environmental agents such as chemicals and radiations acting directly upon germ cells account for at least part of the observed mutation rate. We think in this connection especially of more or less constant bombardment by cosmic rays, terrestrial radiation (from radioactive elements in the earth), ultraviolet light, and the like.

Another property of mutations deserves our attention: They occur in random or haphazard fashion without regard to usefulness or the needs of the organism. This randomness has caused some biologists to conclude that mutations do not afford likely materials for constructive evolutionary change. We shall see, however, that this objection is not insuperable.

A word of qualification is necessary in referring to the mutation process as random. Mutations are random in the sense that they may occur when they are not "needed" and may fail to occur when they are "needed," but their randomness has limits. As emphasized by Blum (1955, Chap. 9), the kinds of mutation that any one gene is capable of producing are limited by the physical and chemical structure of the gene itself and by its thermodynamic properties. Randomness occurs within definite limits. Such limitations on the mutation process impose limitations on the course of evolution itself, helping to determine what directions evolution can take and what directions it cannot take.

INHERITANCE OF ACQUIRED CHARACTERS?

Mutations are changes in the genetic materials, chromosomes and genes. We have said that they may be produced by the direct action on germ cells of such environmental agents as radiations and chemicals. Can such genetic changes also be produced by changes in the body cells (somatic cells) that then are in some way passed on to the germ cells? This would be a two-step process: (1) a change in somatic cells and (2) the change transferred to the germ cells. The question introduces one of the oldest and most long-standing controversies in evolutionary studies. The affirmative answer represents a distinct theory of evolution usually called LAMARCKISM after the French biologist Chevalier de Lamarck, who lived from 1744 to 1829 and hence preceded Darwin.

The essence of Lamarckism is the idea that some changes acquired or developed by individuals during their lifetimes are transmitted to their offspring: This is the so-called "inheritance of acquired characters." We know that as organs or parts of the body are used they develop and increase in strength and size. Thus the college sprinter at the peak of his training has more powerful muscles than he would have had if his most strenuous sport had been bridge. Conversely, organs or parts of the body degenerate if unused. The powerless leg muscles of a person bedridden for a protracted period form a case in point. Lamarck's thesis was that bodily changes of this kind, arising from use or disuse of organs, are passed on to offspring. We see readily that this theory, if correct, would provide a simple and direct means for the production of diversity and evolutionary change.

An example may help to make the application clear. We have seen that the ancestors of the modern horse left the woods and took to life on the dry plains of the West (pp. 214–215). The change was accompanied by a change in the length and structure of the legs; this may have made possible increased speed in running over hard ground. In line with Lamarck's theory we may postulate that the first ancestral horses to venture forth on the plains were chased by predatory animals—packs of wolves, perhaps. In running to evade these predators they would have increased the power of their legs (as our college sprinter increases the power of his by practice). Any gains in muscular strength, efficiency, and length of leg acquired in this manner, according to the theory, would be passed on to the offspring of the animals that acquired them. Thus the offspring would begin life with better legs for running than their parents had when they began life. And this same process might have continued generation after generation, giving rise eventually to the modern horse with its elongated, efficiently muscled legs.

The Lamarckian theory appeals because of its directness and relative simplicity. But we come face to face with the central question: Are characteristics developed by an individual during its lifetime inherited by its offspring? Our everyday observations would lead us to answer in the negative. It is fortunate, for example, that mutilations are not inherited. A man who loses a finger need not fear that his children might be born minus a finger. August Weismann, the German critic of Lamarckism, removed the tails from mice for many generations. Of course the mice in the last generation were born with tails as long as those of the mice of the first generation. Such evidences against Lamarckism have been rightly criticized on the ground that the mutilation is something done to an animal—something in which the animal does not participate actively. Developments produced by the activity of the individual do not seem to offer more convincing evidence in support of Lamarckism, however. If our hypothetical college sprinter continues training after he leaves college and marries, will his sons be born with more highly developed leg muscles than they would otherwise have had? We know that they will not. Is the son of a concert pianist born with more skill in his fingers than other people? While we know that aptitude for music is inherited, we are equally certain that the son will have to begin with simple finger exercises just as his father did before him, despite the years of training the father received before the son's birth.

These observations are not scientific experiments, but experiments have yielded similar negative results when carefully controlled. (Some readers will be interested in the experiments of McDougall, 1938, on the possible inheritance of the effects of training in white rats and in the repetition of those experiments, with adequate controls, by Agar *et al.*, 1954.)

Through the years many experiments of varying kinds have been performed as attempts to demonstrate inheritance of acquired characters, and results of some of them have been interpreted as affording evidence of it. Nevertheless, deficiencies in planning or technique, overlooked sources of error, and the possibility of interpreting experimental data in more than one way have invalidated all experiments known to the author. (Space forbids discussion of the strange resurrection of Lamarckism in the Soviet Union by T. D. Lysenko and his followers. The literature is large; we mention especially Goldschmidt, 1949; and Huxley, 1949; and Caspari and Marshak, 1965).

Evidently we are wisest to answer the question concerning the inheritance of acquired characteristics with the Scotch verdict of "not proven." Will anyone ever present indisputable evidence that the DNA of germ cells has been altered by an alteration of somatic cells (muscles, bone, liver, brain, etc.)?

References and Suggested Readings

Agar, W. E., F. H. Drummond, O. W. Tiegs, and M. M. Gunson, "Fourth (final) report on a test of McDougall's Lamarckian experiment on the training of rats," *Journal of Experimental Biology, 31,* 307–321 (1954).

Beadle, G. W., "Genes and the chemistry of the organism," *American Scientist, 34,* 31–53 (1946).

Beadle, G. W., "Genes and chemical reactions in *Neurospora,*" *Science, 129,* 1715–1719 (1959).

Blum, H. F., *Time's Arrow and Evolution,* 2nd ed., Princeton, Princeton University Press, 1955.

Bonner, D. M., "Genes as determiners of cellular biochemistry," *Science, 108,* 735–739 (1948).

Caspari, E. W., and R. E. Marshak, "The rise and fall of Lysenko," *Science, 149,* 275–278 (1965).

Castle, W. E., "Influence of certain color mutations on body size in mice, rats and rabbits," *Genetics, 26,* 177–191 (1941).

Demerec, M., "Reaction of populations of unicellular organisms to extreme changes in environment," *American Naturalist, 34,* 5–16 (1950).

Dobzhansky, Th., *Genetics and the Origin of Species,* 3rd ed., New York, Columbia University Press, 1951.

Gershenson, S., "Evolutionary studies on the distribution and dynamics of melanism in the hamster (*Cricetus cricetus* L.). I. Distribution of black hamsters in the Ukrainian and Bashkirian Soviet Socialist Republics (U.S.S.R.)," *Genetics 30,* 207–232 (1945).

Goldschmidt, R. B., "Research and politics," *Science, 109,* 219–227 (1949).

Huxley, J., *Heredity East and West,* New York, Henry Schuman, 1949.

Keeler, C. E., "The association of the black (non-agouti) gene with behavior in the Norway rat," *Journal of Heredity, 33,* 371–384 (1942).

Lamarck, J. B., *Zoological Philosophy,* New York, Hafner Publishing, 1963. (Reprint of a translation of Lamarck's *Philosophie Zoologique,* 1809. Lamarck's first detailed statement of his theory.)

McDougall, W., "Fourth report on a Lamarckian experiment," *British Journal of Psychology, 28,* 321–345, 365–395 (1938).

Muller, H. J., "Artificial transmutation of the gene," *Science, 66,* 84–87 (1927).

18

Diversity in Populations

IN THE PRECEDING chapter we discussed means by which genetic differences among individuals arise: recombination and mutation. Now we turn our attention to populations of individuals, since in the larger sense it is the population rather than the individual that is the unit of evolution. What happens to mutations that arise in populations, and how may one population come to differ from another? As a basis for answering these questions we must understand a few principles about what is usually called "population genetics."

In speaking of a population we shall be referring to what Dobzhansky (1950) has called a *Mendelian population*: "a reproductive community of sexual and cross-fertilizing individuals which share in a common gene pool." Other writers have employed the term *deme* for such a population.

GENETIC EQUILIBRIUM

It will be convenient to begin our discussion by referring again to the melanistic hamsters (pp. 358–361). As the result of the cross diagramed in Fig. 17.1 (p. 360) an F_2 generation was produced consisting of $\frac{1}{4}$ homozygous black *(MM)*, $\frac{2}{4}$ heterozygous black *(Mm)*, and $\frac{1}{4}$ homozygous gray *(mm)*. If these F_2 individuals interbreed *at random*, what types of offspring will be expected in the next (F_3) generation and in what proportions will the various types be expected to occur? For present purposes we shall assume that there is nothing about the melanistic condition that affects an individual's mating and that no preference is exercised dependent upon color of the coat. Under such conditions a melanistic individual would be equally likely to mate with another melanistic one or with a gray one, *if* the two were present in equal numbers. Similarly, a gray hamster would be equally likely to mate with a melanistic one or with a gray one, if the two were present in equal numbers. But in this instance the two types are not present in equal numbers; there are three times as many black individuals as there are gray ones. The same principle of random mating will hold, however: The chances of an individual's mating with one type or the other will be in proportion to the relative frequency with which the types occur; or, in terms of this specific example, the chance of any individual hamster's mating with a black individual will be $\frac{3}{4}$ and the chance of its mating with a gray individual will be $\frac{1}{4}$. It is necessary, however, to go one step further and to distinguish between homozygous black hamsters and heterozygous ones. We have seen that the F_2 offspring are as follows: $\frac{1}{4}$ are *MM*, $\frac{2}{4}$ are *Mm*, and $\frac{1}{4}$ are *mm*. Accordingly, the chance that any individual hamster will mate with an *MM* individual is $\frac{1}{4}$, the chance of mating with an *Mm* individual is $\frac{2}{4}$ or $\frac{1}{2}$, and the chance of mating with an *mm* individual is $\frac{1}{4}$.

We can now rephrase the question: What will be the nature of the offspring from a population consisting of $\frac{1}{4}$*MM* individuals, $\frac{1}{2}$*Mm* ones, and $\frac{1}{4}$*mm* ones? (We shall assume that no sex differences are involved, that these proportions are true of both males and females.)

The answer may be obtained by making a "checkerboard" diagram in which the male parents are listed along the left-hand margin and the female parents across the top.

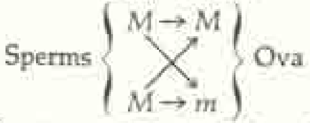
In the body of the diagram are placed the different types of offspring produced and their relative frequencies. The frequencies are obtained for each square by multiplying the fraction representing the proportion of males of the constitution concerned by the fraction repre-

		Female Parents		
		$\frac{1}{4}MM$	$\frac{1}{2}Mm$	$\frac{1}{4}mm$
Male Parents	$\frac{1}{4}MM$	$\frac{1}{16}MM$	$\frac{2}{16}\begin{cases}\frac{1}{16}MM\\ \frac{1}{16}Mm\end{cases}$	$\frac{1}{16}Mm$
	$\frac{1}{2}Mm$	$\frac{2}{16}\begin{cases}\frac{1}{16}MM\\ \frac{1}{16}Mm\end{cases}$	$\frac{4}{16}\begin{cases}\frac{1}{16}MM\\ \frac{2}{16}Mm\\ \frac{1}{16}mm\end{cases}$	$\frac{2}{16}\begin{cases}\frac{1}{16}Mm\\ \frac{1}{16}mm\end{cases}$
	$\frac{1}{4}mm$	$\frac{1}{16}Mm$	$\frac{2}{16}\begin{cases}\frac{1}{16}Mm\\ \frac{1}{16}mm\end{cases}$	$\frac{1}{16}mm$

senting the proportion of females of the constitution concerned. Thus the frequency in the square in the upper left-hand corner is $\frac{1}{4} \cdot \frac{1}{4}$ or $\frac{1}{16}$. The upper row represents the offspring to be expected when the *MM* males, constituting $\frac{1}{4}$ of the total males, mate with the three different types of females in proportion to the relative frequencies of the latter. The diagram shows that $\frac{1}{16}$ of the matings will occur between *MM* males and *MM* females, $\frac{2}{16}$ between *MM* males and *Mm* females, and $\frac{1}{16}$ between *MM* males and *mm* females. The other two horizontal rows are to be interpreted similarly.

The offspring from some of the matings are all of one type—shown in the corner squares of the diagram. In four other squares two types of offspring occurring in equal numbers are shown. An example is the middle square of the top row; here *MM* males are mated to *Mm* females.

MM × *Mm*



Offspring: *MM, MM, Mm, Mm*

In such a mating *MM* offspring and *Mm* offspring are to be expected in equal numbers. Hence, the $\frac{2}{16}$ of the offspring arising from such matings resolves itself into $\frac{1}{16}MM$ offspring and $\frac{1}{16}Mm$ offspring.

The central square of the diagram represents a still more complex situation in that both parents are heterozygous, *Mm* × *Mm*. As we noted earlier, offspring from such parentage are expected to appear in a 1:2:1 ratio; hence the $\frac{4}{16}$ of this square is resolved into $\frac{1}{16}MM$, $\frac{2}{16}Mm$, and $\frac{1}{16}mm$, as indicated.

If we assemble the results shown in the diagram, we find that $\frac{4}{16}$ of the offspring will be expected to be *MM*, $\frac{8}{16}$ will be *Mm*, *and* $\frac{4}{16}$ will be *mm*. This is our 1:2:1 ratio again. The proportions of the different types of individuals are the same in the F_3 generation as they were in F_2. Evidently, then, our artificial population is in *equilibrium;* so long as random mating occurs the proportion of ¼*MM to* ½*Mm to* ¼*mm* may be expected to continue generation after generation.

GENE POOL There is a simpler and more direct way of working the problem discussed above. Let us concentrate upon the genes rather than upon the combinations of genes in the various parents. Turning our attention to the male parents we note that ¼ of the effective sperm cells are produced by *MM* individuals; these sperm cells all will contain gene *M*. Two-fourths of the effective sperm cells are produced by *Mm* individuals; half of these (or ¼ of the total number of sperms) will contain gene *M*. As a result, *half* the total number of sperm cells will contain *M* (¼ from *MM* males plus ¼ from *Mm* males). The other half of the sperm cells will contain gene *m* (¼ from *Mm* males plus ¼ from *mm* males). In the female parents the situation is exactly comparable. Half the ova will contain gene *M* (¼ derived from *MM* females plus ¼ from *Mm* females), and half of the ova will contain gene *m* (¼ from *Mm* females plus ¼ from *mm* females).

As a result we can considerably simplify our checkerboard diagram as follows:

		Ova	
		½*M*	½*m*
Sperms	½*M*	¼*MM*	¼*Mm*
	½*m*	¼*Mm*	¼*mm*

The fraction in each square is obtained by multiplying the fraction of ova having the gene in question by the fraction of sperms having it.

Assembling the results from the chart we find that the offspring occur in the proportions ¼*MM*, 2/4*Mm*, and ¼*mm*—the same result we obtained with the more complicated diagram.

We may even go one step further in our simplification. It is not really necessary to separate the sperms from the ova in our thinking. Grouping the two together we have a "gene pool" in which half the genes (regardless of whether they are in sperms or ova) are recessive, *m*, and half are dominant, *M*. In such a gene pool the equilibrium of ¼*MM*, 2/4*Mm*, and ¼*mm* will be maintained as long as random mating occurs (i.e., as long as choice of mates is entirely a matter of chance and hence obeys the mathematical laws of probability).

An instructive model of such a gene pool is afforded by a box containing red and blue beads (corresponding to gene *M* and gene *m*, respectively) in equal numbers. If without looking you reach into the box and pick up two beads at a time, you may pick up two red ones *(MM)*, a red and a blue one *(Mm)*, or two blue ones *(mm)*. If you do this enough times you will obtain a good approximation of the ratio: $\frac{1}{4}$ both beads of the pair red, $\frac{2}{4}$ one bead red and one blue, and $\frac{1}{4}$ both beads blue.

HARDY-WEINBERG FORMULA We have just noted that offspring derived from a gene pool in which half the genes are dominant and half recessive are expected to consist of $\frac{1}{4}$ homozygous dominants, $\frac{2}{4}$ heterozygotes, and $\frac{1}{4}$ homozygous recessives. In terms of the genes we have used for illustration we may write this as $1MM + 2Mm + 1mm$.

Suppose we now write MM as M^2 and mm as m^2. Our statement then becomes $M^2 + 2Mm + m^2$. Such a statement should begin to stir memories of something we encountered in high school algebra, or more recently as college freshmen. Probably memories will be still further stimulated if we express it with *a*'s and *b*'s: $a^2 + 2ab + b^2$. We now recall that this is the result of multiplying $(a + b)$ by itself: $(a + b)^2$. In other words, $a^2 + 2ab + b^2$ is the expansion to the second power of the binomial $(a + b)$. Evidently the 1:2:1 ratio we have been discussing is a special case of such an expansion.

Instead of employing *a*'s and *b*'s we may follow custom and use *p*'s and *q*'s, those letters we are proverbially admonished to "mind." Let p = the frequency of gene M and q = the frequency of gene m. Then, if random mating occurs, the offspring resulting can be calculated by use of the formula

$$(p + q)^2 = p^2 + 2pq + q^2$$

We may note that this formula is an algebraic equivalent of the small checkerboard diagram (p. 386). Along the left side of the latter we listed the genes carried in the sperm cells together with fractions expressing their frequency: $\frac{1}{2}M + \frac{1}{2}m$. This is equivalent to $p + q$. Along the top we listed the genes carried in the ova together with fractions expressing their frequency: $\frac{1}{2}M + \frac{1}{2}m$. This, also, is equivalent to $p + q$. Filling in the squares of the checkerboard involved multiplying the frequencies of the two kinds of genes carried in the sperm cells by the frequencies of the two kinds of genes carried in the ova: $(\frac{1}{2}M + \frac{1}{2}m)$ $(\frac{1}{2}M + \frac{1}{2}m)$. This is equivalent to $(p + q)$ $(p + q)$ or $(p + q)^2$. Obviously, then, the binomial is *squared* because two parents are involved in the production of offspring. This formula is referred to as the Hardy-Weinberg formula, from the names of the two men who first realized its application to the problems of population genetics.

Let us apply the formula to the situation we have just been discussing, a gene pool in which the numbers of dominant and recessive genes are equal. In such a situation

$$\begin{aligned} p &= \text{the frequency of gene } M = \tfrac{1}{2} \\ q &= \text{the frequency of gene } m = \tfrac{1}{2} \end{aligned}$$

(Note that $p + q = 1$ or unity, standing for the total number of genes. This always must be so since the number of dominant genes plus the number of recessive genes must equal the total number of genes.)

Substituting the numerical values in our formula we obtain

$$\begin{aligned} (p+q)^2 &= p^2 + 2pq + q^2 \\ &= (\tfrac{1}{2})^2 + 2 \cdot \tfrac{1}{2} \cdot \tfrac{1}{2} + (\tfrac{1}{2})^2 \\ &= \tfrac{1}{4} + \tfrac{2}{4} + \tfrac{1}{4} \\ &= \tfrac{1}{4}MM + \tfrac{2}{4}Mm + \tfrac{1}{4}mm \end{aligned}$$

(Recall that p represents gene M in this case; hence p^2 means M^2 or MM. Similarly, pq means Mm, and q^2 means m^2 or mm.)

Thus the Hardy–Weinberg formula affords a means of calculating expectation with regard to offspring without recourse to the checkerboard diagrams previously employed.

So far in our discussion we have confined attention to a situation in which the number of dominant genes equals the number of recessive genes—in which $p = q$. While this situation is common enough in genetics laboratories, it is seldom encountered in a state of nature. There it is much more common for one gene to preponderate in frequency, the other gene being much rarer. Are the principles we have been discussing applicable to such situations?

Suppose we have a population of hamsters in which the gene pool consists of 90 percent M genes and 10 percent m genes. If random mating occurs, what proportion of the offspring may we expect to be black and what proportion gray? The Hardy–Weinberg formula permits an easy solution of the problem:

$$\begin{aligned} p &= \text{frequency of } M = 0.90 \text{ (writing the percentage as a decimal fraction)} \\ q &= \text{frequency of } m = 0.10 \\ (p+q)^2 &= \quad p^2 \quad + \quad 2pq \quad + \quad q^2 \\ &\quad (0.9)^2 + 2 \cdot (0.9) \cdot (0.1) + (.1)^2 \\ &\quad 0.81 \qquad 0.18 \qquad 0.01 \\ &\quad \underbrace{81\%\ MM \quad 18\%\ Mm}_{99\%\ \text{black}} \quad \underbrace{1\%\ mm}_{1\%\ \text{gray}} \end{aligned}$$

We see, then, that under such conditions only 1% of the offspring will be expected to be gray—only one hamster in 100. If random breeding occurs in subsequent generations, the gene pool may be expected to remain the same (90 percent M genes and 10 percent m genes) generation after generation, with the result that gray hamsters may be expected to appear about once in 100 individuals indefinitely. The genetic bases for the occasional appearance of albino individuals among normally pigmented ones, of black sheep among white ones, of cinnamon bears among black ones, of rufous screech owls among gray ones, and so on are doubtless of this type.

We noted earlier (p. 358) that black hamsters appear with varying frequencies in various regions of Europe and Asia; in some places they are rare and in some places common, even approaching 100% of the population. Thoughtful students will readily appreciate that if, knowing the nature of the gene pool, we can calculate the proportion of gray hamsters that will appear, we can reverse the process and calculate the nature of the gene pool if we know the number of gray hamsters occurring. For example, in a certain region 16 percent of the hamsters are gray ones. In what proportions do dominant and recessive genes occur in that gene pool?

The gray hamsters are represented by the q^2 of the Hardy–Weinberg formula. Accordingly, $q^2 = 16\%$ or 0.16; $q = \sqrt{0.16} = 0.4$ or 40 percent. Thus 40 percent of the genes are recessive (m); consequently, the remaining 60 percent must be dominant (M).

Having determined the nature of the gene pool we can do one other thing not possible by direct observation—estimate the proportion of the hamsters that are heterozygous. These are represented by the $2pq$ of the Hardy–Weinberg formula. Substituting the values of p and q, we find that $2 \cdot (.6) \cdot (0.4) = 0.48$ or 48 percent. Thus, in such a population we may expect that 48% of the hamsters are heterozygotes, "carriers" of the gene for gray color. There is interest in obtaining this statistic in view of the role that heterozygotes are observed to play in evolution (see pp. 422–431).

One word of qualification must be added concerning the correctness of calculating the nature of the gene pool from the proportion of individuals exhibiting (and therefore homozygous for) a recessive characteristic. The procedure is valid only insofar as conditions of random mating actually prevail in the population and insofar as the recessive characteristic in question does not affect fertility and viability. Obviously, if gray hamsters were less viable than black ones calculations based on the number of gray hamsters that managed to survive would give an incorrect idea concerning the nature of the gene pool.

So far we have confined our attention to situations in which an equilibrium is already present. What will happen if the population is not in equilibrium at the outset? Suppose a thousand black hamsters, half of them homozygous and half heterozygous, become isolated in some way—marooned on an island, perhaps. What may be expected in future generations of such a population?

The original population has the frequency 50 percent *MM* and 50 percent *Mm*. All the genes contributed by the *MM* individuals are *M*, but only half the genes contributed by the *Mm* individuals are *M*. Thus the frequency of *M* in the gene pool will consist of 50 percent of the total number of genes, contributed by the *MM* parents, plus one-half the genes contributed by the *Mm* parents. The latter contribute 50 percent of the total number of genes; one-half of this 50 percent, or 25 percent, are *M* genes.

$$\begin{aligned}
\text{Thus,}\ p &= 50\% + 25\% = 75\% \text{ or } 0.75\\
q &= 25\% \text{ or } 0.25\\
(p+q)^2 &= p^2 + 2pq + q^2\\
&= (0.75)^2 + 2 \cdot (0.75)\,(0.25) + (0.25)^2\\
&= 0.5625 + 0.375 + 0.0625
\end{aligned}$$

$$56.25\%\ MM + 37.5\%\ Mm + 6.25\%\, mm$$

We note immediately that a change has occurred in the population. There is a somewhat larger proportion of homozygous black hamsters than there was among the parents, and the proportion of heterozygous animals has been somewhat reduced. In addition, a small group of gray hamsters has appeared, although none of the parents were gray. Since this change from the parental generation has occurred it is evident that the original population was not in a state of genetic equilibrium. What is the situation among the offspring?

We answer this question by computing the frequencies of the dominant and the recessive genes, i.e., the values of p and q: 56.25 percent of the individuals have only *M* genes and consequently contribute that percentage of *M* genes to the pool; 37.5 percent of the individuals are heterozygous, half their genes being *M* and half *m*, and thus contribute one-half of 37.5 percent, or 18.75 percent, of *M* genes as well as 18.75 percent of *m* genes. The 6.25 percent consisting of gray hamsters are homozygous *mm* and hence contribute only *m* genes, doing so in proportion to their frequency in the population. Thus,

$$\begin{aligned}
p &= 0.5625 + 0.1875 = 0.75 \text{ or } 75\%\\
q &= 0.1875 + 0.0625 = 0.25 \text{ or } 25\%
\end{aligned}$$

We notice immediately that these values of p and q are exactly the same as those for the original population (see the preceding). Substituting them in the Hardy-Weinberg formula will form a mere repetition of the calculation by which we determined the constitution of the first generation offspring. Evidently, therefore, the population is now in a state of equilibrium and, as long as unmodified random mating occurs, may be expected to continue 56.25 percent *MM*, 37.5 percent *Mm*, and 6.25 percent *mm* generation after generation.

Our hypothetical example has demonstrated that when a population is not in genetic equilibrium with regard to a pair of genes it tends to attain such an equilibrium in one generation of random mating.

SIGNIFICANCE OF GENETIC EQUILIBRIUM FOR EVOLUTION

So far in this chapter we have devoted attention to the manner in which the laws of chance or probability operate upon gene distribution in ways tending to preserve the status quo—to maintain an unchanging equilibrium as generations pass. We have noted that not only is there a tendency to maintain such an equilibrium but if the equilibrium is upset there is a tendency to establish quickly a new equilibrium. Evidently this tendency to equilibrium forms a sort of inertia that must be overcome if evolutionary change is to occur.

Stating the matter so may give the impression that equilibrium is entirely detrimental and obstructive of progress. We should note, therefore, that the equilibrium tendency is *conservative*, in the best sense of that much abused word. It tends to conserve gains that have been made in the past and to prevent too rapid change. "Taking chances" is the price of real achievement and progress in the life of a species, as in the life of a human being. But a species, or a man, who continually gambles everything upon spins of the wheel of fortune leads a precarious existence. Genetic equilibrium helps to ensure that a species will not "put all its eggs in one basket" in undergoing evolutionary change. Radical change may lead to progress; it may also hustle a species down a blind alley to speedy extinction.

An additional conservative function of the equilibrium tendency arises from the manner in which it keeps a store of recessive genes continually in existence even though individuals homozygous for those genes rarely appear. Our discussion will have made clear that there is no inherent tendency for recessive genes to "die out" simply because they are recessive. In the last example, while only about six percent of the hamsters are gray, over 37 percent of them carry the gene for grayness (i.e., are heterozygous). These heterozygous individuals thus form a reservoir of "gray genes" that can be drawn upon in producing future gray individuals. If there is no advantage to be gained from being gray, this matter remains of little importance, but if at any time or under any conditions grayness, or any associated physiological effect, becomes an asset, the reservoir of "gray genes" may assume great significance for the species. We shall return later to this matter of the importance of heterozygotes (pp. 422–431).

Having established a foundation of understanding concerning the tendency to genetic equilibrium we shall now turn our attention to the forces that tend to modify or upset that equilibrium and hence to lead to evolutionary change.

MUTATION PRESSURE AND GENETIC EQUILIBRIUM

In the preceding chapter we emphasized the importance of mutations and mentioned that they occur at a low but fairly constant rate. This continued production of a mutation, even at a low rate, exerts what is called MUTATION PRESSURE on the gene pool since it tends to alter the gene frequencies in this pool and thus the genetic equilibrium we have been discussing.

To refer to our hamsters again, every time a gene that originally produced black color undergoes a chemical change so that it now conditions the appearance of gray color, the gene pool has been altered through decrease by one in number of M genes and through increase by one in number of m genes. Suppose, for example, that a gene pool consists of 50 percent M genes and 50 percent m genes and that the mutation rate is such that one in every thousand M genes mutates to m. It can be demonstrated mathematically that in one generation the gene pool will be shifted to 49.95 percent M genes and 50.05 m genes. This is a small change, but if the same trend continued generation after generation a considerable difference in frequency of the two genes eventually would be accumulated. Indeed, if the trend continued long enough the M genes would be entirely replaced by m genes, assuming that the change from M to m was unopposed. Actually the trend would be opposed by what is known as *reverse mutation*, the mutation of m genes to form M genes. This would also occur at a rather constant rate although, judging by evidence available, at a rate lower than that by which M mutates to m. Thus there are two opposed mutation rates: (1) the rate at which M changes to m and (2) the rate at which m changes to M. The combined action of the two rates is to change the gene frequency until a point is reached at which the number of M genes changing to m genes in any generation balances the number of m genes changing to M at that time. At this point an equilibrium is established. So we see that while mutation pressures by and of themselves may alter genetic equilibriums, their ultimate net effect is to establish equilibrium, even though it is a different equilibrium from that which would otherwise prevail. (The reader is referred to Chap. 3 of

Dobzhansky's *Genetics and the Origin of Species*, 1951, for a more complete discussion of mutation pressure and genetic equilibrium.)

In this connection we may note that a new mutation may not produce a detectable effect until several generations following the actual occurrence of the change in the gene. This is true when a dominant gene mutates to form a completely recessive one. Let us imagine a population of black hamsters all homozygous *MM*. What will be the fate of a single mutation that occurs in this stock? Suppose that in this case the mutation occurs in a sperm-forming cell in a male. As a result one or more of his sperms contains gene *m* instead of the gene *M* possessed by all his other sperm cells. If an *m*-containing sperm functions in fertilization, it must necessarily fertilize an *M*-containing ovum (there are no others). When this occurs an individual of the formula *Mm* is produced. This individual, like its parents, is black; the "new" gray gene still has not produced a visible effect. The *Mm* individual must mate with an *MM* individual of the opposite sex. As we saw on page 385, such a mating (*Mm* × *MM*) is expected to result in offspring that are half *Mm* and half *MM*. Again, these offspring are all black although half of them are heterozygous. Still we have no gray hamsters! How can we obtain gray hamsters? These only can arise if an *Mm* female mates with an *Mm* male. As we saw earlier, one-fourth of the offspring of such a mating are expected to be gray (*mm*) (p. 384). Thus the actual occurrence of a recessive mutation necessarily must be separated from the production of an individual showing the visible effects of that mutation by at least two generations.

Generation I — Black Hamster *MM* (mutation produces an *m*-containing sperm) — Black Hamster *MM*

Generation II — Heterozygous Black Hamster *Mm* × Homozygous Black Hamster *MM*

Generation III — *MM* Black — *MM* Black — *Mm* Black × *Mm* Black

Generation IV — *MM* Black — *Mm* Black — *Mm* Black — *mm* Gray

It will be noted that in order to produce a gray individual in the fewest possible generations we have made use of a brother–sister mating in Generation III. Such matings are not uncommon among lower animals. In modern human societies the nearest approach to them consists of first cousin marriages. These also could bring a recessive gene "to light" in the minimum number of generations if the *Mm* individual in Generation II had a brother or sister of the same constitution and an *Mm* offspring of the latter married one of the *Mm* individuals shown in the diagram.

We mention this matter to emphasize the fact that recessive mutations may occur and be carried by a population as a sort of hidden store, with only occasional homozygous recessive individuals being produced to display the phenotypic effects of the gene. Yet this time lag between the occurrence of a new mutation and the appearance of an individual showing its phenotypic effects occurs only when the new mutation is completely recessive. If the new mutation is not completely recessive, it will produce some phenotypic effect in heterozygotes, even in the first generation offspring. In fact, many so-called recessive genes do have an effect in heterozygotes. As we shall see later, evidence accumulates that frequently the heterozygous state rather than the homozygous one is the more important in evolution.

What is the phenotypic effect when a normally occurring recessive gene mutates to produce its dominant allele (e.g., *m* to *M*)? In this case the new mutation produces a visible effect in the first generation. As we saw earlier, many populations of European hamsters consist entirely of gray individuals. If a black individual suddenly appears in such a population, this individual is the result of a new mutation in a germ cell from one of the parents (assuming that there has been no interbreeding with neighboring populations possessing gene *M*). A like situation is encountered when a melanic individual arises in a population of normally colored peppered moths (*Biston betularia*, pp. 346–351).

GENETIC DRIFT

Let us return in imagination to the population of black hamsters all of which are *MM* except for the one *Mm* individual. We saw that the only mating possible for the latter is to an *MM* individual. We then stated that such a mating (*Mm* × *MM*) is expected to produce offspring that are half *Mm* and half *MM*. Now that statement is true *on the average*, but such theoretically expected ratios are merely expressions of the operation of the laws of probability, as in flipping coins. If parental pairs of *MM* × *Mm* constitution give rise to 200 offspring, about 100 of them would be *MM* and about 100 *Mm*. But let us suppose that this single pair of parents had only *two* offspring—at least, two that lived to reproduce in their turn. Such a situation commonly prevails in populations that are stationary in numbers from generation to generation. If the parents produce only two offspring that live to reproduce, what effects will that fact have upon the fate of the mutation *m* in which we are interested?

$$MM \times Mm$$

$$\begin{tikzcd} \text{Germ cells} & M \arrow[r] \arrow[dr] & M & \text{Germ cells} \\ & M \arrow[r] \arrow[ur] & m & \end{tikzcd}$$

The four arrows in the diagram represent the four possible combinations of germ cells. Probability of occurrence is the same for all four combinations. Two combinations result in *MM* offspring and two in *Mm* offspring. Thus the chance that the *first* offspring will be *MM* is $\frac{1}{2}$ and the chance that the *second* offspring will be *MM* also is $\frac{1}{2}$. Hence, the chance that both of two offspring will be *MM* is $\frac{1}{2} \cdot \frac{1}{2}$ or $\frac{1}{4}$. But if both the offspring are *MM*, an event of great significance has transpired: The *m* gene has been irrevocably lost. The population will revert to its original all *MM* constitution and remain so until such time as a fresh mutation from *M* to *m* occurs. We note, moreover, that the chance of losing a mutation in this way is not a small one; it is one chance in four or 25 percent.

But what other constitutions may the two offspring possess? The chance that the first offspring will be *Mm* is $\frac{1}{2}$; the chance that the second offspring will be *Mm* also is $\frac{1}{2}$. Thus the chance that both of the two will be *Mm* is $\frac{1}{2} \cdot \frac{1}{2}$ or $\frac{1}{4}$. It is to be noted that in this case the number of *m* genes is doubled; the parents, only one of which possessed the *m* gene, have been replaced by two offspring both of which possess the gene.

The chance that the first offspring will be *MM* is $\frac{1}{2}$; the chance that the second will be *Mm* is $\frac{1}{2}$. Hence, the chance that the two will have the designated respective constitutions is $\frac{1}{2} \cdot \frac{1}{2}$ or $\frac{1}{4}$. Finally, the chance that the first offspring will be *Mm* is $\frac{1}{2}$; the chance that the second will be *MM* is $\frac{1}{2}$; and the chance for the combination is $\frac{1}{2} \cdot \frac{1}{2}$ or $\frac{1}{4}$. Thus the chance that either one of the two offspring will be *MM* and the other *Mm* is $\frac{1}{4} + \frac{1}{4}$ or $\frac{1}{2}$. These combinations represent retainment of the *status quo*: The parents *MM* × *Mm*, are merely replaced by two offspring having the same constitutions as themselves. The frequency of the *m* gene has neither increased nor decreased.

In summary we find that, owing to the operation of chance in the reproduction of a relatively stationary population, we may expect "new" mutations to be lost from the population about 25 percent of the time, to be doubled in frequency about 25 percent of the time, and to remain unchanged in frequency about 50 percent of the time.

Suppose we assume that the second possibility is the one that occurs—that the parents are replaced by two offspring, both *Mm* in constitution. If these two are of opposite sex, they may mate together, thus making possible the actual appearance of gray offspring, as diagramed in the preceding (p. 393). But the chances of their mating together are not large; if they do not do so they obviously must mate with *MM* individuals. The result would be two matings like those of the original parents:

Original parents *MM* × *Mm*
/ \
First generation *MM* × *Mm* *Mm* × *MM*

In the case of each of these first generation matings the chances with regard to two offspring are the same as they were for the original parents. Both may be *MM* (the *m* gene being lost as far as that mating is concerned); both may be *Mm* (the frequency of the *m* gene being doubled); and one may be *MM* and the other *Mm* (the frequency of the *m* gene remaining unchanged).

For the sake of illustration, let us suppose that the second possibility materializes in both cases, that the offspring from each mating are both *Mm*.

Original parents *MM* × *Mm*
\ /
First generation *MM* × *Mm* *Mm* × *MM*
\ / \ /
Second generation *Mm* *Mm* *Mm* *Mm*

On this supposition we see that the frequency of the *m* gene has doubled again. Two individuals possessed it in the first generation; four possess it in the second generation.

We might continue on into a third generation, following the matings of the four second-generation individuals. But the principle involved should be evident without more extensive illustration. In small populations producing small numbers of offspring per mating, the frequencies of mutant genes may fluctuate either up or down according to chance. This chance fluctuation in gene frequencies has been termed genetic "drift" by Sewall Wright, who has emphasized its role in evolution. Owing to chance, gene frequencies may "drift" either up or down. In our illustration the frequency of gene *m* might continue to increase generation after generation; if so, actual gray hamsters *(mm)* would soon appear and their breeding would accelerate the spread of the *m* gene. If this trend continued to its culmination, the *m* gene might reach a frequency of 100 percent; i.e., a population entirely composed of gray hamsters might result. Or the trend in the other direction might set in at any time: Matings in which offspring possessing the *m* gene were possible but not inevitable might fail to produce such offspring. As a result the frequency of the *m* gene would decline. If the decline were of sufficient magnitude, the *m* gene might be lost entirely from the population, all the hamsters being homozygous for black coloration. In the former case we should say that the recessive gene had become *fixed*, by chance, and in the latter case that the dominant gene had become fixed. When fixation occurs the drift becomes irreversible, but at any point before fixation is reached reversal of drift may occur.

A model to illustrate the operation of "drift" was constructed by Dubinin and Romaschoff (described in Dobzhansky, 1941, p. 162). In this model the gene pool was represented by 100 marbles in a bowl. Each marble bore a different number. In order to simulate the loss of 25 percent of the mutant genes described above, the investigators discarded from the bowl 25 marbles, taken at random. In order to simulate the doubling in frequency of 25 percent of the mutant genes, they withdrew 25 more marbles at random and then replaced them, accompanying each marble by a second one bearing the same number. In this way the total number of marbles remained 100, but 25 percent of the numbers designating individual marbles were lost and 25 percent of the designating numbers were doubled in frequency. This procedure represented the action of chance in the production of one generation of offspring. The process was then repeated time after time. As the "generations" passed it was found that fewer and fewer different numbers remained in the bowl, until finally all 100 marbles came to bear the same number. This culmination was reached in from 108 to 465 "generations" in different experiments.

In order to demonstrate the influence of size of population upon drift Dubinin and Romaschoff repeated the experiment with a gene pool consisting of but 10 marbles. In this case "homozygosis" (all marbles having one number) was attained much more rapidly than it was in the larger gene pool, only 14 to 51 "generations" being required. This observation emphasizes the point that drift is primarily a phenomenon characteristic of small breeding populations.

Instructive as is the model just described, I felt that a model mimicking more closely the actual conditions of bisexual reproduction might have enhanced value. I also wished to avoid the artificial regularity imposed by discarding 25 percent of a gene pool and doubling another 25 percent at each generation. Accordingly, I devised a simple model in which chance was free to operate in two phenomena at each generation: (1) in arranging of matings and (2) in production of offspring from these matings (Moody, 1947). In the model, individuals were represented by pairs of beads tied together: Two red beads stood for a homozygous dominant individual *(MM);* two blue beads for a homozygous recessive *(mm);* and a pair consisting of one red and one blue bead represented a heterozygous individual *(Mm).*

The model began with a small population conforming to the Hardy–Weinberg equilibrium: 3*MM* : 6*Mm* : 3*mm*. To represent them, three pairs of red beads, six pairs consisting of one red and one blue bead, and three pairs of blue beads were placed in a box and thoroughly mixed. Then the pairs were withdrawn at random, two at a time. Two pairs withdrawn together constituted a "mating," arranged at random. The "matings" actually obtained at one trial were *MM* × *Mm; MM* × *mm; MM* × *Mm; Mm* × *Mm; Mm* × *mm;* and *Mm* × *mm* (Fig. 18.1).

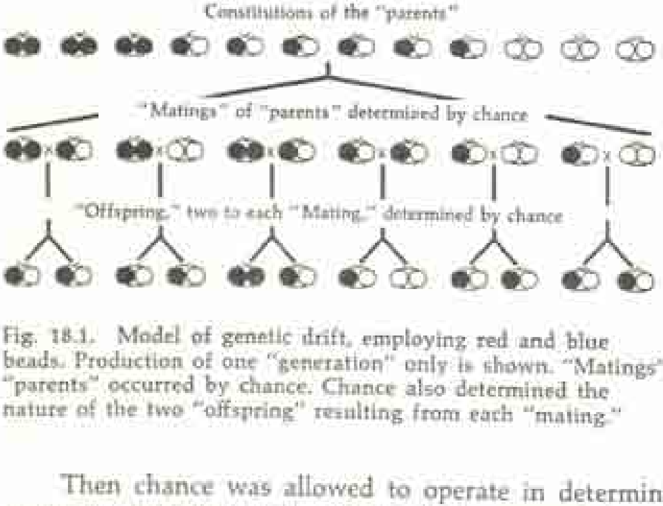

Constitutions of the "parents"
"Matings" of "parents" determined by chance
"Offspring," two to each "Mating," determined by chance

Fig. 18.1. Model of genetic drift, employing red and blue beads. Production of one "generation" only is shown. "Matings" of "parents" occurred by chance. Chance also determined the nature of the two "offspring" resulting from each "mating."

Then chance was allowed to operate in determining the two offspring to arise from each "mating." For example, from the *Mm* × *mm* "mating" two types of offspring are possible, *Mm*, and *mm*. The *mm* parent must contribute an *m* gene; this could be coupled with either an *M* gene or an *m* gene from the *Mm* parent. To permit chance to operate in deciding whether in each case the latter would contribute *M* or *m*, a bowl containing equal numbers of red and blue beads was used. One bead was withdrawn from the bowl at random; if the bead was red, that meant that the *Mm* parent contributed an *M* gene (and the offspring therefore was *Mm*); if the bead was blue, that meant that the *Mm* parent contributed an *m* gene (and the offspring was therefore *mm*). This drawing was done twice, once for each of the two "offspring." The bowl of beads was used in the same way to determine the contribution of a heterozygous parent in the other matings listed. When both parents were heterozygous, as in the fourth "mating" listed, two beads were withdrawn from the bowl at a time, since both parents might contribute either an *M* (red bead) or an *m* (blue bead), the offspring being either *MM* (two red beads), *Mm* (one red and one blue bead), or *mm* (two blue beads). In "matings" like the second listed, in which both parents were homozygous, the offspring must necessarily both be of one constitution (*Mm*, in this instance); hence, no drawing of beads was needed.

In an actual experiment the offspring derived from the "matings" listed above gave the following totals: 1*MM*, 10*Mm*, and 1*mm* (Fig. 18.1).

The process was then repeated to produce a second generation. One pair of red beads, ten pairs consisting of one red bead and one blue bead, and one pair of blue beads were put in the box, mixed, and withdrawn at random two pairs at a time. Thus "matings" were arranged by chance. Then the two offspring from each "mating" were determined, using the bowl of red and blue beads as described above.

The process was repeated "generation" after "generation." Sometimes the number of blue beads increased; sometimes the number of red beads did so. Sometimes beads of one color almost disappeared, the population coming to consist of 11*MM* and 1*Mm* individuals. Then there would be a "rally" on the part of the *m* genes, which became more numerous again. The model demonstrated the tenacity with which the laws of probability as expressed in the Hardy–Weinberg formula tend to maintain equilibrium even in such a tiny "population." Yet eventually "drift" won out, and one gene was entirely lost. The first time the experiment was tried, fixation of one gene did not occur until the 134th generation; members of that generation were all *MM* (12 pairs of red beads). That the large number of generations was of no real significance, however, was attested by another running of the experiment in which the same result was achieved in 17 generations. These results are given in Table 18.1, a study of which will make clear that complete elimination of the blue beads might easily have occurred in even fewer generations.

SIGNIFICANCE OF GENETIC DRIFT FOR EVOLUTION Genetic drift affords a means by which inherited traits may become established in a population without regard to their usefulness. When the size of the population is small some genes may be reduced in frequency or even lost by chance and others may be increased in frequency by chance. Thus the nature of the population is changed without involving the question of the usefulness of the traits.

Table 18.1. RESULTS OF ONE DEMONSTRATION OF THE GENETIC DRIFT MODEL

Generation Number	Distribution of Individuals *MM*	*Mm*	*mm*
Parents	3	6	3
1	3	4	5
2	4	2	6
3	2	5	5
4	2	9	1
5	6	5	1
6	7	5	0
7	8	4	0
8	9	3	0
9	10	1	1
10	10	2	0
11	10	2	0
12	11	1	0
13	11	1	0
14	11	1	0
15	11	1	0
16	11	1	0
17	12	0	0

We have mentioned repeatedly that drift is a phenomenon of small populations. That it is such may at first glance seem to restrict its action to inhabitants of oceanic islands and members of other small, isolated communities. Yet even large, widely ranging assemblages of animals are commonly at least partially divided into smaller breeding groups. A species of field mouse, for example, may range over an entire state and include millions of individuals. If the principles of random mating prevailed, any given individual would be equally likely to mate with any other individual of opposite sex among those millions. Yet that is not the condition that actually obtains. An individual living in one river valley is more likely to mate with an individual in the same valley than with an individual in another one. An individual in one patch of woods is more likely to mate with another individual in the same wood lot than with an individual in woods separated from it by open country. Furthermore, field studies reveal that many animals establish rather definite "home ranges" beyond the limits of which they seldom stray and within which they repel intruders of the same species and sex. Thus the territory within which an individual is likely to secure a mate is still further restricted.

We also should note that many species of animals pass through "bottlenecks" in their yearly life cycles. Among insects, especially, winter is likely to constitute a bottleneck. In a given region there may be thousands of individuals of a certain species throughout the summer, yet only a relatively few may survive the winter to become progenitors of the next summer's population. If the few that survive the winter happen to possess some genetic characteristic in greater frequency than the general population of the preceding summer did, the population of the second summer may differ considerably from that of the first summer. Thus Spencer (1947) found that the fruit flies *(Drosophila)* of a certain small community possessed an unusual frequency of a recessive mutation named "stubble," affecting the length of bristles. In these flies great seasonal fluctuations in number of individuals occur, the parents of a given summer population consisting of a few individuals who succeed in surviving the winter indoors. Since the "stubble" gene seems not to be of significance in the lives of the flies, the explanation for its having attained a considerable frequency of occurrence in this particular locality seems to be genetic drift. By chance, an unusual proportion of the few individuals surviving a winter possessed the "stubble" gene; hence the gene occurred with increased frequency among their offspring, the next summer's population.

In somewhat similar manner an "error of sampling" may occur when, through migration, a small group from a large population establishes a subpopulation in a new locality. The "founders" of the new population may not be entirely typical of the large population from which they came. Suppose, for example, that a large population has in its gene pool equal numbers of genes M and m (i.e., $p = 0.5$ and $q = 0.5$; p. 388). As we noted previously, such a population would be expected to consist of $\frac{1}{4}MM$ individuals, $\frac{2}{4}Mm$ individuals, and $\frac{1}{4}mm$ individuals. Now 10 members of this population migrate to an island, these founders of the island population by chance may not exhibit that 1:2:1 ratio. Perhaps five will be MM, four will be Mm, and one will be mm—or any other chance combination imaginable. In the extreme case all 10 might be MM (or alternatively mm), in which case the island population descended from the 10 individuals would lack completely one of the genes under consideration. In this manner the gene pool of the island population might be very different from the gene pool of the population from which the founders came. This FOUNDER PRINCIPLE, as it is called, may help to explain how small, isolated populations have come to possess the unusual characteristics they sometimes exhibit as compared to characteristics shown by large populations of their relatives and how large populations descended from a few immigrants may differ from the population from which the immigrants came (Mayr, 1963; Sheppard, 1960).

THE QUESTION OF NONADAPTIVE TRAITS We have mentioned that genetic drift is based upon chance and occurs without regard to the usefulness of the traits concerned. This being the case, in theory a population, through drift, could become characterized by traits that are of no significance in the lives of the organisms. Such traits would be adaptively neutral, that is, nonadaptive (p. 324).

Do animals actually possess nonadaptive traits? Many of the differences between related subspecies, and even species, are so small that we have difficulty imagining any possible significance they might have to the organisms concerned. Does it make any difference in the life of a zebra whether its legs are striped down to the hoof or whether the striping extends only part way down the leg (Fig. 13.6, p. 288)?

Questions of this kind are answered both affirmatively and negatively. According to one point of view such nonadaptive traits are commonly found. The other viewpoint is that if an organism has a trait that fact is evidence in itself that the trait must be of some significance to the organism. According to this view, if we do not know what the usefulness of a trait is, that is simply a matter of our ignorance. A trait should be assumed to be useful unless proved otherwise. (Recall here our discussion of pleiotropic genes and their significance; pp. 377–378). So the difference of opinion stands unresolved.

If there *are* nonadaptive traits, how could a population come to possess them? Most of the answers involve genetic drift. At the time this is being written there seems to be a quickening of interest in what has been called "Non-Darwinian Evolution" (King and Jukes, 1969). This refers to evolutionary change not based on natural selection. For example, in Chapter 5 we noted that the DNAs of different organisms differ from each other. Are these differences important to the organisms? In part they undoubtedly are, but King and Jukes (1969) pointed out that because of the degeneracy (synonymity) of the genetic code some genetic change hardly could be of a nature to be acted on by natural selection. For example, the codon UCU can be changed to UCC by substituting cytosine for uricil in the third position (Table 5.2, p. 89). Such a substitution is a mutation by definition. But since both UCU and UCC code for the amino acid serine, what difference to the organism could the mutation make? Again, we noted differences among organisms in the amino acid sequences of their proteins (e.g., cytochrome *c*, pp. 91–93). Experiments indicate that some of the amino acids are so similar in their chemical properties that the substitution of one amino acid for another makes no difference in the functioning of the protein. Hence it would seem that these differences are better accounted for by genetic drift than by natural selection. The drift may have operated long ago in evolutionary history when ancestral populations were small. (See also our discussion of allometry, pp. 452–462, and Van Valen, 1960). We await with anticipation further investigations on the controversial question of nonadaptive traits.

GENETIC DRIFT AND NATURAL SELECTION. We have noted that chance may lead to increased frequency of occurrence of a gene, without regard to usefulness. In this connection it is only fair to state that differences of opinion exist as to the importance of genetic drift in producing the variations in gene frequency actually found in small populations and especially as to the importance of drift in giving rise to the first steps in evolutionary change. Some investigators conclude that the differences between even small populations arise through the action of natural selection rather than through the action of chance in genetic drift.

This point of view was set forth by Ford (1949 and 1964), who described the spread of a gene through an isolated population of moths. Prior to 1929 the frequency of the gene was 1.2 percent; by 1939 it had risen to 9.2 percent, and in 1940 it was 11.1 percent. After that it fluctuated between 6.8 percent and 1.1 percent. The isolated population fluctuated in numbers between 1000 and not over 18,000, but these fluctuations did not seem to affect the relative frequency of the mutant gene under study. Ford concluded (1949), "It has been possible to show that the chances are less than one in a hundred that the observed variations in the gene-ratio could be produced by random survival, indicating that they must be due to the influence of selection, varying in direction and intensity from year to year. This is the first time that these alternatives have been studied experimentally, and the result gives no support to the view that random survival plays a significant part in evolution in populations of 1000 individuals or more." Furthermore, he feels that populations of smaller size than this are not permanent, are particularly liable to extinction, and hence are not likely to contribute significantly to evolution.

Doubtless the conditions of effective population size vary from animal to animal; an effectively small population of butterflies may not have the same size range, in absolute numbers, as an effectively small population of mice, for example. Extremely small populations are sometimes recorded. Thus Miller (1950) recorded a unique dwarf species of fish confined entirely to a single hot spring hole in Death Valley: "Since every fish is in view at one time, reliable estimates of the total population are possible. The number of individuals of this species fluctuates between about 50 and 400. At times the minimum effective breeding population may thus fall below 50 individuals. No doubt the Sewall Wright effect has been a very significant factor in the evolution of this remarkable species, which is one of the most distinctive in the genus." (We suffer from a plethora of terms: "random variation of gene frequency," "genetic drift," "random survival," and "Sewall

Wright effect" all refer to the same phenomenon.) This example is an extreme one in that evolution has proceeded so far that the inhabitants of this spring are regarded as constituting a distinct species. It is not certain that the effective breeding population is abnormally small, however. We should note in this connection that the number of individuals of importance to genetic drift is not the total number in the population but only the portion of the latter that actually contribute genes to the next generation. Immature, sterile, aged, and infirm individuals are not part of the "effective breeding population." Furthermore, in many species the effective breeding population is restricted in size during certain seasons of the year, particularly in the Temperate Zone during the winter. It is this minimum size of effective breeding population that is important in determining the occurrence of random variations in gene frequency.

Students are frequently dismayed by what seem to them flat contradictions, such as those contained in this discussion of genetic drift. We should realize, however, that such differences of opinion are inevitable in a *growing* science. It behooves us not to be dogmatic in the present state of knowledge. We know too little about the genetic constitutions of animals and the varied effects of single genes, about the size of effective breeding populations actually found in nature, about the effectiveness and action of barriers, and particularly about the relationships of animals to their environments, i.e., the ecology of animals. Evolution does not occur in a vacuum. The animal is an integral part of a community of plants and animals played upon by a variety of inanimate environmental factors: temperature, humidity, climate, seasonal changes, nature of the soil, and so on. Until all these animate and inanimate factors in the environment of an animal are understood we cannot have a complete picture of the demands of life faced by that animal and hence of the opportunities for operation of natural selection. Also, recent experiments in natural selection (pp. 420–430) give evidence of the subtlety and rapidity with which natural selection upon occasion can operate. We remember, too, that genes producing structural changes also may affect viability, that the latter effect may be of importance even if the structural change is not (pp. 377–378), and that the genetics of most wild animals is almost totally unknown. All these and other unanswered questions should make us wary of dogmatic statements that natural selection is not, or cannot be, the basis of some particular observed change.

Perhaps we shall be nearest the truth if we think of genetic drift and natural selection as partners in producing the varied gene combinations observed to arise in isolated subpopulations. Whether or not chance may be operative in determining gene frequencies in the early stages of evolutionary change, upon its usefulness depends the final fate of the gene as a contributor to evolution. As Wright (1948) has stated it: "Nonadaptive differentiation is obviously significant only as it ultimately creates adaptive differences."

References and Suggested Readings

Dobzhansky, Th., *Genetics and the Origin of Species,* 2nd and 3rd eds., New York, Columbia University Press, 1941 and 1951.

Dobzhansky, Th., "Mendelian populations and their evolution," *American Naturalist, 84,* 401–418 (1950).

Fisher, R. A., *The Genetical Theory of Natural Selection,* 2nd ed., New York, Dover Publications, 1958.

Ford, E. B., "Early stages in allopatric speciation," in G. L. Jepsen, E. Mayr, and G. G. Simpson (eds.), *Genetics, Paleontology, and Evolution,* Princeton, Princeton University Press, 1949, pp. 309–314.

Ford, E. B., *Ecological Genetics,* New York, John Wiley, 1964.

King, J. L., and T. H. Jukes, "Non-Darwinian Evolution," *Science, 164,* 788–798 (1969).

Mayr, E., *Animal Species and Evolution,* Cambridge, Massachusetts, Harvard University Press, 1963.

Miller, R. R., "Speciation in fishes of the genera *Cyprinodon* and *Empetrichthys,* inhabiting the Death Valley region," *Evolution, 4,* 155–163 (1950).

Moody, P. A., "A simple model of 'drift' in small populations," *Evolution, 1,* 217–218 (1947).

Sheppard, P. M., *Natural Selection and Heredity,* New York, Harper & Row, Torchbook 528, 1960.

Spencer, W. P., "Genetic drift in a population of *Drosophila immigrans,*" *Evolution, 1,* 103–110 (1947).

Van Valen, L., "Nonadaptive aspects of evolution," *The American Naturalist, 94,* 305–308 (1960).

Wright, S., "Evolution in Mendelian populations," *Genetics, 16,* 97–159 (1931).

Wright, S., "On the roles of directed and random changes in gene frequency in the genetics of populations," *Evolution, 2,* 279–294 (1948).

Wright, S., *Evolution and the Genetics of Populations,* vol. 1, *Genetic and Biometric Foundations,* Chicago, University of Chicago Press, 1968.

19

Natural Selection

IN THE PRECEDING chapter we emphasized the point that populations have a tendency to remain in genetic equilibrium but that various forces tend to upset this equilibrium. Of these forces we discussed mutation pressure and genetic drift. Now we turn our attention to the most potent force of all: natural selection. We commence with a discussion of this principle in essentially Darwinian terms.

In Chapter 2 we noted that the concept of natural selection was Darwin's great contribution to thinking on evolution. In *The Origin of Species by Means of Natural Selection* Darwin compared the selective action of nature to selection employed by man in improving strains of plants and animals (artificial selection). When a breeder of cultivated plants or of domestic animals wishes to improve them he selects the individuals showing the desired qualities to be parents of the next generation and prevents individuals lacking the desired characteristics from contributing to the next generation. Thus Luther Burbank, when developing improved varieties of plants such as stoneless plums and spineless cactus, raised seedlings in large numbers. From these he selected only a few that to his practiced eye offered promise of possessing the qualities he desired. The rest of the seedlings were immediately burned; as many as 50,000 condemned plants might be destroyed after a single selection.

It was Darwin's thought that nature selects animals and plants in much the same manner, preserving individuals that have characteristics best fitting them for life in the particular environment in which they find themselves and eliminating individuals less adequately equipped. If such natural selection does indeed occur, what is the driving force behind it and by what means is it accomplished?

TENDENCY TO RAPID INCREASE IN NUMBERS The driving force, according to Darwin, is provided by the tendency of all living things to increase their numbers rapidly. A few examples will typify situations in most animals. Fishes are noted for laying large numbers of eggs. A 25-lb carp in an Iowa lake was found to contain 1,700,000 eggs; the similar prodigality of the salmon in egg production is common knowledge. One female toad may lay as many as 12,000 eggs. It has been calculated that one pair of houseflies breeding in April would have by August, if all eggs hatched and all resulting individuals lived to reproduce in their turn, 191,010,000,000,000,000,000 descendants. Turning to animals that breed more slowly and have longer intervals between generations, we may quote Darwin's statement concerning elephants: "The elephant is reckoned the slowest breeder of all known animals, and I have taken some pains to estimate its probable minimum rate of natural increase; it will be safest to assume that it begins breeding when thirty years old, and goes on breeding till ninety years old, bringing forth six young in the interval, and surviving till one hundred years old; if this be so, after a period of from 740–750 years there would be nearly nineteen million elephants alive descended from the first pair." Other examples might be quoted almost endlessly.

LIMITING FACTORS Why, in actual fact, do we not find our lakes choked solidly with fish, our fields carpeted with toads, the earth overrun with elephants, and so on? Because there are for each species certain checks or limiting factors opposing such an increase in numbers.

One of the most important of these checks is LIMITED FOOD SUPPLY.

Darwin himself was greatly influenced in his thinking by the essay of Malthus on population. It was the thesis of Malthus that population tends to increase in geometric ratio (e.g., by successive multiplication) while the food supply increases more slowly. Hence a population tends to outstrip the food supply available to it. Without doubt, limited food supply is at times an important factor in preventing an unlimited increase in numbers of individuals in a given species.

PREDATORY ANIMALS constitute another check on population size. If the lions were exterminated on the plains of Africa the zebra population would doubtless increase rapidly for a time, until a new limit imposed by available food, and perhaps disease, was reached.

DISEASE is another limiting factor; epidemics occur among animals, particularly if they become overcrowded.

SPACE RESTRICTIONS form another check on unlimited increase. Not only does overcrowding favor disease and starvation, but a certain amount of "elbow room" is required if animals are to live and reproduce normally. In many species the home or nest is surrounded by a certain area of home territory over which the male occupant dominates and in which all other males of the same species are treated as intruders. The density of population that a given region can support is determined in part not by the amount of "standing room" available but by the number of these home territories that can be provided without undue disturbance of the normal living and reproductive habits of the species in question.

Under the term INANIMATE ENVIRONMENT we may include such limiting factors as climate, seasonal changes, and catastrophes of various kinds. Drought and severe heat in summer and severe cold in winter are examples. It has been estimated that during a severe winter half the wild horses inhabiting the southeastern region of the state of Washington perish. This example may suggest the questions: Is it purely a matter of chance which ones perish and which ones survive? What determines which of these horses shall live and which shall die? And we are led to the next element in the process of natural selection.

"THE STRUGGLE FOR EXISTENCE" We have seen that in each generation each species attempts to produce many more individuals than can hope to live to maturity under the limiting conditions prevailing. The result is a competition among the offspring for food, mates, home territories, and the like and a striving to survive the aggressions of predatory animals, disease, and the severities of inanimate nature. This process was called by Darwin "the struggle for existence." In this "struggle" what determines which individuals shall succeed and which shall fail?

We may answer this question by stating that those individuals will succeed that have favorable or advantageous inheritable variations of structure, physiology, and so on. Those individuals will fail that lack such variations or that have unfavorable or harmful ones. In this statement we have mentioned that the variations must be inheritable; while it is true that noninheritable, favorable variations might enable an individual to survive, such variations have no "future" so far as improvement of the species is concerned. (See, however, the "Baldwin effect," pp. 436–437.) The inheritable variations arise as new mutations and as new combinations of genes originating in various ways (Chap. 17). Darwin himself placed great stress on the importance of variations, including individual differences, and he recognized that to be useful in evolution they must be inheritable. He was well acquainted with the fact that variation is universal, that "no two individuals are alike." In his day it was not known to what extent these differences between individual and individual are inheritable or to what extent they are caused by environment and hence not inheritable.

The fact that many of the little variations in structure are not inheritable was brilliantly demonstrated by the Danish geneticist Johannsen. He chose to work with the characteristic of weight in beans. Taking advantage of the fact that beans are self-fertilizing, he established a number of PURE LINES, each descended from one bean. In general, pure lines descended from heavy beans had greater average weight than did pure lines descended from light beans. Since each pure line bred true to a certain average weight generation after generation, hereditary factors must have been involved in the differences in weight. Since in any one pure line (descended from one bean) the hereditary factors must have been identical in all individuals, why were not all individuals identical in weight? The reason is because superimposed upon the identical heredity were the effects of differences in environment (in sunlight, moisture, food supply, etc., available to individual plants and branches as they grew). When Johannsen took the heaviest beans in a certain pure line and raised progeny from them he found that the average weight was the same as that of the pure line itself or the same as he obtained when he took a light bean from the same pure line and raised progeny from it. In brief, selection *within* a pure line was not effective in producing change. Of the many implications of Johannsen's work the one of most significance for us is the demonstration that many observed variations in structure are produced by environment and that selection based on these environmentally induced variations does not result in changes in the resultant progeny. To be effective, selection, either by man or by nature, must utilize inheritable variations—that is, mutations—or recombinations (p. 371).

WHAT CONSTITUTES SUCCESS IN THE "STRUGGLE FOR EXISTENCE"? Darwin laid most stress upon survival; individuals having favorable inheritable variations survive, while their less highly endowed contemporaries perish. This phenomenon has been termed "the survival of the fittest." The "fittest" were thought of as those individuals that possess inheritable characteristics enabling them to succeed in the "struggle for existence" in the particular circumstances and environment in which they find themselves. Since they are the survivors, the "fittest" then become the parents of the next generation, members of which inherit the favorable characteristics from their parents.

A moment's reflection, however, will convince us that survival in itself is not the only, or even the chief, concern. The real point is not survival but *contribution to the next generation*. Obviously a dead animal cannot become a parent, but some living animals cannot, or do not, become parents either. So far as contribution to evolution is concerned, a living animal that does not reproduce might just as well be dead. Indeed, from the standpoint of his species it would probably be better if he were dead, since he consumes food without making any contribution to the species in return. This statement must be qualified for species in which individuals live together in societies. In such species individuals that do not reproduce may nevertheless contribute to the success of the species by rendering essential services to the society of which they are a part. Notable examples are such social insects as ants and bees and man himself (see the discussion of the role of cooperation, pp. 503–505). It is the social unit as a whole whose success is measured in terms of contribution to the next generation. Thus, be it on the individual or on the social level, success in the "struggle for existence" means success in contributing to the next generation. Included among the determinants of this success are all factors favoring effective reproduction. The reproductive process is a complicated one, subject to many influences. Fertility is affected by the health and well-being of the individual, and these in turn depend upon a variety of physiological, and even psychological, factors. In the "struggle for existence" premium is placed, then, both on characteristics that make for survival and on characteristics that make for high fertility.

A somewhat extreme example may help to emphasize the point: Imagine two competing groups of animals, each group consisting at the outset of 1000 young individuals. Of group A, 800 individuals survive to maturity; of group B, only 500 individuals survive. But in group A the reproductive rate is such that each individual is replaced by one descendant, whereas in group B each individual is replaced by two descendants. Which is the more successful group? Obviously group B is, since in the next generation it will number 1000 individuals while group A will number only 800. The most successful individuals or groups are those that contribute their genes in greatest number to the building of the next generation.

"Individuals having most offspring are the fittest ones" (Lerner, 1959). It is well to remember that this is what "fittest" means in natural selection theory. Much mistaken thinking to the contrary notwithstanding, "fittest" does not mean "strongest" or "fastest" or "healthiest" or "most intelligent." Of course individuals or societies lacking in all such traits may not be likely to leave the most offspring. But the measure of their fitness is not possession of the attributes listed; it is the leaving of offspring.

NATURE OF "THE STRUGGLE FOR EXISTENCE" The phrase "struggle for existence" is unfortunate. It carries too many overtones of "Nature red in tooth and claw." True, predatory animals do play a part in reducing the number of surviving members of a population and hence in determining which members shall contribute most to the next generation. But competition for available food supply is also a factor, operating principally in times of exceptional stringency, for example, during droughts, floods, exceptionally severe or prolonged winters, or as a result of extreme overpopulation of a given territory.

So far we have stressed competition between individuals in the same species (for food, territory, etc.): INTRASPECIFIC COMPETITION. We should also note that INTERSPECIFIC COMPETITION occurs and may at times be important in evolution. Two closely related species (recently arisen from a common ancestral species, perhaps) may compete for the same food supply. If this competition is keen it may lead to changes in the two species so that competition will be lessened. Thus two species of ground finch living on the same Galápagos island may come to differ from each other in beak size by virtue of the fact that it is advantageous for one to specialize on large seeds and the other on small seeds. Alternatively, one species may be so much more efficient than the other in utilizing the food supply that the less efficient species becomes extinct (at least in the territory originally shared in common; see Hardin, 1960).

Many important characteristics are less obviously related to struggle and competition than are the examples we have given. Resistance to disease is highly important. Any structural or physiological improvement contributing to vitality and fecundity will tend to confer a differential advantage on some individuals as compared to others. Ability to produce large numbers of viable offspring confers an advantage, particularly in species in which the parents do not care for the young after hatching or birth. Alternatively, increased perfection of postnatal care confers advantages in species that produce few offspring per parent. In the former instance more than the laying of large numbers of eggs is involved. The eggs must be viable, and they must be efficiently fertilized. Young that develop quickly have an advantage over those that develop slowly. When two competing strains differ in speed of individual development, that strain which produces mature offspring in less time will, other things being equal, contribute more of its genes to future generations than will a strain in which sexual maturity is attained more slowly. Offspring of the first strain already may have mated in their turn before offspring of the second strain have matured sufficiently to do so.

These examples are given to emphasize the fact that complex and subtle factors are involved in determining which individuals shall contribute most to the next generation. The familiar matters of escape from predators and competition for food are but two among many important factors.

ESSENCE OF NATURAL SELECTION A brief statement of natural selection may help to bring our discussion into focus. Reduced to its essentials, *natural selection results from the cumulative action of all forces tending to ensure that individuals possessing one genetic constitution shall leave larger numbers of offspring than will individuals possessing some other genetic constitution.* Thus if a mutation contributes in any way to the leaving of larger numbers of offspring it will be perpetuated in increased proportion in the next generation since it will be carried by those "larger numbers of offspring." Contrariwise, if the mutation interferes in any way with the leaving of larger numbers of offspring it will be perpetuated in decreased proportion in the next generation since it will be carried by but a decreased number of individuals in that generation.

We readily appreciate that if natural selection continues for several generations, individuals lacking the favorable mutation may be completely eliminated, with the result that the mutation becomes "standard equipment" for the entire population.

It will be evident, moreover, that these principles apply not only to individual mutations but also to combinations of mutations (Chap. 17).

ORIGIN OF RACES AND SPECIES We recall that the title of Darwin's book emphasizes the origin of *species.* So far we have not accounted for a great amount of evolutionary change; we merely have shown how a population might come to possess a new mutation or combination of mutations. But we have noted previously that one mutation is usually a small change. Few, if any, races, or subspecies differ from each other by a single mutation. How can we account for the origin of larger differences such as those distinguishing separate races and, especially, separate species, genera, and so on? *Addition* of one mutation to another probably accounts for many of these larger differences. Our hypothetical population acquires a certain favorable characteristic, as described above. In later generations a second mutation arises that is an improvement on, or addition to, the first one. Natural selection now works on this second mutation until some generations later the whole population comes to possess it. Thus step by step through the long expanses of geologic time greater and greater evolutionary change is produced by natural selection. The change as we have described it will be in the nature of more perfect *adaptation* to the environment in which the animals are living, i.e., *postadaptation* (pp. 14–15).

Continuing with our hypothetical population, let us suppose that the environment changes. This might result from geologic change in the region inhabited, from climatic change, from biotic change (change in the ecological community of plants and animals), or from the fact that a portion of the population migrates into a different region from that formerly inhabited. Now a premium may be placed on different characteristics from those formerly favored. As a result different mutations will prove advantageous in the "struggle for existence," and in consequence the population, or a portion of it, will gradually come to differ from the ancestral population. Eventually a descendant population may come to differ so much from the ancestral one that a biologist concludes that the two should be regarded as separate species.

An ancestral population may give rise to two or more descendant populations. If these "sister" populations become adapted to different environments they may in the course of time become sufficiently different from each other as to be considered separate races and, if change continues, eventually separate species.

In Chapter 17 we saw how the evolution of the long legs of the horse might be explained according to Lamarck's theory of inheritance of acquired characters. It may help to fix in mind the essentials of natural selection to ask how the same evolutionary change can be explained by the theory of natural selection.

As before, we may postulate that the first ancestral horses to venture forth from the woods onto the plains were chased by predatory animals. The action of the predators would constitute one of the checks upon the too rapid increase in numbers of these ancestral horses. In the resulting competition to survive and leave progeny, which individuals would succeed? If among the population of ancestral horses a mutation arose producing longer legs, possessors of that mutation might be able to run faster than could their fellows. If so, a disproportionately large number of horses *not* possessing the mutation would become food for the predators before they had the opportunity to mate and reproduce. Thus the horses having the mutation for longer legs would produce more than "their share" of offspring, with the result that more of the next generation would inherit longer legs than the parental generation. If selection continued in the same way for several generations the shorter-legged horses might disappear entirely, leaving the field to the possessors of the longer legs. If, now, a second mutation occurred, increasing the length of the legs still more, possessors of that second mutation would be favored in the "struggle for existence," with the result that some generations later all horses would have the second mutation, possessors of the first mutation having been eliminated. And so step by step the progressive lengthening of leg observed in the evolution of the horse might be explained through the operation of natural selection on successive mutations. (For an alternative explanation for this example see pp. 459–460.)

In the preceding example we kept the account as simple as possible in an attempt to paint the broad outlines of the picture without including confusing details. Actually the situation at any time would have been much more complex, both genetically and because many factors in addition to the length of leg enter into determination of which individuals contribute most to subsequent generations.

References and Suggested Readings

Darwin, C., *On the Origin of Species By Means of Natural Selection,* London, John Murray, 1859. (See p. 6 for listing of reprint editions.)

Hardin, G., "The competitive exclusion principle," *Science, 131,* 1292–1297 (1960).

Lerner, I. M., "The concept of natural selection: A centennial view," *Proceedings, American Philosophical Society, 103,* 173–182 (1959).

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Genetic Factors in Natural Selection

IN CHAPTER 19 we discussed the principles of natural selection in essentially Darwinian terms. Darwin himself emphasized variations, recognizing that they must be inheritable to be of significance for evolution. But the modern concept of mutations was unknown to him, as were indeed the principles of Mendelian heredity and the entire modern theory of the gene. What has modern genetics contributed to the theory of natural selection? To answer this question adequately would require a book in itself; in fact many books have been written on the subject. All we can do in our brief discussion is to summarize some basic principles and to indicate where interested readers may find more complete discussions.

MUTATIONS AS RAW MATERIALS FOR NATURAL SELECTION

Let us look more critically at mutations and ask whether they really possess the qualifications for the important role assigned them in the modern theory of natural selection.

Critics of the idea have emphasized the point that most of the mutations we study in our laboratories are harmful, not beneficial. The multitudinous mutations to which students of genetics in *Drosophila* devote themselves are almost all of the nature of abnormalities and malformations. Even when no marked structural abnormality is involved, mutations frequently reduce the viability, or fertility, of their possessors. Since, as we have noted (p. 410), the leaving of disproportionately large numbers of offspring is the principal hallmark of success, reduced viability and fertility are at least as detrimental as are malformations of structure.

Nevertheless the fact that not all mutations are harmful is emphasized by the increasing use man makes of mutations to *improve* cultivated plants. In this case mutations are induced by subjecting plants to irradiation, such as that from x-rays, radioactive cobalt, and even ultraviolet light. Some of the mutations obtained have resulted in barley having increased stiffness of the straw (Gustafsson, 1947); penicillin-producing mold giving greatly increased yields of antibiotic (Raper, 1947); wheat having increased resistance to rust; peanuts having thicker shells and higher yields than usual; and many other things. (For a popular account see Manchester, 1958.) In a state of nature such mutations might be expected to occur, though infrequently. When they did occur, however, if they afforded some advantage to their possessors we might expect natural selection to favor them much as man does when he selects them for propagation.

In Chapter 17 we mentioned the strains of houseflies that have become resistant to the insecticide DDT and the strains of the colon bacillus *(Escherichia coli)* that have become resistant to streptomycin (Demerec, 1950). When this antibiotic is added to a culture of *E. coli* most of the bacteria are killed. But on the average one cell in many million has a mutation that enables it to survive and hence to give rise to a streptomycin resistant strain. Indeed, some of these mutations produce strains that cannot live in the absence of streptomycin; they have become streptomycin dependent. It has been demonstrated that the mutations occur spontaneously and not because of the streptomycin treatment. The streptomycin simply acts as an agent of natural selection favoring the rare cells that possess what, under these circumstances, has become a favorable mutation. Note that under most circumstances in a state of nature a mutation causing a bacterium to be dependent upon streptomycin would be a most unfavorable mutation. This points up the fact that circumstances determine in many cases whether a mutation is harmful or beneficial to its possessor (see the following).

As Dobzhansky and others have pointed out, one reason that great numbers of the mutations we observe today are deleterious is the outcome of the historical process of evolution. We mentioned previously that a given mutation occurs "spontaneously" at a rather constant, though low, rate. There is no reason to doubt that this has been going on throughout geologic time. Each mutation has "popped up" time after time as the eons have passed. Consequently, the favorable mutations, for the most part, have been long since incorporated into the structure of the species. The "normal" characteristics we observe today are the accumulated favorable mutations of past ages; natural selection has incorporated them into the warp and woof of the species. But the deleterious mutations also have put in an appearance time after time. Since they *are* deleterious, however, they have been rejected by natural selection every time they have appeared. But owing to the mutability of the genes they still continue to appear from time to time. Consequently they are the mutations that come to the attenion of modern observers—the deviations from normal, "normal" being comprised of the sum of favorable mutations accumulated in the past.

If the point of view just expressed is valid, we should seldom expect to observe favorable mutations in modern animals that are truly successful in their particular environmental niches. They are successful because they already incorporate most, if not all, the favorable mutations that have occurred. If we really wish to observe favorable mutations, our search should follow two lines: (1) We should examine animals placed in conditions to which they have not been adapted by the historical process of evolution. (2) We should study animals that are not well adapted for life in their environments, i.e., which are not at their "adaptive peaks."

Turning to the first line of approach, we may expect that mutations that are deleterious in some environmental conditions may not necessarily be so under all conditions. We have noted the mutations, of *E. coli* that are unfavorable in an environment lacking streptomycin but that are favorable in an environment containing streptomycin. We have mentioned that many of the mutations of *Drosophila* reduce the viability of the individuals exhibiting them. Timofeeff-Ressovsky (1940) investigated the viability of a number of mutations, using the hatching rate of eggs as a yardstick. He found that when the flies were raised at a temperature of 25°C most of the mutations lowered the viability, though two increased the viability slightly. Furthermore, the viability varied with changes in temperature. One mutation gave above normal viability in flies raised at 25° but slightly below normal viability at 15 and 30°. Another mutation gave slightly subnormal viability at 15° and much more markedly lower viabilities at the higher temperatures. A third mutation showed just the reverse relationships: poor viability at 15°, better at 25°, and almost normal at 30°. Such results demonstrate that environmental factors are influential in determining whether a given mutation shall be harmful or beneficial to its possessor.

As yet only a few instances are known of mutations that increase viability of *Drosophila* above that of normal, wild-type individuals. Perhaps one reason for the lack of data on this point is that the appropriate tests have not been made and the appropriate environmental factors have not been detected and then varied. Such data as we have, however, indicate that mutations that are deleterious under some conditions may be neutral or beneficial under others. If the climate should change, for example, so that *Drosophila* flies in a certain region must exist under more elevated temperatures than prevail today, some of the mutations and gene combinations which are now deleterious might then become beneficial and consequently be favored by natural selection. In the course of time the mutation conferring increased viability at high temperatures might be incorporated into the population as "standard equipment."

Furthermore, individuals possessing a genetic constitution conveying increased viability at high temperatures are *preadapted* for invasion of environments having higher temperatures than the general population could tolerate. Some such preadaptive mutations may well have been involved, for example, in the successful invasion of hot springs such as those in Yellowstone Park by animals and plants now found living in them. Mutations conferring increased viability at low temperatures would correspondingly preadapt their possessors for invasion of cold environmental niches in which the general population could not live.

In actuality, of course, all organisms must be adapted to live in a certain *range* of conditions, including temperatures. Conditions vary between night and day, between wet seasons and dry seasons, and between winter and summer (particularly in the Temperate Zone). To be successful an organism must be able to live in whatever range of conditions it encounters. That populations differ in their ability to tolerate extremes was shown by Timofeeff-Ressovsky (1940) in the case of the "temperature races" of *Drosophila funebris*. He found that flies from eastern Europe and neighboring parts of Asia (dotted area, Fig. 20.1) had greater ability to tolerate extremes of temperature, both high and

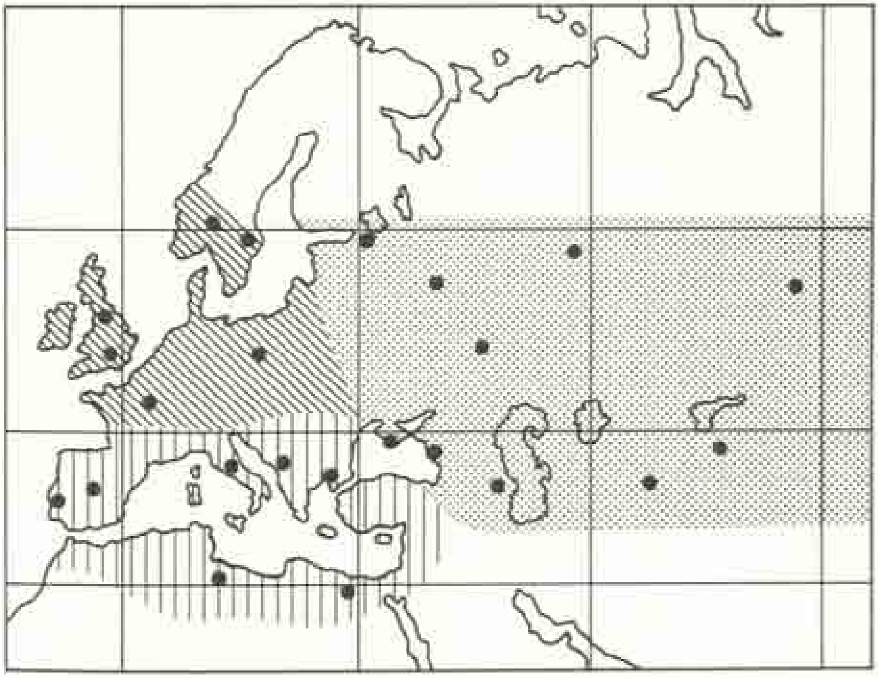

Fig. 20.1. Approximate distribution of three "temperature races" of *Drosophila funebris.* (After Timofeeff-Ressovsky; modified from Allee, Emerson, Park, Park, and Schmidt, *Principles of Animal Ecology,* Philadelphia, W. B. Saunders Company, 1949.)

low, than did flies from western Europe. Among the latter, flies from northwestern Europe (diagonal shading, Fig. 20.1) tolerated low temperatures better than they did high ones while flies from southwestern Europe (vertical shading) tolerated high temperatures better than they did low temperatures. These observations correlate well with the fact that the eastern "temperature race" lives in a more variable climate than do the western "races."

We mentioned previously (p. 378) that many, if not most, mutations have more than one effect on the organism. One of these effects is frequently a change in viability, and it is often of more importance to the organism than are effects more noticeable to observers. Thus the success of a mutation in becoming established in a population may depend upon the mutation's effect on viability, the visible bodily changes involved being more or less incidental accompaniments. We mention this matter because it helps to explain how characteristics of no evident significance to an animal nevertheless may become established in the species. To give a hypothetical example: If a certain mutation changed the color of an insect's eyes from red to black and increased viability at low temperatures, it might eventually be found that mountaintops in the region were inhabited by a black-eyed race of the insect. Such a race would have arisen not because there was any advantage in being black eyed but because there *was* advantage for a mountain dweller in having increased viability at low temperatures

The second line of investigation likely to yield evidence of favorable mutations involves study of animals not already at their "adaptive peaks." We seldom shall find such relatively poorly adapted animals living in a state of nature. Natural selection will have seen to that. But we can produce such animals experimentally and then observe what natural selection does to them. Dobzhansky and Spassky (1947) produced populations of this kind in the form of stocks of *Drosophila* homozygous for one or another of certain chromosomes known to contain recessive genes or gene complexes that reduced viability and produced other deleterious effects. Homozygotes for one such chromosome (designated PA748) had very low viability, were slow in developing to the adult stage, and had small, crumpled wings; elongated, cylindrical abdomens; and sometimes short, crooked legs. Obviously these flies were far below their "adaptive peak." Stocks of flies homozygous for this chromosome were established in culture bottles and raised generation after generation. The culture bottles became overcrowded and were deliberately kept that way to provide a restrictive factor making for natural selection. In the later generations of the experiment natural selection was further abetted by keeping the cultures at a temperature high enough to be deleterious. From time to time, as the generations passed, flies were removed and the PA748 chromosomes they carried were tested to determine whether there had been any improvement in the genes present. It was found that by the tenth generation viability had clearly improved and that by the fiftieth generation it was almost normal. Improvement in the speed of development from egg to adult occurred more slowly, but at some time between the thirty-eighth and fiftieth generations it had become normal. (We recall that rate of development may constitute an important factor in the relative success of a species, see p. 412). By the fiftieth generation, also, the wings and legs had become normal, though the elongated, cylindrical abdomen had remained unchanged. Evidently appropriate mutations for rectifying the abnormalities of the abdomen had not occurred.

All told, Dobzhansky and Spassky performed this experiment with strains of flies homozygous for seven different chromosomes having deleterious effects. Of each strain two stocks were established: one received x-ray treatment; the other was left untreated. It was thought that the radiation might increase the rate at which mutations occurred and hence the rate of evolutionary change. The x-ray treatments seemed to have no particular advantageous effect, however. Ten of the fourteen experimental stocks showed improvements in the genetic contents of the respective chromosomes concerned. Three stocks remained unchanged as the generations passed, and one actually deteriorated. This is exactly the sort of result that would be expected if improvement depended upon the chance occurrence of suitable mutations for natural selection to act upon.

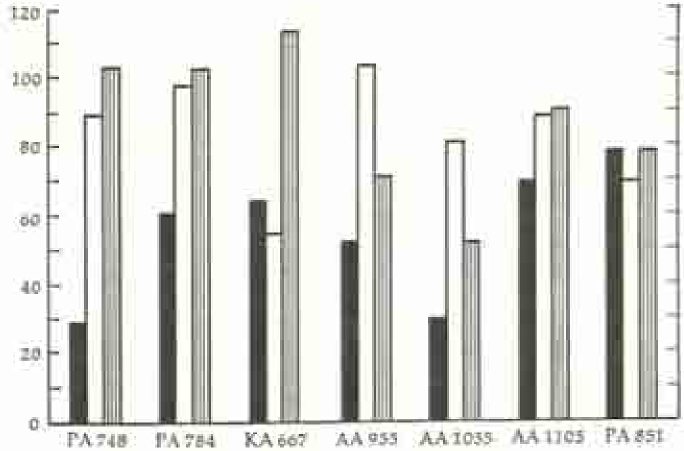

Fig. 20.2 Viability of seven strains of fruit flies before and after 50 generations of homozygosis for chromosomes bearing deleterious genes. Black columns: initial viability before start of the experiments. White columns: viability of homozygous untreated stocks of the respective strains after 50 generations. Shaded columns: viability of homozygous X-ray-treated stocks of the respective strains after 50 generations. Vertical axis: percentages of viability, relative to normal viability. (Redrawn from Dobzhansky, Th., and B. Spassky, "Evolutionary changes in laboratory cultures of *Drosophila pseudoobscura*," *Evolution, 1* (1947), 191–216.)

The results in terms of viability alone are summarized in Fig. 20.2. It may be noted that 11 of the stocks improved in viability—some very markedly and some only slightly. Two stocks declined slightly in viability; one remained unchanged.

Parallel with the stocks just mentioned the authors kept "balanced strains" in which the chromosomes under study were "protected" from the action of natural selection by the presence of normal genes in the other chromosome of the pair. Of the chromosomes possessed by these stocks six remained unchanged or improved slightly, while eight deteriorated markedly. Six of the latter chromosomes eventually came to possess lethal genes or gene combinations.

Evidently in the balanced strains, as in the homozygous ones, both advantageous and harmful mutations occurred. In the homozygous strains the deleterious mutations were "weeded out" by the action of natural selection, which at the same time favored individuals possessed of favorable mutations. In the balanced strains, however, since natural selection did not operate, deleterious mutations, including lethal ones, could become established.

We have placed emphasis upon this investigation because it affords a particularly instructive example of natural selection operating under experimental conditions. We might wish that the individual genes whose mutation resulted in the improvements recorded could have been identified, but that would have entailed a colossal task. As it is, few readers have any conception of the magnitude of the investigation we have summarized so briefly. The authors state that 410,784 flies were classified and recorded! And those must have constituted but a small fraction of the total number of flies raised. While we may not be able to "put a finger on" the individual mutations whose occurrence led to the improvements cited, such favorable mutations evidently occurred, and natural selection utilized them for the improvement of the strains.

THE ROLE OF HETEROZYGOTES

In some cases the significance of a gene for evolution may depend more upon its effect in heterozygotes than on its effect in homozygotes. Many experiments give evidence of this. We select two such experiments as illustrative.

Pioneer experimentation in this field was done by L'Héritier and Teissier (1937), who designed a type of cage for rearing *Drosophila* that made possible the maintenance of a large population over an extended period of time. Experiments began with populations of around 4000 individuals, all of which possessed a certain mutation. A few normal, "wild-type" flies then were introduced into the cage. Thus competition was established between normal individuals and individuals possessing a mutation. Nature was allowed to take its course as time passed and generation followed generation.

In some experiments the flies originally present possessed a malformation of the shape of the eye, called "bar eye." The population was "infected" by the addition of a few normal flies. At first the population was practically 100 percent bar eyed. But in the ensuing competition the proportion of bar-eyed flies declined (Fig. 20.3). At first the decline was rapid, but as the number of bar-eyed flies decreased the rate of decline lessened. By the end of 235 days, in one experiment, bar-eyed individuals constituted only about 28 percent of the population, the

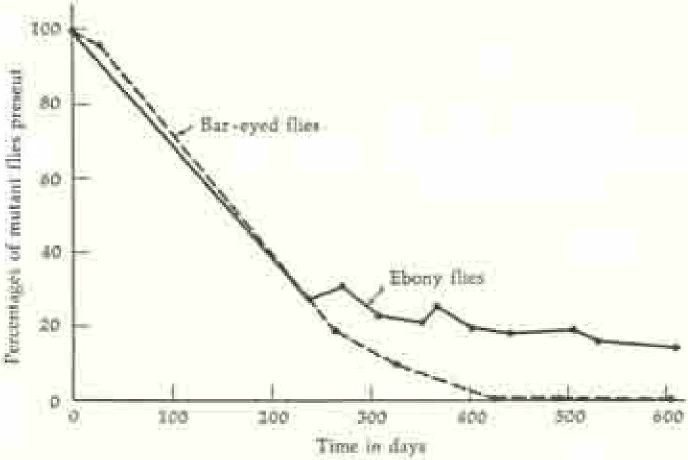

Fig. 20.3. Natural selection operating in (1) competition between normal fruit flies and bar-eyed ones (dashed line) and (2) competition between normal fruit flies and ebony flies (solid line). (Based on data of L'Héritier and Teissier, 1937.)

remaining 72 percent being normal eyed. By the end of 426 days the bar-eyed flies constituted only about 1 percent of the population. They continued at or below this very low frequency as long as the experiment lasted. Here is another example of natural selection operating under experimental conditions. In this case the bar-eyed flies clearly were less well adapted than were normal flies and hence lost out almost completely in competition with the latter.

Another mutation in *Drosophila* is "ebony," the most evident effect of which is darkening of the body color from the normal gray. L'Héritier and Teissier performed the same experiment starting with ebony flies. As shown in Fig. 20.3, the proportion of ebony flies declined rapidly at first: by the 235th day it had reached about 28 percent, the remaining 72 percent consisting of normal flies. But the further course of the experiment differed from that in which the bar-eyed flies were in competition with normal ones. Instead of almost disappearing, ebony flies continued to constitute around 15% of the population as long as the experiment continued. Why did the ebony flies not disappear almost completely, as the bar-eyed ones had? Evidently the normal flies were more efficient or better adapted than were the ebony ones. Yet after the initial decline ebony individuals continued to form a substantial "minority group."

Since "ebony" is a recessive mutation, all flies actually exhibiting this darkened body color are homozygous for the recessive gene, that is, are *ee* in genetic constitution. Evidently such flies were at a disadvantage in competition with normal flies. Many of the homozygous recessive individuals *(ee)* that appeared in any generation, however, were the offspring not of homozygous recessive parents but of heterozygous parents *(Ee)*. It will be recalled that when two such parents mate (*Ee* × *Ee*) one-fourth of their offspring are expected to be homozygous recessive *(ee)*. It seems likely, then, that ebony flies continued to appear generation after generation because they continually arose from heterozygous parents. The latter did not exhibit the ebony trait in their own bodies. Evidently these heterozygous parents *(Ee)* were at no disadvantage in the competition, as compared to homozygous normal parents *(EE)*. Indeed, there is evidence that heterozygotes had one advantage over homozygous normal individuals. In an independent investigation Timofeeff-Ressovsky found that, while homozygous ebony flies had lower viability than did homozygous normal flies, individuals heterozygous for the ebony gene actually had higher viability than did homozygous normal flies. This phenomenon is probably a form of "HYBRID VIGOR" (HETEROSIS), by virtue of which hybrids are frequently larger, stronger, and more vigorous than are purebred strains. The hybrid corn so prevalent on modern farms is a familiar example of hybrid vigor; so is the mule, which possesses some superiorities over either of its parents, the horse and the donkey.

In summary, we see in the experiment involving competition between ebony and normally colored flies that a balance was struck because of opposing tendencies. Natural selection tended to eliminate the ebony flies. Yet these were not eliminatd entirely, since natural selection tended to favor heterozygotes. The equilibrium was reached when about 85 percent of the flies had normal color and 15 percent had ebony color. In each generation this 15 percent of ebony flies arose largely as a "by-product" of the matings of the favored heterozygotes.

In our second illustrative experiment individual genes were not identified; instead, chromosomes of varying types were the subject of investigation. In the larvae of some kinds of flies, including *Drosophila*, the chromosomes in the cells of the salivary glands are relatively huge and are characterized by cross banding so varied in configuration and arrangement of bands that each portion of each chromosome is identifiable under the microscope (Fig. 20.4). Furthermore, investigations have revealed that certain bands are associated with the presence of certain genes. This is not to say that the bands *are* the genes but merely that the sequence in which the bands occur along the chromosome may be taken as a visual indication of the sequence in which the genes occur in that chromosome. In the cells of *Drosophila pseudoobscura* there are four pairs of chromosomes; these are numbered for convenience, one of the larger pairs being referred to as the third

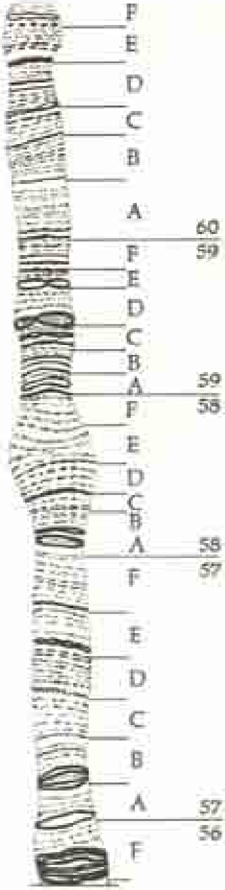

Fig. 20.4. Portion of one of the giant, salivary gland chromosomes of *Drosophila* magnified to show the banding pattern. (After Bridges in the *Journal of Heredity;* redrawn from Wallace, B., *Giant Molecules, and Evolution*, New York, W. W. Norton & Company, 1966.)

chromosomes. In this investigation Dobzhansky (1947 and 1950) concentrated attention on the third chromosome. He found that in some individuals the bands, and hence presumably the genes, of this chromosome were arranged in one sequence and in other individuals in other sequences. INVERSIONS of longer or shorter sections of the chromosome were frequent. For example, if we represent bands, or genes, by letters, we might have a chromosome with the structure ABCDEFGHIJ. This might be called the "standard" arrangement and be found in some individuals of a race or species. Some other individuals might have the same genes in this chromosome but have the section CDEF turned around—inverted. Then the whole chromosome would have the sequence A-B-F-E-D-C-G-H-I-J. If both members of this pair of chromosomes in an individual had the inverted arrangement, the individual would be called an "inversion homozygote." If the individual possessed one uninverted or "standard" chromosome and one inverted chromosome, that individual would be termed an "inversion heterozygote."

In the third chromosome of *D. pseudoobscura* at least 21 different gene sequences have been identified. Not all of these are possessed by individuals in any one portion of the range covered by the species. Indeed, there are definite geographic trends in the distributions of the arrangements, some arrangements being common in one locality and rare in another.

In one locality, Piñon Flats on Mount San Jacinto in southern California, four such arrangements are found. They are identified by the symbols ST, CH, AR, and TL, the meanings of which need not concern us. The point of particular interest at present is that the relative frequencies of these arrangements fluctuate with the seasons. As shown in

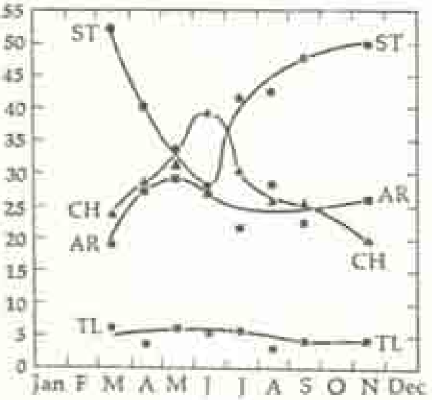

Fig. 20.5. Changes in frequencies of four different gene arrangements in third chromosomes of the population of *Drosophila pseudoobscura* at Piñon Flats, California. Vertical axis: frequencies, in percentage. Horizontal axis: successive months. Combined data for six years of observation. (Redrawn from Dobzhansky, Th., "Adaptive changes induced by natural selection in wild populations of *Drosophila*," *Evolution*, 1 (1947), 1–16.)

Fig. 20.5, in March of each year about 52 percent of the chromosomes found in these flies are ST chromosomes, about 23 percent are CH, about 18 percent AR, and about 7 percent TL. As the spring progresses these frequencies change for the first three mentioned, while the frequency of the TL chromosome fluctuates but little. The ST chromosome rapidly diminishes in frequency, while the CH and AR chromosomes correspondingly increase.

Figure 20.5 shows that the maximum relative frequency of CH is reached in June, when the ST chromosome is at its lowest frequency. In the next few months the frequency of the CH chromosome declines rapidly and that of the ST chromosome increases rapidly, until in November the ST chromosome has practically the same frequency it had in March.

How can we account for these seasonal fluctuations in chromosomal types? We should note that the flies all look alike as far as external visible characteristics are concerned. Only microscopic examination of the chromosomes in the salivary glands of the larvae reveals any differences. Yet differences there must be; we may reasonably suspect that the differences are concerned with viability or fertility or both.

It would seem, for example, that under conditions prevailing in the spring months carriers of CH chromosomes have some advantage over carriers of ST chromosomes, leaving more surviving progeny on the average and thus leading to the observed increase in frequency of CH chromosomes, with a concomitant decrease in frequency of ST chromosomes. Following the same line of thought, we may conclude that conditions during the summer favor carriers of ST chromosomes; hence their numbers increase. The same summer conditions evidently are unfavorable for carriers of CH chromosomes, with a resulting decline in numbers. Perhaps differences in temperature are concerned in the matter. Specifically we might interpret the graph (Fig. 20.5) as indicating that during the heat of summer carriers of ST chromosomes are at a relative advantage (and hence increase in numbers rapidly), while carriers of CH chromosomes are at a relative disadvantage (and hence decrease in numbers).

To test interpretations of the kind suggested, Dobzhansky set up experiments in natural selection, using population cages much like those of L'Héritier and Teissier. In one experiment several hundred flies having two different gene arrangements in the desired proportions were placed in a cage. Within a single generation the population increased to the maximum compatible with the amount of food available—usually to between 2000 and 4000 flies. The experimenter recorded that the numbers of eggs deposited were tens to hundreds of times greater than the number of adult flies that hatched. "The competition for survival is intense." Once a month samples of eggs were taken and the salivary gland chromosomes of larvae hatching from them were studied. In this way changes in the relative frequencies of the different gene arrangements were traced.

It was found that when population cages were kept in the cold (16½°C) no changes in frequencies of gene arrangements occurred. The original relative proportions continued generation after generation. At this temperature there is evidently little if any difference in advantageousness among the various gene arrangements.

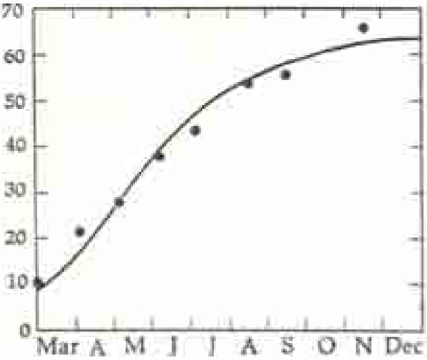

Fig. 20.6. Frequency of ST chromosomes (in percentage) in an experiment in which the ST gene arrangement was in competition with the CH gene arrangement at the temperature of 25° C. (Redrawn from Dobzhansky, Th., "Adaptive changes induced by natural selection in wild populations of *Drosophila*," *Evolution*, 1 (1947), 1–16.)

When the cages were kept at room temperature or higher (25°C), however, progressive changes occurred in many experiments until a definite equilibrium was established. Figure 20.6 shows the results of one such experiment. The population was established in March. In this population 10.7 percent of the third chromosomes were ST and 89.3 percent were CH. As the graph shows, the frequency of ST chromosomes nearly doubled in the first month and continued to rise rapidly in succeeding months (it is to be emphasized that the temperature throughout this time remained constant, at 25°C, i.e., the passing months did not bring temperature changes for the flies). An equilibrium was reached by about the end of December (the graph, Fig. 20.6, does not include the concluding months of the experiment). In experiments involving ST and CH chromosomes equilibrium was reached when about 70 percent of the chromosomes were ST and about 30 percent of them CH. The rapid increase in the relative number of ST chromosomes in a population maintained at a high temperature affords evidence that the conclusion concerning the relative advantage of the ST arrangement in the heat of summer (see the preceding) is valid.

Of equal interest with this conclusion is the fact that an equilibrium is eventually established. If the CH chromosome confers a disadvantage at high temperatures, why does it not disappear entirely? Following mathematical analyses by Sewall Wright the experimenter concluded that the CH chromosomes do not disappear entirely because flies heterozygous for them (i.e., having one CH third chromosome and one ST third chromosome—written ST/CH) are more successful than are either flies homozygous for CH (CH/CH) or flies homozygous for ST (ST/ST). Evidently ST/CH heterozygotes are characterized by that hybrid vigor previously referred to (p. 424) and hence have an advantage over *both* kinds of homozygotes (ST/ST and CH/CH). As Dobzhansky expressed it, "The populations at equilibrium contain the greatest possible proportions of the well adapted heterozygotes compatible with the lowest possible proportions of the relatively ill adapted homozygotes."

One aspect of natural selection evident in this experiment deserves especial emphasis: the *rapidity* with which changes are produced. Traditionally students of evolution have assumed that natural selection must operate very slowly—that time in the bountiful quantities provided by geologic history must be available for detectable results to be achieved. This was an assumption, but one generally accepted. Experiments of the type we have described show that this assumption was not warranted. Natural selection may operate to produce changes within a period of a few weeks or months. Such rapidity and delicacy of control by natural selection came as a distinct, though welcome, surprise. To be sure, these experiments and observations deal with one particular, rapidly breeding organism. But even so the number of generations required for production of significant change is small.

We have described Dobzhansky's experiment in some detail, partly because of its trail-blazing nature and partly because it is typical of results obtained subsequently by other investigators. Succeeding investigations have illuminated many facets of heterozygote superiority.

How frequently does it occur? Not all chromosomal heterozygotes are superior to the corresponding homozygotes. Thus in the experiment we have described, ST/TL heterozygotes are not superior to the homozygotes (ST/ST or TL/TL) but AR/TL heterozygotes are superior to AR/AR or TL/TL. Chromosomes having a given banding pattern (ST, for example) are found in different localities. Superior heterozygotes are more likely to be produced if the chromosomes come from the same locality. For example, we have seen that superior ST/CH heterozygotes are produced if both chromosomes come from flies living at Piñon Flats. But the ST/CH heterozygotes might not be superior if the ST chromosome came from one locality and the CH chromosome from another. Hence Dobzhansky has stated that chromosomes of flies living in one locality have become *coadapted* to each other, with the result that heterozygotes may be superior. This coadaptation presumably is concerned with the genetic contents of the chromosomes. Chromosomes that look alike—have similar banding patterns—but come from different localities may not have the same genes in them.

When chromosomal heterozygotes are superior, in what ways are they superior? We have seen that the ability to live in elevated temperatures is one way. The ability to live on different food supplies (differing species of yeasts and bacteria) is another. Hence "the types of food predominant in a given region may be important in determining the chromosomal composition of the *Drosophila* populations which inhabit this region" (da Cunha, 1955). E. B. Spiess and others have studied the physiological properties of homozygotes and heterozygotes for different gene arrangements, investigating the effect of the latter on such things as egg-laying capacity, longevity, wing beat frequency, and wing dimensions. We can do no more than hint at the multitude of investigations concerning these chromosomal types. Many of the original papers were reprinted in Spiess (1962) and summarized by da Cunha (1955).

In this connection we should note that the chromosomal structures investigated form an example of BALANCED POLYMORPHISM. Genetic polymorphism (literally meaning many forms) is defined by Ford (1964) as "the occurrence together in the same locality of two or more discontinuous forms of a species in such proportions that the rarest of them cannot be maintained merely by recurrent mutation." Black hamsters and gray hamsters and melanic moths and normally colored moths (pp. 346–351) have afforded us examples. Unlike these earlier examples the present polymorphism is revealed only with the aid of a microsope. Previously we noted cases of polymorphism connected with the action of predators (e.g., in industrial melanism). Just *what* is superior about a heterozygote? In most cases necessary investigations have not been made to answer the question. But interestingly enough man himself provides an example of balanced polymorphism maintained in this manner, a case in which the question of what is superior has been determined. Persons suffering from a severe disease known as SICKLE-CELL ANEMIA are homozygous for the gene concerned. Heterozygotes for the gene are not diseased but are detectable by virtue of the fact that their red blood cells will "sickle" (assume unusual shapes when deprived of oxygen). Only a small proportion of sickle-cell homozygotes live to reproduce and pass on the gene. Yet in some sections of Africa the gene remains at a fairly high level of frequency in the gene pool. Why does the gene not disappear? Evidently, as in the experiments described above, it would not disappear if heterozygotes enjoyed some advantage. In this case Allison was able to show what the advantage is: "The sickle-cell heterozygote is relatively resistant to malignant tertian malaria and has as much as a 25 percent better chance of attaining adulthood than the normal homozygote in parts of Africa where malaria is hyperendemic" (Allison, 1959; see also Allison, 1955). Thus the gene remains in a balanced state, the point of equilibrium being established by the tendency of the genes to be lost through low viability of homozygotes, counteracted by the tendency of the genes to increase in number by virtue of the fact that heterozygotes survive better and thus presumably reproduce more than do persons lacking the gene entirely (homozygous "normals"). The small proportion of sickle-cell anemia patients produced in each generation is a price the population pays for the increased ability to survive the ravages of malaria.

GENETIC HOMEOSTASIS Closely linked to heterozygote superiority is the concept of genetic homeostasis, a name for the *self-regulating* ability of a population that enables it to survive environmental change or diversity. The population is said to be "buffered" against change. The idea is analogous to that of the physiological homeostasis of the human body. If one kidney is destroyed or removed, for example, the other kidney will adjust and compensate for the lost organ and the body will continue to function normally. This ability to adjust to change and so to continue normal life is homeostasis. The idea of genetic homeostasis is that populations possess a capability of self-regulation so that they can continue normal existence under a variety of environmental conditions and so survive environmental vicissitudes that would destroy populations less capable of "rolling with the punch."

We may expect that natural selection will favor the development and maintenance by a population of such homeostasis. Evidence is accumulating that populations *heterozygous* for many gene pairs are better buffered against change than are populations composed of homozygotes. This evidence comes from experiments both with such laboratory forms as *Drosophilia* (see Beardmore *et al.*, 1960) and with domestic animals (largely summarized in Lerner, 1954). Beardmore *et al.* found that the superiority of AR/CH chromosomal types over AR/AR and CH/CH homozygotes manifested itself in various ways, including (1) production of greater *biomass* (number of flies multiplied by mean weight per fly) and (2) *less variation* from individual to individual in a number of bodily traits (e.g., wing length).

Apparently both wild populations and successful breeds of domestic animals have a high degree of heterozygosity for genes that are deleterious when homozygous. If attempts are made to rid the population of these genes the population becomes less viable or fertile or able to withstand environmental change. Lerner, for example, described a series of experiments with a hereditary abnormality of chickens known as "crooked toes." The genes for this are probably present in all stocks of chickens. The experimenters attempted by selection and inbreeding to produce a strain of birds free from the gene but met with only partial success since "the fitness of the . . . line has continually dropped and only a few survivors are available each year for reproduction."

The crooked toes example is illustrative of the evidence accumulating that successful, viable populations, wild or domestic, normally consist of individuals having a high degree of heterozygosity. Experimental evidence even suggests that viability can be increased by increasing the degree of heterozygosity artifically by inducing new mutations with irradiation (see Dobzhansky, 1959).

We may note that the view of population structure just described contrasts with the view formerly held that most wild populations consist of individuals homozygous for most of their genes, which are regarded as the "normal" genes. If this were true most mutations would be harmful to homozygotes and, if they produced a phenotypic effect in heterozygotes, to heterozygotes also. (Many investigations demonstrate that many if not most mutations do have some effect upon heterozygotes.) This "classical hypothesis" made possible the separation of "good" genes from "bad" genes. According to the "balance hypothesis" (the terms are Dobzhansky's, 1959), on the other hand, "good" genes contribute to the fitness of individuals heterozygous for them, almost regardless of their effect in individuals homozygous for them.

We say "almost" in this last sentence because we must not forget that there *are* genes that are harmful to both homozygotes and heterozygotes. Thus the majority of *lethal* mutants (those that kill homozygotes) in *Drosophila* are harmful in heterozygotes, even though many mutations that stop short of lethality, when individuals are homozygous for them, form adaptively superior heterozygotes. And in cases not involving lethality heterozygotes for a given pair of genes may be inferior to one or both of the homozygotes (*Aa* inferior to *AA* and/or *aa*). What determines whether *Aa* will be inferior or superior? Many factors are involved, some genetic and some environmental. A gene pair does not operate in a vacuum; it is part of the complete genotype of the individual. Its effects are conditioned by the other genes present. This integrated genotype is the totality that produces the phenotype upon which natural selection operates. Thus all the genes of the individual may be involved in determining in any given instance whether *AA* or *Aa* or *aa* will be adaptively superior.

We see, therefore, that there are elements of truth in both the "classical" and the "balance" hypothesis of population structure. Yet increasing evidence suggests that natural selection frequently, if not usually, favors a balanced population structure composed of many genotypes in which the genes interact to produce a high average of such qualities as superior viability, fertility, and adaptability to change.

What are the advantages of such a population structure? (1) Most of the individuals in a population of this kind have the superior qualities just listed even though a small proportion may be abnormal by-products. (2) The population has genetic reserves upon which it can draw if adaptation to differing conditions becomes necessary or desirable. As we noted earlier, genes that are deleterious in some environments may not be so in others. In other conditions they may be positively advantageous. Thus by keeping these genes and gene arrangements from disappearing natural selection provides a race or species with reserves upon which it may draw if and when conditions change. Referring again to the experiment with *Drosophila* (Fig. 20.5), we recall that the CH gene arrangement is relatively disadvantageous in summer months, although it contributes largely to the building up of the population in the spring. Suppose that by fall of some year the CH chromosome should have disappeared entirely, instead of merely being decreased in frequency. The effect would be to deprive the stock of a gene arrangement that evidently would be of distinct advantage to the species when spring came again. Similarly, if the ST arrangement died out in the spring, the species would have lost a genetic constitution valuable for the increase of its numbers during summer and early fall. Consequently, the genetic mechanism (heterozygote superiority) that leads to a balanced polymorphism, keeping both ST and CH in the population, makes a distinct contribution to the success of the species as it faces the changing seasons. Other genes and gene arrangements kept from disappearance by the means described may not be brought into play by the changing seasons but may be in readiness for use if longer range changes occur in the environment or if the species attempts to invade a different environmental niche. Thus the species may be well adapted to one environment and yet not lose the hereditary plasticity that will enable it to adjust to environmental change or to invade different environmental niches.

In summary, what does natural selection favor? We have spoken previously of the positive action of natural selection in favoring certain mutations or characteristics. Now we can appreciate that the matter is really more complex than such a statement implies. As mentioned previously, the Mendelian population, rather than the individual, is the unit upon which natural selection operates. Such a population has a great variety of genotypes present. Natural selection will favor the development of an aggregate of genotypes that will react to produce for the population a high level of adaptive and homeostatic properties, with resultant high efficiency in reproduction.

GENES AND ADAPTATION

In a population of the sort just mentioned, what does each individual's genotype determine? Usually it is not one rigidly determined phenotype but a certain range of phenotypes possible to enable the individuals to adapt to varying environmental demands. The genotype makes possible a certain NORM OF REACTION (Dobzhansky, 1951) or REACTION RANGE (Simpson, 1953b). Most individuals in a species of mammal, for example, may possess a genotype that will enable the individual to develop a heavy coat of hair in cold regions or seasons and a lighter coat of hair in hot regions or seasons. This reaction range makes for adaptability, which most organisms possess to a greater or lesser extent. The reaction range is determined by the genotype. In dogs, coat density may range all the way from that of the Mexican hairless to that of the Alaskan husky. But it is doubtful that any one dog has a reaction range broad enough so that in a hot climate or season it can be as sparsely covered as the hairless and in a cold climate or season as warmly covered as a husky. The genotypes of the two varieties must be different, but within each variety there are undoubtedly variations in the phenotypes possible. Thus we probably should find that some Mexican hairless individuals transferred to a cold climate would be more able than others to provide themselves with warmer coats, and that some huskies moved to the Tropics would be better able than others to develop lighter coats to help them withstand the heat. The reaction ranges of coat density possible to most varieties of dogs would fall somewhere in between these two extremes.

If the appropriate genetic experimentation were done, we should almost certainly find that coat density depends upon multiple genes or POLYGENES (p. 368). Evidence accumulates that polygenic inheritance is extremely common; in fact, it is probable that "virtually all characters are highly polygenic" (Mayr, 1963). By this we mean that as a rule each phenotype is the product of many genes acting together (plus the effects of environment).

Now let us imagine a species of mammal living in the Temperate Zone. The genotypes possessed by members of the species will be varied, but despite variations the genotypes present will make possible coat densities appropriate to the region and to seasonable variations in climate. Oversimplified models are sometimes useful in making a point clear. Let us construct such a model by supposing that the reaction range in coat densities possible to this species depends upon a minimum of six "capital letter genes" in a polygenic series. Thus the members of the population will have such varied genotypes as *Aa Bb Cc Dd Ee Ff, AA Bb CC Dd Ee Ff, Aa Bb cc DD Ee Ff, Aa BB CC DD Ee ff,* and so on—any genotype with at least six capital letter genes.

Now let us suppose that the opportunity is open for this species to extend its range into arctic regions and that its ability to do so depends upon its ability to develop heavier coats than it previously had developed. A population from the species migrates into the arctic. Some of the immigrants survive, others either do not survive or are in such poor physiological condition that they do not produce "their share" of offspring. In this natural selection, which ones will succeed? Those will succeed that have genotypes making possible the needed heavier coats *in response to the environmental stimulus of low temperature.* In terms of our oversimplified model, we may say that under the stimulus of low temperature individuals having *eight* capital letter genes will succeed; those having fewer will fail. When these successful members of the population interbreed the average number of capital letter genes in the offspring population will tend to rise.

But it would be of advantage to these arctic immigrants to be born with heavier coats or with the ability to develop them quickly while young and *before* the environmental stimulus of low temperature was experienced. Perhaps having *ten* capital letter genes would enable an individual to develop a heavy coat without the stimulus of low temperature that had previously been necessary. We readily understand that individuals having ten such genes would frequently arise from the interbreeding just mentioned (*e.g., Aa BB Cc DD Ee Ff* × *AA Bb CC Dd Ee Ff* would yield some offspring of genotypes *Aa BB Cc DD EE FF* or even of *AA BB CC DD EE FF*). Having an advantage, such offspring would be favored by natural selection. In them heavier coats would have become *hereditary* in the sense that the environmental stimulus originally required was no longer necessary. A heavy coat would have become genetically *assimilated,* in Waddington's terminology (Waddington, 1953, 1956, 1960, and 1961). GENETIC ASSIMILATION in some cases may perhaps have a different genetic basis from the one we have described, but at least the polygenic basis is the most straightforward and easiest to visualize. Mayr (1963), who proposed this explanation, has called it THRESHOLD SELECTION. Natural selection leads to the concentration of polygenes concerned with coat density, in our example, until the number of them becomes high enough to raise the production of heavy coat above a threshold; below that threshold both genes and the environmental stimulus of low temperature had been necessary.

Waddington performed several experiments demonstrating genetic assimilation. One experiment made use of the fact that if pupae of the fruit fly *(Drosophila)* are subjected to a heat shock a certain proportion of them will fail to develop some of the cross veins normally present in the wings. By selecting cross-veinless individuals as parents and continuing the treatment and selection in each generation, Waddington produced a strain in which the percentage of individuals responding to the heat shock was very high. Eventually the point (threshold) was reached where the heat shock was no longer necessary. Waddington then demonstrated that the new cross-veinless strain differed from the original stock in several genes. This fact renders a polygenic explanation likely.

We note that this threshold selection makes use of genetic variability already present in a population. In terms of our oversimplified model, genes, *A, B, C, D, E,* and *F* must already be present if recombination is to make possible an individual having, for example, the genotype *AA BB CC DD Ee FF*. Thus, Waddington (1961) found that if he started his experiment with a highly inbred (and hence largely homozygous) stock, selection was ineffective in producing genetic assimilation of the cross-veinless trait.

But suppose the environment places a premium upon a greater development of a trait than is possible on the basis of genes already present in the population. In terms of our model, suppose that in the Arctic it would be of advantage to have an even heavier coat than the genotype *AA BB CC DD EE FF* will produce. Then a *new mutation* may make possible the needed increase. We may imagine that gene *A* mutates to *A'* and that the latter is a gene having a greater effect on coat density than does *A* itself.

Thus threshold selection (genetic assimilation) affords a means of adaptation based upon recombination of genes already present in a population. The mutational process supplements this by adding new genes to the gene pool of a population.

The idea that organisms enter an environment and there make individual nonhereditary adjustments to the environment until such time as hereditary changes render unnecessary the individual accommodations to the demands of the environment is sometimes called the BALDWIN EFFECT. The essential idea antedates modern genetics (see Simpson, 1953b, for a review). A more precise statement is this: "Characters individually acquired by members of a group of organisms may eventually, under the influence of selection, be reenforced or replaced by similar hereditary characters" (Simpson, 1953b). This is essentially the matter we have been discussing in the preceding paragraphs—in terms of polygenes in populations. The term "Baldwin effect" has been used in the past with a variety of genetical concepts and implications; perhaps it has outlived its usefulness and should be discarded, as suggested by Mayr (1963).

THE ROLES OF ISOLATION

We have seen that large, random-breeding populations have a tendency to maintain a genetic equilibrium that is the antithesis of evolutionary change (pp. 384–392). We may liken such equilibrium to an inertia that evolutionary processes must overcome if change is to be effected. Since the equilibrium is connected with large population size, any factors that tend to break up large populations into smaller ones are likely to contribute to evolutionary change. Thus isolation, and factors giving rise to it, are important in evolution.

TYPES OF ISOLATION GEOGRAPHIC ISOLATION is the most easily visualized type. It exists when two populations, or two parts of one population, are separated by some geographic barrier (examples are listed on p. 285). The effectiveness for evolution of this or any other type of isolation resides in the fact that it prevents, or greatly reduces, the exchange of genes between the populations so isolated. Such isolated populations are more or less completely "out of touch with each other," genetically, and hence the occurrence of new mutations, genetic drift, the action of natural selection, etc., in one population has no effect on the other populations.

As a corollary of the fact that isolation is important only as a means of impeding gene interchange we should note that the only isolation of importance is that concerned with the *breeding* of animals. Most species of higher animals have definite periods of breeding: it is isolation during these periods that counts. Many migratory birds, for example, collect into great flocks and range over vast territories, yet they occupy a more or less restricted range during the breeding season. The prolonged and hazardous migration undertaken by individual salmon in returning to spawn in the stream where they began life is another classic example. It is the relative isolation of these local breeding groups that affects gene distribution and hence is important for evolution.

The local populations just mentioned are frequently not separated from each other by mountain ranges, deserts, and other obvious geographic features. As we noted earlier (p. 400), *distance* is in itself a barrier—if not a complete one, at least one that in practice is effective (see Wright, 1943). Its effectiveness arises in large part from what we may call the homing or territorial tendency of animals. It is the exception rather than the rule for animals to carry on their reproductive activities far from the region in which they themselves first saw the light of day. As mentioned previously, individual animals commonly establish more or less clearly delimited home territories. They do not usually stray far from these, at least at the time of breeding. Whatever the psychological concomitants, "home" evidently has significance in the lives of most animals. Even such able travelers as birds commonly use their wings to return home if removed from it by some accident such as a storm rather than to travel to some other locality and establish a new place of residence, as Mayr has remarked.

ENVIRONMENTAL (ECOLOGICAL or HABITAT) ISOLATION refers to populations that live under different environmental conditions, at least during the breeding period. A fish and a seed-eating bird are environmentally isolated even though they live in the same locality. Similarly, an insect that inhabits only coniferous trees is environmentally isolated from an insect that inhabits only deciduous trees, even though both live in the same wood lot. Beetles that spend their lives burrowing in the ground are environmentally isolated from beetles that spend their lives on trees.

We note that, whereas geographic isolation emphasizes separation in *space*, environmental isolation emphasizes separation resulting from differences in the food, habits, and physiological requirements of animals.

We may well ask: Do we ever find the one type of isolation without the other? Do animals ever occupy somewhat different positions in space without at the same time being faced with somewhat different environmental conditions? Conversely, are animals ever faced with differing environmental conditions while occupying the same position in space? Certainly differences in position in space usually, if not always, involve differences in environment, and differences in environment involve differences in position in space.

If the main difference between the territories occupied by two species is in location; environmental conditions being similar, we say that the species are geographically isolated. In doing so we merely overlook what environmental differences there are. On the other hand, if the main difference between the territories occupied by two species is in environmental conditions (ground dwelling vs tree living, for example), we say that the species are environmentally isolated. In this case we overlook the fact that the two species are also geographically isolated in the sense of not occupying the same position in space—in the vertical dimension of space rather than in its horizontal dimension. All sorts of intermediate conditions exist. Moore (1949) has well said, "The distinction between geographical and habitat isolation is merely quantitative."

Since the amount of distance separating animals that live in different but adjacent habitats is small, ecological isolation by itself is not very effective in preventing interbreeding of animals that move about freely (Mayr, 1963). It is much more effective in plants (Stebbins, 1950).

Under the term REPRODUCTIVE ISOLATION we group a great variety of *biological* restrictions to gene interchange. The two types of isolation just discussed prevent individuals from coming into contact or reduce the likelihood of their doing so. But suppose individuals *do* come into contact, will interbreeding, with consequent interchange of genes, occur? Many factors may prevent the exchange of genes and thus constitute means of biological isolation.

In some cases interbreeding is not *possible*. At least two types of factors may be involved: (1) The anatomies of the two populations may be so unlike that copulation between males of one population and females of the other is impossible. This so-called *mechanical isolation* is sometimes encountered in insects with highly complex genital organs. A comparable situation exists in those plants in which the flower structure is such that cross-pollination cannot occur. (2) *The breeding seasons of the two species may not coincide*. Flowers of one population of plants may open and then disappear before the flowers of another population mature. One population of insects in which adults live but a few days may be effectively isolated from another population if the periods of emergence of adults in the two do not coincide.

In other cases interbreeding is possible but does not occur (*sexual or psychological isolation; ethological isolation*). In many insects copulation is preceded by rather elaborate courtship behavior. Closely related species may differ in details of this ritual. Females readily accept only males that observe the punctilios of courtship behavior characteristic of their species. This behavior may be the expression of a form of preference in the choice of mates. It clearly seems to be such in higher animals. Thus related species of deer mice (*Peromyscus*) are found not to interbreed in a state of nature, although some will do so readily enough when placed in cages together, that is, when the possibility of choice is removed.

That this tendency to selective or preferential mating may be a potent force is suggested by experiments of Reed and Reed (1950). In population cage experiments fruit flies having the mutant gene for "white eye" were placed in competition with normal wild-type (red-eyed) flies. In 25 generations the white-eye gene disappeared from the population completely. The investigators determined that white-eyed flies were not less viable than were wild-type individuals. Tests indicated, however, that the mating behaviors of white-eyed and red-eyed flies were strikingly different. Both red-eyed and white-eyed females "preferred" to mate with red-eyed males. The strength of this preferential mating was determined and expressed mathematically and and the calculations showed that it was sufficient to account for the disappearance of the white-eye gene in the number of generations within which that elimination was observed to occur.

Investigations of ethological (behavioral) factors in reproductive isolation have been numerous. For a survey of the subject as it applies to *Drosophila* see Spieth (1968). Birds also are of great interest in this connection. In them differences in courtship behavior may reduce or prevent hybridization between species. Studies of such phenomena form a lively portion of the rapidly developing science of ethology (see Parsons, 1967).

An interesting type of ethological isolation is found in plants. Here the behavioral traits concerned are not those of the plants but those of the insects and birds that pollinate them. In cases where the pollinating animals feed preferentially on one kind of flower, ignoring others as long as food is available in the preferred variety, cross-pollination is prevented, or at least reduced (see Grant, 1963; see also "Hybridization: Disadvantageous," pp. 442–445.)

Reproductive isolation may exist even in cases in which matings between populations take place. (1) *Fertilization may not occur* as a result of the mating. Sperm cells may fail to reach the eggs, or if they reach them may not enter and fertilize them. In plants, pollen tube growth may be arrested before the ovule is reached. (2) Fertilized eggs may be formed, but the *hybrid individuals may prove to be inviable.* This inviability may express itself at any time: as soon as the fertilized eggs are formed, early in embryonic development, later in embryonic life, or after birth but before sexual maturity is reached. (3) *Hybrids may live to sexual maturity but may be sterile* so that they cannot pass on the genes they have received. Mules, hybrids between horses and donkeys, form well-known examples of this type of isolation (although rare fertile individuals occur).

All of the isolating mechanisms we have enumerated—geographic, environmental, and reproductive—may result in isolation that is complete or partial in its effectiveness. And obviously several of them may be operative simultaneously in any given situation to prevent or reduce gene interchange between populations.

ACTION OF ISOLATION With regard to their function in evolution we may group the three types of isolation into two categories: (1) geographic–environmental and (2) reproductive. The two play different roles in evolution (Mayr, 1959).

Geographic–environmental isolation causes two populations or subpopulations to be separated so that each goes its own way in acquiring mutations, and in being acted upon by such forces as genetic drift and natural selection. Two geographically separated populations are said to be ALLOPATRIC. We should note that isolation between two allopatric populations may not always be complete. If it is not, neighboring populations may interbreed in regions in which they come into contact (frequently the case between neighboring subspecies, pp. 329–330). Or individuals may migrate from one population to another. If interbreeding occurs in either of these ways the gene pools of the two populations will not remain as completely separate as they would under conditions of complete isolation. The effect of this mingling of genes, or gene flow, may be small or large, depending upon the extent to which isolation is incomplete. (See Wright, 1931, and also the discussion of effects of hybridization, pp. 442–448.)

Much evidence indicates that some degree of geographic–environmental isolation is usually a necessary first step in the development of genetic diversity between populations (see Mayr, 1963). So long as a gene pool remains undivided, two differing populations cannot arise from it. Can a gene pool be divided by other than geographic–environmental means? As we shall see, polyploidy is one such means. Other genetic mechanisms have been suggested as serving the same end. But these mechanisms are rare, at least in animals; the *usual* first step in species formation is for two populations to be sufficiently separated in space so that they *do not* interbreed even though they would be capable of doing so. The lack of interbreeding probably need not be absolute; doubtless speciation can occur despite some gene flow. Once separated so that the gene pools are substantially out of touch with each other, the two populations are free to go their separate evolutionary ways. Different mutations occurring in each and differing actions of such factors as drift and natural selection may result in the populations becoming quite unlike. This unlikeness may result in failure of the populations to interbreed if and when they do eventually come into contact (e.g., by migration). If so, reproductive isolation has been attained. When the populations first come into contact this reproductive isolation may be only partial. In this case hybrids may be produced that are sterile or are not as well adapted to existing conditions as are their parents. Such hybrids constitute biological wastage. Natural selection will tend to eliminate this waste by improving and intensifying the means of reproductive isolation until the populations no longer interbreed at all. (See the following discussion of hybridization and also Mayr, 1963, pp. 548 ff.) When this point is reached the populations may live in the same area, i.e., be sympatric, and still retain the integrity of their respective gene pools. They have now become separate species (further discussion of speciation is found on pp. 471–475).

HYBRIDIZATION IN EVOLUTION

Since the primary role of isolation is prevention of hybridization, it is now appropriate to inquire further into the evolutionary significance of interbreeding between populations and of the failure of this to occur. Paradoxically, hybridization is important in evolution when it occurs and when it does not.

HYBRIDIZATION: DISADVANTAGEOUS We may consider first the importance of the failure of hybridization to take place. We have noted that different populations considered to be different species do not usually interbreed, or if they do interbreed they do not usually produce viable hybrids. Moreover, when viable hybrids between species are produced they are generally sterile or of such low fertility that the amount of reproduction is negligible. What is the value to a species of failure to produce "successful" hybrids?

Usually species as we find them under natural conditions are well adapted for particular environmental niches. Thus, as noted above, hybrids, combining some of the characteristics of both species, may not be as well adapted to the environmental niches occupied by the parental species as are these parental species themselves. When this is the case natural selection will tend to eliminate the hybrids as they compete with their parents. So under these circumstances producing hybrids is wasteful. Biological waste also may occur if the hybrids are viable and can compete successfully with their parents but are sterile or of reduced fertility.

In the preceding sentence we said that waste *may* occur under these circumstances. Can production of infertile hybrids ever be of value to the parental species? There is evidence that occasionally, in plants at least, the production of infertile hybrids may serve the useful purpose of keeping intact the gene pools of parental species. Thus Lewis (1969) found that two species in the plant genus *Clarkia* (an evening primrose) readily produce hybrids through cross-pollination by insects whenever the two species come into contact. The hybrids have low fertility, no doubt correlated with the fact that the parental species differ in chromosome number, and the hybrids are chromosomally abnormal. The result of this low hybrid fertility is that "gametes are lost to the extent that hybrids are formed. The effect of this reduction in reproductive potential through hybridization has been to maintain pure colonies except in an area about 10 ft wide along the line of contact" (Lewis, 1969).

Nevertheless, it would seem that among animals, with their greater mobility than plants, infertile hybrids would seldom be likely to provide such a genetic barrier to the mixing of the gene pools of the parental species. We may anticipate, therefore, that animal species that produce hybrids usually will be wasting their energies, and thus will be at a disadvantage in competition with species that concentrate on the production of nonhybrid offspring.

At this point we come upon a debate of long standing, participated in by Darwin himself (Mayr, 1959). There is abundant observational evidence that isolating mechanisms arise as the more or less incidental accompaniment of adaptive changes mainly concerned with such matters as better adaptation to environment, reduction of competition, and the like. The genetic basis involved may lie in the fact that most genes are pleiotropic (p. 378); one of their effects may influence viability or fertility of hybrids. The questions are will natural selection act directly to cause populations to develop isolating mechanisms and will natural selection favor genetic factors that have as their sole or main effect the production or intensification of isolating mechanisms (such as hybrid sterility, preferential mating, and the like)?

We have noted above that one means by which reproductive isolation, and hence failure to hybridize, is achieved is through exercise of "choice" or "preference" in mating (selective or preferential mating). Koopman (1950) found that he was able to obtain intensification of the tendency to selective mating exhibited by fruit flies of the two sibling species *Drosophila pseudoobscura* and *D. persimilis*. These two are so similar that they cannot be told apart by external structure. Yet when hybrids between them are produced, the male hybrids are sterile; the female hybrids when mated with males of either parent species "lay the usual number of eggs, but the larvae arising from these eggs have such poor viability that in competition with the larvae of the pure species, as in population cages, they never reach the adult state." Obviously, then, such hybrids are worthless to the species, representing true biological wastage. The species are somewhat isolated from each other ecologically, preferring slightly different environments, but when they do occur together sexual isolation of the selective mating type tends to prevent the production of hybrids. Using a modified L'Héritier–Teissier population cage, Koopman demonstrated that in artificial mixed populations of *D. pseudoobscura* and *D. persimilis* the number of hybrid individuals could be made to decline rapidly by removing the hybrids that were produced. This had the effect of removing from the gene pools of the two species genes contributed by individuals that tended *not* to mate with members of their own species. Thus the tendency of each species to mate within its own species (homogamic mating) was intensified; consequently the number of hybrids produced decreased markedly in the course of a few generations. Koopman ascribed this decline to the action of natural selection in the population cages since he concluded that the poor viability and sterility of hybrids and their offspring would have prevented their contributing to future generations even if he had not removed them (see also Merrell, 1953).

Similar results were obtained by Knight, Robertson, and Waddington (1956), who employed ebony-bodied and vestigial-winged stocks of *D. melanogaster*. Males and females of both stocks were placed together so that they could either mate with their own kind or cross mate, as they "wished." But in each generation only offspring of homogamic (pure-breeding) matings were used as parents for the next generation. As generations passed, the production of hybrids declined, indicating that some degree of sexual isolation between the stocks had been produced by selection.

Hence the results cited seem to indicate that under experimental conditions, at least, selection will intensify one of the mechanisms of reproductive isolation: selective mating. (See Parsons, 1967.)

Moore (1957) has pointed out that factors increasing reproductive isolation would be of value to the populations concerned only in those regions where the populations were actually in contact. (No advantage to a frog living in Vermont would accrue from having a genetic constitution whose only function would be to render impossible hybridization with a Florida frog with which it would never actually come into contact anyway.) Blair (1955), investigating two species of frogs with overlapping ranges, noted that the greatest difference in mating call and the greatest difference in size between the two species occurred in the region where their ranges overlapped. He concluded: "The existence of the greatest size differences as well as the greatest call differences where the two species are exposed to possible hybridization supports the argument that these potential isolating mechanisms are being reenforced through natural selection.

Such reinforcement is not always encountered, however, e.g., see Volpe (1955). Perhaps some of the conflicting results arise from differences in the animals being investigated; the production of hybrids is not detrimental to all species and under all conditions (see the following). Natural selection, if it does act to favor the development of isolating mechanisms, will only do so under conditions in which hybridization is detrimental. In most instances we know too little of the environmental requirements placed upon species to be able to draw valid conclusions on the extent to which hybridization would be detrimental.

Our tentative conclusion may be that natural selection, under special circumstances, may favor genetic mechanisms having as their principal function the prevention of hybridization. It is important to remember, also, that prevention of hybridization may arise as a by-product of the genetic changes (i.e., pleiotropic mutations) by which two isolated populations become adapted to their respective environments. (In *Rana pipiens*, Vermont frogs and Florida frogs will *not* produce viable hybrids if the experimental attempt is made. Apparently adaptation to development in cold and warm environments, respectively, has carried with it genetic changes that result in constitutions so unlike that hybridization is not possible—Moore, 1955 and 1957.)

Hybridization between species is less frequent in animals than it is in plants. Nevertheless, instances of natural hybridization between animal species exist (see Stebbins, 1959, for a review of the literature in this field). Among vertebrates some hybridization has been found in all groups but seems perhaps to be most common—at least, it has been most studied—in freshwater fishes (e.g., Hubbs, 1955; Hubbs *et al.*, 1943), amphibians (e.g., Blair, 1941, and investigations cited above), and birds (e.g., Sibley, 1954).

HYBRIDIZATION: ADVANTAGEOUS As we have noted, since hybrids sometimes *are* produced, we now may ask under what circumstances might production of hybrids be of advantage in evolution? We have noted that the usual disadvantage faced by hybrids arises from the fact that they are generally not so well adapted for the environmental niche occupied by either parent species as is that parent species itself. In other words, the hybrid is at a disadvantage in competition with its parents and the latter's nonhybrid progeny. Under what circumstances might this situation not be true? It would not be true if there were available to the hybrid other environmental niches than those occupied by the parental species. These other niches would be expected to present somewhat differing living requirements from those presented by the niches occupied by the parental species. Accordingly, some of the combinations of characteristics possessed by the hybrids might prove to be "just the thing" to enable the hybrids to enter and occupy the new niche. They would afford one means of *preadaptation* (see pp. 14–15). Viewed in this light, hybrids are "experiments" in preadaptation; but the experiments will succeed only if suitable environmental niches are available.

Many examples have been found of hybrids between plant species successfully occupying environmental niches unlike those of the parent species. A frequently cited example is afforded by two species of spiderwort studied by Anderson and Hubricht (1938). In the Ozark Mountains one species, *Tradescantia canaliculata*, grows in full sunlight on the tops of the cliffs. The other species, *Tradescantia subaspera*, grows in the woodland shade at the base of the cliffs (Fig. 20.7*A*). In some places where there is a gradual slope connecting the top of a cliff with its base, e.g., in ravines, the forest-dwelling species has extended its range upward and the cliff-top species has extended its range downward. When the two species meet hybrids are produced (Fig. 20.7*B*). The hybrids combine characteristics from the parental species and apparently are successful because the environment is intermediate between that optimal for the forest-dwelling species and that optimal for the cliff-top species. We may speak of it as a "hybrid environment." As a matter of fact, most of the known examples of species hybrids

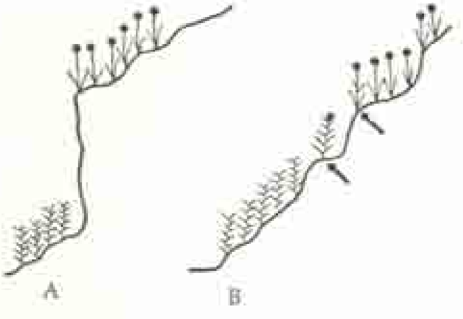

Fig. 20.7. Environmental isolation of two spiderworts, *Tradescantia*. One species grows on the tops of cliffs, the other at the foot of the cliffs. Hybrids are found where the slope is gentle (B), permitting the two species to come into contact. (After Anderson and Hubricht; from *Principles of Genetics* by E. W. Sinnott, L. C. Dunn, and Th. Dobzhansky. Copyright © 1958 by the McGraw-Hill Book Company, Inc. Used with permission of the McGraw-Hill Book Company.)

that have become established in nature have done so when man has "hybridized the habitat," in Anderson's (1949) phrase. By this we mean that most of them have arisen in locations where man has upset natural conditions by cultivation, pasturing of domestic animals, lumbering operations, and so on. Anderson notes that most of the abundant hybrid irises produced spontaneously in southern Louisiana have arisen on patches of land that have been badly overgrazed by domestic animals. Such "hybrid habitats" present living conditions for which the parent species living in undisturbed environments are not adapted.

Deforestation of the hardwood forests in Michigan and Indiana seem to have provided such hybrid habitats for hybrids between the forest-dwelling toad *(Bufo americanus)* and a toad living in more open country *(Bufo fowleri;* Cory and Manion, 1955).

But hybridization of habitat may be produced by agencies other than man. Continental glaciation, so important in Pleistocene history, is a great alterer of habitats. And such natural catastrophes as volcanic action and floods may leave in their wakes changed conditions offering possible opportunities for hybrids. Thus, through preadaptation followed by postadaptation under the spur of natural selection, hybridization may have played a part in the historical process of evolution.

INTROGRESSIVE HYBRIDIZATION What is the effect of hybridization upon the parent species themselves? Apparently hybrids form a means by which genes of one species may be transferred to another species. Let us consider again the two species of spiderwort (Fig. 20.7). The hybrids will breed not only among themselves but also with the two parent species (the latter process being called by geneticists "backcrossing"). The hybrids possess some genes derived from the forest-dwelling species and some genes from the cliff-top species. For example, when the hybrids breed with the cliff-top species they may pass on to the latter some genes *received from the forest-dwelling species*. The reverse, of course, also could occur. Thus the hybrid may serve as a go-between, passing on genes received from one parental species to the other parental species. This process is called INTROGRESSIVE HYBRIDIZATION. As a result of it, genetic variability will be increased over what it otherwise would have been. Genetic variability, as we have seen, furnishes the raw materials upon which natural selection acts. Thus introgressive hybridization in some cases may provide raw materials for evolutionary change. Wide differences of opinion prevail concerning its frequency of occurrence and its effects. Anderson (1949) has postulated that under some conditions introgressive hybridization may be at least as potent a force in introducing genetic variability into a species as is the occurrence of new mutations. Readers are referred to

Anderson (1949), Stebbins (1950), and Sibley (1954) for a more complete discussion of the subject.

A particularly instructive case in animals has been studied by Sibley (1954). The investigation involved two species of the red-eyed towhee (Fig. 20.8). The collared towhee *(Pipilo ocai)* lives in various localities in southern Mexico, primarily in coniferous woodland. The spotted towhee *(Pipilo erythrophthalmus)* lives primarily in oaks and brushy undergrowth in northern Mexico. In at least one locality on the Mexican plateau the species live together without interbreeding. But in other localities the local populations present combinations of the characteristics of the species, a fact suggesting that these populations are composed of hybrids between the latter. These hybrid populations vary greatly from locality to locality. Sibley concluded that "the patterns of variation suggest that the two species, originally ecologically separated, were brought into contact when forests were cleared for

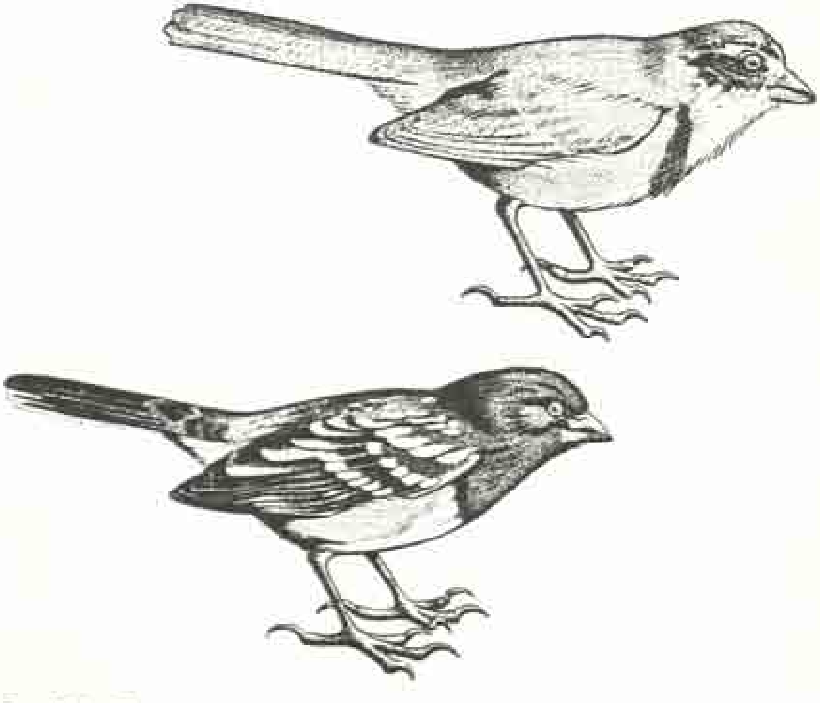

Fig. 20.8. Two species of towhees from Mexico: collared towhee, *Pipilo ocai* (above), and spotted towhee, *Pipilo erythrophthalmus* (below). (After Stebbins and Sibley; reprinted with permission from *Evolution, Genetics, and Man*, by Th. Dobzhansky, 1955, John Wiley & Sons, Inc.)

human purposes." The investigation was not of a nature to disclose whether any of the hybrid populations are better adapted to their "hybrid habitats" than either parental species would have been. This is a possibility. Sibley noted that in some localities with hybrid populations the numbers of towhees present were unusually large. This suggests that the hybrids were at least a successful group. At any rate, this example shows how hybridization can produce variability among populations—a variability which might be acted upon by natural selection.

POLYPLOIDY IN EVOLUTION

In Chapter 17 we discussed the essentials of the genetical phenomenon of polyploidy, that type of chromosomal aberration in which the number of chromosomes is increased by multiples of the haploid number (pp. 374–376). What role has polyploidy played in evolution?

Polyploids may arise in various ways from diploid ancestors. Perhaps the easiest way to visualize this is by means of the production of diploid germ cells by these ancestors (Fig. 17.10, p. 376). Ordinarily germ cells contain one haploid set of chromosomes. But sometimes, owing to abnormality in meiosis, the full number of chromosomes characteristic of the parent's cells finds its way into one germ cell. Thus, a parent whose diploid number is 18 will ordinarily produce germ cells containing nine chromosomes (i.e., 9 chromosomes comprise 1 haploid set in this species). But occasional germ cells may be produced that contain all 18 chromosomes. If a diploid ovum of this kind is fertilized by a diploid pollen grain (also containing eighteen chromosomes), the result is a fertilized ovum containing 36 chromosomes. These 36 chromosomes will comprise four haploid sets (two from the male parent and two from the female), and the resultant individual will be a tetraploid. A tetraploid is likely to differ from its diploid ancestors in a number of ways, presenting quite an altered appearance. Many tetraploids are entirely fertile among themselves, or self-fertile (we recall that production of both pollen and ovules by a single plant is not unusual). But most important of all, there is frequently a high degree of sterility between the polyploid and its diploid progenitors. Thus reproductive isolation arises at one stroke and without the aid of spatial isolation. This point is of interest since usually, as emphasized above, spatial isolation is important in the first stages of species formation.

Polyploidy has formed a common means of speciation in plants. Multitiudes of wild species are polyploids, as are many of our cultivated plants: cotton, wheat, oats, tobacco, potato, banana, coffee, sugarcane, many flowers, and so on. Indeed, plant breeders are constantly employing artificial means of inducing polyploidy to create new varieties.

Frequently polyploidy is linked with hybridization in the production of new varieties and species. The hybrid produced by crossing two diploid species of plants may be partially or completely sterile if it has only the same number of chromosomes as do the parental species (i.e., is itself diploid). On the other hand, if the hybrid is a tetraploid, containing *both* sets of chromosomes from *both* parents, it is likely to be fully fertile and to be reproductively isolated from the diploid parental species. Hence it will "breed true." An instructive

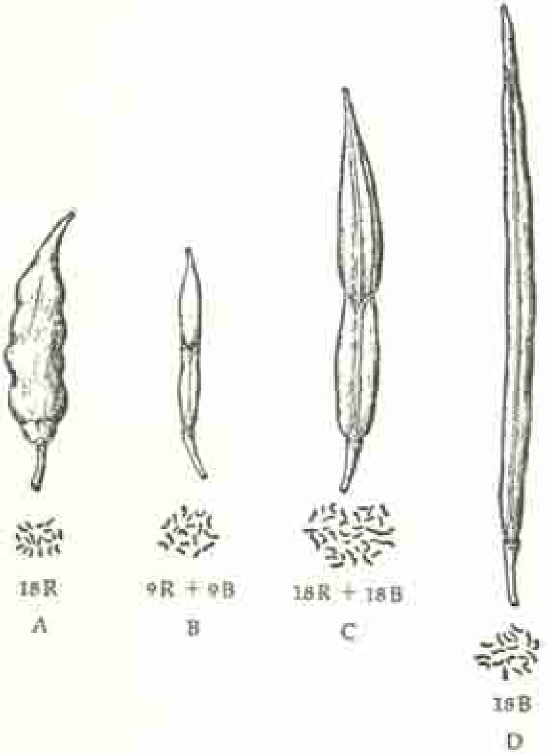

Fig. 20.9. Seed pods and chromosomes of radish (A), of cabbage (D), of their diploid hybrid (B), and of their tetraploid hybrid, *Raphanobrassica* (C). R, radish chromosomes. B, cabbage chromosomes. (After Karpechenko; redrawn from *Principles of Genetics*, by E. W. Sinnott, L. C. Dunn, and Th. Dobzhansky. Copyright © 1958 by the McGraw-Hill Book Company, Inc. Used with permission of the McGraw-Hill Book Company.)

example is the tetraploid hybrid between the radish and the cabbage, produced by Karpechenko (Dobzhansky, 1951; Sinnott *et al.*, 1958). The radish *(Raphanus)* and the cabbage *(Brassica)* both have a diploid number of 18 and a haploid number of nine. The hybrid is a tetraploid, having received two haploid sets of radish chromosomes and two haploid sets of cabbage chromosomes (total 36; Fig. 20.9). Since the hybrid is infertile with both parent species it constitutes a new form that has been named *Raphanobrassica* by combining the names of its parents. The hybrid is intermediate between its parents in many characteristics; the intermediate structure of its seed pod is clearly evident in Fig. 20.9. Unfortunately *Raphanobrassica* seems to have no commercial future since it combines the root of a cabbage with luxuriant leaves resembling those of a radish!

If space permitted, other examples of polyploidy as a means of evolution in plants might be described. Many polyploid species have arisen in a state of nature, and frequently it is possible for botanists to decide which diploid species were their ancestors. The matter has been "clinched" in a few cases by actually "resynthesizing" the polyploid, starting with the diploid species suspected of being its parents.

Although polyploidy is most important in the evolution of plants (for discussions see Stebbins, 1950; Dobzhansky, 1951; Mayr 1963), it has been of almost no importance in animal evolution. It is found in few animals and among that few only in some types that have forsaken reproduction involving two sexes (bisexual) for reproduction in which a single individual produces both ova and sperm (hermaphroditism) or for reproduction by means of unfertilized eggs (parthenogenesis). Apparently the sex-determining mechanism of animals cannot function properly when polyploidy occurs, but there also may be other reasons for its rarity among animals (see Mayr, 1963, pp. 440 ff.).

In summary, we find that plants possess in polyploidy one means, probably the only means in bisexual organisms, by which a new species can arise in one step, achieving reproductive isolation in the absence of spatial isolation. Mayr (1949 and 1963) has termed this phenomenon "instantaneous speciation."

GENETIC CONTROL OF GROWTH RATES

RATE-GENES In earlier chapters we stressed the fact that the main function of genes is to determine the nature of enzymes. Important for evolution are those genes that control the *rates* of metabolic processes and the *times* in the life history (ontogeny) at which the processes act. We are particularly interested in rate-genes expressing their effect during the course of embryonic development since the phenotype of the adult is the resultant of the forces (genetic and environmental) that have acted on it during embryonic life and immediately afterward. This is important. Too often we focus attention on adults only; we must never forget that natural selection operates on an individual during its entire life history, from the time it is a fertilized egg onward.

An easily visualized example of a rate-gene in action is afforded by the research of Ford and Huxley (Huxley, 1932) on eye color in the crustacean *Gammarus* (an amphipod). Early in embryonic life these creatures have bright red eyes. At about the end of the first week of development deposition of melanin (dark brown pigment) begins in the eyes. This continues at such a rapid rate that three or four days later the eyes appear black. The investigators discovered a mutation that causes the eyes of adults to be red, with a faintly brownish cast. They showed that in this case deposition of pigment did not begin until the young were four weeks old and that then it proceeded so slowly that by the time sexual maturity was reached the original red color was but slightly modified. Here we see one mutation with the two effects listed above: it affected the time at which the reaction occurred, and it affected the rate of that reaction.

Of the metabolic processes operative during embryonic development particular interest centers on those affecting *growth* of the parts and organs of the developing individual. Parts and organs grow at different rates; hence genes controlling these relative rates must have great potency in determining the nature of the resulting adult. If so, mutations of genes concerned with differential growth could be highly important in producing the variability upon which natural selection operates. Most of the examples of differential growth rates known at present have not been analyzed genetically. We can scarcely doubt, however, that rate-genes, probably complex systems of them, are involved.

DIFFERENTIAL GROWTH RATES (ALLOMETRY)

The study of differential growth rates of the kind just mentioned is called ALLOMETRY (or heterogony). Although we may seldom think of it, the fact that different parts of the body grow at different rates and that these rates change from time to time is a matter of everyday observation. A glance at Fig. 4.15 (p. 66) will remind us that in the human fetus the head grows much more rapidly than does the rest of the body, the legs especially having a slow rate of growth. After birth the situation changes. An adult man is far from being a newborn baby with all parts of the body increased equally in size. Such an adult would be a most ungainly creature having an enormous head, a large trunk, and short, crooked legs. After birth the head continues to increase in size but at a decelerated rate, while the lower portions of the body, particularly the legs, grow at an increased rate.

Differential growth of one part as compared to another is common in the animal kingdom. Figure 20.10 shows an example among males of a certain species of beetle. In this species small males have large forelegs as compared to males of most beetles. But larger males of the species have forelegs that are proportionately much larger than are those of the smaller males. In other words, a *little* increase in body size is accompanied by much increase in foreleg size. Thus the growth rate of the forelegs must be greater than that of the body as a whole.

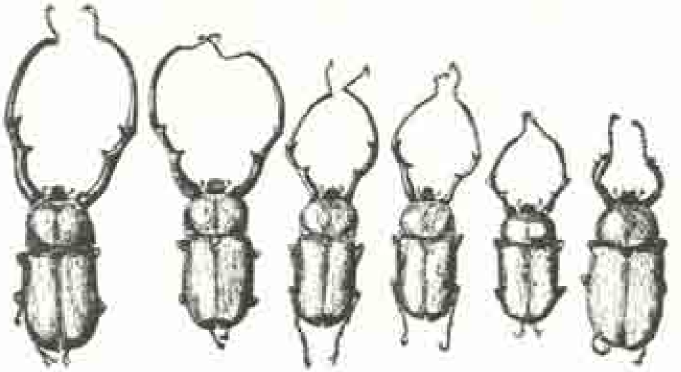

Fig. 20.10. Allometry (differential growth) exhibited by forelimbs of male beetles of the species *Euchirus longimanus*. Specimen at extreme right is a female. Other specimens are males arranged in order according to body size. (From Champy, C., *Sexualité et Hormones*, Paris, Gaston Doin et Cie., 1924.)

In many cases the differential growth rate of one part as compared to that of another is sufficiently precise so that a mathematical statement of it may be made. The formula employed is $y = bx^k$ (or $\log y = k \log x + \log b$). In this formula x is the size or dimension used as a basis for comparison, frequently the general body size; y is the size or dimension of the part of the body being compared; b is the "initial growth index," that is, a constant expressing the size of y when x is 1; and k is a constant indicating the ratio of the growth rate of the organ to the growth rate of the body (in those cases in which the size of the body forms the basis of comparison).

Figure 20.11 presents a hypothetical but true-to-life example of the manner in which differential growth works. Figure 20.11A represents a small, rhinoceroslike animal with a tiny horn on its nose. As indicated, the horn is 2.5 cm long and the length of the head measured from the

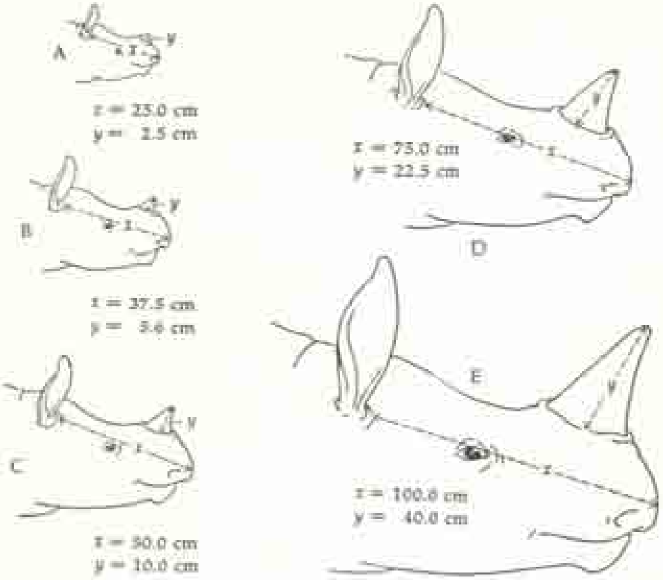

Fig. 20.11. Positive allometry of the nasal horn of a hypothetical rhinoceroslike mammal.

base of the ear to the tip of the snout is 25 cm. Since we wish to study changes in the length of the horn as the head increases in size, we designate the length of the head as x in the above allometry formula and the length of the horn as y. Thus, at the outset $x = 25$ and $y = 2.5$. For the purposes of this example we arbitrarily decide that the value of the constant k shall be 2. If k were 1, the horn would increase in length at the same rate as that at which the head increased in length. A k value of 2 provides that the horn shall increase in length more rapidly than does the head.

The initial growth index b can now be determined by substituting the values of x, y, and k in the formula:

$$y = bx^k \qquad b = \frac{y}{x^k} \qquad b = \frac{2.5}{25^2} = \frac{2.5}{625} \qquad b = 0.004$$

We are now in a position to utilize the formula in determining the horn sizes that will accompany an increase in the length of the head. We may inquire what will be the change in the length of the horn when the length of the head increases from 25 to 37.5 cm (Fig. 20.11B); x is now 37.5 cm.

$$y = bx^k \qquad y = 0.004 \cdot 37.5^2 \qquad y = 5.6 \text{ cm}$$

Figure 20.11C shows the increase in horn length when the head length has increased to 50 cm. The length of the horn is calculated using the same constants as before but assigning x a value of 50. We note that y now equals 10 cm. In other words, while the head has doubled in length, the horn has become four times as long as it was at the outset.

D and E in Fig. 20.11, show the increase in horn length with an additional increase in the length of the head. In E the length of the head has increased to four times its original length, but the horn is 16 times as long as it was at first.

Our hypothetical example assumes added significance when we note that Fig. 20.11 may be interpreted in one or all of three different ways: (1) The series of heads shown may represent stages in the growth and development of an *individual* rhinoceroslike animal. In this case A is the head of a young, perhaps newborn, animal and the succeeding diagrams show stages in the animal's development as it becomes adult. In other words, the diagrams may represent an ontogenetic series. (2) On the other hand, the series of heads may represent adult individuals of varying sizes. In this case A would represent an adult of a dwarf species of a rhinoceroslike animal, E an adult of a relatively giant species, and the intervening forms adults of species of intermediate size. (3) Or again, the series of heads may represent an evolutionary series. In this case A would represent an adult of a prehistoric ancestor, E its modern descendant, and the intervening forms intermediate steps in the sequence of forms leading from A to E. Such series of fossils, marked by increasing size, are frequently encountered; we recall particularly the evolutionary sequences leading to the modern horse and to the modern elephant (pp. 212–224). Thus the series of diagrams in Fig. 20.11 may represent a phylogenetic series.

ALLOMETRY IN HORSES Let us turn from a hypothetical example to one based on actual data. In our discussion of the evolution of the horse (pp. 207–208) we noted that during evolution the facial or preorbital portion of the skull increased in length disproportionally to the increase in size of the skull as a whole (Fig. 11.3, p. 208). The same trend is noted in the ontogeny of modern horses. Line *A* in Fig. 20.12 shows the increase in length of face as compared to length of braincase (cranium) in modern horses of different sizes and ages. The lowest point on the line represents a foetal horse; other points represent colts and adults of varying sizes. As the cranium increases in length the face increases in length at a somewhat faster rate (k = about 1.5) until a cranium length of about 15 cm is reached (in colts 6–8 months old). From that point on $k = 1$; in other words, growth is *isometric*, the face and cranium increasing in length at the same rate.

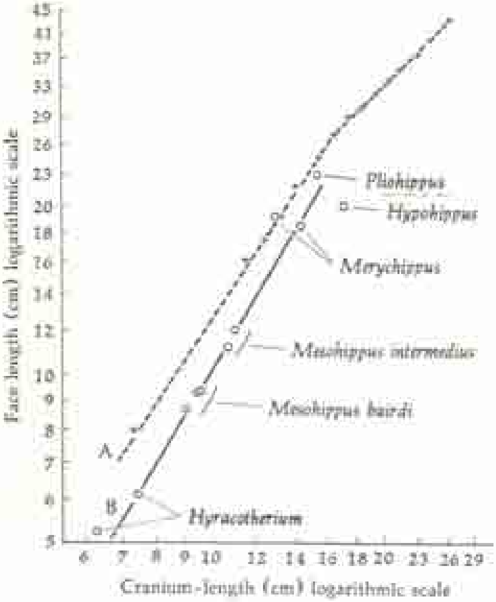

Fig. 20.12. Allometry of facial length in horses. Line A: allometry in the ontogeny of the modern horse. Line B: allometry in the ancestral line leading to the modern horse. Plus signs indicate modern horses (*Equus*); open circles indicate prehistoric horses. (Redrawn from Reeve, E. C. R., and P. D. F. Murray, "Evolution in the horses's skull," *Nature, 150* (1942), 402–403.

Line B (Fig. 20.12) represents allometry in the phylogenetic line leading to the modern horse. Here the growth ratio *k* seems to be slightly greater than it is in the ontogeny of the modern horse (about 1.8). But each point on the graph is based on a single specimen; the difference from 1.5 might not be found to be significant if a large number of specimens were measured. Reeve and Murray (1942) pointed out that simple allometry of face growth to cranium growth seemed to prevail until about the time of *Merychippus*, when a change in skull proportions occurred "by an increase in size of the facial rudiment at a very early stage of growth." In terms of the allometry equation this may have represented an increase in the initial growth constant *b* (Simpson, 1953a). We recall that *Merychippus* initiated many adaptations to life on dry plains. Accordingly, the change in *b* seems to have occurred in connection with these adaptations. From *Pliohippus* on through the ancestral species of *Equus* facial growth and cranium growth may well have been nearly isometric as they are in later stages of the ontogeny of

Equus (upper portion of line *A*, Fig. 20.12), but we need more data on this point.

Thus in horses the face increases in length faster than does the cranium. Up to a certain size, small horses have short faces and larger horses have disproportionately longer ones. This is true today; it was true in prehistoric times. The observed evolutionary trend through at least the larger *Mesohippus* (Fig. 20.12) can be explained without assuming any change in the genes concerned. The larger the horse, the longer the face. Thus, if by evolutionary change we mean change in the genes, genetic change, we can not say that the horses underwent evolutionary change in facial length until the *Merychippus* stage was reached. Before that an increase in the length of the face had been an automatic accompaniment of an increase in body size. Genetic change was evidently introduced with *Merychippus*, however.

By way of contrast to the line leading to *Equus*, the "forest horse" *Hypohippus* is included in Fig. 20.12. Note that the point representing it falls at some distance from either of the two lines. *Hypohippus* did not have hypsodont teeth; its face was only three-quarters as long as that of a modern horse having the same cranium length (Reeve and Murray, 1942).

What has allometry to do with evolution? As noted previously, genes control the rates at which developmental processes, including those of growth, occur in the body. Thus, for example, genes would control the rate at which the horn of our hypothetical rhinoceroslike animal (Fig. 20.11) would grow; other genes would control the rate at which the length of the head as a whole would increase. In the example shown we need only suppose that the genes controlling growth of the horn determine that the horn shall grow at a more rapid rate than the rate of growth of the body as a whole. Then, if for any reason the head becomes larger, the horn will automatically become disproportionately larger, as shown in the figure.

Perhaps it is important for a large rhinoceros to have a relatively longer horn than its small ancestor. Then we may expect that in the evolutionary line leading to the large descendant natural selection will have favored changes in growth rate genes so that the length of the horn will increase more rapidly than the increase in body size. Such genetic changes will be reflected in changes in the constants b or k, or both, of the allometry formula. Conceivably, change in a single gene controlling relative rate of growth might be all that was needed to produce large changes in horn length as the body increases in size. This would remove the necessity of postulating many mutations, each one increasing horn length by a small amount.

Alternatively, there might be circumstances in which it would *not* be important for a large rhinoceros to have a relatively longer horn than its small ancestor had—yet the large descendant was observed to have such a horn. Perhaps in this case natural selection had seen to it that growth rates were adequate to produce the horn length needed by the ancestor, but by accident these rates were such that if the body increased greatly in size a relatively longer horn would develop, not because greater relative length was *needed* but as the automatic result of the fact that the growth rate established in the ancestor had not changed. The disproportionately longer horn would develop as a sort of by-product in this case. Just so long as having a longer horn was not positively detrimental, natural selection would not operate to change the growth rate gene.

On the other hand, the time might come when the horn would become so large as to be a positive handicap. Then natural selection would tend to eliminate possessors of the oversized horns. Among prehistoric animals some instances are observed of animals possessing horns and other structures so huge that they seem to have passed the point of maximum usefulness. The huge spread of antlers possessed by the Irish stag affords a case in point. Whether the excessive antler development contributed to the animal's extinction is still the subject of debate. But we may feel reasonably confident that the tendency of these big stags to develop disproportionately huge antlers represented the culmination of such a process of differential growth as we have been discussing. (See Huxley, 1932, for a discussion of allometry of antlers.)

We may well mention in passing that the observed tendency of a part or organ to change progressively in size is sometimes given as an example of what is called ORTHOGENESIS, evolution in a straight line. In such a terminology the steady increase in the length of the horn in our rhinoceroslike animal would form an example of an orthogenetic series. Orthogenesis as a descriptive term indicating the occurrence of progressive changes is sometimes useful. Unfortunately, it has at times been endowed with an occult meaning and presented as an evolutionary force in its own right, as though there were some inner force in animals tending to cause them to evolve in straight lines. Further discussion of orthogenesis is not appropriate here; readers are referred to Jepsen (1949) and Simpson (1953a) for a more extended treatment of the controversial subject. We recall that the "line" leading from *Hyracotherium* to *Equus* (Fig. 11.7, p. 213), frequently cited as an orthogenetic line, was in reality singled out for attention from among many other lines actually existing. We may quote with approval Simpson's conclusion that much apparent orthogenesis is "a product rather of the tendency of the minds of scientists to move in straight lines than of a tendency for nature to do so" and note further that at least some of the progressive series that *are* observed are explicable as the result of differential growth rates. Other progressive series are explicable as the result of the operation of natural selection on organisms living in a stable environment or an environment that is changing with a constant trend (e.g., becoming increasingly dry). Under such conditions natural selection promotes more and more perfect adaptation to that environment and the resulting changes may take the form of a progressive series. Natural selection operating in this manner is sometimes called ORTHOSELECTION.

The changes in the feet of horses resulting in the one-toed condition characteristic of modern horses presents a somewhat similar situation. We recall (Fig. 11.7, p. 213) that there were many lines of three-toed horses, one of which eventually gave rise to the one-toed genus. It has been shown (work of Robb, summarized by Simpson, 1944) that the relationship between the growth rate of the lateral digits and that of the cannon bone remained constant among these three-toed horses ($y = 1.5x^{0.97 \text{ to } 0.98}$, in which y is the length of the lateral digits and x is the length of the cannon bone). There was no evolutionary, i.e., genetic, change among them; changes in the proportionate length of digits were the automatic accompaniment of whatever changes in the size of foot (typified by changes in size of cannon bone) occurred. But in the one-toed horse line there *was* an abrupt change in proportion, as compared to the proportions of three-toed ancestors. This change took the form of a sudden *relative* decrease in the length of lateral digits as compared to the length of the cannon bone. The change is expressed in the allometry formula by a reduction of the constant b to about half its former value: $y = 0.76x^{0.99 \text{ to } 1.00}$. Once inaugurated, this changed value has continued and is found to apply to modern adult horses of various sizes and to size changes encountered in the ontogeny of modern horses.

Viewed in the light of allometry, horse evolution assumes quite a different complexion from what it has in other lights. According to this view, the important evolutionary change at first was in size. It is doubtless of advantage to a horse to be large. For one thing, large animals do not fall so easy prey to predators as do small ones. Thus natural selection would tend to favor genetic changes making for an increase in size. As the horses became larger their faces became longer, not because of further genetic changes but because genes controlling the rate of facial growth determined greater rate of growth than that characterizing the body as a whole. Eventually, at the *Merychippus* stage, a genetic change occurred. This change may well have been connected with an increased adaptation for grazing (recall the adaptive value to the modern horse of its long face, p. 207). Since then there has been little change in the relative lengths of face and cranium.

Similarly, in most horse lines the three toes retained about the same proportions to each other. But in the line leading to the one-toed horses a sudden genetic change occurred, with the result that there was an abrupt decrease in the relative size of the lateral digits. Presumably this change was favored by natural selection in connection with the development of efficient foot structure adapted for rapid movement on dry plains (see pp. 214–216).

Thus we see that allometry removes the necessity for postulating large numbers of more or less independent mutations, each affecting some particular structure of the body and each acted on by natural selection. In the evolution of the face and legs of the horse two principal genetic changes seem to have occurred: (1) an increase in the growth rate of the face, inaugurated at the *Merychippus* stage and (2) a decrease in the growth rate of the lateral digits when the horses reached a functionally one-toed state. Once inaugurated, these changed growth rates persisted.

NEGATIVE ALLOMETRY So far we have emphasized cases in which the growth rate of a part has been greater than that of the body as a whole. This is called positive allometry and is exemplified in Fig. 20.11. In positive allometry the constant k is greater than 1. If the value of k is 1, growth of the part proceeds at the same rate as does growth of the whole. This is called isometric growth. If the growth of the horn in our rhinoceroslike animal had been isometric, when the head increased in length fourfold (Fig. 20.11E) the horn would also have increased in length fourfold, i.e., would have been 10 cm long. If the value of k is less than 1, i.e., is a fraction, the part in question increases in size more slowly than does the body as a whole. This process is called negative allometry. If this had been true of our rhinoceroslike animal, the horn of the largest animal (Fig. 20.11E) would have been even less than 10 cm long; it would have been relatively shorter than it was in the smallest individual (Fig. 20.11A). Negative allometric growth may help to account for the relative reduction in size observed in some organs during evolutionary history. Recall that k is slightly less than 1 in the allometry formula describing the relationship between lateral digits and cannon bone in the feet of three-toed horses.

Finally, we should note that changes in the genes controlling growth rate would constitute mutations having large effects. In Fig. 20.11 we presented a hypothetical example of horn evolution involving a gene that determines that the horn shall grow in length faster than the head increases in length. Suppose that in an immediate descendant of animal

A that gene underwent a mutation, the effect being to lower the rate of growth so that the horn increased in size more slowly than did the body as a whole. That is, the mutation changed the allometric growth rate from positive to negative. Then, through isolation, genetic drift, and other forces discussed on earlier pages, two populations might become established—one population possessing the unchanged gene and the other the mutated one. If body size increased in both populations, we should find them coming to differ greatly in the character of the nasal horn. The population with the unchanged gene would develop long horns, as shown in Fig. 20.11. On the other hand, the population with the mutated gene would develop relatively short horns; indeed, as the animals became large the horns might have become reduced to mere blunt, bony calluses (Fig. 20.13A). What a difference in the end products of the two evolutionary lines! And the difference may have been the result of a single mutation occurring early in evolutionary history.

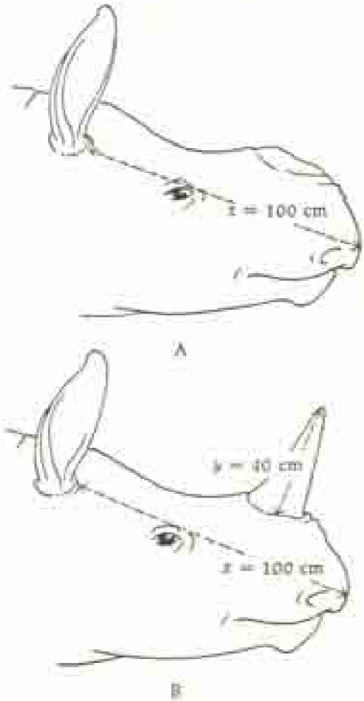

Fig. 20.13. A, negative allometry of the nasal horn of a hypothetical rhinoceroslike mammal. B, positive allometry in length of nasal horn coupled with isometric growth in width (cf. E, Fig. 20.11).

For the sake of simplicity we have confined our discussion of allometry to single dimensions, e.g., *length* of horn. But material objects have three dimensions, and growth in one dimension is not always proportional to growth in the other two. In drawing Fig. 20.11 we actually have shown the horn increasing in breadth as well as in length, although the point was not mentioned previously. Suppose growth in breadth had been isometric, relative to an increase of the head length. The result would have been a much more slender horn (Fig. 20.13B) than that shown in Fig. 20.11E.

CARTESIAN COORDINATES In closing this phase of our discussion we may well mention the Cartesian coordinate method utilized by D'Arcy Thompson (1942) for representing simultaneous change in two dimensions. Figure 20.14 shows one of his most famous examples. The figure at the right approximates the outline of a huge marine sunfish of most unusual proportions, almost circular in profile. A close relative is the fish shown at the left, a creature of smaller size and more "usual"

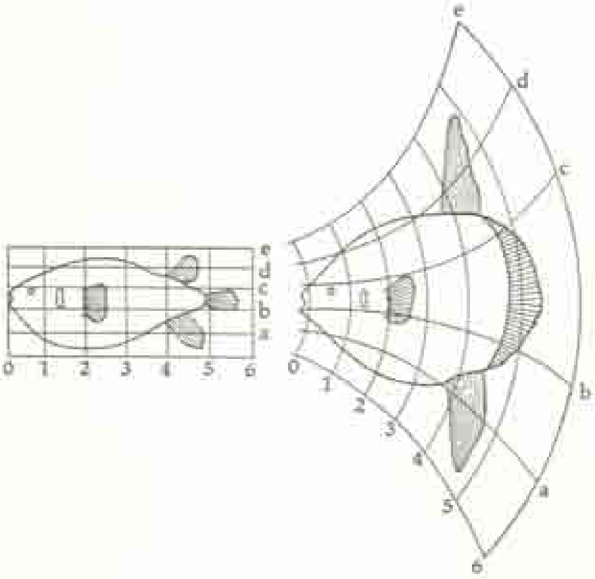

Fig. 20.14. Transformation of the body outline of a teleost fish, *Diodon* (left), to give the outline of the giant sunfish, *Orthagoriscus* (right). The outline of *Diodon* was inscribed in a framework of rectangular coordinates and the latter was then distorted in a regular manner as indicated. (Redrawn from D'Arcy Thompson, *On Growth and Form*, Cambridge University Press, 1942.)

proportions, resembling the presumed ancestor of the fantastic sunfish. If this outline of a "normal" fish is inscribed in a grid of rectangular coordinates, as shown, and then this system of coordinates is distorted in the regular way indicated at the right, the result is the shape possessed by the weird sunfish. What does such distortion of a system of coordinates mean in terms of biological processes? The diagram would be interpreted to indicate that a center of very active growth in the vertical dimension developed in the tail region and that the growth rate declined progressively from tail to head. Presumably these changed growth rates arose as the result of mutation occurring in the evolutionary line leading to the strange sunfish. Consequently, as the descendants increased in size the posterior regions of the body increased in height more rapidly than did the anterior regions, with the result observed.

The reader is referred to Thompson's stimulating classic *On Growth and Form* (1942) for other and more complicated applications of the method, including that to changes in skull shape encountered in the evolution of the horse. The method offers an admirable description of observed trends, but the physiologic and genetic forces at work in the production of the trends remain largely undetermined. This condition should not be permitted to continue. Thompson's studies offer a real challenge to anyone interested in the evolution of animals as *wholes*. That this technique of analysis is not being entirely neglected is indicated by its application to changes in skull shape in evolutionary lines of prehistoric mammals (e.g., Colbert, 1935; Patterson, 1949).

In conclusion, we would not convey the impression that allometry offers the key to *all* evolutionary change. But it illustrates how evolution can occur by means of the mutation of genes controlling growth rates during embryonic development.

Furthermore, allometry aids in explaining the development of neutral or nonadaptive characteristics—those which have little or no significance in the lives of their possessors. Natural selection itself can account only for characteristics that are useful. But a horn or a spine on the thorax of a beetle may become disproportionately long as the body itself becomes larger, even though the lengthening is of no value to its possessor. We need only suppose that the genes controlling the growth of the horn or spine determine a disproportionately high rate of growth. So long as the lengthening remains neither beneficial nor harmful natural selection will not operate either for or against the rate-gene. As noted previously, other indifferent or nonadaptive traits may be accounted for by the side effects of pleiotropic genes (pp. 377–378) or by the random fixation of genes through genetic drift (pp. 399–402). Other genetic explanations for nonadaptive traits have been suggested (Van Valen, 1960).

References and Suggested Readings

Allison, A. C., "Aspects of polymorphism in man," *Cold Spring Harbor Symposia on Quantitative Biology, 20,* 239–255 (1955).

Allison, A. C., "Metabolic polymorphisms in mammals and their bearing on problems of biochemical genetics," *American Naturalist, 93,* 5–16 (1959).

Anderson, E., *Introgressive Hybridization,* New York, John Wiley, 1949.

Anderson, E., and L. Hubricht, "Hybridization in *Tradescantia.* III. The evidence for introgressive hybridization," *American Journal of Botany, 25,* 396–402 (1938).

Beardmore, J. A., Th. Dobzhansky, and O. A. Pavlovsky, "An attempt to compare the fitness of polymorphic and monomorphic experimental populations of *Drosophila pseudoobscura,*" *Heredity, 14,* 19–33 (1960).

Blair, A. P., "Variation, isolating mechanisms, and hybridization in certain toads," *Genetics, 26,* 398–417 (1941).

Blair, W. F., "Size difference as a possible isolating mechanism in Microhyla," *American Naturalist, 89,* 297–301 (1955).

Colbert, E. H., "Siwalik mammals in the American Museum of Natural History," *Transactions of the American Philosophical Society, 26,* 1–401 (1935).

Cory, L., and J. J. Manion, "Ecology and hybridization in the genus *Bufo* in the Michigan-Indiana region," *Evolution, 9,* 42–51 (1955).

da Cunha, A. B., "Chromosomal polymorphism in the Diptera," in M. Demerec (ed.), *Advances in Genetics,* vol. 7, New York, Academic Press, 1955.

Demerec, M., "Reaction of populations of unicellular organisms to extreme changes in environment," *American Naturalist, 84,* 5–16 (1950).

Dobzhansky, Th., "Adaptive changes induced by natural selection in wild populations of *Drosophila,*" *Evolution, 1,* 1–16 (1947).

Dobzhansky, Th., "The genetic basis of evolution," *Scientific American, 182,* 32–41 (1950).

Dobzhansky, Th., *Genetics and the Origin of Species,* 3rd ed., New York, Columbia University Press, 1951.

Dobzhansky, Th., "Variation and evolution," *Proceedings, American Philosophical Society, 103,* 252–263 (1959).

Dobzhansky, Th., and B. Spassky, "Evolutionary change in laboratory cultures of *Drosophila pseudoobscura,*" *Evolution, 1,* 191–216 (1947).

Ford, E. B., *Ecological Genetics*, New York, John Wiley, 1964.

Grant, V., *The Origin of Adaptations*, New York, Columbia University Press, 1963.

Gustafsson, A., "Mutations in agricultural plants," *Hereditas, 33,* 1–100 (1947).

Hubbs, C. L., "Hybridization between fish species in nature," *Systematic Zoology, 4,* 1–20 (1955).

Hubbs, C. L., B. W. Walker, and R. E. Johnson, "Hybridization in nature between species of American cyprinodont fishes," *Contributions, Laboratory of Vertebrate Biology, University of Michigan* No. 23, 1–21 (1943).

Huxley, J. S., *Problems of Relative Growth*, New York, Dial Press, 1932.

Jepsen, G. L., "Selection, 'orthogenesis,' and the fossil record," *Proceedings, American Philosophical Society, 93,* 479–500 (1949).

Knight, G. R., A. Robertson, and C. H. Waddington, "Selection for sexual isolation within a species," *Evolution, 10,* 14–22 (1956).

Koopman, K. F., "Natural selection for reproductive isolation between *Drosophila pseudoobscura* and *Drosphila persimilis*," *Evolution, 4,* 135–148 (1950).

Lerner, I. M., *Genetic Homeostasis*, New York, John Wiley, 1954.

Lewis, H., "Evolutionary processes in the ecosystem," *BioScience, 19,* 223–227 (1969).

L'Héritier, Ph., and G. Teissier, "Élimination des formes mutantes dans le populations de Drosophiles," *Comptes Rendus Société de Biologie, 124,* 880–884 (1937).

Manchester, H., "The new age of 'atomic crops,'" *Reader's Digest*, 135–140 (November 1958). *Popular Mechanics*, 106–110, 282–288 (October 1958).

Mayr, E., "Speciation and systematics," in G. L. Jepsen, E. Mayr, and G. G. Simpson (eds.), *Genetics, Paleontology, and Evolution*, Princeton, Princeton University Press, 1949, pp. 281–298.

Mayr, E., "Isolation as an evolutionary factor," *Proceedings, American Philosophical Society, 103,* 221–230 (1959).

Mayr, E., *Animal Species and Evolution*, Cambridge, Massachusetts, Harvard University Press, 1963.

Merrell, D. J., "Selective mating as a cause of gene frequency changes in laboratory populations of *Drosophila melanogaster*," *Evolution, 7,* 287–296 (1953).

Moore, J. A., "Patterns of evolution in the genus *Rana*," in G. L. Jepsen, E. Mayr, and G. G. Simpson (eds.), *Genetics, Paleontology, and Evolution*, Princeton, Princeton University Press, 1949, pp. 315–338.

Moore, J. A., "Abnormal combinations of nuclear and cytoplasmic systems in frogs and toads," in M. Demerec (ed.), *Advances in Genetics*, vol. 7, New York, Academic Press, 1955, pp. 139–182.

Moore, J. A., "An embryologist's view of the species concept," in E. Mayr (ed.), *The Species Problem*, publ. 50, Washington, D.C., American Association for the Advancement of Science, 1957, pp. 325–358.

Parsons, P. A., *The Genetic Analysis of Behaviour*, London, Methuen, 1967.

Patterson, B., "Rates of evolution in Taeniodonts," in G. L. Jepsen, E. Mayr, and G. G. Simpson (eds.), *Genetics, Paleontology, and Evolution*, Princeton, Princeton University Press, 1949, pp. 243–278.

Raper, K. B., "Penicillin," in *The Yearbook of Agriculture 1943–1947*, Washington, D.C., United States Department of Agriculture, 1947, p. 699–710.

Reed, S. C., and E. W. Reed, "Natural selection in laboratory populations of *Drosophila*. II. Competition between a white-eye gene and its wild type allele," *Evolution*, *4*, 34–42 (1950).

Reeve, E. C. R., and P. D. F. Murray, "Evolution in the horse's skull," *Nature*, *150*, 402–403 (1942).

Sibley, C. G., "Hybridization in the Red-Eyed Towhees of Mexico," *Evolution*, *8*, 252–290 (1954).

Simpson, G. G., *Tempo and Mode in Evolution*, New York, Columbia University Press, 1944.

Simpson, G. G., *The Major Features of Evolution*, New York, Columbia University Press, 1953a.

Simpson, G. G., "The Baldwin effect," *Evolution*, *7*, 110–117 (1953b).

Sinnott, E. W., L. C. Dunn, and Th. Dobzhansky, *Principles of Genetics*, 5th ed., New York, McGraw-Hill, 1958.

Spiess, E. B. (ed.), *Papers on Animal Population Genetics*, Boston, Little, Brown, 1962.

Spieth, H. T., "Evolutionary implications of sexual behavior in *Drosophila*," in Dobzhansky, Th., M. K. Hecht, and W. C. Steere (eds.), *Evolutionary Biology*, vol. 2, New York, Appleton-Century-Crofts, 1968, pp. 157–193.

Stebbins, G. L., Jr., *Variation and Evolution in Plants*, New York, Columbia University Press, 1950.

Stebbins, G. L., Jr., "The role of hybridization in evolution," *Proceedings, American Philosophical Society*, *103*, 231–251 (1959).

Thompson, D'A. W., *On Growth and Form*, 2nd ed., Cambridge, Cambridge University Press, 1942; abridged ed., 1961.

Timofeeff-Ressovsky, N. W., "Mutations and geographical variation," in J. Huxley (ed.), *The New Systematics*, Oxford, Oxford University Press, 1940, pp. 73–136.

Van Valen, L., "Nonadaptive aspects of evolution," *American Naturalist*, *94*, 305–308 (1960).

Volpe, E. P., "Intensity of reproductive isolation between sympatric and allopatric populations of *Bufo americanus* and *Bufo fowleri*," *American Naturalist*, *89*, 303–317 (1955).

Waddington, C. H., "Genetic assimilation of an acquired character," *Evolution*, *7*, 118–126 (1953).

Waddington, C. H., "Genetic assimilation of the *bithorax* phenotype," *Evolution*, *10*, 1–13 (1956).

Waddington, C. H., "Evolutionary adaptation," in S. Tax (ed.), *Evolution After Darwin*, vol. I, *The Evolution of Life*, Chicago, University of Chicago Press, 1960, pp. 381–428.

Waddington, C. H., "Genetic assimilation," in E. W. Caspari and J. M. Thoday (eds.), *Advances in Genetics*, vol. 10, 1961, pp. 257–293.

Wallace, B., *Chromosomes, Giant Molecules, and Evolution*, New York, W. W. Norton, 1966.

Wright, S., "Evolution in Mendelian populations," *Genetics*, *16*, 97–159 (1931).

Wright, S., "Isolation by distance," *Genetics*, *28*, 114–138 (1943).

Wright, S., *Evolution and the Genetics of Populations*, vol. 1, *Genetic and Biometric Foundations*, Chicago, University of Chicago Press, 1968.

21

Origin of Races, Species, and Higher Categories

THE PRECEDING CHAPTERS surveyed a variety of factors and forces concerned with evolutionary change. At this point it will be helpful to pull the threads together by summarizing our discussion in outline form:

I. Sources of Variability
   A. New Mutations. These include gene mutations and chromosomal mutations or aberrations (pp. 371–378). Aside from the "instantaneous speciation" possible to plants by *polyploidy* (pp. 449–451), chemical changes in genes seem on the whole to produce more radical changes than do chromosomal aberrations.
      1. Effects. (a) *Structure,* (b) *physiology,* (c) *viability,* (d) *fertility,*

and other aspects of the organism and its life may be affected by mutation. One gene may affect several aspects (be *pleiotropic*), and conversely many genes may affect any one aspect. Effects may be small or large. Some of the large effects may be the result of mutations occurring in genes controlling *differential growth rates* of different parts of the body (pp. 452–463).

  2. Mutation Pressure. New mutations are produced at a continual though low rate, thus providing raw materials for evolutionary change.

B. New Combinations of Genes
  1. Mendelian Recombination. Accumulated genetic variability inherited from preceding generations constitutes a store of genetic diversity, which in bisexual organisms is constantly shuffled and reshuffled into ever changing combinations (pp. 362–371).
  2. Gene Flow. Migration of individuals from one population to another may introduce genes new to the population entered by the migrants.
  3. Introgressive Hybridization. If two populations interbreed in the region where they come into contact, a hybrid population may form in this region. By backcrossing with the parent populations, this hybrid population may pass genes from one parent population to the other (pp. 447–449).

C. Norm of Reaction or Reaction Range of a Genotype. The fact that a genotype confers upon an organism some degree of flexibility in meeting environmental demands forms a source of variability (pp. 434–437).

II. Forces Operative Upon the Variability Present in a Population
  A. Tendency to Equilibrium
    1. Mechanisms of Mendelian Inheritance. These tend to establishment and maintenance of equilibrium in a population; this is expressed by the Hardy–Weinberg formula (pp. 387–392).
    2. Stabilizing Selection (Schmalhausen, 1949). This is an aspect of natural selection tending to maintain the status quo of a population already well adapted to its environment. Stabilizing selection may operate by (a) weeding out ill-adapted deviates and (b) favoring the production of a genotype that confers upon its possessors a high adaptability to environmental change, that is, a genotype characterized by *homeostasis*.
  B. Factors and Forces Tending to Disturb Equilibrium
    1. Isolation. Populations are isolated from each other primarily by *geographic–environmental factors* (pp. 437–439) involving

some element of isolation in space. Such isolation may be reinforced by, and in later stages of speciation even supplanted by, various physiological and behavioral adaptations that prevent the interchange of genes between populations. These mechanisms of *reproductive isolation* include selective mating (pp. 439–440). Within isolated populations or subpopulations the following forces may be operative:

2. Genetic Drift. Especially if the subpopulation is small, *chance* may increase or decrease the frequency of a gene or genotype (p. 399). If the genotype increased in frequency in this manner has elements of superiority, the way is paved for the action of natural selection.
3. Natural Selection. Natural selection will act in these subpopulations upon the store of genetic variability submitted to it, tending always toward production of populations having a large capacity for reproduction. This will mean in most, if not all, instances a population adapted to its environment and well "buffered" to withstand some range of environmental diversity.
   a. *Postadaptation.* Insofar as the characteristics that become established in a subpopulation are of value to their possessors, they usually will have the effect of adapting the subpopulation to its particular environmental niche.
   b. *Preadaptation* (prospective adaptation). At times a subpopulation may attain adaptations of wider applicability than merely to the environmental niche in which it lives at the time. If so, the population may take up life in a different environment. Usually this can happen only if the new environmental niche is unoccupied.

FORMATION OF RACES (SUBSPECIATION)

Successful species tend to expand their ranges. As they do so each species becomes divided into subpopulations, as we have stressed. The subpopulations are separated from each other by distance and in many cases by other barriers of different types. Within these subpopulations drift may operate, as mentioned above, and so may natural selection. In many cases the environments faced by the different subpopulations may differ. If so, natural selection (always tending toward adaptation to environment) will eventually produce differences between the subpopulations. The subpopulations have now become microgeographic races or, if the magnitudes of difference and of territory are greater, geographic races (pp. 331–334).

Because of the effectiveness of the barriers producing isolation, animals inhabiting oceanic islands afford particularly instructive examples of this phenomenon. One such example is diagramed in Fig. 21.1, which represents the varieties or races of the golden whistler found on various of the Solomon Islands. The varied colorations and patterns of plumage that have developed in these isolated populations are evident. We may well conclude that we are seeing the results of genetic drift plus, perhaps, some measure of natural selection. Here is an example of the formation of varieties or geographic races comparable to the subspecies of zebras discussed earlier (pp. 328–329) and, on reduced scale, to the races of man (pp. 262–267).

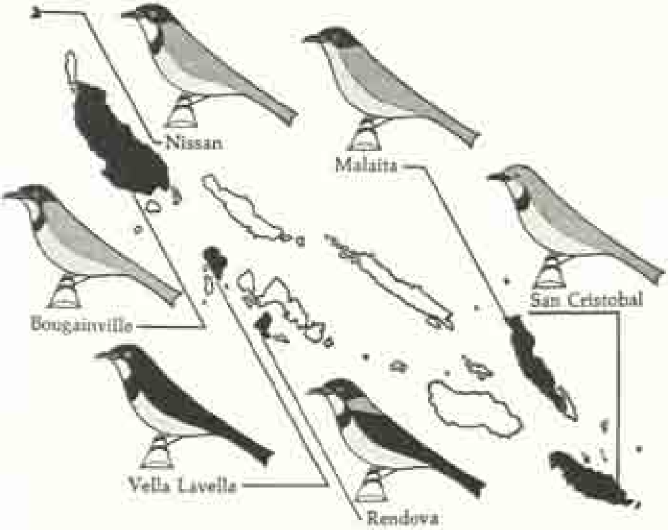

Fig. 21.1. Geographic races of the golden whistler *(Pachycephala pectoralis)* on various of the Solomon Islands. The races differ in black, white, and colored markings. Dark gray areas represent green markings, light gray areas yellow markings. (Redrawn from Dobzhansky, Th., "The genetic basis of evolution," *Scientific American, 182* (1950), 32–41. Copyright © 1950 by Scientific American, Inc. All rights reserved.)

Investigated examples of subspeciation are numerous. A valuable survey of them was made by Goldschmidt (1940), who called the process *microevolution.*

FORMATION OF SPECIES (SPECIATION)

Most biologists believe that the process we have just described, if carried one step farther, will lead to the formation of distinct species.

As we have noted before, the "step farther" is the development of reproductive isolation. If, while isolated, two subpopulations accumulate sufficient genetic differences so that they will no longer exchange genes if and when they come into contact, those subpopulations have become separate species. We have already discussed the roles played in this process by the various types of isolation (pp. 437–442) and the development of methods for the prevention of hybridization when hybrid production would constitute biological waste (pp. 442–445). In our discussion of Darwin's finches we presented an example of how these factors might have worked to produce the diversity observed at the present time (pp. 309–310).

When two populations, arisen in isolation and having at least some measure of reproductive isolation, come together in the same territory, what happens? As mentioned previously (p. 442), perfection of means of reproductive isolation is likely to occur. In many cases the genetic differences acquired while the populations were isolated will have included behavioral (ethological) differences—differences in mating patterns and behavior, for example—that will suppress interbreeding when the populations come together. Natural selection is now likely to intensify these differences, as well as any physical differences connected with the mating process. Sometimes it is observed that when the ranges of two species overlap somewhat but not completely the characteristics by which the species differ from each other are accentuated or increased in the area of overlap, as compared to parts of their ranges in which the two species do not come into contact. Color differences between the species, for example, may be more striking in the region of overlap than in other regions. This phenomenon is called CHARACTER DISPLACEMENT (Brown and Wilson, 1956). It is not of universal occurrence, but when it does occur it frequently seems to be connected with the maintenance of reproductive isolation. If species differences are accentuated, males and females of a species are less likely than they otherwise would be to make "mistakes" and mate with members of the "wrong" species. As mentioned previously, Lack (1947) demonstrated that in Darwin's finches differences in the beak are important in enabling members of a species to recognize each other.

During their period of isolation the populations we are considering may or may not have become adapted to different ecological conditions—food supplies, for example. If they have come to depend upon different foods they will not be in competition now that they occupy the same territory—have become sympatric, in part, at least. That is, they will not be in competition for *food*, though they may be in competition in other ways, e.g., for breeding or nesting territories. To simplify our discussion we shall concentrate on the matter of food.

Suppose that the two species both depend on the same food supply. Will they then be in competition with each other? In the first place we should note that "competition" is a relative term. So long as the food supply is abundant enough to feed all members of both species there will be no real competition (for food). So, other things being equal, the two species can live together in harmony. But such conditions of plenty are not likely to last indefinitely. Adverse conditions may reduce the food supply—by droughts, for example, if the food supply consists of plants or plant products such as seeds. Or, while the quantity of food may not change, the populations of the species dependent on it may become so large that there is no longer sufficient food for all. When this time comes, the species will be in competition with each other.

This brings us to a much-debated idea that, in slightly different versions, is called GAUSE'S LAW (Gause, 1934) or the COMPETITIVE EXCLUSION PRINCIPLE (Hardin, 1960). The essence of the idea is that two species having the same ecological requirements cannot continue to occupy indefinitely the same habitat (environmental niche). The word "indefinitely" is important here. So long as there is enough food for everyone two species may live together very well (remember that we are using food as an example; the shared resource may often be some ecological factor other than food). But the time will come when there is not enough food for all. Then, so runs the thinking, one species will supplant the other. Why? Because it is unlikely that both species will be *exactly* alike in their efficiency in utilizing the food supply or, in more general terms, will have exactly the same degree of adaptation to the environmental niche shared by both. We mentioned that this principle is "much debated." Instances are cited in which it seems not to apply—cases in which two species with apparently the same ecological requirements live together in complete harmony. But perhaps in these cases the shared resources are abundant enough for both. And perhaps in some cases the ecological requirements have not been analyzed in sufficient detail to detect subtle differences. If the shared resources are abundant at present, what will happen when a time of stringency arrives?

Assuming that the stringency is concerned with the food supply, what may happen? (1) The less successful species may become extinct. (2) The less successful species may migrate to other regions or retract its range so that there is no longer an area where it is sympatric with the more successful species. (3) The less successful species may undergo evolutionary change—it may change its food requirements. If it is a seed-eating bird, for example, natural selection may cause the species to develop a stronger, heavier beak so that it can cope with larger seeds than can be utilized by its competitor. Or it may change its food entirely. The stimulus of a dwindling supply of seeds relative to population size is usually credited with having caused some of Darwin's finches to enter a variety of unfinchlike environmental niches: woodpeckerlike insect eating, cactus feeding, and so on (Chap. 14).

Throughout our discussion we have emphasized the point that in sexually reproducing animals, at least, some degree of spatial isolation (geographic–environmental isolation, p. 441) is important at the outset if two subpopulations derived from a common source are to begin the process of acquiring genetic differences.

Lack (1947 and 1949) presented as an example of the necessity for initial spatial separation the case of the finch inhabiting Cocos Island (Fig. 14.2, p. 300). This finch is so unlike other Darwin's finches that it is placed in a separate genus, suggesting that it has been on the island for a long time. Yet this genus contains but one species, which is not even divided into subspecies. Lack wrote: "Cocos resembles the Galápagos in providing varied habitats and in having a great paucity of other land-birds, but it differs in one essential respect: it is a single island, not an archipelago. Hence there has been no opportunity for the geographical isolation of populations and hence no evolution of new species or of an adaptive radiation." The one species present has presumably undergone progressive evolutionary change, but without dividing into separate species. Adaptive radiations of birds occur on archipelagos but not on single oceanic islands; such radiations also occur on continents, which are large enough so that means of geographic isolation other than stretches of ocean are operative. Obviously for other animals than such accomplished travelers as birds smaller barriers and distances will suffice to produce the needed isolation. The point is that some effective means of spatial isolation seems usually to be essential as an initial step in speciation.

EFFECT OF POPULATION SIZE Our discussion of speciation has emphasized the breaking up of large populations into relatively small, isolated subpopulations. Students of the subject are now generally agreed that optimal conditions for evolutionary change are provided by such conditions (see Wright, 1949). Our preceding discussion will have made it evident that a large population not divided in this way would not be favorable for evolutionary change since random breeding of large numbers of individuals results in population equilibrium resistant to change. A change in conditions or an increase in the severity of natural selection acting on such a large population might result in some shift in gene frequencies, changing them to a new equilibrium that then would be maintained as long as the new conditions persisted (Wright, 1931). But the change would be slow and would be reversible whenever conditions altered again. Thus, while some increased adaptation might be brought about by this means, no considerable evolutionary change would be produced.

Conversely, very small populations are not favorable for evolutionary change. If a gene is lost by chance (genetic drift), a very small population will less frequently than a large one reacquire that gene through mutation, since mutation rates are so low. So when a very small population loses reserves of genetic variability these are less likely to be replaced than they are if the population is larger. Owing to genetic drift, also, members of a very small population all may come to possess genetic characteristics of no particular value or that even are deleterious. Thus observers of species inhabiting small oceanic islands find, on the one hand, reduced variability among them and, on the other hand, possession of a variety of seemingly nonadaptive characteristics. The disharmonic nature of the fauna of oceanic islands (p. 295) frequently results in the absence of competitors for a given environmental niche. Therefore, relatively ill-adapted animals can continue to exist—even animals so ill adapted that they would not succeed in the stiffer competition characterizing life on continents. Zimmerman (1948) recorded the unusual number of flightless insects on the Hawaiian Islands and explained many of them as mutant forms that can survive under conditions of reduced competition found on oceanic islands. The influence of size of population on variability was clearly demonstrated in the observation of an isolated colony of butterflies over a prolonged period by Ford (1949). For the first few years specimens remained rare; it was noted that those taken were very constant in appearance. In later years the species increased greatly in numbers: "An extraordinary outburst of variation took place while the numbers were rapidly increasing, and many of the more extreme aberrations were deformed." The author continued, "When the population became stabilized again at the new and high value, uniformity was restored, yet the constant form which was then established differed in appearance from that which existed before the outburst of variability."

Populations broken up into subpopulations provide a means by which nature can make "experiments," to employ a figure of speech suggested by Muller (1949), without risking the fate of the entire species on the outcome of an experiment. The various "experiments" increase the diversity characterizing the species as a whole and, as stressed repeatedly, diversity is essential for evolution.

SEXUAL SELECTION

We have stressed the importance of reproductive isolation in the process of speciation. In the preceding chapter (p. 439) we mentioned the importance of behavioral patterns in reproductive isolation—courtship rituals that served to stimulate reproductive activity, for example. Many times the courtship behavior is connected with structural differences between the sexes: the SECONDARY SEX CHARACTERISTICS. The primary sex characteristics, of course, are the male and female reproductive organs. But in addition to the latter, males usually differ from females in a variety of bodily structures. The bright plumages and elaborate songs of many male birds, contrasted with the duller plumages and relative tunelessness of the females, form a familiar example. Among mammals it is the male lion that develops a mane, the male goat that possesses a beard, and the male deer that displays many-pronged antlers. Darwin felt that such differences between the sexes are not vital enough to the welfare of the species to arise through the operation of natural selection. Hence, he advanced the supplemental theory of SEXUAL SELECTION to explain their development.

Although one would not expect it from the abbreviated title by which the book is usually known, the theory is set forth in detail in Darwin's book *The Descent of Man* (1871). Bodily characteristics with which the theory is concerned may be divided into two main types: (1) those of use in combat between rival males and (2) those used for display purposes.

Male birds and mammals are sometimes observed to fight. Why do they do so? Darwin postulated that males may fight for possession of a female. When this occurred males with superior implements of warfare—horns or antlers, for example—might be expected to be most successful, becoming the fathers of a disproportionate share of the next generation. The male offspring of such fathers might be expected to inherit superior fighting equipment, and if the process continued long enough males of that species might become quite unlike the females in terms of bodily equipment specifically connected with fighting.

But how about the development of features concerned with display—bright colors, ornate plumages, songs, posturing, dancing, and the like? The theory accounts for their development by assuming that females possess an aesthetic sense and employ it in deciding which suitor to accept. Thus the male with the brightest colors, the most intricately ornamental plumage, the most beautiful song, or the most skill in courtship wins the female, in competition with his less endowed brethren. In consequence, he fathers a disproportionate share of the next generation, the males of which inherit superior attractions. If females continue generation after generation to select as mates the brightest-colored or otherwise most ornamental males, male pulchritude may be expected to increase in the species.

Despite the fact that Darwin marshaled a great array of circumstantial evidence in support of the theory, sexual selection is generally considered to have but limited applicability. Since Darwin's day much has been learned about animal behavior (ethology). Evidence accumulates, for example, that in many species when males fight they fight over possession of a certain *territory* rather than over possession of a female. Females then mate with possessors of suitable territories for home or nest, instead of mating with males that have not been able to secure and defend such a territory. Territoriality in animals has been investigated extensively. Interested readers will find surveys of many of these investigators in the popular writings of Robert Ardrey (1961 and 1966). The point we wish to make here is that since any activities making for successful reproduction are important for the success of a species, such activities will be important for *natural* selection itself. No special theory of sexual selection is needed in such cases.

Even when males fight for possession of a female, combat is seldom to the death, an eventuality which would, of course, permanently eliminate one potential father. Furthermore, according to the theory, after the fight is over the victor wins the female. This may or may not be the outcome. Moreover, in species in which the individuals are monogamous (pairing for a season or longer), sexual selection would work only if there were more males than females. If the sexes were equal in number, every male would eventually find a mate regardless of his prowess in combat. In a species in which polygamy is the rule sexual selection might be expected to be more effective, since the successful males would amass the largest "harems" of females or would otherwise mate with the largest number. It is noteworthy that some of the most elaborate displays are possessed by male birds that are polygamous (e.g., the argus pheasant). Under such circumstances, since one male may mate many times and other males not at all, a high premium is placed on elaborate display. Such cases are perhaps our best example of sexual selection in the Darwinian sense.

What we have said about combat also applies in the main to the matter of display on the part of the males for the benefit of the watching females. Evidently some of the display of bright and ornate plumages or other male adornments, accompanied by the courtship ritual appropriate to the species, does have the effect of arousing the female so that she will accept the male. But there is little evidence that females sit in judgment upon the quality of ornamentation or posturing of males of their own species and decide upon that basis which male to accept. Indeed, "in most monogamous birds, display begins only after pairing up for the season has occurred" (Huxley, 1938). And in polygamous species, so long as the courtship behavior is adequately exciting and orthodox for the species, the females usually are rather passive in the matter of which individual male is accepted. On the other hand, evidence accumulates that females detect small irregularities in the courtship behavior and that even seemingly minor irregularities may be sufficient to cause a female to refuse a male. As mentioned earlier such refusal appears to form a means by which interbreeding between closely related species is prevented. And that brings us back to reproductive isolation again.

Returning to such matters as the bright colors and songs of male birds, we note that investigators have found that many of these features do not have as their principal function the pleasing of females. Some bright colors are warning or threatening devices. Observation and experiment on the common robin of England have demonstrated that the red breast, conspicuously displayed during the breeding season, is a device for threatening other males that might seek to invade the territory the individual has claimed for himself. The same is true of conspicuous plumages of other birds that establish home territories. The songs of male birds serve the same purpose. Song has "its prime function as a 'distance threat' to rival males and its secondary function as an advertisement, so long as the singer is unmated, to unmated females" (Huxley, 1942). If the distance threat is unsuccessful and a would-be invader approaches too closely, the proprietor of the territory resorts to display activities, frequently involving its bright colorings, with the apparent object of bluffing the intruder into leaving. If all else fails they may fight. But frequently this fighting is a more or less ritualized performance rather than lethal combat. And usually the proprietor of the territory wins. This is all part of the territorial system mentioned above. As we have implied, if the establishment of home territories is advantageous to the species, in terms of welfare of the young, characteristics that aid in the establishment and maintenance of the territorial system will be furthered by *natural* selection.

Conspicuous colorings of the male also may serve as recognition characters by means of which a female recognizes a male of her own species. And in some cases bright colorings and courtship activities stimulate the reproductive processes themselves. In birds, for example, the activity of the ovaries is largely under the control of the higher brain (cerebral) centers. Psychological stimulation, as by bright colors, mating displays, and dances, is necessary to induce ovulation and hence reproduction. All this is grist for the mill of natural selection.

ORIGIN OF HIGHER CATEGORIES

By the term "higher categories" we refer to the units of classification called genus, family, order, class, and phylum. We need say little about the genus other than to mention that a genus consists of a group of species having certain similarities. We usually say "a group of *related* species," thereby implying the evolutionary interpretation of the origin of similarities stressed throughout this book. We recall, for example, that the genus *Equus* includes horses, donkeys, and zebras. Recall also the attention we gave to genus *Homo* in Chapter 12.

Modern members of genus *Equus* and their prehistoric relatives and ancestors are included in the family Equidae. How do such families arise in evolution?

In the first place we should note that families, and even more strikingly orders, consist of groups of animals that have a characteristic similarity in their manner of life. In earlier discussions we have spoken of environmental (ecological) "niches." A comparable figure of speech for the broader limits of adaptation characterizing families and orders is ADAPTIVE ZONE (Simpson, 1953). Thus modern members of the family Equidae occupy the adaptive zone of being one-toed grazers (Fig. 11.7, p. 213). Because they resembled modern equines in many ways and some were clearly ancestral to them, three-toed browsing mammals extending back to *Hyracotherium* also are included in the family Equidae (pp. 212–216).

According to the views most widely held, the processes of speciation we have described above will lead to the formation of families (and orders) if a species is fortunate enough to find a broad adaptive zone open to it. For most species this opportunity will not be present; for them the processes of speciation lead to adaptation to narrower environmental niches. Such niches may continue to exist for a long time, or they may disappear as the environment changes. If they disappear, occupants of the niche usually become extinct, though a small minority may be able to shift to another niche—another way of life. But occasionally a species is offered a larger opportunity. Apparently this was true of early members of the horse line back in Eocene and Oligocene times; they formed a successful group of browsing mammals in the forests of those times.

As we noted in our discussion of the evolution of the horse (Chap. 11), *Hyracotherium* was very unlike our modern horse. In fact it was more closely similar to certain of the Condylarthra (archaic mammals, p. 205). Why, then, do we place *Hyracotherium* and *Equus* in the same family? We do so because the fossil record indicates that *Hyracotherium* was ancestral to lines one of which led eventually to *Equus*. "A higher category is higher because it *became* distinctive, varied, or both to a higher degree and not directly because of characteristics it had when it was arising. . . . In effect, there was no family

Equidae when eohippus [*Hyracotherium*] lived. The family and all its distinctive characters developed gradually as time went on. . . . There is no particular time at which the Equidae became a family rather than a genus or a species; the whole process is gradual and we assign the categorical rank after the result is before us" (Simpson, 1953).

According to the view we have expressed, once populations of organisms have achieved reproductive isolation they are free to follow their own separate evolutionary destinies. The few fortunate enough to find available a broad adaptive zone undergo far-reaching change until they eventually become as unlike the ancestor as *Equus* is unlike *Hyracotherium*. We visualize these extensive changes as arising through the action of natural selection upon such genetic raw materials as mutations and recombinations. In other words, the origin of higher categories is speciation carried farther; it is "more of the same." This is the view most widely held at the present time; for a dissenting opinion both on the origin of species and of higher categories see pp. 483–484.

Broad adaptive zones are frequently divided into subzones, and so at any given time a taxonomic family is likely to contain subdivisions adapted to these subzones. So in the early Pliocene we find three-toed browsers in the forest and three-toed grazers on the plains (Fig. 11.7, p. 213). In other words, adaptive radiations occur. *Miohippus,* for example, in addition to giving rise to *Parahippus* was ancestral to *Anchitherium* and *Archeohippus,* two "horses" we have not mentioned previously. They became extinct; only *Parahippus* gave rise to a higher type of horse: *Merychippus,* a three-toed grazer. *Merychippus,* in turn, was ancestral to at least six lines of descendants, most of them three-toed grazers; but one of them, *Pliohippus,* was the first one-toed grazer (p. 215).

When we turn our attention from families to orders we find that adaptive zones are still broader. Most orders of mammals, for example, consist of assemblages of families that have some striking characteristic in common—some adaptive trait that characterizes them all. The multitudinous members of the order Rodentia, for example, all have gnawing incisor teeth. Members of the order Cetacea, whales and porpoises, have their well-known adaptations for aquatic life. The order Proboscidea, elephants, mastodons, and their ancestors, we have already discussed (pp. 216–224). Bats, of the order Chiroptera, have wings. Members of the order Carnivora—e.g., cats of all kinds, wolves, bears, weasels, and skunks—have teeth adapted for flesh eating. And so it goes. Of the other orders we mention especially Perissodactyla, the odd-toed hoofed mammals, and Artiodactyla, the even-toed hoofed mammals. Both orders are herbivorous and have developed long legs for running away from enemies. On an earlier page we cited them as an example of parallel evolution (p. 31).

As mentioned earlier, both perissodactyls and artiodactyls are believed to have arisen from Paleocene condylarths (p. 205). What was the fundamental difference between the two lines back when the "parting of the ways" occurred? The big difference was in the manner in which the weight of the body was distributed in the limbs. In perissodactyls the weight-bearing axis runs through the third digit (Fig. 3.2, p. 24). In artiodactyls the weight is borne equally by the third and fourth digits. Presumably this difference in the manner of body support arose among the condylarths. Condylarths starting the trend toward prominence of the third digit gave rise eventually to rhinoceroses, tapirs, horses, and so on. Condylarths starting the trend toward equal prominence of the third and fourth digits gave rise eventually to antelopes, deer, cattle, pigs, buffalo, camels, and their numerous relatives—a much larger assemblage than that of the perissodactyls. Quite certainly the condylarths that started these two trends would not have been so unlike each other that a biologist seeing them would have placed them in separate orders. They might have been regarded as related genera even though the event proved that one was to give rise eventually to the order Perissodactyla and the other to the order Artiodactyla. This emphasizes again the fact that, as Simpson (1953) stated, "Our recognition of a higher category is *ex post facto.*"

In the above example we have assumed that all perissodactyls had one common ancestor and that artiodactyls had one common ancestor. In the case of orders, and especially of classes, there is always the possibility that not all the organisms placed in one order or class did in fact inherit the distinctive trait from a single ancestral group. We must never forget the possibility of parallel evolution. Might not more than one group of condylarths have given rise to lines of descendants in which the weight of the body was shared equally by the third and fourth digits? And in the case of the class Mammalia itself we noted that several lines of therapsid reptiles became essentially mammalian (p. 198). The question of whether a given taxonomic group is *monophyletic* (composed of organisms all inheriting from a common ancestor) or *polyphyletic* (composed of organisms of diverse ancestries) is much debated. No one answer applicable to all orders and all classes can be given, and in many instances definite answers must await further evidence from the fossil record.

There is much more to be said about the evolution of higher categories, but space forbids our saying it. Interested readers are referred especially to Simpson's *The Major Features of Evolution* (1953).

RATES OF EVOLUTIONARY CHANGE

Two groups of factors are involved in determining the rate of evolutionary change: factors within the organism and factors external to the organism.

INTERNAL FACTORS Of the internal factors involved, primacy must be accorded the *rate* with which mutations occur, since mutations are the raw materials of evolutionary change. Other things being equal, we should expect a population in which mutations occurred at a high rate to change more rapidly than would a population having a low mutation rate. In the former population the genetic equilibrium would be much more radically modified (p. 392) by the occurrence of new mutations than in the latter population. Unfortunately, positive evidence of the actual importance of this factor in determining rates of evolution in specific groups of organisms is almost completely lacking. Different evolutionary lines are observed to differ in rate of change, and one evolutionary line may be observed to undergo alteration in rate of change during the course of its history. But there is little clear evidence that differences or changes in mutation rate underlie the differences and changes in the rate of evolution. Indeed, there is some evidence to the contrary (see Stebbins, 1949). At the same time we must remember that our present actual knowledge of mutation rates in wild populations of plants and animals is still very fragmentary.

An interesting discovery in this connection is that of genes that increase the rates at which other genes undergo mutation. The possible evolutionary significance of such genes is discussed by Ives (1950), who describes a high mutation rate gene in *Drosophila*. This gene has the effect of increasing the mutation rates of some other genes about tenfold. Such genes increase the rate of supply of "raw materials" and hence, under some conditions, might affect the rate of evolution.

EXTERNAL FACTORS On the whole, evidence available seems to indicate that differing rates of change are more dependent upon external factors than they are upon internal ones—always provided, of course, that the mutation rate is *adequate* to furnish the raw materials.

Such quantitative studies as have been possible on rates of evolution among prehistoric animals seem to indicate that there is an average rate of evolution approximated by many evolutionary lines. Simpson (1953) has used the term HOROTELIC to designate the average rate of evolution. Other evolutionary lines group themselves around a lower mean rate of evolution termed BRADYTELIC. Clearly, cockroaches, mentioned on a preceding page (p. 163) as having undergone little change since the Pennsylvanian period, are bradytelic. Many forms have changed little over long periods of time during which other forms underwent great changes. Oysters were practically the same 200 million years ago as they are today. Our opossum has changed but little from the closing days of the dinosaurs down to the present.

The term TACHYTELIC has been assigned evolutionary lines in which the mean rate of evolution is above the average, or horotelic, rate. Apparently there are no evolutionary lines in which the rate of change remains permanently at the tachytelic level. This rapid evolution is exceptional in that in any given line it is "effective only during certain crucial relatively short evolutionary episodes" (Simpson, 1949).

What causes a line that has been evolving at its average, or horotelic, rate to make a sudden evolutionary spurt and become for a time tachytelic in its evolution? We have suggested that the answer is probably not to be found mainly in an increased rate of mutation. Rather it seems to lie in the field of what Simpson terms the "organism-environment relationship." Throughout our discussions, for example, we have referred repeatedly to the emergence of vertebrates from life in the water to life on land. This was certainly one of the largest evolutionary changes in all history. The bodily changes involved were clearly associated with meeting the needs of the new environment. Similarly, the changes involved in the evolution of horses, elephants, and many other groups not cited in our brief discussion have been of a nature to adapt animals to conditions of life facing them. Accordingly, it seems that a change in environment is a primary factor in the speeding up of evolution. This change in environment may occur in one of two ways: (1) The environment in which the species is living may change, e.g., as a result of geologic change, or (2) the species may enter a new environment. The entering of new adaptive zones, new ways of life, seems to have provided the stimulus for the most radical and rapid evolutionary changes.

MEGA-EVOLUTION Goldschmidt (1940) divided evolution into "microevolution" (that of subspecies) and "macroevolution" (that of species and genera and perhaps also of higher categories). Simpson (1953) has proposed the additional term "mega-evolution" for really large-scale evolution, such as that of families, orders, classes, and phyla. Evolution at these levels receives much attention from students of the fossil record. Unfortunately, on the other hand, most experimental studies of the evolution of living animals perforce must concentrate on differences between subspecies, species, and at times genera. But principles revealed by these studies can be applied with caution to explanation of the origin of the larger differences between families, orders, classes, and phyla. The large evolutionary changes, connected as we have seen with major changes of environment, constitute the most important accomplishments of evolution. Accordingly, brief consideration of mega-evolution will form a fitting climax to our discussion.

Evidence accumulates that the *extent* and the *rapidity* of evolutionary change are connected. So far as we can judge from the geologic record, large changes seem usually to have arisen rather suddenly in terms of geologic time. This fact has been one of the reasons that a special type of large mutation, "systemic mutation," has been postulated by Goldschmidt (1940) as necessary to account for the large changes observed in evolution. By "systemic mutation" Goldschmidt meant a complete repatterning of the chromosomes—"the arrangement of the serial chemical constituents of the chromosomes into a new, spatially different order; i.e., a new chromosomal pattern." Chromosomal aberrations (pp. 371–376) qualify as systemic mutations under this definition. But are chromosomal aberrations of great importance in producing major evolutionary change? While we have seen that new species of plants may arise suddenly by polyploidy (pp. 449–451), it is noteworthy that chromosomal aberrations frequently produce less marked effects upon their possessors than do gene mutations. In other words, the *arrangement* of the genes present usually makes less difference than does their *nature*, whatever their arrangement in the chromosomes. Hence most students of the subject regard gene mutations as of more importance to evolution than are those "systemic mutations" known to us (i.e., chromosomal aberrations).

In bisexual organisms a radical change would have great difficulty in becoming established in a population. An individual possessing such a change frequently would not be capable of breeding with unchanged members of the population. In such a case at least two "hopeful monsters," as they are sometimes called, of opposite sex would have to arise simultaneously if a new species were to be formed.

What explanation other than that of "systemic mutations" can we find for the rapid occurrence of large changes? As noted before, rapid change may be expected to occur when an organism faces the demands of a new adaptive zone radically different from the one formerly occupied. Under such conditions the severity of natural selection will be greatly increased, with a resultant increase in the rate of evolution. We recall recent experimental evidence (pp. 424–429) indicating that upon occasion natural selection can operate with surprising swiftness. Organisms faced with radically new conditions of life will adapt rapidly to those conditions under the stimulus of a severe natural selection operating upon the raw materials provided in the form of mutations and other types of genetic variability. We recall, also, that such factors as differential growth rates may magnify the effects produced by single mutations.

Rather than confining our discussion to generalities, we summarize current thinking concerning the causation of large evolutionary change in terms of a specific example—that of bats, order Chiroptera. Bats resemble insectivores in many ways but differ from them by having wings. Bats have existed since at least the beginning of the Cenozoic era, and the early bats had wings as well developed as those of their modern descendants (Fig. 21.2). No transitional forms with partially developed wings are known as fossils. If we grant that bats did not arise by a single "systemic mutation" converting certain insectivores into bats "overnight," how can we explain the observed facts?

In the first place, it seems clear that bats did *not* arise by a long process of accumulating slight changes in structure over a great span of time. Bat evolution has been bradytelic in the extreme since early in the Cenozoic era. Indeed, bats' wings have changed so little since the Eocene that if such an extremely slow rate of change had prevailed throughout the evolution of the wing, the time required to develop the wing from a typical pentadactyl limb might be longer than the age of the earth itself (Simpson, 1953). Hence there must have been a tachytelic phase in the evolution of bats prior to the Eocene. Such a spurt in evolution, involving change from one adaptive zone to another, has been termed by Simpson *quantum evolution*.

Can we imagine the conditions that would lead to quantum evolution among certain arboreal insectivores, giving rise to bats? One adaptive zone is that of *flying insect eaters*. That it is not an easy niche to enter is attested to by the fact that only three vertebrates have entered it: small pterosaurs (Fig. 3.1, p. 22), some birds, and bats. Pterosaurs had either disappeared or were about to disappear at the time bats were evolving. At any rate, bats filled the niche much more efficiently than these flying reptiles. Birds are highly efficient occupants of the niche, but most insectivorous birds do their insect feeding by day (as, probably, the pterosaurs did also) while bats are active by night. The adaptive zone found open by these early arboreal insectivores, then, was that of nocturnal, flying insect eaters. We recall that they were already insect eaters, and probably nocturnal, so the change called for was primarily development of the power of flight.

Most of the arboreal insectivores of that day had no capability for entering the vacant zone. But somewhere there must have existed a small group of them, a subpopulation in terms of our previous dis-

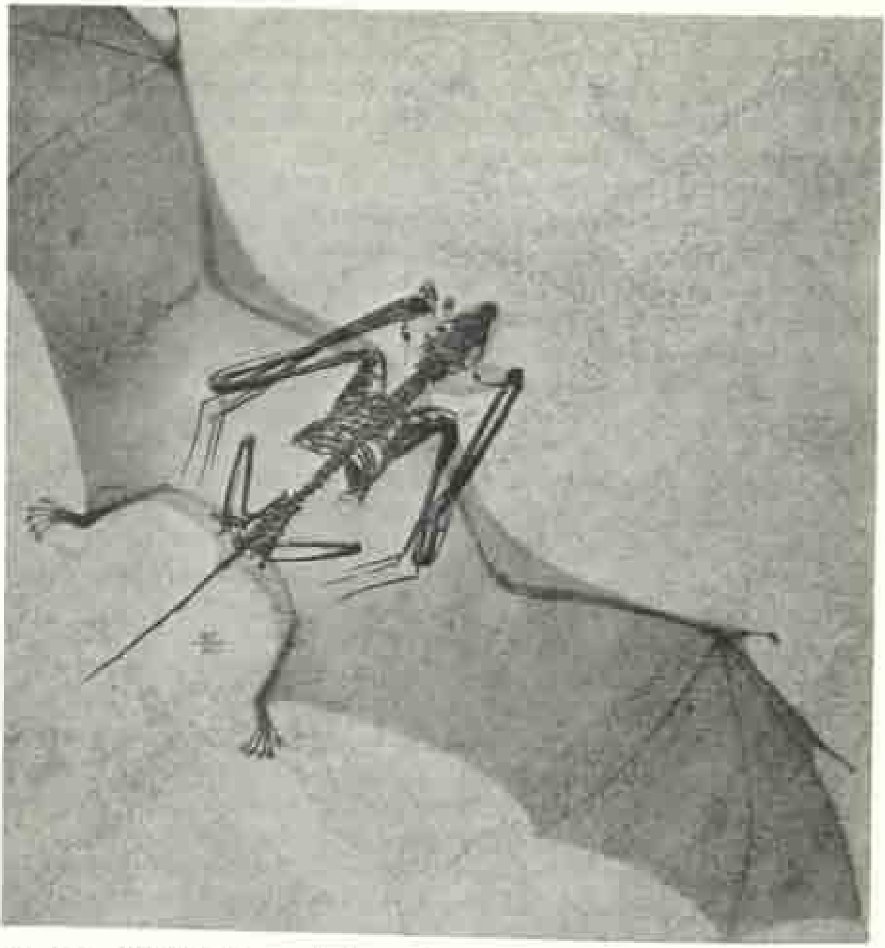

Fig. 21.2. Skeleton of an early Eocene bat. The wings of the fossil are folded but the shadowed outline indicates what their appearance would be if they were extended. (Courtesy of Glenn L. Jepsen. Cover illustration accompanying Jepsen, G. L., "Early Eocene bat from Wyoming," *Science, 154* (1966), 1333–1339. Copyright 1966 by the American Association for the Advancement of Science.)

cussion, that underwent rapid evolution in developing wings. We recall that the division of a population into subpopulations affords optimal conditions for evolutionary change. In some such subpopulation genetic variability of types previously enumerated must have combined to alter the structure of the forelimb toward that of a wing. This alteration may have been spread through the subpopulation by genetic drift; it was certainly favored by natural selection. Probably, though not necessarily, the modified forelimb was first used for gliding from tree to tree; various vertebrates have achieved one type of structure or another for gliding through the air. But gliding does not provide the means for entering the flying insect eater niche. The ancestors that essayed to enter this niche could have done so only by developing forelimbs capable of true flight. This would make possible the pursuit of insects on the wing in a manner not possible to mere gliders. So perhaps the change from gliding to flying was initiated by a change in *behavior*. Probably a certain small group of gliding insectivores attempted to change to an adaptive zone characterized by the active pursuit of insects. The evolutionary role of behavior has not been fully appreciated in the past, but its importance is being recognized increasingly (see the summary in Mayr, 1963, pp. 604–606). Mayr states: "A shift into a new niche or adaptive zone is, almost without exception, initiated by a change in behavior."

Once committed to insect pursuit as a means of obtaining food, the bat ancestors evidently evolved rapidly in perfecting the flight mechanism and their sonar system for locating moving and stationary objects.

Now we can understand why our fossil collections contain no transitional forms between insectivores and bats. If our interpretation is correct, this evolution occurred rapidly, in terms of geologic time, and in only a small population of animals. That small population lived under conditions that did not favor fossil formation. Perhaps no fossils of that small group ever were formed: if some were, they have not yet been discovered.

Using bat evolution as an example we have explained major evolutionary change in terms of small populations entering new adaptive zones and being subjected to severe natural selection. This combination of factors results in rapid change to a new type of organism. Once the zone has been "conquered" the pressure of natural selection relaxes. Consequently, the perfection of details of adaptation proceeds at a slower rate. A slower rate also characterizes the accumulation of the partly adaptive and partly nonadaptive changes that eventually results in the subdivision of the descendants of the new type of organism into subspecies, species, and other subordinate groupings of classification.

We do not wish to imply that other factors are not involved in producing large evolutionary change. But space limitations preclude a further discussion (see Simpson 1953, 1961; Mayr 1963).

L'ENVOI

Now that we have surveyed some of the modern ideas on the means and methods of evolutionary change, let us select some half-dozen books that would be most useful in helping us to delve deeper into these ideas:

We begin with two books that avowedly deal with the plant and animal kingdoms, respectively: G. Ledyard Stebbins' *Variation and Evolution in Plants* (1950) and Ernst Mayr's *Animal Species and Evolution* (1963). Both are most important books.

Then for a lucid and scholarly treatment of general principles: George Gaylord Simpson's *The Major Features of Evolution* (1953), a book often quoted in the preceding pages.

We must include the third edition of one of the most influential books on evolution written in this century: Th. Dobzhansky's *Genetics and the Origin of Species* (1951).

One of the broadest and most readable discussions of evolutionary principles is Verne Grant's *The Origin of Adaptations* (1963).

Then to round out the half-dozen books and to introduce readers to the modern British school of investigators in evolution: E. B. Ford's *Ecological Genetics* (1964).

My apologies to the authors of many valuable books on evolution not included in the above list. Many of these are included in bibliographies at the ends of the chapters in this book. And readers of any or all of the six books listed above will learn of these other books, as well as of the vast literature of original research reports.

Finally we mention the book that was first in directing thinking on evolution into modern channels: Charles R. Darwin's *On the Origin of Species by Means of Natural Selection* (1859). Appropriately and affectionately known to generations of students of evolution as *The Origin*, this book is timeless, and should be read by all. You will find it surprisingly "modern" in basic thinking.

References and Suggested Readings

Amadon, D., "The Hawaiian honeycreepers (Aves, Drepaniidae)," *Bulletin, American Museum of Natural History*, *95*, 155–262 (1950).

Ardrey, R., *African Genesis*, New York, Dell Publishing, 1961, Delta Book 0036.

Ardrey, R., *The Territorial Imperative*, New York, Atheneum Press, 1966.

Brown, W. L., Jr., and E. O. Wilson, "Character displacement," *Systematic Zoology*, *5*, 49–64 (1956).

Darwin, C. R., *On the Origin of Species By Means of Natural Selection*, London, John Murray, 1859. (See p. 6 for listing of reprint editions.)

Darwin, C. R., *The Descent of Man and Selection in Relation to Sex,* 1871. (Available in the Modern Library series, bound in one volume with *The Origin of Species,* Random House, New York.)

Dobzhansky, Th., *Genetics and the Origin of Species,* 3rd ed., New York, Columbia University Press, 1951.

Ford, E. B., "Early stages in allopatric speciation," in G. L. Jepsen, E. Mayr, and G. G. Simpson (eds.), *Genetics, Paleontology, and Evolution,* Princeton, Princeton University Press, 1949, pp. 309–314.

Ford, E. B., *Ecological Genetics,* New York, John Wiley, 1964.

Gause, G. F., *The Struggle for Existence,* Baltimore, Williams & Wilkins, 1934.

Goldschmidt, R., *The Material Basis of Evolution,* New Haven, Yale University Press, 1940.

Grant, V., *The Origin of Adaptations,* New York, Columbia University Press, 1963.

Hardin, G., "The competitive exclusion principle," *Science, 131,* 1292–1297 (1960).

Huxley, J. S., "Darwin's theory of sexual selection and the data subsumed by it, in the light of recent research," *American Naturalist, 72,* 416–433 (1938).

Huxley, J. S., *Evolution: The Modern Synthesis,* New York, Harper & Row, 1942.

Huxley, J. S., *Evolution in Action,* New York, Harper & Row, 1953.

Ives, P. T., "The importance of mutation rate genes in evolution," *Evolution, 4,* 236–252 (1950).

Lack, D., *Darwin's Finches,* Cambridge, Cambridge University Press, 1947. Available as Harper Torchbook TB544, New York, Harper & Row.

Lack, D., "The significance of ecological isolation," in G. L. Jepsen, E. Mayr, and G. G. Simpson (eds.), *Genetics, Paleontology, and Evolution,* Princeton, Princeton University Press, 1949, pp. 299–308.

Mayr, E., *Animal Species and Evolution,* Cambridge, Massachusetts, Harvard University Press, 1963.

Muller, H. J., "Redintegration of the symposium on genetics, paleontology, and evolution," in G. L. Jepsen, E. Mayr, and G. G. Simpson (eds.), *Genetics, Paleontology, and Evolution,* Princeton, Princeton University Press, 1949, pp. 421–445.

Schmalhausen, I. I., *Factors of Evolution. The Theory of Stabilizing Selection,* Philadelphia, Blakiston, 1949.

Simpson, G. G., "Rates of evolution in animals," in G. L. Jepsen, E. Mayr, and G. G. Simpson (eds.), *Genetics, Paleontology, and*

Evolution, Princeton, Princeton University Press, 1949, pp. 205–228.

Simpson, G. G., *The Major Features of Evolution*, New York, Columbia University Press, 1953.

Simpson, G. G., *Principles of Animal Taxonomy*, New York, Columbia University Press, 1961.

Simpson, G. G., *The Meaning of Evolution*, 2nd ed., New Haven, Yale University Press, 1967.

Stebbins, G. L., Jr., "Rates of evolution in plants," in G. L. Jepsen, E. Mayr, and G. G. Simpson (eds.), *Genetics, Paleontology, and Evolution*, Princeton, Princeton University Press, 1949, pp. 229–242.

Stebbins, G. L., Jr., *Variation and Evolution in Plants*, New York, Columbia University Press, 1950.

Wright, S., "Evolution in Mendelian populations," *Genetics, 16*, 97–159 (1931).

Wright, S., "Adaptation and selection," in G. L. Jepsen, E. Mayr, and G. G. Simpson (eds.), *Genetics, Paleontology, and Evolution*, Princeton, Princeton University Press, 1949, pp. 365–398.

Zimmerman, E. C., *Insects of Hawaii*, vol. 1, *Introduction*, Honolulu, University of Hawaii Press, 1948.

22

What of It? An Open Letter to Students

> Those of you who specialize in science will find it hard to understand religion unless you feel, as Voltaire did, that the harmony of the spheres reveals a cosmic mind, and unless you realize, as Rousseau did, that man does not live by intellect alone. We are such microscopic particles in so immense a universe that none of us is in a position to understand the world, much less to dogmatize about it. Let us be careful how we pit our pitiful generalizations against the infinite variety, scope and subtlety of the world.
>
> —WILL DURANT*

THIS CHAPTER WILL be devoted to a brief discussion of the bearing of evolution on some other facets of our intellectual lives—particularly on religion. Such a discussion does not constitute an integral part of a scientific treatise on evolution. If this book were being written for scientists or primarily for advanced students of biology, this last chapter would not be included. But I realize that for many of my readers this book will constitute the only formal excursion into evolutionary literature and that for them evolution is of most interest as it

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*From a commencement address; quoted from *The Reader's Digest*, 74, 94–96 (June 1959).

relates to other aspects of their lives. Of these other aspects religion is the one usually considered most affected by "belief in" evolution. Experience has taught me that when a scientist follows his natural inclination to treat evolution objectively, without reference to such matters as religion, his silence on the subject is frequently misinterpreted as indifference or hostility to religion. Accordingly, after long consideration, I have decided to doff the cloak of scientific objectivity, to sit down at your elbow, so to speak, and to talk over with you some of the implications of evolution for your outlook on life in general, including religion. Although I lay no claim to having originated most of the ideas and viewpoints, I shall write this chapter largely in the first person as a constant reminder that the opinions expressed are personal ones. If some of you find my viewpoints helpful, my inclusion of this discussion will have been justified. Yet you have complete freedom to ignore any of the ideas which seem to you unfruitful or unacceptable.

EVOLUTION AND RELIGION One question about evolution is in the minds of a large proportion of the students who study the subject with me. Occasionally they say something about it in class, or when they stop to see me after class, but for the most part they wonder about it in private or in the small circle of their "bull sessions." This is the question of the relation of evolution to the stories of creation contained in the Bible. As children at home and in their churches they learned about how things started; now at college they hear an entirely different story. That is a really unsettling experience when it involves the book that forms the principal document of our religion. In the light of scientific discoveries must we discard the Bible and with it our religion?

The whole difficulty here lies in the fact that we try to use the Bible in ways for which it was never intended. *It is a book of religion, not a book of science.* If that fact becomes thoroughly established in our minds most of our difficulty vanishes. The Bible as we know it is the work of many writers, writing at widely diverse periods in human history. The contributions of these multitudinous writers are almost inextricably mixed, although modern Biblical scholars have done much to untangle the intertwining strands. All of the writers had this in common: They were interested in religion, not science, and they did their writing long before *anyone* knew anything about modern science. If in writing of religion they had occasion to refer to science they inevitably did so in terms of the science known in their day. So if we piece together these scattered references to the physical world we obtain a picture of the world and solar system as these people thought them to be. And by reading other writers who wrote at the same periods, in

Babylonia, for example, we learn that these ideas of the world were widely current at the time.

As Fosdick (1924) has pointed out, to a considerable extent these people relied on their senses and thought that the universe was as it seemed to be. They thought the earth was flat and that a sea lay under it (Psalm 136:6; Psalm 24:1–2; Genesis 7:11). They thought that the heavens were like a tent or an upturned bowl above the flat earth (Job 37:18; Genesis 1:6–8; Isaiah 40:22; Psalm 104:2). They thought that the earth was stationary (Psalm 93:1; Psalm 104:5) and that the sun, moon, and stars moved through the heavens for the special purpose of illuminating the earth (Genesis 1:14–18). They thought that there was a sea above the sky (Genesis 1:7; Psalm 148:4) and that there were windows in the sky through which the rain came down (Psalm 78:23; Genesis 7:11). They thought various other things that we know to be incorrect, but this sample will suffice.

I hope you will take your Bible and read the references given above. If you do I am sure you will be struck by one thought—that the references to the nature of the universe are purely incidental to the writers' main objectives in writing. The fact that the passages reveal something of the writers' ideas of the universe is entirely secondary and of no consequence to the writings themselves. Many of the references are to the great religious poems we call the Psalms. Their authors were writing of religion; if in doing so they made an inaccurate allusion to the nature of the universe that is a fact of no real importance. Their writing stands or falls on the basis of its worth to religion, not of its worth to science.

What we have just been saying seems pretty obvious. It seems so obviously true to me that I often wonder how anyone can think otherwise. Yet people have thought otherwise, vehemently; and some people still do. Take the matter of the earth's being stationary, for example. When the Copernican astronomy became established, with its proof that the earth revolves (instead of the sun, moon, and stars revolving around the earth as they seem to do), various religious leaders were extremely upset. Father Inchofer, for example, "went off the deep end" as follows: "The opinion of the earth's motion is of all heresies the most abominable, the most pernicious, the most scandalous; the immovability of the earth is thrice sacred; argument against the immortality of the soul, the existence of God, and the incarnation should be tolerated sooner than an argument to prove that the earth moves" (Fosdick, 1926). And even such a generally wise religious leader as Martin Luther attacked Copernicus in these intemperate words: "People gave ear to an upstart astrologer who strove to show that the earth revolves, not the heavens or the firmament, the sun and the moon.

Whoever wishes to appear clever must devise some new system, which of all systems is, of course, the very best. This fool wishes to reverse the entire science of astronomy, but sacred Scripture tells us that Joshua commanded the sun to stand still, and not the earth."

What was the matter with such people? They failed to make the differentiation I am recommending to you. They failed to recognize that the Bible is a book of religion but not a book of science.

This conflict over whether or not the earth revolves seems remote and unreal to us today (though there is at least one religious sect in the United States that still maintains that the Bible must be regarded as the scientific authority on this point). For the most part the church long ago adjusted itself to the new findings of science concerning the physical universe and has found essential religion to be little affected by the adjustment.

This point brings us to evolution—a relative newcomer in the history of science, so far as general attention is concerned at least. Most people had thought little about the subject before 1859, when Darwin published his *Origin of Species*. Then the storm broke all over again! Religious leaders who had become entirely reconciled to the Copernican astronomy, despite its contradiction of Scripture, maintained that the stories of creation in Genesis must be accepted as literal history. What peculiar inconsistency they showed in recognizing that the Bible is not a scientific book in matters of astronomy and yet refusing to recognize that the Bible is not a scientific book in matters of biology! The conflict during the latter part of the nineteenth century was bitter and is not yet completely dead. Yet again, for the most part, religious leaders recognize the Bible for what it is, a book of religion but not a book of science (not even of biology). And again essential religion is little affected by the adjustment.

Since many people still maintain that they regard the creation stories in Genesis as literal history, however, we may be interested to look at them a little. Perhaps you are surprised that I write of them in the plural: the creation "stories." Most people do not realize that the early chapters of Genesis contain two such stories and that they differ greatly. This situation arose from the fact mentioned earlier that the Bible had many authors, writing at different times, and that these varied writings were assembled together without indication of the sources of the various portions and without much attempt to remove inconsistencies and contradictions. By dint of painstaking sleuthing biblical scholars have done much to unscramble the various portions.

The Pentateuch (the first five books of the Bible) is "a composite production made out of sources old and new that have been blended, brought up to date, and supplemented" (Moffatt, 1926). One of the sources was the Judahite or "J" narrative written as the religious book of the kingdom of Judah. The northern kingdom of Israel also had its narrative, usually called the "E" narrative. When the kingdoms were subsequently united their two sacred books were combined and supplemented from other sources. Although neither the J nor the E narrative was written earlier than the ninth century B.C., both tell of the founding of the Jewish nation centuries earlier. The E narrative starts with Abraham, but the J narrative begins with the creation. This most ancient account of creation is now found in our Bible in the second chapter of Genesis—Genesis 2:4b–23, beginning "in the day that the Lord God made the earth and the heavens." I hope you will read this passage. According to this account God made the earth suitable for life ("watered the whole face of the ground") and then "formed man of the dust of the ground." Then he planted a garden for the man Adam to live in, creating a variety of trees for his use and enjoyment. Following that God created the beasts of the field and the fowls and brought them to Adam to name. Afterward God created Woman from one of Adam's ribs. Note that in this account man was created *before* the lower animals were and that the creation was not represented as divided into separate days.

When the J and E narratives were united and added to, the ancient Judahite account of creation was left intact but ahead of it was placed another and differing account of creation: Genesis 1 and 2:1–4a. This later account is the familiar one divided into six days. In this narrative plants were created first (on the third day) and then the sun, moon, and stars were created (certainly an improbable sequence!). Then water-dwelling animals and fowls were created, followed on the next day by beasts and "creeping things." Finally on the sixth day man was created ("male and female created he them"; no mention here of Adam and his rib).

So we find together in these first two chapters of Genesis two entirely different stories of creation, conflicting in detail and chronology at practically every point. Both of them cannot be the literal history of what occurred, so why regard either of them as being that?

Why were these accounts of creation written? Were they intended as textbooks of instruction in the *facts* of creation? Partly, perhaps, and to that extent they are outmoded. But mainly their emphasis is *religious*, not historical. "In the beginning *God* created the heavens and the earth." These early writers were striving to impress the thought of a divine Creator of all things, and the later writers at least were especially intent upon establishing the point that all this was the work of *one* God, not many gods, as most other people of that time believed. In describing the creative work of this omnipotent Deity they wrote in terms of such scientific ideas as were prevalent in their day. Somewhat similar accounts of creation are found in ancient Babylonian documents, but with this important difference: The latter are full of the quarrels of many gods, the fear of primeval dragons, and the like. "When one turns from this welter of mythology to the first chapter of Genesis, with its stately and glorious exordium, 'In the beginning God created the heavens and the earth,' one feels as though he had left miasmic marshes for a high mountain with clean air to breathe and great horizons to look upon. Here a victory was gained for pure religion for which we never can be too thankful" (Fosdick, 1924).

Yes, the first chapters of Genesis are great religion. Why worry about the fact that they are not valid science? The Bible is a book of religion, not a book of science. Acceptance of its religion is in no way dependent upon acceptance of such scientific allusions as it chances to contain. It is just as possible to worship a God who works through natural laws, slowly evolving life on this planet, as it is to worship a God who creates by sudden command. In fact, is not our concept of the Creator immeasurably heightened when we understand more and more of the intricate workings of this marvelous universe? Such a Creator is of far greater stature than would be a miracle worker who created things once and for all back in 4004 B.C.

I know the question in the minds of many of you who have followed me to this point: "Does not science prove that there is no Creator?" Emphatically, science does *not* prove that! Actually science proves nothing about *first causes* at all. As we mentioned in an earlier chapter, science deals with phenomena that can be studied by the physical senses, particularly the sense of sight, aided by all manner of methods of extending those senses: microscopes, telescopes, varied measuring devices, and so on. As we perfect these "tools" and become more and more adept in their use and in the interpretation of the data they supply we learn more and more about the facts of the universe. But we do not arrive at the first causes of those facts. Science enables us to determine that "phenomenon Z" is caused by "phenomenon Y," for example. Further research may demonstrate that "phenomenon Y," in turn, is caused by "phenomenon X." But what causes "phenomenon X"? Researchers work on the problem and eventually discover "phenomenon W," which is a necessary precursor of "phenomenon X." Or perhaps they discover a "phenomenon W" and a "phenomenon V" both of which are necessary if "phenomenon X" is to occur. Now we have to determine the causes of "phenomenon V" and "phenomenon W." And so we go back, step by step discovering more and more causes of causes, but not arriving at first causes ("phenomenon A" of our hypothetical series). Will science, as such *ever* arrive at first causes ("phenomenon A")? That, of course, is a question we cannot answer. If it ever does, science will then be in position to prove whether or not there is a Creator. But that time is certainly far removed from the present. Until it arrives science can neither prove that there is a Creator nor prove that there is not a Creator.

If your question had been: "Do not many scientists believe that there is no Creator?" I should have answered, "Yes." But that is quite another matter from science's proving that there is no Creator. Scientists, like other fallible human beings, *believe* many things not proved by science. If we took a poll of bankers or bakers or machinists or farmers we should find that many of them do not believe in a Creator either. What we *believe* to be true is determined by numerous factors, conscious and subconscious, many of which have nothing to do with scientific demonstration. This statement is as true of scientists as it is of other people. Scientists are not a race apart; they had impressionable childhoods, molded by varying influences, and lead private lives, too. Accordingly, in matters of *belief* they are much like other people. Many of them believe in a Creator; many of them do not. But if they are thoughtful and honest they readily recognize that their belief one way or the other is not equivalent to scientific demonstration.

All right, the question is in your mind; why not ask it? How about me, do I believe in a Creator? As I mentioned earlier, this letter is intended to give you an idea of how things look to me, so the question is not out of order and I shall answer frankly, "Yes, I do." Then, of course, you want to know, "Why?" Probably it would be impossible for me to answer that question fully even if space permitted. Certainly a powerful influence in the direction of belief in God was exerted by the deeply religious home in which I grew up. Suppose we change the question slightly and ask: "Granted that science cannot *prove* either that there is or that there is not a Creator, has my study of science contributed in any way to belief in a Creator?" Again let me warn you that my answer is a purely personal one and that many persons, some of them more profound than myself, will consider it totally inadequate. But after all, this is *my* letter! The more I study science the more I am impressed with the thought that this world and universe have a definite *design*—and a design suggests a *designer*. It may be possible to have design without a designer, a picture without an artist, but *my* mind is unable to conceive of such a situation.

Evidences of design are everywhere about us; the forces producing the design are the so-called "laws of nature," many of which science has disclosed to us and many of which still await discovery. The greatest aspect of design visible to us is in the ordered movement of the stars and planets in this solar system and in other solar systems extending on and on through space—a design almost incomprehensibly large. At the other extreme we find all matter composed of invisible atoms, each of which in turn is a solar system almost inconceivably small, with electrons swinging in orbits around the atomic nuclei somewhat as planets circle about the sun. And everywhere in between these extremes we find evidence of design. Atoms are arranged in definite patterns to form molecules. Molecules arrange themselves in perfect patterns to form crystals. While design is most regular and easily seen in the inorganic world, it is also apparent in living things. The outward patterning observable in the bodies of plants and animals is a reflection of the inner patterning of organs, tissues, and cells; and this patterning in turn is a reflection of the patterning of genes in chromosomes. And the genes are composed of complex but regular arrangements of atoms. And so it goes—everywhere there is design. Everything is conforming to definite forces acting upon it, is obeying natural laws applicable to its particular state. Whence come these natural laws? There we find the Creator.

It may seem to you that we have drifted rather far from the subject of evolution, but in reality we have not. Evolution is part of the great design, or better it is the way in which certain parts of the design are being produced. The principles of evolutionary change discussed in previous chapters are the means employed by the artist to paint the picture—to create the design. In other words, the design was not completed in its entirety at some distant time in the past; it is not completed even yet. The process is a continuing one and the end is not in sight.

Now I am perfectly well aware that some students of evolution conclude that there is no design in evolution, that the whole process is haphazard, without direction or goal. They point to the many evolutionary blind alleys up which animals have gone, only to become extinct. They emphasize the fact that evolution is not steadily progressive, that progress is frequently followed by retrogression. They stress the point that animals do not seem to evolve according to an established pattern, that how animals evolve depends upon the opportunities that chance to befall them. All these things are matters of observation, yet may not they in themselves form part of the pattern? Why should we assume that the laws of the universe, including those of evolution, must be so organized as to reach a goal by what seems to our human minds the most direct route? And why should we conclude that if the natural laws do not seem to be leading toward a goal by what seems to us a direct route there is no goal at all?

Admittedly these are matters of speculation. Perhaps the universe, including evolution on this planet, has no design and no goal. But exercising the prerogative of voicing my own opinion here, I submit that the point is far from proved. My own "hunch" is that all organic evolution is following a pattern that constitutes one portion of the great design of the universe. Of course, I cannot *prove* that such is the case any more than those who hold the opposite view can *prove* their position.

A word seems appropriate at this point concerning the statement sometimes made that the universe and everything in it arose by *chance*. The statement usually carries the implication that if a thing occurs by chance it obeys no laws and follows no design whatever. As should be clear to you from our previous discussions, such an implication reveals a fundamental misunderstanding of the nature of chance. Chance itself follows statistical laws—the laws of probability that we saw to be so fundamental in Mendelian inheritance (pp. 358–371), in population genetics (that is, Hardy–Weinberg law, pp. 387–391), and hence in evolution. These laws are clearly as much a part of the design of the universe as is the law of gravitation. They express the regularities with which phenomena occur. Probable events occur frequently; less probable events occur less frequently. But even highly improbable events do occur. We are told, for example, that on a roulette wheel at Monte Carlo red once came up 32 times in a row. The probability of such an occurrence is about one in four billion. Yet this high degree of improbability did not prevent the occurrence from happening. Similarly, some new evolutionary developments may have been dependent on very "improbable" combinations of genes and mutations. It was doubtless "improbable" that a climbing or gliding insectivore would become possessed of a limb structure for flight (pp. 485–487). Yet, as with the roulette wheel, the improbable event did occur, and having occurred it altered all subsequent evolutionary history of the group by making possible the origin of bats.

We should note that the occurrence of highly improbable phenomena is not a "breaking" of the laws of chance. The laws of chance provide for improbable phenomena as well as for probable ones and even predict the frequency with which improbable events may be expected.

I suspect that one reason some people doubt the existence of a design or pattern in the universe, and all of us discern the pattern so dimly if at all, is because we are part of it. If we imagine a dab of paint on a canvas endowed with the sense of sight, we readily appreciate that this bit of paint would find it well-nigh impossible to see the painted landscape of which it was a minute part. It might well deny that it was part of any landscape or any design at all!

Not only is our perspective likely to be faulty; our knowledge and understanding of the universe are strictly limited by the nature of our sensory equipment and minds. We frequently overlook these limitations. If, for example, you look at a postage stamp through a compound microscope you see only a tiny bit of the stamp, greatly magnified. In your small field of view you see irregular and apparently meaningless blotches of colored ink on a light background. If you move the stamp other patches of ink come into view. Moving the stamp further you see still different ink spots. But these spots do not seem to "add up to" anything. If you never saw a postage stamp except through the high powers of a microscope you might feel entirely justified in concluding that postage stamps have no pattern, that their surface is covered with ink spots distributed at random, forming no design. Here and there, on the other hand, you might by careful study detect arrangements of spots suggesting that a pattern really exists. Yet you would probably not be able to determine the actual nature of the design. We are much in that position as we look at the universe and at evolution. What we perceive and what we understand are strictly limited by the nature of our sense organs and of our minds. If we had different sense organs and different minds our perceptions and understandings might be quite other than they now are. So it behooves us to be cautious about concluding that if we see no pattern in the universe there necessarily must be no pattern. The design may be there; in fact we see evidence that it is. Yet our sense organs and minds may have such limitations that we can no more perceive the complete scope and nature of the design than a student viewing a postage stamp with high-power magnification can make out the face engraved upon it.

What is the outcome of the matter? Personally, it is that I am impressed with *design* permeating all things great and small. For me, design necessitates a designer. And I suspect that the design has a goal —an objective that gives significance and meaning to the whole. But I would not presume to state that I know what that objective is, and I suspect that I am not mentally equipped to comprehend it.

We are touching here on important matters. It is essential for each of us to feel that his life has significance. A sense of being part of a great pattern or plan contributes mightily to one's feeling of personal significance. I have testified to a belief that the universe and everything in it is characterized by design and goal. Perhaps some of you are unable to follow me in this belief. Does that mean that you must regard your own life as without significance, as meaningless and without goal or objective? Not at all. As we shall mention shortly, there has been added to biological evolution in the case of man an entirely new form of evolution: *social evolution*. Social evolution is dependent upon learning and the passing on of acquired wisdom from generation to generation. Whether or not you agree with me that the universe and organic evolution give evidence of purpose and plan, you will recognize readily enough that this new evolution, under human control, is characterized by purpose and plan, "because man has purposes and he makes plans" (Simpson, 1967). The quotation is from the pen of a distinguished contributor to evolutionary thinking who does not agree with the point of view I have expressed—that the universe gives evidence of being characterized by pattern and goal. Nevertheless he finds pattern and goal in man's social evolution sufficient to confer significance upon human life. His discussion merits thoughtful reading.

LOOKING AT MAN AND HIS FUTURE If space permitted I should like to discuss at some length the influence of evolution upon our conception of man and upon human institutions and society. I must content myself with only a few points, however. In the first place, what is the influence of evolutionary thinking upon our ideas concerning man himself? Succinctly, it changes our viewpoint so that we regard man no longer as a "fallen angel" but instead as a "risen animal." Some people, mostly of an older generation, are sincerely distressed by this changed viewpoint. For them there was comfort in the thought that man once was perfect and that his principal task is to regain that perfect state. Then along came knowledge of evolution, demonstrating that the first men were not perfect at all. The more we learn of prehistoric men and their predecessors the more we appreciate the fact that they were less "perfect" in the higher human attributes than are we. This means that man, as found from the dawn of civilization down to the present, represents the finest fruit of the evolutionary process. It does not necessarily mean that no finer fruit ever will be produced, but if superior types of man do arise they will be a new development, not a reversion to a perfect human state once existent but subsequently lost. Accordingly it seems to me that evolution forms the optimistic viewpoint from which to look at man. From this viewpoint we may well believe that the great days for humanity are yet ahead of us, not behind us.

In the preceding paragraph I spoke bluntly of man as a "risen animal." You may have thought that in so doing I was casting aspersion upon man. Not at all; the emphasis is upon the "risen." In other words, we do not regard man as "just an animal"; he is an animal who has achieved heights attained by no other inhabitant of this planet. His use of tools has enabled him increasingly to adapt his environment to himself instead of adapting himself to his environment. His development of spoken and written language has made possible the development of a *social inheritance* that forms a unique addition to his biological inheritance. Through this social inheritance the ideas and achievements of past generations are handed on to descendants, so that one generation builds upon the achievements of its predecessors in a manner totally unlike anything possible to lower animals. Because one generation thus builds on the achievements of its predecessors we have the possibility of *social evolution,* an evolution independent of biological evolution. The importance of this new evolution cannot be overemphasized. It is a unique achievement of man, and it enables him increasingly to control his own destinies.

We noted in earlier chapters that biological evolution varies from animal to animal and from time to time. Some animals, like the cockroach, remain virtually unchanging for vast periods of time while other animals undergo great changes. Still other animals, whose ancestors were highly developed, become simpler in structure, losing many of the ancestral structures—particularly animals that develop parasitic modes of life. Evolution, then, does not always mean *progress,* in the sense in which we usually employ the word, for any particular species. Yet viewed as a whole the broad trend of evolution has been progressive, producing ever higher types of organisms. Thus progress seems to be part of the design to which I referred earlier. But it is not constant in rate, and it does not involve all forms of life equally. While some forms progress, others retrogress, and still others travel down evolutionary blind alleys until they become extinct. At any given time in the earth's history it would be practically impossible for an observer to tell which forms were progressing and which were moving toward extinction. With the wisdom of hindsight we see that in the latter days of the Mesozoic era the dinosaurs were heading for extinction, while the future belonged to the descendants of the insignificant little mammals. But would an observer living at the time have drawn any such conclusion? It seems most unlikely.

So it is with human evolution. Some human societies remain almost static for centuries, others progress rapidly, and still other retrogress. By analogy we may feel confident that some societies will develop into something higher while others, possessing the seeds of their own destruction, will become extinct. But as observers of the current scene we are as little likely to be able to "pick the winner" as would have been our hypothetical observer of the late Mesozoic scene. Thus while we may feel confident that progress will be achieved, we cannot feel confident that it will necessarily be achieved through one particular form of society that we may regard as "best." Perhaps *our* socioeconomic system is in the evolutionary blind alley and peoples of some other cultures are on the road to progress. If it sounds like heresy to suggest that the people with the most and best machines, the most potent engines of destruction, and the most devastating bombs are not surely on the road to progress, recall that the dinosaurs were the most powerful destroyers in their day also! As a student of evolution I find strange fascination in that most controversial of the Beatitudes: "Blessed are the meek: for they shall inherit the earth" (Matthew 5:5). Perhaps the future will demonstrate that this and its companion—"all they that take the sword shall perish with the sword" (Matthew 26:52)—were correct prophecies.

Though we cannot predict with certainty that ours is the society that is on the road to progress, our knowledge of biological and social evolution does provide us with inklings as to what may constitute the hallmarks of progress. First we may note a grave error made by some of the immediate followers of Darwin. Darwin himself stressed the struggle for existence. One phase of this struggle is between individuals for supremacy and survival. Emphasis on this phase led to a school of thought called Social Darwinism, in which great emphasis was placed upon the value of struggle for supremacy between individuals and between societies. This was the "nature red in tooth and claw" concept applied to human life and society. According to this view, ruthless economic competition, the exploitation of "inferior peoples," and warfare constituted the accepted means of evolutionary progress. "Might makes right" and "the devil take the hindmost." So in the decades following publication of the *Origin of Species* the idea of natural selection was taken as justification for all manner of exploitation, economic and military. Those who were strong proved to themselves that they were "the fittest" by exploiting the weak. Cutthroat competition and the exploitation of colonial peoples were the order of the day. No wonder evolution fell into disrepute with sensitive and thoughtful people.

Fortunately a reaction set in. Kropotkin was a leader in this with his *Mutual Aid; A Factor of Evolution* (1917), and other voices were heard calling attention to the fact that *cooperation* is as valid a factor in evolution as is competition (see Allee, 1951; Montagu, 1950 and 1952). On an earlier page (p. 410) we mentioned the "survival value" of cooperation for animals living together in societies. Man is such an animal. Clearly, cooperation between individuals in a society is of the highest value for the success of that society. In fact, we may anticipate that the society will be most successful that achieves the most perfect state of cooperative living. For man, then, cooperation is clearly a hallmark of progress.

How inclusive must this cooperation be? In the time of the biblical patriarchs the members of one family cooperated together, but each family was more or less continually at war with other families. In later times families joined together to form cities, but each city-state was more or less constantly at war with every other one. Eventually the city-states joined to form confederations, and these finally became nations. Each change enlarged the circle within which cooperation was operative. We have now reached the stage when it seems imperative that for the good of mankind nations shall join into superstates, enlarging the cooperative circle still further. At present we seem destined to have two such cooperative circles, one labeled "the East" and the other "the West." The two circles are pitted against each other, but this conflict seems unlikely to be a permanent condition. By some means, peaceful or otherwise, the circles will merge to form one—the "One World" of Wendell Willkie (1943).

Man has become so powerful in controlling his own social evolution, including the invention of means for his own destruction, that nothing short of complete cooperation by all peoples on our "shrinking planet" will suffice. If any people or society finds itself unable to adapt to such cooperative living on a global scale we may predict that that people or society will go the way of the dinosaurs, leaving the earth to those peoples who can make the adjustment. Natural selection is not dead; but in the modern world natural selection is placing a premium on the ability to live cooperatively, not competitively.

Each of us is naturally interested that *his* society shall be among the survivors. It is not pleasant to imagine a future in which our particular race or nation shall have no part. How can we help to ensure that our group shall not be eliminated by natural selection? Evidently, since social evolution is so largely under human control, we can contribute most by supporting all measures that further cooperative living on this earth.

Perhaps all peoples will be able to make the adjustment to cooperative living on a global scale. On the other hand, being as pessimistic as possible for the moment, we may ask: What will happen if *no* peoples can make the necessary adaptation? Then we may feel sure that mankind as a whole will become as extinct as the dinosaurs (probably through self-destruction), leaving our environmental niches free for exploitation by some other form of life. What form of life? We should have as great difficulty predicting that as a dinosaur would have had predicting that the mammals would inherit his place on earth.

But such pessimism is untimely. Possibly the way of progress will be found to lie through some form other than man. We have reason to doubt that this will be the case, however. Increasingly man controls his own evolution, especially his social evolution. Development of cooperative living is one process in that social evolution. We may feel confident that man, or at least some groups of men, will develop the qualities necessary for cooperation on the scale required. If so, there now seems no ascertainable limit to man's supremacy. Each of us can make his own contribution toward creating a mental and spiritual climate in which the necessary cooperation can thrive. "Cooperation begins at home," but it must not end until it encompasses the earth. Each of us can contribute to this end.

In closing this letter on an optimistic note I may be laying myself open to the accusation of being a "Pollyanna." After all, none of us can really foretell the future—most especially the distant future. But optimism seems at least as warranted as pessimism, especially when we recall the brief space in which our social evolution has been operative. In Chapter 8 we noted that on a time scale in which 2000 years becomes the equivalent of one minute, the Age of Mammals (Cenozoic) began about 22 days ago. But man himself has been in existence only about 14½ hours (even when we include the australopithecines as men), and the most ancient civilization for which we have written records began less than two minutes ago. What great social evolution has taken place in that two minutes! This fact gives us confidence that much more will occur before man's time on earth equals that of many of his predecessors. Our social evolution is near its beginning, not its ending. Knowledge of evolution, then, gives us the perspective for optimism. We say that these are "dark days"; thoughtful reading of history will convince us that most if not all days have been dark in the sense we have in mind. But out of the darkness has come progress in the past. That fact gives us optimism that progress also will characterize the long trends of the future.

References and Suggested Readings

Allee, W. C., *Cooperation Among Animals,* rev. ed., New York, Henry Schuman, 1951.

Fosdick, H. E., *The Modern Use of the Bible,* New York, Macmillan, 1924.

Fosdick, H. E., *Adventurous Religion,* New York, Harper & Row, 1926.

Genesis, the first book of the Bible, Chaps. 1 and 2.

Kropotkin, P. A., *Mutual Aid; A Factor of Evolution,* New York, Alfred A. Knopf, 1917.

Moffatt, J., "Introduction" to *The Holy Bible. A New Translation,* New York, George H. Doran, 1926.

Montagu, M. F. Ashley, *On Being Human,* New York, Henry Schuman, 1950.

Montagu, M. F. Ashley, *Darwin: Competition and Cooperation,* New York, Abelard-Schuman, 1952.

Persons, S. (ed.), *Evolutionary Thought in America,* New Haven, Yale University Press, 1950.

Simpson, G. G., *The Meaning of Evolution,* 2nd ed., New Haven, Yale University Press, 1967.

Sullivan, J. W. N., *The Limitations of Science,* New York, Viking Press, 1933. (Available as Mentor MD35, New York, New American Library.

Willkie, W. L., *One World,* New York, Simon & Schuster, 1943.

Appendix

THIS APPENDIX IS a supplement to Chapter 17. It will be especially useful to readers who are unfamiliar with the manner in which the chromosomes are distributed when gametes (ova and sperms) are produced (meiosis) and the way in which this distribution explains the distribution and assortment of genes discussed in Chapter 17.

MEIOSIS As a specific example, we take a heterozygous black male hamster (p. 358). His body cells contain chromosomes arranged in pairs; one member of each pair came from his mother and one from his father. Early in his embryonic development certain cells were set aside to form the sperm cells that he would require when he reached sexual maturity. These primordial

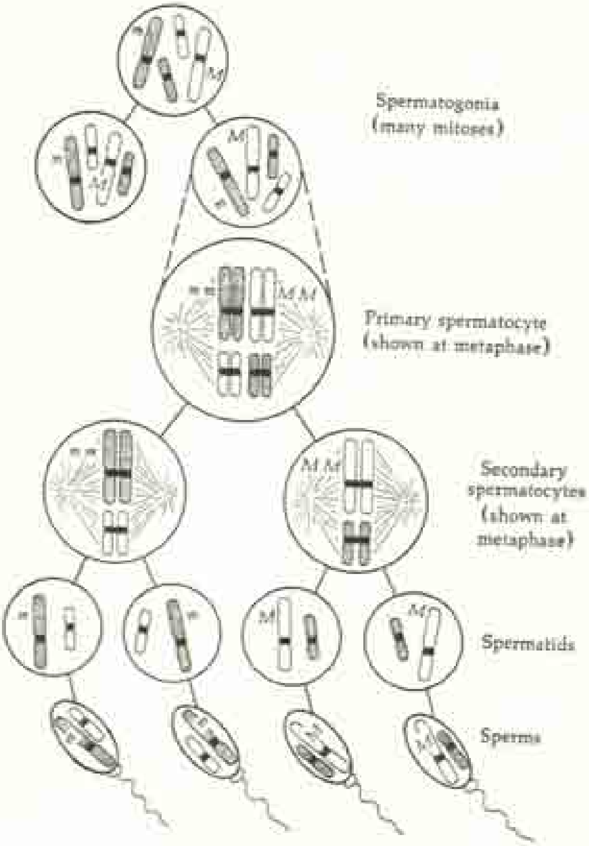
Spermatogonia
(many mitoses)
Primary spermatocyte
(shown at metaphase)
Secondary spermatocytes
(shown at metaphase)
Spermatids
Sperms
M
m
M M
m m

Fig. Ap.1. Meiosis (spermatogenesis) in the male. The genes are in the chromosomes but for clarity the symbols for them are placed outside the latter.

germs cells are called spermatogonia. They contain chromosomes in pairs just as do the body cells. At the top of Fig. Ap. 1 we see spermatogonia containing a long pair of chromosomes and a short pair. (For the sake of simplicity only two pairs are shown.) One member of each pair is white and one is shaded. The white member may be thought of as the one derived from the mother, the maternal one, and the shaded member as the one derived from the father, the paternal one. Somewhere on each chromosome there is a centromere. This is represented as a large dot in the diagram.

The spermatogonia, originally few in number, multiply by the ordinary process of cell division, mitosis. For the sake of simplicity in the diagram only one of these mitoses is indicated, and this is done without including all the stages in the process (see Fig. 7.4, p. 132). Eventually each resulting spermatogonium becomes a primary spermatocyte. By this time each chromosome has duplicated itself. The two resulting duplicate chromosomes

(CHROMATIDS) for the time being are held together by the centromere (Fig. Ap. 1). As the primary spermatocyte prepares to divide, the chromosomes come together in pairs; e.g., the two chromatids representing the maternal "long chromosome" pair with the two chromatids representing the paternal "long chromosome." This pairing is called SYNAPSIS, and during it the chromatids are frequently twisted around each other instead of lying smoothly side by side as shown in the diagram. At this time part of one chromatid may be exchanged with part of another one. This exchange is called CROSSING OVER and has important genetic consequences (pp. 365–367).

Eventually each primary spermatocyte divides to form two SECONDARY SPERMATOCYTES. In this division each centromere remains intact, carrying with it its two chromatids. Thus, in terms of our diagram, each secondary spermatocyte receives the chromatids representing one "long chromosome" and one "short chromosome." The chromatids representing the maternal "long chromosome" (white) go to one secondary spermatocyte; those representing the paternal "long chromosome" (shaded) go to the other. It is important to note that what the "long" chromatids do in this respect does not influence what the "short" chromatids do. In the diagram of the primary spermatocyte we have shown the maternal "long" chromatids on the right and the paternal ones on the left and the paternal "short" chromatids on the right and the maternal ones on the left. This is a matter of chance. About half the time this arrangement would be expected; about half the time the maternal members of both "long" and "short" chromosomes would line up on the same side and the paternal members of both on the other side.

Each secondary spermatocyte divides to form two SPERMATIDS. In this division each centromere splits so that the chromatids separate, one "long" chromatid and one "short" one going into each spermatid. Each spermatid undergoes a metamorphosis, developing a swimming tail, and becomes a mature SPERM cell. We note that each sperm cell contains only half as many chromosomes as did the spermatogonium and that one member of each pair of chromosomes present in the spermatogonium is present in the sperm cell. The number of singly occurring chromosomes in a mature germ cell (e.g., sperm) is called the HAPLOID number. In our diagram the haploid number is 2. On the other hand, the number of chromosomes occurring in pairs in primordial germ cells, and in body cells, is called the DIPLOID number. In our diagram the diploid number is 4. The process we have described is called MEIOSIS; it results in the production of haploid germ cells from diploid primordial cells.

As noted above, we have pictured meiosis in a heterozygous black male hamster. Let us suppose that he inherited the gene for melanism (*M*) from his mother and the gene for grayness (*m*) from his father and that these genes are in the "long chromosomes" (Fig. Ap. 1). When each chromosome duplicates itself to form a pair of chromatids the genes are duplicated too (as shown in the primary spermatocyte of Fig. Ap. 1). In the figure the maternal "long chromosomes," with their duplicated *M* genes, are shown going to the secondary spermatocyte on the right and the paternal "long chromosomes," with their "*m*" genes, to the secondary spermatocyte on the left. Then, when the chromatids separate, each of the pair of spermatids on the right receives a maternal chromosome containing *M* and each of the pair of spermatids on the left receives a paternal chromosome containing *m*. As a result, half the sperm cells in such a heterozygous male receive maternal chromosomes containing gene *M* and half receive paternal chromosomes containing gene *m*. It will be readily appreciated that the hamster in which this occurred might have inherited *m* from his mother and *M* from his father, in which case the *m* gene would have been contained in the maternal chromosome and the *M* gene in the paternal one. But the genetic results would have been the same: Half the sperm cells would contain *M* and half would contain *m*.

Meiosis in females differs from meiosis in males only in details. The primordial germ cells are called OOGONIA. These multiply by mitosis. Even-

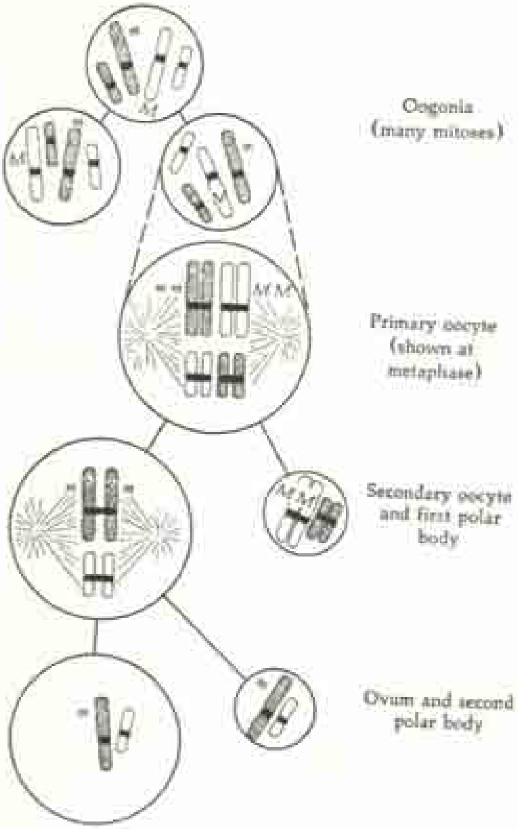
Oogonia
(many mitoses)
Primary oocyte
(shown at
metaphase)
Secondary oocyte
and first polar
body
Ovum and second
polar body
m
M
m m
M M
m
M M
m
m
m

Fig. Ap.2. Meiosis (oogenesis) in the female. The genes are in the chromosomes but for clarity the symbols for them are placed outside the latter.

tually each daughter oogonium increases in size, and the chromosomes duplicate themselves and pair in synapsis, forming a PRIMARY OOCYTE stage (Fig. Ap. 2). Whereas the primary spermatocyte divides into two secondary spermatocytes of equal size, the primary oocyte divides into two cells of very unequal size: the SECONDARY OOCYTE of the FIRST POLAR BODY. The secondary oocyte contains practically all the cytoplasm of the primary oocyte. The polar body containing only enough cytoplasm to enclose the chromosomes. Despite the unequal partitioning of cytoplasm, the secondary oocyte and the polar body contain equivalent chromosomes: In our example each contains the chromatids representing one "long chromosome" and one "short chromosome" (Fig. Ap. 2).

When the secondary oocyte divides, the cytoplasmic division is again unequal, the products being the large OVUM and the tiny SECOND POLAR BODY. But, as shown, each receives one chromatid of each pair contained in the secondary oocyte. The polar bodies disintegrate; hence each primary oocyte gives rise to but one ovum. This ovum contains one chromosome for each pair of chromosomes contained in the oogonium from which it arose. Thus meiosis in the female resembles meiosis in the male in that haploid germ cells are produced from diploid primordial cells.

Figure Ap. 2 pictures meiosis in a heterozygous black female hamster that inherited the gene *M* from its mother and the gene *m* from its father. In the figure the paternal "long chromatids" with gene *m* are shown as passing into the secondary oocyte and the maternal "long chromatids" with the gene *M* as being discarded in the first polar body. The result is that the ovum shown contains *m*. But the fate of the chromosomes when the primary oocyte divides is determined by chance. Thus it is as likely that the paternal "long chromosome" will be discarded in the first polar body as it is that the maternal one will be. In this case the secondary oocyte, and hence the ovum, would contain *M*. Hence in the long run half the ova produced by such a heterozygous female may be expected to contain *M* and half to contain *m*.

As a result of meiosis in both sexes haploid cells are produced. When a sperm cell (haploid) fertilizes an ovum (haploid) the two cells fuse and the diploid number is restored (Fig. Ap. 3). The fertilized ovum undergoes mitosis, dividing into two cells each with the diploid number. Such mitoses

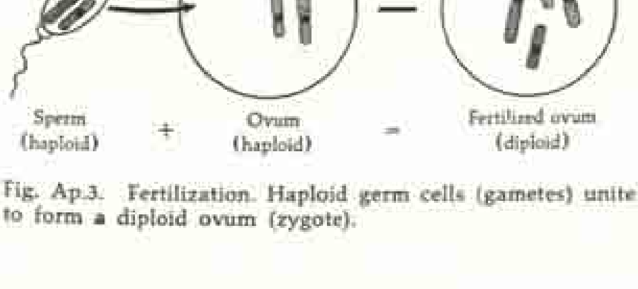

Fig. Ap.3. Fertilization. Haploid germ cells (gametes) unite to form a diploid ovum (zygote).

continue, and eventually an embryo takes shape, the cells all containing the diploid number of chromosomes derived from the fertilized ovum. Some of the cells in the embryo are set aside as primordial germ cells, which in time undergo meiosis, and so the cycle is continued generation after generation.

Returning to the genetic implications of meiosis, we note that the behavior of the chromosomes in this process provides the mechanism for Mendel's "law of segregation" (p. 359)—the means by which each germ cell receives but one member of each pair of genes. The chromosomes also provide the mechanism for the Mendelian "law of independent assortment." This is the principle that different pairs of genes are independent of each other in the manner in which they are distributed to the germ cells.

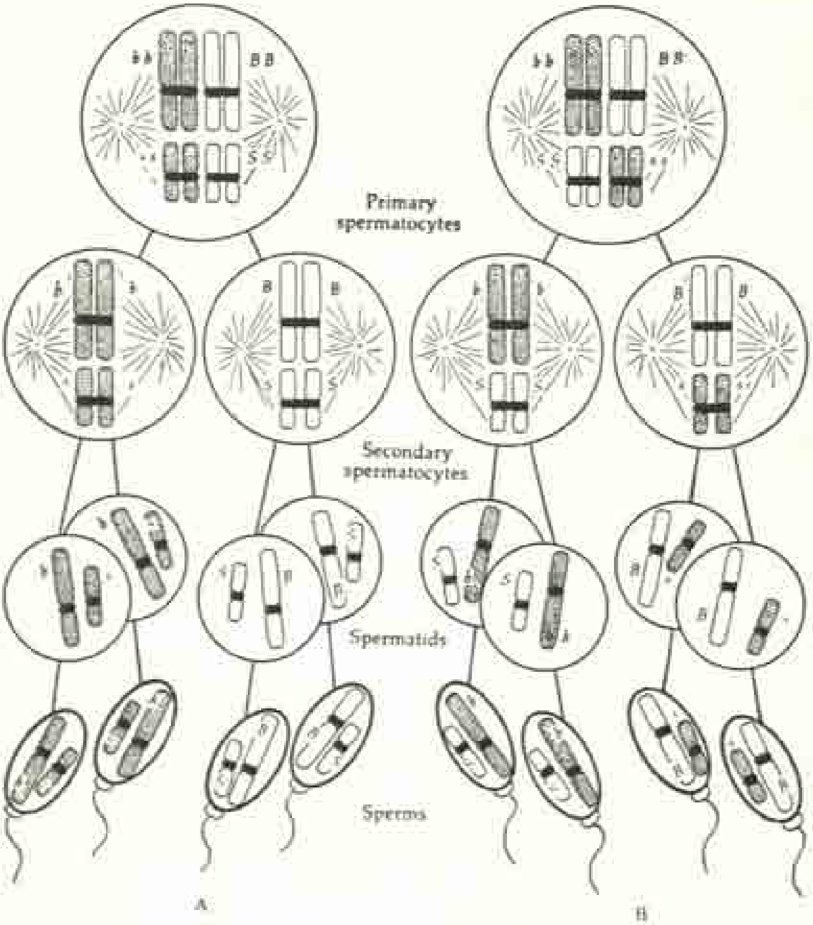

Fig. Ap.4. Chromosomal basis of the independent assortment of genes in meiosis. The genes are in the chromosomes but for clarity the symbols for them are placed outside the latter.

MEIOSIS AND INDEPENDENT ASSORTMENT In the example of independent assortment of genes discussed in Chapter 17, two contrasting pairs of characteristics in guinea pigs were used: (1) black vs white and (2) short hair vs long. Individuals heterozygous for both pairs of genes are black and have short hair. The result of mating such doubly heterozygous individuals to each other is shown in Fig. 17.2 (p. 363). Figure Ap. 4 shows how meiosis produced the four kinds of sperm cells shown in Fig. 17.2. It is assumed that the male in which this meiosis is occurring inherited blackness and short-hairedness from his mother, the opposite characteristics from his father. Thus the gene *B* is in the maternal (white) "long chromosome" and the gene *S* is in the maternal "short chromosome." In the diagram the spermatogonia have been omitted, the first stage shown being the primary spermatocyte. The pairs of chromatids are shown in synapsis. In Fig. Ap. 4A they are lined up in such a manner that the paternal pairs of chromatids are on the left in both cases. As a result two kinds of sperm cells are produced in equal numbers: (1) those containing the maternal "long chromosome" (with gene *B*) and the maternal "short chromosome" (with gene *S*) and (2) those containing the paternal "long chromosome" (with gene *b*) and the paternal "short chromosome" (with gene *s*).

It is to be noted, however, that the arrangement of chromatid pairs in synapsis is a chance affair. Sometimes they will line up as shown in Fig. Ap. 4A, but they are equally likely to line up as shown in Fig. Ap. 4B, with the pair representing the paternal "long chromosome" on the left and the pair representing the paternal "short chromosome" on the right. As a result of this arrangement sperm cells containing one maternal chromosome and one paternal one are formed, with the accompanying *Bs* and *bS* combinations of genes.

The two arrangements of chromatid pairs are equally likely to occur; hence the four kinds of sperm cells shown in Fig. Ap. 4 will occur with equal frequency: *BS*, *bs*, *Bs*, and *bS*. By a somewhat comparable operation of the laws of chance in female meiosis, a doubly heterozygous black, short-haired female will produce ova of these same four types (Fig. 17.2).

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