COMPARATIVE ANATOMY

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To

JAMES F. PORTER

IN ADMIRATION AND
AFFECTION

PREFACE

In one of the frescoes of the Sistine Chapel, Michelangelo portrays Adam after his creation by Jahveh. The frontispiece of this book shows only enough of this painting to suggest that Jahveh had a hand in the event; but how Jahveh accomplished his creative work is left to biologists who have tried to solve by scientific methods the problem of the genesis of the human body. Such scientific investigation is not concerned with the question of the ultimate origin of the universe nor of the presence or absence of God in the cosmos, but with the secondary factors which determine physical events in the physical world.

The scientific evidence which bears upon the problem of the genesis of the human body is derived chiefly from the sciences of paleontology, comparative anatomy, and embryology. These sciences provide the factual support of the evolution theory, which in turn furnishes the clue to the origin of species, including the human species. The remarkable development of these sciences since Darwin's day may be attributed to the conviction of biologists that by means of them light may be thrown on the history of organisms in general and of the human body in particular. Today such courses form standard constituents of the biological curricula of universities and colleges.

American undergraduates study comparative anatomy not so much from interest in lower animals as to gain the best approach to an understanding of human structure and function. The details of comparative anatomy in themselves interest the average undergraduate slightly if at all. To elicit the attention of the student the facts must be interpreted for him and given meaning in terms of function or of genetic relations. The earlier books in comparative anatomy served better as works of reference than as college texts. The multiplicity of facts presented in them tended to confuse the student, who consequently was unable to see the woods for the trees.

The facts presented in this book have been selected chiefly because they throw light upon the important problem of man's place in nature and because they help the student to understand the major functions of his body. If greater stress is laid upon morphological than upon physiological matters, this is done, not because students are more interested in morphological problems, but because the authors are convinced that the central problem of life is that of form. The best approach to this problem is through the study of the changes which the body undergoes in ontogenesis and phylogenesis. College and medical courses in physiology usually assume that the student has a basis for them in a knowledge of the facts of anatomy.

Among the difficulties which confront the teacher of comparative anatomy is the reluctance of students to acquire a vocabulary of technical terms. As far as possible in this text familiar, non-technical language is used. Unfortunately, it is impossible to eliminate technical terms wholly from an anatomical text. In defense of their use it should be emphasized that they avoid much circumlocution and thus make for brevity.

This book is not intended to be used as a laboratory manual but as a text to supplement, interpret, and integrate the facts acquired in the laboratory. The foundations of a course in comparative anatomy should be laid in the laboratory so that the student may have first-hand acquaintance with at least a fish and a mammal—and if possible a tailed amphibian also. For such laboratory work a suitable laboratory manual should be used. Since this text deals comparatively with each of the various organ systems in turn, a laboratory manual which follows this plan is desirable.

For some years this text in mimeographed form has had the benefit of student criticism, with the consequent elimination of many obscurities and inconsistences. The typescript copy has been read by Mr. Edwin Tenney Brewster of Andover, Massachusetts, and by Professors A. Brazier Howell and W. L. Straus, Jr. of the Johns Hopkins University. For what these have done to improve the book the authors are deeply grateful. The authors consider themselves most fortunate to have had the efficient services of John Howell Neal who has drawn or redrawn most of the text figures. All new drawings required for the chapters on reproduction and histology (chapters 2 and 3) were made by Mary B. Marks. Of the text-books in comparative anatomy which have been consulted those of Goodrich, Ihle, Kingsley, Plate, Stempell and Wilder have been especially valuable. For embryological facts and figures, the authors have leaned heavily upon Arey, Corning, Kellicott, MacBride, and Patten. In human anatomy, the text-books of Braus and of Morris have been much used. In histology, Bremer's text, and in neurology, the text-books of Herrick and of Ranson have been most helpful.

In this text-book the discussion of each organ or organ-system is divided into three parts—phylogenesis, ontogenesis, and anatomy. Since it may be assumed that the student has first-hand acquaintance with the anatomy of such a mammal as the cat, and since he presumably is more interested in the human species than in any other mammal, anatomical description in this text emphasizes human anatomy. The descriptions of ontogenesis are also mostly based upon the human embryo. If, as the authors believe, the main purpose of a course in comparative anatomy is to throw light upon the structure of the human body, to ignore it as some text-books do seems like a performance of Hamlet with the Prince left out.

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INTRODUCTION

"Grant a simple archetypal creature like the mudfish or Lepidosiren, with the five senses and some vestiges of mind, and I believe natural selection will account for the production of every vertebrate animal." Darwin to Lyell in 1859.

One of Gauguin's best-known paintings portrays a group of human figures, some standing, some reclining, all in an attitude of melancholy thoughtfulness. The picture might well serve as an illustration of Tennyson's "Lotus Eaters." The painter, however, has entitled it "Where do we come from? Where are we now? Where are we going?" These persistent problems interest the biologist also as well as the poet and artist. "The question of questions," says the elder Huxley, "the problem which underlies all others and is more deeply interesting than any other, is the ascertainment of the place which man occupies in nature and of his relations to the universe of things."

The answer is to be found, if it is to be found at all, through scientific methods of investigation and these seem to point inevitably to some form of evolution. Evolution is the scientific theory that organisms have arisen in nature by "continuous progressive change according to certain laws and by means of resident forces." The theory assumes the mutability of species, their blood relationship to one another, and their origin in accordance with natural law by means of resident factors. For its factual support evolutionists appeal to circumstantial evidence. Geological evidence provides the strongest argument for evolution. For the evidence from the rocks demonstrates that the earth has existed for many millions of years, and that during this time the bodies of organisms have progressively changed, so as to resemble, more and more, the forms now living.

Many objections have been raised against the evolution theory, most of them based upon misunderstanding. A few of these may be mentioned. First, it is asserted that the foundations of the theory are weak, since it depends upon circumstantial evidence. In reply to this objection it may be pointed out that there is no more trustworthy evidence than circumstantial. Courts have found that eye witnesses are notoriously unreliable.

It is sometimes asked how it happens, if there has been evolution, that there are any lower animals left. "Why haven't all monkeys turned into men?" This supposed difficulty is evidently based upon the assumption that evolutionary change is bound to occur, under whatsoever circumstances. Evolution, however, is not the notion that organisms are bound to change regardless of conditions. If an animal is adapted to a particular environment, as the monkey is to the forest, and the forest persists, we should not expect the monkey to change. It may be said in this connexion, however, that evolution is not the theory that man came from a monkey, but that the bodies of the two have had a common animal origin.

Evolution is sometimes said to be "only a theory," as if it were no more than an unfounded guess or pure assumption. On the contrary it is doubtful if any other scientific theory has greater factual support.

A frequent objection raised against evolution is that "it cannot explain the origin of life." It may candidly be admitted that we know nothing about the origin of life. But the primary question of evolution is not how life *began* but how organisms have *changed* since their origin. The geological record leaves us in no doubt as to the fact of change. As to the *origin* of life, L. J. Henderson is probably justified in saying that "any theory about the origin of life is nothing but an unfounded guess."

Again, it is charged that the evolution theory "degrades" man by making a monkey of him. In reply to this supposed objection it may be said that the differences between man and monkeys obtain whatever may have been their origin. "A man's a man for a' that." Values are not determined by origins. The value of the Venus of Melos is not affected by the fact that the block of marble from which the statue was carved came from a quarry.

Our ignorance of the causes of evolution has been considered an objection to the theory. It must be admitted that it has been found easier to prove that evolution has taken place than to explain how it has been brought about. Undoubtedly the nineteenth century belief that Darwin's hypothesis of natural selection explained organic evolution led men to accept this theory more readily than they otherwise would have done. Nevertheless, the case for evolution does not depend upon the ability to state its cause any more than the existence of light depends upon our ability to explain how it reaches the earth.

Of the hypotheses advanced to explain evolution, three have best survived criticism. Briefly stated they are:

1. The Lamarckian hypothesis assumes that organic evolution is due to four factors:

1. The will to live
2. The use or disuse of organs
3. The influence of environment
4. The inheritance of the bodily modifications due to use or disuse or to the influence of environment.

The theory leaves unexplained how bodily modifications effect corresponding changes in the germ cells which transmit inherited traits. On the whole, experimental evidence does not support the assumption of the inheritance of bodily modifications.

2. According the Darwin's hypothesis of natural selection, four factors effect organic evolution:

1. Variation
2. Multiplication
3. Competition
4. The inheritance of useful variations

The theory asserts that no two individuals are precisely alike, and that many more are born than can possibly live. The result is a struggle for existence so severe that only those types survive whose variations favor them in the struggle. These transmit their favorable traits through heredity to their offspring. Carried on through many thousands of generations, such changes would, it is assumed, eventually produce new species.

3. During the twentieth century, Hugo De Vries has advanced a third view, which he calls the Mutation Theory. According to the Mutation Theory, new species arise suddenly, discontinuously, not, as Darwin thought, by slow accumulation of slight differences. De Vries conceives of an organism as a mosaic of traits. A new combination of characteristics constitutes a new species. Breeding evening primroses in his Amsterdam garden, De Vries discovered that mutations are inherited. In other words, mutants breed true. After it arises, a mutant species is subject to natural selection or elimination, but its origin, like that of the fluctuating variations of Darwin, is not dependent upon this struggle for existence. The factors in evolution, therefore, according to De Vries are:

1. Mutation
2. Heredity

The laws of heredity are found to be in accord with the mutation theory. The theory has, however, been criticised as failing to explain the origin of adaptive mutations. Since the cause of adaptive change must affect the germ-cell in order to be inherited, and since biologists are still searching for the factors which determine *adaptive* mutation, it must be admitted that the cause or causes of evolution are unknown. Of the three hypotheses mentioned, the Lamarckian is least acceptable to biologists.

At the present time two divergent conceptions of evolution are held by biologists—*mechanical* and *emergent*.

According to the mechanical conception of evolution, the universe is a machine operating in accordance with "immutable" laws. The entire universe or any part of it consists of particles in motion grouped into various systems. Changes in these groupings constitute what we call evolution. Random samplings of all parts of the universe—possible through the spectroscope—prove that all consist of the same kinds of particles moving in accordance with the same laws of motion. Hence from a knowledge of any part of the universe it follows logically that we can know about all the rest. Reduced to its lowest terms, the universe consists simply of matter and energy. Since the total amount of matter and energy is constant and evolution consists of changes in the distribution of matter, it would be theoretically possible, if we knew enough, to calculate the future changes in arrangement, and predict the course of evolution. Since living organisms consist of the same kinds of particles as are found in the lifeless world and no form of energy peculiar to the living has been discovered, prediction of what will happen in the living world involves no new factors.

Against such a mechanical conception of evolution and of the universe most minds revolt. To accept such a conception would mean the rejection of the most cherished beliefs of mankind. If the universe be a great machine, and nothing more, there is obviously no place for freedom, moral responsibility, or for values of any sort. Might and might alone prevails. In a mechanical world, ideas, ideals, and aspirations, if they existed, could have no more influence in the course of events than do shadows cast on a summer day. But, it may be asked, if the universe is in reality a giant machine in which all changes are only alterations of systems of moving particles, how could there be any evolution at all? Mechanical changes undoubtedly do occur in the universe as, for example, in the revolutions of the planets around the sun. But changes like these are not truly evolutionary at all. A mechanical universe which started with matter and energy could consistently have only matter and energy in the end. From such a point of view, the universe could contain only "eternally old things." But evolution is above all else a process of novelty production. Life and consciousness are such novelties. By no hocus pocus could a magician with matter and energy in his hat conjure such entities as mind or ethics. The mechanists, says Carrel, referring to living organisms, have "built a machine, and like the vitalists, they were the engineers of the machine. Then as Woodger pointed out, they forgot the existence of that engineer." Mechanical evolutionists have made the same mistake.

While the mechanical conception of evolution may appear simple, clear, and logical, it ignores too many facts to be true. The facts accord better with the opposing emergent conception of evolution. According to the doctrine of emergent evolution, evolution is above all else a process of novelty-production. The differences which distinguish higher from lower organisms are not simply quantitative but qualitative. The differences are such that it is impossible to reduce the higher to terms of the lower. Biology is found to be not simply biochemistry and biophysics, but a science in its own right. Mechanism is inadequate to life. The notion that, from a knowledge of masses and motions, the future course of organic evolution might be predicted is ridiculous.

The basis of the emergent conception of evolution is found in the empirical fact that an *organized* whole—such as a living creature—has characteristics which are *qualitatively* different from those of the elements which enter into it. The properties of electrons give no clue to the properties of the atoms which they form. The properties of atoms are not found in the chemical compounds which they form. Add ten carbon atoms together and they have the same properties which one atom has. Add hydrogen atoms together and their properties remain the same. But when carbon atoms are combined chemically with hydrogen atoms, the hydrocarbons formed have entirely new properties. It seems increasingly clear that "an organized whole is more and other than the additive sum of its parts." For the appearance of such new properties science has today no explanation to offer. Indeed, the concept of causation does not seem to apply to such phenomena since cause and effect in the mechanical sense involves a transfer of energy from the cause to the effect. Spaulding has well called this process of formation of new characteristics through the organization of parts into wholes "creative synthesis," since the properties of the whole, or at least some of them, are *new*.

"From separate organic compounds to organized living protoplasm," says G. H. Parker, "we pass from one plane of organization to another and consequently from one set of properties to another. The essential properties of living protoplasm are at present no more to be understood from its constituent compounds than are the properties of water from those of hydrogen and oxygen. The properties of living protoplasm are too manifold for description. They are those properties whereby living protoplasm acts otherwise than its chemical constituents do."

Nineteenth century mechanism failed because it failed to consider the factor of organization. But, as L. J. Henderson says, "there is that which organizes matter in time and space." Consequently, if we are to understand how new properties and capacities arise in nature, we must add to the categories of matter and energy (which were considered sufficient in the nineteenth century) a third category of *organization*. In a strict sense this organizing factor is not "mechanistic." Certainly, organization has up to the present not been recognized as a mechanistic factor by physicists or chemists. But the evidence of such a factor in life is indisputable. Without it, the evolutionary process is incomprehensible.

As mechanical evolution is a contradiction in terms, so emergent evolution is a redundant expression. If there is no emergence there is no evolution. The facts speak loudly in favor of emergent evolution.

"Things living," says Jennings, "behave themselves as if emergent evolution were a true doctrine."

The acceptance of the doctrine of emergent evolution has greatly relieved the minds of many who were depressed by "mechanical mythology" as applied to man. According to emergent evolution, man, like all other creatures, is a unique product. Consequently, man's capacities and powers are what we find them to be in experience, and are not to be logically deduced from the properties of lower animals. The doctrine of emergent evolution also relieves the evolution theory of the charge of materialism. If evolution be an emergent process, as it evidently is, we can understand how the "strata" of reality assumed by pluralist philosophers have arisen. Out of the lifeless has emerged the living, out of the living the conscious, out of the conscious the ethical.

This text-book undertakes to answer the questions "Where do we come from?" and "Where are we now?" on the assumption that the human body has evolved. It seems unnecessary and undesirable to present here the mass of evidence gathered by Darwin and his successors in support of this opinion. Most of the facts stated in this book have a bearing, either direct or indirect, upon it. If this book proves anything, it is that the body of man is best understood in the light of its animal origin.

No attempt is made, however, to convey the impression that evolutionary change can be adequately explained at the present time. The hypotheses of Lamarck, Darwin, and De Vries appear today less satisfactory than they did a generation ago, and biologists are still searching for the causes of adaptive evolution. To give students the impression that we know the factors of evolution is to mislead them. A recent textbook states that "it would seem that the immediate cause for the development of dermal bones from tooth-bases . . . was the early need for teeth and tooth supports in the young carnivorous larvae." Such an assertion evidently raises more problems than it attempts to answer. As a causal factor in morphology, need is probably about as effective as it is in economic life in raising our balance at the bank. A future advantage or possibility may influence human behavior, but teleology is ruled out of scientific explanations.

To determine man's ancestry, three kinds of evidence are used—paleontological, anatomical, and embryological. Except for skeletal structures, paleontological evidence is generally incomplete. Consequently, for the history of other organs morphologists have to depend upon anatomical and embryological evidence. Unfortunately, evidence from these two sources is sometimes equivocal or conflicting. Ontogenesis does not always repeat the history of the race. There are too many exceptions to the fundamental law of biogenesis. When embryological and comparative anatomical evidence conflict with one another, the difficulties of interpretation are enhanced and morphological opinion is likely to be divided. Where evidence conflicts, there is no criterion by which the more reliable clues may be recognized. Anatomists tend to value anatomical evidence more highly; embryologists favor ontogenetic evidence. In such matters, personal opinion looms large. Frequent differences of opinion among morphologists have given the impression that phylogenetic conclusions are exceptionally speculative and uncertain. Much of this divergence, however, is due to lack of sufficient evidence. The history of morphology shows that with increasing knowledge there has been an increase of agreement on controverted issues. As the recent upheaval in theoretical physics has shown, speculation is not peculiar to morphology. Even if it be admitted that the methods of the morphologist resemble those of Sherlock Holmes, this similarity does not invalidate his conclusions.

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COMPARATIVE ANATOMY

CHAPTER I

THE ANIMAL KINGDOM

Since some of the so-called lower animals, living or extinct, more or less resemble hypothetical ancestors of man, some knowledge of them is necessary for a proper understanding of the history of the human body. Moreover, certain highly complex and obscure organs of man are most easily understood in the light of the simpler conditions of lower forms. Even the plants, so unlike us in outward appearance, contribute something to our knowledge of ourselves.

But the organic world is so enormously complex that no human mind can carry its detail adequately without some system by which facts are classified and summarized. Most useful of such systems are those based on natural relations, which, therefore, exhibit the course of evolution of each species, and place it correctly in an evolutionary scheme. For evolution, nowadays, is the key to all genetic animal relationships.

Such an evolutionary scheme begins by dividing all living things into plants and animals. Plants are creatures which contain chlorophyl, and therefore, can, produce or make their food directly out of inorganic materials, or else they are, obviously, such creatures as have lost their chlorophyl and adopted the feeding habits of the simpler animals. Animals may or may not have descended from plants; only rarely do they contain chlorophyl, hence all their structure and habits rest on other means of obtaining food. There are, however, many simple organisms; for example, the slime molds, which are as much one as the other, plants or animals indifferently. Even some of the higher plants, like the venus fly-trap, catch and devour insects; and some of the unicellular algae also feed like animals.

The animal kingdom as a whole is commonly divided into about a dozen phyla, the precise number and the precise definitions of which have not yet been agreed upon by taxonomists. These phyla, in turn, are split into classes, the classes into orders, the orders into genera, and the genera into species. It is sometimes convenient, also to recognize sub-orders and sub-classes, and to combine similar genera into families.

Scientific naming is by genera and species, a scheme devised by the great naturalist Linnaeus, or Linné, about the middle of the eighteenth