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FOUNDATIONS OF BIOLOGY

BY

LORANDE LOSS WOODRUFF

PROFESSOR OF PROTOZOÖLOGY IN YALE UNIVERSITY

FOURTH EDITION

New York

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PREFACE TO THE FOURTH EDITION

The opportunity to reset the entire text in larger form for the fourth edition of the *Foundations of Biology* has made it possible to introduce recent advances in biological science and the various constructive suggestions offered by biologists in many different institutions who have used the book in their courses, as well as once again to take advantage of the knowledge and experience of my colleagues in the Osborn Zoölogical Laboratory at Yale University. There are few pages on which changes have not been made, particularly looking toward simplification of expression and reduction of technical terms to the residual minimum inherent in exact scientific presentation. However, the body of the text has been altered chiefly by assigning separate chapters to certain important problems, thereby allowing for more adequate discussion, and by a change in the order of treatment of several subjects so that it may more readily accord with certain limits imposed by organized laboratory study. These additions and other changes have involved a further emphasis on the zoölogical aspect of biology, particularly in relation to Man himself. Accordingly the book is still better adapted than before for courses in general zoölogy.

Furthermore, the illustrations and their legends have been thoroughly revised. Many figures have been redrawn and still more new ones have been made by Mr. R. E. Harrison, so it is believed that also in this phase of the book the experience derived from many sources has been incorporated. Acknowledgments are due to the authors and publishers of the following works, who generously have supplied some of the new illustrations included in this edition: Calkins' *Biology of the Protozoa* (Lea & Febiger); Chapman's *Handbook of the Birds of Eastern North America* (D. Appleton & Co.); Chandler's *Animal Parasites and Human Disease*, Curtis and Guthrie's *General Zoölogy* (John Wiley & Sons); Martin's *Human Body* (Henry Holt & Co.); Morgan's *Evolution and Genetics* (Princeton University Press); Metcalf and Flint's *Destructive and Useful Insects* (McGraw-Hill Book Co.);

Peabody and Hunt's *Biology and Human Welfare*, Lindsey's *Evolution and Genetics*, Newman's *General Zoölogy*, Smith, Overton, Gilbert, Denniston, Bryan, and Allen's *General Botany* (The Macmillan Co.); Rockefeller Foundation's *Annual Report*; and Thompson's *Concerning Evolution*, and Wilson's *Physical Basis of Life* (Yale University Press).

Professor Baitsell again has read the complete manuscript, and has incorporated all the necessary changes in a new edition of his *Manual of Biology*, designed to supply the details of morphology and physiology of selected types, as well as directions for their study in the laboratory, which obviously would be out of place in the present book.

Finally, it should be emphasized that the utmost care has been exercised not to obscure the basic spirit of the book in its presentation of a broad survey of the "fundamental principles of biology for the college student and the general reader," which has been so widely accorded the approval of instructors in biology.

YALE UNIVERSITY,
April, 1930.

L. L. WOODRUFF.

PREFACE TO THE FIRST EDITION

The present volume brings together in brief form the fundamental principles of biology for the college student and the general reader.

It is well recognized that there is no adequate substitute for detailed laboratory work on the structure and physiology of representative organisms as a means of affording a first-hand knowledge of the facts and methods of biology. However, the author has realized with increasing force that the student's correlation of the laboratory data from day to day and accordingly his appreciation of the broader aspects of the subject are greatly enhanced by a synchronous 'running account' of the underlying principles. The material in this volume has proved to be of great value for this purpose in a course on General Biology elected each year by several hundred Yale undergraduates.

The large problems of life are common to both zoölogy and botany, and therefore both animals and plants have been drawn upon for illustration and discussion. This method of presentation accords with the author's conviction that the general biological viewpoint is the most favorable means of approach both to a broad knowledge of living phenomena as a part of a 'liberal' education, and to more advanced studies in zoölogy and botany which are prerequisite for medicine, forestry, etc. As is natural, however, the zoölogical aspect has been emphasized since it affords indispensable data for the interpretation of Man himself. For courses in general zoölogy, therefore, the book will be found adequate in its treatment of animals, while chapters VIII and IX on plants may readily be omitted without breaking the continuity of the discussion.

The author is indebted, of course, to innumerable sources for the facts and principles outlined. The content has grown by accretions year by year. Nearly all the standard treatises have been drawn upon, but those which have been most generally suggestive are listed in the bibliographies of the respective chapters. Specific mention, however, should be made here of Professor Wilder's *History of the Human Body*, Professor Conklin's *Heredity and En-*

vironment in the Development of Men, Professor Ganong's Textbook of Botany, and Professor Coulter's Evolution of Sex in Plants.

The author has availed himself of the constructive criticism generously given by Professor B. W. Kunkel of Lafayette College, Professor E. H. Cameron of the University of Illinois, and his colleagues at Yale, Professors R. G. Harrison, W. R. Coe, A. Petrunkevitch, F. P. Underhill, Henry Laurens, G. A. Batsell, W. W. Swingle, and Dr. J. W. Buchanan, who have read the book either in manuscript or in the mimeographed form in which it has been used by the Yale classes. And Professor Batsell's interest in the work of the courses has made it possible to impose upon him the added task of reading the book at each stage of its development. Miss Hope Spencer of the Yale Laboratory has assumed with enthusiasm a considerable portion of the editorial work involved in seeing the book through the press. Finally, the author's indebtedness to the criticism and coöperation of his wife, Margaret Mitchell Woodruff, must not remain unmentioned, though it cannot be adequately expressed.

The original illustrations as well as those from other sources which have been modified or merely redrawn are, with a few exceptions, the work of Mr. R. E. Harrison, Yale, 1923. In most cases these figures have been selected because of their proved pedagogic value. Acknowledgments are due to the authors and publishers of the following works, from which illustrations have been reproduced by permission: Coulter, Barnes, and Cowles' Textbook of Botany, Coulter's Plant Life and Plant Uses (American Book Co.); Kellcott's Social Direction of Human Evolution, Jordan and Kellogg's Evolution and Animal Life, Darwin's Life and Selected Letters, Huxley's Life and Letters (D. Appleton & Co.); Folsom's Entomology, Gager's Fundamentals of Botany (P. Blakiston's Sons & Co.); Jennings' Behavior of the Lower Organisms (Columbia University Press); Bergen's Foundations of Botany, Bergen and Caldwell's Practical Botany, Bergen and Davis' Principles of Botany, Densmore's General Botany, Hough and Sedgwick's The Human Mechanism, Linville and Kelly's General Zoölogy (Ginn & Co.); Kellicott's General Embryology, Sedgwick and Wilson's General Biology (Henry Holt & Co.); Morgan's Physical Basis of Heredity (J. P. Lippincott & Co.); Romanes' Darwin and After Darwin (Open Court Publishing Co.); Conklin's Heredity and Environment in the Development of Men (Princeton University

Press); Conn and Budington's Physiology and Hygiene (Silver, Burdett & Co.); Coulter's Evolution of Sex in Plants (University of Chicago Press); Abbott's General Biology, Buchanan and Buchanan's Bacteriology, Campbell's University Textbook of Botany, Ganong's Textbook of Botany for Colleges, Hegner's College Zoölogy, and Introduction to Zoölogy, Holmes' Biology of the Frog, Huxley's Physiology, Lankester's Treatise on Zoölogy, Lull's Organic Evolution, Packard's Textbook of Entomology, Parker's The Elementary Nervous System, Parker and Haswell's Textbook of Zoölogy, Parker and Parker's Practical Zoölogy, Scott's The Theory of Evolution, Shipley and McBride's Zoölogy, Verworn's General Physiology, Walter's Genetics, and The Human Skeleton, Wiedersheim's Comparative Anatomy of Vertebrates, Wilson's The Cell (The Macmillan Co.). To the Macmillan Company is also due the author's appreciation of the liberal attitude which they have assumed in all the arrangements attendant upon the publication of the book.

L. L. WOODRUFF.

YALE UNIVERSITY,
May, 1922.

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FOUNDATIONS OF BIOLOGY

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CHAPTER I

THE SCOPE OF BIOLOGY

Science is, in its source, eternal; in its scope, unmeasurable; in its problem, endless; in its goal, unattainable. — *von Baer*.

THE oldest as well as the most obvious classification of the objects composing the world about us is into non-living and living; and the knowledge accumulated during many centuries in regard to the former is to-day represented in the physical sciences, while that of the latter comprises the content of BIOLOGY, the science of matter in the living state. Biology, like all science, has as its ultimate object the description of its phenomena in terms of what may be regarded as basic concepts — matter and energy acting in space and time; but it is needless to say that the attainment of this object is not imminent in any department of knowledge, and least so in the science of living things. These exhibit a state of matter and energy which altogether transcends the classifications of physicist and chemist to-day — a condition which expresses in its highest manifestations what we call our ‘life.’

Whether the ‘riddle of life’ will ultimately be solved is a question which everyone would like to answer but only the rash would attempt to predict. Suffice it to say that biologists who are on the firing line of progress to-day are directing their attention solely to the description and measurement of the phenomena exhibited by living things — those phenomena which distinguish life from lifeless — in an attempt to relate them to the familiar and more readily accessible phenomena of which we have some exact knowledge in the realm of the non-living. But this should by no means be taken to indicate that biologists do not recognize the stupendous problems they face, or do not appreciate to the full — indeed more fully than others — the enormous gap that separates even the simplest forms of life from the inorganic world.

Our present interest, however, is not in discussing the theoretical

goal of biology, but in drawing in bold strokes an outline picture of the present-day knowledge of the subject which represents the cumulative results of the application, to problems of life, of the scientific method. This method is not peculiar to science, but is merely a perfected concentration of our human resources of observation, experimentation, and reflection. Thus far this has been a most productive method and certainly has given no evidence that its usefulness is being exhausted. But, of course, "in ultimate analysis everything is incomprehensible, and the whole object of science is simply to reduce the fundamental incomprehensibilities to the smallest possible number."

A. ORIGIN OF LIFE LORE

The foundations of the scientific study of living nature were laid by Aristotle and Theophrastus over 2000 years ago. On the basis of collecting, dissecting, classifying, and pondering they reached generalizations, many of which have but recently been put on a firm basis of fact. Indeed, they seem to have raised nearly all the broad questions which are fundamental to-day; but from the Greeks until about the fifteenth century there is little to record. There were many additions to the body of knowledge during this long slumber period, but fact and fancy were so intermingled that the truth was largely obscured. (Figs. 272, 273.)

The feeling that, though Man is of nature, he is still apart, was expressed at the revival of learning, during the sixteenth century and later, in the broad classification of all knowledge as history of nature and history of Man; the former recording the "history of such facts or effects of nature as have no dependence on Man's will, such as the histories of metals, plants, animals, regions, and the like"; the latter treating of the voluntary actions of men in communities. Thus all record of facts was either NATURAL HISTORY or civil history. From this general field of natural history the present-day sciences of astronomy, physics, chemistry, geology, and biology became separated as relatively independent bodies of facts as each gained content, clearness, and individuality. Astronomy, physics or natural philosophy, and chemistry were set apart first owing to the fact that their material was more readily susceptible to mathematical and experimental treatment, thus leaving the histories of the Earth, animals and plants, or so-called observational sciences, as the residue for natural history.

It remained, however, for Lamarck in particular, during the opening years of the nineteenth century, to attain a vision of the unity of animal and plant life — the unity of zoölogy and botany — and to express it in the term BIOLOGY. But biology is something more than a union of botany and zoölogy under one name — for it endeavors, in addition to describing the characteristics of animals and plants, to unfold the general principles underlying both.

B. BIOLOGICAL SCIENCES

Thus the biologist has as his field the study of living things — what they are, what they do, and how they do it. He asks, how

FIG. 1. — The chief divisions of Biology.

this animal or that plant is constructed and how it works — and this he attempts to answer. He would like to ask, and often does ask, why it is so constructed and why it works the way it does, but then he passes beyond the scope of science into the realm of philosophy.

These queries of the biologist reflect the two primary viewpoints from which biological phenomena may be approached: the *morphological* in which interest centers upon the form and structure of

living things; and the *physiological* in which attention is concentrated upon the functions performed — the mechanical and chemical engineering of living machines. Clearly, however, it is impossible to draw a hard and fast distinction between morphology and physiology because in the final analysis structure must be interpreted in terms of function, and vice versa. But again, the fields of morphology and physiology naturally resolve themselves into special departments of study, depending on the level of analysis of structure or of function which is emphasized. Thus MORPHOLOGY stresses the general form of the animal or plant; ANATOMY, the gross structure of individual parts, or *organs*; HISTOLOGY, the microscopic structure of organs, or *tissues*; CYTOLOGY, the component elements of tissues, or *cells*, and the physical basis of life, or *protoplasm*. Similarly, PHYSIOLOGY investigates the activities of animals and plants, the functions of organs, the properties of tissues, the phases of cell life, and finally the physico-chemical characteristics of protoplasm. So much for the study of the adult individual animal or plant — but this is not all. The origin and development of the individual, GENETICS and EMBRYOLOGY; and the origin and development of species, ORGANIC EVOLUTION, are other wide fields which must be approached from both the structural and functional aspect if any real advance is to be made toward a comprehensive appreciation of life. (Fig. 1.)¹

Thus, just as the various physical sciences have expanded and become specialized until they are beyond the grasp of a single man, so biology and its subdivisions, or the BIOLOGICAL SCIENCES, are now distributed among many specialists. Although specialization results in a narrowing and isolating of the fields of study, as deeper levels of investigation have been reached in all the sciences there has been a tendency for the basic phenomena to meet on the common ground of the fundamental sciences, physics and chemistry — for in the last analysis the biologist must assume as a *working hypothesis* that the properties of protoplasm are the resultant of the properties and interrelationships of the chemical elements which compose it. “In one direction, supported by chemistry and physics, biology becomes biochemistry and biophysics. In a contrary direction it forms a connection with the psychical sciences which relate to human nature, with psychology

¹ In order not to interrupt the continuity of the narrative, formal definitions of technical terms are usually omitted from the text. See the GLOSSARY, Appendix III.

and sociology, with ethics and religion." Indeed, it is not an exaggeration to regard all knowledge as really biological, since the process of knowing is a life process which is basal to every art and its practice, to every science and its application, and to every philosophy and its exposition.

C. BIOLOGY AND HUMAN PROGRESS

Probably the value of a knowledge of biological principles, and of the order of nature in general, cannot be better emphasized than in the words of the founder of modern methods of biological teaching. Huxley wrote: "Suppose it were perfectly certain that the life and fortune of every one of us would, one day or other, depend upon his winning or losing a game of chess. Don't you think that we should all consider it to be a primary duty to learn at least the names and the moves of the pieces? . . . Do you not think we should look with disapprobation upon the parent who allowed his child, or the state that allowed its members, to grow up without knowing a pawn from a knight? Yet it is a very plain and elementary truth that the life, the fortune, and the happiness of every one of us, and, more or less, of all who are connected with us, do depend upon our knowing something of the rules of a game infinitely more difficult and complicated than chess. It is a game which has been played for untold ages, every man and woman of us being one of the two players in a game of his or her own. The chessboard is the world, the pieces are the phenomena of the universe, the rules of the game are what we call the laws of Nature. The player on the other side is hidden from us. . . . To the man who plays well, the fullest stakes are paid with an overflowing generosity. And one who plays ill is checkmated."

The contributions of the biological sciences to human welfare — the rules of the game of life — we shall consider later more fully. At this point it is merely necessary to emphasize that biology affords certain fundamental principles which are of universal application — principles of so great importance that they have revolutionized modern thought and action in nearly every field of human endeavor, and color civilized Man's entire mental outlook on the world about him. Biology is the supreme agent of adjustment of human life to human life-conditions, and life goes on solely by reason of the adequacy of such adaptations. Specifically, of course, biology forms the indispensable foundations of

medicine — health, and of agriculture — food and raiment. Together these spell wealth: without them we would be poor indeed.

Thus biology meets many of the physical needs of mankind and so adds enormously to the basis of human welfare, but it also has another equally important aspect. The appeal of biology for its high place as a contributor to the progress of humanity *combines* its practical gifts with the more subtle development of aesthetic values which naturally flow from the pregnant thought of the unity of nature — the oneness of life — based on the firm and ever-increasing sense of control as knowledge grows, which “robs life of none of its mystery but rather serves to link it securely with the larger mystery of the universe and the Infinite back of it all.” Man, though one with all living beings, has the unique and all-important power consciously to study the ways, to direct the forces of nature, and to adapt himself to them. When the grandeur of this view of life to which biology leads is appreciated to the full, no reassurance is necessary of Man’s commanding position as an intellectual, emotional, and moral being.

CHAPTER II

ORGANIZATIONAL UNITS OF PLANTS AND ANIMALS

Science never destroys wonder, but only shifts it, higher and deeper. — *Thomson*.

WITH a synoptic view of the scope and importance of biology before us, we now turn directly to the study of life itself in the only form it is known — the bodies of plants and animals.

A thin slice of material from the surface of the skin of a Frog or the leaf of a Buttercup when examined under the microscope shows the same general structure. Each appears to be composed of innumerable small bodies, no two of which are exactly alike

FIG. 2. — Cells, highly magnified, from the surface of the Frog's skin (A), and a plant leaf (B).

even in the same piece, though all are similar enough to be one and the same type of unit. And if we extend our study to other parts of the Buttercup or the Frog or, indeed, to any part of any familiar plant or animal — or to the human body — we find essentially similar units of structure in every case. In fact, the bodies of all living things either consist of a single organic unit or of millions of essentially similar units called **CELLS**. (Figs. 2, 3, 4.)

Each cell is itself the theater of all the fundamental vital processes — each is alive. This, of course, is obvious when a cell forms the whole body of a **UNICELLULAR** plant or animal, but not so apparent when it is only one of myriads forming a **MULTICELLULAR** organism. But actually the life of the organism as a whole is, in

final analysis, the product of the life of the component cells: the expression of their harmonious coöperation. Accordingly the cells are the basic units of the actual living matter, termed PROTOPLASM.

FIG. 3. — Vertical section (highly magnified) of a leaf to show its cellular structure. *a*, guard cells, at opening (stoma) through epidermis; *b*, cells containing chlorophyll; *c*, upper and lower epidermal cells. (From Abbott, after Bailey.)

Such being the case, we reach the first great biological generalization: all animals and plants have the same elementary cellular structure. Indeed, the specific local differentiations in the living

FIG. 4. — Transverse section (highly magnified) of a simple animal (*Hydra*) to show the cellular structure. Outer layer, ectoderm; inner layer, endoderm; central cavity, enteron.

materials of the various parts of animals and plants are made possible largely because the protoplasm is disposed in microscopic unit masses, or cells.

A. THE CELL

With the diversity of gross structure of animals and plants in mind, one is not surprised that there are considerable, even great, variations in their component cells. In fact, the characteristics of an organism or part of an organism are determined by those of the cells. But there are certain fundamental cell characters which are common to all cells — by virtue of which they are cells — and it is important to emphasize these. (Fig. 5.)

In its simplest form a cell is a small, more or less spherical mass of protoplasm. Such are the eggs of various animals and the complete body of some of the lowest plants and animals. Cells forming

FIG. 5. — Diagram of cubical cell shown (a) as a solid body; and (b) in optical section, through plane $x-y$ of a , as it appears under the microscope.

the units of multicellular organisms, however, frequently exhibit more or less hexagonal surfaces on account of stresses and strains incident to their position among other cells, while specializations and differentiations, for one purpose or another, produce forms which are characteristic of different parts of the organism, as, for example, the long spindle-shaped cells of certain muscles, and the widely branching cells of parts of the brains of animals. Broadly speaking, the greater diversity of cell form is found in animals, while in plants, owing to the more general presence of rigid CELL WALLS about the protoplasm, the cells more frequently present symmetrical, angular outlines. (Figs. 6, 7, 41.)

The term cell is a relic of the time when the cell wall was regarded as the more important part, and its protoplasmic contents, if observed at all, were considered as only of secondary importance,

if not a waste product. Now we recognize many cells which are essentially naked masses of protoplasm, such as *Amoeba* and white blood cells. In other words, the protoplasm is the actual living part — the cell wall frequently being a non-living accessory which more or less sharply separates one unit mass of protoplasm from another and lends rigidity and form to the group of cells as a whole.

The living material of cells is highly organized into various complex structures, some of which are present in all cells and others only in cells adapted for special functions. For the present, however, it is only necessary to emphasize that the protoplasm of all typical cells is differentiated into two chief parts: the cyto-

FIG. 6. — A simple animal (*Amoeba proteus*) which consists of a single cell (highly magnified). Locomotion is by streaming of the protoplasm forming temporary protrusions, or pseudopodia.

PLASM, or general groundwork which makes up the bulk of the cell; and the NUCLEUS, a more or less clearly defined spherical body, situated near the center of the cytoplasmic mass.

Cytoplasm and nucleus, looked at from the functional viewpoint, represent a *physiological division of labor* within the confines of the cell. Experiments have shown that they are mutually necessary for cell life; the removal of the nucleus putting an end to constructive processes — assimilation, repair, and growth — and thus leading rapidly to death. Accordingly the nucleus may be considered as the center of the synthetic activities of the cell, and the cytoplasm, if not as the area in which destructive processes are chiefly involved, at least as a neutral region which translocates material toward and away from the nucleus. It seems clear that the nucleus is the controlling center in cell activity, and hence a

FIG. 7. — Various types of cells, highly magnified: *A*, female germ cell, egg of a Cat. *B*, male germ cell, sperm of a Snake. *C*, three ciliated epithelial cells from the digestive tract of a Clam. *D*, supporting tissue (cartilage) of a Squid. *E*, voluntary (striated) muscle fiber from an Insect. *F*, involuntary (smooth) muscle fibers from the bladder of a Calf. *G*, nerve cell from the brain of Man. *H*, white blood cell (corpuscle) of Frog. *I*, red blood cell of Frog. *J*, same, edge view. *nu*, nucleus. (From Dahlgren and Kepner, and Parker.)

primary factor in growth, development, and transmission of specific qualities from cell to cell, and so from one generation to the next.

B. CELL DIVISION

All the evidence indicates that, at the present time at least, living matter never arises except under the influence of preëxisting living matter. That is, protoplasm grows — cells grow and, having attained a certain size, reproduce by dividing into two essentially equal parts. Then there are two cells — the parent cell has lost

FIG. 8. — An Amoeba in six successive stages of division. The dark body surrounded by a clear area is the nucleus. (After Schultze.)

its identity in its offspring. Cell division is reproduction. Indeed, in final analysis reproduction is always cell division, though this primary fact is largely obscured by accompanying phenomena in higher animals and plants. (Figs. 8, 16.)

The process of cell division involves the division of both cytoplasm and nucleus, and therefore we must enlarge our conception of a cell as a small mass of protoplasm differentiated into cytoplasm and nucleus, by adding that both cytoplasm and nucleus arise through the division of the corresponding elements of a preëxisting cell.

We shall later have occasion to make a study of the details of cell division, known as MITOSIS, but from what has been said it must occur to the reader that, since cells arise only by division, those of the present day, whether complete free-living organisms or units composing the bodies of higher plants and animals, including Man, are actually lineal descendants in unbroken series from the beginning of cellular life on the Earth. (Fig. 164.)

CHAPTER III

THE PHYSICAL BASIS OF LIFE

Over the structure of the chemical molecule rises the structure of the living substance as a broader and higher kind of organization.

— *Hertwig.*

THE realization that all animals and plants possess a fundamentally similar organization — the structural and physiological units, or cells — leads quite naturally to an intensive study of the material of which the cells are composed — the physical basis of life itself. Accordingly we must now consider more specifically the characteristics of this actual life-stuff — protoplasm.

The old saying that the materials forming the human body change completely every seven years is a tacit recognition that lifeless material, in the form of food, is gradually transformed into similar living matter under the influence of the body. Indeed, just as a geyser retains its individuality from moment to moment though it is at no two instants composed of the same molecules of water identically placed, so the living individual is a focus into which materials enter, play a part for a time, and then emerge to become dissipated in the environment. But here the analogy stops. For in the living organism the materials which enter as food, endowed with POTENTIAL ENERGY, are arranged and rearranged until specific molecular combinations result, which in turn are transformed into integral parts of the organization of life itself. However, to live is to work, and to work means expenditure — the transformation of the potential into KINETIC energy — with the result that materials in relatively simple form and largely or entirely devoid of energy are returned to the realm of the non-living. And note, the living organism must continuously utilize energy in order merely to maintain itself. Cessation is death.

Thus we reach a fact of prime importance: so far as we know, living matter — protoplasm — is merely ordinary matter that has assumed, for the time being, a peculiar structural relation in which it displays the remarkable series of phenomena which we recognize as LIFE.

But non-living matter is always closely associated with living matter in the bodies of animals and plants. Indeed, the two are so intimately related that it is frequently difficult to distinguish sharply between them. Obviously, in the body of Man, for instance, the visible parts of hair and nails, a large part of bone, and the liquid part of blood are non-living material. But the non-living is not confined to gross structures, for the dead among the living are still revealed until the penetrating power of the microscope fails us.

A. THE PROTOPLASM CONCEPT

Although there is a continuous stream of matter and energy flowing through the living individual, nevertheless the physical and chemical study of living matter from whatever source we take it — Mold or Elm, Amoeba or Man — reveals a striking similarity in its fundamental factors, and this is the basis of the protoplasm concept held by modern biologists.

As the finer structure of animals and plants came within the range of vision through improvements in microscope lenses, it was gradually recognized that the ultimate living part appeared to be a granular, viscid fluid. This started a long series of studies on the materials of the bodies of unicellular organisms similar to Amoeba and of the cellular elements of higher animals and plants, which finally led, about the middle of the last century, to the complete demonstration of the full morphological and physiological significance of protoplasm. There is, in truth, an essentially similar, fundamental, living material of both animals and plants — a common physical basis of life. This reduction of all life phenomena to a common denominator laid the foundations for — indeed, actually established — the life-science, biology. (Figs. 6, 9.)

Although we speak of a common 'physical basis of life,' it is of paramount importance to bear in mind that the protoplasm of no two animals or plants or, indeed, of different parts of the same animal or plant is exactly the same. Identity of protoplasm would mean identity of structure and function — identity of life itself. The concept protoplasm merely emphasizes that, after allowances are made for all the variations, we still have the similarities far outnumbering the dissimilarities in the 'agent of vital manifestations.'

The physical chemists tell us that protoplasm consists of matter

in the colloidal state — a condition of matter that chemists have long been familiar with in the inorganic world. A COLLOID has been described as matter divided into particles larger than one molecule and suspended in a medium of different matter. Therefore butter and cream are each colloids: the former consisting of water finely divided and suspended in oil, and the latter essentially of finely divided oil in water. But protoplasm is a stupendously more complex colloidal system. It comprises not two, but very many substances, some in simple and others in highly complex molecular form, so finely divided that they are invisible with the ordinary microscope.

Now colloidal systems in general are characterized by tremendous surface activity — the result of energy relations between the contact surfaces of the particles of the different component substances. This being so, and protoplasm being a colloid composed of very many different kinds of materials, the total surface area between suspended substances and suspending media is very great, and thus affords the requisite conditions for an exceedingly intricate system of energy relations. And when we add to this the fact that at such surfaces chemical changes, some involving changes in electrical potential, occur; and also that mechanical changes are induced by precipitation, coagulation, and constant redistribution between the suspending media and the substances in suspension, we begin to get at least a glimpse of the exceedingly intricate and delicate *energy-transforming system* that protoplasm really is. To work out these intricacies is one of the imposing tasks still before the biologist, chemist, and physicist.

But the statement that protoplasm is a colloidal system leaves the reader without any clear conception of the appearance of protoplasm. As a matter of fact it is as difficult to describe the appearance of protoplasm as it is to define it. Protoplasm must be seen under the microscope to be appreciated. With a moderate magnification, it presents a fairly characteristic picture, appearing like a translucent, colorless, viscid fluid containing many minute granules as well as clear spaces or vacuoles. If it is examined in water it exhibits no tendency to mix with the surrounding medium, though investigations show that OSMOTIC interchanges are constantly going on. For this reason it is impossible to consider protoplasm except in connection with its surroundings, whatever they

may be — variations in its environment and variations in its activities being reflected directly or indirectly in its appearance. (Fig. 6.)

Under the highest magnifications, not only does the finer structure of protoplasm differ in various specimens, but also in the same cell under slightly different physiological conditions. At one time it presents the appearance of a fairly definite net-like structure, or *reticulum*, the meshes of which enclose a more fluid substance; at another, a frothy, or *alveolar*, appearance due to a more liquid substance scattered or emulsified as spherical bodies in a less liquid medium. Again, at other times, the denser portion seems

FIG. 9. — Protoplasm of the living Starfish egg (highly magnified), exhibiting alveolar, or foam-like, structure. This arises by the appearance, growth, and crowding together of minute bodies in a homogeneous ground substance. (From Wilson.)

to take the form of minute rods, or *fibers*, distributed in a somewhat fluid matrix. (Fig. 9.)

These appearances have given rise to various theories which emphasize one or another as the universal formula for the physical structure of protoplasm, from which the other appearances are merely secondarily derived. But the trend of recent work has been to indicate that although the general similarity of protoplasmic activity, wherever we find it, might lead us to expect to find also a visible fundamental structural basis, such does not exist within the range of magnifications at our command. Reticular, alveolar, and fibrillar structures which our microscopes reveal are, as it were, merely surface ripples from underlying physico-chemical changes which, thus far, have proved unfathomable.

B. UNIQUE CHARACTERISTICS OF LIVING MATTER

Since the phenomena of life are without exception the results of protoplasmic activity, it is obvious that we must look to protoplasm for the primary attributes of living matter. The properties which are absolutely characteristic of living matter are its specific organization, chemical composition, metabolism including the power of waste and repair, growth by intussusception, power of reproduction, and power of adaptation.

1. *Organization*

It must be emphasized that living things are not homogeneous, but possess structural and physiological ORGANIZATION. Animals and plants are made up of various parts adapted for certain purposes. They exhibit 'a viable unity' and so stand in sharp contrast with objects comprising the inorganic world as, for instance, rocks and rivers. Accordingly animals and plants are referred to as ORGANISMS. Moreover, as we have seen, the organizational units of all living things are cells, and so it follows that cell structure is a direct or indirect expression of all the unique life characteristics that we are about to survey. A few of the details of cell structure are necessary for an appreciation of the organization of organisms.

It will be recalled that the protoplasm of all typical cells is differentiated into two chief parts: the *cytoplasm*, or general groundwork which makes up the bulk of the cell; and the *nucleus*, a more or less clearly defined spherical body, situated near the center of the cytoplasmic mass.

CYTOPLASM. The cytoplasm may be considered the less specialized protoplasm of the cell, and its appearance and other characteristics are those which have been outlined in our discussion of protoplasm. With that in mind, for the sake of definiteness, we may consider its basis as consisting of a meshwork, composed of innumerable, minute granules which permeate an apparently homogeneous ground-substance, or HYALOPASM. Distributed throughout the cytoplasm are usually various lifeless inclusions such as granules of food, droplets of water or oil, vacuoles of cell sap, crystals, etc., representing materials which are to be, or have been, a part of the living complex, or are by-products of the vital processes. This passive material is frequently referred to as META-

PLASM, but it is quite evident that such a term stands for no essential morphological part of the cell, and we have no absolute criterion to distinguish between some granules which are regarded as metaplastic in nature and others which are ordinarily considered active elements of the cytoplasm. But there are various undoubtedly active bodies besides the nucleus in the cytoplasm. Chief among these are the CENTROSOME which plays an essential part in cell

FIG. 10. — Detailed diagram of a cell. (From Wilson, slightly modified.)

reproduction; and the PLASTIDS, MITOCHONDRIA, and GOLGI BODIES which apparently are the seat of various special physiological activities. (Fig. 10.)

The cytoplasm, since it forms the general groundwork, is that part of the cell which comes most closely into relations with the environment, and accordingly near the surface it is frequently modified somewhat in texture and consistency so that an outer CORTICAL region, or ECTOPLASM, may be distinguished from an

inner, or ENDOPLASM. The ectoplasm is limited externally by a PLASMA-MEMBRANE just beneath the cell wall. The plasma-membrane is certainly a part of the living cytoplasm, while the cell wall must be regarded as non-living, though in many cases it is a direct transformation of the living material which grows and plays, in connection with the plasma-membrane, an important part in controlling the flow of matter and energy to and from the cell and its surroundings.

NUCLEUS. As already mentioned, within the cytoplasmic mass there is an area of clearly differentiated material, which typically has a rounded form, bounded by a membrane, so that it appears as a definite body of protoplasm called the NUCLEUS. The structural basis of the nucleus appears to be essentially similar to that of the cytoplasm — the so-called LININ meshwork and KARYOLYMPH being comparable respectively to the granular meshwork and hyaline ground-substance of the cytoplasm. But superimposed upon this, as it were, is the highly characteristic nuclear material, or CHROMATIN, which takes various forms during different phases of cell activity but generally gives the appearance of a network of tiny granules with one or more dense 'knots' of chromatin (KARYOSOMES). Frequently there is a conspicuous round achromatic body within the nucleus known as the NUCLEOLUS. Later it will be necessary to describe some of the important changes in chromatin arrangement that occur during various phases of cell activity, especially during cell division, but it is sufficient at this moment to emphasize that the nucleus is a differentiated area of the cell protoplasm which is the arena of the chromatin. Indeed, the nucleus probably represents the highest type of organization in the organism.

2. Chemical Composition

It is impossible to make an analysis of living matter because the disturbance of its molecular organization by chemical reagents kills it. Therefore our knowledge of its chemical composition has of necessity been derived from a study of dead protoplasm. However, since in the transformation from the living to the non-living state there is clearly no loss of weight, it follows that the complete material basis of life is still present for examination. In other words, the death of protoplasm is a result of *disorganization*.

Chemical analysis of protoplasm shows that it invariably comprises the elements CARBON, OXYGEN, HYDROGEN, NITROGEN, SULFUR, and PHOSPHORUS; and usually also CHLORINE, POTASSIUM, SODIUM, MAGNESIUM, CALCIUM, and IRON. Occasionally a number of other elements are found normally in the protoplasm of certain parts of various species of animals and plants.

The average composition of the human body is about as follows:

Oxygen.....	65.00%
Carbon.....	18.00
Hydrogen.....	10.00
Nitrogen.....	3.00
Calcium.....	2.00
Phosphorus.....	1.00
Potassium.....	0.35
Sulfur.....	0.25
Sodium.....	0.15
Chlorine.....	0.15
Magnesium.....	0.05
Iron.....	0.004
Iodine.....	<i>traces</i>
Fluorine.....	<i>traces</i>
Silicon.....	<i>traces</i>

At first glance there is nothing very striking about this list of elements. They are all common ones with which the chemist is familiar in the non-living world. The materials of Man's body are worth less than one dollar! Furthermore, quantitatively the most important compound is nothing more complex or mysterious than WATER (H_2O). It composes more than two-thirds of the human body. But there are *combinations* of the elements which are highly significant and characteristic, and result from the capacity of carbon, hydrogen, and oxygen, or carbon and hydrogen together, to form the numerous complex compounds which in turn supply the basis for intimate associations with other elements. As a matter of fact, the bulk of protoplasm is composed of carbon, oxygen, hydrogen, and nitrogen associated with each other in an apparently infinite series of relationships, in which the carbon seems to play the leading rôle — the indispensable bond that links all other elements in organic unity. Some of these compounds are relatively simple, but the majority consist of elaborate atomic arrangements and not a few represent molecular complexes of hundreds and even thousands of atoms.

The COMPOUNDS OF CARBON which are characteristic of protoplasm fall into three chief groups: proteins, carbohydrates, and fats.

PROTEINS invariably consist of the elements carbon, oxygen, hydrogen, nitrogen, and sulfur, and frequently phosphorus and iron. Examples are ALBUMIN of the white of egg, CASEIN of milk, GLUTEN of cereals, and MYOSIN of lean meat. The *nitrogen* particularly distinguishes proteins from the other compounds of the living complex and, as we shall see later when considering the chemical processes in animals and plants, is largely responsible for their commanding position as "the chemical nucleus or pivot around which revolve a multitude of reactions characteristic of biological phenomena." Study of the relationship of nitrogen to the other chemical elements of proteins has revealed that the protein molecule is a huge complex of linked AMINO ACIDS — an amino acid being an organic acid in which one hydrogen atom is replaced by the amino group, NH_2 . The amino acids are the nitrogenous units with which organisms deal physiologically, rather than the proteins themselves. An animal, for example, with various proteins available in its food, chemically disrupts these into their amino acid constituents, and then takes an amino acid here and another there and synthesizes the specific proteins it demands. And further, if individual amino acids are supplied, the animal employs them. So it seems highly probable that the specific structure of an organism depends upon the chemical specificity of its proteins.

Although the presence of proteins and the power of forming them is the chief diagnostic chemical characteristic of living matter, at the present stage of our knowledge it is impossible to define proteins satisfactorily on the basis of chemical or physiological properties. The most we can say is that the biochemist describes proteins as "huge molecules, complex in structure, labile in character, and therefore prone to chemical change" — and the latter characteristic undoubtedly is closely associated with the plasticity and responsiveness of the protoplasmic system itself.

CARBOHYDRATES consist of various combinations of carbon, hydrogen, and oxygen, the latter elements invariably being present in the proportion found in water (H_2O). Though more simple in chemical structure than proteins, they range in complexity from the simple sugars, or monosaccharids such as GLUCOSE and FRUCTOSE, to polysaccharids such as DEXTRINS, STARCHES, and CELLULOSE.

FATS are composed of the same elements as the carbohydrates, but in quite different arrangements. The proportion of oxygen is always less, and therefore they are more oxidizable and richer in potential energy. Fats represent the union of an acid (fatty acid) and glycerol. Examples are butter and all oils of plant or animal origin.

Thus proteins, carbohydrates, and fats represent large classes of substances which are distinctly characteristic of living matter, not being found in nature except as the result of protoplasmic activity; although biochemists now can artificially construct certain fats and carbohydrates as well as the amino acid constituents of some proteins. Proteins undoubtedly play the most important part in the organization of protoplasm, while the carbohydrates and fats contribute largely to the supply of available energy. However, it is impossible to draw a hard and fast distinction in regard to their respective contributions because, for example, as we shall see later, carbohydrates form the foundation upon which proteins are built by green plants.

Proteins, carbohydrates, and fats are frequently referred to as the foodstuffs, but it will be recognized that while, in a way, they constitute the chief groups, all the constituents of protoplasm must be available. Accordingly, inorganic salts, water, and free oxygen are really foodstuffs. Furthermore, recent investigation has disclosed another class of organic substances which are absolutely necessary for the constructive phases of protoplasmic activity. These are termed VITAMINES and must be classified as accessory food substances, although as yet little is known in regard to their chemical structure or mode of action. And then, finally, on the border line of food substances may be mentioned a great group of organic catalyzers, called ENZYMES, which play a major rôle in the chemical processes of animals and plants. But, when all is said, our knowledge of the chemical complexities of protoplasm affords no adequate conception of how they are related to the phenomena of life. This is beyond present-day biology.

3. *Metabolism*

We have emphasized that living matter is continually changing, and this fundamental fact is reflected in nearly all attempts to define life. Aristotle described life as "the assemblage of operations of nutrition, growth, and destruction"; deBlainville, as a

“twofold internal movement of composition and decomposition”; and Spencer, as “the continuous adjustment of internal relations to external relations.”

This interaction consists of chemical and physical processes in which combustion or oxidation plays the chief rôle. Over a century ago it was shown that animal heat results from a slow burning of the materials of the body, involving the consumption of oxygen and the liberation of carbon dioxide; and further, that for a given consumption of oxygen and liberation of carbon dioxide, about the same amount of heat is produced by an animal as by a burning candle. In other words, the oxidation of the complex compounds which enter the body as food is definitely proportional to the amount of energy which the body gives out, just in the same way as the amount of work performed by a steam engine and the amount of heat it liberates bear a strict proportion to its consumption of fuel.

This is an important discovery, because it goes far toward establishing the fact that at least certain characteristic vital phenomena are in accord with the laws which hold in the non-living world. But the processes involved in life are not so simple as perhaps might be imagined from the results just mentioned. Heat represents but one of the many energy transformations within the organism, and biologists are at work trying to interpret one after another in terms that are equally applicable in the realms of the living and the lifeless.

One naturally asks whether living matter possesses some special form of energy — ‘vital force’ — which is quite different from chemical and physical energy. This is the philosophically important question of VITALISM. From the standpoint of biology we may say that no instrument ever devised has detected such energy, and until some unique vital energy can be made evident to one of the human senses, it does not fall within the scope of science — science can neither deny nor affirm its existence. However, although the grosser phenomena of life are being gradually restated in terms of the physical sciences, it is interesting to note that these sciences, in turn, are developing formulae that carry much of the mysticism attaching to life. Indeed, time, space, matter, and perhaps energy are approaching the melting pot.

Thus, for practical purposes at least, it is necessary to consider the organism as a system for transforming energy — transforming

the potential energy stored in chemical complexes of its own substance into the various vital processes of living — into work performed. And it is in this transfer of energy from one kind to another that we find exhibited the activities which are most distinctive of living things. In these processes many complex substances rich in potential energy, which have entered as food and have been, in whole or part, added to the protoplasmic system, are reduced to simpler and simpler conditions and finally, with their energy content nearly or entirely exhausted, are eliminated as EXCRETIONS. Obviously, if life is to persist, this continual waste must be counterbalanced by a proportionate intake of food in order to renew the supply of energy and to provide the materials which, after preliminary changes, are made into an integral part of the living organism.

Thus in living the animal or plant is partially consuming and rebuilding itself continually. This dual process is METABOLISM. When constructive metabolism, ANABOLISM, keeps pace with destructive metabolism, KATABOLISM, the individual remains essentially unchanged and this is the normal condition of adult life. During youth the anabolic phases are in the ascendancy and growth occurs, while old age is characterized by a predominance of katabolic processes.

4. *Growth*

One of the most obvious results of metabolism is growth, or permanent increase in the size of the individual. As a rule growth is most rapid during the early part of the individual's existence, or youth. Indeed, at birth a child is about a billion times larger than the egg cell from which it has developed. Later in life, when a certain physiological balance, or maturity, is attained, growth chiefly occurs in making good, in so far as may be, the wear and tear incidental to living, and in providing for reproduction.

Growth means that the organism makes over the materials which it receives in the form of food from its environment, transforms them and fits them into the protoplasmic organization here and there throughout as needed. This method of addition of materials, which is termed growth by INTUSSUSCEPTION, is highly characteristic of life. It is in striking contrast to growth in the non-living world, which is by ACCRETION, as, for example, in crystals that increase in size merely by the addition to the surface

of new material of the same kind from the saturated solution, the mother liquid, in which they are suspended. But protoplasm, with materials and energy taken from its environment, constructs more protoplasm — endows the non-living with its own unique organization. It makes more life-stuff. And, if the available materials are adequate, the specifically organized living substance tends to increase indefinitely.

5. *Reproduction*

So far as is known, living matter arises only by the activities of preëxisting living matter. We have seen that this transformation is continually going on in the constructive phase of metabolism in the animal or plant, and brings about repair and growth of the individual; but it is in reproduction that what may be termed the overgrowth of the individual results in the production of a new one. A larger or smaller part of the parent generation is detached and becomes the new generation. In ultimate analysis, reproduction is cell division. This is a unique characteristic of living things which provides for the continuation of the race. (Figs. 8, 16.)

6. *Adaptation*

The discussion of metabolism has emphasized the close interrelationship between the living organism and its surroundings, and the dependence of life upon the interplay and interchange between protoplasm and its environment. As a matter of fact the plant or animal retains its individuality — lives — solely by its powers of developing and maintaining exquisite adjustments to its surroundings. This results from the IRRITABILITY of living substance: its inherent capacity of reacting to environmental changes by changes in the equilibrium of its matter and energy. The inciting changes, known as STIMULI, may be chemical, electrical, thermal, photic, or mechanical, but the nature of the response is determined rather by the fundamental character of protoplasm itself than by the nature of the stimulus. Thus muscle cells respond by contracting, regardless of the nature of the stimulus.

The reaction of living matter by virtue of its irritability implies not only *response* to a stimulus but also *conduction* so that the cell, or group of cells, as a whole is directly or indirectly influenced. It responds as a coördinated unit — an individual. It adapts itself structurally and functionally to the necessities of its existence.

This power of adaptation, as exhibited in active adjustment between internal and external relations, overshadows every manifestation of life and contributes, more than any other factor, to the enormous gap that separates even the lowest forms of life from the inorganic world.

The characteristics which we have described — specific organization, chemical composition, metabolism including waste and repair, growth by intussusception, reproduction, and adaptation — individually and collectively are characteristic of living matter. It is possible, to be sure, to take exception to one or another; for instance, to say that growth by intussusception occurs in non-living things when a salt is dissolved in water; but such formal objections only emphasize the unique conditions which obtain in life.

FIG. 11. — Amoeboïd movement. Successive changes in form assumed by an Amoeba. The clear ectoplasm flows forward, followed by the granular endoplasm with the nucleus (darker) and contractile vacuole (lighter). See Fig. 6. (After Verworn.)

C. MOVEMENT

The reader may be surprised to note that the power of *movement* has not been mentioned as a characteristic of life, but a moment's thought will make it apparent that visible movement is not confined to living matter. Though this is so, movement is one of the most obvious manifestations of life and depends, of course, in

every instance, upon tumultuous ultramicroscopic chemical changes of protoplasm itself.

Thus it is to these changes that, in the last analysis, we must turn for the energy which brings about the visible movements in animals and plants, such as the contraction of the muscles of animals, the streaming movement (AMOEBOID movement) of the simple unicellular animals known as Amoebae, the rotation and circulation of the protoplasm in certain of the cells of plants and, finally, the lashing of threads of protoplasm (CILIA) which not only enables many a tiny plant and animal to swim, but also aids in numerous ways in certain parts of the bodies of higher organisms. The phenomena of life are quite generally expressed in visible movements, but movement itself is not peculiar to living things. (Figs. 11, 13.)

In our discussion thus far, we have endeavored to describe the characteristics of life in terms of its organizational units — cells, and of its physical basis — protoplasm. But we have not attempted formally to define 'life' or 'protoplasm' because, since they are unique, it is impossible to resort to the trick of comparing them with something else; and because the expressions 'protoplasm' and 'life' are generalizations. The former indicates that all animals and plants have an essentially similar foundation, and the latter that they exhibit certain characteristic actions and reactions. The living organism exhibits a permanence and continuity of individuality correlated with specific behavior, and this it transmits to other matter which it makes a part of itself, and to its offspring in reproduction.

CHAPTER IV

METABOLISM OF GREEN PLANTS

Matter and force are the two names of the one Artist who fashions the living as well as the lifeless. — *Huxley*.

LIFE is only known to us in the form of individual organisms, so we turn now to concrete examples of unicellular plants and animals which present, in relatively simple form within the confines of a cell, the essentials of all the fundamental life processes that we shall later have occasion to study in their complex expressions in the higher animals and plants.

Unicellular green plants are distributed all over the world and adapted to a great variety of conditions. We find them, for example, forming green coatings on the bark of trees, scums on puddles and ponds, or being blown about in dust by wind. Of the many hundreds of species we select *Pleurococcus vulgaris* because of the simplicity of its structure and life history, and because it is readily obtained for study.

A. STRUCTURE AND LIFE HISTORY OF PLEUROCOCCUS

A single *Pleurococcus* is invisible to the naked eye, but like many another microscopic form, it makes up in numbers for the small size of the individual, and frequently gives a greenish color to moist surfaces of rocks, tree trunks, fence posts, and flower pots.

Examined under the microscope, the organism is seen to consist of a spherical mass of protoplasm with a nucleus centrally located. Most of the cytoplasm surrounding the nucleus is specialized to form a PLASTID which contains a green pigment. The whole organism, the PROTOPLAST, is enclosed within a distinct, rigid cell wall which has been secreted by the protoplasm and is composed of CELLULOSE: a carbohydrate especially characteristic of plants. It is evident that the organism is a single cell. (Fig. 12.)

Since *Pleurococcus* is a single cell, we find reproduction presented in its simplest terms: under favorable conditions the cell divides and the two daughter cells sooner or later separate. Sometimes, however, several divisions occur before the cells are sep-

arated and thus there is formed, as it were, a temporary multicellular body, but one without any physiological division of labor between the cells because all are independent in their vital activities. Moreover, this tendency to form temporary cell groups suggests the type of step that was taken when the multicellular body was established during plant evolution.

B. METABOLISM IN PLEUROCOCCLUS

We may now turn our attention to the point *Pleurococcus* was chosen especially to illustrate — the characteristic life processes of green plants. At first glance it may appear that a multicellular plant, such as a tree or shrub, would afford a more suitable example, but since the fundamental distinction between plants and animals is chiefly a question of metabolism, there are advantages in studying it in a single cell, where one's attention is not distracted by root, stem, and leaf.

FIG. 12. — *Pleurococcus vulgaris*, a unicellular Green Plant. Separate individual and temporary cell groups formed by cell division.

Since *Pleurococcus* lives, grows, and multiplies in moisture exposed to sunlight, it is to this environment that we must look for the materials with which it constructs protoplasm, and the energy which it employs in the process. And, furthermore, since the organism is enclosed within a cell wall, its income and outgo must be materials in solution in order to pass through to the living protoplasm.

1. Food Making

In short, *Pleurococcus* takes materials from its surroundings in the form of simple compounds, as carbon dioxide, water, and mineral salts, which are relatively stable and therefore practically devoid of energy, and, through the radiant energy of sunlight, shifts and recombines their elements in such a way that products rich in potential energy result. *Pleurococcus* thus exhibits the prime distinguishing characteristic of green plants — the power to construct its own foodstuffs.

The key to this power of chemical synthesis by light — PHOTOSYNTHESIS — resides in a complex chemical substance called CHLOROPHYLL.¹ This pigment, which is segregated in special cytoplasmic bodies, the plastids, gives to *Pleurococcus* during its active phases and to the foliage of plants in general their characteristic green color. Plastids bearing chlorophyll are known as CHLOROPLASTIDS. The chlorophyll arrests and transforms a small part of the energy of the sunlight which reaches it in such a way that the protoplasm can employ this energy for food synthesis.

The first great step in the constructive process is a combination of carbon with hydrogen and oxygen to form a carbohydrate. *Pleurococcus* gets these elements from carbon dioxide and water by a process of molecular disruption. We know that when charcoal, for instance, is burned, carbon and oxygen *unite* to form carbon dioxide, and energy in the form of light and heat is liberated. Obviously *Pleurococcus* must employ an equal amount of energy in separating the carbon and oxygen of carbon dioxide; that is, in overcoming their chemical affinity. And this kinetic energy which the plant employs is then represented in the chemical potential which exists between the oxidizable carbon and free oxygen — it has become potential energy. Thus the plant in sunlight is continually separating the carbon from the oxygen of carbon dioxide. The oxygen is liberated as free oxygen, while the carbon which has been separated from the oxygen is combined with molecules of water to form carbohydrates — grape sugar (glucose) and fruit sugar (fructose).

The conventional equation for this reaction is:

It should be emphasized, however, that the processes involved are by no means so simple as is implied above; but since there is little conclusive data in regard to the details, the equation as stated affords a formal explanation which is adequate for the present discussion.

The first great step in food synthesis, the formation of a *sugar*, having been accomplished, the green plant transforms the sugar

¹ A rough approximation of the formula of chlorophyll has been given as: $(\text{Mg-N}_4\text{C}_{32}\text{H}_{30}\text{OO}) (\text{COOCH}_3) (\text{COOC}_{20}\text{H}_{39})$. A slight chemical modification of chlorophyll results in hematochrome, which gives the reddish tinge to certain unicellular plants closely related to *Pleurococcus*.

and stores it as *starch* for future use as fuel or as the basis of further synthesis. Starch is the first *visible* product of photosynthesis.

We have seen that the characteristic of proteins as compared with carbohydrates (sugars, starches) is the presence of nitrogen, and this element must be added to the CHO basis already constructed as the next step toward protein synthesis. The green plant not only can, but must employ nitrogen in such simple combinations as *nitrates*, and this is a fact of prime importance, for typically, as will appear later, animals and most colorless plants require nitrogen in more complex combinations. By the addition, then, of nitrogen to the carbohydrate basis a very simple nitrogen compound, such as an *amine* (e.g., asparagine = $C_4H_8N_2O_3$), is built up, which may be transformed into a *protein* by the addition of sulfur and other elements secured from sulfates, phosphates, etc. Again, we do not know how this is done, or, after it is done, how the protein becomes an intrinsic part of the living material itself. But it is evident that synthesizing ENZYMES play a crucial part. These are chemical bodies which are only known as products of living protoplasm and are the activating agents (catalytic agents) for chemical transformations in which, however, they themselves take no integral part. The chemical composition and constitution of enzymes is undetermined.

Pleurococcus thus takes the raw elements, so to speak, of living matter and by the radiant energy of sunlight, which its chlorophyll traps, constructs carbohydrate, protein, protoplasm. In other words, the green plant is a synthesizing agent, building up highly complex and unstable molecular aggregates brimming over with the energy received from the Sun. So the green plant, whether Pleurococcus or Elm, manufactures its own food for itself: and incidentally, as it were, for the living world in general, including Man.

2. Respiration

As we have already stated, protoplasm is always at work — to live is to work — and this means expenditure of energy: the same energy that chlorophyll has secured for the plant and stored away in its food. Therefore the food must be oxidized — burned — in order to release the energy, and for this the plant must have available a supply of free oxygen. Pleurococcus obtains this oxygen dissolved in water and also, in sunlight, from that liberated

through photosynthesis. The process involved, for the sake of simplicity, may be represented by the equation:

which, it will be noted, is the reverse of the equation for photosynthesis. This intake of free oxygen by the cell and outgo of carbon dioxide and water, the chief products of combustion, is known as RESPIRATION. It is essentially the securing of energy from food, involving the exchange of carbon dioxide for oxygen by protoplasm. And this interchange of gases between the living matter and its surroundings is not only characteristic of *Pleurococcus* and all green plants, but of all living things. Plants respire just as truly as animals, though the more active life and complex bodies of most of the latter requires an elaborate respiratory apparatus in order that an adequate gaseous interchange may be effected with the necessary rapidity.

Thus the green plant may be regarded as a chemical machine for the transformation of energy — the radiant energy from the Sun — into lifework; the matter and energy which enters, forms, and leaves the organism obeying, to the best of our knowledge, the fundamental laws of matter and energy of the non-living world.

We have now obtained some idea of one living organism, *Pleurococcus vulgaris*, a green plant reduced to the simplest terms — a single cell provided with chlorophyll. And we have seen that this chlorophyll is the key to the photosynthetic activity of the green plant. In other words, the expression 'green plant' does not refer specifically to the color of a plant (in some cases it may appear red or brown), but to the fact that there is present a complex pigment functionally similar to chlorophyll by virtue of which the plant is a constructive agent in nature. It has the power to manufacture its own foodstuffs from relatively simple compounds largely devoid of energy and, in particular, is able to utilize nitrogen in the form of nitrates.

We pass now from the essentially constructive agents in nature to the chiefly destructive; from the collectors of energy to the energy dissipators; from the green plants to animals and then to 'colorless' plants.

CHAPTER V

METABOLISM OF ANIMALS

The most important discoveries of the laws, methods, and progress of Nature have nearly always sprung from the examination of the smallest objects which she contains, and from apparently the most insignificant enquiries. — *Lamarck*.

THERE is probably no better introduction to the study of the biology of an animal than that afforded by *PARAMECIUM*, a common organism of ponds, ditches, and decaying vegetable infusions. *Amoeba*, frequently referred to as the simplest animal, and *Paramecium* are representatives of some 15,000 kinds of single-celled animals, or *PROTOZOA*. Members of this group are found in almost every niche in nature and, like the *PROTOPHYTA*, as the unicellular plants are sometimes called, are important because although small in size the number of individuals is inconceivably large. Collectively they produce profound changes in their environment, whether living free or within the bodies of other organisms. The subdivision of zoölogy devoted to the investigation of the Protozoa is known as *PROTOZOÖLOGY*. (Figs. 6, 8, 11, 13.)

A. STRUCTURE AND LIFE HISTORY OF *PARAMECIUM*

Paramecium is a giant among the Protozoa, though just visible to the naked eye as a whitish speck if the water in which it is swimming is properly illuminated. But in order to make out the details of structure it is necessary to magnify it several hundred times. This done, it appears as a more or less slipper-shaped organism which one would not consider, at first glance, a single cell because it shows highly specialized parts. However, careful study reveals the fact that the organism really consists of a single protoplasmic unit differentiated into cytoplasm and nucleus, though each of these regions shows specializations. (Fig. 14.)

The nuclear material, instead of forming a single body as it does in most cells, in *Paramecium* is distributed in two parts: a larger body, or *MACRONUCLEUS*, and a smaller body, or *MICRONUCLEUS*.¹

¹ The several species of *Paramecium* differ in regard to micronuclear number; e.g., *P. caudatum* has one micronucleus, *P. aurelia* and *P. calkinsi* have two, and *P. polycaryum* and *P. woodruffi* have several micronuclei.

FIG. 13. — Some common fresh-water Protozoa, greatly magnified. (From Curtis and Guthrie.)

Strictly speaking, the macronucleus and micronucleus together constitute the nucleus of the cell, and represent a sort of physiological division of labor in the chromatin complex.

But it is in the cytoplasm that specialization is most conspicuous. Not only are there general differentiations into ectoplasm

FIG. 14. — *Paramecium calkinsi*. Diagrammatic. *a*, contractile vacuole surrounded by radiating canals; *b*, macronucleus; *c*, mouth; *d*, undulating membrane extending lengthwise in gullet; *e*, gastric vacuole in process of formation at end of gullet; *f*, contractile vacuole, fully formed; *g*, gastric vacuoles; *h*, endoplasm; *i*, micronuclei; *j*, peristome and peristomal cilia; *k*, trichocysts in ectoplasm; *l*, cilia.

FIG. 15. — Section of a dividing *Paramecium caudatum*. *M*, dividing macronucleus; *m*, *c.st.*, dividing micronucleus; *g.v.*, gastric vacuole; *tr.*, trichocysts; *e.tr.*, extruded trichocysts. (From Calkins.)

and endoplasm, but these regions also have local

specializations such as CILIA for locomotion and securing food, TRICHO CYSTS for defense, PERISTOME, MOUTH, and GULLET for the intake of solid food, GASTRIC VACUOLES for digestion, and CONTRACTILE VACUOLES for excretion. And withal, recent investiga-

tions indicate that various parts of the cell are coördinated by a NEUROMOTOR apparatus. (Figs. 14, 135, 229.)

Paramecium, under favorable conditions, grows rapidly and, when it has attained the size limit characteristic of the species, cell division, termed BINARY FISSION, takes place, with the result that from the single large cell there are formed two smaller individuals which soon become complete in all respects. These, in turn, grow and repeat the process in about ten hours so that, as in the case of *Pleurococcus*, within a few days the original Paramecium has divided its individuality, so to speak, among a multitude of descendants. (Figs. 15, 16.)

FIG. 16. — Diagram of reproduction by division, or binary fission, in Paramecium.

This process of multiplying by dividing can go on indefinitely under favorable environmental conditions. But periodically Paramecium undergoes an internal nuclear reorganization process (ENDOMIXIS). Also now and then individuals temporarily fuse in pairs and interchange nuclear material (CONJUGATION) — an expression of fundamental sex phenomena, involving FERTILIZATION, which we shall have occasion to consider later. (Figs. 17, 170, 171.)

B. METABOLISM IN PARAMECIUM

Paramecium thus affords some idea of the complexities of structure and function which a cell may exhibit when it forms the whole

animal organism. The Protozoa are the simplest, though by no means simple animals. But the great structural differences between *Pleurococcus* and *Paramecium*, though to a certain extent representative of plants on the one hand and animals on the other, are not essentially diagnostic, because, as we have suggested before, in the last analysis it is a matter of metabolism. And it is largely for this reason that these two organisms, shorn of all or nearly all non-essentials, have been selected as illustrations.

FIG. 17. —Position assumed by conjugating *Paramecia*.

1. Food Taking

The food of *Paramecium* is chiefly microscopic, colorless plants known as BACTERIA which are present in countless numbers in decaying vegetable infusions. As *Paramecium* swims about by means of its cilia, a current of water laden with Bacteria is whirled down the peristome on one side of the animal and some passes through the mouth and gullet into the endoplasm. Here the Bacteria are surrounded by a droplet of fluid — a gastric vacuole — into which the endoplasm secretes chemical substances (enzymes, etc.) which gradually simplify — DIGEST — the complex proteins, carbohydrates, etc., of the plant cells. Finally, this material which shortly before was Bacteria protoplasm is incorporated into *Paramecium* protoplasm — matter and energy is supplied and the animal lives and grows. (Fig. 230.)

This is, in most regards, a strikingly different condition from that which we have seen in *Pleurococcus*. In *Paramecium* solid particles of food — Bacteria — are taken into the cell, and since the chief organic constituents of protoplasm are proteins, associated with carbohydrates and fats, it is clear that the income of the animal organism is, unlike that of the green plant, chiefly ready-made complex foodstuffs. In other words, *Paramecium*, like all animals, requires relatively complex chemical compounds rich in potential energy: proteins, carbohydrates, and fats. Of these, proteins or their constituent amino acids are absolutely indispensable because it is only from this source that nitrogen is available for the animal. But the green plant, through its chlorophyll apparatus, is able to take materials largely devoid of energy

and to rearrange them and endow them with potential energy which it has received in the kinetic form from sunlight.

2. *Respiration and Excretion*

Of course, during life the animal, like the green plant, is continually breaking down its food and its own protoplasm by a process of combustion which involves an intake of free oxygen and the liberation of carbon dioxide and water. Nitrogenous wastes, chiefly URIC ACID or UREA, as well as inorganic salts, are also excreted. So the animal, like the plant, returns to its environment the elements in simple combinations which are devoid or nearly devoid of energy. We have stated that green plants are essentially constructive and animals essentially destructive agents in nature. It is now apparent that green plants are *both* constructive and destructive, while animals are essentially destructive. The constructive processes of green plants are necessary and sufficient not only for themselves but for all living things.

A little consideration of the income and outgo of green plants and animals will show that, although the animals are dependent on the plants for their complex foodstuffs, they do not return, for example, the nitrogen to the outer world in a form simple enough to be available for green plants. For example urea, $(\text{NH}_2)_2\text{CO}$, which still has a little energy left that the animal is unable to extract, must be transformed into nitrates.

Furthermore, since plants die, which are not consumed by animals, and animals die, which are not devoured by other animals, large stores of matter and energy are locked up in the complex compounds of their dead tissues. Clearly, there must be some way of completing the cycle of the elements, for if there were not, life, as we know it, could not have continued long on the Earth. This gap is filled by the so-called COLORLESS PLANTS; that is, plants which, because chlorophyll is not present, lack the power of photosynthesis and so in most cases are dependent for food on more complex substances than green plants demand, though not so complex as animals require.

CHAPTER VI

METABOLISM OF COLORLESS PLANTS

Nature, which governs the whole, will soon change all things which thou seest, and out of their substance will make other things and again other things from the substance of them, in order that the world may be ever new. — *Marcus Aurelius*.

As representative of the diverse types of colorless plants which, lacking chlorophyll or a functionally similar pigment, are without the power of photosynthesis, we select the vast group known as the BACTERIA. For reasons that will appear later, it is not practical to focus attention on one particular species of Bacteria, as we have just done in considering green plants and animals. Instead we shall discuss in very general terms the group as a whole, referring now and then to special kinds of Bacteria to illustrate particular points.

A. THE BACTERIA

The wide distribution of the Protozoa is exceeded by the Bacteria. Representatives are literally found everywhere: floating with dust particles in the air; in salt and fresh water; in the water of hot springs; frozen in ice; in the upper layers of the soil; and in the bodies of plants and animals. Bacteria have received a considerable notoriety under the names of 'microbes' and 'germs,' owing to the fact that certain types subsist within the human body as parasites and bring about disturbances, chiefly chemical, which we interpret as disease. But aside from these forms which, though all too many, are relatively few in number, human life and life in general on the Earth could not long continue without their services. Indeed, the Bacteria have practically ruled the world since they first secured a foothold when the Earth was young. It is this aspect of the Bacteria which concerns us at present.

Among the Bacteria are the smallest organisms known. Some species are less than one fifty-thousandth of an inch in length and much less in breadth. None of the typical forms comes within the range of unaided vision, while some are not revealed by the

highest powers of the microscope — indeed there is room and to spare for thousands of millions of Bacteria to live in a thimble-full of sour milk. The small size and similarity of structure of many of the Bacteria render their study particularly difficult, and accordingly they are grouped and classified largely on the basis of chemical changes which they produce in their surroundings, rather than on structural characteristics. However, there are three chief morphological types: the rod-like forms or *BACILLI*; the spherical forms or *COCCI*; and the spiral forms or *SPIRILLA*. Bacilli or cocci may be associated in linear, branching, or plate-like series, or grouped together in colonies. (Fig. 18.)

The individual bacterium is regarded as a single cell, though in most species there is no definite nuclear body; the chromatin material being distributed in the form of granules throughout the cytoplasm. A cell wall chemically similar to protein is usually present. Some forms show active movements by means of thread-like prolongations of the cytoplasm, or *FLAGELLA*, as in the case of the common *Spirillum* of decaying vegetable infusions.

Reproduction is by a process of cell division which, under favorable conditions, may occur as often as every fifteen minutes. The vast multitude of cells thus produced before long exhaust the food supply and contaminate with excretion products the medium in which they are living, so that further growth is inhibited. In many species, under these circumstances the protoplasm within the cell wall assumes a spherical form and secretes a protecting coat about itself, and thus enters upon a resting state. In this *SPORE* form the Bacteria can withstand drying, variations in temperature, and other conditions — in certain cases even strong carbolic acid — to which in the active state they would readily succumb, and thereby the organisms tide over periods of unfavorable conditions and are ready to start active life again when the opportunity occurs. It is certainly fortunate for Man that most disease-producing Bacteria are unable to form spores. (Fig. 204.)

FIG. 18. — Chief types of Bacteria. A, cocci; B, bacilli; C, spirilla; D, branched filamentous form. — Types of flagellation in Bacteria. 1, without flagella; 2, 3, with flagella. (From Buchanan.)

FIG. 19. — A Bracket Fungus (*Pleurotus ulmarius*) on the trunk of a Maple tree. The spores gain access to the tissues through wounds and the resulting mycelium causes the decay of valuable timber. The visible part of this Fungus (a Basidiomycete) is merely the spore-bearing surface, similar to a 'Toadstool.' (From Bergen and Davis, after Freeman.)

B. CYCLE OF THE ELEMENTS IN NATURE

We have seen that carbon dioxide is the source from which green plants derive the carbon which they synthesize into carbohydrates, fats, and proteins. Animals directly or indirectly feed

FIG. 20. — Bread Mold (*Rhizopus nigricans*), highly magnified. A type of colorless plant very much more complex in structure than the Bacteria. A, older plant, with stolon (*st*) giving rise to new plant, B. The mycelia (*myc*) are processes which permeate the bread and give rise to the sporangiophores (*sph*) bearing the spore cases (sporangia, *sp*) with their contained spores. (From Gager.)

on plants, so that the ultimate source of the carbon of animals is likewise the carbon dioxide of the atmosphere. Although both plants and animals by their respiratory process are continually returning to the outer world some of this carbon as carbon dioxide, it is evident that relatively enormous amounts of carbon are nev-

FIG. 21. — Yeast cells, very highly magnified. A, cell showing granular cytoplasm and a large vacuole; B, showing nucleus; C, cell budding; D, mother cell and bud after division is completed.

ertheless being taken out of circulation and locked up in the bodies of the plants and animals. For example, it has been estimated that about one-half the weight of a dried tree trunk is contributed by carbon.

The same general segregation is going on in regard to nitrogen. The green plants take it in the form of nitrates, for instance, and store it away in the proteins; and again animals get their nitrogen from plant proteins, so that the ultimate source of the animal nitrogen is the same. In a somewhat similar manner we might trace the fate of the other chemical elements necessary for protoplasm, but that of carbon and nitrogen is particularly striking and instructive, and is sufficient to illustrate the fact that although both green plants and animals are continually taking elements

FIG. 22. — The Carbon Cycle. A schematic representation of the circulation of carbon in nature.

from and returning them to their environment, nevertheless more is taken away than is returned. (Figs. 22, 23.)

The agents which restore to the inorganic world the elements removed by green plants and animals are the colorless plants, such as the Bacteria, Molds, Yeasts, etc. As we know, when an animal or plant dies, DECAY sets in almost immediately; that is, the complex chemical compounds are slowly but surely reduced to simpler and simpler forms until 'dust' remains. Although undoubtedly many of these compounds would automatically, so to speak, tend to simplify, nevertheless this is not only hastened, but chiefly carried out by organisms of decay such as the Bacteria. Through enzymes, or ferments, which they form, FERMENTATION occurs.

The carbohydrates and fats are resolved into carbon dioxide and water, and the proteins are reduced to carbon dioxide, water, and ammonia (NH_3) or free nitrogen, while the nitrogenous waste (urea, etc.) of animals is similarly broken down.

Practically all of these long series of chemical reactions are carried on by different kinds of Bacteria. Most green plants, however, take their nitrogen chiefly in the form of nitrates and accordingly we find that another type of Bacteria (NITRITE BACTERIA) acts upon the ammonia and transforms it into nitrous acid (HNO_2).

FIG. 23. — The Nitrogen Cycle. A schematic representation of the circulation of nitrogen in nature.

After certain chemical reactions in the soil, forming, *e.g.*, potassium nitrite or ammonium nitrite, still another type (NITRATE BACTERIA) oxidizes the nitrites into nitrates (*e.g.*, KNO_3 or NH_4NO_3), so that again this nitrogen is in a form which is available for green plants.

But, still confining our attention to the nitrogen, it is obvious that there is a leak from this cycle, since some of the nitrogen in the form of ammonia or free nitrogen escapes to the atmosphere. The greatest loss, however, is brought about by a group of DENITRIFYING BACTERIA whose activities are largely spent in changing nitrates into gaseous nitrogen which escapes into the air, and so is placed beyond the reach of green plants and animals. But fortunately there are many kinds of NITROGEN-FIXING BACTERIA

which rescue the nitrogen from the atmosphere and return it to the cycle of elements in living nature. These organisms are widely distributed, some living freely in the soil and others in tiny nodules which they produce on the rootlets of higher plants, such as Beans, Clover, and Alfalfa; and this accounts for the fact, long known but not understood, that these plants when plowed under are particularly efficient in enriching the soil. (Fig. 24.)

FIG. 24. — Root nodules caused by symbiotic Nitrogen-fixing Bacteria.
(From Bergen and Caldwell.)

In brief, there is a cycle of the elements in nature through green plants and animals and back again to the inorganic world through the Bacteria and other colorless plants. Such is the reciprocal nature of the nutritive processes of living organisms.

It is hardly necessary to state that the chemical changes produced by the Bacteria are either the direct results of, or are incidental to the process of nutrition in these organisms. Therefore the material taken as food by certain groups is relatively complex, for example, by those which bring about the early putrefactive changes in proteins; while that employed by others is very simple since they find adequate chemical combinations less complex

than those needed by green plants. Indeed, it appears possible that certain Bacteria are able to utilize carbon dioxide and water just as do green plants, but instead of obtaining energy for the synthesis from sunlight, they derive it from chemical energy liberated by the oxidation of substances in their environment. Such a process possibly represents the most primitive method of nutrition from which all the others have been derived in the evolution of life.

C. THE HAY INFUSION MICROCOSM

The importance of the complex nutritional interdependence of organisms in general as well as the cosmical function of green plants — the link they supply in the circulation of the elements in nature — may be emphasized and summarized by a brief description of a 'hay infusion.'

Probably nowhere is the 'web of life' more conveniently or convincingly exhibited than in the kaleidoscopic sequence of events — physical, chemical, and biological — which are initiated when a few wisps of hay are added to a beaker of water. Apparently the chief components of a hay infusion are hay and water, but these merely supply the matter and energy for the interplay of various forms of life. Most of these are beyond the scope of unaided vision though chiefly responsible for the obvious changes which occur from day to day in their environment.

Ordinary tapwater, for instance, contains free oxygen and various inorganic salts in solution, and not infrequently different species of Bacteria, unicellular green plants, and Protozoa. The hay soaking in the water contributes soluble salts, carbohydrates, proteins, etc. It also supplies many microscopic animals and plants which have adhered to it in dormant form and are only awaiting suitable surroundings to assume active life again. (Fig. 25.)

A microscopical examination of an infusion when it is first made shows very few active organisms, but within a day or so, depending largely on the temperature, it reveals countless numbers of Bacteria which have arisen by division from the relatively small number of dormant and active specimens originally present. At first the Bacteria are fairly evenly distributed in the infusion, but as conditions change, largely through the chemical and physical transformations which they themselves bring about, those species which can employ oxygen in combined form (that is, in chemical

compounds) find existence possible and competition less keen at the bottom of the beaker, while those types of Bacteria which are dependent upon free oxygen gather nearer the surface where the supply is being replenished constantly from the atmosphere.

Up to this point the life of our microcosm is largely bacterial — unicellular SAPROPHYTIC plants which employ as food the complex decomposition products of the proteins, etc., of the hay. The

FIG. 25. — Some representative types of Protozoa found in infusions. A, B, two species of Monads. (Mastigophora.) C, a Flagellate (*Euglena viridis*) with chlorophyll like a green plant. (Mastigophora.) D, a Vorticellid, one of the most complex ciliated Protozoa. (Infusoria.) *aSp*, adoral zone of specialized cilia; *Ch*, chloroplastid, bearing chlorophyll; *cv*, contractile vacuole; *Fi*, myoneme; *L*, lip of peristome; *Mm*, vibrating membranes in gullet; *My*, bundle of myonemes (contractile element) of stalk; *N* (in C), nucleus; *N* (in D), macronucleus; *Na*, gastric vacuole; *Nn*, micronucleus; *R*, reservoir of contractile vacuole; *S*, stigma ('eye spot'); *Um*, undulating membrane in peristome; *V*, mouth opening into gullet. (From Doflein.)

process is essentially destructive and the simplified products are represented in the relatively simple excretions of the Bacteria.

But during bacterial ascendancy another factor has been gradually intruding itself almost imperceptibly into the drama. This is the microscopic animal life which has been multiplying with increasing rapidity as conditions became more favorable, and forthwith assumes the dominant life phase in the infusion. Among

the animal forms, the first to appear are exceedingly minute flagellated Protozoa, known as Monads, many species of which absorb products of organic disintegration brought about by the Bacteria, while others ingest solid food — the Bacteria themselves. Then tiny ciliated animals, close relatives of *Paramecium*, appear in untold numbers and feed upon the Bacteria. The dominance of these smaller ciliates is brought to an end after a few days by the ascendancy of larger ciliates, which, though feeding to a certain extent upon the already greatly depleted bacterial population, obtain most of their food by eating the smaller ciliates. And so the cycle of life continues — saprophytic forms gradually being replaced in dominance by herbivorous and these in turn by carnivorous organisms. (Fig. 25.)

But obviously this chain of events must sooner or later come to an end through the dissipation of energy brought about by the metabolic processes of the colorless plants and animals. Sooner or later the supply of potential energy stored up in the chemical compounds of the hay will have become nearly or completely exhausted — transformed into the kinetic form and expressed in the life activities of the plant and animal population.

Thus, after a few weeks, the hay infusion world has reached a standstill — extermination faces the population and inevitably occurs unless microscopic green plants, close relatives of *Pleurococcus*, find opportunity to develop in the energy-exhausted environment and proceed to entrap the kinetic energy of sunlight, store it up in carbohydrates and proteins, and thus restore energy in the potential form to the hay infusion.

If such occurs, the hay infusion world is a microcosm indeed — green plants, colorless plants, and animals gradually become reciprocally adjusted so that a self-perpetuating condition of practically stable equilibrium is established; in other words, what is termed a 'balanced aquarium.' The rise and fall of teeming populations, made possible by the rapidly changing environmental conditions which the bringing together of hay and water initiated, is replaced by an apparently harmonious interdependence of organisms demanding different food conditions, such as we are familiar with in the world at large.

CHAPTER VII

THE MULTICELLULAR ORGANISM

Over the structure of the cell rises the structure of plants and animals, which exhibit the yet more complicated, elaborate combinations of millions and billions of cells coördinated and differentiated in the most extremely different ways. — *Hertwig*.

It has been pointed out that all organisms consist either of one free living cell or of many cells, and some idea has been gained of unicellular forms from *Pleurococcus*, *Paramecium*, and the Bacteria which were selected to illustrate various types of nutrition. We are now in a position to consider the origin and organization of the individual in the METAZOA and METAPHYTA, as the multicellular animals and plants are sometimes called.

Every individual, with exceptions to be noted later, begins its existence as a single cell which has been set free as a SPORE from the parent, or which has been formed by the fusion of two cells, or GAMETES, each typically derived from a separate parent individual: one MALE, the other FEMALE. The former method is known as UNIPARENTAL, or ASEXUAL, reproduction and the latter as BIPARENTAL, or SEXUAL, reproduction. The union of male and female gametes (SPERM and EGG) in sexual reproduction to form the ZYGOTE is termed FERTILIZATION. Both asexual and sexual methods are widespread among plants and animals, frequently alternating in regular sequence in the same species to give what is termed an ALTERNATION OF GENERATIONS.

The most remarkable fact about a reproductive cell is its power to develop into an organism similar to the parent from which it has separated. Both the spore and the zygote (fertilized egg) are set, one may say, to go through a series of changes which transform an apparently simple cell into an obviously complex multicellular plant or animal with all the tissues and organs characteristic of the species. It is important, at this point, to review the typical method by which the development of the adult is accomplished.

Briefly, the general method of development is cell division accompanied by differentiation. The spore (asexual) or the zygote (sexual) by a succession of cell divisions, termed **CLEAVAGE**, passes from the single-cell stage to a two-cell stage and then, with more or less regularity, to four-cell, eight-cell, sixteen-cell stages, etc. If these cells separated after each division, the same general condition would occur here which has been seen in the *Protophyta* and *Protozoa*, where each organism is a complete free-living cell. Or again, if cleavage merely resulted in a group of so many exactly similar cells, there would arise a **COLONY** of unicellular individuals rather than a multicellular organism.

Such colonial forms are, in fact, numerous among the lower plants and animals, and show nearly all grades of complexity from simple associations of a few identical cells, as for example in *Spondylomorom*, to groups of many thousands of cells in which some of the individuals are specialized for certain functions. *Volvox* affords an instructive example of the latter condition. The majority of the cells, ten thousand or more, that form the relatively large

spherical colony are flagellated individuals, each of which lives a practically independent existence in organic union with its fellows. The chief contribution of each of these cells to the economy of the whole results from the lashing of its flagella, which helps to propel the colony through the water. But, under certain conditions, some of the cells become specialized for reproduction, both asexual and sexual, and form new colonies which sooner or later are set free. Thus we have a differentiation of reproductive (**GERM**) cells from body (**SOMATIC**) cells, and a foreshadowing of that further specialization and physiological division of labor between cells which is the most characteristic feature of the *Metaphyta* and *Metazoa*. (Figs. 26, 27, 154.)

Indeed, the complex bodies of multicellular organisms are made possible by cell differentiation and cell coöperation. All protoplasm possesses, for instance, the primary attribute of contractility, but

FIG. 26. — A simple colony of unicellular organisms (*Spondylomorom*) each of which carries on all the functions of life, including reproduction. (From Hegner, after Oltmanns.)

in the muscle cells of animals we find the capacity for contraction very greatly developed, and to a certain extent at the expense of other powers. But this differentiation would be ineffective were not innumerable similarly specialized cells grouped together—

FIG. 27. — *Volvox globator*, a large colony of flagellated unicellular organisms in which the various cells have become organically connected, and certain cells specialized for reproduction. *A*, mature colony (highly magnified) showing sperm, ♂, and eggs, ♀, in various stages of development. *B*, four cells (more highly magnified) showing the connections between three 'somatic' cells, and the early differentiation of a reproductive cell, *rp*; *cv*, contractile vacuole; *st*, 'eyespot' or stigma. (From Kölliker.)

marshalled to perform a certain function. The power of a muscle results from the combined action of its component muscle cells. Differentiation without coöperation between cells we have seen in unicellular organisms. Paramecium has highly specialized parts; other Protozoa have still more — perhaps the limit of possibilities of the single cell. But the multicellular body solves the difficulty by removing the limit — by assigning special functions to groups of cells rather than to parts of one cell.

Thus cell division (cleavage) involving differentiation and its attendant physiological division of labor is the keynote of development in the higher animals and plants. Among animals, for example, the cells which arise from the cleaving egg (zygote) usually

FIG. 28. — Early stages in the development of the egg of a Sea Urchin. *A-F*, cleavage and formation of the blastula; *G*, section of blastula showing the beginning of gastrulation; *H-I*, early and later gastrula stages. *a*, ectoderm; *b*, endoderm; *c*, blastocoel; *d*, blastopore, leading into the enteric cavity; *e*, cells, arising from the endoderm, destined to form the mesoderm.

become arranged so that they form the surface of a hollow sphere of cells known as a **BLASTULA**. All the cells at first appear essentially similar, but soon those at one side of the blastula become invaginated until the central cavity, termed the **BLASTOCOEI**, is

largely obliterated. Accordingly there results the GASTRULA stage, which may be roughly compared to a sack, with an opening to the exterior termed the BLASTOPORE, composed of two layers of cells. The outer layer is known as the ECTODERM, and the inner, which lines the gastrula cavity (ENTERIC CAVITY), as the ENDODERM. The ectoderm comprises cells which are already somewhat differentiated among themselves for special purposes, but which, as a whole, form a primary tissue with general functions of its own, chiefly sensory and locomotor. Similarly the endoderm consists

FIG. 29. — Portion of a cross section of the small intestine of the Frog, highly magnified to show cellular differentiation and tissues. *a*, ordinary absorptive epithelial cells lining the intestine; *b*, unicellular glands; *c*, connective tissue; *d*, blood vessel in connective tissue; *e*, circular muscle cells; *f*, longitudinal muscle cells; *g*, peritoneal membrane; *h*, blood vessels in longitudinal muscle.

of cells which, as a group, form the nutritive cells of the embryonic animal. (Fig. 28.)

In the gastrula stage of most animals, a third layer of cells arises typically from the endoderm and becomes disposed between the ectoderm and endoderm. This new middle layer is the MESODERM. In this way the so-called three PRIMARY GERM LAYERS are established which are characteristic of the developing animal, and from these are derived the specialized tissues which compose the various organs of the adult. For example, the ectoderm by cell division and differentiation gives rise to the outer skin and central nervous system; the mesoderm to muscular and supporting tissues and the

blood vascular system; while the endoderm forms the layer of cells which lines the alimentary canal of the adult organism.

This grouping of more or less similar cells into functional systems, or **TISSUES**, is at the basis of the architecture of multicellular organisms, and thus we have now reached another level in the analysis of their structure. Although the unit of organization is the cell, these are associated in groups, or tissues, which represent a morphological unit of a higher order — a division of labor among the cells that makes possible the multicellular body with its attendant complexity. A tissue may be defined as a group of essentially

FIG. 30. — Portion of a cross section of a young plant stem, magnified to show cellular differentiation and tissues. *ca*, cambium; *co*, cortex; *e*, epidermis; *p*, pith; *ph*, phloem; *x*, xylem.

similar cells specialized to perform a certain function. Examples are bone, muscle, and nerve in animals; and wood and bark in plants. (Figs. 29, 30.)

Since the similar cell components of multicellular organisms are grouped to form tissues, it follows that the major working units, or **ORGANS**, of the animal or plant body as a whole are formed of tissues. In other words, an organ is a complex of tissues which has assumed a definite form for the performance of a certain function: for example, the human hand composed of bone, muscle, nerve, etc.; or the plant stem of wood, bark, etc.

As one would naturally expect, among the lowest Metaphyta and Metazoa there are forms in which the body is relatively simple, without highly specialized tissues and organs, but in most animals specialization is carried still another step forward by the

grouping of organs devoted to the performance of some one general function into an ORGAN SYSTEM. An animal has many muscles, each of which is an organ but which collectively constitute a working unit, the muscular system; or it has stomach, intestine, liver, etc., forming the digestive system. On the other hand, even in the highest plants, differentiation has proceeded neither in just the same way, nor so far, since the body is composed of tissue systems rather than organ systems. This point will be clear when the structure of the plant and animal body has been considered.

In truth, the multicellular plant or animal — the organism as a whole — is the resultant of the action and interaction of organs, tissues, and cells; and in the final analysis the body is a multitude of coöperating protoplasmic units. However, we must not overlook the whole which is greater than its parts. The cells merge their individuality in that of the entire organism, and as long as its cells remain associated they are to be regarded, not as individuals, but as specialized centers of action and reaction of the living body itself, by means of which physiological division of labor is made possible.

CHAPTER VIII

THE PLANT BODY

The evidence seems to show beyond question that our present species of plants have descended by gradual evolution from simpler and fewer species which formerly existed — back, it is possible, to a single kind which thrived in remotest antiquity. — *Ganong*.

NEARLY all stages exist between the simplest unicellular plant body such as is exhibited by *Pleurococcus*, and the highly complex multicellular body of the familiar Flowering Plants, technically

FIG. 31. — *Spirogyra*. *A*, one cell of a filament. *B*, dividing cell shown in section. (From Smith and others.)

known as the SEED PLANTS or SPERMATOPHYTES. A simple type is found among the thread-like, or filamentous, green Algae commonly called Pond Scums. Thus in *Spirogyra*, the body of the plant consists of a series of similar cells placed end to end and, therefore, from one point of view, may be looked upon as a colony of cells

since the individual cells of the filament are essentially independent. In *Ulothrix*, another simple form, the filament instead of floating free is attached by a more or less specialized cell devoid of chlorophyll. (Figs. 31, 62.)

Still more common are plant bodies composed of branching filaments of cells. The branches may all be similar, or there may be a chief axis with lateral branches of different form. Frequently the

FIG. 32. — A common Seaweed (*Fucus*). One of the Brown Algae, showing comparatively simple thallus structure. (From Coulter.)

branches, though still composed merely of filaments of cells placed end to end, may show, for example, larger chloroplasts and thus be more active in photosynthesis. This is essentially the same general division of labor that occurs between the stem and leaves of higher plants, but without the attendant structural differentiation of these parts into various tissues.

The next specialization we find is in regard to the character of the growth. Whereas, in simple unbranched filamentous forms, growth takes place, as a rule, by the division of all of the cells composing it, in the branched types this is usually restricted to one or more cells near the

end of each filament. Thus, depending on the character of the growth from the apical cells, various complex forms of massive branching structures arise as, for instance, in many of the Red Seaweeds. In these plants the chloroplasts are chiefly developed in the cells on the surface; which again indicates the physiological division of labor referred to above and suggests that many, if not all of the modifications of the simple plant bodies thus far considered are provisions for the purpose of bringing about the most favorable exposure to light of the photosynthetic apparatus.

Another method of attaining the same object is found in other Seaweeds. In the common Sea Lettuce (*Ulva*) and the Rockweed (*Fucus*) the plant body takes the form of a plate of cells, as a result

FIG. 33. — The Giant Kelp (order *Laminariales*). A marine Alga which may attain more than 200 feet in length. A thallus plant exhibiting distinct leaf-like and stem-like structures supported by the water, and a holdfast that anchors it to the bottom. (From Ganong.)

of cell division occurring in two planes, and then this THALLUS usually becomes thicker by division of the cells in a third plane also. Moreover, as a result of further modifications of the thallus, the single attaching cell of the simple filamentous types is replaced

FIG. 34. — Gulfweed (*Sargassum*) showing the 'stem,' 'leaves,' and the berry-like floats of the thallus. (From Coulter, Barnes, and Cowles.)

in the larger Seaweeds by massive HOLDFASTS which anchor them securely to rocks. Still there is no marked differentiation in the cellular components of the holdfasts because they perform only this one function of the roots of higher forms; the absorption of food

materials dissolved in the water being carried on by the individual cells of the whole plant. Although among the most complex Seaweeds, for example in the Kelps and Gulfweed, the form of the thallus is highly modified into divisions which serve certain of the functions of root, stem, and leaf of higher plants, still none of the fundamental tissue differentiations so characteristic of the higher forms occur. Similarity of *function* has given rise to ANALOGOUS structures. (Figs. 32-34.)

It is among the higher groups — the Ferns and Seed Plants — that the most specialized plant bodies occur. As will be explained in more detail later, these plants exhibit in their life history an alternation of generations: a sexual plant (GAMETOPHYTE) bearing gametes gives rise to a non-sexual spore-bearing plant (SPOROPHYTE) which in turn produces a gametophyte. These two generations exhibit marked differences in structure. The gametophyte body is relatively very simple, consisting merely of a few cells, the main function of which is to develop male and female gametes. On the other hand, the sporophyte is composed of a number of specialized tissues and organs, and is the conspicuous generation which is recognized by everyone as a 'Fern' or a 'Seed Plant.' Accordingly, for the present, attention will be directed to the sporophyte.

A. STRUCTURE

The body of the sporophyte of a typical Seed Plant is clearly differentiated into two parts, ROOT and SHOOT. The root is the organ of attachment, as well as of absorption of food material in solution. The shoot consists of STEM and LEAVES. The stem is largely a passive structure and forms the connecting link between the root and the photosynthetic apparatus of the leaf. The reproductive organs that produce the spores are usually developed on modified leaves which are grouped, with certain accessory structures, to form a FLOWER.

In order to obtain a mental picture of the essential working plan of the tissue distribution in these major parts of the body of a higher Seed Plant, we shall consider first an ideal vertical section through a generalized plant. (Fig. 35.)

The root and shoot system together constitute a continuous body, which may be regarded as forming a long narrow cylinder of cells, the bottom of which is the growing point of the primary

FIG. 35. — Ideal vertical section through a generalized plant, showing the typical distribution of the systems of tissues. The central cylinder, or stele, comprises the pith (coarse dotted), xylem (diagonally lined), phloem (cross lined), with cambium (fine dotted) between and extending to growing points of root and shoot. The cortical system (crosses) forms the 'hollow' cylinder which surrounds the central cylinder and is, in turn, enclosed by the outer 'hollow' cylinder (double lined), or dermal system. (From Ganong.)

root, and the top, the growing point of the shoot. This *primary cylinder*, in turn, is made up of a solid *central cylinder* of cells, surrounded by *two concentric 'hollow' cylinders*. The inner of these concentric hollow cylinders surrounds the central cylinder, and in turn is surrounded by the outer cylinder. The latter forms the surface of the primary cylinder, or the outer layer of cells of the plant. These three cylinders comprise the PRIMARY TISSUE SYSTEMS.

The central cylinder, known as the STELE, runs continuously throughout root and stem, and extends into the branches so that certain of its elements enter the leaves to form the VEINS. It provides the PITH, or primary axial tissue, and the VASCULAR BUNDLES. The latter include the food-conducting tissue (PHLOEM), the water-conducting tissue (XYLEM), and between them the actively growing tissue (CAMBIUM). The cambium becomes continuous with the tissues at the growing points of stem and roots, and together these embryonic tissues, called MERISTEM, may be regarded as the GROWTH SYSTEM of the plant.

The hollow cylinder, immediately surrounding the solid central cylinder, comprises the CORTICAL SYSTEM which provides the chlorophyll-bearing tissue of the young stem and of the leaves, and also the CORTEX of bark and root.

The outside cylinder forms the DERMAL SYSTEM which supplies the hair layer of the surface of the young root and the protective EPIDERMIS covering the stem and leaf.

Bearing in mind this diagrammatic plan of the root and shoot and of their component tissue systems, we are in a position to survey some of the common forms assumed by the root, stem, and leaf of the higher Seed Plants, and also to analyze their tissue systems by the study of transverse and longitudinal sections under the microscope.

1. *Types of Roots*

The PRIMARY ROOT of a young plant, which is usually a continuation downward from the shoot, may persist throughout the life of the plant as the chief root and merely give off laterally small secondary roots. Such a root system, known as a TAP root, is common in many herbs, as for example the Dandelion. More often the primary root is entirely replaced by the SECONDARY ROOTS which radiate and branch in all directions from the main axis of

the plant until they form a complex underground structure. This may equal in size the part of the plant body which is developed above the surface by the shoot system. (Fig. 36.)

FIG. 36. — *A*, tap root of the Dandelion; *B*, fibrous roots of a grass; *C*, clustered and fleshy roots of the Dahlia. (From Bergen and Davis.)

In plants which live through two years (**BIENNIALS**), often the first year is spent in storing up food. Sometimes this is in the roots, in which case they are greatly enlarged to form a reservoir of material, at the expense of which during the second season the plant rapidly develops flowers and seeds. These **STORAGE** roots may be tap roots as in the Turnip, or lateral roots as in the Dahlia and Sweet Potato. (Fig. 36, *C*.)

Although the contact of the plant with its environment through its roots is ordinarily underground, tropical plants in particular frequently develop **AERIAL** roots from the stem or its branches. Roots which rise from such unusual places are called **ADVENTITIOUS** roots. In certain species the aerial roots hang free in the air and absorb moisture from the atmosphere. In addition, such roots

FIG. 37. — English Ivy, showing the aerial roots which enable it to cling to walls. (From Ganong, after LeMaout and Decaisne.)

may develop chlorophyll and so perform the characteristic function of leaves. In the Fig tree the aerial roots grow from the branches down to the earth where they become attached, and eventually form a stout trunk which functions as a stem. Comparable to these roots are the so-called PROP roots of some Palms and of the familiar Indian Corn. (Figs. 37, 81.)

FIG. 38. — Dodder, a parasitic Seed Plant, entwined about the stem of its host, a Golden Rod. *A*, cross section of stem of host to show its penetration by the Dodder roots (haustoria). *C*, several Dodder seedlings growing in the soil before attachment to a host. *h*, stem of host; *l*, scale-like leaves; *r*, haustoria; *s*, seedlings. (From Bergen and Davis.)

Many plants depend chiefly or entirely on other plants for their food materials. The roots of such PARASITIC species frequently grow into the tissues of their HOST, and become more or less modified into suckers, or HAUSTORIA. In the Dodder and Mistletoe,

the haustoria enter the tissues of the stem of the host, while in many of the false Foxgloves (*Gerardia*) they enter the tissues of the roots. In some aquatic and parasitic plants roots are absent, their function being taken over by other parts of the body such as stem or leaves. (Fig. 38.)

Without multiplying examples, it is clear that the part of a plant which the botanist calls a root, and which typically anchors the

FIG. 39. — Cell division and tissue differentiation in a growing root tip. Diagram of root (a) shaded to show the several regions from which the highly magnified sections (b, c, d, d', e) are taken. (From Densmore.)

plant to the earth and takes water with food materials in solution from the soil, frequently is highly modified and even assumes the duties of other organs in certain plants which are adapted for special places in the economy of nature.

2. Histology of Roots

An examination with the microscope of the tip of a root shows that it is covered with a large number of cells which form the ROOT CAP. These cells are gradually rubbed away as the root

works through the soil and continually replaced by new ones from the GROWING POINT which is immediately above. The numerous, small, densely-packed cells constituting the growing point represent the region of cell formation for the entire root tip, since near the center is a group of cells from which smaller cells are divided off, and these in turn absorb food materials and gradually attain

FIG. 40. — Root hair (very highly magnified) showing its relation to adjoining cells of the root and to particles of the soil. *a*, vacuole filled with cell sap; *b*, cytoplasm (dotted); *c*, soil particles; *d*, nucleus within the cytoplasm lining the cell membrane.

the normal size. It will be recalled that the growing point is continuous with the cambium region above, and it thus represents the growth system (meristem) at the root tip. (Fig. 39.)

Just above the growing point is the GROWTH ZONE which includes cells recently formed by the tip in its growth downward. In this region the cells enlarge rapidly, especially in length, and at the same time retain relatively thin cell walls. The cytoplasm of these cells, by the development and fusion of large vacuoles of CELL SAP (water, sugar, and other substances in solution), soon forms merely a lining closely applied to the wall; a condition characteristic of many plant cells in contrast with those of animals. In the growth zone also is clearly seen on the surface the protective layer, or epidermis, and, just within, the cortex made up of several layers of cells. Still further toward the center of the root, the central cylinder appears, which shows differentiating vascular bundles.

Passing now to a point a little above, we find the growth zone merging imperceptibly into a region in which many of the epidermal cells on the outer surface of the root are modified into ROOT HAIRS. It has been emphasized above that the primary function of the root is the intake of certain of the elements of food in

solution. This function is performed almost entirely by OSMOSIS through the extensive area afforded by the surface of the root hairs, and accordingly cells of this type form the vital point of contact between the root and its environment. The root hairs exhibit the

FIG. 41. — Optical section (highly magnified) of a generalized plant cell. (From Ganong.)

selective power of protoplasm to a remarkable degree. For example, Red Clover plants and Barley plants when burned yield about the same proportion of mineral matter as ash. But the Barley ash contains nearly twenty times as much silica as the

FIG. 42. — Propagation of the Strawberry plant by runners. A, parent plant; B, young plant; b, modified leaf; r, runner or stem. (From Bergen and Caldwell.)

Clover, while the latter contains nearly six times as much lime as the Barley. (Figs. 40, 57.)

In the zone in which root hairs are present, the central cylinder of the root shows still more cellular specialization. The young

vascular bundles are differentiated into the phloem tissue, characterized by its small angular ducts; while the developing xylem, with its large ducts, has obliterated the primitive ground tissue, or pith. Between the xylem and the phloem appears the developing cambium, but this begins its characteristic growth contribution somewhat above the hair zone. Indeed, as we pass upward from the region where the root hairs are developed, the cellular structure becomes more and more similar to that of the stem; the older woody roots of trees and shrubs being, from the standpoint of both structure and function, stems. (Figs. 35, 39.)

3. *Types of Stems*

The stem is the axis of the shoot and has two primary functions. First, to support and raise the leaves into a position of vantage with respect to light; and, second, to act as the medium of communication between the absorbing organs, or roots, and the photosynthetic organs, or leaves. But, like the root, it may be modified and diverted from its typical structure and take over more or less of the functions of other parts.

FIG. 43. — Bulb of a Hyacinth, in section, showing roots, stem, bases of leaves of previous year stored with food, and new foliage leaves about the flower cluster. (After Figuier.)

For the purpose of propagation, creeping stems occur, such as the surface RUNNERS of the Strawberry, and the underground RHIZOMES of many Sedges, Grasses, and common Ferns. Sometimes the stem to a large extent replaces the root system, but more often it acts as an underground reservoir in which food material is stored up during the short growth period for the rapid development of the flowering shoot. This is well seen in some of the early spring Seed Plants of New England such as Bloodroot and Trillium. (Figs. 42, 51.)

Again, the stem is greatly shortened to form a BULB or a CORM; types particularly common in plants adapted to dry soil. Extremely arid regions are characterized by plants, such as the Cacti, in which the leaves are completely suppressed to prevent rapid evaporation; their function being taken over by the stem which is pro-

vided with well-developed chlorophyll-bearing tissue. Sometimes parts, BRANCHES, of the stem may superficially resemble a leaf by being flattened or otherwise modified, as in the Prickly Pear, the apparent leaves of the so-called Smilax (*Myrsiphyllum*), and the filamentous 'leaves' of Asparagus. Finally, the versatility of the stem is illustrated by the THORNS of the Honey Locust, the twining

FIG. 44. — Stem of Smilax (*Myrsiphyllum*). *cl*, leaf-like branch, or cladophyll, situated in the axil of a leaf; *l*, leaf; *ped*, flower stalk. (From Bergen.)

TENDRILS of the Grape, and the TUBER of the Potato which is essentially a 'concentrated rhizome.' (Figs. 43, 44.)

4. Histology of Stems

Just as cell division in the meristem tissue of the growing tip of the root proceeds in such a way that the direction of growth is typically downward, so in the similar region at the growing point (bud) of the shoot we find that cell multiplication results in progress upward. In other words, from the region where root and shoot merge, the growth of the plant is in opposite directions.

The general character of the embryonic tissue is essentially the same in both the root and shoot regions, being composed of densely packed, more or less cubical cells which are completely filled with protoplasm. At this stage the cells have not become modified for

FIG. 45. — Diagram of the structure of the woody stem of a vine, a Dicotyledon. (Modified, after Ray.)

special functions by the formation of vacuoles of cell sap, or in other ways. But all the tissues of the stem are derived from the cells of the growing point, so that slightly below this region three areas are to be noted in which differentiations are in progress. These result in the formation of the outer cylinder (epidermis), the intermediate cylinder (cortex), and the central cylinder (stele) in which the ground tissue (pith) is gradually encroached upon by the developing vascular bundles. The general arrangement

FIG. 46. — Portion of a cross section of the woody stem of Oak. *m*, pith and medullary rays, from center to bark; *r*, annual rings; *b*, boundaries between rings, porous from presence of many ducts; *i*, interior fibrous layers of dead bark. (From Bergen and Caldwell.)

FIG. 47. — Leaf of a Seed Plant, showing blade, or lamina, petiole, and two stipules at the leaf base. (From Ganong, after Gray.)

of these fundamental tissue systems may be seen, for instance, in a transverse section of the stem of a vine such as *Aristolochia*, which affords almost a diagrammatical picture of the plan of stem anatomy in one of the two great divisions (Dicotyledons) of Seed Plants. (Figs. 30, 45, 46, 56.)

5. *Types of Leaves*

Leaves and roots form the two chief points of contact between the plant and its surroundings. The fundamental functions of

FIG. 48. — Branch of Horse Chestnut showing winter buds enclosed by thick scale leaves. (From Smith and others.)

FIG. 49. — Onion leaf, cut longitudinally
bl, blade; *int*, hollow interior of blade; *s*, thin sheath of leaf; *sca*, thickened base of leaf. (From Bergen and Davis, after Sachs.)

FIG. 50. — Leaves of Sundew during digestion of captured prey. The one at the left has all the tentacles closed; the one at the right, only half of them closed over the prey. (From Bergen.)

leaves are to expose to the sunlight the chlorophyll apparatus and to afford a surface for evaporation and the exchange of gases with the environment. Accordingly the principal part of a typical leaf is a broad blade, or LAMINA, which affords the optimum conditions for exposure. The leaf is usually attached to the stem by a stalk, or PETIOLE, which is somewhat modified at the point of union with the stem into a LEAF BASE from which arise leaf-like appendages, or STIPULES. When the petiole is absent, the lamina of such a sessile leaf appears to arise directly from the stem. (Figs. 47, 55, 56.)

The leaf, like the root and the stem, exhibits numerous modifications in adaptation to other functions. The chlorophyll-bearing tissue may be nearly or completely suppressed, as in the SCALES which enclose WINTER BUDS in a protective case. These are conspicuously developed in the Horse Chestnut and also in the Hickory. Or the scale leaves, in addition to affording protection, may act as reservoirs in which food materials are stored, an example of which is the familiar Onion. Indeed, all transitions between scale leaves and typical foliage leaves may frequently be seen in an unfolding leaf bud. Still more marked departures from the

FIG. 51. — The Sensitive Fern (*Onoclea sensibilis*), showing vegetative leaf, and spore leaf, or sporophyll, arising from the rhizome. (From Bergen and Davis.)

usual leaf-form are the TENDRILS of some climbing plants such as the Sweet Pea, the SPINES of the Barberry and the Thistle, and the 'INSECT TRAPS' of Pitcher-plants and Sundews which capture small living animals. (Figs. 48-50.)

Leaf modification in another direction occurs in the spore-bearing structures of Ferns and Seed Plants. In some Ferns the spore cases (SPORANGIA) are borne upon typical leaves, and in others on special leaves with the chlorophyll-bearing tissue partly or completely suppressed. Such leaves which are given over to the production of spores, as in the common Sensitive Fern, are known as SPOROPHYLLS. In the Seed Plants, the FLOWER is a group of

FIG. 52. — The floral parts of the Alpine Azalea (*Loiseleuria*). Collectively the sepals constitute the calyx, and the petals, the corolla. The pistil represents several united carpels. (From Bergen and Caldwell, after Müller.)

sporophylls, known as CARPELS and STAMENS, associated in most cases with certain sterile leaf structures, termed SEPALS and PETALS, which afford protection to the sporophylls and offer attraction to insect visitors. We shall consider the structure of the flower in more detail when discussing reproduction in plants. (Figs. 51, 52, 73.)

6. Histology of Leaves

The embryonic cells forming the growing point, or bud, of the shoot comprise, as we have seen, the fundamentals of both stem and leaves; that is to say, stem and leaves arise together in buds. The method of formation of stem and leaves is well seen in the buds of a common water plant, *Elodea*. Here the rounded end of the stem is composed of the characteristic embryonic tissue. The rudiment of each individual leaf is first visible on the surface as

an enlarged cell, which by division and differentiation gradually develops into a flat projection of epidermal, cortical, and vascular tissue, constituting the fully formed leaf. (Fig. 53.)

The fundamental structure of a typical leaf is well illustrated by a transverse section. The essential features consist of upper and lower limiting membranes (epidermis) which are continuous at the edges of the blade, and thus enclose the supporting and conducting tissues consisting of vascular bundles (veins), and the chlorophyll-bearing cells (CHLORENCHYMA) that carry on the work of photosynthesis. (Fig. 54.)

The walls of the epidermal cells are impervious to water and gases, and accordingly the epidermis is perforated with tiny pores (STOMATA) which lead to air spaces among the chlorenchyma cells. It is estimated that the number of stomata in the epidermis of typical leaves averages about 500 per square millimeter. Each stoma is enclosed by two specialized epidermal cells, termed GUARD CELLS, which regulate the size of the opening according to varying internal and external conditions.

The veins, as we have seen, are merely the extensions into the leaf of the chief elements of the vascular bundles of the stem. They form the framework of the leaf, as well as the complex network of highways for the transportation of materials between the blade as a whole and the stem. In transverse section the larger veins

FIG. 53. — Diagram of a section through a terminal naked bud of *Elodea*, showing the development of leaves. (From Smith and others.)

show the essential features of the vascular bundles seen in the stem, lacking, however, the cambium.

The major tissues of the leaf consist of chlorophyll-bearing cells. Immediately under the upper epidermis these cells are arranged in a definite layer known as the **PALISADE TISSUE**. Below this region the cells are more or less irregularly disposed so that there are larger and smaller **AIR SPACES** between them. These air spaces in the **SPONGY TISSUE** form a practically continuous system of passages

FIG. 54. — Diagram of a portion of the blade of a leaf, showing the relations of the various tissues. (From Smith and others.)

and thereby facilitate the interchange of oxygen, carbon dioxide, and water vapor between the leaf cells and the outer world through the stomata.

The cytoplasm within the thin walls of the chlorenchyma cells forms merely a lining in which are situated the nucleus and numerous specialized, disc-shaped, cytoplasmic bodies, the chloroplastids, which contain chlorophyll and therefore appear green. It will be recalled that these are the essential agents of photosynthesis. The center of the cell is occupied by a large vacuole filled with cell sap. This sap is usually under pressure, which accounts for the close application of the cytoplasm to the inside of the cell

wall and produces the rigidity, or **TURGOR**, characteristic not only of the chlorenchyma cells, but also of many other types of plant cells as well. The wilting of the leaves of cut plants is due chiefly to the escape of water from the cell vacuoles resulting in loss of turgor. (Fig. 41.)

FIG. 55. — Diagram of characteristic structures of Monocotyledonous Seed Plants. A, leaf, parallel-veined; B, stem with vascular bundles scattered through the pith; C, flower with parts in 3's (transverse section); D, flower; E, seed having embryo with *one* cotyledon (transverse section). See Fig. 56. (From Gager.)

B. PHYSIOLOGY

We have now outlined the essential structure of a generalized Seed Plant, with the exception of the parts modified for reproduc-

tion. Before turning to the flower, the function of which has to do with the race rather than the individual, it is important to consider the organism as a whole — how the various cells, tissues, and organs coöperate in the nutrition of the living plant. For nutrition,

FIG. 56. — Diagram of characteristic structures of Dicotyledonous Seed Plants. A, leaf, netted-veined; B, stem with vascular bundles arranged so that wood forms annual rings; C, flower with parts in 5's (transverse section); D, flower; E, seed having embryo with *two* cotyledons (transverse section). See Fig. 55. (From Gager.)

it will be recalled, is the function of primary importance to the individual.

The essentials of nutrition were readily described in the simple green plant *Pleurococcus*, because the whole organism comprises but a single cell which directly interchanges matter and energy with its environment. But with the establishment of the complex plant body, an organization of many millions of highly specialized

cells, the intricate interrelationship of the various parts to the nutrition of the whole becomes a problem in itself.

1. *Circulation Paths*

The green plant, as we know, takes in the raw materials and builds them up into its foodstuffs. In the case of the higher plants, water in large amounts is taken in through the root hairs. Dissolved in this water are various substances — nitrates, phosphates, sulfates, etc. — supplying most of the elements that are necessary for the make-up of protoplasm. The leaves admit carbon dioxide through the stomata. Thus the substances which are to be built up into foodstuffs enter at the opposite ends of the plant, and must be brought together in a chemical laboratory, as it were, in order that their union may be effected. The organ in which food construction takes place is the leaf, and, specifically, in the chloroplastids. Accordingly we must consider the highways which bring the raw materials from the root hairs to the leaves, and those which distribute the finished products to the various parts of the plant for their use. (Fig. 57.)

The water which enters the root hairs is given a start up the stem by ROOT PRESSURE due to osmotic phenomena in the multitude of cells of the root. This pressure in an actively growing tree in spring may be nearly forty pounds to the square inch. Passing from the xylem of the root the ascending water enters the similar region of the stem. Here the conducting vessels are of two kinds: namely, greatly elongated single cells, known as TRACHEIDS, and DUCTS. The latter are really tubes which have been formed by the

FIG. 57. — Diagram of the path of water with solutes from the soil through a root hair and internal cells of a root to the xylem. (From Smith and others.)

absorption of the adjoining walls of many long cells arranged end to end. The mature tracheids and ducts, though originally derived from living cells, are devoid of protoplasm, and form a series of non-living tubes extending up the stem to the leaves, through which they are distributed in the veins. This is the fluid-conducting highway from root to leaf. (Fig. 58.)

FIG. 58. — Diagrammatic presentation of the chief physiological activities of a Seed Plant (Bean). The first leaves (seed leaves, or cotyledons) are richly stored with food but contribute only slightly to photosynthesis. (From Densmore.)

The supply of carbon which the plant needs is obtained from carbon dioxide which enters the leaves through the stomata. The water, containing various salts in solution, which has been taken in by the roots, meets the carbon dioxide in the chlorophyll-bearing cells; and it is here that these raw materials are manufactured into food. As we know, through the radiant energy of light a complicated series of chemical reactions are initiated by which

carbon, oxygen, and hydrogen are united to form a sugar. In this process, free oxygen is evolved which may be used in respiration or liberated through the stomata. Part of the sugar thus formed is directly utilized by the plant as fuel, and part is employed as the basis for the manufacture of proteins and the living material itself by the addition of nitrogen and various other chemical elements.

Therefore the leaves are the organs specialized for assembling the materials of the inorganic world and forming from them new

FIG. 59. — The seasonal history of an annual plant, a Bean.
(From Densmore.)

chemical compounds of such a character that they can be utilized as building material for the plant body, and as sources of energy for carrying on the vital functions. In other words, the new compounds are the food of the plant — and, incidentally, of the rest of the living world.

In every case all types of food built up in the leaves must be distributed to the organism as a whole. This occurs chiefly by diffusion in the form of soluble carbohydrates (*e.g.*, grape sugar) or in soluble nitrogenous form (*e.g.*, amines or soluble proteins) to the smallest veinlets and then on to larger and larger veins, which finally lead to the stem.

In the stem, the course taken by the food depends upon the immediate needs of the plant. It may pass either up or down through the phloem, or some may be transferred to the xylem and carried to the growing tip or the developing flower, etc., for immediate use. When growth is not active, most of the food passes downward through the phloem to supply the cambium and to be stored, chiefly as starch, in stem and root. In brief, all the living cells of the plant directly or indirectly draw upon the supply of food circulating through the phloem, so we may look upon the phloem as primarily a food-distributing system from the leaf,

FIG. 60. — The seasonal history of a biennial plant, White Sweet Clover. (From Densmore.)

just as we have seen that the xylem is the system for carrying water and solutes from root to leaf. The raw materials pass up through the wood and the finished products pass down through the bark.

2. Dynamics of Circulation

The question will naturally arise in the mind of the reader: what is the force which brings about the circulation of all these fluids in the plant body? We have mentioned that water containing solutes enters the root hairs and passes to the cortical cells and ducts of the xylem chiefly by the physical process of osmosis — a 'push' from below referred to as root pressure. It is also believed that osmosis in the leaves draws water from the ducts of

the stem into the cells of the leaf, and therefore plays an essential part in lifting water to the tops of even the tallest trees. But also apparently involved in the dynamics of this rise of sap is the interesting physical phenomenon that water when confined in tiny tubes, such as those of plant stems, possesses remarkable tensile strength — “it is as strong as wire” — and evaporation at the upper end of the water column in the leaves serves to pull up the water.

The outgo of water through the stomata of the leaves by evaporation is termed *TRANSPIRATION*, and is brought about by heat energy from the surrounding atmosphere. In the last analysis, if the explanation suggested above is correct, the energy of heat, resulting in evaporation from the leaves, is chiefly responsible for the movement of the column of water which is continually passing through the plant — entering the root with various substances in solution and emerging through the stomata as water vapor. The fact that much more water usually is evaporated from a forest than from an equal area of a lake, affords some conception of the part played by vegetation not only in returning water to the atmosphere but also in ‘consuming’ heat energy — cooling the summer air.

The dynamics of the circulation through the xylem, however, are probably by no means so simple as might appear from the theory just outlined; and, moreover, there is no satisfactory explanation of the causes of food distribution in the phloem, further than that osmotic phenomena play an important rôle. But, as might be anticipated, recent work seems to show that there is an inherent activity in the stem itself independent of the root and leaf. The cellular mechanism is highly sensitive, being automatically adjusted for serving the welfare of the plant. Apparently local depression or stimulation makes the sap move toward the depressed or away from the overstimulated region, so that chemical substances stored in one region may be transferred to other parts. By this ‘hydraulic mechanism’ the plant as a whole becomes an organized unit.

3. *Food Utilization*

The food which the plant has constructed and distributed to the various parts of its body must be employed by the individual cells in supplying the material and energy for their life processes. It is

important not to lose sight of the cells in the larger organization which they form, for although the cells suppress their individuality in the complex body, the life of the plant is as truly the life of the component cells as is the life of a human community resident in the individual citizens.

The cells select from the food stream not only the materials essential for their individual life, but in addition those which they require for the performance of their particular part in the economy of the whole. But doing this implies work, and work means expenditure of energy — the same energy of sunlight which was stored in the food during its construction by the chlorophyll-bearing cells of the leaf. In order to release this energy RESPIRATION must occur. Carbohydrates, fats, and proteins must be oxidized, that is, burned, and consequently free oxygen transmitted throughout the plant to the various cells, and carbon dioxide carried away. This is effected by an intercellular system of air spaces which ramifies throughout the plant and communicates with the surrounding atmosphere chiefly by way of the stomata, but also to some extent through stomata-like pores (LENTICELS) on the surface of the stem. (Figs. 45, 58.)

We have now considered, in such detail as the scope of the present work requires, the structure and functions of a typical higher plant as a whole, and have indicated how the organism is specialized for the chief function which primarily concerns the individual: that is, nutrition, or the transformation of matter and energy into life and work. Since, however, the duration of the existence of the individual is relatively limited, it is obvious that some provision must exist for the continuation of the race. In other words, new individuals must be formed. Reproduction occurs.

CHAPTER IX

REPRODUCTION IN PLANTS

The synthetic act by which the organism maintains itself is fundamentally of the same nature as that by which it repairs itself when it has undergone mutilation, and by which it multiplies and reproduces itself. — *Bernard*.

We have considered briefly the gradual increase in complexity of the plant body from the unicellular condition, through colonies of essentially similar cells and the thallus type, to that of some typical higher plants, placing emphasis on organs directly or indirectly associated with nutrition. It is necessary now to review in a similar manner the specializations of structure and function which exist in the plant kingdom for the multiplication of individuals.

As has been seen, in *Pleurococcus* all the life processes essential to the individual are exhibited in relative simplicity and without obviously complicated machinery. Moreover, the continuation of the race is provided for by the individual cell dividing to form two new cells. Neglecting for the time being the mechanism of cell division, it is clear that reproduction in *Pleurococcus*, since it is not complicated by specialized organs for its performance, is a comparatively simple process.

It may be well to reiterate here that reproduction and growth are phenomena which are intrinsically the same—both are the result of a preponderance of the constructive phase of metabolism. The single cell, whether a whole organism or a single unit of a complex body, increases in volume up to a certain limit and then divides. In the former case two new individuals replace the parent cell; in the latter, the complex body has been increased to the extent of one cell. In both cases cell division has resulted in cell reproduction. Thus cell division is always reproduction, though it is customary and convenient to restrict the term reproduction to cell divisions which result in the formation of new individuals—single cells or groups of cells which sooner or later separate from the parent organism.

A. SPORE FORMATION

That cell division in multicellular plants results in the growth of the single individual is well illustrated by the simpler Green Algae, such as *Spirogyra* and *Ulothrix*, in which the plant body consists

FIG. 61. — Life history of *Sphaerella lacustris*. *a*, *b*, *c*, *d*, asexual cycle; *a*, *w*, *x*, *y*, *z*, sexual cycle. *a*, dormant cell enclosed within a protective cyst wall which has ruptured to allow the enclosed protoplast to escape; *b*, division of the protoplast to form four spores (*c*) each of which grows, develops two flagella, and assumes the typical 'adult' free living form of *Sphaerella* (*d*). This may divide many times, but each cell eventually assumes the dormant form (*a*) again. Under other circumstances the protoplast from the dormant form may divide until 32 or 64 small cells (*w*) are formed. These make their escape and are gametes (*x*) since they fuse in pairs (*y*). The composite cell resulting from fertilization is a zygote (*z*) which soon forms a cyst wall and assumes the dormant phase.

of a series of similar cells placed end to end to form a long thread-like body. In such cases, cell division merely increases the length of the filament constituting the plant body, unless the newly formed cell becomes detached from the parent plant. As a matter of fact, in some species, under certain conditions the protoplasmic content actually does make its escape from the cell wall and swims

about in the surrounding water. This independent protoplast is a spore. (Figs. 31, 62.)

Moreover, this spore now begins a series of cell divisions which result in a new filament, or individual. It will be noted that the potentialities of the spore and the protoplasts which continue to retain their stations in the parent body are intrinsically the same, but the opportunity of the spore is different. In brief, the fact that the spore has separated from the parent stock appears to be the reason why it reproduces. Therefore a spore may be regarded as a

FIG. 62. — *Ulothrix*, a filamentous Green Alga. *A*, modified cell for attachment at the base of a filament. *B*, cells of a filament which have formed spores. From three cells the spores have been liberated. *C*, part of a filament liberating spores (below), and gametes (above) which pair to form zygotes. (From Coulter.)

cell, or the essential part of a cell, the protoplast, which has separated from one plant body and is capable of producing another plant body. This statement might, at first glance, seem to indicate that spore formation is restricted to plants with multicellular bodies, while, as a matter of fact, spore formation occurs in the life history of many unicellular plants as, for example, *Sphaerella*. However, this apparent contradiction is cleared away when we note that in such unicellular forms the cell divisions which produce the spores do not involve the cell wall; merely the protoplast within divides and the daughter cells make their escape.

Therefore spore formation is not a necessary result of the establishment of a multicellular body, but an inheritance from unicellular forms which makes possible one of the two effective types of asexual reproduction in the Metaphyta. The other type is **FRAGMENTATION** which consists essentially in the separation from the body of larger or smaller parts, which later reproduce the whole plant. It is a familiar fact that, under proper conditions, cuttings, buds, bulbs, and sometimes pieces of leaves may reproduce or, as it is sometimes stated, **REGENERATE** a complete plant. This is just an expression of the same power which the spore, though a single cell, exhibits. It regenerates, as it were, a plant body similar to the one from which it has separated.

B. GAMETE FORMATION

During the life history of *Sphaerella*, under certain conditions a cell, instead of dividing twice to form four spores, divides five or

FIG. 63. — *Spirogyra*. Stages in the union of gametes and the formation of the zygote. See Fig. 31. (From Smith and others.)

six times and forms 32 to 64 small cells. These are gametes. Now it is not the structure but the behavior of the gametes which particularly distinguishes them from spores. From the standpoint of their origin, gametes may be regarded as spores which have developed the habit of fusing to form a zygote. Moreover, the origin of gametes is the origin of **SEX**, so that sexuality arose in

plants when spores, instead of reproducing, developed the habit of pairing and thus became gametes. The act of fusing is FERTILIZATION and the gametes which unite are sex cells. (Figs. 61, 63.)

Another example may emphasize this important point. The body of a filamentous Alga, *Ulothrix*, is composed of a linear series of cells all of which are essentially the same in structure and function. Under favorable conditions the cells divide and the plant grows in length. New individuals are not formed by this process, although the mechanical breaking, fragmentation, of the filament into two parts, owing to the simplicity of the body, gives two individuals. When conditions become less favorable for vegetative growth, some of the cells cease to contribute to the elongation of the filament. Instead, the protoplasts begin to divide within their cell walls, and thus each forms from 2 to 64 or more spores of different sizes, depending upon the number of divisions the parent protoplast undergoes. (Fig. 62.)

The largest spores are provided with four, and the smallest with two flagella by means of which they swim actively in the water when discharged from the parent plant body. However, the number of flagella is apparently of no importance since the cells of intermediate size may have either two or four. Nevertheless the behavior of the spores of different sizes is characteristic and significant. The largest spores soon settle down and, attaching themselves by the flagellated end, begin to develop into new filaments. The spores intermediate in size likewise form new individuals, but the process is much less rapid; while the smallest spores not only germinate very slowly, but give rise to dwarf filaments with vigor below the normal. As a matter of fact very few of the smallest spores germinate at all. Instead, they unite in pairs, each pair fusing to form a large single cell. It is apparent that the small spores by fusing, instead of feebly germinating, behave sexually and therefore, are gametes, while the product of this process of fertilization is a zygote. Nothing could indicate more clearly the primary relationship of gametes to spores than the origin of sex and sexual reproduction through the assumption by certain spores of the habit of pairing to form a zygote before germination.

It should be noted that sexual reproduction is not a different kind of reproduction, but merely reproduction *preceded* by the formation of a zygote; a fact very readily lost sight of in the higher forms where accessory phenomena connected with sexuality ob-

secure the essential features, but quite apparent in *Ulothrix* because here the zygote does not form directly a new filament. Instead, after passing a longer or shorter time in a dormant condition protected by a heavy wall, the protoplast (zygote) within divides to form a number of spores, each of which then germinates into a

new individual. Thus in *Ulothrix*, as in *Sphaerella*, reproduction is solely by spores, "sexual 'reproduction' not reproducing, but only protecting a spore-forming protoplast."

C. SEX DIFFERENTIATION

So far we have seen that sex cells, the gametes, arose with the establishment of the habit of reduced spores uniting in pairs. This is obviously a statement of fact rather than an explanation of sex. Although the two cells which fuse show no morphological characters by which they can be distinguished from each other, there is certainly a *physiological* basis of sex which induces them to swim toward each other, to become oriented so that fusion begins at the flagellated ends, and to melt into a single cell. This is a reorganized cell with the complicated structural and physiological equipment of the two cells which entered into its make-up. The zygote thus is a cell which *combines* the characteristics of both the contributing gametes, and to this significant

fact must be attributed the profound importance of sex phenomena in the life history of plants as well as of animals.

Although sexuality is fundamentally a physiological difference between gametes which leads to their characteristic behavior (zygote formation), even among the lower plants *structural* differentiations appear. In fact, a series of plants can be arranged showing a gradual transition from gametes which are morpholog-

FIG. 64. — Oedogonium, a filamentous Green Alga. A, young filament. B, portion of a filament forming gametes (egg and sperm). Below are two sperm which have just been liberated; above is a large egg with a sperm just coming into contact with it to form a zygote. (From Coulter.)

ically identical to those which differ so widely that they appear to have little in common. *Oedogonium*, another filamentous Alga, will suffice as an example, since it affords an excellent illustration of an intermediate stage in gamete differentiation. One form of *Oedogonium* gamete, representing an entire protoplast of a greatly enlarged cell, is richly supplied with food materials and chloroplasts and remains motionless within the cell wall. The other type develops in pairs in small cells with greatly reduced chloroplasts and food content. Instead of being motionless, each cell is provided with a circle of cilia by which it leaves its place of origin, swims actively in the water and, entering a cleft in the wall surrounding a large gamete, fuses with it to form a zygote. (Figs. 64, 65.)

FIG. 65. — *Oedogonium*. *A*, zygote emerging from cell of parent filament. *B*, division of zygote into four spores. *C*, mature spores ready to escape and develop into new filaments. Note that the zygote does not directly give rise to a filament, but to spores. (From Coulter.)

In short, one gamete, designated the EGG, is a large non-motile cell stored with food materials, while the other gamete, or SPERM, is a small active cell largely devoid of food. This is typical of the conditions which are at the foundation of gamete differentiation throughout the plant and animal kingdoms — eggs and sperm expressing a physiological division of labor which entails structural specialization in opposite directions.

In *Oedogonium* sexuality is apparent both in the behavior and in the structure of the gametes, so that it is possible to identify the sex cells as MALE gametes, or sperm, and FEMALE gametes, or eggs. It will be noted that this is not the origin of sex, for sex arose when spores by their behavior became gametes. In other

words, the sex act is the fusion of two cells which reorganize as a single cell; and all modifications of these cells, which enable them to function as gametes, are secondary.

D. REPRODUCTIVE ORGANS

Hand in hand with the specialization of spores and gametes there is a progressive modification of the cells or groups of cells which produce them, until highly developed REPRODUCTIVE ORGANS

FIG. 66. — A Brown Alga, *Ectocarpus*. A, portion of a filament with a sporangium and a liberated spore; B, portion of a filament with a gametangium and a liberated gamete. (From Coulter.)

arise. The asexual reproductive cells, or spores, are formed in SPORANGIA, which may be merely vegetative cells in which the protoplast becomes transformed into a spore, or elaborate multicellular structures set aside for this one function. Similarly, with the origin of sexuality, the sex cells, or gametes, arise in GAMETANGIA, which later are distinguished as ANTHERIDIA, or sperm-producing, and ARCHEGONIA, or egg-producing organs. Moreover, although the terms male and female are strictly applicable only to the sperm and eggs respectively, the antheridia and archegonia are called male and female organs; while a plant body which bears only male reproductive organs is designated as a male plant and one which bears female reproductive organs is known as a female

plant. In short, the sexuality of the gametes is reflected back, as it were, to the organs and then to the individual which bears them; although the gametes are the actual sex cells. If this is kept clearly in mind it will obviate confusion in considering the remarkably specialized secondary features which sexuality imposes on the bodies of higher plants and animals. (Fig. 66.)

We may now review the facts before proceeding to further complications. Reproduction, divested of its specialized features, is merely growth expressed in cell divisions. This primary potentiality of all cells may exist side by side with the development of cells specialized for asexual reproduction (spores) and sexual reproduction (gametes). In either case the products become separated from the parent body and develop new bodies. Furthermore, spores which in the lowest forms are developed from any of the vegetative cells of the plant body, in somewhat higher forms arise in asexual reproductive organs (sporangia), while gametes are produced in sexual reproductive organs (gametangia). With the morphological differentiation of gametes into sperm and eggs, a further specialization of the gamete-forming organs results in male and female reproductive organs (antheridia and archegonia). When sporangia and gametangia are borne by separate individuals, asexual plants (SPOROPHYTES) and sexual plants (GAMETOPHYTES) result. Finally, the sperm and eggs may be borne on separate gametophytes, in which case male and female gametophytes result.

E. ALTERNATION OF GENERATIONS

From the standpoint of the evolution of the higher plants the most significant fact stated above is that sporangia and gametangia may be borne by separate individuals, for this clearly involves an asexual, spore-bearing generation, and a sexual, gamete-bearing generation. We shall outline this ALTERNATION OF GENERATIONS in the life history of a typical Moss and Fern as an introduction to the problem of reproduction in the higher Seed Plants.

1. *The Moss*

The common Mosses of woods, hillsides, and fields are a relatively inconspicuous but nevertheless an important part of our flora, since they form heavy growths or carpets of vegetation which hold back much of the rainfall so that it sinks into the soil. Although there are over 8000 species which botanists include in the

order *Bryales* of the Phylum BRYOPHYTA, a general description of a typical common Moss, such as *Polytrichum commune*, will suffice for the purpose at hand. (See Appendix I: Classification.)

The shoot of a moss plant is differentiated into stem and leaves which are of very simple construction compared with those of the

FIG. 67. — The life history of a Moss, chiefly *Polytrichum*. *a*, the entire plant (gametophyte and sporophyte), $\times \frac{1}{2}$. *b*, median vertical section of the capsule in which spores are formed, $\times 6$, with spore (*c*) and germinating spore (*d*), $\times 300$; *e*, spore germinated to a protonema with a bud which forms leafy plant (gametophyte), $\times 75$; *f*, tip of gametophyte with two archegonia, $\times 2$; *g*, archegonium in section showing egg, $\times 16$; *h*, tip of gametophyte with antheridia, $\times 2$; *i*, antheridium, $\times 16$; *j*, a single liberated sperm, $\times 600$; *k*, gametophyte with sporophyte developing in enlarged and transformed archegonium. (After Ganong, Dodel-Port and others.)

Seed Plant we have studied. True roots are not present, but their function is performed by filamentous outgrowths called RHIZOIDS. At the top of the leafy moss plant, inconspicuous reproductive organs are developed. Some species bear both antheridia and archegonia on the same plant, while others have only one type. The leafy moss plant is thus a sexual individual, or gametophyte. When the reproductive organs are mature, sperm escape from the

antheridia and, swimming about in moisture which has collected on the leaves, are attracted to the archegonia containing the eggs, apparently by a chemical substance secreted within these organs. A single sperm which has made its way down into an archegonium fuses with the egg to form a zygote. The fertilized egg retains its position in the archegonium and germinates. The result is a rod-shaped embryo which grows not only upward through the archegonium and so out into the world, but also downward into the tissues of the gametophyte, from which it secures practically all of its food materials. (Fig. 67.)

The essentially parasitic nature of the new individual renders the development of leaves superfluous, so it consists of a simple upright stalk at the top of which reproductive organs are borne. These are sporangia and accordingly the individual is a sporophyte. The ripe spores are liberated and, falling to the ground, each forms a filamentous outgrowth called a PROTONEMA. Soon a bud arises on the protonema which develops into a leafy moss plant. The cycle is complete.

A common Moss thus exhibits in its life history an alternation of sexual and asexual generations. The leafy moss plant, with antheridia and archegonia, produces gametes and is the gametophyte. The leafless generation, which develops from the fertilized egg in the archegonium, produces spores and is the sporophyte. So the gametophyte arises asexually, but is itself sexual; the sporophyte arises sexually but is itself asexual. The dominant generation from the viewpoint of both structure and nutrition — the plant one thinks of as a 'moss' — is the gametophyte.

2. *The Fern*

The common Ferns comprise the largest group of one of the major divisions of the plant kingdom known as the PTERIDOPHYTES. Although the forms of different species are remarkably varied, the ensemble of characters and in particular the foliage is quite distinctive, so that one would recognize practically any member of the group as a 'fern.' The stems may be short and close to the ground, or upright as in the Tree Ferns, though creeping and underground stems (RHIZOMES) are more common. The leaves, known as FRONDS, either arise in clusters from the tip of the stem (Tree Ferns), or are distributed along the creeping and underground stems. Roots bring the stem into intimate contact

with the food materials of the soil, though rhizomes function to a certain extent as roots. An examination of the cellular structure of a common Fern, such as *Aspidium marginale*, shows that it is much more complex than a Moss, the tissues of stem and leaves being essentially like those we have seen in the Seed Plants, and accordingly Ferns and Seed Plants are frequently referred to as VASCULAR PLANTS. (Figs. 51, 69.)

FIG. 68. — The life history of a common Fern, chiefly *Aspidium*. *a*, the entire sporophyte, $\times 10$; *b*, portion of a leaf showing groups of sporangia (sori), $\times \frac{1}{2}$; *c*, a sorus showing sporangia, $\times 10$; *d*, a sporangium, $\times 50$; *e*, a single spore, $\times 100$; *f*, ventral view, $\times 3$, and *g*, a median section, $\times 6$, of a prothallus showing rhizoids, antheridia, and archegonia; *h*, antheridium liberating sperm, $\times 120$; *i*, single sperm still attached to a remnant of 'mother cell,' $\times 300$; *j*, open archegonium with sperm passing down to egg, $\times 120$; *k*, young sporophyte developing from zygote. (From Ganong.)

The leafy fern plant bears, on certain of its fronds, reproductive organs which are sporangia. These, of course, produce spores and therefore the plant commonly recognized as a Fern is a sporophyte. The spores when ripe are liberated from the sporangia and fall to the ground, where they germinate. From the spore arises a tiny body, about a quarter of an inch in diameter, called a PROTHALLUS, which is essentially a plate of chlorophyll-bearing cells with rhizoids attaching it to the ground. On its lower surface are developed reproductive organs, antheridia and archegonia,

which form gametes. The prothallus therefore is a gametophyte. (Fig. 68.)

Sperm are liberated from the antheridia and swim in the moisture, from dew or rain, to the archegonia. A single sperm works its way down an archegonium and fuses with the egg to form a zygote. Then the zygote, which remains in the archegonium, proceeds to

FIG. 69. — Tree Ferns (*Alsophila*) in the Federated Malay States. (From Campbell.)

divide and forms at first a small plant, with stem and leaf which grows upward and root which seeks the soil. During the process of root and shoot development the plant retains its attachment to the parent prothallus from which its food is secured. Later, when direct communication with the environment has been established by its own root and leaf, the new generation becomes entirely independent of the prothallus, which then degenerates and dies. The young plant gradually grows into the typical asexual leafy plant, which itself in due time produces spores. The cycle is complete.

It is clear that in the Fern, as in the Moss, there is an alternation of generations. The leafy fern plant (sporophyte) gives rise to the prothallus (gametophyte). The leafy fern arises sexually, but is itself asexual; the prothallus arises asexually, but is itself sexual. The significant fact, however, is that the conspicuous leafy moss plant is a gametophyte, while the large leafy fern plant is a sporophyte; or, one may say, the 'moss' is a sexual plant and the 'fern' is an asexual plant. This ascendancy in dominance of the

FIG. 70. — Diagram to illustrate the decline of the gametophyte generation and the advance of the sporophyte generation. (From Coulter.)

asexual and suppression of the sexual generation, which is so characteristic of the fern as compared with the moss life history, is carried still further in the higher Ferns and finally culminates in the Seed Plants.

3. *Higher Ferns*

As we have seen, the sporophyte of the common Ferns produces spores on ordinary vegetative fronds or sometimes on more or less specialized sporophylls. In either case but one kind of spore is formed. Among the higher Ferns, however, spores of two kinds occur which, since they differ greatly in size, are called MICRO-SPORES and MEGASPORES. The production of two kinds of spores is known as HETEROSPORY and leads to the differentiation of the sporophylls into MICROSPOROPHYLLS and MEGASPOROPHYLLS. Moreover, the microspores on germination form gametophytes which produce sperm, and therefore are called MALE GAMETOPHYTES, while the megaspores develop into gametophytes bearing eggs, and accordingly are known as FEMALE GAMETOPHYTES.

Finally, in these heterosporous forms the gametophytes are no longer even small independent plants, such as the prothallus of the common Ferns, but both male and female gametophytes are so greatly reduced that they practically remain permanently in the parent microspore and megaspore, respectively, which supply

them with food. This, it will be noted, is just the reverse of the condition which exists in the Moss, where it is the sporophyte which is the dependent generation. (Figs. 51, 71, 72.)

FIG. 71. — Stages in the life history of a 'higher Fern' (*Marsilia*). *A*, microspore, enclosing the male gametophyte with two groups of sperm mother cells, and prothallial cells (*p*); *B*, sperm; *C*, megaspore, enclosing food material (starch grains), and female gametophyte comprising a single archegonium (with egg) at one end of the spore; *D*, a week-old embryo sporophyte, still attached to the megaspore, with first leaf (*l*) and root (*r*). (From Bergen and Davis.)

FIG. 72. — A microspore and megaspore of a 'higher Fern,' *Selaginella*, magnified and drawn to the same scale. (From Coulter.)

FIG. 73. — Diagram of a typical flower. *a*, the receptacle; *b*, calyx; *c*, corolla; *d*, stamens; *e*, pistil formed of fused carpels.

4. Seed Plants

Passing to the Seed Plants, we find that these are heterosporous sporophytes, and the FLOWER represents a greatly modified stem (branch), the leaves of which are specialized as sporophylls and

accessory structures. In order to make this clear it is necessary to review the structure of a typical flower. (Figs. 52, 73.)

FIG. 74. — Transition between petals and stamens in a Water Lily. (After Gray.)

above the calyx is the second circle (COROLLA) formed of larger leaves (PETALS) which are usually brightly colored. The calyx and corolla together form the PERIANTH, or floral envelope which surrounds the primary floral organs, the STAMENS and CARPELS.

The stamens represent the third circle of leaves, but are so highly modified that their leaf origin is not immediately apparent. Each consists of a slender FILAMENT at the apex of which is a small case known as the ANTHHER. Within the anther POLLEN GRAINS are formed. The pollen grains are microspores and, therefore, it is apparent that the pollen sacs of the anthers are MICROSPORANGIA and the stamens are microsporophylls. (Fig. 74.)

Finally, just within the circle of stamens is the fourth whorl of floral leaves, the carpels, in which specialization has gone so far that practically no suggestion of leaf structure remains. Each carpel consists of three parts: a lower, expanded portion termed the OVULE CASE, merging above into the elongated, slender STYLE the tip of which is the STIGMA. Such a fully developed carpel is known as a PISTIL and when, as frequently happens, the various carpels fuse to form a composite structure, this is termed a compound pistil. Within the

A complete flower consists of four whorls of modified leaves. These arise near together at the top of a RECEPTACLE, representing the enlarged tip of the floral branch, which connects the flower proper with the main tissue systems of the plant as a whole. The outermost and lowest circle of leaves (CALYX) is composed of several parts (SEPALs) which usually are green and retain a leaf-like appearance. Just within and

FIG. 75. — Diagram to illustrate the method of union of three carpels (megasporophylls) to form the ovule case of a pistil (compound). The edges which unite form the point of attachment of the ovules. (After Gray.)

ovule case are developed the reproductive bodies known as **OVULES** which are essentially **MEGASPORANGIA**, for within each is formed a megaspore, commonly known as an **EMBRYO SAC**. A carpel, therefore, is a megasporophyll. (Fig. 75.)

So far it is clear that a flower is a group of sporophylls which produce microspores and megaspores. Since, however, such reproductive bodies always form male and female gametophytes, their development must now be considered.

FIG. 76. — The life history of a higher Seed Plant, from various species. *a*, shoot of a Flax with flowers, $\times \frac{1}{3}$; *b*, vertical section of a flower, $\times \frac{1}{1}$; *c*, an anther cut to show four microsporangia containing pollen grains (microspores), $\times 6$; *d*, an ungerminated pollen grain, and one, *e*, which has formed tube (male gametophyte), $\times 110$; *f*, longitudinal section of an ovule enclosing megaspore and its contents (female gametophyte), $\times 20$; *g*, an ovule transformed into a seed with young embryo sporophyte and endosperm, $\times 10$; *h*, a mature seed, $\times 5$; *i*, young sporophyte from the germination of the seed, $\times \frac{1}{2}$. (From Ganong.)

The first fact to have clearly in mind is that the megaspore is never liberated by the megasporangium. And further that the latter remains just where it arose in the ovule case of the pistil. Consequently the megaspore germinates within the pistil, and it forms there a female gametophyte composed of only a few cells, including the female gamete, or egg. Thus the female gametophyte generation of Seed Plants is invisible unless the contents of the pistil are examined with the microscope. (Fig. 76.)

The pollen grain is a typical microspore, a single cell enclosed within a protective wall. Germination starts, while the pollen is still in the anther, by the division of the spore nucleus into two, one of which divides again. Further development does not occur unless the pollen is transferred in some way, usually by insects or the wind, to the stigma of the pistil. The stigma secretes fluids suitable for the germination of the ripe pollen grain, which bursts its rigid wall and puts forth a cytoplasmic tube. This grows down

FIG. 77. — Diagram of a flower, showing pollination and fertilization.
(From Peabody and Hunt.)

through the tissues of the pistil until its tip enters the ovule case, and carries with it the nuclei, two of which represent sperm. The pollen has now completed its development and thus the contents of the pollen grain plus the tube itself constitute a greatly reduced male gametophyte. (Fig. 77.)

By the time the pollen tube reaches the ovule case, the megaspore within has formed, as already described, the female gametophyte with its egg. One of the sperm nuclei unites with the egg and forms a zygote, which remains just where it is, surrounded by the tissues of the pistil base, and proceeds to divide to form an embryo sporo-

phyte with rudimentary root, stem, and leaf. Concurrently, the ovule case and associated tissues of the base of the pistil undergo more or less profound changes ('ripen') and become transformed into a **FRUIT**. The young sporophyte within, together with food material for its further development, is hermetically sealed up in a special packet — it has become a **SEED**. In this form the new

FIG. 78. — Types of fruits. A, 'fruit' of the Fig, comprising the hollow end of a branch enclosing a number of true fruits; B, Apple: pome type of fruit; C, stone fruit (drupe) of Peach, showing pit enclosing the seed; D, aggregate fruit of the Blackberry.

generation is prepared not only to leave the parent plant and withstand adverse conditions for a long time, but also to continue rapidly its development into an adult sporophyte when it falls upon favorable soil. Incidentally, it may be mentioned that the establishment of seed formation is probably chiefly responsible for the dominant position which the flowering plants hold in the flora of to-day. (Figs. 76, 78, 80.)

Thus it is clear that the gametophyte generation of Seed Plants

is reduced to practically its lowest terms — a few nuclear divisions little more than sufficient to form the gametes. The whole generation is telescoped, as it were, within the flower of the previous sporophyte generation, so that sporophyte seems to produce sporophyte; whereas, as a matter of fact, *three* distinct generations contribute directly to the formation of the seed. A seed is really a highly modified megasporangium with its contents and covering. The seed coat comprises tissue from the megasporangium of the parent sporophyte bearing the flower (first generation).

FIG. 79. — Seed of a Violet. At left, hard seed coat; at right, section showing the endosperm (female gametophyte) enclosing the young sporophyte, with plumule (first bud) above and radicle (primary root) below. (From Coulter.)

Certain nutritive tissues (ENDOSPERM) represent the female gametophyte (second generation). The product of the fertilized egg is a young sporophyte (third generation). (Fig. 79.)

The great reduction of the gametophyte generation in Seed Plants is accompanied by a transference of some of the phenomena associated with sexuality to the sporophyte, so that the latter, though intrinsically asexual, comes secondarily to exhibit certain sexual characters, chiefly in the flower. Thus, although the stamens and pistil (carpels) are actually sporophylls of the non-sexual generation, they are frequently referred to as the male and female organs of the flower. Likewise POLLINATION, or the transference of the pollen grains from anther to stigma, is often called the fertilization of the flower; whereas, as we have seen, it is merely a preliminary step which makes it possible for gametophytes to meet on common ground so that the sperm, which themselves have suffered reduction and lost their motility, can reach the egg and perform the act of fertilization. Frequently this sexual differentiation extends to the flower as a whole, since some flowers bear only stamens and others only carpels and are known as male and as female flowers respectively. Moreover, male and female flowers may be borne on separate plants, in which case the plants themselves are called male and female. In brief, the terminology which rightly is applicable only to the sexual generation is, for convenience, transferred to the asexual generation, in conse-

FIG. 80. — Fruits and seeds dispersed by wind (upper), and by animals (lower).

FIG. 81. — Corn (Maize).

Fig. 82. — Evolution of plant structures. (After Ganev, slightly modified.)

quence of the fact that accessory sexual functions are reflected back to it through the almost complete suppression of the actual sexual generation itself.

If we glance back over the reproductive processes in plants, we are impressed with the fact that reproduction is, to a very large extent, asexual. The great masses of thallus vegetation, represented by Seaweeds and their allies, increase in bulk chiefly by vegetative cell division, and new individuals are formed in profusion by fragmentation and spore formation. In the Mosses, where the sexual generation is prominent, beds of moss are developed chiefly by the asexual budding of the sexual plant, while spore formation holds a prominent place in the increase and dissemination of individuals. In the Ferns and Seed Plants, which are to all intents and purposes asexual plants, since the sexual phase is relegated to an increasingly obscure position in the life history, reproduction is not only by spores, but also by cuttings, bulbs, fragments of leaves, etc. In brief, reproduction, unaccompanied by sexual phenomena, is apparently amply sufficient for the propagation of plants.

However, it will be noted that sexuality has persisted from its simple origin when spores of unicellular plants performed the sexual act and became gametes. The gametophyte generation in the life history, which sexuality induces, decreases in importance structurally as we proceed from the lower to the highest plants; but in spite of this the sex act itself is retained and shows its modifying powers even in the asexual generation. Obviously some advantages must be gained in the long run by fertilization, other than the establishment of another generation in the life history, or such complex devices culminating in the flower would not have been evolved for its preservation. We shall leave this large problem until we take up the question of sex in animals, since sexuality is a fundamental attribute of both plants and animals which profoundly affects their morphology and physiology.

CHAPTER X

THE ANIMAL BODY:

INVERTEBRATE

Nature is so varied in her manifestations that many must unite their knowledge and efforts in order to comprehend her. — *Laplace*.

THE most obvious characteristic which distinguishes familiar plants and animals is the power of locomotion of the latter. This criterion, however, fails among the lowest forms; for example, *Sphaerella*, as we have seen, swims as actively as *Paramecium*. Moreover, among multicellular animals there are innumerable permanently attached forms, such as the typical stages of the Sponges, Hydroids, Barnacles, etc. Although the power of locomotion is not a diagnostic character of animals as compared with plants — this, as has been explained, being chiefly a matter of metabolism — it is a fact that the great dissimilarity between the bodies of multicellular plants and animals is a direct or indirect result of the loss by plants and the development by animals of the primitive power of locomotion which most unicellular organisms possess. At the basis of this difference is probably the fact that early in the evolution of plants comparatively rigid cell walls of cellulose were established, which directed the development of the body along relatively fixed lines. On the other hand, animal cells, unhampered by the limitations imposed by rigid confining walls, were free to respond in more ways to environmental conditions, and this made possible the extremely diverse forms of mobile bodies characteristic of the animal kingdom.

A. THE CHIEF GROUPS OF ANIMALS

The animal kingdom may be divided into two main groups: on the one hand, the unicellular animals, or **PROTOZOA**, comprising about fifteen thousand known kinds, nearly all of which are microscopic, such as *Amoeba*, *Paramecium*, and their allies; and on the other hand, multicellular forms, or **METAZOA**. The latter

division includes animals ranging in size from those which are so small that hundreds can sport in a drop of water, to the giant Whales of to-day and the Dinosaurs of the geologic past.

Although the actual stages in the transition from the Protozoa to the Metazoa are unknown, among the more complex colonial Protozoa there are forms, as already noted, in which the various cells become organically connected so that a primitive type of body results, and, furthermore, certain cells are set aside for reproduction. In other words, coöperation involving a physiological division of labor takes place between the individuals of a group of cells, and this results in the establishment of an individual body of somatic cells associated with germ cells. (Fig. 27.)

The Metazoa proper may be divided into two large groups known as INVERTEBRATES and VERTEBRATES. The former group, frequently referred to as the lower animals, comprises about a million living species and exhibits an enormous variety of form and complexity of structure ranging from the Sponges and Hydroids to the Molluscs, Crustacea, and Insects. On the other hand, the Vertebrates, or higher animals, form a relatively homogeneous group of about fifty thousand species, including the FISHES, AMPHIBIA, REPTILES, BIRDS, and MAMMALS. The Birds and Mammals in contrast with all other animals are referred to as warm-blooded, because their body temperature is practically constant and usually above that of their surroundings. (See Appendix: Classification.)

The highly complicated and varied organization of animals renders it impossible to present a concise and adequate plan of a typical animal body, and it is therefore necessary in the present work to select one group of animals as the basis of study and then to compare with this, in so far as comparisons are possible without confusion, a few of the most significant morphological and physiological variations presented by other groups. We naturally select the group of Vertebrates for chief consideration not only because its relative homogeneity renders it the most available, but because it includes Man. However, even before we focus attention on the Vertebrates, it is necessary to make a preliminary survey of certain morphological principles as exhibited among the Invertebrates — selecting as types the Hydra, Earthworm, and Crayfish — in order to afford a background for the consideration of Vertebrate structure and function.

B. HYDRA

In discussing the development of animals, it was pointed out that the dividing egg typically forms first a blastula which, in turn, becomes transformed into the gastrula stage. The gastrula is essentially a sac composed of two layers of cells: an outer, or ectoderm,

FIG. 83. — Hydra. Longitudinal section, magnified. 1, mouth; 2, tentacles; 3, early stage in budding; 4, older bud; 5, ectoderm; 6, endoderm; 7, enteric cavity; 8, testis; 9, ovary. (From Linville and Kelly, after Parker.)

and an inner, or endoderm, layer. Although no adult animals retain this simple gastrula form, those composing the group known as the COELENTERATES are to all intents and purposes permanent gastrulae since their bodies are built on the plan of a two-layered sac. This is well exhibited in Hydra, an almost microscopic, fresh-water Coelenterate which is commonly found attached to submerged vegetation or stones in brooks and ponds (Fig. 28.)

The body of Hydra somewhat resembles a long narrow sac, the base constituting the foot, and the opening at the opposite end forming the MOUTH. Surrounding the mouth is a circle of outpocketings of the body wall termed TENTA-

CLES. The main axis of the body extends from foot to mouth, and every plane passing through this axis divides the body into symmetrical halves. In other words, the parts of the body are symmetrically disposed about, or radiate from the main axis, and so Hydra affords an example of RADIAL SYMMETRY. (Figs. 83, 158.)

The body wall of Hydra is composed of two distinct cell layers, ectoderm and endoderm, separated by a thin non-cellular supporting layer of jelly-like material (MESOGLOEA) secreted by the cells

of both ectoderm and endoderm. Hydra thus illustrates a simple type of Metazoan structure in which but two primary tissues exist; such specializations as are necessary for the performance of the essential life functions being confined to the various cells that compose these layers. The majority of the cells of the endoderm which line the ENTERIC CAVITY are concerned with the digestion of solid food taken in through the mouth, while those of the ectoderm are variously modified for protection, and the other relations of the individual to its surroundings, as well as for reproduction.

FIG. 84. — Hydra. Transverse section, highly magnified. Outer layer of cells, ectoderm; inner layer, endoderm. Between, mesogloea represented by a line.

In short, in the organization of Hydra the *primary* tissues (ectoderm and endoderm) have not become differentiated into *secondary* specialized tissues (muscular tissue, nerve tissue, etc.) for one function or another — the simple life processes of the animal are adequately provided for by the specialization of isolated cells or small cell groups within ectoderm and endoderm. (Fig. 84.)

C. EARTHWORM

The bodies of all animals above the Coelenterates are built of three primary layers, which, as development of the individual proceeds, give rise to the secondary tissues and thereby form a relatively complex body. This third primary layer (tissue), the MESODERM, typically is developed, as we have described earlier,

from the endoderm and comes to occupy the position held by the mesogloea of *Hydra*; that is, between the ectoderm and the endoderm. (Fig. 173.)

The development of the mesoderm is the key to the advance in body organization of higher animals, because it makes possible a radical change in plan that involves the establishment of a body cavity, or COELOM, in which are disposed many of the chief organs. Accordingly the Coelentrates, since they lack the coelom, are often

FIG. 85. — Diagrams of the body plan of the Earthworm. *A* and *C*, longitudinal sections; *B*, a transverse section. *a*, aortic loops of the blood vascular system; *al*, alimentary canal; *an*, anus; *c.g.*, brain (cerebral ganglion); *co*, coelom; *c.v.*, blood vessels to the intestinal wall; *ds*, partitions (septa) between the segments; *d.v.*, dorsal blood vessel; *m*, mouth; *n*, nephridia; *o*, ovary; *o.d.*, oviduct; *s.i.*, ventral blood vessel; *v.g.*, ganglia. (From Sedgwick and Wilson.)

referred to as ACOELOMATES, and the animals above the Coelentrates, since they possess the coelom, are known as the COELOMATES. The difference in structure can best be made clear by comparing the body plan of a higher Invertebrate, such as the common Earthworm, with that of *Hydra*.

1. Body Plan

Whereas the *Hydra* body is essentially a sac composed of two layers of cells surrounding the enteric cavity, the body of the Earthworm is built on the plan of a tube within a tube — the

outer tube forming the BODY WALL, and the inner, the wall of the digestive tract, or ALIMENTARY CANAL. The walls of these tubes merge into each other at both ends, and thus together they enclose a space, the coelom. Or, to state it another way: the outer tube, or body wall, surrounds a space, the coelom; through the coelom runs a second tube, the alimentary canal, which opens to the exterior at either end forming the MOUTH and ANUS. (Figs. 85, 86.)

The coelom of the Earthworm is divided by a large number of transverse partitions, called SEPTA, which extend from the inner surface of the body wall to the outer surface of the alimentary canal. The result is that the worm's body cavity is not a continuous space running from one end of the animal to the other, but consists of a linear series of chambers through the center of which runs the alimentary canal. The limits of these chambers are indicated on the outside of the worm by a series of grooves which encircle the body wall. In short, the body is made up of a series of essentially similar units known as SEGMENTS, and thus affords a simple example of SEGMENTATION, which is a characteristic expressed in varying degrees in nearly all the higher animals.

Many of the chief organs of the Earthworm are developed as outgrowths from the walls enclosing the coelom, so that it is in this cavity that we find, for example, the main organs devoted to circulation, excretion, coördination, and reproduction. Moreover, the organs are symmetrically arranged with respect to the long axis of the body which passes from mouth to anus. For instance, the chief blood vessels and the nerve cord lie in the long axis and extend from end to end, while the excretory and reproductive organs are disposed in pairs on either side of this axis. Thus there may be passed through the main axis a single plane which divides the body into symmetrical halves, each of which is a 'mirror image' of the other. The main axis, therefore, extends from the mouth (ANTERIOR END) to the anus (POSTERIOR END), and the plane which divides the body into right and left sides passes through the upper (DORSAL) and lower (VENTRAL) side: the body exhibits BILATERAL SYMMETRY which is characteristic of higher animals. (Fig. 87.)

2. *Tissues and Organs*

Bilateral symmetry practically implies the existence of definitive parts of the body, or organs and organ systems, and these we find

Fig. 86. — Dissection of an Earthworm (*Lumbricus terrestris*), lateral view. Portion of lateral body wall turned down. 1, Prostomium, upper lip; 2, 3, first and second segments; 4, cavity of pharynx; 5, muscular wall of pharynx; 6, retractor muscle of pharynx; 7, beginning of esophagus; 8, seventh segment; 9, position of first aortic loop; 10, septum: one of the partitions between segments; 11, lateral blood vessel; 12, calciferous gland; 13, fifth aortic loop; 14, parietal blood vessel; 15, dorsal blood vessel; 16, posterior seminal vesicle; 17, posterior end of esophagus; 18, crop: food reservoir; 19, gizzard: muscular chamber which grinds the food; 20, beginning of intestine; 21, mouth; 22, cerebral ganglion: brain; 23, subesophageal ganglion; 24, body wall of fifth segment; 25, ventral blood vessel; 26, subneural blood vessel; 27, internal opening of a nephridium; 28, end of nephridium opening to exterior; 29, 30, seminal receptacles; 31, basal part of seminal vesicles; 32, ovary; 33, oviduct; 34, ventral nerve cord. (Modified, after Linville and Kelly.)

highly developed in the Earthworm. Again, the presence of organs demands a much greater differentiation of tissues than occurs in Hydra where local modifications of ectoderm and endoderm serve the purposes of its relatively simple organization. Accordingly in the Earthworm and in all higher forms the mesoderm is added to the two primary cell layers, and from these three there is developed a great variety of special tissues. It is convenient to distinguish

FIG. 87. — Transverse section through the middle region of the body of the Earthworm. (From Hegner, after Marshall and Hurst.)

six main groups of tissues: epithelial, supporting, muscular, circulating, nervous, and germinal.

The importance of EPITHELIAL TISSUES is evident from the fact that the body is covered and lined with these cellular membranes so they form the point of contact between the organism and its environment. For example, food before it is really inside the body must pass through an epithelium lining the digestive tract, and before it can do that it must be digested by enzymes secreted by the epithelium. Furthermore, the waste products of metabolism must be excreted and pass from the body through epithelial membranes. Specialization for secretion and excretion leads to GLAND

formation. Glands may be unicellular and scattered here and there in the surface of the cellular membrane, or they may be grouped at certain points of vantage. Just as often, however, many cells combine to form multicellular glands, which sink, as it were, below the surface as simple or complex tubes or sacs of secreting cells, and thus amplify many-fold the effective surface within a given space. And finally, specialized epithelial cells form important elements of sense organs — the outposts of the nervous system.

Obviously the larger and more complex the organism, the greater is the necessity for sustaining and binding material; and therefore

FIG. 88. — Diagrams of glands. A, B, unicellular glands (*gc*) in surface epithelium (*se*); C, D, E, F, multicellular glands with ducts (*d*) leading to the surface. (From Curtis and Guthrie.)

as we ascend the animal scale we find, in general, an increase in SUPPORTING TISSUE. Whereas in epithelia the cells themselves form the major part of the tissue, in supporting tissues it is direct or indirect products of the cells, known as intercellular material or matrix, that gives character to the tissue. Thus the function of *connective tissue* is performed chiefly by intercellular bundles of fibers. Later we shall find that the same principle is true for the *cartilage* and *bone* forming the internal skeletons of higher animals.

MUSCULAR TISSUE is responsible for the power of motion and locomotion so characteristic of most animals, and also for the necessary movements performed by the internal organs in carrying on the various life processes. Muscle cells have in a highly de-

veloped and specialized form a fundamental property of all protoplasm, contractility, which they exhibit by shortening and broadening when stimulated by impulses coming chiefly through the nervous system. A muscle is a coöperating group of muscle cells, usually bound together by connective tissue and richly supplied with blood vessels and nerves. (Figs. 7, 87, 97.)

One seldom thinks of BLOOD, LYMPH, and other fluids, that transport materials in the body, as tissues, but in truth they must be regarded as CIRCULATING TISSUE in which the living cells, or CORPUSCLES, are suspended in a fluid matrix, the PLASMA. Circulating tissues minister to, and are in intimate contact with, every tissue and cell of the organism.

All protoplasm is irritable — it responds to stimuli — but obviously the larger and more complex the body becomes, the more necessary it is that the actions and reactions of its component cells be instantly coördinated so that the parts act as a whole — an organism. This function is performed by NERVOUS TISSUE.

And finally, within the body — though perhaps not of the body — is the GERMINAL TISSUE destined to contribute not to the individual but to the propagation of the race during reproduction.

So the Earthworm and higher animals present a great advance over the two-layer body plan exhibited by Hydra. But, of course, this advance involves the coöperation of several tissues to form organs, and the coöperation of organs to form ORGAN SYSTEMS, each of which plays a particular part in the economy of the whole.

3. *Organ Systems*

The organ systems may be classified as the INTEGUMENTARY and SUPPORTING SYSTEMS which constitute the covering and the framework of the individual; the ALIMENTARY, RESPIRATORY, CIRCULATORY, and EXCRETORY SYSTEMS which directly or indirectly are concerned with nutrition; the NERVOUS SYSTEM which, in coöperation with the system of SENSE ORGANS, the MUSCULAR SYSTEM, etc., not only coördinates the various parts of the individual, but also orients the whole with respect to its environment; and, finally, the REPRODUCTIVE SYSTEM which makes possible the continuation of the race. The fundamental life processes for which these systems provide must be carried on by all animals, and the chief differences in the structure of animals, from the lowest to the highest, is a resultant of the means adopted to serve these

essential functions under different conditions imposed by the environment and mode of life.

Thus it is clear that the body plan of the Earthworm and all higher forms is radically different from that of Hydra, exhibiting as it does such essential new features as mesoderm, coelom, bilateral symmetry, segmentation, specialized tissues, definitive organs, and complex organ systems. The persistence and development of this basic plan from Earthworm to Man is interpreted by biologists as evidence of evolution.

D. CRAYFISH

Bearing in mind the general plan of the body of the Earthworm, we must next consider briefly the main principle underlying the changes in this plan which give rise to many of the diverse forms

FIG. 89. — Diagrammatic representation of the structure of a primitive Arthropod in which very little specialization of the segments has occurred. (After Schmeil.)

among the higher Invertebrates. This principle appears to be chiefly a specialization of the individual segments so that the body, instead of consisting of a large number of essentially similar segments, is formed of a linear series of segments, many of which are quite different from the rest. Moreover, by the partial or complete fusion of two or more segments and the suppression of segmentation, definite regions of the body are marked off. This principle is well illustrated by animals of the group known as the ARTHROPODA, or 'jointed-footed' Invertebrates, such as Lobsters, Insects, Millipedes, and Spiders. Altogether the Arthropoda comprises over half a million living species.

The body of a primitive Arthropod differs from that of the Earthworm chiefly in the reduction of the number of segments and the development of paired jointed appendages as outgrowths from the body in each segment. From such a primitive type all

FIG. 90. — Dissection of a Crayfish (*Cambarus affinis*). 1, antennules; 2, antenna; 3, position of statolith ('ear'); 4, rostrum; 5, eye; 6, cerebral ganglion; brain; 7-7', extent of cephalothorax; 8, esophagus opening into stomach; 9, stomach; 10, gastric mill; grinding organ in stomach; 11, posterior part of stomach; 12, anterior median artery; 13, coelom, filled with digestive gland (not shown); 14, heart; 15, one of the openings into heart; 16, intestine; 17, dorsal artery; 18-18', extent of abdomen; 19, abdominal muscle; 20, anus; 21, opening of nephridium (green gland); 22, mouth; 23, cheliped; first thoracic leg; 24, mandible; 25, 26, 27, maxillipeds; 28, sub-esophageal ganglion; 29, first thoracic ganglion of ventral nerve cord; 30, base of second thoracic leg; 31, ventral artery; 32, sternal artery; 33, opening of sperm duct; 34, 35, first two abdominal appendages of male modified for copulation; 36, 37, third and sixth (last) abdominal appendages; 38, telson.

the multitude of diverse forms of Arthropod bodies can be derived. For instance, in the Crayfish, which is essentially a fresh-water Lobster, the body consists of twenty-one segments, of which segments 1 to 6 together form the HEAD; segments 7 to 14, the THORAX; and segments 15 to 21, the ABDOMEN. In other words, by the union or complete fusion of certain segments, the body has become divided into more or less distinct regions. Furthermore, the primitive locomotor appendages of the respective segments have become modified into organs for the performance of widely different functions: those of the head, as sensory organs, jaws, etc.; those of the thorax, as organs for grasping, offense and defense, and walking; and those of the abdomen for swimming, etc. Thus change in structure has gone on hand in hand with change in function, so that although there is no obvious resemblance between the jaws of the Crayfish and the legs employed for swimming, nevertheless a study of their development shows beyond doubt that they owe their

FIG. 91. — Typical appendages of a Crayfish. All have been derived from a simple biramous appendage. Protopodite, endopodite, and exopodite are homologous throughout the series. A. 1,

antennule; A. 2, antenna; L. 4, fourth walking leg; M., mandible; Mp. 1, first maxilliped; Mp. 2, second maxilliped; Mp. 3, third maxilliped; Mx. 1, first maxilla; Mx. 2, second maxilla. (From Hegner, after Kerr.)

origin to modifications of one primary type. Accordingly the various appendages are said to be **HOMOLOGOUS**, signifying a fundamental similarity of structure based on descent from a common antecedent form. (Figs. 89-91.)

On the other hand, organs of fundamentally dissimilar structure, which nevertheless perform the same function, are called **ANALOGOUS**. In the group of the Arthropods known as the Insects, the series of head appendages and the legs are homologous with those of the primitive Arthropod type, while the wings are new, unrelated structures and not modifications of the primitive serial appendages of the ancestral form. However, as we shall see later, the wing of a Bird and the arm of Man are homologous, while the wing of an Insect and the wing of a Bird are analogous structures. One of the chief tasks of the branch of biology known as **COMPARATIVE ANATOMY** is to determine the various parts of plants or of animals which are homologous and to study the adaptive changes which are associated with change of function. (Fig. 231.)

We have considered the principle of specialization and fusion of the segments of the higher Arthropods in so far as it affects external structures, but profound modifications of the internal organs also occur. In the first place, the partitions between the various segments which are present in the Earthworm have disappeared in the Crayfish. Again, the alimentary canal of the Earthworm is a nearly straight tube extending through the coelom, with relatively slight modifications in certain segments for the elaboration of the food material as it passes along from mouth to anus; while in the Crayfish we see the accentuation of such modified regions, and the development of large outpocketings, or glands, which are specialized for the formation of chemical substances to **DIGEST** the food material. That is, to change the food into a

FIG. 92. — Diagram of the anterior portion of the central nervous system of an Earthworm (A) and a Crayfish (B). *a*, brain (cerebral, or supraesophageal, ganglion); *b*, nerve commissures, encircling the pharynx (shown in section); *c*, subesophageal ganglion; *d*, ganglia of the ventral nerve cord, with nerves emerging.

soluble form so that it can pass through the cellular membrane which lines the digestive tract and thus actually pass to the circulatory system for distribution to the tissues of the animal.

As a final illustration we may take the nervous system. In the Earthworm this consists of a NERVE CORD which runs along the body in the mid-ventral line below the digestive tract. At the anterior end, it divides into two branches which encircle the digestive tract and unite above in a relatively large body of nervous tissue which constitutes the cerebral ganglion, or BRAIN. In each

FIG. 93. — Dissection of a Fresh-Water Mussel (*Anodonta fluviatilis*). *a*, foot; *b*, mouth; *c*, anterior adductor muscle; *d*, stomach; *e*, liver; *f*, intestine; *g*, auricle of heart; *h*, pericardium; *i*, ventricle of heart; *j*, posterior retractor muscle; *k*, posterior adductor muscle; *l*, anus; *m*, cloacal chamber and exhalant siphon; *n*, branchial chamber; *o*, edge of inhalant siphon; *p*, gill. (From Simpson.)

segment the nerve cord also is somewhat enlarged to form masses of nerve tissue (GANGLIA) from which NERVES pass to the organs in the vicinity. The nervous system of the Crayfish exhibits the same general plan as that of the Earthworm, but certain modifications have been brought about by the uniting of segments in the region of the head and thorax. This process has resulted in the fusion of the segmental ganglia in this region into larger ganglionic masses. The brain of the Crayfish, for example, comprises the primitive ganglia of the segments which have united to form the head. (Fig. 92.)

We have now considered the fundamental body plan of Hydra, Earthworm, and Crayfish chiefly to afford a background for a proper understanding of the body structure of the Vertebrate groups. It will be recalled that Hydra exhibits the simple two-layered condition (ectoderm and endoderm) which is a transient phase in the early development of higher forms. The Earthworm illustrates bilateral symmetry, an alimentary canal opening to the exterior by an anterior mouth and a posterior anus, segmentation, mesoderm, coelom, definite organs and organ systems. The Crayfish shows, in simple form, certain general principles underlying the modification of the Earthworm type, which involve the specialization of various regions of the body in connection with the change of functions of the parts to fulfil more complex life-conditions.

Before passing to a consideration of the Vertebrates, it perhaps should be emphasized again that we have selected from the groups of Invertebrates certain types which illustrate several of the fundamental structural principles which are to be found in the Vertebrate body, but that there are other Invertebrate groups that exhibit body plans which superficially depart very widely from the types described. Although it is believed that these forms do not break the general evolutionary continuity of the Invertebrate series, such a brief consideration, as the limits of this volume would impose, of the morphology of the groups which comprise the Flatworms, Rotifers, Sea Urchins, Clams, etc., would but tend to obscure those principles which are requisite for a proper interpretation of the structure and functions of the Vertebrates, including Man. (Figs. 93, 163, 251.)

FIG. 94. — General anatomy of a primitive Chordate, *Amphioxus* (*Branchiostoma lanceolatus*), a near relative of the lowest Vertebrates.

CHAPTER XI

THE ANIMAL BODY:

VERTEBRATE

If we contemplate the method of Nature, we see that everywhere vast results are brought about by accumulating minute actions. —*Spencer*.

THE Vertebrates form one of the most clearly defined divisions of the animal kingdom and include all the larger and more familiar forms — Fishes, Amphibians, Reptiles, Birds, and Mammals — so that in the popular mind the words animal and Vertebrate are essentially synonymous.

A Fish, as everyone knows, is an aquatic backboned animal which breathes by means of gills and moves by fins. An Amphibian, such as a Frog, may be thought of as a Fish which early in life — at the end of the tadpole stage — discards its gills, develops lungs, substitutes five-toed limbs for fins, and takes up a terrestrial existence. In the same general way, a Reptile may be pictured as an Amphibian which has relegated, as it were, the tadpole stage to the egg, and therefore emerges with limbs and lungs. Birds and Mammals may be regarded as derivatives of the reptilian stock which have transformed the scales of the reptile into feathers and hair respectively, and have developed a special care for their young; the Birds by incubation of the eggs and the Mammals by retention of the young within the body of the female until birth occurs. (Figs. 106-109.)

It will be appreciated, of course, that other important characteristics — some of which will be apparent as we proceed — distinguish these chief Vertebrate groups; but there is, in fact, less diversity in structure among the Vertebrates as a whole than is present, for example, in the one subdivision of the Arthropods, the Crustacea, of which the Crayfish is a member. Accordingly we shall confine our attention largely to a description of the structure and physiology of an 'ideal' Vertebrate, and mention incidentally some of the chief modifications of general significance which appear in the different groups, and specifically in Man.

A. BODY PLAN

The ideal Vertebrate body is more or less cylindrical in form, and is bilaterally symmetrical with respect to a plane passed vertically through the main axis which extends from the anterior to the posterior end. Three regions of the body may be distinguished,

FIG. 95. — Diagrammatic body-plan of an ideal Vertebrate. *A*, longitudinal section of body (female); *B*, transverse section through trunk.

HEAD, TRUNK, and TAIL. The head forms the anterior end and contains the brain, eyes, ears, and nostrils, as well as the mouth and throat, or PHARYNX. On either side of the head is a series of openings, or GILL SLITS, leading into the pharynx which, however, in air-breathing Vertebrates disappear before the adult condition is attained. The trunk forms the body proper and its cavity, or

coelom, contains the major part of the alimentary canal, leading posteriorly to the exterior by the anus, as well as the chief circulatory, excretory, and reproductive organs. The tail comprises the region posterior to the coelom and anus. (Fig. 95.)

The Vertebrate coelom, in contrast with the condition in the Earthworm, essentially comprises only two chambers — a large ABDOMINAL cavity which contains most of the chief viscera, and a small, anterior, PERICARDIAL cavity in which the heart is situated. In the Mammals, including Man, however, the anterior chamber, or THORACIC cavity, contains the esophagus, heart, and lungs and is separated from the ABDOMINAL cavity by a muscular partition, or DIAPHRAGM. The lining membrane of the coelom, known as the PERITONEUM, forms the innermost layer of the body wall and also supplies broad bands of membrane, the MESENTERIES, in which most of the viscera are suspended. (Figs. 107, 108.)

In aquatic forms thin extensions from the trunk and tail form median and paired FINS, the latter comprising the PECTORAL fins, situated near the junction of head and trunk, and the PELVIC fins, just lateral to the anus. The pectoral and pelvic fins, or the FORE-LIMBS and HIND-LIMBS which replace them in all forms above the Fishes, are the only lateral appendages typically found in Vertebrates.

B. SKIN

The surface of the body which comes in direct contact with the environment is covered by an integument, or SKIN, which, though primarily protective and sensory in function, takes part to a greater or less degree in respiration, excretion, and secretion. Scales, feathers, claws, horns, hoofs, nails, teeth, etc., are derivatives of the skin. The skin, unlike that of the Invertebrates, is formed of two layers: an outer epithelial tissue, the EPIDERMIS, derived from the ectoderm; and an inner DERMIS from the mesoderm of the embryo. (Fig. 96.)

C. MUSCLES

The body wall proper is chiefly composed of muscular tissue, commonly spoken of as 'flesh,' which varies in thickness in different parts of the body. In the mid-dorsal region it surrounds the brain and spinal cord (CENTRAL NERVOUS SYSTEM) and the axial supporting structure (NOTOCHORD), while ventrally it forms the wall of the coelom. In the lower Vertebrates and the embryonic

FIG. 96. — Vertical section of human skin, highly magnified, to show its composite structure.

FIG. 97. — Types of muscle cells. A, B, unstriated muscle cells; C, two fragments of striated muscle fibers (cells), at left showing the end of a fiber. Highly magnified. (From Verworn.)

stages of higher forms the muscular layer is composed of segments known as MYOTOMES. But in the adult stage of the latter this evidence of Vertebrate segmentation largely disappears, since the muscular tissue for the most part assumes the form of highly complex longitudinal bands, extensions from which pass into the paired appendages. (Figs. 94, 95 B.)

Muscles, such as those attached to the bones, in which contraction can be brought about at will, are termed VOLUNTARY muscles, while those which cause most of the movements of the viscera are known as INVOLUNTARY muscles. From the standpoint of their microscopic structure, muscle cells are of three kinds. Voluntary muscles consist of STRIATED muscle cells, and involuntary muscles, except those of the heart, are composed of UNSTRIATED muscle cells. The cells of the heart approach somewhat in structure those of voluntary muscles and are known as CARDIAC muscle cells. (Figs. 7, 97, 98.)

D. SKELETON

The form of the Vertebrate body is maintained by a system of supporting and protecting structures, termed the SKELETON. Although various outgrowths of the skin, such as scales, feathers, and hair, form a part of the skeletal system known as the EXOSKELETON which is comparable to the protective coverings of the Invertebrates, it is a bony ENDOSKELETON which is characteristic of the higher animals. This internal skeleton, which is largely mesodermal in origin, exhibits such great diversity and complexity that its study, known as OSTEOLOGY, forms an important subdivision of comparative anatomy.

In the lower Fishes the endoskeleton is composed of a firm elastic tissue, CARTILAGE, or gristle, but from the 'bony' Fishes to Man most of the cartilage becomes OSSIFIED: that is, impregnated with lime salts and transformed into BONE. The human skeleton is formed of about 200 separate bones, but the number varies at different periods of life, because some bones which at first are distinct later become fused. (Figs. 99, 103-105.)

While it is true that the bones constitute the main supporting framework of the body, they are entirely inadequate to knit together the organism into a working unit. We find therefore various kinds of connective tissue interwoven between the integral parts of the body. These tissues form sheaths about most of the organs

and also supply the connecting links between muscle and muscle, muscle and bone — TENDONS; and bone and bone — LIGAMENTS.

FIG. 98. — Muscles of an Amphibian, the Frog (*Rana temporaria*), ventral view. (From Hegner, after Parker and Haswell.)

Endoskeletal tissues, of which bone, cartilage, and connective tissue form the chief groups, are characterized by the development of large amounts of resistant non-living material in or between the

FIG. 99. — Skeleton of a bony Fish, *Perca fluviatilis*. *a*, quadrate bone, *b*, dentary part of lower jaw bearing teeth; *c*, premaxilla, part of upper jaw, *d*, prenasal; *e*, nasal; *f*, optic capsule; *g*, frontal; *h*, parietal; *i*, supraoccipital; *j*, operculum, flap covering the gill openings; *k*, centre of vertebra; *l*, skeleton of median dorsal fins; *m*, attachment of caudal fin to vertebral column; *n*, caudal fin rays; *o*, haemal spines; *p*, anal fin; *q*, interspinous bones; *r*, first caudal vertebra; *s*, ribs; *t*, styliform processes; *u*, pelvic fin rays; *v*, proximal portion of ventral fin, 'pelvic bone'; *w*, pectoral fin rays; *x*, *y*, *z*, coracoid, scapula, and clavicle of pectoral girdle.

component cells themselves; the character of the skeletal tissue being determined chiefly by the nature of this matrix.

The primitive axis of the skeleton consists of a cylindrical cord or rod of cells (NOTOCHORD), which lies in the mid-dorsal line of the body wall just below the brain and spinal cord and above the coelom. In most Vertebrates, however, the notochord in its original form is only a temporary structure, being partially or completely replaced during later development by a linear series of cartilaginous or bony elements, known as VERTEBRAE, which form

FIG. 100. — Diagram of a longitudinal section through a developing vertebral column to show the invasion of the notochordal sheath by cartilage to form the centra of the vertebrae. *a*, notochord; *b*, notochordal sheath; *c*, blood vessel in connective tissue; *d*, growing cartilage invading notochord; *e*, bone developing to form vertebra; *f*, muscle tissue.

the VERTEBRAL COLUMN, or backbone. This is the most characteristic structure of Vertebrates as compared with Invertebrates, or backboneless animals. (Figs. 94, 95, 100.)

A typical vertebra of the higher animals consists of a basal portion, known as the CENTRUM, and a NEURAL ARCH which it supports. These form a protecting ring of bone about the spinal cord. From various parts of the vertebra as a whole arise PROCESSES for movable articulation with its neighbors, the attachment of muscles, etc. Between the vertebrae of the Mammals are cushions of cartilage which absorb shock. (Fig. 101.)

In some forms, RIBS are attached to the transverse processes of certain vertebrae. These extend outward and downward within the body wall, and become attached in the mid-ventral line to the breast bone (STERNUM). Thus, in the adult of the higher Vertebrates, the series of centra of the vertebrae come to occupy the position formerly held by the notochord; while above, the neural arches encircle the NEURAL CANAL containing the spinal cord; and below, the transverse processes, ribs, and sternum surround the anterior portion of the coelom. (Figs. 95, 101, 105.)

The Vertebrate head, containing the anterior end of the alimentary and neural canals, the brain, and the chief sense organs, is protected in the lower Fishes by a case of cartilage. In higher forms the cartilage is replaced by a bony SKULL which articulates with the first vertebra of the backbone. JAWS, or supporting structures of the mouth, are attached to the skull.

The skull and vertebral column form the main SKELETAL AXIS from which is suspended the APPENDICULAR skeleton, or bony framework of the paired appendages (FINS or LIMBS) and their supporting structures (GIRDLES). This is relatively simple in the anterior (pectoral) and posterior (pelvic) paired fins of Fishes, which merely act as paddles; but when these are modified into paired limbs for progression on land, the mechanical problems involve the development of complex limb skeletons to support the body, and to act as levers for the limb muscles to move in locomotion. In response to this need an elaborate series of bones is developed which, in all cases, however, may be referred to a common plan, known as the PENTADACTYL LIMB in allusion to the five digits (FINGERS and TOES) in which it usually terminates. The limbs are attached directly or indirectly to the vertebral column by groups of bones which form respectively the PECTORAL and PELVIC GIRDLES. (Figs. 102-105, 231, 232.)

FIG. 101. — A typical human vertebra (tenth thoracic). *a*, neural spine; *b*, transverse process; *c*, neural arch; *d*, anterior articulating surface; *e*, neural canal through which spinal cord passes; *f*, centrum which has replaced notochord of early embryo.

E. DISTINCTIVE VERTEBRATE CHARACTERS

As a summary of this general outline of the structure of the Vertebrate body, we may emphasize three characters which are of prime diagnostic importance.

In the first place, whereas the skeletal structures of Invertebrates typically consist, as in the Crayfish, of an exoskeleton of hard non-living materials deposited on the surface of the body, the chief function of which is protection, the Vertebrate skeleton is primarily a living endoskeleton. It is an organic part of the

FIG. 102. — Diagram of the plan of the Vertebrate limbs. A, fore limb and pectoral girdle; B, hind limb and pelvic girdle. (From Hegner, after Parker and Haswell.)

organism which, although it affords protection for delicate parts, provides adequately for support and supplies muscle levers, and thus makes practicable the relatively large bodies of the higher animals. The notochord is at once the foundation and axis of the Vertebrate internal skeleton and either persists throughout life as such, or simply long enough to function as a scaffolding about which the vertebral column is built. In recognition of the prime importance of the notochord, the Vertebrates and their nearest allies (*e.g.*, the Tunicates and *Amphioxus*) are technically known as CHORDATES. (See Appendix: Classification.)

In the second place, it will be recalled that the central nervous system of the Earthworm and Crayfish consists of a ventral nerve cord running along in the coelom below the digestive tract, except at the anterior end where it encircles the pharynx to form the

FIG. 103. — Skeleton of an Amphibian, the Frog (*Rana temporaria*). Dorsal aspect; the left half of the shoulder girdle and the left fore and hind limbs are removed, as also are the membrane bones on the left side of the skull. Permanently cartilaginous parts dotted. (After Howes, slightly altered.)

brain above. The position of the Vertebrate brain is similar, though the spinal cord is not a 'cord' but a nerve tube, which lies in the neural canal imbedded in the muscles of the body wall *above* the digestive tract and, of course, outside of the coelom. Thus the spinal cord itself and its location are highly characteristic.

A third fundamental characteristic is a series of perforations or slits through the throat and body wall. In the lower forms the gill slits provide an exit for the current of water entering by the mouth and, being richly supplied with blood, afford the chief

FIG. 104. — Skeleton of the Cat. 1, premaxilla (bone of skull); 2, maxilla; 3, nasal; 4, optic capsule; 5, frontal; 6, malar; 7, squamosal; 8, parietal; 9, supraoccipital; 10, atlas (1st cervical vertebra); 11, axis (2d cervical vertebra); 12, neural spine of first thoracic vertebra; 13, centrum of seventh thoracic vertebra; 14, rib; 15, first lumbar vertebra; 16, anterior and posterior articulating processes of fifth lumbar vertebra; 17, three sacral, followed by twenty-two caudal vertebrae; 18, ilium; 19, pubis; 20, ischium; 21, femur; 22, patella (knee cap); 23, fibula; 24, tibia; 25, tarsals; 26, metatarsals; 27, phalanges of hind limb (toes); 28, phalanges of fore limb; 29, metacarpals; 30, carpals; 31, ulna; 32, radius; 33, humerus; 34, anterior end of sternum; 35, scapula; 36, hyoid apparatus; 37, auditory capsule; 38, zygomatic arch; 39, mandible; 40, molar teeth; 41, premolar teeth; 42, canine tooth; 43, incisor teeth.

means of respiratory interchange between the animal and the surrounding medium. In the higher Vertebrates the gill slits are present merely during a transient phase in the development of the individual, since the function of aerating the blood is taken over by the lungs. (Figs. 94, 95, 117, 239.)

FIG. 105. — Skeleton of Man. (From Peabody and Hunt.)

FIG. 106.—Dissection of a bony Fish, the Yellow Perch (*Percula flavescens*). 1, roof of mouth; 2, position of external nostrils; 3, position of right eye; 4, olfactory nerve; 5, optic nerve; 6, left cerebral hemisphere; 7, left optic lobe; 8, cerebellum, dorsal and anterior to medulla; 9, skull (cranium); 10, cord from air bladder to alimentary canal; 11, air bladder (hydrostatic organ); 12, dorsal fin; 13, an interspinal bone; 14, spinal cord; 15, centrum of a vertebra; 16, tongue; 17, pharynx; 18, gill slits and gills; 19, aorta; 20, ventricle of heart; 21, auricle; 22, liver; 23, gall bladder; 24, stomach; 25, bile duct; 26, pyloric caecum; 27, spleen; 28, fat mass; 29, right pelvic fin; 30, intestine; 31, gonad; 32, right ureter (from right kidney, mesonephros, not shown); 33, urinary bladder (dilation of ureter or mesonephric duct); 34, anus; 35, urogenital pore; 36, anal fin.

FIG. 107.—Dissection of an Amphibian, the Frog (*Rana clamitans*). 1. Cartilage of lower jaw; 2, opening of Eustachian tube from ear; 3, teeth on upper jaw; 4, nasal bone; 5, internal nares; 6, olfactory lobe of brain; 7, left cerebral hemisphere; 8, eye; 9, left optic lobe; 10, cerebellum; 11, skull (cranium); 12, medulla; 13, trachea; 14, esophagus; 15, spinal cord; 16, left lung; 17, a vertebra; 18, right lung; 19, fat body; 20, right testis; 21, right kidney (mesonephros); 22, adrenal body; 23, urostyle—end of spinal column; 24, ureter (mesonephric duct); 25, opening of left ureter into cloaca; 26, opening of cloaca; 27, opening of urinary bladder into cloaca; 28, socket in pelvic girdle for left femur; 29, muscles of left hind leg; 30, urinary bladder; 31, large intestine; 32, mesentery with blood vessels, etc., to small intestine; 33, spleen; 34, pancreas; 35, small intestine; 36, gall bladder; 37, stomach; 38, lobe of liver; 39, ventricle of heart; 40, left auricle; 41, right auricle; 42, 43, branches of aorta leaving heart; 44, glottis; 45, pharynx; 46, tongue.

FIG. 108. — Dissection of a Mammal, the Gray Squirrel (*Sciurus carolinensis*). 1, incisor tooth; 2, tongue; 3, nostrils (external nares); 4, olfactory lobe of brain; 5, cranium; 6, optic nerve; 7, trigeminal nerve; 8, left cerebral hemisphere; 9, cerebellum; 10, medulla; 11, pharynx; 12, esophagus; 13, spinal cord; 14, anterior vena cava; 15, pulmonary artery; 16, pulmonary vein; 17, posterior vena cava; 18, left lung; 19, diaphragm; 20, adrenal body; 21, left kidney (metanephros); 22, spleen; 23, ureter; 24, mesorehium — mesentery supporting testis; 25, sperm duct; 26, uterus masculinus; 27, urethra; 28, large intestine; 29, penis; 30, prostate gland; 31, urinary bladder; 32, left testis; 33, scrotum; 34, Cowper's gland; 35, penis; 36, blood vessels in mesentery of intestine; 37, stomach; 38, pancreas; 39, small intestine; 40, liver; 41, bile duct; 42, left auricle; 43, left ventricle; 44, pericardium; 45, aorta; 46, sternum; 47, thymus gland; 48, trachea; 49, thyroid gland; 50, epiglottis; 51, internal nares. (Redrawn, after Linville and Kelly.)

FIG. 109. — Diagrammatic median section of the human body. 1, cranium; 2, nostrils (external nares); 3, mouth; 4, internal nares; 5, pharynx; 6, larynx, 'Adam's apple'; 7, trachea; 8, esophagus; 9, sternum (breast bone) imbedded in body wall; 10, lungs; 11, heart; 12, thoracic cavity (part of coelom); 13, diaphragm; 14, abdominal cavity (part of coelom); 15, liver; 16, stomach; 17, large intestine; 18, kidney; 19, small intestine; 20, ureter; 21, vermiform appendix of large intestine; 22, urinary bladder; 23, pubis of pelvic girdle; 24, urethra; 25, anus; 26, coccyx; 27, posterior part of neural canal; 28, centrum of vertebra; 29, neural spines of vertebrae; 30, spinal cord; 31, medulla; 32, cerebellum; 33, cerebral hemisphere.

CHAPTER XII

NUTRITION IN ANIMALS

I do not know how it may be with others, but it is a great satisfaction for me to know when regaling on my humble fare that I am putting in motion the most beautiful machinery with which we have any acquaintance. — *Dickens*.

AMONG the single-celled animals, such as *Paramecium*, nutrition is reduced to its simplest terms. The food material enters the cell and is acted upon by substances formed by the protoplasm in its vicinity: the food is chemically changed, or digested, so that it becomes available for the use of the cell. In *Hydra* a special layer of cells, the endoderm, is largely devoted to digestion. Although some of the endoderm cells actually engulf small particles of food and digest them within the cell (INTRACELLULAR DIGESTION), the major part of digestion is brought about within the enteric cavity by secretions from the endoderm cells. Digestion of the latter type (INTERCELLULAR) is characteristic of the Earthworm and all higher animals.

We have considered the form and supporting structures of the body wall of a typical Vertebrate — the outer tube which surrounds and contains the viscera — and therefore we recall that through this outer tube, just as in the case of the Earthworm and Crayfish, there runs from mouth to anus a second or inner tube, the digestive tract, or ALIMENTARY CANAL. The alimentary canal is essentially a tubular chemical laboratory which passes the food on by its own muscular activity from one part to another. Each of these regions, in turn, supplies the chemical reagents which it uses for changing the food into a soluble form so that it can pass through the walls and be distributed to the cells of the organism as a whole. Indeed, the complex food materials which enter the human mouth run the gauntlet of a whole series of digestive fluids.

The wall of the alimentary canal consists of three chief cellular layers: a lining epithelium, a connective tissue layer, and a muscular layer. The epithelium which lines the alimentary canal and its derivatives is the digestive tract proper in the sense that it is

of prime functional importance in secreting the digestive fluids and in absorbing the products of digestion. The other layers per-

FIG. 110. — Diagram of the alimentary canal and its derivatives in Man. *a*, mouth; *b*, salivary glands; *c*, pharynx, showing the embryonic position of five pairs of gill pouches, the second pair probably giving rise to the tonsils, and the third and fourth to the thymus glands; *d*, thyroid gland; *e*, trachea; *f*, thymus gland; *g*, lungs; *h*, esophagus; *i*, diaphragm — the muscular partition between the thorax and abdomen; *j*, liver; *k*, gall bladder; *l*, stomach; *m*, pancreas; *n*, small intestine; *o*, large intestine; *p*, vermiform appendix; *q*, rectum leading to exterior by the anus.

form accessory functions such as support, conduction of blood vessels, and movements of the canal. (Fig. 29.)

A. BUCCAL CAVITY, PHARYNX, AND ESOPHAGUS

The entrance to the alimentary canal is the mouth, a transverse aperture in the head, which leads into the mouth-chamber, or

BUCCAL CAVITY, supported by the jaws. The buccal cavity gradually merges into the throat, or PHARYNX, which in the Vertebrates acts as a passage both for the food and the respiratory gases. The respiratory current of water in aquatic forms soon passes to the exterior by a series of perforations, the GILL SLITS, through the pharynx and body wall; while the respiratory current of air in higher forms enters the LUNGS. On the other hand, in all Vertebrates the preparation of the food for its passage through the alimentary canal starts in the buccal cavity. (Figs. 110, 117.)

FIG. 111. — Diagram of a gland, in section, together with the surrounding connective tissue and blood vessels. Highly magnified. See Fig. 88. (From Hough and Sedgwick.)

The human buccal cavity is lined with a membrane, continuous at the LIPS with the outer skin, which is provided with unicellular glands that secrete MUCUS. This serves to lubricate the food so that it may be more readily moved about by the TONGUE for mastication by the teeth and then passed on toward the gullet. Furthermore, the secretion, SALIVA, from three pairs of large SALIVARY GLANDS, aids in the same process, but also contributes to the digestion of one class of foods, the starches. This is due to a special chemical substance, an enzyme termed PTYALIN, which in an alkaline medium converts starch into a sugar, MALTOSE. But

only a small proportion of the starch is digested by ptyalin during the rapid passage of food through the mouth region, and the activity of the enzyme ceases soon after it reaches the stomach where the alkaline reaction of the mouth gives place to an acid reaction.

So the mouthful of food, masticated, moistened, and with some of its starch digested, is rolled by the tongue and passed along the pharynx into the ESOPHAGUS. Henceforth it is beyond voluntary recovery, because it is pushed along by involuntary rhythmical contractions, PERISTALSIS, of the digestive tract wall. The esophagus is a muscular tube which passes posteriorly through the thorax, and rapidly delivers the food without further digestion to the STOMACH.

B. STOMACH

The stomach, really the first stopping place of food that has been swallowed, is a thick-walled sac situated just below the diaphragm in Mammals. In common with most of the viscera, the stomach is suspended in the abdominal cavity by broad loops of a membrane, the MESENTERY, which is continuous with the peritoneal membrane lining the cavity. Within the mesentery, blood vessels, nerves, etc., pass to the stomach. (Figs. 106-110.)

Here the work of the digestive tract actively progresses by the action of specific chemical substances present in the GASTRIC JUICE which is secreted by innumerable GASTRIC GLANDS. The latter are tiny pits in the stomach wall lined with special glandular cells. Human gastric juice is a complex fluid comprising water — over 99 per cent; a protein-splitting enzyme, PEPSIN; a milk-curdling enzyme, RENNIN; common salt, NaCl; and a free acid, HCl. This array of components of gastric juice softens the food mass, gives it an acid reaction, curdles the milk, and simplifies the proteins — transforms the average meal in the course of an hour or so into CHYME which gradually passes through the PYLORIC VALVE into the INTESTINE.

C. SMALL INTESTINE

The human intestine is a much coiled tube that extends from the stomach to the anus, and it is in the upper part, known as the SMALL INTESTINE, that not only the most radical chemical changes in the food take place — digestion is completed; but also most of the products of digestion pass through its walls into the body proper — absorption occurs. Accordingly we find various glands

to elaborate and secrete the digestive fluids — cells that take from the circulatory system not only the materials necessary for their own life but also other substances which they transform chemically for the use of the organism as a whole. Some are unicellular or simple multicellular tubular glands imbedded in the

FIG. 112. — Liver and pancreas of the Frog, showing their ducts. *L*, lobes of liver turned forward; *G*, gall bladder; *C*, cystic ducts which unite with hepatic ducts (*H*) and finally lead into the common bile duct (*B*). The latter passes through the pancreas (*P*), receives further hepatic ducts (*H*₁) and pancreatic ducts (*P*₁), and (*D*) leaves the pancreas, opening into the upper part of small intestine (*Du*) at *O*. *S*, stomach; *Y*, pylorus.

intestinal wall; others are highly complex and far removed from the intestine into which they pour their products through long ducts. But, as we know, even in the latter case the glands are really derivatives of the intestine — cellular areas sunk, as it were, below the membrane to which they really belong — because they arise during development as outpocketings of its wall: the ducts being the sole remaining connection with the point of origin. (Fig. 111.)

1. *Liver and Pancreas*

The largest gland in the body, the LIVER, and an equally important one, the PANCREAS, pour their secretions into ducts which unite to form a single duct. This carries the secretions to the upper part of the small intestine. The secretion of the liver, termed BILE, which is constantly formed but may be stored until needed in the GALL BLADDER, is a highly complex mixture of substances. Most of them probably are waste products — excretions — which, on their way out of the body through the intestine, contribute incidentally to digestion by coöperating with the actual enzymes from other glands. However, the liver is still more versatile, as will appear beyond. (Fig. 112.)

LOCATION	SECRETION	ENZYMES	SUBSTANCES CHANGED	INTER- MEDIATE PRODUCTS	PRODUCTS READY FOR ABSORPTION
Mouth	Saliva	Ptyalin	Starch	Maltose	
Stomach	Gastric juice	Pepsin Rennin	Protein Protein of Milk	Proteoses Peptones Casein	
Small intestine	Pancreatic juice	Amylopsin	Starch	Maltose	
		Lipase	Fats		Fatty acid and Glycerol
		Trypsin	Proteins		Amino acids
	Intestinal juice	Maltase Sucrase Lactase	Maltose Cane sugar Milk sugar		Simple sugars
		Erepsin	Proteoses Peptones Casein		Amino acids

FIG. 113. — Chief chemical activities of the human digestive tract.

The pancreas, or 'sweetbread,' may be regarded as the chief digestive gland in the Vertebrate body though it also performs additional functions. The gland in Man lies just below the stomach and secretes into the small intestine each day nearly two pints of strongly alkaline PANCREATIC JUICE containing three enzymes — TRYPSIN acting on proteins, AMYLOPSIN on starches, and LIPASE on fats. (Fig. 113.)

Thus food that has run the gauntlet of the enzymes of the upper digestive tract is now attacked by the pancreatic juice. But this is not all: as if to make digestion doubly sure, innumerable minute glands imbedded in the intestinal wall contribute the so-called **INTESTINAL JUICE** armed with four enzymes — again one of them, **EREPSIN**, to act on certain proteins, and the others to convert complex sugars into simple sugars.

2. Absorption

But, of course, the chief purpose of digestion is to make the food soluble so that it may enter the body proper: pass through the epithelium lining the digestive tract wall. This passage into the body, or **ABSORPTION**, occurs chiefly in the small intestine, the walls of which are lined with millions of minute projections, or **VILLI**, that bring tiny vessels into intimate contact with the absorptive membrane while greatly increasing the effective absorptive surface. The transportation system of vessels within the villi consists of **BLOOD** vessels which take up the absorbed products of protein and carbohydrate digestion, and **LYMPH** vessels, here called **LACTEALS**, which receive the derivatives of the fats. Both also take absorbed water and salts. (Fig. 114.)

FIG. 114. — Diagram of a section through a villus. (From Peabody and Hunt.)

3. Distribution

Accordingly the path through which the proteins and carbohydrates are transported differs from that of the fats. The blood vessels returning blood from the digestive organs finally merge to form a large vessel, the **PORTAL VEIN**, which proceeds to the liver to allow that organ to regulate certain of the blood constituents — in particular to store up sugar, in the form of **GLYCOGEN**, after a meal and later dole it out to the blood as conditions demand. On the other hand, the lacteals merge into larger and larger lymph

vessels and finally into the THORACIC DUCT which empties into the blood vascular system — the fats being switched, as it were, around the liver so that they do not directly enter the blood supply to that organ. (Fig. 115.)

D. LARGE INTESTINE

During the passage of food through the small intestine, digestion is practically completed and absorption has progressed far. The

FIG. 115. — A, diagram of paths of absorbed food from the human digestive tract. Proteins and carbohydrates by veins; fats by lymphatics. B, plan of distribution of the chief lymphatic vessels in the human body.

remaining material, termed CHYLE, then passes through a constriction into the LARGE INTESTINE where absorption is completed and the undigested materials, or FECES, are carried to the exterior through the anus. The latter either leads into a terminal cavity, the

CLOACA, into which also open the urogenital ducts, or directly out on the ventral surface, as in Man.

Finally, we must not overlook certain accessories of the alimentary canal which lose all direct connection with it as development proceeds — really glands that have carried, as it were, the process of outpocketing from the digestive tract to the breaking point and become DUCTLESS GLANDS. Such, for instance, are the THYROID and THYMUS glands near the anterior end of the esophagus. The thymus in Man degenerates during early childhood, while the thyroid delivers its secretion, a HORMONE, directly into the blood stream as an INTERNAL, or ENDOCRINE SECRETION. We shall have occasion later to discuss the important coördinating functions carried out by hormones secreted by ductless glands and other endocrine organs. (Fig. 110.)

One naturally wonders how it is that the living tissues of the digestive tract, and especially of the glands themselves, withstand the digestive activities of their own enzymes, although the stomach or intestine of an animal killed during active digestion will begin self-digestion. A partial explanation of immunity during life appears to be that the enzymes are not in an active form while they are within the glands, but are later activated by certain conditions that they meet in the digestive tract when food is actually present.

Certainly, at first glance, the complicated digestive system of the Vertebrate may seem to have little in common with that of the Earthworm, but as a matter of fact the fundamental plan is the same. The differences which are present are the result of an increase of the working area of the alimentary canal, not only to afford greater secretive and absorptive surface and a larger variety and amount of digestive substances, but also to prolong the length of time the food is subjected to treatment. This increase in area has been effected by folds and elevations of the inner surface of the tract; by outpushings of limited areas of the tube to form large glands which in most cases contribute their products to their point of origin through ducts; and by increasing the length of the inner tube as compared with the outer tube, or body wall, which results in throwing the intestine into various convolutions within the body cavity. Thus is met the increasingly complex nutritional demands of more highly organized animals.

CHAPTER XIII

RESPIRATION IN ANIMALS

The living body is the theatre of many chemical and physical operations in line with those of the inorganic domain. — *Thomson.*

As we have seen, the essential factor of respiration is an interchange of gases between protoplasm and the environment: an intake of free oxygen for combustion, and an outgo of the waste products, chiefly carbon dioxide and water. In the unicellular organisms, such as *Pleurococcus* and *Paramecium*, and in simple multicellular animals like *Hydra*, this appears to be a relatively simple process since an elaborate mechanism is not necessary to facilitate the interchange. But with the establishment of a highly differentiated multicellular body, fewer and fewer cells are in direct contact with the aërating medium and so various provisions are necessary to transfer the gases to and from the outer world and the individual cells themselves.

In all forms the SKIN functions to some extent; in the Earthworm, in fact, it acts as the chief respiratory membrane since a profuse supply of blood vessels to the moist surface of the body effects a sufficiently rapid gaseous interchange for the relatively inactive life of the organism. The Crayfish meets the problem of respiration by finger-form outpocketings of the body wall, the GILLS: a method of bathing a large area of the respiratory membrane in the respiratory medium, the surrounding water. Insects, however, instead of bringing the blood to the surface, develop a network of tubes, or TRACHEAE, which ramify throughout the body tissues and conduct air directly to the cells. (Fig. 116.)

Among the lower Vertebrates, as has been indicated, the anterior end of the digestive tract functions as a common food and respiratory passage. In Fishes, the respiratory water current which enters the mouth makes its exit by way of the gill pouches and gill slits; the lining of the pouches — outpocketings of the lining of the alimentary canal — functioning as the respiratory membrane. (Fig. 117.)

Among the air-breathing Vertebrates there are the added problems of protecting and keeping moist the greatly increased respiratory surface which their more active metabolism — proportionally greater energy requirements — demand. Accordingly the gill slits persist merely as transient embryonic reminders of evolutionary history; the function of the gill pouches being taken over by a huge outpocketing of the ventral wall of the pharynx into the anterior portion of the body cavity, which constitutes the LUNGS. Thus, even in Man, the respiratory membrane which lines the lungs is, from the standpoint of development, a specialized

FIG. 116. — Diagram of the respiratory (tracheal) system of an Insect.

FIG. 117. — Diagram of a vertical section through the head region of Fish (above) and Reptile or Bird (below) to show the paths of the respiratory currents (*a*) and food (*b*). See Fig. 109.

part of the epithelium of the alimentary canal. Furthermore, the establishment of lungs entails, in turn, a complex respiratory mechanism so that the air within them may be changed at frequent intervals. (Fig. 239.)

A. LUNGS

In the human respiratory process, air after passing through the nose to the pharynx is drawn through the windpipe, or TRACHEA, toward the lungs. The opening (GLOTTIS) from the pharynx into the trachea is situated just back of the tongue and is covered by a lid, the EPIGLOTTIS, which offers no hindrance to the passage of air except when it shuts down during the process of swallowing to prevent food from 'going down the wrong way.'

As the lower end of the trachea enters the chest, or THORAX, it

divides into right and left branches, the **BRONCHIAL TUBES**, which thereupon directly enter the lungs, each of which is a bag of elastic, spongy tissue. Within the lungs, the bronchial tubes divide into smaller and again smaller branches, until finally they form micro-

FIG. 118. — Diagram of a vertical section through the right half of the human thorax. *A*, muscles, ribs, etc., of the body wall; *B*, pleura, lining the same; *C*, pleural cavity; *D*, pleural covering of the lung; *E*, connective tissue of the lung; *F*, alveoli of the lung; *G*, diaphragm; *H*, trachea; *I*, right bronchial tube; *K*, the pericardial space in which lies the heart. (From Hough and Sedgwick.)

scopic twigs, each ending in one or more tiny air sacs, or **ALVEOLI**. Thus there are many thousands of alveoli in the human lungs, every one in direct communication with the outer air. Furthermore, each alveolus is profusely supplied with tiny thin-walled blood vessels, or **CAPILLARIES**, through which flows blood sent by the heart and soon to return to the heart so that it may be

distributed to every part of the body. It is while the blood is in the capillaries of the alveoli that it gives up to the air in the alveoli carbon dioxide, water, and heat taken from the tissues, and at the same time receives oxygen. This is effected through the delicate walls of the capillaries and alveoli. So the alveoli are really the effective surface of the lungs. (Fig. 118.)

B. RESPIRATORY MECHANISM

In order for the lungs to play their part in respiration, it is evident that the air within them must be periodically renewed, and this rhythmical process of INHALATION and EXHALATION is what one usually refers to as breathing. The complex mechanism involved and its method of operation may be briefly outlined.

The lungs are elastic sacs suspended in an air-tight cavity, the thorax, which can be enlarged by raising the RIBS and lowering the DIAPHRAGM, a muscular partition between the thoracic and abdominal cavities. The sole entrance to the lungs is through the trachea, and accordingly an atmospheric pressure of approximately fifteen pounds to the square inch is exerted down through the trachea on the inner walls of the lungs and keeps them constantly in close contact with the walls of the thoracic cavity — otherwise there would be a vacuum between the lungs and the thoracic wall. Therefore when the thoracic cavity is enlarged by contraction of the muscles of the ribs and diaphragm, the elastic lungs expand in maintaining contact with its walls — inspiration takes place; and when the thoracic cavity is decreased, by relaxation of the same muscles, expiration occurs. The lungs play an entirely passive part in the process. Of course, if through injury the thorax is punctured, then there is equal atmospheric pressure on both sides of the walls of the lungs, and they collapse. (Fig. 119.)

Since the rhythmical respiratory movements are due to the contractions of muscles, it follows that stimuli reach the muscles from the nervous system; because muscles, excepting those of the heart and alimentary canal, do not contract automatically. Now we know that nerve impulses arise in the so-called RESPIRATORY CENTER in the lower part (MEDULLA) of the brain, just before it merges into the spinal cord, and pass by nerves to the muscles involved. Usually it is the oxygen-carbon dioxide content of the blood reaching the respiratory center which determines the rate of the respiratory movements that it induces; though there are

nerves that carry nerve impulses from the lungs which contribute to the rhythm of breathing by holding in check the activities of the center itself. Indeed, the center can be influenced by stimuli from nearly any part of the body: witness the effect of a cold plunge on breathing. The action of the center is, of course, chiefly involuntary — we breathe when we are asleep; but obviously it

FIG. 119. — Diagram to illustrate the mechanism of diaphragm breathing. The lungs of a small Mammal are in a closed bell-jar. As the rubber membrane below (representing the diaphragm) is pulled down enlarging the cavity, air enters through the tube (trachea) and the lungs are distended. (From Conn and Budington, after Tigerstedt.)

can be controlled by the will — we can ‘hold the breath.’ If this center is destroyed or the nerves are severed, respiratory movements immediately and finally cease.

C. RESPIRATORY INTERCHANGE

The respiratory mechanism has attained its objective when air and blood are brought into such close relationship in the lungs that gaseous interchange can occur, and heat be transferred. Inhaled air varies very widely in temperature but in our homes is perhaps most frequently about 21° C. (70° F.). Exhaled air is about 36° C., or very nearly the same as that of the human body. Thus under usual circumstances the exhaled air is warmer than when it entered the lungs — the blood has lost heat. Again, the amount of water in the inhaled air is variable, being low on a dry day and high on a wet day; but the exhaled air is practically

saturated with water vapor — the blood has lost water. Furthermore, the inhaled air contains merely a trace of carbon dioxide, while when it leaves the lungs it bears about four per cent — the blood has given up carbon dioxide. And finally, air entering the lungs contains approximately twenty per cent of oxygen, while when exhaled there is only about sixteen per cent — the blood has received oxygen. In short, the blood by its traffic with the air in the lungs gives up heat, moisture, and carbon dioxide, and takes up oxygen.

One naturally is interested to know how the blood while passing through the lungs acquires the oxygen, since this is the element demanded by every cell in its life processes. At least two phenomena are involved. In the first place, the air contains a considerable amount of oxygen under relatively high pressure and therefore some oxygen passes into the liquid plasma of the blood where the oxygen conditions are just the opposite. But the amount of oxygen gained in this way by the blood is by no means equal to the demands of the tissues, and so the emergency is met by special blood cells known as RED BLOOD CORPUSCLES. These carry a complex chemical substance, HEMOGLOBIN, which has a high chemical affinity for free oxygen: it is oxidized to form a loose chemical compound, OXYHEMOGLOBIN. Accordingly the millions of red blood corpuscles leave the lungs with the oxygen affinity of the hemoglobin satisfied and return to the heart to be distributed throughout the body.

The oxygen is actually delivered to the tissue cells through the capillaries in the tissues where the oxygen content is low — just the opposite of the condition in the lungs — because the various cells use the oxygen nearly as rapidly as it is received. So the corpuscles give up their oxygen — oxyhemoglobin is reduced to hemoglobin — and the blood receives in exchange, as it were, carbon dioxide, and also water and heat resulting from oxidative processes — combustion — in the tissue cells. The carbon dioxide is carried by the blood plasma, in combination with sodium as sodium bicarbonate, and perhaps to a slight extent by the hemoglobin in the corpuscles.

And now the blood, after its passage — lasting about one second — through the capillaries, proceeds on its way back to the heart which sends it to the lungs so that it can transfer to the air in the alveoli water, heat, and carbon dioxide. The latter passes

to the air because it is under higher tension in the blood than in the air. The transportation cycle is complete.

Such, in brief, is the elaborate apparatus present in the higher animals, and Man, to provide for the new conditions arising because of the removal of many of their component cells further and further from the source of oxygen, and the demand for more and more facilities for securing it as their life processes increased in activity. We shall have occasion later to consider the attendant changes in the blood vessels; but now it is only necessary to be sure that the mechanism does not obscure its object — to reiterate that, although one ordinarily thinks of the movements involved in the renewal of the air in lungs as respiration, it is neither inhalation and exhalation, nor the interchange of gases between blood and air or between blood and tissue cells. The essential feature of respiration is the same here as it is in unicellular plants and animals: the protoplasm of each and every cell of the body securing energy from food by combustion, involving the appropriation of oxygen and the liberation of carbon dioxide. All else is accessory — though necessary.

CHAPTER XIV

CIRCULATION IN ANIMALS

I finally saw that the blood, forced by the action of the left ventricle into the arteries, was distributed to the body at large, and its several parts, in the same manner as it is sent through the lungs, impelled by the right ventricle into the pulmonary artery, and that it then passed through the veins and along the vena cava, and so round to the left ventricle . . . which motion we may be allowed to call circular.

— *Harvey*, 1628.

THE crucial points of contact between the higher animal and its environment, in so far as the intake of matter and energy is concerned, are the membranes which line the DIGESTIVE TRACT and a large diverticulum from it, the LUNGS. Through the former must pass all the materials which are to be assembled as integral parts of the organism and the fuel which is to supply the energy for the vital processes, while through the latter must pass the oxygen which is to release this energy. Only when these membranes have been passed are the materials really within the body and at its disposal for distribution by the CIRCULATORY SYSTEM to the individual cells of the various organs which are to use them.

In addition to carrying the fuel and the oxygen, the circulatory system must remove the waste products of metabolism from the cells and deliver them to the proper EXCRETORY ORGANS, such as the lungs or kidneys, to be passed to the outside world. The circulatory system is therefore the essential connecting link between the points of intake, utilization, and outgo of materials — a distributing system which in coöperation with the NERVOUS SYSTEM unifies the organs into an organism.

A. CIRCULATION IN THE LOWER VERTEBRATES

It has been shown previously that in the higher plants the movement of water and food in solution through the conducting systems is affected chiefly by physical forces which are, to a certain extent, independent of, though directed by the activity of the plant cells. In the higher animals, on the other hand, circulation is brought

about by an active system which forces as well as conducts throughout the body a fluid tissue, the BLOOD and its derivative, LYMPH.

Many stages in the evolution of this elaborate circulatory system can be traced from the lowest coelomate Invertebrates — in which it consists merely of a single cavity or several connected cavities filled with a fluid containing various types of cells — through forms in which more and more of the spaces are replaced by definite *tubes* for the conduction of the fluid.

With the establishment of closed vessels, the contractions of various organs and the movements of the body as a whole can no longer be entirely depended on for the movement of the fluid, and accordingly, in certain regions, a *muscular layer* is developed in the walls of the tubes, which by rhythmic pulsation forces the fluid along. Thus, for example, in the Earthworm there is a fluid (COELOMIC FLUID) within the body cavity which is forced about by the movements of the worm and bathes most of the internal organs; and also a system of vessels, a part of which contracts rhythmically and distributes the blood to the individual cells. (Fig. 86.)

In the higher forms a *closed* vascular system gradually takes the ascendancy and becomes what one ordinarily has in mind when speaking of 'the circulatory system,' but the primitive type of open system still functions as an auxiliary of no mean importance even in Man. The highly developed Vertebrate circulatory system, therefore, really consists of two parts. First, a closed system of vessels containing blood: a lifeless liquid plasma in which float detached cells, the red and the white blood corpuscles. Second, a series of spaces, channels, and vessels, closely associated with the blood vascular system, which is filled with lymph. Lymph consists of some of the liquid plasma of the blood, with some white corpuscles, which has passed through the thin walls of the smallest blood vessels and bathes the individual tissue cells. The lymphatic system really acts as an intermediary between the blood and the tissues. It supplies food materials, etc., to the cells, and finally returns the waste products to the blood vascular system. (Figs. 7, H, I, J; 115.)

The essential elements of the blood vascular system are, first, a muscular organ for propulsion of the blood, the HEART, which lies near the mid-ventral line in the anterior part of the coelom; and, second, tubes which convey the blood to the heart, the VEINS, and away from the heart, the ARTERIES. The arteries divide and sub-

FIG. 120. — Diagrammatic lateral view of the vascular system of a Shark (Dogfish). *a.br.a.*, afferent branchial artery; *au*, auricle; *br.cl. 1-5*, branchial clefts; *ca*, carotid artery; *c.art.*, conus arteriosus; *cd.a.*, caudal artery; *cd.v.*, caudal vein; *cl.a.*, coeliac artery; *cd.v.*, cardinal vein; *d.a.o.*, dorsal aorta; *e.br.a.*, efferent branchial artery; *gon*, gonad; *h.a.*, hepatic artery; *h.p.v.*, hepatic portal vein; *h.v.*, hepatic vein; *il.a.*, iliac artery; *il.v.*, iliac vein; *int*, intestine; *j.v.*, jugular vein; *k*, kidney; *lat.v.*, lateral vein; *lr*, liver; *ms.a.*, mesenteric artery; *pn*, pancreas; *pr.cd.v.*, precaval vein; *r.a.*, renal artery; *r.p.v.*, renal portal vein; *r.v.*, renal vein; *scl.a.*, subclavian artery; *scl.v.*, subclavian vein; *sp.a.*, spermatic artery; *spl*, spleen; *sp.v.*, spermatic vein; *st*, stomach; *s.v.*, sinus venosus; *v*, ventricle; *v.a.o.*, ventral aorta. Aërated, 'pure,' blood shown in red; non-aërated, 'impure,' blood shown in blue. (From Parker.)

divide to form smaller and smaller vessels (ARTERIOLES) which finally merge into exceedingly delicate tubes (CAPILLARIES) that permeate the tissues of the body. The capillaries, in turn, deliver the blood to VEINLETS which pass it on through larger and larger veins to the heart. Consequently the blood flows in a circle from heart to heart again, through a closed system of vessels. (Figs. 120, 121.)

The heart represents that part of the vascular system in which the power of rhythmic contraction has concentrated, and can be regarded as a blood vessel whose walls have become highly modified by an excessive development of the muscular layer. In the lowest Vertebrates and in embryonic stages of higher forms the heart consists typically of two chief chambers, an AURICLE and a VENTRICLE, fitted with muscular flaps, or VALVES, which allow the blood to flow in one direction only; that is, from auricle to ventricle. An enlargement, the SINUS VENOSUS, connects the veins (VENOUS SYSTEM) with the auricle, and there is frequently another, called the CONUS ARTERIOSUS, in a similar position at the arterial end. The heart is thus essentially a linear series of chambers. The sinus venosus and auricle function mainly as reservoirs to fill rapidly the especially muscular ventricle. The latter, acting both as a suction and force pump, passes the blood on to the conus arteriosus and from there to the ARTERIAL SYSTEM as a whole. For our purposes, however, we may consider the heart in the lowest Vertebrates (Fishes) as composed of the two chambers, auricle and ventricle. (Fig. 120.)

The arterial system is the distributing system of vessels which carries the blood to all regions of the body. Soon after its origin at the heart, the circuit in the aquatic forms is temporarily interrupted to allow the blood to pass through the GILLS and exchange carbon dioxide for a supply of oxygen. To facilitate this gaseous interchange, the arteries (AFFERENT BRANCHIAL) as they enter the gill membrane break up into smaller and smaller vessels which finally are of microscopic caliber and consist of but a single layer of cells. These capillaries, in turn, merge into larger vessels (EFFERENT BRANCHIAL ARTERIES) which finally lead into the chief artery of the body, the DORSAL AORTA. This extends along the median dorsal line of the body just below the vertebral column, and sends branches to the various organs.

The branches of the dorsal aorta, on reaching the location which

FIG. 121. — Plan of the vascular system of a Fish (A), Amphibian (B), and Mammal (C). 'Pure' blood, unshaded; 'impure' blood, shaded. *a*, capillaries of head region; *b*, chief arteries leading to head region; *c*, capillaries of lungs; *ca*, conus arteriosus; *d*, (in A), vessel from heart dividing up into the afferent branchial arteries of gills; *d* (in B and C), pulmonary artery to lungs; *e* (in A), artery from gills formed by union of efferent branchial arteries (capillaries of gills, connecting afferent and efferent branchial arteries, not shown); *e* (in B and C), pulmonary vein to left auricle; *f*, artery from ventricle to skin; *g*, chief artery (dorsal aorta) to posterior parts of body; *h*, hepatic artery to liver; *i*, arterial blood supply to stomach, intestine, etc.; *j*, capillaries of stomach, intestine, etc.; *k*, portal vein; *l*, blood supply to kidneys by renal arteries; *m*, capillaries of posterior extremities; *n*, renal portal vein; *o*, capillaries of the kidneys; *p*, abdominal vein; *q*, renal veins; *r*, capillaries of posterior vein; *t*, main venous current from posterior parts of body to heart; *u*, capillaries of skin; *v*, cutaneous vein; *w*, return venous current from the head region; *x*, sinus venosus; *y*, auricle in A, right auricle in B and C; *y'*, left auricle; *z*, ventricle in A and B, right ventricle in C; *z'*, left ventricle. Arrows indicate direction of blood flow.

they supply with arterial blood, break up into capillaries similar to those in the gills, and pass to the tissues the blood carrying food and oxygen. The blood receives in return various waste products of metabolism, including carbon dioxide and, in certain cases, absorbed food materials from the intestine, and special secretions chiefly from endocrine glands. The fine capillaries lead into veinlets and these into veins of constantly increasing caliber which sooner or later complete the circuit by returning the blood to the heart.

The return current, however, is not quite so simple as would appear from the above statement because, just as all the outgoing stream is interrupted for the respiratory interchange in the gills, so a part of the return current is temporarily side-tracked through the liver. The veins returning blood from the digestive organs merge to form the PORTAL VEIN which proceeds to the liver, where it resolves into capillaries to allow that organ to regulate certain of the blood constituents. These capillaries then pass the blood into the HEPATIC VEIN, which conveys it toward the heart. Thus the liver receives blood from two sources: an artery providing blood primarily for the use of the organ itself, and a vein (portal vein) delivering blood, containing a large amount of food material, solely to receive special treatment before being sent back to the heart and then all over the body. This special arrangement for a venous blood supply to the liver is known as the HEPATIC PORTAL SYSTEM.

Moreover, in Vertebrates lower than the Birds, the venous blood from the posterior part of the body makes a detour through the capillaries in the kidneys on its way back to the heart. This constitutes what is termed the RENAL PORTAL SYSTEM. Therefore in these forms the kidneys as well as the liver receive blood from two sources, an artery and a vein. It will be noted that both the hepatic portal vein and the renal portal vein arise in capillaries and terminate in capillaries. (Figs. 115, 120, 121.)

Such is the general plan of the blood vascular system of the lower Vertebrates. The modifications of this which occur in higher forms are related chiefly to changes in the respiratory mechanism necessitated by abandoning an aquatic for a terrestrial mode of life, with consequent dependence on the free oxygen of the atmosphere instead of that dissolved in the water.

B. CIRCULATION IN THE HIGHER VERTEBRATES

We may now note some of the far-reaching changes that the blood vascular system undergoes as a result of the substitution of

FIG. 122. — Diagram to show the transformation of the six pairs of primitive gill slit arteries (aortic arches) in the ascending series of Vertebrates. *A*, primitive condition, embryonic; *B*, Fish; *C*, Amphibian (Frog); *D*, Reptile; *E*, Bird; *F*, Mammal. *a*, dorsal aorta; *b*, ventral artery from heart; *c*, internal carotids; *d*, external carotids; *e*, *e'*, right and left aortic arches; *f*, pulmonary arteries; *g*, *g'*, subclavian arteries to fore limbs.

lungs for gills. In the first place the series of paired branchial arteries, which formerly supplied the gills, no longer break up into capillaries, but instead lead directly into the dorsal aorta, and

accordingly are termed AORTIC ARCHES. Thus Fishes bequeath, as it were, to higher forms a series of pairs of aortic arches which, though they are no longer of use in their former capacity, appear in the developmental stages. Some disappear at that time and others are modified and diverted to various uses in the adult. (Fig. 122.)

For our purpose it is sufficient to emphasize that in Man's body one branchial arch continues to carry blood directly from the heart to the dorsal aorta, while parts of another deliver blood from the heart to the lungs and back again to the heart. Thus there is established a second current of blood through the heart, which necessitates a median partition in both the auricle and ventricle in order to keep the two currents separate.

In this way a four-chambered heart arises which consists of right and left auricles and ventricles. The RIGHT AURICLE receives blood from the venous system of the body and passes it through the

FIG. 123. — Diagram of human heart and associated blood vessels. The direction of blood flow is indicated by arrows. (From Peabody and Hunt.)

TRICUSPID VALVE into the RIGHT VENTRICLE to be pumped through the PULMONARY ARTERY to the lungs. After traversing the capillaries of the lungs, the blood is returned by the PULMONARY VEIN to the LEFT AURICLE, thence through the MITRAL VALVE into the LEFT VENTRICLE, which forces it into the AORTA and so on its way about the body as a whole. To all intents and purposes, the higher Vertebrates have two hearts which act in unison — a right, or pulmonary, heart receiving non-aërated blood from the entire body and pumping it to the lungs, and a left, or systemic, heart receiving aërated blood from the lungs and delivering it to the body as a whole. Thus the blood vessels of the primitive aquatic respiratory apparatus are transformed by gradual additions and subtractions into the PULMONARY SYSTEM of the higher Vertebrates, including Man. (Figs. 121, C; 123.)

The blood vascular system of the higher Vertebrates, in spite, shall we say, of its makeshift origin, is a highly efficient apparatus. Day in and day out throughout life the human heart, beating rhythmically at an average rate of 70 times per minute, does about 175,000 foot-pounds of work. This power is expended in moving the weight of the blood, in imparting to it the velocity of its motion, and in maintaining pressure in the aorta and pulmonary artery. In its circulation through the body of a man, the blood passes through a series of vessels that, if they could be arranged continuously, would encircle the Earth!

The RATE of flow is greatest when the blood leaves the heart and gradually diminishes until, in the capillaries of both the pulmonary and systemic systems, it is reduced to a minimum. On

FIG. 124. — Diagram of the intimate relations between capillaries, lymphatics, and tissue cells. (From Peabody and Hunt.)

the return trip from the capillaries through the veins the rate of flow gradually increases, though it reënters the heart at a slower rate than it departed. Thus of the 23 seconds which it takes a unit of blood to make the complete circuit in Man, about two seconds are spent in the capillaries — a relatively long time when it is realized that the average length of the capillary path is about one fiftieth of an inch. The principle underlying the change in rate is simple. The blood, driven throughout its course by the same force — the heart beat — varies in rate with the width of the bed through which it is flowing. Although the area afforded individually by the arteries and veins is greater than that by any single capillary, nevertheless the total area afforded by the capillary system is enormously greater than that by either the arterial or venous system. The total surface of the capillaries of a man is about equal to the area of a city block.

Moreover, since a liquid in a closed system of tubes must flow from a region of high to one of low pressure, the blood PRESSURE continuously diminishes from heart back to heart again. But, it should be noted, that although the pressure in the capillaries of any region as a whole is greater than in the veins which they supply, nevertheless the pressure in a single capillary is very low, as is demanded by its delicate wall.

Thus it is apparent that in the capillaries the blood moves very slowly under low pressure — for it is here that the blood does its work. All the rest of the vascular system — heart, arteries, and veins — is arranged to give the blood just this opportunity in the capillaries.

It is in the capillaries that the blood vascular system turns over the work of distribution to the LYMPHATIC SYSTEM. As has been said, lymph essentially consists of plasma and white corpuscles from the blood which have passed through the thin capillary walls, carrying along food materials, oxygen, etc., to exchange for the various waste products of metabolism of the cells which it bathes. Thus there is a continuous drainage of lymph from the capillaries into intercellular LYMPH SPACES. Some of the fluid, with waste products, etc., passes immediately into the capillaries again, but the excess passes from lymph spaces into small LYMPH VESSELS, and from these into large lymph vessels. The latter, in turn, empty into the venous system and so restore the materials to the blood. (Figs. 115, 124–126.)

FIG. 125. — The superficial and some of the deeper lymphatics of the human hand. (From Hough and Sedgwick.)

With such a marvellously complex transportation system, clearly some provision must exist for regulating the blood flow in order to meet the varying local demands of the organs of the body under different physiological conditions. This is attended to chiefly by nerve impulses which are conducted by a system of VASOMOTOR

nerves and bring about the dilation or contraction of the smaller blood vessels (arterioles) leading to an organ, and thus increase or decrease the volume of the blood which it receives. Since the total volume of blood in the body is practically constant, an extra supply to one part obviously necessitates a reduced supply to another. So it happens, for instance, that after a hearty meal more blood is concentrated where digestion is actively going on, leaving less for the other organs — the reduced supply to the brain resulting in the proverbial drowsiness at such times.

FIG. 126. — Diagram to illustrate how a suitable cell environment is maintained by the flow of blood. (From Martin.)

The elaborate mechanism in HOMOTHERMAL animals (Birds and Mammals) that maintains a practically constant body temperature is largely dependent upon heat distribution, heat loss, and heat conservation by the blood vascular system. For instance, when the muscles are rapidly contracting, as in running a race, an unusually large amount of heat is being liberated by the muscle cells. This superfluous heat is carried by the blood to the skin, which becomes flushed by the distension of its blood vessels, and heat is radiated from the skin, perhaps aided by perspiration. Thus the body is losing heat, but we 'feel warm' because the sense organs that make us aware of temperature are situated in the skin. We 'feel cold' when blood is withdrawn from the skin

to the internal organs and heat is being conserved. This makes clear the apparent paradox — one is apt to 'feel warm when catching cold.'

So much for the paths and duties of the blood and lymph that circulate through the body — just enough, perhaps, to emphasize that with increase in size and complexity of the animal body there goes hand in hand an elaboration of the transportation system. It is gradually transformed to meet the new demands made upon it, and so leaves in higher forms evidence of their origin.

CHAPTER XV

EXCRETION IN ANIMALS

The mathematically accurate end-reaction of a chain of known and unknown causes and effects. — *Noyes*.

PROVISIONS for eliminating from the organism the waste products of metabolism are not less important than those for supplying the matter and energy by which the vital processes are carried on. In many of the unicellular forms the whole surface of the organism functions as an excretory organ, but it will be recalled that even in some of these, such as *Paramecium*, contractile vacuoles facilitate the removal of useless metabolic products. Indeed, in all but a few of the lowest Metazoa there are highly specialized organs devoted chiefly or entirely to excretion. In the Vertebrates we find the KIDNEYS assigned solely to excretion; the GILLS or the LUNGS, largely to excretion; and the SKIN and LIVER acting in subsidiary capacities. In nearly every case the essential parts of the excretory organ are gland cells which select from the blood supply at their disposal one or another waste product. This material they secrete in more or less changed form so that it eventually leaves the body as an excretion.

There is therefore an essential distinction between an excretion, which represents chemical waste from the vital processes, and the major part of the material which is ejected from the digestive tract as feces. The latter is almost entirely indigestible material taken in with the food which has not directly contributed to the metabolic processes of the organism. Accordingly the digestive tract is not included in the list of excretory organs, though it will be recalled that certain waste products excreted by the liver reach the outside world with the feces.

The nature and amount of the material eliminated by the excretory organs is, of course, determined by what is brought to them by the blood, and this, in final analysis, is dependent upon the food — the fuel that has been burned — and the disintegration of protoplasm from the wear and tear of life. Carbohydrates and

fats yield carbon dioxide and water, while proteins give in addition UREA, URIC ACID, CREATININE, AMMONIA, etc., the products of nitrogenous metabolism.

A. GILLS AND LUNGS

We have already emphasized the elimination of carbon dioxide by the gills or the lungs. Here the cells of the respiratory membranes play essentially a passive rôle in excretion, since the carbon dioxide, which is under higher tension in the blood than in the water or air, follows the physical laws of diffusion of gases and passes from the blood. In addition to carbon dioxide, the blood of homo-thermal animals loses a large amount of water and heat; the amount depending on the moisture and temperature of the air which enters the lungs. When the air is exhaled, its temperature is essentially that of the body and it is saturated with water vapor. In Man about one-third of the water eliminated is excreted by the lungs. (Fig. 118.)

B. SKIN

The skin of some of the lower Vertebrates, for instance the Frog, is an exceedingly important excretory organ, because more carbon dioxide is eliminated through it than through the lungs; but in most of the higher forms, including Man, excretion by the skin is confined to the SWEAT GLANDS. There are nearly three millions of them, with a total length of about eight miles, opening on the surface of the human body. They take from the blood, in addition to large quantities of water, traces of nitrogenous waste or urea, fatty acids, and salts, which form a residue on the surface of the skin when the PERSPIRATION evaporates. However, most of the water may be regarded as a secretion rather than an excretion because it is of use to the body, being employed in regulating the body temperature. Everyone knows that evaporation of perspiration accelerates the loss of heat by the skin. In addition to sweat

FIG. 127. — Diagram of a sweat gland. (From Conn and Budington.)

glands, the skin is provided with SEBACEOUS GLANDS which open, as a rule, at the base of hairs and deliver a true secretion — a lubricant for hair and skin, and a conserver of body heat. (Figs. 96, 127.)

C. LIVER

The liver, in addition to its various other functions, aids in no small way in excretion. On the one hand, the liver removes deleterious compounds of ammonia from the blood and converts them into urea. Then it secretes the urea into the blood from which it is later removed by the kidneys. On the other hand, the liver collects other waste products, etc., from the blood, which form the bile. This passes to the GALL BLADDER for temporary storage, or directly to the intestine. (Fig. 112.)

D. KIDNEYS

The kidneys are, in a way, the chief excretory organs of Vertebrates, and any serious interference with their activity rapidly leads to a poisoning of the body with its own waste products. Certain cells of the kidneys remove the urea from the blood stream which reaches them, while water and various solutes are drained from the blood. In Man about ninety per cent of the nitrogenous waste is eliminated in the form of urea. (Figs. 130, 131.)

1. *Urine*

The total excretion of the kidneys, known as URINE, passes from the kidneys through the URETERS to the URINARY BLADDER where it is stored temporarily until passed to the exterior through the URETHRA. Since urine is the medium for the elimination not only of nearly all the normal products of katabolism, but also of the majority of abnormal substances that may enter or be formed by the organism, there is no better indication of the general metabolic condition of the human body than that afforded by a chemical and microscopical analysis of the urine. Thus in Bright's disease protein appears; in diabetes, glucose (grape sugar) and other abnormal substances; while in gout the uric acid is present in abnormal quantity in the urine.

However, the interpretation of the analysis is of first importance in every case because the urine rapidly reflects normal changes in the physiological condition as well as those that are abnormal: even the nervous tension of an examination may well be evidenced

by the appearance of grape sugar. Again, the amount of urine excreted depends upon many factors. Under normal conditions with a given intake of water, the volume of urine varies chiefly with the temperature and moisture of the atmosphere. For instance, when the atmosphere is hot and dry, a relatively large amount of water is eliminated as perspiration. Accordingly the intake of water should be greater in order to carry off readily the waste products of metabolism through the kidneys.

2. *Evolution of Kidneys*

Aside from their functional importance, the kidneys are of considerable interest to the comparative anatomist because of their complicated evolutionary history — indeed the structure of the human kidneys is intelligible only in the light of the relatively simple excretory organs of Invertebrates, such as the Earthworm, and of lower Vertebrates. (Figs. 85–87, 128.)

The chief excretory organs of the Earthworm consist of pairs of coiled tubes, or NEPHRIDIA, segmentally arranged in the coelom on either side of the alimentary canal. Each nephridium begins as an open funnel in the coelom of one segment, passes through the partition to the next posterior segment and there, after coiling, passes to the ventral surface and opens to the exterior by a pore. Thus, reduced to its

FIG. 128. — Diagram to show the general structural plan of a nephridium of an Earthworm, anterior end toward the right. *a*, internal opening of nephridium; *b*, external opening; *c*, capillary network about the coiled, glandular portion.

simplest terms, a nephridium is a tube communicating between the coelom and the outer world, and affording a path of egress for the waste matter in the coelomic fluid.

But the closed blood vascular system of the worm collects various waste products in addition to the carbon dioxide which it delivers to the skin. Nitrogenous waste, inorganic salts, etc., are carried to the coiled part of the nephridial tube where gland cells take them from the blood and deliver them to the interior of the tube to be passed out of the body. Now strange as it may seem, although the primitive segmentation of the coelom has disappeared in the

FIG. 129. — Diagram of the fundamental plan of the urogenital system of Vertebrates. A, Pronephric system — primitive and early embryonic type in all Vertebrates; functional in the Frog tadpole. B, Mesonephric system — embryonic type in all Vertebrates, and adult type in the lowest Vertebrates (Cyclostomes). C, Mesonephric system and the male (σ) reproductive system in adult Fishes and Amphibians (Frog). D, the same, female (φ). E, Metanephric system, and male (σ) reproductive system in adult Reptiles, Birds, and Mammals. F, the same, female (φ). a, gonad; testis in male, ovary in female; b, cloaca or terminal portion of alimentary canal; c, pronephros, c₁, the same, vestigial; d, pronephric duct, d₁, the same, vestigial; e, mesonephros; f, mesonephric duct (originally posterior portion of pronephric duct); f₁, mesonephric duct acting also as sperm duct; f₂, mesonephric duct acting solely as sperm duct; f₃, mesonephric duct, vestigial; g, metanephros; h, metanephric duct; i, oviduct; j, uterus. See Figs. 106–109.

Vertebrates, nevertheless there are good grounds for believing that the archaic, segmentally arranged nephridia have been taken over, as it were, and made the basis of the essential excretory elements of the kidneys.

In the lowest Vertebrates the primitive type of kidney, or PRONEPHROS as it is called, consists of a series of segmentally arranged nephridia in the dorsal part of the anterior end of the coelom. These, however, instead of opening independently to the exterior, discharge their products into a common tube (PRONEPHRIC DUCT) which passes them to the outside. In higher forms the pronephros disappears, and its function is taken over by another series of nephridia which appears in the coelom posterior to the pronephros. This series constitutes the MESONEPHROS, and opens into the pronephric duct which accordingly now is called the MESONEPHRIC DUCT. Finally, in still higher Vertebrates this second urinary organ is replaced by a third, the kidney proper (METANEPHROS) and its special duct, the ureter. (Fig. 129.)

FIG. 130. — Diagram of the human urinary system. (From Peabody and Hunt.)

Thus as we ascend the Vertebrate series three distinct kidney systems appear, in each case by the development and grouping of nephridium-like elements into a definitive organ. In this process the primitive communication of the individual nephridia with the body cavity is lost and the activity of the glandular portion increased, until, in the higher forms, all the waste products are taken solely and directly from the blood. It is therefore apparent that each of the relatively large, compact kidneys of the higher Vertebrates, including Man, may be regarded as a large group of nephridium-like elements, the tubules, bound together by connective tissue and covered with a protective coat. The tubules within

the kidney deliver the materials taken from the blood, the urine to the pelvis of the kidney, from which it passes down the ureter, on to the urinary bladder, and finally to the exterior. (Figs. 130, 131.)

FIG. 131. — A. Longitudinal section of the human kidney. *Ct*, cortex, or region in which the essential nephridial elements, the tubules, come into functional association with the capillaries; *M*, medullary portion, through which the tubules extend to open on the summits of the pyramids (*Py*); *P*, pelvis of kidney; *RA*, renal artery; *U*, ureter. B. Diagram of the course of the tubules in the kidney. *r*, cortical portion answering to *Ct* in A, *k*, being close to the surface of the kidney; *g*, *p*, medullary portion, *p* reaching to the summit of a pyramid. *I*, Malpighian capsule; *II*, *V*, convoluted tubules; *III*, descending limb, and *IV*, ascending limb, of the loop of Henle; *VI*, *VII*, *VIII*, collecting tubules; *IX*, discharging tubule. (From Huxley.) C. Diagram of the blood supply to a kidney tubule. *a*, arteriole from renal artery forming a knot of capillaries (glomerulus) within a Malpighian capsule; *e*, capillaries to convoluted portion; *v*, veinlet leading toward renal vein. (After Conn and Budington.)

Such, in broad outline, is the historical viewpoint from which the kidneys of Man must be interpreted. As a matter of fact, however, the evolutionary transformation is still further complicated by anatomical, though not physiological, relations with the

reproductive system. As will be pointed out later, this neighboring system now and again foists, as it were, some of its accessory responsibilities upon parts of the excretory (urinary) system, and even takes over portions and makes them integral parts of its own when they have been permanently abandoned by the urinary system in its evolutionary development.

CHAPTER XVI

REPRODUCTION IN ANIMALS

Let us first understand the facts, and then we may seek the cause. — *Aristotle*.

REPRODUCTION, as we know, is in the final analysis cell division, whether it is binary fission in unicellular forms such as *Paramecium*, or the setting free by the multicellular organism of cells with the power of going through a complex series of changes by which they rapidly become transformed into the complex individual, similar to the parent. In most plants and animals this process is complicated at the start by sexual phenomena: the fusion of two germ cells, the male and female GAMETES, to form the fertilized egg, or ZYGOTE.

Disregarding for the time being the actual origin of the germ cells in the body, we find in the Metazoa special organs in which the germ cells reside and undergo changes preparatory to their liberation. Such reproductive organs, or GONADS, ordinarily contain germ cells of one kind, and accordingly are either OVARIES (egg-producing organs) or TESTES (sperm-producing organs).

A. INVERTEBRATES

In many of the simpler animals, the gonads are merely temporary structures which appear during certain seasons of the year when conditions favor sexual reproduction. In some species the same individual produces both eggs and sperm, in which case the sexuality of the germ cells is not reflected back, so to speak, to the organism as a whole, which accordingly is known as a HERMAPHRODITE. Such is the condition in *Hydra*, where the testes appear as small swellings in the ectoderm a little below the circle of tentacles; and the ovary, which is usually single, is a somewhat larger projection near the opposite end of the animal. Both the testis and the ovary at first appear to be a group of ectoderm cells, which in one case gives rise to many sperm and in the other to a

single egg. The mature sperm are set free from the testis and swim about in the water, but sooner or later one enters the now ruptured covering of the ovary and fuses with the egg. With the conclusion of fertilization the zygote begins to divide and forms an embryo, which at an early stage becomes detached from the parent. Thus in *Hydra* there is no complicated apparatus for sexual reproduction; merely now and again the temporary development of the primary sex organs, ovaries and testes. (Fig. 83.)

The complex bodies of most animals, however, demand more or less permanent gonads, as well as means for transferring the gametes directly or indirectly to the exterior. This is brought about by the fact that in coelomate animals the gonads come to lie, not on the outside of the body, but within the coelom. In the Earthworm, which also is hermaphroditic, the testes and ovaries are permanent organs attached to the partitions between certain segments. The sexual products are set free in the coelom, where they are taken up by SPERM DUCTS and OVIDUCTS and carried to the outside. Although each Earthworm possesses both male and female reproductive organs, two worms copulate and exchange sperm which are stored in the respective sperm receptacles. Later, when the eggs pass to the exterior, the 'foreign' sperm are shed on them. Thus cross-fertilization is insured in this hermaphroditic form. In the Crayfish the sexes are represented by separate individuals, males and females, and the appendages of the first and second abdominal segments of the male are modified into copulatory organs for the transfer of the sperm to the body of the female, where they are retained until egg-laying. (Figs. 86, 90.)

B. VERTEBRATES

Throughout all the chief Vertebrate groups the sexes are distinct, although in rare instances abnormal hermaphroditic individuals occur. The definitive primordial germ cells first appear as localized areas of the epithelium lining the coelom, on either side of the vertebral column. As the germ cells develop they become associated with connective tissue, blood vessels, and nerves and form the paired gonads. In the most primitive Vertebrates a condition more simple than in the Earthworm is found, for both male and female gametes merely break out of the gonads and find their way to the exterior by a pair of minute ABDOMINAL PORES. In higher forms, however, special sperm ducts and ovi-

ducts are developed in close relationship with the urinary system. (Fig. 132.)

In most terrestrial Vertebrates, including Man, fertilization occurs while the eggs are still within the oviducts; the copulatory organ transferring the sperm directly to the terminal portion of the ducts through which they make their way up to meet the de-

FIG. 132. — Urogenital organs of male and female Frog.

scending eggs. After fertilization the zygote may soon pass to the exterior, usually, as in the case of the familiar hen's egg, after being wrapped up in nutritive and protective coats secreted about it during its passage down the oviduct. Or, as is the case rarely among lower forms and the rule among the highest Vertebrates, the Mammals, the zygote on reaching the lower part of the oviduct may become attached to the wall of an enlargement of the oviduct, or of a chamber formed by the union of the two oviducts, called the UTERUS. Here the embryo proceeds far along in development before birth occurs. (Figs. 134, 169.)

1. Uterine Development

In the human body, the attachment of the fertilized egg in the uterus is followed by the very rapid development of what may be regarded as a new uterine lining, profusely supplied with blood vessels. This soon surrounds the embryo and, as pregnancy proceeds, the embryo protected by EMBRYONIC MEMBRANES projects

FIG. 133. — Human egg and sperm. A, four sperm (left); and egg (right) just removed from the ovary, surrounded by follicle cells of the ovary and a clear membrane. The central part of the egg contains metaplastic bodies and the large nucleus. Superficially there is a clear ectoplasmic region. (Magnified about 400 times.) B, two views of the human sperm. *c*, centrosome; *h*, head consisting of the nucleus surrounded by a cytoplasmic envelope; *m*, *ne*, middle piece; *t*, tail or flagellum. (Magnified about 2000 times.)

into, and finally completely fills the gradually increasing uterine cavity. As the uterus enlarges, it exerts increasing pressure on the adjacent organs, and later shifts higher up in the abdominal cavity where the flexible body wall more readily accommodates it. Throughout the entire period of pregnancy the embryo leads essentially a parasitic existence at the expense of the mother's body which supplies it with food and oxygen, and removes carbon dioxide, urea, and other metabolic wastes. This, of course, imposes a

considerable amount of extra work on the various maternal organs, especially the lungs, kidneys, and digestive system, and therefore special provisions must be made for this intimate interchange of materials between the blood vascular systems of mother and offspring. (Fig. 134.)

The embryo at first is nourished by materials absorbed from the rich blood supply of the uterine wall, but soon this proves in-

FIG. 134. — Diagrammatic section of the human uterus with developing embryo. The embryo (*h*) is suspended in a fluid-filled cavity (*c*) surrounded by embryonic membranes (*e*) and by tissue (*f*) from the uterus itself. The sole path of communication between embryo and mother is by blood in vessels passing up through the umbilical cord (*i*), spreading out into capillaries in the placenta (*b*) and there coming into close relations with the maternal blood supply. The openings of the oviducts (*d*) into the uterus become closed during the development of the embryo. *a*, dorsal wall of uterus; *b*, placenta; *c*, fluid-filled cavity of amnion; *d*, openings of oviducts (Fallopian tubes); *e*, embryonic membranes; *f*, uterine tissue; *g*, uterine cavity; *h*, embryo; *i*, umbilical cord.

adequate for the rapidly increasing demands of the growing embryo, and a new structure, the **PLACENTA**, is formed jointly by the uterus and embryo to meet the need. The connection of the body proper of the embryo with the placenta is by the **UMBILICAL CORD**. The blood of the embryo passes by its arteries through the

umbilical cord to capillaries in the placenta, and after interchanging wastes for food by diffusion with the blood supply in the maternal capillaries, returns to the embryo. Accordingly there is no direct intermixture of maternal and embryonic blood: the embryo from the beginning is a separate organism whose blood supply interchanges materials with that of the mother through the placenta. This temporary dependence is terminated when the child is expelled from the uterus, or born.

Thus, except in the simplest animals, there is a special reproductive system: a series of organs connected with the reproductive function. But it must be emphasized that the essential organs are the gonads themselves and all the rest are accessory. Furthermore, in relation to the sexual differentiation of male and female individuals, many so-called SECONDARY SEXUAL CHARACTERS arise which are not directly connected with the reproductive organs, but nevertheless depend very largely for their development upon HORMONES liberated by the gonads. For example, early castration of the Stag inhibits the growth of a distinctive male secondary sexual character, the antlers; while if performed later when the antlers are full grown, they are shed and abnormal ones take their place. Similarly, the development and functioning of the mammary glands during pregnancy in the human female is induced by hormones produced, not by the ovary itself, but by its product, the developing embryo within the uterus. Here at least two hormones are involved; one directly stimulates the development of the glands, while another prevents their active functioning until it is removed by the birth of the offspring.

2. *The Urogenital System*

We must now outline the structural interrelations of the urinary and reproductive organs forming the UROGENITAL SYSTEM. It has been pointed out that the nephridia, which combine to form the kidneys in some of the lower Vertebrates, retain their funnel-like openings into the coelom and therefore afford a direct exit for waste material in the coelomic fluid. It is some of these nephridia which are employed in the lower Fishes for the transfer of the germ cells to the outside. The testes of the male, which lie close to the kidneys, become connected with the nephridia (mesonephros) by a series of short delicate tubes. Through these tubes the SPERMATIC FLUID, containing the sperm from the testes, is transferred to the

nephridia and by them to the kidney (mesonephric) ducts and so to the exterior with the urinary waste. In this way, during the period of sexual activity of the male, the kidney tubules satisfactorily perform two functions, and the mesonephric ducts become UROGENITAL CANALS. (Fig. 129, C.)

Turning to the female, we find that the ovaries, which are situated in about the same position with relation to the kidneys as the testes in the male, do not enter into communication with a set of nephridia of the kidneys (mesonephros); probably because the eggs are too large to pass through the tubules. Instead, what appears to be the coelomic opening of a single nephridium-like structure on either side (which fails, so to speak, to enter the kidney complex) enlarges and becomes the funnel which connects up with a new duct opening into the cloaca. Thus there arises from the female urinary system a pair of entirely distinct oviducts. An egg, liberated from the ovary into the coelom, finds its way into one of the oviducts and descends directly to the outside, or into an enlargement (uterus) of the terminal portion of the duct where development proceeds until birth occurs. (Fig. 129, D.)

The female reproductive system, though derived from the mesonephric system, has become entirely independent of it. Accordingly the disappearance of the mesonephros and duct in higher Vertebrates, when it is replaced by the metanephros and the ureter as the functional urinary system, has little effect on the female reproductive system. As a matter of fact, the abandoned mesonephros and duct degenerate and disappear in the female, while in the male the mesonephric duct remains and becomes completely appropriated by the reproductive system. The sperm now pass directly into the former mesonephric duct, which thereby becomes solely a sperm duct. (Fig. 129, E, F.)

Such is the historical origin of the foundations of the reproductive system as it occurs in the Reptiles, Birds, and Mammals. Each of these groups, building on this foundation, has developed modifications and additions demanded by its special lines of evolution. Nature, whenever possible, apparently turns to structures at hand to construct what is to be, and thereby weaves in the woof and warp of higher forms a record of their ancestry.

CHAPTER XVII

COÖRDINATION IN ANIMALS

It seems that Nature, after elaborating mechanisms to meet particular vicissitudes, has lumped all other vicissitudes into one and made a means of meeting them all. — *Mathews*.

SINCE a primary attribute of protoplasm is irritability — the power of responding to environmental changes by variations in the equilibrium of its own matter and energy — it is not strange that the cells of an organism mutually influence each other's activities and reciprocal interrelationships have been established during their long evolutionary history. The various cells, tissues, organs, and organ systems are unified into an organism by what may be called the chemical interplay between its various parts, which is made possible by the facilities for distribution afforded by the circulatory system; and also by the directing influence of the nervous system which supplies a central station with lines for instantaneous intercommunication with every part of the body.

A. CHEMICAL COÖRDINATION

It is only with the recent increase in knowledge of the general problem of metabolism that the far-reaching importance of the chemical control of bodily processes has gradually been brought to the fore. Although we may properly think of the various chemical regulators, or HORMONES, as forming a coördinating system in so far as their collective action has such a result, in the present stage of our knowledge it is possible to cite only the specific action of individual hormones as examples of the general method of chemical regulation which their study, ENDOCRINOLOGY, is revealing.

Certain hormones are elaborated by special cells imbedded in organs, such as the pancreas and reproductive organs, largely devoted to other functions. Other hormones are secreted by organs whose sole function is their production, such as the various ductless, or endocrine, glands.

As an example of a hormone secreted by specialized cells within the tissue of an organ devoted primarily to other functions, we may select **INSULIN** which reaches the blood directly from the pancreas, and is not delivered with the other secretions of this organ to the intestine through the pancreatic duct.

Diabetes has long been known to be the result of an abnormal condition of the pancreas producing a lack of coördination of the chemical processes by which the body uses carbohydrates to supply energy. The storage of sugar by the liver is unregulated. Evidences of this disease are chiefly an increase in the sugar content of the blood and the presence of sugar in the urine. Now we know that a close approach to the normal metabolic condition can be attained by administering to diabetics the hormone insulin extracted from the pancreas of sheep or other animals. Insulin thus takes the place of the secretion which the diseased pancreas fails to afford, and so removes the pall of hopelessness from many of the most acute and desperate cases of diabetes.

Turning now to a gland devoted solely to the secretion of a hormone, we may select the thyroid which, as has been seen, arises as an outpocketing of the digestive tract in the neck region and finally loses all connection with its point of origin and becomes a ductless gland. (Fig. 110.)

The general effect of the thyroid hormone, **THYROXINE**, on metabolism is a regulation of the rate of oxidation in the body to meet changing physiological demands. An excess of thyroxine induces such vigorous fuel consumption that no surplus remains in the body to be stored as fat; while a deficiency in the glandular secretion results in a tendency toward fat formation. Accordingly the administration of thyroid extract or thyroxine is often an efficient means of reducing fat by increasing the oxidative processes of the body. A deficiency of the hormone during adult life frequently results in a type of mental deterioration called **MYXEDEMA**. Children in whom the development of the thyroid is suppressed become dwarfish idiots known as **CRETINS**, while overdevelopment of the gland induces increased nervous activity and mental disorders. Feeding with thyroid material prevents or retards the development of cretinism and cures myxedema, while a surgical removal of part of the gland may cure the nervous instability and other symptoms due to an excessive amount of the hormone. **GOITER** is a pathological enlargement of the thyroid

due to a deficiency in iodine needed to manufacture its iodine-containing thyroxine.

The almost uncanny potency of hormones in general will be evident from the fact that about 1/30,000th of an ounce of thyroxine is sufficient to induce a two per cent increase of the total oxidation of the resting adult human body. The amount of thyroxine required by the body during a whole year is less than 1/11th of an ounce, while the amount in use at any one time is approximately 1/176th of an ounce. "But this pinch of material spells all the difference between complete imbecility and normal health"—a fact that should give pause not only to the biologist but also to the sociologist.

Finally as a further indication of the nicety of the reciprocal adjustments within the organism, it may be mentioned that the thyroid gland itself is subject to regulating stimuli reaching it through the nervous system, and also, apparently, by a hormone derived from the PITUITARY BODY which is another endocrine gland situated in conjunction with the lower part of the brain. Glimpses of such interrelationships are being gradually afforded as one hormone after another is discovered and studied.

FIG. 135. — Neuromotor apparatus of *Paramecium*. Side view showing the 'fibers' arising from a 'coördinating center' situated above the mouth. (Modified, after Rees.)

B. COÖRDINATION BY THE NERVOUS SYSTEM

Although hormones are indispensable as a means of regulating many of the processes of the organism, especially the slower ones such as growth, they are entirely inadequate for the instantaneous correlation of diverse parts of an animal and also for the adjustment of the whole animal to its surroundings. This need is supplied in the Metazoa by the NERVOUS SYSTEM: a complicated arrangement of cellular elements in which irritability and conduction are highly developed.

Even in some unicellular organisms certain portions of the protoplasm are especially differentiated for receiving and conducting stimuli, and others for making effective such stimuli by contractions of the whole or parts of the cell. Indeed, *Paramecium* and

its allies apparently possess a NEUROMOTOR apparatus. But it is in the lower Metazoa, such as Hydra and its allies, that we find the establishment of definite NERVE CELLS, some of which are specialized for receiving stimuli and others for conducting the excitation to cells specialized for contracting (muscle cells), etc. Thus a simple RECEPTOR-EFFECTOR system arises which may be regarded as the basis for the development of the elaborate NEURO-MUSCULAR MECHANISM of higher forms. Although from the functional point of view it is impossible to differentiate the receiving

FIG. 136. — Diagram of a simple type of receptor-effector system, found in some Hydra-like animals. It comprises receptors (*b*), or sense cells, reaching to the body surface (*a*), with basal nerve net (*c*) connecting with muscle cells (*d*). (Slightly modified, after G. H. Parker.)

FIG. 137. — Diagram of a more complex type of receptor-effector system, found in some Hydra-like animals. It comprises, in addition to the receptor (*b*) with nerve net (*c*) and the muscle cells (*e*), another nerve (ganglion) cell (*d*) interpolated in the nerve net. *a*, body surface. (After G. H. Parker.)

and conducting elements from those which make them effective (muscular system) in the economy of the organism, from the standpoint of anatomy the former constitutes a definite entity, the nervous system proper. (Figs. 135-137.)

The structural elements of the nervous system of all animals consist of cells known as nerve cells, or NEURONS. In the lower forms these cells are permanently united so that they form NERVE NETS which surround and permeate the tissues which they stimulate to action. In more highly developed animals the net arrangement is relegated to the control of relatively minor functions (Fig. 140), while the main nervous system consists of neurons arranged in groups, or GANGLIA, and prolongations of the neurons, or nerve

FIBERS, bound together into cables, or NERVES. The neurons, which are imbedded in protective sheaths of connective tissue in the ganglia, are in physiological continuity one with another by 'transmitting contacts,' or SYNAPSES; but each neuron, it is believed, remains structurally distinct. (Figs. 138, 139.)

1. Brain and Spinal Cord

It will be recalled that the first great differentiation during the development of a multicellular animal establishes an outer ectoderm and inner endoderm, and thus separates the functions of protection and general reactions to the environment from that of nutrition. It is natural therefore that the ectoderm should become the seat of those specializations which have evolved into the nervous system and sense organs. Such is the case in all forms from the lowest to the highest, and thus the development and comparative anatomy of the nervous system of Vertebrates, in particular, affords strong evidence of the genetic continuity of the whole series, including Man.

In the development of a Vertebrate, the first indication of the nervous system is a longitudinal *groove* in the ectoderm along the dorsal surface, which soon becomes converted into a *tube* by the apposition and, finally, the fusion of its edges. This NEURAL TUBE then becomes separated from, and sinks below the surface ectoderm, and in time forms the CENTRAL nervous system consisting of the BRAIN and SPINAL CORD. As development proceeds, outgrowths from the central nervous system establish the PERIPHERAL and the AUTONOMIC nervous systems, so that structurally as well as physiologically the whole nervous system represents a unit; a single organ, as it were, which secondarily becomes closely identified here and there with sense organ, muscle, or gland, as the case may be. (Figs. 143, 174.)

FIG. 138. — Diagram of stages in the differentiation of nerve cells (neurons). A, primitive neuron from the nerve net of Hydra-like animals; B, motor neuron of the Earthworm; C, a primary motor neuron of a Vertebrate. In B and C the nerve impulse passes from below upward. (After G. H. Parker.)

The first marked structural modifications in the developing central nervous system of Vertebrates are two constrictions of the enlarged anterior end of the neural tube, which establish the three primary brain vesicles: FORE-BRAIN, MID-BRAIN, and HIND-BRAIN. Thus very early in embryonic development, one end of the neural tube is molded into the brain, leaving the rest to become the spinal cord. (Fig. 141.)

The three-vesicle brain now becomes transformed into one of five vesicles by a hollow outpocketing from the anterior end of the fore-brain and a dorsal outpocketing from the hind-brain. In some of the lowest Vertebrates the brain throughout life consists of these

FIG. 139. — Diagram of a primary sensory (*sf*) and motor (*mf*) neuron of the ventral nerve cord of an Earthworm, showing their connections with the skin (*ep*) and the muscles (*lm*) to form a simple reflex arc. *cm*, circular muscles; *ep*, epidermis; *lm*, longitudinal muscles; *mc*, motor neuron cell body (in a ventral ganglion), with fiber (*mf*); *sc*, sensory neuron cell body with fiber (*sf*) entering ganglion to form synapses with processes of motor neuron. See Fig. 87. (After G. H. Parker, and Retzius.)

divisions, known as TELENCEPHALON, DIENCEPHALON, MID-BRAIN, CEREBELLUM, and MEDULLA OBLONGATA, the latter merging into the spinal cord. Usually, however, the telencephalon gives rise to a pair of CEREBRAL HEMISPHERES, which are destined gradually to overshadow in size and importance all the other parts of the brain and to become the seat of consciousness as well as of the higher mental life in general.

Finally, the development from the telencephalon or its derivatives, the cerebral hemispheres, of a pair of OLFACTORY LOBES completes the establishment of the chief brain chambers. The further changes which transform the more or less linear series of vesicles into the increasingly complex and compact brain of higher forms are due to bendings, or FLEXURES, and to unequal thicken-

ings and outgrowths of the chamber walls. For instance, the upper and lower surfaces of the diencephalon give rise to the PINEAL BODY and the INFUNDIBULUM respectively, while from similar regions of the mid-brain are developed the OPTIC LOBES and CRURA CEREBRI. Hand in hand with these changes the primary cavities of the chambers undergo a gradual restriction, but throughout all there persists at least a remnant of the original tubular cavity which is continuous with that of the spinal cord. (Figs. 109, 142.)

2. Cranial and Spinal Nerves

The brain and spinal cord are, as we know, protected and isolated by a cartilaginous or bony tube, formed by the skull and neural arches of the vertebrae, which is imbedded in the muscles forming the dorsal part of the body wall. The sole paths of nervous communication between the central system and the rest of the organism and its surroundings are a series of pairs of CRANIAL and SPINAL NERVES. These arise at fairly regular intervals from one end of the brain and cord to the other, and pass out through openings in the skull and between or through the vertebrae to constitute the PERIPHERAL nervous system. (Fig. 143.)

It is usually considered that the primitive segmental condition of the Vertebrate body is well exhibited in the arrangement of the cranial and spinal nerves, and that the origin of the cranial nerves from the brain affords a partial index to the primary series of segments which apparently have been merged to form the Vertebrate head. Conditions as they exist at the present time can perhaps be most readily understood by imagining a simple, ancestral

FIG. 140. — Diagram of a section (highly magnified) of the wall of the intestine of a Vertebrate to show its *intrinsic* nervous organization which brings about the movements of the tube. The two plexuses consist essentially of simple neurons arranged as nerve nets. *a*, food absorbing surface of the intestine; *b*, mucous layer; *c*, plexus of neurons (submucous); *d*, circular muscle; *e*, plexus of neurons (myenteric); *f*, longitudinal muscle; *g*, serous layer. (From Parker, after Lewis.)

segmented worm-like form in which the dorsal neural tube gives off a pair of nerves to each segment of the body. As the result of a gradual shifting forward, union, and finally complete fusion of

FIG. 141. — Diagrams to illustrate the general method of transformation of the anterior end of the neural tube into the brain. A, B, C, median vertical sections; D, dorsal view of C. *a*, fore-brain; *b*, mid-brain; *c*, hind-brain; *d*, telencephalon; *e*, diencephalon; *f*, cerebellum; *g*, medulla oblongata; *h*, cerebral hemispheres; *i*, olfactory lobes; *j*, pineal body; *k*, infundibulum.

certain segments near the anterior end, there is formed a head region with its brain, battery of sense organs, and skull, more or less distinct from a trunk region with its spinal cord, vertebral column, paired limbs, etc. This naturally involves a corresponding shifting and modification of the primitive condition of the paired

FIG. 142.—Dorsal view of the brain of A, bony Fish (Perch); B, Amphibian (Frog); C, Reptile (Alligator); D, Bird (Pigeon); E, Mammal (Cat). *a*, olfactory lobes; *b*, cerebral hemispheres; *c*, pineal body; *d*, optic lobes; *e*, cerebellum; *f*, medulla; *g*, spinal cord.

nerves; especially since the innervation of a group of cells in normal development is apparently rarely changed — a nerve following the part which it originally supplied through many of the transformations and even migrations of the latter.

If this point of view is accepted, the cranial and spinal nerves are, historically considered, similar structures. But the former, synchronously with the changes in the head region, have departed somewhat widely from their ancestral condition and have even been augmented by nerves of diverse origin. The spinal nerves, on the other hand, continue to issue from the cord at about equal intervals and in segmental arrangement as indicated by muscle segments and skeletal structures, although those of certain regions unite in the body cavity to form groups, or PLEXUSES, to afford an adequate nerve supply to the appendages.

From the standpoint of function the nerves are of two classes, SENSORY and MOTOR. The former are distributed mainly to the skin and sense organs of the head, and are the paths over which excitations (NERVE IMPULSES) due to external stimuli are conducted to the cord and brain. The motor nerves, on the other hand, are the media for distributing impulses from the

FIG. 143. — Ventral view of the nervous system of the Frog. *Br*, second and third spinal nerves (brachial plexus); *Js*, sciatic nerve leading from the sciatic plexus; *O*, eye; *Ol*, olfactory nerve; *Op*, optic nerve; *Sg 1-10*, ten ganglia of autonomic system; *Spn 1*, first spinal nerve; *Sp 4*, fourth spinal nerve; *Vg*, trigeminal ganglion; *Xg*, ganglion of 10th cranial nerve (vagus). (After Ecker.)

brain and cord to muscle cells, gland cells, etc., and thus induce the response of the organism.

In discussing nerves, it must be kept in mind that a nerve is actually a bundle of nerve fibers; the fibers themselves in turn being prolongations of nerve cells, the cell bodies of which are usually in groups, or **GANGLIA**. Moreover, nerve impulses are not transmitted by a nerve as a whole, but by one component cell process, a nerve fiber; that is, by way of a definite cell path through the nerve. The same is equally true of the cord and the brain,

FIG. 144. — Diagram of a section of the spinal cord to show the paths of nerve impulses. *c.c.*, central canal; *col.*, collateral fibers; *c. cort.*, cells of the cortex of the cerebral hemispheres of the brain; *c.g.*, smaller cerebral cells; *d.c.*, cells in dorsal part of gray matter; *d.r.*, dorsal root of spinal nerve; *g.*, ganglion of dorsal root; *g.c.*, cell body of sensory neuron; *g.m.*, gray matter of cord; *M.*, muscle; *m.c.*, nerve cell in medulla; *m.f.*, fiber (axon) of motor neuron; *s.*, sensory surface; *s.f.*, fiber of sensory neuron; *s.p.c.*, spinal cord; *v.c.*, cells in ventral part of gray matter; *v.r.*, ventral root of spinal nerve; *w.m.*, white matter of cord. The arrows indicate the direction of the impulses. (After Parker and Parker.)

which differ from nerves largely in that they comprise more cell processes and also the cell bodies themselves. In other words, the brain and cord comprise the elements of both ganglia and nerves.

A given nerve may conduct impulses both to and from the central organ if it contains *afferent* and *efferent* cell paths, or fibers. As a matter of fact all the peripheral nerves primarily are **MIXED** nerves, because typically they arise by two roots from the central organ; the **DORSAL ROOT** containing only sensory (afferent) fibers and the **VENTRAL ROOT** only motor (efferent) fibers. This condition is preserved by the spinal nerves of higher forms since each arises by two roots. But some of the cranial nerves, in response to the

profound modifications that have been wrought in the head region, have only one root, and so are either solely sensory, as those to the sense organs, or only motor, as those innervating the muscles which move the eye. (Fig. 144.)

3. *Autonomic System*

So far we have considered the central system — the brain and spinal cord; and its lines of communication with the body as a whole, the peripheral system — the cranial and spinal nerves. In point of fact, however, the peripheral system gives rise to an auxiliary series of ganglia and nerves which are charged with the regulation of certain of the internal organs, particularly the alimentary canal and arteries that are not directly under voluntary control. This AUTONOMIC SYSTEM in the higher Vertebrates consists essentially of a double nerve chain situated chiefly within the coelom just ventral to the spinal column. It communicates with the central system by way of the sensory roots of the spinal and some of the cranial nerves. (Fig. 143.)

Such in essence is the distribution throughout the body of the nervous system which, although it arises as an infolding of the ectoderm and therefore is primarily external, comes to be internal and so chiefly dependent upon more or less isolated groups of SENSORY cells for the reception of stimuli. Some of these, termed EXTERNAL RECEPTORS, remain at the surface to receive stimuli from the outer world, while others, known as INTERNAL RECEPTORS, are situated within the body for the reception of stimuli arising there. The external receptors are what one ordinarily thinks of as sense organs.

C. SENSE ORGANS

Although among some of the Protozoa certain regions of the cell are specialized so that they are more sensitive to one or another kind of stimulation, the great majority show no trace of sense organs. Nevertheless all forms, in common with all protoplasm, possess the power of receiving and responding to environmental changes. Thus Paramecium reacts to mechanical, thermal, chemical, and electrical stimulation: the entire surface of the cell is sensitive to stimuli, and the excitations are conducted from one part to another essentially by the protoplasm as a whole, aided apparently by the neuromotor apparatus. In some Invertebrates,

such as *Hydra* and the Earthworm, the entire surface of the body is still depended upon as a receiving organ for all kinds of stimuli, and only simple sense cells are developed. In the majority of animals, however, although all the cells, of course, retain to some extent their power of irritability, environmental changes exert their influence chiefly upon complex receptors, which are specialized to respond most readily to particular forms of energy. The energy, for example of heat or light, is transformed by appropriate mechanisms into the energy of a nerve impulse, and accordingly the sense organs constitute the outposts of the nervous system.

Since we necessarily gain our knowledge of the outside world solely through the data afforded by our sense organs, it follows that we judge the capacity of the sense organs of other animals merely by comparing them with our own. This is a safe procedure only in the case of sense organs that more or less correspond in structure to those which we possess. In the Crayfish, for example, we find complex sense organs which, without doubt, are eyes, and others which are ears, or at least perform one of the functions of our ears, equilibration; while some of the head appendages are particularly adapted to receive sensations of touch. The senses of smell and taste are also probably present, but here we are on less sure ground.

It is, indeed, almost certain that environmental changes which are without effect on the sense organs of the human body, and so play no recognizable part in the 'world' of Man, may stimulate receptors in lower organisms. But Man's ingenuity has in certain cases devised apparatus to minimize his limitations: witness the radio receiver.

The simplest form of sense organ in Vertebrates is a single epithelial cell for the reception of stimuli, connected with a nerve fiber for the conduction of the nerve impulse to a sensory center.

FIG. 145. — Diagram of stages in the differentiation of sense cells. A, primitive sensory neuron of *Hydra*-like animals; B, sensory neuron of a Mollusc; C, primary sensory neuron of a Vertebrate. In each case the sensory surface is represented below, and therefore the nerve impulse passes upward. (After G. H. Parker.)

Usually, however, many associated cells are arranged to respond and are aided by accessory structures for intensifying the stimulus, protection, etc., so that the whole forms a highly complex sense organ. (Figs. 145, 150.)

1. *Cutaneous Senses*

Confining our attention to the Vertebrates, we find that practically the entire surface of the body constitutes a sense organ, because the skin is permeated with a network of sensory nerves. Certain regions are supplied with special PRESSURE RECEPTORS, which may take the form of a regular system of sense organs, such as the LATERAL LINE ORGANS of Fishes and Amphibians, or of groups of TACTILE CORPUSCLES as in Man. In addition to pressure receptors, the whole surface of the human body is provided with PAIN, HEAT, and COLD SENSE SPOTS.

2. *Sense of Taste*

In the higher Vertebrates the sense of taste is restricted to the cavity of the mouth, particularly to the tongue, where special

FIG. 146. — A, Cells of olfactory epithelium from human nose. B, Cells of a taste bud in epithelium of tongue. The sensory cells terminate externally in hair-like processes that are able to receive the chemical stimuli of smell or taste. *ep*, epithelium of tongue; *gc*, gustatory cell; *oc*, olfactory cell; *p*, pore or external opening of epithelial cup in which the taste bud is located; *sc*, supporting non-sensory cell. (From Curtis and Guthrie.)

receptors known as TASTE BUDS are in communication with the brain by two of the cranial nerves; but in some Fishes they are scattered quite generally, so that the whole body surface is sensitive to such qualities as sweet, sour, and salt. (Fig. 146.)

3. Sense of Smell

The special sense organs of smell, or **OLFACTORY BUDS**, reside in the membrane which lines a pair of invaginations of the anterior end of the head, termed **OLFACTORY POUCHES**. The buds are in communication with the brain by the olfactory, or first pair of cranial nerves. The pouches constitute relatively simple sacs in the lower Vertebrates, but in the air-breathing forms, and especially in the Mammals, the walls of the pouches are thrown into folds, ridges, and secondary pouches. This is necessitated by the concentration of the olfactory surface to the air passages of the **NOSE** which lead to the lungs. However, in Man the olfactory apparatus has fallen somewhat from the complexity which it attains in the lower Mammals, as is attested not only by its structure in the adult but also by transient remnants in the human embryo. (Fig. 146.)

4. The Ear

The **EARS**, or organs of hearing and equilibration, arise as paired depressions of the ectoderm of the head, which, in all Vertebrates above the lower Fishes, lose their connection with the exterior and form the so-called **INNER EAR**, or **LABYRINTH**. This becomes divided into two chief parts, the **SACCULUS** and the **UTRICULUS** from which are developed three **SEMICIRCULAR CANALS**, one in each plane of space. The sacculus is largely devoted to the reception of vibrations of the surrounding medium, that is to hearing in the usual sense of the word. Accordingly the sacculus becomes progressively differentiated as we ascend the Vertebrate scale — a complex derivative in the mammalian ear being the **COCHLEA**.

On the other hand, the utriculus and the semicircular canals provide for sensations of loss of equilibrium, or orientation of the body in space, and show far less change. It is probable that

FIG. 147. — Semidiagrammatic figure of the left membranous labyrinth of a lower Vertebrate to show the sacculus (*s, l*), utricle (*u, rec*), and the three semicircular canals (*aa, ca; ae, ce, and ap, cp*). *l*, lagena, a derivative of the sacculus which becomes the cochlea in higher Vertebrates; *cus*, utriculo-sacculus canal; *de, se*, endolymphatic duct and sac; *as, sp, ss*, utricular sinuses. (After Wiedersheim.)

equilibration is the chief function of the entire labyrinth in Fishes, as it is of the so-called auditory organs of many Invertebrates, such as the Crayfish. With the progressive specialization of the labyrinth, the essential sensory cells, which are in communication with the brain by the eighth, or AUDITORY NERVE, become limited to a few definite areas. These sensory cells are provided with auditory hairs which project into the cavity of the labyrinth and so are stimulated by movements of the fluid which fills it. (Fig. 147.)

The ears of Fishes lie immediately below the skull roof, where they are readily accessible to vibrations transmitted by the water.

FIG. 148. — Front view of the human organ of hearing, right side. *a*, pinna of outer ear; *b*, bone of skull; *c*, *d*, *l*, transmitting mechanism of three bones — malleus, incus, and stapes; *e*, one of the three semicircular canals; *g*, vestibule; *h*, auditory nerve; *i*, cochlea; *j*, Eustachian tube leading to the throat; *k*, tympanic chamber or middle ear; *l*, stapes; *m*, tympanic membrane; *n*, external auditory passage, or outer ear; *o*, cartilage.

But with the substitution of air for water as the surrounding medium, there arises the necessity of a more delicate method for conducting and also for collecting and augmenting the sound waves. The result is that, in ascending the Vertebrate series, we find the ear proper receding farther and farther below the surface.

Soon, between the labyrinth, or inner ear, and the surface of the head, a simple resonating chamber is added which is provided with a vibrating TYMPANIC membrane, or EAR DRUM, situated just under the skin. Then this is improved by the development of a bony transmitting mechanism between the tympanic membrane and the inner ear. This consists of a single bone until we reach the Mam-

mals, when two more bones are added by being diverted from their earlier function of articulating the jaws with the skull! Finally, the resonating (tympanic) chamber recedes farther below the surface and becomes the MIDDLE EAR to which sound waves are conducted through a tubular passage, the OUTER EAR. In some forms, as in Man, there is an external funnel-like collecting appendage, the PINNA. Nature apparently accomplishes much by accumulating minute changes during the ages. (Fig. 148.)

5. *The Eye*

The organs of sight are the most complex sense organs of animals and reach a very high degree of specialization even in some of the Invertebrate forms. Among the latter the essential sensory element (RETINA) of the eye usually arises by the invagination of a limited area of ectoderm, the cells of which become differentiated for receiving the photic stimuli that produce nerve impulses to be transmitted to the central nervous system. Among Vertebrates the sensory cells are also of ectodermic origin, but only secondarily so, since the OPTIC VESICLES arise as outpocketings directly from the sides of the fore-brain. (Fig. 149.)

A retina alone such as exists in some of the lower Invertebrates can afford no visual sensations other than light and darkness, and perhaps in some cases the ability to distinguish light of one color from that of another. In order that not merely degrees of the intensity of light may be perceived, but that objects may be seen, many of the higher Invertebrates have developed various kinds of complicated apparatus for bringing the rays from a given point to a focus at one point on the retina. These culminate, on the one hand, in the compound eye of the Arthropods; and on the other, in the 'camera' eye of certain Molluscs such as the Squid. In the latter case the mechanism is very much like that found in the Vertebrates, but since it occurs in Molluscs which cannot be considered in the direct evolutionary line of the Vertebrates, it affords an example of similar responses of different organisms to similar needs giving rise to *analogous* structures. (Fig. 150.)

The wall of the Vertebrate eye, or EYEBALL, forms a more or less hollow sphere which can be rotated by several relatively large muscles. The anterior exposed part of the eyeball consists of two transparent layers: the delicate CONJUNCTIVA, continuous with the inner lining of the eyelid, and the rigid CORNEA beneath. The sides

FIG. 149. — Diagrams illustrating the method of formation of the eye of an Invertebrate (A) and a Vertebrate (B, C, D, E, — successive stages). Note that the *opposite* surface of the retinal cells is exposed to the light rays in the Vertebrate as compared with the Invertebrate eye. *a*, ectoderm; *b*, retinal area; *c*, future position of optic nerve; *d*, cavity of the diencephalon; *e*, optic vesicle; *f*, stalk of optic vesicle later replaced by the optic nerve; *g*, vitreous chamber within optic cup; *h*, developing lens.

and posterior part are also composed of two layers, the outer **SCLEROTIC** coat and the inner **CHOROID** coat. Suspended within the eyeball is the **LENS** which divides the cavity into two chief parts; the one posterior to the lens, known as the **VITREOUS CHAMBER**, being lined by the retina whose nerve cells supply the nerve fibers forming the **OPTIC**, or second cranial nerve.

FIG. 150. — The Vertebrate eye (human). A, vertical section of the eye *in situ*. B, horizontal section to show relation of optic nerve to fovea centralis through which the optical axis passes. *a*, eyelash; *b*, lid; *c*, bony orbit; *d*, superior rectus, one of the six muscles which revolve the eyeball; *e*, muscle to upper lid; *f*, optic nerve (bundles of fibers cut obliquely); *g*, inferior rectus muscle of eyeball; *h*, anterior chamber filled with aqueous humor; *i*, pupil opening to posterior chamber, also filled with aqueous humor, between iris and lens; *j*, conjunctiva, a transparent membrane, continuous with the lining of the eyelid; *k*, cornea; *l*, iris; *m*, lens; *n*, suspensory ligament of lens; *o*, retina; *p*, choroid coat; *q*, sclerotic coat; *r*, muscles to ligament suspending lens; *s*, vitreous chamber containing vitreous humor; *t*, point of entrance of optic nerve (blind spot); *u*, fatty connective tissue; *x*, fovea centralis at posterior end of axis of eyeball.

The Vertebrate eye is an optical apparatus that may be compared roughly with a camera, but this conspicuous difference must be noted. A camera is focussed by altering the distance between the lens and the film, whereas the eye is focussed by changing the curvature of the lens. Thus light waves passing through the conjunctiva, cornea, and an opening (**PUPIL**) in a regulating diaphragm (**IRIS**), reach the lens and are focussed on

the retina. The sensory stimulation thus brought about is transmitted by the optic nerve to the brain. The brain itself interprets the nerve impulses and composes — 'sees' — the picture. How this is done, nobody knows. (Fig. 151.)

A broad survey of the sense organs of Vertebrates from the lowest to the highest impresses one with the fact that, taken by and large, the improvements, though considerable, are not so marked

FIG. 151. — Diagram of the nervous elements in the Vertebrate retina (human). *gr*, *gr'*, granular layers; *nc*, *nc'*, *nc''*, *nc'''*, nerve cells; *nu''*, nuclear layer of rods and cones; *on*, fibers of optic nerve; *r*, sensory cells (rods and cones). The tips (*r*) of these are imbedded in a pigmented layer (not shown) which is the retinal layer farthest from the vitreous chamber, and in contact with the choroid coat. (After Stöhr.)

as one might expect when the great development of the nervous system, particularly the brain, is considered. The brain increases enormously in volume and complexity from Fish to Man. In many Fishes it seems to be little more than a slight modification of the anterior end of the spinal cord, while in the Frog the brain and cord weigh about the same. But the human brain weighs about three pounds, nearly fifty times as much as the cord, and comprises some twelve thousand million nerve cells. So apparently

we must look to the general influence of the sensory stimuli themselves for the underlying factor in the development of the brain during its long evolutionary history — the brain, in turn, being enabled to make more out of the same stimuli and create in Man the higher mental life with all that it implies. It is, indeed, an appalling thought that all human mental states are represented by a few thimblefuls of cells constituting the cerebral cortex of the brain — and when their activities go astray, insanity.

CHAPTER XVIII

ORIGIN OF LIFE

The mystery of life will always remain. Science is not the death, but the birth of mystery, awe, and reverence. — *Donnan*.

A GENERAL background of biological facts and principles has now been established, and we are therefore in a position to take up from an advantageous viewpoint some of the broad questions raised by the science. For its antiquity as well as its universal interest, the problem of the origin of life takes precedence.

A. BIOGENESIS AND ABIOGENESIS

It must seem strange to the reader, with some of the complexities of organisms before him, that the best minds up to the seventeenth century saw nothing more remarkable in the spontaneous origin of plants and animals of all kinds from mud and decaying matter, than does the boy of to-day who believes that horse hairs soaked in water are transformed into worms. As a matter of fact, we find that even Aristotle, who laid such broad foundations for the science and philosophy of the organism, believed that certain of the Vertebrates, such as Eels, arose spontaneously.

Similar ideas are voiced repeatedly through more than twenty centuries by scientists and philosophers, poets and theologians. Van Helmont, one of the founders of chemical physiology during the seventeenth century, gives particularly specific directions for the experimental production of scorpions and mice; while Kircher actually figures animals that he states arose under his own eyes through the influence of water on the stems of plants. The following ironical reflections, aroused by Sir Thomas Browne's doubts in regard to mice arising by putrefaction, are quite typical of opinion of the time: "So we may doubt whether, in cheese and timber, worms are generated or if beetles and wasps in cow dung, or if butterflies, shellfish, eels, and such life be procreated of putrefied matter. To question this is to question reasons, sense, and experience. If he doubts this, let him go to Egypt, and there he

will find the fields swarming with mice begot of the mud of the Nile, to the great calamity of the inhabitants."

Naturally, with the gradual increase in knowledge of the complexity of organisms, the idea of ABIOGENESIS, or SPONTANEOUS GENERATION, was restricted more and more to the lower forms. It remained, however, for Francisco Redi during the latter part of the seventeenth century to question seriously the general proposition, and to substitute direct experimentation for discussion and hearsay. By the simple expedient — it seems simple to-day — of protecting decaying meat from contamination by flies, he demonstrated that these insects are not developed from the flesh and that the apparent transformation of meat into maggots is due solely to the development of the eggs deposited thereon by flies.

One may imagine that the practical man of affairs scoffed at Redi toiling under the Italian sun with meat and maggots to satisfy a scientific curiosity, and little dreamed that the practical results which germinated from this 'folly' would be among the most important factors in twentieth-century civilization. Indeed, it is difficult to overestimate the importance of Redi's conclusion from either the theoretical or practical viewpoint, for with it was definitely formulated the theory that matter does not assume the living state, at the present time at least, except from preëxisting living matter.

The influence of this work gradually became evident in scholarly literature. One author during the next century states that "spontaneous generation is a doctrine so generally exploded that I shall not undertake to explode it. It is so evident that all animals, yea and vegetables, too, owe their production to parent animals and vegetables, that I have often admired the sloth and prejudices of ancient philosophers in taking it upon trust." Another writes that he "would as soon say that rocks and woods engender stags and elephants as affirm that a piece of cheese generates mites."

But it is not to be supposed that the time-honored doctrine of spontaneous generation actually had been so easily relegated to the myths of the past, Redi's work and these eighteenth-century opinions to the contrary. Indeed, the history of the establishment of BIOGENESIS — all life from life — extends down almost to the present time, for no sooner had experiment apparently disposed of spontaneous generation than it arose again with fresh vigor in a slightly different form demanding further investigation.

The difficulties came from two chief sources. In the first place, Redi himself had been baffled by the presence of parasites within certain internal organs of higher animals, such as the brains of sheep. How did they get there if not by spontaneous generation? The answer to this had to await the working out of the marvelously complex life histories of the parasitic worms and allied forms which showed that they all arise from parents like themselves. In the second place, improvements in microscope lenses contributed to the discovery of smaller and smaller living creatures. Countless numbers and myriads of kinds of "animalcules" appearing almost overnight in decaying organic infusions aroused widespread interest and amazement, and proved to be the chief riddle. The plausible explanation seemed to be spontaneous generation. (Figs. 25, 251, 252.)

Among others, Needham studied the problem and believed that he had demonstrated the spontaneous origin of minute organisms in infusions that he had boiled and sealed in flasks. His results attracted considerable attention because the famous French naturalist, Buffon, found in them support for his theory that the bodies of all organisms are composed of indestructible living units, which upon the death of the individual are scattered in nature and later brought together again to form the units of new generations.

Needham's and similar results, however, were shown by Spallanzani and other to be inconclusive because they were obtained by insufficient sterilization and sealing of the flasks containing the infusions. But at this point objections came from another source: the chemists who had recently discovered the important part played by free oxygen for life processes and for the putrefaction and fermentation of organic substances. They argued that the treatment to which Spallanzani and other experimenters subjected the infusions might well have changed the organic matter, excluded oxygen, etc., so that it was impossible for life to be produced.

This objection was met by a long series of experiments by various investigators during the first half of the last century, which showed conclusively that thoroughly sterilized infusions never developed living organisms even when air was admitted, provided the latter had been rendered sterile by heat or by having all suspended 'dust' particles removed. Thus the chemists were answered — the infusions possessed all the conditions necessary to support life — but life did not arise. The biologist who contributed most to

the establishment of this conclusion was Pasteur. His masterly and comprehensive work was not only convincing and final, but it also demonstrated the source of the life that so rapidly appeared in infusions that are exposed to the air. It is the air. A considerable part of so-called 'dust' is made up of microorganisms in a dormant state ready to resume active life when moisture and other suitable conditions are encountered. Furthermore, these organisms are not the result, but the cause of decay — their own activities bring about chemical changes: putrefaction, fermentation, and, in the bodies of higher organisms, disease. And this is amply attested by the methods now universally used in food

FIG. 152. — Flask used by Pasteur in his experiments on spontaneous generation. After the contents were poured in, the top of the flask was sealed. The opening at the end was sealed against the entrance of germs, but not oxygen, etc., by the water of condensation that accumulated at the bend. Life did not develop in the flask. (After McFarland.)

preservation and aseptic surgery — to mention but two instances. (Figs. 152, 153, 278.)

But, though highly improbable, of course it is not impossible that simple life is even at the present time arising spontaneously under special environmental conditions, perhaps in the ocean depths, but is unable to come to fruition in competition with existing highly specialized protoplasm of ancient pedigree. Indeed, if such living matter is arising, it must be very simple compared with protoplasm as we know it to-day; so simple, in fact, that we would not recognize it as such, because the protoplasm of even the simplest organisms has had a long evolutionary history.

So we may consider it firmly established that, so far as human observation and experiment go, no form of life arises to-day except from preëxisting life by reproduction. The evidence from innumer-

able sources converges overwhelmingly to the support of biogenesis. There is no evidence in support of abiogenesis.

B. ORIGIN OF LIFE ON THE EARTH

If we accept the testimony of astronomer and geologist, the Earth was at one time in a condition in which life could not exist, and so we are face to face with the problem of how it came to be

FIG. 153. — Apparatus used by Tyndall in his experiments on spontaneous generation. The front and side windows (*w*, *w*) of the cabinet are made of glass. Air can enter through the two tubes (*a*, *b*). The optical test for the purity of the atmosphere within the cabinet was made by passing a powerful beam of light from the lamp (*l*) through the side windows. When the atmosphere contained no suspended 'dust' particles, the tubes (*c*) within were filled, through the pipet (*p*) with sterile culture medium suitable for the growth of germs, but none developed. (After Tyndall.)

established on the Earth in the past — the remote past, since the geological record affords convincing proof that life has existed continuously on the Earth for some hundreds of millions of years.

Accordingly, unless one is willing to ascribe life's origin to SPECIAL CREATION — which at once removes it from the sphere of science and so beyond the present discussion — we have the fol-

lowing alternative: either life came to this planet from some other part of the universe; or it arose spontaneously from non-living matter at one period at least in the past as a natural result of the evolution of the Earth and its elements. With these in mind, a review may be made of several modern theories of the origin of life. It is nearly, if not quite, as important "to define our area of ignorance as to extend our area of knowledge."

1. *Cosmozoa Theory*

The establishment of biogenesis, and the dawning realization of the unique complexity of the structure of matter in the living state have led several scientists to suggest that life has *never* arisen *de novo* on the Earth but has been carried hither from elsewhere in the universe — the so-called COSMOZOA theory.

On the assumption that some of the heavenly bodies have always been the abode of life, and from the fact that small solid particles, which presumably have been a part of such bodies, are moving everywhere in space, these particles have been pictured as the vehicles which disseminate the simplest forms of life through interstellar space to find lodgment and development upon such planets as afford a suitable environment. Clearly, from this point of view, life may be as old as the universe itself.

The plausibility of the cosmozoa theory depends on two assumptions: that life exists elsewhere in the universe, and that life can be maintained during the interstellar voyage. Neither assumption has, of course, any foundation of established fact whatsoever, though the second offers at least something tangible for discussion.

As we know, many of the Bacteria and Protozoa, especially when under the influence of unfavorable surroundings, have the power of developing protective coverings about themselves and of assuming a dormant condition in which all the metabolic activities are reduced to the lowest ebb. In this spore or encysted state they can endure extremes of temperature and dryness which would quickly prove fatal during active life. For instance, it seems clear that the spores of certain kinds of Bacteria can survive a temperature approaching that below which no chemical reactions are known to occur, and others can endure as high as 120°C. for a short time. The cysts of some relatively highly specialized Protozoa can retain their vitality for at least half a century, while the seeds of some plants have been found to retain the power of germi-

nation for nearly a century; though statements that grain from ancient Egyptian tombs still maintains its power of growth has been positively disproved.

But the hardships to which living matter would be exposed when started on its interstellar journey are not to be minimized. Meteors in their fall through the Earth's atmosphere become heated to incandescence and, if they are the vehicle of transfer, it would only be conceivable for life to survive far below their surface where the temperature is lower. To avoid this and other difficulties it has been suggested that the radiant pressure of light is sufficient to overcome the attraction of gravitation for particles of the extraordinary minuteness of some of the lower forms of life, and that isolated germs might make the journey to the Earth. But on the assumption that an organism were forced out into space by the mechanical pressure of light waves from the Sun of the nearest solar system, it would require many thousand years for it to reach the Earth. However, certain scientists believe that, owing to the exceedingly low temperature and absence of water vapor which must prevail in cosmic space, there is no reason why spores should lose appreciably more of their germinating power in ten thousand years than in six months.

Without further discussion, it is apparent that the cosmozoa theory is one which cannot be proved or disproved. It removes the origin of life to a "conveniently inaccessible corner of the universe where its solution is impossible." Although at first thought it seems almost absurd, with its strictly scientific formulation by recent physicists and biologists, and especially in view of our increasing knowledge of the powers of life in the latent state, we are justified, perhaps, in seriously wondering whether after all life has ever arisen, whether it may not be as old as matter, and whether its germs, passing from one world to another, may not have developed where they found favorable soil.

But the majority of biologists undoubtedly would agree that, "knowing what we know, and believing what we believe, as to the part played by evolution in the development of terrestrial matter, we are, without denying the possibility of the existence of life in other parts of the universe, justified in regarding cosmic theories as inherently improbable." Accordingly we may turn to theories which attempt to picture the evolutionary origin of life from the inorganic upon the Earth.

2. *Pflüger's Theory*

Assuming that the Earth was at one time in an incandescent condition, Pflüger imagines that there arose from this superheated mass a combination of carbon and nitrogen to form the radical CYANOGEN, CN. This union involves the taking up of a large amount of energy in the form of heat, and therefore cyanogen contributes energy to organic compounds and, in particular, to proteins of which he believes it to be the unique life-principle. Accordingly the problem of the origin of life is essentially the origin of cyanogen, and since cyanogen and its compounds arise only at exceedingly high temperatures, Pflüger holds that life is essentially derived from fire.

Thus, if Pflüger's hypothesis is valid, once the cyanogen has energized organic compounds they are on their way to proteins and protoplasm, and finally to the evolution of the highly specialized protoplasm of organic life to-day.

3. *Moore's Theory*

Moore essays to picture with rather bold strokes the origin of life from the inorganic elements of the cooling Earth, by a continuation of the process of complexification which he sees inherent in the nature of matter. This he expresses in a general way as a "law universal in its application to all matter, and holding throughout all space as generally as the law of gravitation — a law which might be called the LAW OF COMPLEXITY — that matter, so far as its energy environment will permit, tends to assume more and more complex forms in labile equilibrium. Atoms, molecules, colloids, and living organisms arise as a result of the operations of this law, and in the higher regions of complexity it induces organic evolution and all the many thousands of living forms." In this manner he conceives that the chasm between non-living and living things can be bridged over, and that life arose as an orderly development, which comes to every earth in the universe in the maturity of creation when the conditions arrive within suitable limits.

4. *Allen's Theory*

Allen maintains that it is simplest to believe that life arose when the physical conditions of the Earth came to be nearly what they

are at present, and therefore does not attempt to trace it to actual Earth beginnings. If life formerly existed actively outside of the range of the freezing and boiling points of water, it must, he says, have been quite different from life as we know it. Allen imagines some such reactions as the following to have occurred: solar energy, acting on the water or damp earth containing the raw materials, caused dissociation and rearrangement of the atoms; the nitrogen abstracting oxygen from its compounds with carbon, hydrogen, sulfur, and other elements and delivering it to the atmosphere. Not much energy would be absorbed by a transparent liquid; but such reactions would occur particularly in water containing compounds of iron in solution or suspension since these compounds would absorb the solar energy. In this way compounds of nitrogen, carbon, etc., accumulated in the water or damp earth; and further reactions, anabolic and katabolic, occurred among them by virtue of the lability of the nitrogen compounds. Life at this stage was of the humblest kind since there were no definite organisms, only diffuse substances trading in energy, and between this stage and the evolution of cellular organisms an immense period elapsed.

5. *Troland's Theory*

With the increasing realization of the importance of enzymes in the economy of organisms, it is not strange that in these chemical bodies has been sought the key to life's origin, and accordingly we find Troland stating that life is something which has been built up about the ENZYME. This author assumes that, at some moment in Earth history, a small amount of a certain autocatalytic enzyme suddenly appeared at a definite point within the yet warm ocean waters which contained in solution various substances reacting very slowly to produce an oily liquid which did not mix with water. If, when this occurred, the enzyme became related to the reaction in such a way as to greatly increase its rate, Troland believes it is obvious that the enzyme would become enveloped in the oily material resulting from the reaction, and the little oil drop would increase until it was split into smaller globules, provided the original substances which combined were soluble in oil as well as in water. Thus arose, according to Troland, the first and simplest life-substance, possessing the power of indefinitely continued growth.

6. *Osborn's Theory*

Starting with the assumption that the primal earth, air, and water contained all the chemical elements and three of the more simple but important chemical compounds — water, nitrates, and carbon dioxide, Osborn suggests that an initial step in the origin of life was the bringing of these elements into combined action. This took place when the Earth's surface and waters had temperatures between 6° and 89° C. and before the atmospheric vapors admitted a regular supply of sunlight. The earliest function of living matter, he thinks, was to capture and transform the electric energy of the chemical elements characteristic of protoplasm, and this power probably developed only in the presence of heat energy derived from the Earth or the Sun.

An early step then, in the organization of living matter, was the assemblage of several of the 'life elements,' and next their grouping in a state of colloidal suspension — "they were gradually bound by a new form of mutual attraction, whereby the actions and reactions of a group of life elements established a new form of unity in the cosmos, an organic unity, or organism, quite distinct from the larger and smaller aggregations of inorganic matter previously held or brought together by the forces of gravity."

7. *Huxley's Statement*

Such is an outline of some of the foremost attempts of biologists to conceive the origin of the living state of matter from the elements of the Earth. It will be noted that all, except the cosmozoa theory, have one assumption in common — the 'chance' assemblage of the various elements of protoplasm: an assumption not unreasonable when the stupenduous duration of time and the almost infinite variations in conditions that were at the disposal of Nature are appreciated. But the statements of the respective theories necessarily have been presented so briefly here as hardly to be fair to their authors. However, our purpose is attained if they provide an instructive illustration not only of the evolutionary trend which biological thought follows in this problem, but also of the divergent results reached by the scientific imagination when it has few or no facts to guide it.

So we may more profitably turn to a consideration of the present-day manifestations of life, and dismiss the insolvable problem of

the origin of life on the Earth with the conservative statement penned more than half a century ago by Huxley: "Looking back through the prodigious vista of the past, I find no record of the commencement of life, and therefore I am devoid of any means of forming a definite conclusion as to the conditions of its appearance. Belief, in the scientific sense of the word, is a serious matter, and needs strong foundations. To say, therefore, in the admitted absence of evidence, that I have any belief as to the mode in which existing forms of life have originated, would be using words in a wrong sense. But expectation is permissible where belief is not; and if it were given to me to look beyond the abyss of geologically recorded time to the still more remote period when the Earth was passing through physical and chemical conditions, which it can no more see again than a man can recall his infancy, I should expect to be a witness of the evolution of living protoplasm from not living matter. . . . That is the expectation to which analogical reasoning leads me; but I beg you once more to recollect that I have no right to call my opinion anything but an act of philosophical faith."

CHAPTER XIX

THE CONTINUITY OF LIFE

Owing to the imperfection of language the offspring is termed a new animal, but is in truth a branch or elongation of the parent.

—*Erasmus Darwin.*

SINCE so far as is known all life now arises from preëxisting life and has done so since matter first assumed the living state, it apparently follows that the stream of life is continuous from the remote geological past to the present and that all organisms of to-day have an ancient pedigree. It is to the establishment of this as the reasonable conclusion from the data accumulated during recent years, that from now on our attention is somewhat more particularly directed; and accordingly it is necessary first of all to consider in some detail the relation of parent to offspring in present-day forms as exhibited by reproduction.

A. REPRODUCTION

The power of producing new individuals specifically similar to the parent is, as has been seen, one of the most important characteristics of living in contrast with lifeless matter. Furthermore, reproduction is typically cell division. This is quite evident in unicellular plants and animals, but by no means so obvious in higher organisms where, as we know, special gonads and highly complex accessory organs are developed in furtherance of reproduction.

It will be recalled that in *Paramecium*, for example, the nucleus and cytoplasm divide into two parts, so that by cell division, here called BINARY FISSION, the identity of the parent organism is merged into the two new cells. Simple as this seems, the fission of *Paramecium* actually involves considerably more than the halving of the original cell, because, as a matter of fact, each half must *reorganize* into a complete new individual with all parts characteristic of the parent. (Fig. 15.)

Among some unicellular organisms (*e.g.*, *Sphaerella*) the parent cell, instead of merely forming two cells by binary fission, becomes resolved into many cells by a series of practically simultaneous

divisions known as **MULTIPLE FISSION**, or **SPORULATION**. This is usually preceded by a considerable growth of the parent cell and its enclosure in a protective covering, or **CYST**, which ruptures to liberate the spores. Other unicellular forms, such as the Yeasts — colorless plants chiefly responsible for alcoholic fermentation — exhibit a modified form of fission, in which the parent cell forms one or several outgrowths, or **BUDS**, which gradually assume the characteristic adult form and sooner or later become detached as complete similar individuals. (Figs. 61, 155.)

In a considerable number of instances, however, the cells arising by multiple fission or budding remain closely associated or organically connected so that they form a **COLONY**. In some colonial organisms the component cells are all alike and each retains its

A. Paramecium.

B. Volvox.

C. Hydra.

D. Earthworm.

FIG. 154. — Diagrams to illustrate the general reproductive cell cycle in (A) a unicellular organism (*Paramecium*); (B) a colony of cells (*Volvox*); (C) a simple Metazoön (*Hydra*); and (D) a more complex Metazoön (*Earthworm*). (After Hegner, slightly modified.)

individuality, while in others certain cells are restricted more or less in their functions, so that a physiological division of labor is established which involves the shifting of individuality from the cells to the colony as a whole. This specialization is exhibited chiefly with regard to reproduction and reaches its highest expression among colonial PROTISTA (Protozoa and Protophyta) in *VOLVOX*, where among ten thousand or so cells, perhaps a score are specialized for reproduction and the rest are somatic. Usually each of the reproductive cells (germ cells) divides to form a group which is set free as a miniature colony; but in certain cases some of the reproductive cells become transformed into male and others into female gametes. After fertilization of the eggs, usually by sperm from another colony, the zygotes develop into new colonies

FIG. 155. — Yeast cells, very highly magnified. A, cell showing granular cytoplasm and a large vacuole; B, showing nucleus; C, cell budding; D, mother cell and bud after division is completed.

which eventually are liberated from the parent colony. (Figs. 26, 27.)

As has been previously suggested, the physiological division of labor in the colonial Protista, involving, as it does, a segregation of reproductive from somatic structures, affords a logical transition from the unicellular condition to that characteristic of the multicellular forms. These, to all intents and purposes, may be considered highly complex colonies of cells in which specialization, no longer confined merely to demarking germinal and somatic regions, has transformed the latter into a complex of tissues and organs, the body (SOMA) of the individual, while the germinal tissue (GERM) is confined to the essential reproductive organs.

It is customary, therefore, to draw a more or less sharp distinction between the soma and germ — to consider the soma the individual which harbors, as it were, the germ destined to continue the race. This theory of GERMINAL CONTINUITY, which is chiefly associated with the name of Weismann, recognizes that the germ contains living material which has come down in unbroken con-

tinuity ever since the origin of life and which is destined to persist in some form as long as life itself. On the other hand, the soma may be said to arise anew in each generation as a derivative or offshoot of the germ; and, after playing its part for a while as the vehicle of the germ, to pass the germ on at reproduction, and then die. The germinal continuity concept has altered the attitude of biologists toward certain fundamental questions in heredity and evolution, as will be apparent when these subjects are considered. (Figs. 154, 181, 289.)

FIG. 156. — Hydra reproducing asexually by dividing lengthwise. (After Koelitz.)

Though Volvox and other colonial forms afford a glimpse of the conditions which probably prevailed when the evolutionary bridge from unicellular to multicellular organisms was crossed, the varied methods of reproduction of the latter by no means indicate the early establishment of a hard and fast boundary between soma and germ. Many of the Invertebrates, such as Hydra and various types of worms, reproduce not only by germ cells, but also by strictly asexual processes which are known as **FISSION** and **BUDDING**. These processes are comparable merely in a superficial way with the similarly named methods in the Protista. In some forms the whole complex body divides into two or more parts, each of which reforms — **REGENERATES** — what was lost and so becomes a complete though a smaller individual. In other species, as well as in Hydra itself, buds arise as outgrowths from the body and assume the form of the parent either before or after becoming detached. (Figs. 156, 157.)

FIG. 157. — An unsegmented worm (Flatworm) in process of fission. (After Child.)

In many of the nearest allies of Hydra the buds remain permanently attached so that eventually a large colony of organically connected hydra-like individuals (**HYDRANTHS**) is developed. Moreover, this condition leads to a physiological division of labor between the various hydranths which may become more or less changed in structure so that, for instance, feeding, protective, and repro-

ductive individuals are established, and thereby the HYDROID COLONY exhibits what is termed POLYMORPHISM. Our present interest is confined to the *reproductive* hydranths, which in many of the Hydroids are so modified that they are dependent upon the colony as a whole for all the necessities of life and are merely

FIG. 158. — Life history of *Obelia*. A, portion of a colony: 1, ectoderm; 2, endoderm; 3, mouth; 4, enteric cavity; 5, stalk of colony; 6, 7, and 10, exoskeleton; 8, reproductive hydranth (blastostyle); 9, medusa bud. B, free swimming medusa. C, ciliated larva of closely related species. (After Parker and Haswell, Shipley and MacBride, and Allman.)

bodies which form by budding other individuals known as MEDUSAE. The medusae, which become detached and swim away, usually bear no superficial resemblance to any of the other individuals of the colony on which they arose, but a study of their structure shows that they are built on the same fundamental plan and are essentially free-swimming, sexual hydranths, some of

which produce sperm and other eggs. The medusae liberate their sexual products in the water where fertilization occurs, and the zygote gives rise to a free-swimming embryo (LARVA). This soon becomes attached to some submerged object and develops into a Hydroid colony. (Figs. 83, 158, 159.)

Thus the common Hydroids, such as *Obelia*, exhibit two distinct phases, or generations, in their life history — the fixed, polymorphic colony of hydranths which is produced sexually but is itself asexual; and the free-swimming medusae which are produced asexually but are themselves sexual. The asexual and sexual gen-

FIG. 159. — Diagrams to show the fundamentally similar structure of Hydra or of a hydranth of *Obelia* (A) and of a medusa (B). *cir. c.*, circular canal; *ect.*, ectoderm; *end.*, endoderm; *ent. cav.*, enteric cavity; *hyp.*, *mnb.*, region of mouth (*mth*); *mscl.*, mesogloea; *nv.*, *nv*¹, nerve rings; *rad.*, radial canal; *t.*, tentacle; *v.*, velum. (From Parker.)

erations alternate with each other in regular sequence, so that an ALTERNATION OF GENERATIONS occurs, which recalls in a general way the conditions that exist in certain plants.

Alternation of asexual and sexual methods of reproduction, attended by more or less difference in structure of the individuals of the generations, is fairly widespread among the Invertebrate groups, particularly in forms which have adopted a *parasitic* mode of life. Frequently the life histories are exceedingly complicated: several asexual, sexual, and parthenogenetic generations succeeding one another in response to the special conditions imposed by adaptation to a life within another animal or series of animals. (Fig. 251.)

It is clear from such life histories that the conception of special

germ *cells* early set aside, as it were, from the somatic cells must not be taken too literally. The same point is emphasized by the power exhibited by plants and animals in restoring parts lost by mutilations of one kind or another. Among many plants, pieces of the root, stem, or, in special cases, of the leaf may give rise to individuals complete in every respect. Until the middle of the eighteenth century this was considered a property peculiar to plants, and soon after *Hydra* was discovered experiments were made to determine whether the organism was a plant or an animal. Specimens were cut into several pieces and it was found that each piece developed into a complete *Hydra*. This result, from the ideas of the time, should have led to the conclusion that *Hydra* is a plant,

FIG. 160. — Regeneration in *Hydra*. A, normal *Hydra* (lines show where piece was cut out); B, 1-4, changes in a piece of A as seen from side; C, 1-4, same as seen from end; D, E, F, later changes in same piece. (From Morgan.)

but additional characteristics were observed which outweighed all other considerations. Accordingly *Hydra* was recognized as an animal with the power of replacing lost parts. (Fig. 160.)

Since the classic work on *Hydra* the power of regeneration has come to be recognized as a fundamental property of all animals. It is exhibited to the greatest degree among the lower animals, while in the higher Vertebrates it is confined chiefly to the replacement of cells which especially suffer from wear and tear, such as those forming the outer layer of the skin. Regeneration is one phase of a fundamental property of protoplasm, namely growth, whether it consists in restoring a part of a *Paramecium*, transforming a bit of a Flatworm into a complete animal, or replacing half of an Earthworm, the head of a Snail, the claw of a Crayfish,

or the leg of a Salamander. But, it will be recognized that associated with growth there are complex processes of simplification (dedifferentiation) of tissues and organs, and later a rebuilding (differentiation) in order that a part may become again a normally organized whole. Witness certain marine Flatworms that can be cut down to less than one two-hundred-thousandth of their original size and still become miniature worms like the original.

The experimental study of regeneration phenomena has opened up a new vista of the regulatory powers of living things from

FIG. 161. — Regeneration in a Flatworm (*Lineus socialis*). A, normal worm; B, B', section cut from body and its appearance after twelve days; C, same after thirty days, cut in planes 3-3, and 4-4. Successive cuttings and regenerations indicated by arrows. M, M', similar experiments and results on posterior end of body. (From Coe.)

Protist to Vertebrate and from egg to adult, and has afforded a means of approach to some fundamental biological problems. And withal it has a practical value. The surgeon now knows more about the regeneration of tissues in general and of nerves in particular in wound healing, and the oysterman knows — or should know — that his attempt to destroy Starfish by tearing them up and throwing the pieces overboard, may serve merely to increase this enemy of the Oyster. (Figs. 161-163, 177, 178.)

The power of fragments of distinctively somatic tissue, as in many lower animals and plants, to form a complete organism

FIG. 162. — Regeneration and grafting in the Earthworm. *A*, regeneration of removed anterior segments by the posterior piece. *B*, regeneration of posterior segments by the posterior part, so that the worm has a 'tail' at either end. *C*, regeneration of removed posterior end by the anterior piece. *D*, three pieces grafted together to make a long worm; *E*, two pieces grafted to form a worm with two 'tails'; *F*, short anterior and posterior pieces grafted together. Regenerated portions are dotted. (From Morgan.)

FIG. 163. — Regeneration of a Flatworm (*Planaria maculata*). *A*, normal worm; cut across at line indicated. *B*, *B'*, and *C*, *C'*, regeneration of anterior and posterior parts of *A* to form complete worms. *D*, piece cut from a worm; *D*¹, *D*², *D*³, *D*⁴, successive stages in the regeneration of *D*. *E*, 'head' from which rest of animal has been cut off. *E*¹, *E*², *E*³, successive stages in the regeneration by *E* of a complete body. *F*, similar experiment to *E*, but a new 'head' in reversed position is regenerated instead of a body, *F*¹. (From Hegner, after Morgan.)

including the reproductive organs and germ cells, indicates that we must postulate at least a potential supply of the germ residing in the somatic tissue, which can make good the definitive germ cells when they are lost. At first glance this may seem to be a far cry to save an idea, but it is a fact that there is a continuity of the *nuclear* complex (GERM PLASM) whether the germ cells are set aside early in individual development, or later by the transformation of what seem to be typical somatic cells. That this is really the crux of the question will be appreciated after the details of cell division have been discussed.

B. ORIGIN OF THE GERM CELLS

Among the Vertebrates, as previously described, the germ cells reside during adult life in definite organs, the ovaries and testes, and upon these cells the power of reproduction of the individual is solely dependent. It seems clear, however, that the primary germ cells do not arise as such by division in the tissues which during development form the ovaries and testes. Just when the germ cells are set aside in Vertebrates is uncertain, but it would seem to occur very early in embryonic life, perhaps during the cleavage of the egg. Then by shiftings of the tissues during growth, and possibly also by amoeboid movements of the germ cells themselves, they finally reach definite positions in the epithelium lining the dorsal wall of the coelom, which becomes an integral part of the gonads as development proceeds.

With regard to the fate of the PRIMORDIAL GERM CELLS, once they have reached testis or ovary, we are on surer ground and can trace with considerable exactness their divisions and transformations which give rise to the gametes: sperm and eggs. In the first place the primordial germ cells proceed to divide in the testis and ovary so that they produce a large number of relatively small germ cells known as SPERMATOGONIA and OÖGONIA respectively. (Fig. 166, A, B.)

1. *Mitosis*

Before taking up the origin of the gametes by division from the spermatogonia and oögonia, it will be necessary to describe in some detail the complicated internal process involved in all typical cell divisions, known as MITOSIS, which was dismissed when considering the origin of cells until the reader would be in a position to appreciate to the full its significance. (Fig. 10.)

Reduced to its simplest terms, a typical resting cell, that is one which is not dividing, consists of a mass of CYTOPLASM surrounding a NUCLEUS; the latter with its chromatin distributed so that it presents a net-like appearance. In addition to the nucleus, it will be recalled that there is present another important cell organ, the CENTROSOME, which appears like a tiny granule situated in the cytoplasm near the nucleus of the resting cell. For all practical purposes we may consider the cytoplasm as the arena in which mitosis takes place, the centrosome as the dynamic agent, and the nucleus, or more specifically its CHROMATIN, as the essential element which the complicated process is to distribute with exactness to the daughter cells that are in process of formation. With this in mind we may proceed to an outline of the chief stages of mitosis, though perhaps it should be emphasized that variations in the details are as numerous as the different types of cells, and that any general account can do no more than present the fundamental plan of operations.

Broadly speaking, mitosis can be divided into four chief stages: PROPHASE, METAPHASE, ANAPHASE, and TELOPHASE, during each of which characteristic changes take place in the nucleus, cytoplasm, and centrosome. (Fig. 164.)

At the beginning of the prophase, or earlier, the centrosome divides to form two, each of which becomes surrounded by what appears to be a halo (ASTER) of radiating fibers which possibly are cytoplasmic currents—the visible expression of physico-chemical forces. The centrosomes and asters now proceed to move apart, take up positions at opposite sides of the nucleus, and the astral fibers between lengthen until they form a CENTRAL SPINDLE. While these changes are going on, the nucleus is not inactive. The nuclear membrane gradually disappears and the chromatin granules, originally in a net-like arrangement, seem to become rearranged in a more or less continuous thread of chromatin called the SPIREME. This, however, actually represents a number of definite chromatin entities, termed CHROMOSOMES, which gradually by chromatin concentration become distinctly individual. The number of chromosomes varies greatly in different species, but is typically an even number and the same for all the cells of a given species.

When the chromosomes have assumed definitive form, the preliminary events which constitute the prophase of mitosis are brought to a close by the chromosomes being drawn to the center of

the spindle. Here they are arranged in a plane at right angles to the long axis of the central spindle, midway between the two centrosomes, and form the **EQUATORIAL PLATE**.

And now the stage is set for what is apparently the climax of mitosis, designated the metaphase. Each of the chromosomes sep-

FIG. 164. — Typical stages of mitosis (somatic) in which the chromosome number is assumed to be eight. *A*, prophase (start): chromatin still exhibiting net-like arrangement, centrosome divided and surrounded by aster; *B*, prophase (early): chromatin in spireme form, centrosomes moving apart and spindle arising between; *C* and *D*, prophases (later): nuclear membrane disappearing, constituent chromosomes of spireme separating; *E* and *F*, metaphase and anaphase (early): chromosomes arranged in equatorial plate and each separating into two along a longitudinal split; *G*, anaphase (later): a set of eight chromosomes approaching each aster; *H*, telophase: gradual loss of visibility of distinct chromosomes, asters and spindle disappearing, division of cytoplasm beginning; *I*, mitosis completed, two cells.

arates into two parts along the line of a *longitudinal* split, in such a manner that each of the thousands of chromatin granules which make up a chromosome is equally divided. Two sets of similar daughter chromosomes are thus formed.

With chromosomal division consummated, the metaphase merges

into the anaphase which is devoted to a shifting of a daughter set of chromosomes along the fibers to either end of the spindle. In this way each centrosome becomes associated with one set of daughter chromosomes.

The last stage, or telophase, is one of nuclear reconstruction and division of the cytoplasm. The chromosomes become indistinct as they spin out to form the net-like arrangement of the chromatin in the nucleus of each daughter cell; a nuclear membrane arises; and the nucleus again assumes the form of a definite spherical body characteristic of the resting cell. It must be emphasized, however, that although the chromosomes usually disappear from view as definitive entities in the resting nucleus, nevertheless the individuality of each persists and the same chromosomes emerge from the nuclear complex at the next division period.

Simultaneously with these nuclear changes, and before the spindle and asters — the machinery of mitosis — disappear, the division of the cytoplasm is initiated as indicated by an indentation of the cell wall, encircling the cell at the equator. This becomes deeper as it gradually extends through the cytoplasm in the same plane which the equatorial plate formerly occupied, until the cytoplasm is cut into two separate masses, each containing one of the daughter nuclei and centrosomes. Thus one cell has merged its individuality into two daughter cells by mitotic division. Cell division — reproduction — has occurred.

What is the main thought that we carry away from this brief view of a phenomenon that has been going on for untold ages; is going on now in every living thing; is being enacted with the same nicety in various cells of our own bodies this very instant? Surely it seems that whereas the mitotic process apparently results in merely a mass division of the cytoplasm, the chromatin material is rearranged and distributed in a manner which makes it possible for each cell to receive a very definite share. Each daughter cell receives the same number of chromosomes, although in many cases there is a very great difference in the size of the resulting cells. Indeed, exactness of chromatin distribution appears to be the primary object of mitosis.

For the sake of emphasizing chromatin behavior during mitosis, we may resort to a crude analogy. If one had a hank of yarn, every inch of which was qualitatively different, and desired to distribute it equally to two persons; it would be necessary to disentangle it,

then convenient to cut it up into small pieces, and finally necessary to split each piece lengthwise. In truth, the spireme, and accordingly each chromosome, is qualitatively different from one end to the other, and these qualitatively different parts of the chromosomes, known as GENES, are the determiners of characters which are handed on from cell to cell. And since cell division is reproduction, the chromosomes are the chief agents in the transmission of characters from parent to offspring in inheritance. We shall consider this important fact when we discuss heredity, but now we must return to the origin of the gametes.

2. *Chromosomes of the Germ Cells*

It is clear that the spermatogonia and oögonia in the reproductive organs, together with all the cells forming the body proper, are direct descendants by mitotic cell division from the fertilized egg which gave rise to the individual organism. This, we have just seen, is equally true of the chromosomes and, therefore, every cell of the animal body has the same number of chromosomes as the fertilized egg. Furthermore, since fertilization always consists in the fusion of two gametes — a fusion of nucleus with nucleus and cytoplasm with cytoplasm to form a zygote — one of two things must happen. Either the zygote, which is one cell reconstructed from two, must have double the chromosome number, that is, a set contributed by both egg and sperm; or some method must exist by which the chromosomes of the gametes are reduced in number to one-half that characteristic of the somatic cells.

As a matter of fact, a reduction in the number of chromosomes always does take place sometime during the life history. In plants such as the Mosses, Ferns, and Seed Plants, it occurs at the formation of the spores. Thus it follows that the gametophyte contains half as many chromosomes as the sporophyte, and the sporophyte number is restored by the union of the gametes. It must be borne in mind, however, that the familiar plants are sporophytes which, for all practical purposes, directly produce sporophytes because the gametophyte is reduced almost to the vanishing point. The chromosome number of the parent sporophyte and the sporophyte in the seed is the same. However, attention must be concentrated on the conditions as they exist in animals, in which the somatic number of chromosomes is reduced one-half at the formation of the gametes. From the standpoint of chromosome number, the

FIG. 165. — Schematic representation of the life history of an animal (A) and of a plant, *e.g.*, Fern, (B) from the standpoint of the diploid and haploid condition of the chromosomes.

sporophyte is comparable to the animal soma and the gametophyte is represented by merely a couple of cell generations during the formation of the gametes in animals. (Fig. 165.)

The MATURATION or 'ripening' of the germ cells of animals involves two cell divisions by which each spermatogonium gives rise to four sperm, and each oögonium to one functional egg and three tiny, abortive cells known as POLOCYTES; each and all with one-half the number of chromosomes of the somatic cells and of the germ cells up to this point in their development. Consequently these two divisions, termed MATURATION DIVISIONS, must be examined in some detail if we are to appreciate the nicety of the process by which the chromosome number is reduced one-half without impairing the chromatin heritage from cell to cell. We shall describe first the origin of the sperm which, though it is fundamentally the same as that of the egg, is somewhat simpler to understand.

3. *Spermatogenesis*

A given SPERMATOGONIUM, with, let us say, eight chromosomes characteristic of the species, proceeds to increase in size preparatory to the first maturation mitosis, and is designated a PRIMARY SPERMATOCYTE. At the close of the growth period, when this cell is preparing to divide, the chromosomes are arranged in pairs by a process termed SYNAPSIS. The number of such pairs will obviously be half that of the chromosome number. The SYNAPTIC PAIRS are then distributed in the equator of the spindle exactly as the single chromosomes are in ordinary mitosis. But, and this is the crucial point, in the early anaphase the members of each pair are separated, one synaptic mate going to each pole of the spindle. Thus each of the daughter cells — SECONDARY SPERMATOCYTES — receives half the total number of chromosomes that were present in the primary spermatocyte. It will be noted that the essential difference between this type of mitosis (REDUCTION DIVISION) and that of all other nuclear divisions (EQUATION DIVISIONS) lies in the *separation* of entire chromosomes (SYNAPTIC MATES) instead of the splitting of each chromosome.

Both the secondary spermatocytes now divide by typical mitosis, equation division, thus distributing to each of the resulting cells (SPERMATIDS) half the somatic number of chromosomes. The spermatids are presently transformed into sperm and thus

FIG. 166. — Diagram of the general plan of spermatogenesis and oögenesis in animals. The somatic, or diploid, number of chromosomes (duplex group) is assumed to be eight. Male, to the left; female, to the right. *A*, primordial germ cells; *B*, spermatogonia and oögonia, many of which arise during the period of multiplication; *C*, primary spermatocyte and oöocyte, after the growth period, with chromosomes in synapsis; *D*, secondary spermatocytes and oöocytes, with haploid number (simplex group) of chromosomes, which have arisen by the first maturation (reduction) division; *E*, spermatids (which become transformed into sperm) and egg and three polocytes which have arisen by the second maturation (equation) division; *F*, union of sperm and egg (fertilization) to form zygote with diploid number (duplex group) of chromosomes; *G*, chromosome complex of cells after first division of the zygote, and of all subsequent somatic cells, and germ cells until maturation.

each spermatogonium with eight chromosomes gives rise to four sperm with four chromosomes apiece. (Fig. 166.)

4. *Oögenesis*

The maturation of the egg, as already intimated, follows the same plan as that of the sperm, and the reduction of the chromosomes is the same. Such modifications as occur are related to the fact that the egg is usually a relatively large, passive cell stored with nutritive materials for use during the developmental process, while the sperm is among the smallest of cells — essentially a nucleus surrounded with a delicate envelope of cytoplasm. Accordingly it is only necessary to emphasize that the growth period of egg formation, in which the OÖGONIUM becomes transformed into the PRIMARY OÖCYTE, is characterized by a much greater increase in size than is the case in the corresponding period in spermatogenesis; and that the following two cell divisions (one a reduction and the other an equational division) involve very unequal divisions of the cytoplasm. Thus one SECONDARY OÖCYTE is very large, while the other is a tiny cell termed the FIRST POLOCYTE.

Both the large secondary oöcyte and first polocyte now divide again; the former giving rise to a large cell, the mature EGG, and a tiny SECOND POLOCYTE; while the first polocyte divides equally to form two polocytes. In this way arise the four cells, comparable to the four sperm in spermatogenesis, each with half the somatic number of chromosomes. But only one of these, the egg, functions as a gamete. The three polocytes, although possessing a similar chromosome complex, are sacrificed in providing one cell, the egg, with its special cytoplasmic equipment. The polocytes get just enough cytoplasm to be regarded as cells, and soon degenerate and disappear.

Such is the outline of the essentials of spermatogenesis and oögenesis in animals; processes which involve at one stage a modification of ordinary mitosis to give each gamete half the somatic number of chromosomes characteristic of the species. It is clear that this is not merely a mass reduction of chromatin material, but is a separation and SEGREGATION after synapsis of definite chromatin entities, the chromosomes, so that the gametes receive the reduced number.

Throughout the animal kingdom, wherever sexual reproduction occurs, phenomena which can be interpreted as nuclear reduction

have been observed in the formation of gametes. In some of the Protozoa this seems to be merely an extrusion of a certain amount of chromatin, but since whenever chromosomes can be observed and counted the process has been found to follow in principle essentially the same lines described above, we have every reason to believe that it is never a haphazard mass reduction, and that the ripe gametes emerge with a definite chromatin heritage, relatively simple as this may be in the lowest forms.

5. *The Chromosome Cycle*

We have now surveyed the *germ cell cycle* from the fertilized egg through the germ plasm in the adult to the gametes again, but before proceeding to consider the details of the fusion of egg and sperm — the fertilization process — it may clarify matters to glance back to the *chromosome* condition in the fertilized egg at the *beginning* of the cycle that has just been considered.

Obviously this fertilized egg (zygote) contained two groups of chromosomes, one of which belonged to the egg and therefore may be termed MATERNAL, and one of which was derived from the sperm and thus is PATERNAL. When the zygote divided by mitosis to form the body and germ, every cell received two groups of chromosomes directly derived from these two original groups in the zygote. It logically follows, and all observations indicate, that each and every cell, both of the body and of the germinal tissue, possesses two groups of chromosomes, one of maternal and one of paternal origin — in other words, direct lineal descendants of the combined set formed at fertilization.

So it happens that each body cell really has a *double* set (DUPLEX GROUP, DIPLOID NUMBER) of chromosomes — and the same is true of the germ cells until maturation. Then at synapsis corresponding (HOMOLOGOUS) maternal and paternal chromosomes pair and, after the reduction division, the secondary spermatocytes and oöcytes and the gametes themselves have a single set (SIMPLEX GROUP, HAPLOID NUMBER). (Figs. 165, A; 167.)

Thus far we have emphasized chromosome reduction as the main result of the complicated maturation phenomena. The question now arises: Is this chromatin distributed so that all the gametes receive the same heritage?

As already stated, the evidence indicates not only that chromosomes differ qualitatively one from another, but also that the va-

FIG. 167. — Diagram of the chromosome cycle of an animal. Somatic (diploid) chromosome number assumed to be eight. Paternal chromosomes (from sperm) = ABCD; maternal (from egg) = abcd. I, union of nuclei of gametes, each with a simplex group (haploid number) of chromosomes, in the zygote at fertilization to form a duplex group (diploid number) of chromosomes. II, III, IV, somatic divisions or divisions of germ cells before maturation (duplex groups of chromosomes). V, synapsis, involving pairing of homologous paternal and maternal chromosomes to give the haploid number of paired chromosomes. VI, reduction division — separation of pairs into single chromosomes again. VII, two gametes, with simplex groups (haploid number) of chromosomes; there are 14 more possible combinations of the chromosomes, or types of gametes, which are not shown. (After Wilson, slightly modified.)

rious parts of each chromosome are qualitatively distinct. And further that these qualitative differences are the physical basis of inheritance — the determiners (genes) of characters which will be realized in the individual or the race to which the cell containing them contributes. Such being the case, the chromosomal complex of the nuclei which arises after synapsis — that is, the nuclei of the gametes — depends on how the various chromosomes happen to be distributed during the two maturation divisions. As a matter of fact, all the chromosomal combinations occur that are mathematically possible with the available number of chromosomes in a given species, but with one limitation: every cell must receive one member of each synaptic pair of chromosomes, so that each and every gamete receives a complete simplex group of chromosomes, but rarely the same groups (maternal and paternal) which existed before maturation. For example, if the somatic (diploid) number of chromosomes is eight, sixteen different types of gametes are possible. In Man with 48 somatic chromosomes, and after synapsis 24 pairs of paternal and maternal chromosomes, there are 2^{24} , or about seventeen million possible types of gametes in each sex; and since these combine at random at fertilization, the possible number of different types of zygotes from one parental pair mounts far up in the trillions. No wonder the children of a family differ — there is *variation*!

In a way, therefore, fertilization is not consummated, so far as its influence on the race is concerned, until the maturation of the gametes in the new generation to which it has given rise. We must defer until later the consideration of the significance of these facts in BIPARENTAL inheritance, and merely emphasize again that the continuity of life implies not only the continuity of cells but also of their nuclear elements, the chromosomes.

CHAPTER XX

FERTILIZATION

The entire organism may be compared to a web of which the warp is derived from the female and the woof from the male. — *Huxley*.

Now that we are familiar with the method of gamete formation and its contribution to the continuity of life, it is in order to consider some important details of the structure of the gametes themselves, and the significance of the complex series of phenomena that they initiate at fertilization. The biological importance of fertilization and the part it plays in the life of the individual organism and the race has aroused the interest of philosophers and scientists since the time of Aristotle, but it is only within the past half-century that at least a partial answer has been forthcoming from a critical analysis of the gametes and their product, the zygote.

A. GAMETES

The gametes, while exhibiting in certain cases peculiar adaptations to special conditions, are remarkably similar in general structure throughout the animal series. It is possible in animals, just as in plants, to arrange a series of lower forms which shows various stages in sex differentiation. Beginning with animals in which both gametes are structurally similar, we pass by slow gradations to others in which the egg is a relatively large, passive, food-laden cell and the sperm a minute, active, flagellated cell.

As a matter of fact, the egg is subject to somewhat more variation in size and general appearance than the sperm, for after fertilization it must be adapted to meet the special conditions of development peculiar to the species. Thus, for instance, the actual size of the egg in both plants and animals is determined chiefly by whether the developing embryo is in the main dependent upon food stored in the cytoplasm of the egg itself, or upon some outside source, such as the sea water in which it floats, or the tissues of the parent. The first case is well illustrated by a Bird's egg in which the so-called YOLK is the egg cell proper, hugely distended

by stored food, and surrounded by nutritive and protective envelopes consisting of the 'white of the egg,' shell membranes, and shell which are formed by secretions from the walls of the oviduct during the passage of the egg to the exterior. On the other hand, the eggs of Mammals, for instance of the Rabbit and Man, are very small — the human egg being less than $1/125$ th of an inch in diameter — since their essentially parasitic method of development in the uterus renders superfluous the storage of any

FIG. 168. — A, section through the egg of a primitive Vertebrate, the Lamprey. B, sperm of the same species, drawn to scale. *d.en.*, dense endoplasm; *i.m.*, inner membrane, *o.m.*, outer membrane; *p.*, granular 'polar' cytoplasm; *v.en.*, vacuolated endoplasm; *v.ex.*, vacuolated ectoplasm; *I*, first polarocyte; *II*, spindle for second polarocyte. (From Kellicott.)

considerable amount of food material in the egg cytoplasm. (Figs. 7, 133, 168.)

With the specialization of the egg along lines which render it non-motile, it has devolved upon the sperm to assume the function of seeking out the egg for fertilization. It does this in most cases by active lashing of its flagellum. This necessitates a fluid medium in which the sperm can swim, and such is provided by the environment in which the organism lives or, in the case of most higher animals, where fertilization takes place within the oviduct, by special fluids secreted for the purpose. In the highest plants, how-

ever, it will be recalled that the characteristic motility of the sperm is lost in the excessive specialization attendant upon gametophyte reduction — the sperm nucleus reaching the egg by the growth of the pollen tube down through the tissues of the style. (Fig. 77.)

A question of much interest is how the actual meeting of the gametes is brought about. In many cases it is undoubtedly merely by chance: the random swimming of the sperm sooner or later bringing one in contact with an egg. In other cases the movements of the sperm seem to indicate some definite attraction by the egg. It has been shown, for example, that the sperm of some Mosses and Ferns are attracted by exceedingly dilute solutions of cane sugar and malic acid respectively, traces of which are secreted by the tissues in the vicinity of the egg. Also the sperm of some of the lower animals seem to be attracted by substances eliminated by the egg at maturation. In such instances there can be but little doubt that chemical stimulation of the sperm by specific substances plays a part in bringing the gametes together. This is an example of **CHEMOTAXIS**: a phenomenon of considerable importance, especially in the behavior of free-living cells.

B. UNION OF GAMETES

Once a single sperm has come into functional contact with the egg, it initiates a chain of events which constitutes fertilization. Although, as might be expected, the variations in details are legion, they do not obscure the main facts. The first reaction on the part of the egg is to prevent the entrance of other sperm and thereby to insure a free field for the operations of the first arrival. In some of the lower plants this is accomplished by instantly secreting a chemical substance which repels other sperm. Frequently among animals a jelly-like layer is formed about the egg, or if a membrane is already present this may be rendered impermeable or still another formed. In cases where the egg is surrounded originally by a dense and resistant wall, the tiny opening provided for the entrance of the sperm is closed. However, the accessory wrappings about certain eggs, such as those of Birds, have no relation to the present subject since they are secreted, not by the egg itself, but by glands in the wall of the oviduct, some time after fertilization has occurred, when the egg is passing down. (Fig. 169.)

The reactions of the egg cytoplasm that exclude accessory sperm are overshadowed in importance by others which upset the stable

equilibrium of the egg and render its surface permeable, so that extensive osmotic interchanges take place between the cytoplasm of the egg and its surroundings. Most often this is visible merely in a shrinkage of the cytoplasm due to loss of water, but sometimes contractions, amoeboid movements, or flowing of special cytoplasmic materials to definite regions of the egg are visible. In any event it is certain that profound changes occur in the cytoplasm —

FIG. 169. — Diagram of the egg of the domestic Fowl, before incubation.

its organization as a gamete soon gives place to a reorganization that establishes the general outlines of its subsequent development as a new individual. (Fig. 177, A, B.)

1. *Synkaryon*

Turning now to the nuclei, known as male and female GAMETIC NUCLEI, the union of which to form the single nucleus (SYNKARYON) of the zygote is the climax of fertilization. Disregarding the flagellum of the sperm, which disappears as it enters the egg, we find that the sperm nucleus moves through a quite definite path toward the center of the egg where it is met by the egg nucleus. Both the gametic nuclei now become resolved into chromosomes which lie free in the cytoplasm, while two centrosomes, each surrounded by an aster, appear and take up positions on either side of the chromosomes to form a typical mitotic figure. The two sets of chromosomes form an equatorial plate at the center of the spindle, thus establishing at once not only the mitotic apparatus for the first division of the egg, but also the intimate association on equal terms of chromosomes, with their potentialities from the two parents.

to form a common structure — the nuclear complex of the new individual. (Fig. 167, I, II.)

Such are the outstanding facts of fertilization which a host of investigators have brought to light chiefly within the past sixty years. It was not until 1839 that Schwann, with the establishment of the cell theory, recognized the egg as a cell, and sixteen years more before the sperm was similarly understood; while the first realization that fertilization is an orderly fusion of two cells to form one came during the seventies of the past century. Then it became evident that in sexual reproduction each individual contributes to the formation of the offspring a single cell, in which must be sought the solution of the problems of sex, fertilization, development, and inheritance. However, the concentration of attention on the cell has not simplified the solution of these fundamental problems; but rather it has contributed to an ever-increasing appreciation of the complexities of cell phenomena and the difficulties of formulating them in general terms.

With a realization of the intricacies of the phenomena involved and that they are *cell* phenomena, we may turn to a consideration of the significance of fertilization.

2. *Significance of Fertilization*

Quite naturally the original view, emphasized during many centuries, was that fertilization fundamentally is reproduction, and echoes of this idea are preserved in certain present-day hypotheses, on the basis of such facts as the following. The mature egg pauses in development and usually comes to naught unless fertilized — the entrance of the sperm affording a necessary stimulus for the resumption of cell division which is to transform the egg into the adult. Again, the egg typically contains only half the somatic chromosome complex (simplex group, haploid number) and most of the cytoplasm, while the sperm contributes a reciprocal simplex group of chromosomes; in short, transforms what is, apparently, a half into a whole.

However, it does not necessarily follow from these facts that fertilization is primarily reproduction. The evidence against this conclusion is derived largely from the relations of fertilization and reproduction in the Protista, and from the development, in certain cases, of eggs without fertilization, or by parthenogenesis. A single example of each class of facts will suffice.

PROTISTA. The life histories of nearly all Protozoa and Proto-phyta that have been carefully studied include a period in which fertilization occurs. Under usual environmental conditions, *Paramecium*, for instance, reproduces by binary fission two or three times a day so that in a remarkably short period the one cell is replaced by a host of descendants. Sooner or later, however, the individuals exhibit a tendency to unite temporarily in pairs, or CONJUGATE. During conjugation complicated changes take place in the nuclei of the cells, involving chromosome reduction and the formation of two gametic nuclei in each individual of the pair of conjugants. Then one of the gametic nuclei in each conjugant migrates over and fuses with the stationary gametic nucleus of the other to form a synkaryon, or fertilization nucleus, in each cell. After this the two *Paramecia* separate, reconstruct their characteristic vegetative nuclear apparatus, and proceed to reproduce by division as before. (Fig. 170.)

This is fertilization in *Paramecium*, and it is generally conceded that the primary significance of synkaryon formation must be sought among unicellular forms of which this is an example. Accordingly a large amount of experimental breeding has been carried out on *Paramecium* and its allies. The earlier results seemed to demonstrate conclusively that *Paramecium* can divide only a limited number of times, say a couple of hundred, after which the cells die from exhaustion or SENILE DEGENERATION unless fertilization takes place. In other words, it was believed that periodic REJUVENATION by fertilization is a necessity for the continuance of the life of the race. And therefore, so the natural conclusion ran, protoplasm is unable to grow indefinitely; there is an inherent tendency for the destructive phases of metabolism to gain ascendancy over the constructive, and fertilization serves to maintain or restore the youthful condition and thus secure the continuance of the race.

In this connection, the life history of *Paramecium* from one period of fertilization to the next is often compared to the life of a multicellular organism from its origin as the fertilized egg through youth and adult life to old age. The striking difference is that, in the case of *Paramecium*, the products of division of the animal which has conjugated (EXCONJUGANT) separate as so many independent cells, all of which are alike and, in later generations, capable of fertilization; while all the products of division of the fertilized

FIG. 170. — Diagram of the nuclear changes during fertilization (conjugation) in *Paramecium aurelia*. A, union of two individuals along the peristomal region; B, degeneration of macronucleus and first division of the micronuclei; C, second division of micronuclei; D, seven of the eight micronuclei in each conjugant degenerate (indicated by circles) and disappear; E, each conjugant with a single remaining micronucleus; F, this nucleus divides into a stationary micronucleus and a migratory micronucleus — the gametic nuclei. The migratory micronuclei are exchanged by the conjugants and fuse with the respective stationary micronuclei to form the synkarya. This is fertilization. G, conjugants, with synkarya, separate (only one is followed from this point); H, first division of synkaryon to form two micronuclei; I, second reconstruction division; J, transformation of two micronuclei into macronuclei; K, division of micronuclei accompanied by cell division; L, typical nuclear condition restored.

egg of multicellular forms remain together as a unit and become differentiated for particular functions in the individual, except a few, the germ cells, which retain the power of forming new individuals. Pushing this comparison a little further, it is stated that after fertilization in *Paramecium* we have the period of greatest cell vigor, or youth, followed by maturity when the cells are ripe for fertilization again, and in the absence of fertilization — and only then — the onset of old age, and death. Thus death has no normal place in the life history of *Paramecium*, for all the cells at the period of maturity are capable of fertilization. On the other hand, in multicellular forms only some of the cells, the germ cells, retain this power — the somatic cells have paid the penalty of specialization and must die. Thus death of the individual except by accident does not occur among unicellular forms because fertilization 'rejuvenates' the cell, and the cell and the individual are one and the same. With the origin of multicellular forms, involving the segregation of soma from germ, death became possible, and was established — it is the 'price paid for the body.' (Figs. 154, C, D; 181.)

Suggestive as is this comparison and contrast — and it is not without some justification — the cardinal fact remains that recent work has demonstrated that *Paramecium*, under favorable environmental conditions, can continue reproduction indefinitely, at least for twenty years and some twelve thousand generations, without fertilization and without any signs of degeneration. In other words, fertilization is not a necessary antidote for inherent senescence, and this, taken in connection with other data which point in the same direction, such as the fact that in many plants sexual propagation is seldom if ever resorted to, renders it fairly safe to make the general statement that the need of fertilization is not a primary attribute of living matter. Now, reproduction *is* such an attribute and therefore the evidence at hand indicates that reproduction and fertilization are intrinsically separate processes which, however, have become closely associated, especially in higher forms.

So far our conclusion is entirely negative — fertilization is not reproduction and is not intrinsically necessary for reproduction. What then is its significance? Though fertilization may not be necessary in the life of simple organisms under favorable conditions, this does not indicate that it may not be a stimulus to protoplasmic activity when it does occur — perhaps a very important

factor under special environmental conditions. Indeed there is no doubt that conjugation in certain cases directly results in stimulating the vital processes of the cell, including reproduction. But it

FIG. 171. — Diagram of the nuclear changes during endomixis in *Paramecium aurelia*. A, typical nuclear condition; B, degeneration of macronucleus and first division of micronuclei; C, second division of micronuclei; D, degeneration of six of the eight micronuclei; E, division of the cell; F, first reconstruction micronuclear division; G, second reconstruction micronuclear division; H, transformation of two micronuclei into macronuclei; I, micronuclear and cell division; J, typical nuclear condition restored.

would seem that the essential factor in this stimulation is *not* the essence of fertilization, which is *syngaryon formation*, and for this reason. In *Paramecium*, for example, an internal nuclear reorganization process known as **ENDOMIXIS** occurs periodically, which

is carried on by each cell without the coöperation of another cell, and therefore *without* synkaryon formation. Nevertheless it apparently effects a physiological stimulation similar to that which follows synkaryon formation during fertilization. Accordingly the factor common to both fertilization and endomixis, that is general nuclear reorganization, and not synkaryon formation which is peculiar to fertilization, must be responsible for the 'dynamic' effects. (Fig. 171.)

METAZOA. Turning from *Paramecium* and its allies, we may consider some evidence among higher forms in regard to the dynamic influence of fertilization. Although fertilization is usually necessary for the resumption of the series of cell divisions which paused after the maturation divisions, and which are to transform egg into adult, there are many exceptional but entirely normal cases where the egg proceeds to divide of its own accord. Such **PARTHENOGENETIC** eggs are formed like other eggs, though sometimes without synapsis and therefore without chromosome reduction. Thus the eggs of the Honey Bee, to cite the most interesting case, develop either with or without fertilization — fertilized eggs forming females and unfertilized eggs, males. Certain species of Rotifers and Roundworms apparently reproduce solely by parthenogenesis, males not being known. Leaving out of the question the effect on the chromosome complex, it is at once apparent that the mere fact that an egg divides without the influence of a sperm indicates clearly that, in such cases at least, neither structural additions nor physiological influences of the sperm are necessary to initiate development.

It may with justice be urged, however, that such cases of normal parthenogenesis are special adaptations to peculiar conditions in which the egg has usurped, as it were, the usual sperm function, and that therefore the evidence is of little weight in determining the primary significance of fertilization. Accordingly the data from so-called **ARTIFICIAL PARTHENOGENESIS** are particularly cogent. Within recent years it has been found that the eggs of a considerable number of Invertebrates and even of Vertebrates, such as some Fishes and Frogs, which normally require fertilization, can be induced to start development parthenogenetically by various artificial means such as subjection to certain chemicals, unusual temperature changes, shaking, or the prick of a needle — the effective stimulus varying with different species.

Just what happens in the egg as a result of such treatment is open to discussion, but for our purposes it is sufficient to know that the egg begins to divide in normal fashion. This shows conclusively that even eggs which normally require fertilization are intrinsically self-sufficient at least to start to develop, and therefore this strongly indicates that an incidental and not the main function of fertilization is to stimulate cell division.

Restating the evidence in its bearings on the meaning of fertilization, we may say that fertilization is not fundamentally an indispensable event in the life history of the Protozoa living under favorable environmental conditions; and further that whatever stimulus is associated with fertilization is also provided by endomixis which does not involve synkaryon formation. Similarly in the Metazoa, both normal and artificial parthenogenesis indicate that the egg itself comprises a mechanism which is capable of initiating and carrying on development. From this viewpoint, fertilization may be satisfactorily interpreted as a means of insuring under special or unfavorable environmental conditions in unicellular organisms, and under usual conditions in the eggs of multicellular forms, a suitable stimulus which otherwise might be unavailable at the proper time.

Granting then that one aspect of fertilization is dynamic, what is its main significance? Many lines of evidence surely converge toward the view that the opportunities which fertilization affords for changes in the complex of the germ are of paramount importance. Fertilization establishes new duplex groups of hereditary characters by combining diverse simplex groups from the two gametes. Careful studies show, in *Paramecium*, for instance, that variation is greater after than before fertilization, and therefore that the process affords new combinations, some of which will more effectually meet — be better adapted to — the exigencies of the environment, and so have a survival value for the organism in the struggle for existence. So whatever the primary meaning of fertilization may be, its importance in establishing the essentially dual nature of every sexually produced organism is settled beyond dispute, and it is the cardinal fact of heredity.

It may seem strange that such a fundamental phenomenon and one so generally distributed throughout the animal and plant kingdoms should so long have eluded solution. The truth probably is that therein lies the secret of the difficulty. Whatever

fertilization may have been originally, it is no longer a simple process, but has undergone specialization hand in hand with that of other functions and with the structure of organisms. To-day one or another of its various aspects — rejuvenation, stimulus to development, control of variation, or basis of biparental inheritance — may assume the chief rôle or, at any rate, loom largest in the mind of the student.

Reproduction, in the final analysis, is division — cell division or the detachment of a portion of the substance of a living organism to constitute another. Fertilization is a phenomenon associated with reproduction — so closely associated in nearly all organisms that the two processes, evolving together from relative simplicity to great complexity, have reciprocally influenced one another until in higher forms they seem to be related as cause and effect, and reproduction becomes dependent on fertilization. The popular idea that fertilization *is* reproduction is due to the fact that in higher organisms, if fertilization is to occur at all, it must take place at that period in the life history when the individual is but a single cell detached from the parent — that is, *at* reproduction.

CHAPTER XXI

ANIMAL DEVELOPMENT

The student of Nature wonders the more and is astonished the less, the more conversant he becomes with her operations; but of all the perennial miracles she offers to his inspection, perhaps the most worthy of admiration is the development of a plant or animal from its embryo. — *Huxley*.

THE new individual, established by the orderly merging of a cell detached from each parent in sexually reproducing species, has before it first of all the problem of assuming the adult form by a complicated developmental process. As we have shown, this involves cleavage of the egg, followed, in the Metazoa, by blastula and gastrula stages during which the primary germ layers are established — the fundament out of which the definitive form, organs, and organ systems of the adult are evolved. The description and comparison of these processes in different organisms constitute the content of one aspect of EMBRYOLOGY.

It is unnecessary — indeed, it is impossible — for us to survey the immense field included under embryology. We must be satisfied with the realization that animal development, though it varies widely in producing the immensely diverse body forms, exhibits throughout a thread of similarity in its fundamental features; and the appreciation of the marvellous intricacy of the developmental process even in the lowly animals. This perhaps may be gained by concrete examples — first the embryological development of the Earthworm from the zygote to the establishment of the general body plan.

A. EMBRYOLOGY OF THE EARTHWORM

The egg of the Earthworm, after fertilization, proceeds to divide first into two cells, then four cells, eight cells, and so on, with more or less regularity, until a condition is attained in which many relatively small cells are arranged about a central cavity. This stage of the embryo will be recognized as the blastula.

The various cells of the blastula appear essentially the same ex-

cept that those at one end are somewhat larger than at the other. The larger cells now sink into and nearly obliterate the central cavity of the blastula, thus forming a typical gastrula stage com-

FIG. 172. — Early stages in the development of the egg of a Sea Urchin. *A-F*, cleavage and formation of the blastula; *G*, section of blastula showing the beginning of gastrulation; *H-I*, early and later gastrula stages. *a*, ectoderm; *b*, endoderm; *c*, blastocoel; *d*, blastopore, leading into the enteric cavity; *e*, cells, arising from the endoderm, destined to form the mesoderm.

posed of two layers of cells, ectoderm on the outside and endoderm on the inside. The infolded endoderm pouch (ENTERIC POUCH) enclosing the enteric cavity eventually becomes the main part of the alimentary canal of the worm, its present opening to the exterior (BLASTOPORE) forming the mouth. So the developing worm

has now reached a transient state which is broadly comparable to the permanent adult condition of Hydra. (Figs. 172, 173.)

While these two primary germ layers are being established, the developing embryo shows the rudiments of the third primary germ layer (mesoderm) in the form of two cells (POLE CELLS) which leave their original position in the wall of the embryo and take up a place between the ectoderm and endoderm; that is, in the remnant of the cavity of the blastula which the invagination process during gastrulation has not completely obliterated. Here the pole cells, by division, form on either side of the enteric pouch a linear series, or band, of mesoderm cells. These MESODERM BANDS gradually increase in size and spread out until finally they unite above and below, that is encircle, the enteric pouch. Thus they form a continuous mesoderm layer between ectoderm and endoderm. Simultaneously with the growth of the mesoderm bands to form a definite middle layer, a linear series of spaces appears in each band which presages the future segmentation of the worm's body. These cavities increase in size and, when the bands unite around the enteric pouch, the corresponding cavities of each band also become continuous in the same regions. (Fig. 173, *C-H*.)

In this way the mesoderm itself becomes divided into what are essentially two cellular layers, an outer, or SOMATIC LAYER, next to the ectoderm, and an inner, or SPLANCHNIC LAYER, in contact with the endoderm. The space between these layers of the mesoderm is the body cavity, or coelom. The coelom, however, is not a continuous cavity from one end of the embryo to the other, because the mesodermal cells which separated the linear series of cavities in the respective mesodermal bands persist. These cells form a regular series of connecting sheets of tissue between the somatic and splanchnic mesoderm layers and thus divide the body of the worm into a series of essentially similar segments, the limits of which are indicated on the outside by a series of grooves which encircle the worm's body. (Fig. 173, *I, J*.)

While these processes are transforming the two-layered gastrula into an embryo composed of three primary layers, and exhibiting segmentation, coelom, etc., — in short, the 'tube within a tube' body-plan characteristic of higher forms — the embryo is gradually increasing in size and elongating. The mouth, representing the blastopore, remains at one end, which is therefore designated as anterior, while growth is chiefly in the opposite direction or

FIG. 173. — Development of the Earthworm. *A*, blastula (within a membrane); *B*, section of blastula; *C*, later blastula; developing mesoderm bands; *D*, start of gastrulation; *E*, gastrula showing invagination, which leaves the mesoderm bands on either side of the body as indicated by the cells with dotted outline; *F*, section of *E*, along the line *s-s* to show pole cells, mesoderm bands, and enteric cavity; *G*, later stage showing cavities in the mesoderm bands; *H*, the same (*G*) in cross section; *I*, longitudinal section after formation of mouth and anus; *J*, the same in cross section; *K*, later stage in cross section. *al*, alimentary canal; *an*, anus; *ar*, enteric cavity; *coe*, coelom; *ec*, ectoderm; *en*, endoderm; *m*, pole cells; *m*², mesoderm; *mh*, mouth; *n*, nerve cord; *s*, cavity of segment; *sc*, blastocoele; *sm*, somatic mesoderm; *spl.m.*, splanchnic mesoderm. (From Sedgwick and Wilson.)

toward the posterior. At this end (the blind end of the enteric pouch formed at gastrulation) an opening to the exterior, the anus, is formed so that the enteric pouch now communicates with the exterior at both ends and becomes the alimentary canal. Thus antero-posterior differentiation is clearly established.

A cross section perpendicular to the main axis of the developing worm at this stage presents the appearance of a circle within a circle. The smaller circle surrounds the enteric cavity and is the wall of the alimentary canal. It is separated by a space, the coelom, from the larger circle, or body wall. Moreover, each of these circles is composed of two tissue layers: the alimentary canal, formed internally of endoderm and externally of splanchnic mesoderm; and the body wall, internally of somatic mesoderm and externally of ectoderm. Thus the coelomic cavity is entirely enclosed by mesoderm. (Fig. 173, *K*.)

It is from these three primary layers of cells (ectoderm, somatic and splanchnic mesoderm, and endoderm) that all of the tissues and organs of the adult worm arise through later differentiation, thickenings, foldings, outgrowths, etc. For example, the nervous system is formed by the ingrowth of a thickened region of the ectoderm; the blood vascular system develops by a specialization of cells throughout the mesoderm; while the reproductive system first appears as thickenings of the somatic mesoderm which, as development proceeds, become largely separated from it as independent organs in the coelom. (Figs. 85-87.)

B. EMBRYOLOGY AND METAMORPHOSIS OF THE FROG

As an example of Vertebrate development we may take that of the Frog, though it must be borne in mind that just as other Invertebrates differ in their embryology from the Earthworm, so the embryology of other Vertebrates departs widely from that of the Frog — chiefly fundamental and highly significant similarities persisting.

The fertilized egg of the Frog contains a large amount of stored food material, or yolk, which influences the character of the cleavage of the egg. Thus cell division is progressively more rapid, and accordingly the cells smaller, in the region with little yolk, the upper (animal) pole, than in the yolk-laden lower (vegetal) pole. The first and second division planes are from pole to pole, and give rise to four cells of equal size. The third division plane

FIG. 174. — Early development of the Frog. *A, B, C*, egg at two-, four-, and eight-cell stage; *D*, early blastula; *E*, section of *D*; *F*, late blastula; *G*, early gastrula: overgrowth of ectoderm (cells of ectoderm now too small to be shown in figure); *H*, section of *G* showing germ layers, etc. (*Blcl.*, blastocoel); *I*, late gastrula: formation of neural groove and folds representing the foundations of the nervous system; *J*, older embryo, with neural groove closed, assuming tadpole form; *K*, section of *J*.

is just above the equator of the egg, at right angles to the former planes, and establishes four dark, pigmented cells above, and four larger pale, yolk-laden cells below the equator. As division proceeds, soon there are many cells arranged in the form of a hollow sphere which will be recognized as the blastula. (Fig. 174.)

The transformation, in due course, of the blastula into the gastrula by typical invagination is somewhat obscured by the large amount of yolk in the prospective endoderm cells. In fact, the endoderm is formed by a flat infolding of cells, just below the edge of the small dark cells, that finally results in a crescentic groove on the surface, which is the edge of the blastopore. But gastrulation is not completed until all the large endoderm cells are enclosed by ectoderm cells, and this is accomplished chiefly by the latter gradually creeping and folding over the exposed, pale endoderm cells (YOLK PLUG) until merely a small blastopore remains leading into the enteron.

The development of the third germ layer, or mesoderm, takes place by the ingrowth of a layer of cells between ectoderm and endoderm along the edge of the blastopore where these two layers merge. When the mesoderm has grown forward and spread out between the ectoderm and endoderm, the lower portion (LATERAL PLATE) splits into a somatic and splanchnic layer and thus gives rise to the coelomic cavity between. The upper portion of the mesoderm (VERTEBRAL PLATE) exhibits traces of primitive segmentation as it forms a series of muscle plates, or MYOTOMES, on either side of the NOTOCHORD which, in the meantime, has arisen from an axial, dorsal strip of endoderm.

During the later stages of gastrulation, the foundations of the central nervous system are established by the differentiation of a plate of ectoderm cells, the MEDULLARY PLATE, on the dorsal surface of the embryo. Then a groove appears in the medullary plate which is finally completely enclosed by the growth upward, over, and then fusion of the edges of the medullary plate. Thus the open groove is converted into the NEURAL TUBE which is soon to be differentiated into fore-brain, mid-brain, hind-brain, and spinal cord.

Simultaneously with the establishment of the central nervous system, the differentiation of the enteron into the alimentary canal, opening by mouth and anus, and also various other internal transformations have proceeded apace. Furthermore, the embryo

has been gradually elongating so that it is nearly twice as long as broad by the time it begins locomotion by means of cilia distributed over the body surface. And soon thereafter the larva, or TADPOLE,

FIG. 175. — Larval development and metamorphosis of the Frog. 1, tadpole, just hatched, ventral aspect; 2, 3, older tadpoles, side view; 4, 5, later stages, dorsal views showing external gills and development of operculum; 6, tadpole with the gills covered, leaving only a small opening on the left side; 7, older stage, right side, showing further development; 8 and 10, lateral view of two later stages showing development of hind-legs; 9, dissection of tadpole to show internal gills, spiral intestine, and anterior legs developed within operculum; 11, advanced tadpole just before metamorphosis; 12, 13, 14, stages in metamorphosis, showing gradual resorption of tail; 15, juvenile frog after metamorphosis. (From Newman, after Leuckart and Nitsche.)

assumes a somewhat fish-like form, with a vertically flattened tail edged by a fin which provides for locomotion during the rest of the animal's purely aquatic life. (Fig. 175.)

Independent existence demands sense organs, and these are

already functioning in the head region. It also demands the intake of food which earlier was supplied by the yolk stored in the egg, and so the mouth develops a hard rim for scraping food material from the surface of aquatic plants. Moreover, increased respiration is necessary, and this is met by the appearance of branched external gills on the sides of the head, which are the first of a series of three different respiratory organs that succeed one another during the life history. Indeed, these external gills are soon covered over by a fold of the skin, the OPERCULUM, which finally leaves but a single opening, the SPIRACLE, to the exterior. And no sooner is the operculum fully developed, than the external gills are resorbed and a new set of fish-like internal gills take their place in the gill slits. Then hind-legs slowly make their appearance, followed by the fore-legs, already developed under the operculum.

Now the larva is ready for METAMORPHOSIS — its transformation from a gill-breathing tadpole to a lung-breathing juvenile Frog. During metamorphosis one stage melts rapidly into the next: the tail is resorbed, the legs increase in size, the long coiled intestine becomes shorter and specialized to digest animal food, the internal gills are resorbed, and lungs are developed which make it necessary for the tadpole to come to the surface of the water for air. Finally, as a juvenile Frog, the animal transfers its abode largely to land, and grows.

The process of metamorphosis varies in length from a few weeks to several years in different species of Frogs. In all cases it is sometime after metamorphosis before sexual maturity arises. Preceding the first breeding season, the gonads develop rapidly, their ducts become fully differentiated, and adult male and female individuals are established. (Fig. 132.)

C. EMBRYONIC MEMBRANES OF THE HIGHER VERTEBRATES

The embryological development of the higher Vertebrates departs rather widely in certain ways from that of the Earthworm and the Frog, chiefly as a result of adaptations to terrestrial life. Thus the eggs of Reptiles and Birds contain much more yolk than the egg of the Frog, with a consequent greater obscuring—though not obliteration—of the characteristic blastula, gastrula, etc. Furthermore, the development of various EMBRYONIC MEMBRANES, to meet new conditions of embryonic existence, makes possible not

FIG. 176. — Diagrammatic figures illustrating the formation of the embryonic membranes of a Mammal. *A*, embryo before appearance of amnion; *B*, embryo with yolk-sac and developing amnion; *C*, embryo with amnion closing and developing allantois; *D*, embryo with villous subzonal membrane, and with mouth and anus; *E*, embryo in which vascular layer of allantois is applied to subzonal membrane, and has grown into the villi of the latter forming the fetal placenta; yolk-sac reduced; amniotic cavity increasing. (From Hegner, after Kölliker.)

only a more rapid and sure interchange of materials between the embryo and its surroundings, but also affords greater protection for the growth of complicated structures. Finally, the eggs of Mammals, including Man, though not provided with so large an amount of yolk because food is supplied to the developing embryo by the blood vascular system of the mother, nevertheless inherit, as it were, from lower forms the embryonic membranes. These are, in part, modified and diverted to meet new conditions demanded by the uterine life of the Mammalian embryo. (Figs. 133, 134, 169, 176.)

With merely this outline of some of the chief features of the embryology of the Earthworm, Frog, and higher forms before us, it is possible to gain some appreciation of the similarity of the basic method of development which is ever present in the animal kingdom—cleavage, blastula, gastrula, primary germ layers, etc. In general, it may be said that in all the higher animals the ectoderm forms the outer skin and nervous system; the endoderm supplies the lining membrane of the major part of the alimentary tract; while the mesoderm contributes muscles, blood vessels, reproductive organs, and the membrane lining the coelom. This similarity in origin of the organ systems from the primary germ layers, throughout the animal series above *Hydra* and its allies, is of the highest significance because it indicates a fundamental structural similarity in the body plan of all these forms. It is exhibited in the developmental process in each generation, even though the adult body in the various groups differs widely in form and arrangement of organs. Such a state of affairs clearly suggests an hereditary relationship throughout the animal series—the origin of the diverse forms by evolution. (Figs. 172, 174.)

D. PROBLEMS OF DEVELOPMENT

Embryology is something more than the description of the kaleidoscopic series of stages which seem to melt one into the other as development progresses. It attempts, especially at the present time, to look below and beyond structure to the processes involved, and to determine how the sequence of events is brought about. This is but a repetition of the stages of progress in all science; a passage from the *descriptive* to the *experimental*. The results thus far secured have raised many, and answered some problems of

development that are of great practical importance and theoretical interest.

From what the pioneer students of embryology during the seventeenth and eighteenth centuries saw, or thought they saw, with simple lens and newly invented compound microscope, there were gradually formulated two opposing views of development which, though long since swept aside in their original form as a result of the increase of knowledge, raised the problem of problems that is still before the embryologist to-day.

In brief, one view virtually denied development by maintaining that the adult organism is nearly or completely formed within the germ, either in the egg or the sperm, which merely by expansion, unfolding, and growth gives rise to the new generation. In this first crude form the PREFORMATION theory demanded the 'encasement' of all future generations one within another in the germ of existing organisms, so that when it was computed that the progenitor of the human race must have contained some two hundred million homunculi (a conservative estimate, to say the least) the *reductio ad absurdum* was irresistible.

The other view was reached by careful studies on the transformation of the Hen's egg into the chick which soon made it clear that the chick is not preformed in the egg. The embryo arises by a gradual process of progressive differentiation from an apparently simple fundament—it is a true process of development, or EPIGENESIS. But the upholders of epigenesis versus preformation were before long beyond their depth and in danger of attempting to get something out of nothing—lost in the miraculous!

A statement in such succinct form tends to accentuate the crudities of these two conflicting views—"preformation explaining development by denying it and epigenesis explaining development by reaffirming it"—and it may be well to remark that the early embryologists with the means at their command faced a stupendous task of which only recent work has brought a full appreciation.

The path to progress cleared by the realization that adult structures are not preformed as such in the egg, and that development is not an expansion but the formation—the 'becoming'—by an orderly sequence of events of structures of great complexity out of apparent simplicity, the problem of the embryologist was to determine what the egg structure actually is, and how it is related to that of the adult. To trace the development of these studies

would involve the history of embryology since the formulation of the cell theory. We must confine ourselves to the bare statement of the new guise in which the old theories of preformation and epigenesis confront us to-day as a result of recent research.

The reader already recognizes the fertilized egg as a cell, with its nucleus comprising a complex of quite definite elements — the chromosomes — contributed jointly by the two gametes. To this extent, then, the nucleus and therefore the egg exhibits a ready-formed structural basis which (as we have already suggested, and will have occasion to elaborate later) seems to be definitely related to characters which appear in the offspring.

Turning to the egg cytoplasm, we are confronted with conditions which are not so uniform but nevertheless highly suggestive. In the first place, before fertilization the egg possesses a definite POLARITY, expressed, for example, in the position of the nucleus and the distribution of food material (yolk), pigment granules, and vacuoles. This polarity is traceable, in part at least, to the polarity of the oögonia, and through them to the germinal epithelium. In brief, the egg as a whole is *organized*; the invisible organization of the fundamental matrix of the cytoplasm being revealed, in part, by the disposition of various elements of the cell. Now in some cases this cytoplasmic organization remains essentially undisturbed at fertilization and persists as that of the zygote, while in others it is superseded sooner or later by a reorganization which establishes that of the new organism. Herein, apparently, is to be sought the explanation of the difference in behavior — in potentialities — of various types of eggs during cleavage stages. Clear-cut examples of the two chief types will serve to bring the main facts before us.

The *first type* is well illustrated by the egg of a Mollusc, Dentalium, and a primitive Chordate, Styela. The egg of the latter shows at the first division five clearly differentiated cytoplasmic regions. For the sake of simplicity these may be described as white, light and dark gray, and light and dark yellow. As cleavage proceeds, these substances are distributed with great regularity to definite cell groups, which in turn form special organs or organ systems of the animal. Thus cells which receive the white region form the ectoderm; those which receive the dark gray, the endoderm; while the cells with light or dark yellow form mesodermal structures, and so on. And further, the experimental removal of a

FIG. 177. — Development of a Mollusc (*Dentalium*), after removal of the 'polar lobe.' A, egg, shortly after being extruded and before maturation is completed, showing three differentiated regions. B, section through an egg after fertilization, showing cytoplasmic rearrangement involving the segregation of clear polar lobe at *p*. C, normal eight-cell stage with polar lobe in cell D; D, normal sixteen-cell stage, with materials of polar lobe now in cell X; E, sixteen-cell stage, from an egg with the polar lobe removed at the first division; F, normal larva at end of twenty-four hours; G, larva (abnormal) of same age developed from egg from which polar lobe was removed; H, normal larva of seventy-two hours. I, abnormal larva of same age from 'lobeless' egg. (From Kellicott, after Wilson.)

cell or cell group in which a certain substance is segregated results in an embryo deficient in the very structures which this normally forms. In other words, the egg cytoplasm seems to be a mosaic of ORGAN-FORMING SUBSTANCES, which either themselves directly, or through more fundamental conditions of which they are but the visible expression, have a causal relation to definite adult structures. Just in so far as this is true, the adult is *predelineated* in bold lines, though not actually preformed, in the egg. (Fig. 177.)

Passing now to the *second type*, represented by the eggs of Amphioxus and the Sea Urchins, the results which we obtain seem to be diametrically opposite. Although in the egg of the Sea Urchin more or less clearly differentiated cytoplasmic regions appear to exist, the removal of a part of the egg before division, or of one or more cells during cleavage, blastula, or gastrula stages, has no permanent effect on the structural integrity of the developing embryo. Furthermore each of the cells, apparently even as late as the eight-cell stage, has the power to develop into an embryo complete in every respect, but smaller than the normal. Or, to put it another way: at the eight-cell stage, a single cell which normally forms, let us say, one-eighth of the embryo, if isolated with two other cells, will form one-third of a normal embryo; if isolated with three other cells, will form one-quarter; and so on. What now has become of the egg organization? Or, if we lean toward a mechanistic interpretation of development or life, what kind of a 'machine' is it which has such potentialities? (Fig. 178.)

At first glance the behavior of these two classes of eggs seems to afford results which are irreconcilable — the former supporting the doctrine of preformation in a refined form, and the latter its antithesis, epigenesis. But an explanation is not far to seek. The difference apparently depends upon the time when differentiation of the egg cytoplasm is chiefly established. If this occurs before or at fertilization, so that the early divisions give rise to dissimilarly organized cells, then each of the cells is not TOTIPOTENT and the mosaic type of development results; but if the initial differentiation is delayed until later, or is relatively slight so that the cells of the early stages are all essentially similar, then during this period each cell is totipotent — the whole forms an EQUIPOTENTIAL SYSTEM — as exhibited by the early stages of the Sea Urchin. Thus we may bring under one viewpoint the apparently

contradictory behavior of the two classes of eggs, for it turns out to be reducible to the common factor, *differentiation*. In one case this has progressed further than in the other during the early embryonic stages. In both cases, therefore, development is epigenetic in its obvious features. (Fig. 179.)

However, since cytoplasmic differentiation is a fact whether it appears early or late, we have merely pushed the solution of the

FIG. 178. — Diagram to show development of whole eggs and isolated cells of the two-cell stage. *A*, *Dentalium*: at the left, development of the whole egg; at the right, development of the first two cells, when separated, into two *abnormal* larvae. *B*, *Amphioxus*: identical experiment at the two-cell stage resulting in two *perfect* small larvae. (From Wilson.)

problem further back and the question becomes: Is there a primary differentiation and, if so, where? It is not possible to present here the specific evidence on this point, but the reader's knowledge of the nucleus, and particularly its definite chromosomal architecture, will lead him to anticipate that modern research tends more and more to emphasize the chromosome as representing a material configuration — a packet of chemicals, may we say — which is transmitted, in a way, 'preformed' from generation to generation

and determines the cytoplasmic characteristics of the cells. As to how the specific physical basis of inheritance, constituting the chromosomes, is related to cytoplasmic organization and to characters which arise later, we can offer no satisfactory explanation or even guess. We must be content with a discussion, in the next

FIG. 179. — Diagram of zones of cytoplasmic differentiation and their distribution at the first division of the egg. *A*, immature egg, assumed to have no definite segregation of cytoplasmic stuffs; *B*, mature egg, with cytoplasmic zones established; *C*, first division of egg; *D* and *E*, two types of two-cell stages; *D*, Dentalium or Styela type, with one cytoplasmic zone entirely distributed to one of the cells, and therefore each of the two cells, if separated, gives rise to an abnormal larva; *E*, Sea Urchin or Amphioxus type, with equal distribution of the zones to both cells, and therefore, if separated, each of the two cells gives rise to a normal larva. (From Wilson.)

chapter, of some of the facts of heredity which show that certain chromosomes are causally related to the inheritance of certain characters.

But in so far as the nucleus possesses an organization which is definitely related to differentiations of the cytoplasm, organ-forming substances, or characters of embryo and adult, we may look upon the chromatin to this extent as representing a sort of

primary preformation which is realized by a process of building up — epigenesis — as one character after another becomes established in the development of the individual. This is the guise in which the old problem of preformation versus epigenesis faces the biologist to-day.

So the early embryologists were right when, studying the egg of the Frog or Hen, they maintained that development *is* development and not merely the unfolding of an organism already fashioned in more or less definite adult form. But it took two centuries of research to reveal the fact that, below and beyond its superficial aspects, there is a germ of truth in the principle of preformation hidden in the nuclear architecture — that the origin of the individual, though obviously through epigenesis, is fundamentally from a sort of preformed basis. We no longer bother ourselves with the old conundrum as to which is more complex, the egg or the adult, but recognize that each is complex in its way — the simplicity of the egg being more apparent than real, as is attested by every endeavor to analyze cytoplasm, nucleus, chromosomes, chromatin, and beyond.

CHAPTER XXII

INHERITANCE

So careful of the type . . .

So careless of the single life. — *Tennyson*.

THE old adage that 'like begets like' expresses the general fact of HEREDITY. Everyone recognizes that parent and offspring agree in their fundamental characteristics: they 'belong to the same species.' And everyone realizes that the resemblance may be strikingly exact even in details of form or behavior. Family traits crop out. The mere statement of striking resemblances among the individuals of a family is a tacit admission that no two individuals are exactly alike; in other words, heredity is "organic *resemblance* based on descent"—inheritance of the characters exhibited by the parents is not complete, there is VARIATION. Indeed "variation is the most invariable thing in nature," but one must guard against the impression that there is an antithesis between heredity and variation. "Living beings do not exhibit unity and diversity, but unity in diversity. Inheritance and variation are not two things, but two imperfect views of a single process."

We may now address ourselves to the problems of heredity and variation which are at the basis not only of what organisms have been in the past and are at the present, but also of whatever the future may have in store for them. Variations are the raw materials of evolutionary progression or regression. From a broad point of view, the origin of species and the origin of individuals are essentially the same question. If we can solve the relations of parent and offspring, the origin of species will largely take care of itself. As a matter of fact, historically the question of species origin was approached first, and through the work of Darwin became of paramount interest in the latter half of the nineteenth century. The twentieth century finds the individual—the hereditary relation of parent and offspring—the center of investigation, and it forms the science of genetics. ORGANIC EVOLUTION attempts to establish the general fact that all organisms are related by descent; GENETICS attempts to show how specific individuals are related.

Even further has the pendulum swung from the general to the particular. To-day the most intense investigation is centered not on the heritage of the individual as a whole, but on particular characters of the individual. The concept has arisen from recent experimental work that, for practical purposes, the individual may be regarded as an aggregate of essentially separate characters, both structural and physiological, that are relatively stable and may be inherited more or less as units. But the analysis does not stop even at this level. Each character is regarded as represented in the chromosomes of the germ cells by one or more determining factors, or GENES; and whether or not a given character will be present in a tree or a man depends upon whether the genes for this particular character entered into the nuclear complex of the fertilized egg which formed the individual. Therefore, geneticists are now studying the relative positions which the genes occupy on certain chromosomes; how they may 'cross-over' from one chromosome to the other of a synaptic pair; how they mutually influence one another, etc.

At present we are witnessing great advances in knowledge of the underlying factors of heredity, and the data recently accumulated are so vast that we can attempt here no more than to indicate the character and promise of the principles already discovered.

We may survey the field before us by a concrete example. About twenty-five years ago, just at the opening of the modern concentrated attack on genetic problems, an association of British millers awoke to the fact that some active means must be taken to offset the increasingly great deficiency in quantity and quality of the wheat yield. Accordingly they commissioned a specially trained biologist to investigate the matter. He collected many different varieties of domestic and foreign Wheat, each known to have one or more good qualities, and studied how these were inherited. Making use of the data thus secured, in the course of a few years he produced a wheat which combined the good qualities of several varieties; including high content of gluten, beardlessness, immunity to Rust, and large yield. And this 'made to order' wheat proved successful in the British Isles. But with the opening up of new territory in western Canada another obstacle was encountered: the growing season was too short for the finest varieties of wheat. This condition was quickly met by transferring the quality of early ripening from an inferior grade of wheat to a wheat possessing several other valuable characters.

In a similar fashion, a host of workers have performed the impossible of a few years ago. Corn of desirable percentage content of starch or sugar; cotton with long fibers of foreign varieties and quick maturing qualities to escape insect ravages; Sheep combining choice mutton qualities of one breed with the fine wool of another and the hornlessness of a third; and so on almost without end. Furthermore, there is no limit in sight to the new stable races of plants and animals which are forthcoming as the principles already known are applied, and subsidiary ones are discovered. And last

FIG. 180. — Effect of crossing two varieties of wheat, one 'bearded' and the other 'beardless.' The parents are shown on either side and the hybrid offspring in the middle. A case of so-called blending inheritance.

but not least, Man has begun to study himself as a product of heredity and the process of evolution—to determine the distribution of characters in the family, and the consequences of their combinations in the physical and mental make-up of the individual.

A. HERITABILITY OF VARIATIONS

What then are the basic principles of heredity which are to-day at the command of the scientific breeder? To answer this question it is necessary to go into some details because no real appreciation of the underlying principles involved is otherwise forthcoming. Most of these details have been acquired through patient investigations

made from the standpoint of so-called pure science—one more proof of the indebtedness of the 'practical man of affairs' to the biological laboratory.

In the Protista the problems of heredity confront us in their simplest, though by no means simple form. *Pleurococcus* or *Paramecium*, as we know, divides into two cells which through growth and reorganization soon are to all intents and purposes

FIG. 181. — Scheme to illustrate the continuity of the germplasm. Each triangle represents an individual composed of *germplasm* (dotted) and *somatoplasm* (clear). The beginning of the life cycle of each individual is at the apex of the triangle where both germplasm and somatoplasm are present. In biparental (sexual) reproduction the germplasms of two individuals become associated in a common stream which is the germplasm and gives rise to the somatoplasm of the new generation. This continuity is indicated by the heavy broken line and the collateral contributions at each succeeding generation by light broken lines. (From Walter.)

exactly similar to the parent cell. The parent has merged its individuality into that of its offspring. Thus stated, one does not wonder that parent and offspring are alike—each is composed of essentially the same protoplasm. But when we come to multicellular forms in which reproduction is restricted to special germ cells which involve fertilization, confusion is apt to arise unless one keeps clearly in mind—and perhaps exaggerates for the sake of concreteness—the distinction between germ and soma which has been

previously discussed. Since in higher forms, to which brevity demands that our attention be confined, the sole connection between parent and offspring is through the germ cells, it follows that this must be the sole path of inheritance. In other words, whatever characters the body actually *inherits* must have been represented by genes in the fertilized egg from which it has arisen: and conversely, any characters which the individual can transmit must be represented in its germ cells. (Fig. 181.)

1. *Modifications*

Every individual organism—a man, for instance—is a composite not only of inherited characters, but also of MODIFICATIONS of the soma produced by external conditions during embryonic development or later. The individual's environment, food, friends, enemies, the world as he finds it, on the one hand, and on the other his education, work, and general reactions to this environment, all have their influence on body and mind and determine to a considerable extent the realization of the possibilities derived from the germ—what he makes of his endowment. He acquires, let us say, the strong arm of the blacksmith, the sensitive fingers of the violinist, or the command of higher mathematics. In other words, what he *is* depends on his heritage and what he does with it. Now, if he does develop an inherited capacity, can he transmit to his offspring this talent in a more highly developed form than he himself received it? Or must his children begin at the same rung of the ladder at which he started and make their own way up in the world? This is the old question of the inheritance of modifications, or so-called ACQUIRED CHARACTERS.

Is the great length of the Giraffe's neck, to take a classic though crude example, due to a stretching toward the branches of trees during many successive generations, with the result that a slightly longer neck has been gained in each generation and inherited by the following? If so, it is a result of the inheritance of modifications because the changes were somatic in origin. Or is the length of the neck the result of the survival in each generation of those individuals which 'happened to be born' with longer necks and accordingly were better adapted to foliage conditions than those which varied toward shorter necks? If so, it is a result of MUTATIONS (surviving through natural selection) because the changes were germinal in origin. (Pp. 275, 276.)

To-day biologists almost unanimously deny the former and accept the latter interpretation—the consensus of opinion is certainly that modifications, or changes in the individual body due to nurture, use, and disuse, are not transmitted as such. This conclusion is held chiefly because there is no positive evidence of the inheritance of modifications while there is much negative evidence; and also because there is no known mechanism by which a specific modification of the soma can so influence the germ complex that this modification will be reproduced as such or in any representative degree. However, it should be emphasized that biologists in general recognize the potent influence of environment and the organism's reactions to the environment on the destinies of the race, even though they see, at present, no grounds for a belief that any specific modification can enter the heritage and so be reproduced.

In this connection the question of the inheritance of disease will undoubtedly arise in the reader's mind. But this is really not a special case. If the disease is the result of a defect in the germinal constitution, it may be inherited just as any other character, physiological or morphological, that has a germinal basis. But if the disease is a disturbance set up in the body by some accident of life or through infection by specific microorganisms, before birth or later, it is a modification and inheritance does not occur. Of course, it is well known that susceptibility or immunity to disease-producing organisms—the 'soil' for their development—may be inherited, but this is a different question. It may, however, be suggested in passing that from the standpoint of the individual born malformed, structurally or mentally, as a result of parental alcoholism, syphilis, or other obliquities, it probably will not appear of the first moment that the sins have been visited otherwise than by actual inheritance. (Fig. 250.)

The whole question of the non-heritability of modifications, or acquired characters, is a relatively new point of view which has been fostered by the elusiveness of crucial experimental evidence, by an ever-increasing knowledge of the details of the chromosome mechanism of inheritance, and by the general influence of Weismann's contrast of the soma and germ. Indeed, Lamarck did not question the inheritance of acquired characters and made it the corner-stone of his theory of evolution, while some have even gone so far as to say that either there has been inheritance of acquired

characters, or there has been no evolution. But the question is not so serious as that, as will be seen later on; though it obviously is profoundly important from many viewpoints, biological, educational, and sociological.

2. *Combinations*

Turning from modifications, which appear to be useless to the geneticist, and concentrating attention on characters which represent an expression of germinal factors, we see that, in the final analysis, heredity is *germinal* resemblance among organisms related by descent — a consequence of the continuity of cells by division. Hereditary differences which appear in offspring are either COMBINATIONS of ancestral characters — apparently new characters which owe their origin to recombinations of the germinal factors, genes, of old characters — or MUTATIONS due to fundamental changes in the organization of the germinal constitution or in the genes themselves.

For our purposes we may somewhat arbitrarily classify the obvious hereditary differences following fertilization which are the result of recombinations of parental characters represented in the egg and sperm: that is, cases in which nothing is apparent which is not clearly related to the conditions expressed in the ancestors. In the first place the offspring may exhibit a character, eye color let us say, of one parent to the exclusion of that of the other — the character appearing unmodified. This may be termed ALTERNATIVE inheritance. Or the offspring may seem to be a sort of mosaic of the characters of its progenitors. Each parent contributes a certain character but not to the exclusion of that of the other and without blending — the offspring exhibits MOSAIC inheritance. Sometimes the parental traits seem to fuse so that the progeny exhibit a more or less intermediate and different condition, as in the color of the skin of mulattoes. Such a result is known as BLENDING inheritance. Or again, certain characters are transmitted from males solely to female offspring. This is an example of SEX-LINKED inheritance. In still other instances characters of parents which are invisible, or 'latent,' in their children appear again in their grandchildren. This has long been known as ATAVISM. Finally, characters of still more remote ancestors may crop out, and constitute REVERSION.

3. *Mutations*

But quite different results now and then occur. Characters which have no place in the ancestry appear and are transmitted to the descendants. Sometimes these new inherited variations are only slight departures from the parental condition, while in other instances they are quite abrupt. However, there is no fundamental difference between the two classes — it is chiefly one of degree — and so we speak of all heritable variations, which are not the result of recombinations, as *MUTATIONS*. Thus combinations and mutations contrast sharply with modifications which are not transmitted to the offspring and are the results of environing conditions on the soma during embryonic development or later. The importance of this distinction can hardly be overemphasized because it makes comprehensible many of the inconsistencies of earlier work on genetics, as will immediately appear.

B. GALTON'S LAWS

The studies of Galton, a cousin of Darwin, on the inheritance of definite characters open the modern era of scientific investigations in genetics. In particular, his work on the inheritance of characters in Man, such as stature and intellectual capacity, is a biological classic judged by the momentous consequences which followed from the discussion it evoked. As a result of the statistical treatment of data, Galton formulated two principles of heredity which may be briefly stated as follows:

Law of Ancestral Inheritance. The two parents contribute between them, on the average, one-half of each inherited faculty; each of them contributing one-quarter of it. The four grandparents contribute between them one-quarter, or each of them one-sixteenth, and so on.

Law of Filial Regression. On the average any deviation of the parents from the racial type is transmitted to the progeny in a diminished degree; the deviation from the racial mean being two-thirds as great as that of the parents. (Fig. 182.)

These so-called laws, taken by and large, undoubtedly express general truths — offspring inherit much more from their immediate than from their remote ancestors; and offspring of gifted or deficient parents, judged by the average standard of a mixed population, regress toward mediocrity: that is, toward the popu-

lation average. But the 'laws' are not particularly helpful in arriving at the fundamental principles involved in heredity because the data upon which they are founded include indiscriminately both heritable variations and modifications. The individual's somatic characters, which form the data, belie in many cases the underlying germinal constitution — what will be transmitted to the progeny. Thus, for instance, experiments show that when

FIG. 182. — Scheme illustrating Galton's law of filial regression, as shown in the stature of parents and children. The circles represent the height of graded groups of parents and the arrow heads show the average heights of their children. The length of the arrows indicates the amount of 'regression' toward mediocrity. (From Walter.)

the *germinal* make-up of all the members of a population is the same, the regression is complete, no matter how far the particular parents may diverge *somatically* from the population average. The somatic divergence represents chiefly modifications which are not inherited. Conversely, when the divergence of the parents from the population average is due to characters which represent expressions of their germinal constitution, then there is no regression.

C. MENDELISM

It was reserved for Mendel to apply statistical methods to facts observed in the progeny derived from carefully controlled

FIG. 183. — Inheritance of size in a cross between a tall and a dwarf race of garden Peas. (From Morgan.)

experiments in breeding. In other words, to substitute for 'ancestral generations,' controlled pedigrees — to look forward as well as backward and thus largely to remove the unknown and unknowable quantity which rendered the materials of Galton somewhat delusive. Mendel's studies actually were made a score of years before Galton's, but failed to reach the attention of the biological world engrossed in the evolution theory; in fact were not known by Darwin to whom they would have meant so much in his work to secure experimental data in heredity. To-day Mendelism is essentially a science in itself, with its own vocabulary of technical terms. We can attempt no more than to make clear its fundamental features by a few concrete examples; the first from Mendel's own work. (Fig. 290.)

Mendel chose seven pairs of ALTERNATIVE characters which he found were constant in certain varieties of edible Peas, such as the form and color of the seeds, whether round or wrinkled, yellow or green; and the length of the stem, whether tall or dwarf: and these he studied in the HYBRIDS. One ordinarily thinks of a hybrid as a cross between two species or, at least, two characteristically distinct varieties of animals or plants; but as a matter of fact the offspring of all sexually reproducing organisms are really hybrids because two parents seldom, if ever, are exactly the same in all of their germinal characters. Consequently the offspring are hybrids with respect to the characters in which the parents differ.

1. *Monohybrids*

Mendel found, in crossing tall and dwarf varieties of Peas, that all of the progeny of this PARENTAL (P) generation, in the FIRST FILIAL (F_1) generation, were tall like one parent, there being no visible evidence of their actual hybrid character. Accordingly tallness was designated a DOMINANT (D) and dwarfness a RECESSIVE (d) character.

Mendel's next step was to follow the behavior of these characters in succeeding generations. Therefore the tall hybrids (F_1) were inbred (self-fertilized) and their offspring, the SECOND FILIAL (F_2) generation, were found to be tall and dwarf in the ratio of three to one (3D : 1d). This is now the broadly established MENDELIAN RATIO. Of course, in dealing with a small number of individuals this ratio is merely approximate; the greater the number of

offspring, the closer it is approached. In this particular case Mendel obtained 787 dominant and 277 recessive individuals. (Fig. 183.)

Continuing the work, Mendel found that the dwarfs (recessives) when inbred gave only recessives generation after generation, and accordingly were pure. On the other hand, the tall plants (dominants) when inbred proved to be of two kinds: one-third pure dominants which bred true indefinitely, and two-thirds hybrids like their parents, giving when inbred the same ratio of three dominants to one recessive in the THIRD FILIAL (F_3) generation.

Aside from his masterly foresight in realizing that success depended on simplifying the problem by dealing with definite alternative characters, Mendel's claim to fame lies chiefly in his discovery of a simple principle by which the results may be explained. Since the hybrids when inbred always give rise to hybrids and also to each of the parental types in a *pure* form, it must be that the factors (genes) which determine the characters in question are sorted out, or SEGREGATED, in the ripe germ cells, or gametes. Assuming for illustrative purposes that a single gene determines a given character, it follows that after segregation the genes are distributed so that some gametes bear the gene for one character and other gametes bear the gene for the other character, but no gamete ever bears the genes for both characters. If the gametes of the original tall parent contained the gene for tallness (S), and those of the dwarf parent the gene for dwarfness (s) — then the hybrids will arise from a zygote which combines both genes (Ss), and since tallness is dominant over dwarfness all will be tall. Further, when the germ cells of this hybrid (Ss) mature, if these genes segregate so that, as a rule, half of the gametes bear S and half bear s, then when such plants, each with this germinal constitution, are inbred there will be equal chances for gametes bearing the same and for gametes bearing different genes to meet in fertilization.

The zygotes are 1 SS : 2 Ss : 1 ss. But, since S is dominant, the resulting organisms will be in the ratio of 3 tall to 1 dwarf, which is the familiar 3 : 1 Mendelian ratio of dominants to recessives in the F_2 generation. The important point, however, is that these tall plants, although they all *appear* alike and therefore belong to the same PHENOTYPE, are actually different with respect to their

germinal constitution; because one-third bear gametes all of which contain the gene *S*, and two-thirds bear gametes half of which contain *S* and the other half *s*. Consequently the tall phenotype is composed of two GENOTYPES which are distinguishable only by what they produce. (Fig. 184.)

It is thus apparent why the pure tall plants always breed true, and why the pure dwarfs do the same — all the gametes of one bear *S* and those of the other, *s*. The pure plants are HOMOZYGOUS with respect to the characters in question. It is also clear why the hybrids give rise to hybrids and pure dominants and recessives — half of their gametes bear *S*, and half bear *s*. The hybrid plants are HETEROZYGOUS.

The real difference then between the F_2 hybrids (*Ss*) and the pure dominants (*SS*) is that the former are heterozygous and the latter are homozygous. In order to tell which is which, since they are phenotypically the same, it is necessary to breed them. When self-fertilization can be practiced, as in the case of most plants, we get the result directly; that is an individual's progeny are either all dominants or dominants and recessives in 3 : 1 ratio, and thus the gametic constitution of the parent is immediately known. However, in the case of animals, where self-fertilization is impossible, the determination can be made by mating the dominants with recessives; for a homozygous (pure) dominant then will give all

FIG. 184. — Diagram of a Mendelian monohybrid. Results of crossing tall (*S*) and dwarf (*s*) Pea plants. The circles represent the zygotes and the characters of the soma (phenotype); the letters within the circles, the germinal constitution (genotype). The letters outside the recombination square represent the gametes. Note that each of the parents (*P*) represents a different phenotype and genotype; all the F_1 (one shown) belong to the same phenotype and genotype; while the F_2 represent two phenotypes and three genotypes. The relative number of individuals composing the F_2 phenotypes is 3:1.

dominants, while a heterozygous (hybrid) dominant will give half dominants and half recessives. Thus:

Gametes	=	$\begin{array}{cc} D & D \\ & \\ d & d \end{array}$	$\begin{array}{cc} D & d \\ & \\ d & d \end{array}$
Gametes	=		
Possible zygotes	=	100% Dd	50% Dd + 50% dd

So far we have considered the inheritance of one pair of alternative characters — the resultant of a pair of genes termed ALLELOMORPHS — but if the reader has grasped the principles involved in MONOHYBRIDS, we may pass rapidly over cases where two, three, or more pairs are concerned: that is DIHYBRIDS, TRIHYBRIDS, and POLYHYBRIDS.

2. Dihybrids

Mendel investigated inheritance in dihybrids by crossing, for example, a Pea producing yellow round seeds with one producing green wrinkled seeds. The plants in the F_1 generations bear only yellow round seeds, and therefore yellow and round are each dominant characters when paired with green and wrinkled. After self-fertilization such hybrid plant sproduce offspring (F_2) with seeds showing all the possible combinations of the four characters, and in the ratio of 9 yellow round to 3 yellow wrinkled to 3 green round to 1 green wrinkled. (Fig. 185.)

This logically can only be interpreted as indicating that one of the original parent plants bore gametes all containing the genes for yellow and for round peas (YR), while the other parent plant bore gametes all containing the genes for green and for wrinkled (yr). Such being the case, the resulting zygote is YRyr, and the hybrid which it forms develops gametes with all the possible combinations of these genes (except, of course, Rr and Yy) which are YR, Yr, yR, and yr. Now, in turn, at fertilization there are sixteen possible combinations of gametes, since there are four different kinds of sperm and four different kinds of eggs with respect to the characters in question. Accordingly the F_2 generation, which is produced by the union of these gametes, is represented by one pure dominant (YRYR), one pure recessive (yryr), four (including the former two) homozygotes, and twelve heterozygotes. These sixteen individuals form nine genotypes but, since only the dominant character is expressed when dominant and recessive genes combine, they are resolvable into four phenotypes (YR, Yr, yR, yr) in

the ratio 9 YR : 3 Yr : 3 yR : 1 yr. Thus the 9 : 3 : 3 : 1. Mendelian ratio for two pairs of alternative characters is merely the mono-

FIG. 185. — Diagram of a Mendelian dihybrid. Results of crossing yellow round seeded (YYRR) Peas with green wrinkled seeded (yyrr). The circles represent the zygotes and the characters of the soma (phenotype); the letters within the circles, the germinal constitution (genotype). The letter groups outside the recombination square represent gametes. The hybrids of the F_1 generation are all yellow round seeded since green and wrinkled are recessive. The F_1 plants form four types of gametes which affords sixteen possible types of zygotes, representing four phenotypes (shown graphically) and nine genotypes (numbered). There is one pure dominant (1) and one pure recessive (9). The zygotes numbered 4 are identical with the F_1 generation. Four are homozygotes (1, 7, 8, 9) and the rest are heterozygotes. The relative number of individuals composing the phenotypes is 9:3:3:1.

hybrid 3 : 1 expanded. Both rest on the same fundamental assumption that there is an independent assortment of the genes and that those for alternative characters segregate — both members of a pair of allelomorphs can never occur in the same gamete.

FIG. 186. — Diagram of a Mendelian trihybrid. Results of crossing tall Peas bearing yellow round seeds (*SYR*) with dwarf Peas bearing green wrinkled seeds (*syr*). The circles represent the zygotes and the characters of the soma (phenotype); the letters within the circles, the germinal constitution (genotype). The letter groups outside the recombination square represent the gametes. The *F*₁ hybrids form eight types of gametes, giving sixty-four possible types of zygotes, representing eight phenotypes (shown graphically) and twenty-seven genotypes. There is one pure dominant (in upper left corner) and one recessive (in lower right corner). Eight are homozygotes (diagonal from upper left to lower right corner) and the rest are heterozygotes. The zygotes in the diagonal from upper right to lower left are identical with the *F*₁ generation. The relative number of individuals composing the phenotypes is 27 : 9 : 9 : 9 : 3 : 3 : 3 : 1.

3. *Trihybrids*

Similarly, Mendelian trihybrids, for example the cross between tall Peas bearing yellow round seeds and dwarfs bearing green wrinkled seeds, give in the F_2 generation 27 genotypes and 8 phenotypes; the number of individuals in the phenotypes being in the ratio 27 : 9 : 9 : 9 : 3 : 3 : 3 : 1. Of course, in nature there are few instances in which parents and offspring differ by only one, two, or three characters, but since characters arising from each pair of allelomorphs can usually be treated singly, convenience demands that the analysis be made with respect to one or two pairs at a time, which therefore is the usual method of procedure. (Figs. 186, 187.)

4. *General Principles*

Before passing to certain modifications and extensions of Mendelian principles, it may serve to clarify the subject if we restate it in slightly different form and thus emphasize the essential facts thus far discussed on the basis of Mendel's own work.

Every cell of the soma of an individual may be regarded as bearing a pair of genes for each alternative character (*e.g.*, size in the case of the garden Pea), one member of each pair having been derived from each gamete which contributed to the individual's make-up. When both genes are identical (*e.g.*, either SS or ss) they are expressed in the soma (*e.g.*, the plant is tall or dwarf). The individual is homozygous with respect to size. But when the two genes are not identical (*e.g.*, S and s), then one, the dominant (S), is expressed in the soma (the plant is tall), while the other, the recessive (s), is not expressed. The individual is heterozygous with respect to the character in question (*e.g.*, size).

At the reduction division during the maturation of the germ cells of the individual, an independent assortment, or segregation, of the genes occurs with the result that each gamete receives only one gene for each character. Thus the gametes of homozygous individuals are all alike with respect to the gene in question (*e.g.*, all bear either S or s), while the gametes of heterozygous individuals are of two numerically equal classes (*e.g.*, half bear S and the other half bear s).

When the determining genes (allelomorphs) for each of a pair of alternative characters are present in the zygote, one (the domi-

SPR

SpR

sPR

SPr

spR

Spr

sPr

spr

FIG. 187. — The eight phenotypically different kinds of Guinea-pigs in the F_2 generation of a trihybrid. S = short hairs, s = long hair, P = pigmented coat, p = non-pigmented coat or albino, R = rough coat, r = smooth coat. The hybrid parents (F_1) were phenotypically SPR.

nant) is expressed in the resulting individual; but the other (the recessive) is also present in all of its somatic cells and in half of its gametes. In other words, the recessive is not expressed in the soma unless it is present in duplicate, *i.e.*, unless it has been received from both parents.

SEGREGATION. The genes for each of a pair of alternative characters are never both present in the same gamete. Therefore the gametes of hybrids fall into two numerically equal classes: in one the gene of the dominant character and in the other the gene of the recessive character is segregated. This is the so-called purity of the ripe germ cells, or gametes.

D. NEO-MENDELISM

It becomes more and more apparent as data accumulate that it is necessary to revise somewhat our ideas regarding the importance of dominance, and to accentuate the principle of segregation as the prime Mendelian contribution. A few examples will bring the main facts before us.

The seven pairs of alternative characters in Peas which Mendel studied showed essentially complete dominance of one character in each pair, and therefore, quite naturally, he laid stress on this principle. But as a matter of fact we now know innumerable cases in which the hybrid (F_1) shows a different condition from either of the parents. For instance, on crossing homozygous *red* and *white* races of the Four-o'clock, all the progeny in the heterozygous (F_1) generation bear *pink* flowers, or, we may say, flowers intermediate in color between the two parents. Neither red nor white is dominant: the result is BLENDING inheritance. But inbreeding the hybrids gives a F_2 of 1 red: 2 pink: 1 white. Thus the typical Mendelian 3 : 1 ratio is, so to speak, automatically resolved into the 1 : 2 : 1 ratio which, when one character is dominant, is evident only on further breeding. Segregation actually occurs as usual, because the homozygous progeny of the hybrid exhibit the original parental characters unmodified. (Fig. 188.)

In certain other cases, the hybrids, instead of being true intermediates, really exhibit the characters of *both* parents: neither character is recessive. Thus in Shorthorn cattle, red and white when mated give roan, a color effect resulting from a close intermingling of red and white hairs in the coat. This is MOSAIC inheritance. Accordingly roan Shorthorns are always heterozygous,

but their offspring give the expected ratio of 1 red : 2 roan : 1 white which is clear evidence of segregation. Perhaps a more striking case of mosaic inheritance is the well-known blue Andalusian fowl. This will not breed true because it is a hybrid. Its offspring show the ratio of 1 black : 2 blue Andalusian : 1 white-splashed-with-blue. In order to obtain all blue Andalusians — the type

FIG. 188. — Diagram to illustrate the results from crossing white and red flowered races of Four-o'clocks (*Mirabilis jalapa*). The somatic condition (phenotype) is shown graphically; the small circles represent the genes which are involved.

recognized by poultrymen — obviously it is necessary to mate black with white-splashed-with-blue birds. So again it is clear that mosaic inheritance involves segregation. (Fig. 189.)

But many other complications occur in inheritance; thus sometimes blending inheritance is not the result of lack of dominance, but of the CUMULATIVE action of several pairs of genes as illustrated by the cross of white and black races of Man. The mulatto (F₁) is

intermediate in skin color between the parental types, and in the F_2 and later generations gives a series of gradations between white and black but rarely pure white or black offspring. However an adequate explanation is not far to seek. Assuming that three pairs of genes are involved, the genetic constitution of the black race may be represented by AABBCc and that of the white race by

FIG. 189. — Cross of white-splashed-with-blue and black fowls, giving in the F_1 all blue Andalusians, and in the F_2 one white-splashed-with-blue to two blue Andalusians, to one black.

aabbcc. Accordingly the hybrid, or mulatto, has the genetic constitution AaBbCc and is intermediate in color since only half of the genes for black pigmentation are present in cumulative action. Furthermore, the progeny (F_2) of mulattoes show different degrees of color ranging from pure white to pure black owing to the sixty-four possible recombinations of genes according to the trihybrid formula: the more 'black' genes present, the darker the pigmentation of the skin. The infrequent appearance of pure whites or blacks in the F_2 generation is because the chances are slight that in segregation all the separate genes for black or white will be brought

together in a single gamete and, further, that such a gamete at fertilization will meet another similarly endowed. (Fig. 190.)

From these few examples, selected almost at random from the wealth of data at hand, it is apparent that blending and mosaic inheritance, as well as alternative inheritance, can be satisfactorily interpreted on the fundamental Mendelian principle of segregation. It is merely necessary to bear in mind that it is the genes, which condition the development of characters, and not the characters themselves that behave as units; for now we know that most characters are determined by MULTIPLE genes. And further, that dominance is a relation between a pair of genes rather than between their expressions, characters. Blending inheritance may be the result of lack of dominance, but more frequently it is an expression of the action of many pairs of genes, each gene displaying dominance for one member of a pair; while mosaic inheritance may represent the extreme where each gene's influence is exhibited to the full in the hybrid. Segregation is the rule.

Within the past few years geneticists have been able by the multiple gene hypothesis to bring into line with the Mendelian interpretation the inheritance of a large number of characters, especially in the higher animals. Thus stature, proportions of the parts of the body, build, as well as nearly all of the physiological and mental characteristics in Man are evidently dependent upon multiple genes. In certain Fruit Flies eye color is influenced

FIG. 190. — The distribution of the sixty-four possible recombinations in the F_2 generation when three similar genes, cumulative in action, produce a character; *e.g.*, the offspring of mulattoes. The figures indicate the number of genes (*e.g.*, for black) present in the individuals represented by the column above. (From Walter.)

by more than forty pairs of genes and the wings by upward of ninety. Thus it is becoming increasingly clear that what a given gene will produce is determined by the constitution of the gene plus its interaction with many, if not all of the other genes of the complex. And, furthermore, what the gene complex will produce bears an intimate relationship to the environment. For instance, in Fruit Flies the abnormal condition of extra legs is inherited in typical Mendelian manner when the flies are reared at a low temperature; whereas supernumerary legs do not appear in flies with the *same* gene heritage when bred at a higher temperature.

So it happens, as is usually the case, the more a problem is studied the more complex it appears to become. Suffice it to say that, although our knowledge of inheritance is to-day very much broader than Mendel conceived on the basis of his classic experiments, it is evident that he supplied us with basic principles which are affording a common denominator for an ever-increasing number of facts in genetics. It appears that all inheritance will prove to be Mendelian.

E. MECHANISM OF MENDELIAN INHERITANCE

With this general outline of the Mendelian principles before us, it is now necessary to bring them into relation with the facts so far discovered in regard to the structure of the germ cells. In other words, we have assumed, on the basis of the experimental results derived from breeding plants and animals, the existence of genes, the occurrence of segregation, etc., but has the actual study of cells (CYTOLOGY) by means of the microscope given any evidence of the physical basis of genes and of a segregating mechanism? The reader will at once answer this in the affirmative on the basis of our discussion of the origin and structure of the germ cells and their behavior in fertilization. But all of these cardinal facts were unknown when Mendel worked and this makes still more remarkable his prevision in interpreting his results in the terms he did. (Fig. 166.)

The essential facts may now be restated from a slightly different viewpoint. The egg and sperm each carry a definite number of chromosomes and consequently after fertilization the zygote contains a double set. For each chromosome contributed by the sperm there is a corresponding, or HOMOLOGOUS, chromosome contributed by the egg. In other words, there are two chromosomes of each kind which may be considered as pairs. When division of the

zygote takes place each chromosome splits into two chromosomes, so that each daughter cell receives a daughter chromosome derived

FIG. 191. — Diagram of the chromosome cycle of an animal. Somatic (diploid) chromosome number assumed to be eight. Paternal chromosomes (from sperm) = ABCD; maternal (from egg) = abcd. I, union of nuclei of gametes, each with a simplex group (haploid number) of chromosomes, in the zygote at fertilization to form a duplex group (diploid number) of chromosomes. II, III, IV, somatic divisions or divisions of germ cells before maturation (duplex groups of chromosomes). V, synapsis, involving pairing of homologous paternal and maternal chromosomes to give the haploid number of paired chromosomes. VI, reduction division — separation of pairs into single chromosomes again. VII, two gametes, with simplex groups (haploid number) of chromosomes; there are 14 more possible combinations of the chromosomes, or types of gametes, which are not shown. See Fig. 192. (After Wilson, slightly modified.)

from each of the original ones. Since all the cells of the organism are lineal descendants by similar mitotic cell divisions, all of its cells contain the double set of chromosomes — half paternal and half maternal; and since the primordial germ cells have a similar origin, they also have a double set of chromosomes. But during the maturation process SYNAPSIS occurs: that is, homologous chromosomes of paternal and maternal origin unite in pairs — the process of fertilization which gave rise to the individual being consummated in the ripening of its own germ cells. But this union is only temporary; a succeeding mitosis (reduction division), instead of dividing each chromosome as usual, separates the maternal and paternal chromosomes of each synaptic pair and delivers one of each (though rarely all of the same maternal or paternal set) to the two arising cells. Thus each mature germ cell, or gamete, contains one member of every

chromosome pair and the number of chromosomes is reduced one-half.¹ (Fig. 191.)

Mendel assumed that the genes for alternative characters segregate in the formation of the gametes of hybrids so that a single gamete bears one and not both genes of a pair of allelo-

FIG. 192. — Diagram to show the union of simplex groups of either the chromosomes or of the genes of the gametes to form the duplex condition of the zygote and animal body; and then their pairing at synapsis, and segregation in the gametes. With four pairs of chromosomes or of genes (Aa, Bb, Cc, Dd) there are sixteen possible types of gametes. (From Wilson.)

morphs. That is the genes, which come together in the zygote that forms the hybrid, separate again in the formation of its own gametes. This is just what cytological studies show. Chromosome behavior exactly parallels the typical behavior of the Mendelian gene, because after synapsis, during spermatogenesis and oögenesis, each chromosome of paternal origin separates from the corresponding chromosome of maternal origin. The genes similarly

¹ It will be recalled that in plants exhibiting an alternation of generations, the chromosome reduction occurs at the formation of the spores. (Fig. 165.) A little thought will convince the reader that this difference is of no importance from the standpoint of the present discussion, because we are interested in inheritance from sporophyte to sporophyte and can neglect the almost suppressed gametophyte generation which intervenes in Seed Plants.

situated on homologous paternal and maternal chromosomes are allelomorphs and are segregated during gamete formation.

Furthermore, in considering Mendelian dihybrids we found, for instance, that genes for yellow and round, and green and wrinkled seeds were inherited in a fashion which indicated that yellow and round, let us say, are segregated independently of each other, because all possible combinations with green and wrinkled occur. This clearly is fully accounted for, provided the gene for yellow and the gene for round are not borne by the same chromosome, since following synapsis the gametes secure one of each pair of homologous chromosomes (a *SIMPLEX* group), but not necessarily all of maternal or paternal origin. (Fig. 192.)

In short, when two gametes unite they each contribute to the zygote two corresponding simplex groups of genes with the result that the offspring is of a double, or *DUPLEX* gene constitution. Similarly, the gametes contribute two simplex chromosome groups so that the zygote is of a duplex chromosome constitution. Thus both the *chromosomes* and the *characters* (genes) are in the simplex condition in the gametes and duplex in the zygote. This close parallelism of character and chromosome behavior affords almost positive evidence that the chromosomes supply the physical basis of inheritance, and that Mendelian segregation and related phenomena are facts. For all practical purposes A, B, C, D, and a, b, c, d, in Figures 191 and 192 may be interpreted either as chromosomes or as characters.

Turning now to the inheritance of characters whose genes are borne by the *same* chromosome: these would seem to be indissolvably linked together. And since the chromosome number is usually not large — there are twenty-four chromosomes in the gametes of Man — compared with that of heritable characters, we would expect sometimes to find characters linked together. That is, not separately inherited as are yellow and round in our example. In reality many cases are known in which characters are inherited in groups. The inheritance of sex and sex-linked characters will make the main point clear, and at the same time serve to bring before us the essential facts in regard to the determination of sex.

1. Sex Determination

Intensive studies of the chromosomes in the somatic cells and in the germ cells before the reduction division have shown that usually

in *male* animals two members of a certain pair of homologous chromosomes (synaptic mates) differ recognizably one from the other in size or form or both. For example, one member, referred to as the X chromosome, may be similar in size to the other chromosomes, while its mate, called the Y chromosome, is very much smaller and apparently practically functionless. Indeed, in many species it has never been discovered and probably does not exist. Furthermore, it has been found that in corresponding cells of *females* there are two X chromosomes — another X chromosome taking the place of the Y chromosome of the male. Thus the

FIG. 193. — Diagram to show the relation of the two classes of sperm in fertilization. The formation of gametes in the male is shown at the left, in the female at the right; fertilization, producing the male or female zygote, in the center. Somatic chromosome number assumed to be six. X chromosome (large) and Y chromosome (small) in black.

chromosome groups of males possess an X-Y pair, and those of females, an X-X pair. This difference between the chromosomes of the sexes naturally suggests that the X chromosome bears an essential determiner for sex, and this has proved to be the case. (Fig. 193.)

During spermatogenesis the reduction division following synapsis distributes an X chromosome to one cell and a Y chromosome to the other — segregates the synaptic mates (X-Y) in the regular way — so that two classes of sperm result: half the sperm bear the X chromosome and half bear the Y chromosome. Furthermore, in oögenesis the reduction division distributes an X chromosome (from the X-X pair) to each cell, and accordingly every egg bears

an X chromosome. Thus, in Man the somatic number of chromosomes is 48; males having 46 plus an X-Y pair, and females 46 plus an X-X pair. Half the sperm bear 23 plus X, and half bear 23 plus Y; while all the eggs bear 23 plus X.

Since there are equal numbers of sperm with and without the X chromosome, on the average as many eggs will be fertilized by one class of sperm as the other, with the result that half of the zygotes will contain one X and half two X chromosomes. Obviously the former will develop into males and the latter into females, since the somatic cells of males have the X chromosome and therefore the 'sex gene' in the simplex condition, and similar cells of females have it in the duplex condition.

Thus there is good cytological evidence that sex inheritance follows the Mendelian formula. The male carries one 'sex gene' (on the single X chromosome) and the female two 'sex genes' (one on each of the X chromosomes). At maturation these segregate so that the male is heterozygous and the female is homozygous in regard to sex, and therefore all possible combinations of gametes result in the 1:1 ratio of males to females. In passing, we may emphasize that this shows that the sex of an individual is typically determined at the time of fertilization, and not subsequently as most of the well-known theories contend. But obviously we must guard against thinking of either the X chromosome or the 'sex gene' as 'producing' sex. Sex is a complex character whose full development is undoubtedly conditioned by hormones, etc., but since the X chromosome is the differential in the sexes, it is to that extent sex-determining.

2. *Linkage*

Since sex is regulated by an internal mechanism which appears to be the same as that which determines the distribution of characters in Mendelian inheritance, it might be supposed that the genes of other characters as well are carried by the X chromosome. As a matter of fact the behavior in inheritance of certain characters is such that it can only reasonably be explained on this assumption. Accordingly such characters are known as SEX-LINKED. This brings us again to the point at which we digressed to consider sex—the discussion of genes associated on the same chromosome. One example will bring out the main facts.

The common form of COLOR-BLINDNESS known as Daltonism, in

FIG. 194. — Diagram to show the inheritance of color-blindness from the male. A color-blind man (shown in black) transmits the character to half of his grandsons. * indicates the 'sex' chromosome with the gene for color-blindness.

FIG. 195. — Diagram to show the inheritance of color-blindness from the female. A color-blind woman (shown in black) transmits the character to all of her sons, and to half of her grandsons, and to half of her granddaughters.

which the affected individual is unable to distinguish red from green, has long been known to be inheritable, but in a peculiar *criss-cross* way. The abnormality is usually transmitted from a color-blind man through his daughters, who are normal, to half of his grandsons; and from a color-blind woman to all of her sons and none of her daughters. When both parents are color-blind, all the children show the defect. This behavior is readily accounted for if

FIG. 196. — Diagram to show a possible mechanism of crossing-over during synapsis of homologous paternal and maternal chromosomes. The segments indicate the assumed linear arrangement of the genes with allelomorphs opposite each other. I, pair of chromosomes which have entered and emerged from the synaptic state without any crossing-over; IIa, chromosomes winding about each other at synapsis; IIb, separation of these chromosomes, involving breaking at the points of crossing; IIc, their emergence from synapsis with the members of the pairs of allelomorphs genes interchanged. (From Wilson.)

we assume that the gene for color-blindness when present is associated with the gene for sex on the X chromosome, and that color-blindness develops in males, just as 'maleness,' when it is simplex, or from one parent, and develops in females when it is duplex, or from both parents. Thus a color-blind man is always heterozygous for the character, while a color-blind woman is homozygous. A woman who is heterozygous is phenotypically normal, but is a 'carrier.' It is obvious why color-blindness is very much less frequent in women than in men. (Figs. 194, 195.)

Color-blindness thus serves to illustrate the association

of genes of different characters on the same chromosome and the association later of their respective characters in the adult. Incidentally, it also clearly shows that whatever characters are borne by the X chromosome are not transmitted by a father to his sons, and so minimizes, from the standpoint of heredity, the importance usually ascribed to descent in the direct male line.

However, the presence of different genes on the same chromosome — indeed, chromosomes are really linkage groups of genes — by no means indicates that such genes must always be distributed together, for there is considerable evidence that during synapsis

genes may reciprocally cross-over from one synaptic mate to the other, and thus become separated from their former gene associates on the same chromosome. When this CROSSING-OVER has occurred they may be independently segregated, and accordingly crossing-over removes the limitations which, at first glance, would seem to confine the possible number of characters capable of independent segregation in Mendelian inheritance to that of the chromosome number, and renders invalid any objections to the universality of Mendelism which are based on the chromosome mechanism as at present understood.

And further, the crossing-over gives an opportunity to determine the relative positions of different genes in a chromosome, on the assumption that the distance between two genes in a chromosome is proportional to the percentage of crossing-over which these genes show — the longer the distance, the more likely is crossing-over to occur within it. (Fig. 196.)

F. NATURE *versus* NURTURE

From one viewpoint, then, the individual may be considered as a composite of very many characters which behave in a definite way in inheritance. "Expressed otherwise, and somewhat fancifully, individuals are temporary kaleidoscopic combinations of the various genes belonging to the species; the act of reproduction, especially the reduction division, involving segregation, and subsequent fertilization, providing the new turn of the kaleidoscope."

But since the life of an organism is one continuous series of reactions with its surroundings, it follows that nurture plays an immensely important part in molding the individual on the basis of its heritage. Indeed we are apt to overlook the fact that every character is a product both of factors of the heritage and of the environment and can be reproduced only when both are present. Those characters that appear regularly in successive generations are those whose development depends upon factors always present in the normal surroundings. Other characters, potentially present, do not become realized unless the unusual environmental conditions necessary for their development happen to be met.

To disentangle the closely interwoven influences of heredity and environment is one of the most important and perplexing problems of the science of genetics. This is especially true in the case of Man. Development is a form of behavior, and how a child develops

physically and mentally is determined not by its heritage alone nor by its environing conditions alone, but by both in intricate combination.

Although apparently we do not inherit the effects on our forebears of their surroundings and training, nevertheless we are the heirs to their customs — each generation builds upon the intellectual and material foundations of all of its predecessors — and this entails added responsibilities as well as opportunities for each suc-

FIG. 197. — Corn of a single variety (Leaming dent): at the left, grown well spaced; at the right, badly crowded. The heredity of each plot of corn is the same; the striking differences in growth are therefore solely due to environment. They are modifications. (From Blakeslee.)

ceeding generation. Already in certain fields the applications of science to human affairs tax the ability of Man to use them wisely. Thus 'social heredity' bids fair to outstrip our conservative and essentially unchanging inherited nature. The EUTHENIST emphasizes nurture, the EUGENIST emphasizes nature. As is so often the case, however, when doctrines are opposed, the truth combines both; though we cannot doubt, knowing what we know of the genetic constitution of organisms, that from the standpoint of permanent advance — racial rather than individual — the path to progress is chiefly through EUGENICS, the science of being well born.

This distinction between heritage and acquirements leaves a fatalistic impression in many minds, which to a slight extent is justified. "We cannot get away from inheritance. On the other hand, although the organism changes slowly in its heritable organization, it is very modifiable individually; and this is Man's particular secret — to correct his internal organic inheritance by what we may call his external heritage of material and spiritual influences." (Thomson.) (Figs. 197, 198.)

It is therefore clear that the problem of human improvement has two aspects: in the first place, the effects of culture on the

FIG. 198. — Scheme to illustrate the contributions of nature and nurture to the make-up of the individual. The triangles represent various types of individuals which may be produced by the same germ cells (heritage) if environment and training are variable. The foundation of the 'triangle of life' is heritage. (After Conklin.)

individual which, though not inherited, are cumulative from generation to generation through training; and secondly, racial betterment through breeding the best. But we may well ask: What is the possibility of anything much better than the present best if heredity is essentially a recombination of the characters of our forebears — a turn of the kaleidoscope?

Although we are wofully ignorant of the *cause* of variations, the difficulty is more apparent than real and arises from our absolute ignorance of what genes really are. We may conceive them to be chemical molecules, and if so they can change only by an alteration of their chemical constitution. And for all we know, this may occur. Or, without any change in the genes themselves, their expression —

the chemical effects which they produce — may change by the alteration of other substances with which they react. If we interpret such phenomena as recombinations, they are profoundly more subtle and far-reaching than are called to mind by our simile of a kaleidoscope. They may be essentially infinite in number and infinite in potentialities for variations in the germ plasm and therefore for inheritable variations expressed in the soma. Again, there is evidence that inheritable variations — mutations — are often the result of the 'accidental' loss or gain of groups of genes, or even entire chromosomes, during synapsis or mitosis. Thus, for example, one member of a pair of synaptic mates may leave with the other member certain genes for which it gets none in return: only half of the crossing-over process occurs. All these phenomena apparently profoundly modify the constitution of both chromosomes involved and accordingly the organisms to which they contribute.

It would appear that all such types of mutations must be important raw materials for evolution: but in regard to the factors that actually induce mutations in nature, there is very little evidence. However, recently certain laboratory experiments, involving the subjection of the germ cells of flies to irradiation (X-rays, etc.), have produced inheritable variations and thus have opened up an apparently important field for investigation.

FIG. 199. — Diagram to illustrate a quart (population) of beans assorted according to weight.

G. SELECTION

For more than half a century selection has been something to conjure with — a sort of creative principle to explain the progressive changes in plants and animals. It was assumed that the SELECTION of a certain type of individual for breeding would result in a gradual and continuous transformation of the race or species in the direction of the selection. But Darwin recognized that selection in itself can produce nothing — its efficacy depends on the materials afforded by variation. He did not and, in fact, could not make the modern sharp distinction between modifications, combinations, and mutations, although he questioned the inheritability of modifications. In general he accepted all variations as at the disposal of selection.

But recent work indicates that selection of certain types of variations effects only an apparent and not a real change. An example will make this clear. (Fig. 199.)

Take, say, a quart of beans and sort them into groups according to the weight of each bean. Then put each group into a separate cylinder and arrange the cylinders in a series according to the weight of the enclosed beans. Now if we imagine a line connecting the tops of the bean piles in each cylinder, it takes the form of a normal *curve of probability*, or *variability curve*. A similar figure would be obtained by the statistical treatment of nearly all fluc-

FIG. 200. — Normal variability curve plotted from measurements of the height of 1,052 women (population). The height of each rectangle is proportional to the number of individuals of each given height. (From Kellicott, after Pearson.)

tuating characters among the members of any large group of organisms, or of the size of the grains in a handful of sand, or the deviations of shots from the bull's-eye in a shooting match. Therefore the variations with respect to a given character very closely approximate the expectation from the mathematical theory of probability, or chance, and the reasonable conclusion is that such finely graded variations, or FLUCTUATIONS, are a resultant of a large number of factors, each of which contributes its slight and variable quota to the expression in a given individual. (Fig. 200.)

The question is, what results are obtained by breeding from individuals which exhibit such a fluctuating variation to, let us say, a greater degree than that of the mean of a mixed POPULATION?

With Galton's theory of filial regression in mind, one will naturally expect, and rightly, that the offspring usually will exhibit the character to a less degree than the parents but to a greater degree than the population. The top (mode) of the curve will have moved, so to speak, slightly in the direction of selection. Now, by continuing generation after generation to select as parents the extreme individuals, is it possible, with due allowance for some regression, to take one step after another indefinitely, or until the character in question is expressed to a degree which did not exist previously? The experience of practical breeders gives a partial answer, since the continual selection of the best animals for mating and the best plants for seed has been a profitable procedure. But it has long

FIG. 201. — Schematic representation of the effect of selection from the viewpoint of Galton's 'law of filial regression.' (1) Mode before selection; 2, 3, 4, new (successive) modes, the results of selections of individuals at 2', 3', 4'. The mode has been shifted in the direction of selection (toward the right). But there has been each time an amount of regression indicated by the length of the arrows.

been known that after a certain amount of selection has been practiced it ceases to be so effective, and thenceforth serves chiefly to keep the character at the higher level attained. (Fig. 201.)

The crux of the matter is in regard to exactly what the fluctuations are. Modifications (non-heritable) and frequently combinations (heritable) give a normal variability curve, and both may be included in fluctuations. This mixture of heritable and non-heritable variations is what makes confusion. If we rule out combinations, by inbreeding or by self-fertilization of homozygous individuals — establish *PURE LINES* — then the fluctuations are all modifications and selection is ineffectual with characters which are not inherited.

Pure Lines

The importance of this point was discovered by careful experiments on the inheritance of characters in single pure lines; particu-

larly those of Johannsen on inheritance in a brown variety of the common garden Bean. For example, by keeping the progeny of each individual bean separate from that of all the rest, he was able to isolate a number of pure lines which differed in regard to the average weight of the beans. Selection did nothing but resolve the species, or the bean population with which he began, into its constituent 'weight types,' or lines, each of which exhibited a characteristic variability curve of its own with a mode departing more or less from that of the population. But when Johannsen selected *within* a pure line (ruled out combinations) nothing at all resulted; he was unable to shift the mode because he was dealing with non-heritable characters. In other words, the effect of selection is one of isolation and not creation. As a rule it sorts out preëxisting pure lines (lines with homogeneous germinal constitution) from a population and then stops — though if selection is stopped the isolated lines usually soon merge again into the original population. A mutation must occur in a pure line for selection to be effective — but by the mutation the single pure line becomes two. (Fig. 202.)

Thus the pure line concept has served to clarify our ideas in regard to selection by focussing attention on the actual nature of the variation being dealt with — on the fact that variations are of three sorts: modifications which are not heritable and combinations and mutations which are heritable. Most of the variations within pure lines apparently are the result of environmental influences recurrent in each generation, but the germ plasm is homogeneous. The variability within a population is the composite variability of its component pure lines, but the germ plasm is not the same in all individuals — these may be segregated into groups, the pure lines. Thus, very liberally interpreted, the pure line concept is a formal expression of the fact that most of the variations which we recognize are either somatic or the result of recombinations of diverse parental genes. Accordingly when the genes of the gametes are identical (as in pure lines) the latter source of variation does not exist, and selection is powerless except when comparatively rarely mutations occur.

However, some recent work indicates that under certain conditions selection may be effective, at least to a limited degree, within a pure line. We have seen that many, probably most characters are the expression of multiple genes. In some such cases one gene

is, so to speak, the determining gene for the character as a whole, while associated with this gene there is a series of modifying genes which themselves do not find expression without the presence of the determining gene, but chiefly serve to alter the character expression

FIG. 202. — Diagram to illustrate a population of beans and its five component pure lines. The beans are assorted according to weight. Tubes containing beans of the same weight are placed in the same *vertical* row. See Fig. 199. (From Walter, after Johannsen.)

of the latter. Under such conditions it is possible to modify the character by selection — to add or subtract or otherwise change the relationships of the modifying genes to the primary gene. Although at first glance it would seem that the effectiveness of selection of this sort would be relatively limited in any particular case,

present research is revealing previously unappreciated possibilities for changes through the mutual interaction of genes which may necessitate a somewhat broader, though fundamentally unchanged, interpretation of the pure line concept.

When all is said, the recognition that variations differ in regard to inheritability, taken in connection with the pure line concept, has given new significance to the problem of selection. The appreciation of its limitations has but accentuated its possibilities. Selection is not shorn of its importance either practical or theoretical. Artificial selection is useful in separating one line from another, as is attested by practical breeders everywhere, and in taking advantage of mutations when they occur. Most of the 'new creations' in horticulture and animal breeding are the result of hybridization and the rigid selection of individuals exhibiting desirable new combinations and sometimes mutations which hybridizing seems to induce. NATURAL SELECTION, in a quite similar manner, may act as a 'sieve' and sort out the new combinations and mutations presented — retain the fit and discard the unfit — and so afford a natural explanation of the adaptation of organisms to their envioning conditions. (Fig. 243 ; p. 369.)

SUMMARY

Before leaving the subject a summary of the most important general principles which the study of genetics has thus far afforded may be helpful.

In the first place, it appears clear that the basis of inheritance is in the germinal rather than in the somatic constitution of the individual. A character to be inherited must be represented by one or more genes in the germ cells, although the environment is not unimportant in the development of the character from the gene complex.

Secondly, there is no satisfactory evidence that modifications of the body, 'acquired characters,' can be transferred from the body to the germ complex and so be inherited.

Thirdly, the germinal basis of characters, genes, may be dealt with essentially as units. The chromosomes — linkage groups of genes — follow Mendelian principles of segregation and recombination in the formation of the gametes of an individual, so that paternal and maternal contributions are readjusted in all the combinations which are mathematically possible.

And finally, the germinal factor basis of characters, the gene complex, is remarkably constant. Selection is apparently powerless directly to alter it, but sorts out what is already there, or, taking advantage of such changes (mutations) as do occur, determines their survival value for their possessor in the struggle for existence.

CHAPTER XXIII

ADAPTATION OF ORGANISMS

Every creature is a bundle of adaptations. Indeed, when we take away the adaptations, what have we left? — *Thomson and Geddes.*

SINCE organisms are dependent for their life processes upon energy liberated by physico-chemical processes in protoplasm, any and all influences which induce changes in the structure or functions of an organism must initially modify the underlying metabolic phenomena. In other words, organic response is a problem of metabolism. Although it is highly important that this cardinal fact be clearly grasped, the science of biology to-day is not in a position to interpret the responses of organisms in these fundamental terms. Accordingly we can merely present some representative instances to illustrate the fact that the response of organisms, as exhibited in active adjustment — ADAPTATION — of internal and external relations, overshadows in uniqueness all other characteristics of life and at one stroke differentiates even the simplest organism from the inorganic.

Overwhelmingly striking as is the fitness of organisms to their physical surroundings, we must not lose sight of the fact that the environment itself presents a reciprocal fitness. This results from the "unique or nearly unique properties of water, carbonic acid, the compounds of carbon, hydrogen, and oxygen. . . . No other environment consisting of primary constituents made up of other known elements, or lacking water and carbonic acid, could possess a like number of fit characteristics, or in any manner such great fitness to promote complexity, durability, and active metabolism in the organic mechanism which we call life." (Henderson.)

A. ADAPTATIONS TO THE PHYSICAL ENVIRONMENT

In any consideration of the reciprocal relations which must exist between organisms and their surroundings, of first importance is the inconstancy of the latter. Uncertainty is the one certainty in nature and accordingly the response of living things — their

adaptability to environmental change — is at once the most striking and indispensable adaptation.

1. *Adaptations Essentially Functional*

Although the changes of the environment are almost inconceivably complex — witness the kaleidoscopic series of events exhibited in the hay infusion microcosm — there are certain general conditions which every environment must supply, and without which life cannot exist. These are food, including water and oxygen, and certain limits of temperature and pressure. (Fig. 25.)

FOOD. As we know, food represents the stream of matter and energy which is demanded for the metabolic processes of living matter. And each and every element which forms an integral part of protoplasm must be available. Since all protoplasm consists chiefly of a dozen chemical elements, these, of course, must be present; and further, since protoplasm is a colloidal complex in which water plays a fundamental rôle, life processes without water are impossible. But the old adage that what is food for one is another's poison has a broader significance than is immediately

FIG. 203. — Portion of filaments of *Beggiatoa alba* (a), and two cells of *Beggiatoa mirabilis* (b) showing enclosed sulfur granules. (From Buchanan.)

apparent. Although it is true there are general 'food-elements' which all life demands, it is equally true that the combinations in which these elements must be presented to the organism, in order to be available for its metabolic processes, are subject to the widest variation.

We have emphasized and contrasted the nutrition of a typical animal, green plant, and colorless plant, and have seen the reciprocal part which they play in the circulation of the elements in nature; so it is only necessary, with these facts in mind, to cite special cases in order to illustrate the adaptation of certain groups of organisms to special conditions of existence. The demands of the so-called Sulfur Bacteria and the Yeasts are in point.

The Sulfur Bacteria (*Beggiatoa*) live in water containing sulfuretted hydrogen, from which, by oxidation, they obtain energy and store up within the protoplasm free sulfur in the form of tiny

granules. And then by further oxidation they transform the sulfur into sulfuric acid and excrete it. Thus a gas which is poisonous to nearly all organisms is for *Beggiatoa* a necessary life condition. (Fig. 203.)

The Yeasts include a host of microscopic colorless plants which play an important part in the simplification of organic compounds. Since they are devoid of chlorophyll, Yeasts, of course, lack photosynthetic powers, though like many other colorless plants they are not dependent upon proteins for nitrogen but obtain it in less complex form. But the essential fact of interest at present is the chemical changes associated with Yeast metabolism — the transformation of a large proportion of the sugar content of the medium in which they live into alcohol and carbon dioxide. This process of ALCOHOLIC FERMENTATION may be approximately expressed by the formula:

The explanation is not far to seek. Deprived of an adequate supply of air, Yeasts resort to the energy released when, with the decomposition of the sugar, the carbon and oxygen unite as CO_2 . The formation of alcohol by the remnants of the sugar molecules is, from the standpoint of the Yeasts, a mere incidental factor which is, so to speak, unavoidable. On the other hand, from the broad viewpoint, the waste products of the action of the Yeast plants' enzymes represent an important phase in the general simplification of organic compounds in nature. And Man turns to account in numerous ways both products of the Yeasts' destructive powers — the alcohol and the carbon dioxide. (Fig. 21.)

Thus the Yeasts are practically independent of free oxygen and in this they agree with many kinds of Bacteria as well as some animals, chiefly parasitic worms, which are able to secure the necessary energy by the rearrangement of the atoms within, or the disruption of molecules containing oxygen. Indeed, certain species of Bacteria not only do not need free oxygen at all, but are killed when it is present in any considerable amount. All such organisms are termed ANAEROBES. A common example is *Bacillus tetani* which inhabits garden soil and street dust and produces TETANUS, or lockjaw, in Man and certain domesticated animals when it gains entrance and develops in the tissues.

TEMPERATURE. Although protoplasmic activity is restricted to

ranges of temperature which do not seriously interfere with the chemico-physical processes involved, it is a commonplace that various species are adapted to different degrees of temperature. The great majority of organisms, however, find their optimum temperature between 20°C. and 40°C. , though species inhabiting the polar and tropical regions show adaptations to the temperature extremes of their surroundings. As a matter of fact, it is not possible to state the upper and lower limits beyond which active life ceases, but some Algae and Protozoa are known to multiply in the water

of hot springs, certainly at temperatures higher than 50°C. , and others in water until freezing actually occurs.

But many of the lower forms of life, such as the Bacteria and Protozoa, have the power of developing, particularly under unfavorable surroundings, protective coverings of various sorts about themselves and of assuming a resting condition in which all the metabolic processes characteristic of active life are reduced to the lowest terms. In this spore or encysted state they are immune to extremes of temperature and of dryness to which they readily succumb during active life. Thus some types of Bacteria can successfully

withstand a temperature of nearly -200°C. for six months, and about -250°C. for shorter periods, while others can endure a temperature as high as 120°C. for a short time. (Fig. 204.)

It is clear that the great majority of organisms are at the mercy of environmental temperatures. This is true of all except the higher Vertebrates, the Birds and Mammals. These homothermal animals possess a highly complex mechanism which maintains their body temperature practically constant; *e.g.*, in Man at 37°C. (98.6°F.).

The heat regulatory mechanism represents, so to speak, the final result of the assembling and elaborating, throughout Vertebrate evolution, of various elements, the origin of which is found among the Fishes. In the Mammals it comprises insulating material in the skin, a closed blood vascular system, power of rapid

FIG. 204. — Spore formation and germination in Bacteria. A, B, C, a pair of rods forming spores, drawn at one hour intervals; D, a five-celled rod, with three fully-formed spores, which was allowed to dry for several days and then placed in a nutrient medium; E, F, the same spores at one, and three hours later; G, a pair of typical vegetative rods. (From Sedgwick and Wilson, after deBarry.) See Fig. 18.

oxidation, endocrinal and other glandular products, evaporation surface of the lungs and skin, 'trophic' and 'temperature' nerves, coördinating centers, etc., — the whole complex rendering its possessors largely independent of the surrounding temperature and making possible a carrying on of the various bodily functions with such nicety as the life of these forms demands. It is hardly possible that the human brain, for instance, could have developed to function as it does if its cells were subject to wide temperature variations such as are those of a Fish or Frog.

PRESSURE. The metabolism of organisms, in common with chemical processes in general, is influenced by the surrounding mechanical pressure. Therefore it is evident that the pressure of either the water or air plays an important part in the operation of the life functions. We find organisms adapted to the greatest depths of the ocean where the water pressure is several hundred atmospheres — so great that some forms burst when rapidly brought to the surface; while others are adapted to live at high altitudes where the air pressure is relatively low. And again, the higher Vertebrates present an adaptive mechanism which renders them less dependent on a constant atmospheric pressure.

These few examples must suffice to emphasize the general environmental conditions which are necessary for life, as we know it, to exist, and to suggest that within these broad limits organisms are adapted to special environmental conditions so that there is scarcely a niche in nature untenanted.

2. Adaptations Essentially Structural

We may now broaden our view of the plasticity of organisms by a brief consideration of adaptations which are essentially structural. But here as elsewhere it is absolutely impossible to sharply distinguish between structure and function which, obviously, are only reciprocal aspects of the fitness of living creatures.

ADAPTIVE RADIATION OF MAMMALS. In the group of Mammals, forms are to be found which are extraordinarily modified in adaptation to the most diverse environmental conditions. From a more or less primitive type, or focus, there radiate, as it were, types which are specialized for very different habitats and modes of life. We may select from the highest subclass of the Mammals, the Eutheria, a small Malayan insectivorous animal known as Gym-

FIG. 205. — *Gymnura*. (From Lull, after Horsfield and Vigors.)

FIG. 206. — Diagram of the adaptive radiation of Eutherian Mammals as exhibited in limb structure. (From Lull.)

nura, which is allied to the Hedgehogs, as most similar among living Mammals to the generalized or focal type of terrestrial Mammal. *Gymnura* has relatively short pentadactyl limbs with the entire palms and soles resting flat upon the ground (PLANTIGRADE) and therefore essentially adapted for comparatively slow progression. (Figs. 205, 206.)

Radiating from this focus, adaptations for rapid running (CURSORIAL adaptations) are chiefly evident in a lengthening of the limbs. Thus, for example, in the Dogs, Foxes, and Wolves, the effective limb length is increased by raising the wrist and heel from the ground and walking merely upon the digits (DIGITIGRADE); while in Antelopes, Horses, and hoofed runners in general, the chief limb bones themselves are lengthened, subsidiary ones are suppressed, and the wrist and ankle are raised still further from the ground, so that merely the tips of one or two digits of each limb support the animal (UNGULIGRADE). Thus the typical cursorial forms represent the culmination of Mammalian adaptation to plains and steppes; regions in which long distances must frequently be traversed in quest of food, and safety is to the swift. (Fig. 207.)

Another line of adaptive radiation is presented by the tree dwellers: ARBOREAL forms which make their own the world of foliage high above the ground. Such

FIG. 207. — Foot postures of Mammals. A, plantigrade; B, digitigrade; C, unguligrade. (From Lull, after Pander and D'Alton.)

are, for instance, the Sloths which are really tree climbers that walk and sleep upside down suspended from branches; the Man-like

FIG. 208. — A Sloth, *Choloepus*, walking suspended from a branch.
(From Allen.)

Apes that swing among the boughs chiefly by their arms; and the Squirrels that scamper along the branches. Some Squirrels and the so-called Flying Lemurs take long soaring leaps supported by

FIG. 209. — Skeleton of a Mole, *Talpa europaea*. (From Pander and D'Alton.)

wide folds of skin between the sides of the body and the extended limbs. But the Mammals have not left the air untenanted, for truly VOLANT forms are represented by the Bats in which the fore

FIG. 210. — Skeleton of a Porpoise. The vestigial pelvic bones are shown imbedded in the flesh. (From Pander and D'Alton.)

limbs with greatly elongated fingers form the framework of true wings. (Figs. 208, 211, 212.)

Passing below the surface of the earth, FOSSORIAL Mammals are found such as the Woodchucks, Gophers, and especially the Moles,

which are adapted to a subterranean existence by bodily modifications which facilitate digging. Furthermore, the gap between ter-

FIG. 211. — 'Flying Lemur,' *Galeopithecus volans*. (From Lull.)

restrial and aquatic Mammals is bridged by the Muskrats, Beavers, Otters, and Seals which are more or less equally at home on land and in the water. (Fig. 209.)

FIG. 212. — A Bat, *Vespertilio noctula*. (From Lull.)

The truly AQUATIC Mammals are the Porpoises and Whales which have completely abandoned the land of their ancestors of the

geological past and to-day approach, in adaptations to a marine life, the general contour of the primitively adapted aquatic Vertebrates, the Fishes. (Fig. 210.)

Thus the various lines of adaptive radiation of the Mammals from a generalized terrestrial type, such as *Gymnura*, have provided Mammals fitted for all sorts and conditions of the environment — representatives are competing with members of other groups beneath, on, and above the earth and in the water. Somewhat similar adaptive radiations are traceable in other animal and plant groups, though there seems no doubt that the adaptability of the Mammal stock — its potential of evolution — is in no small degree responsible for the dominant position which the

FIG. 213. — Diagram of the adaptive radiation of a group of Insects, the Hemiptera or Bugs. (From Lindsey.)

Mammals hold in the animal world of to-day. Man is a Mammal. (Fig. 213.)

ANIMAL COLORATION. Perhaps the most generally striking characteristic of organisms is their color and color pattern. Among plants this applies chiefly to the flowers and fruit of the higher forms, though here and there throughout the plant series the typical green color is replaced or rendered inconspicuous by others. But the absence of photosynthetic pigments in animals and their relatively active life have permitted more latitude in body color, and accordingly it is in the animal world that color adaptations are more numerous and varied. Some colors and color patterns are, of course, merely incidental to the chemical composition of the whole or parts of the body. Others, however, irresistibly arouse our interest and seem to demand a less simple explanation because they are ap-

parently of special service to their possessors. A few examples will serve to bring the problem before us and indicate the class of facts involved.

The color and color patterns of many animals are such that they harmonize or fuse with the usual surroundings of the creatures and render them practically indistinguishable from their immediate environment. Every frequenter of the open knows innumerable instances. The song of the green Katydid readily guides one to its immediate vicinity, but it is quite another matter to distinguish its leaf-green wings among the foliage of its retreat. Again, one is attracted by the striking colors of an Underwing Moth while in flight, but is at a loss to find the insect when scarlet or orange is obscured by the overlapping grayish-mottled fore-wings blending with the tree trunk where it has come to rest. (Figs. 214, 215.)

FIG. 214. — The common green Katydid, *Microcentrum*. (After Riley.)

The white of the Foxes, Hares, and Owls of alpine and arctic regions; the green color of foliage-dwelling Insects and Frogs; the tendency toward fawn and gray of desert Insects, Reptiles, Birds, and Mammals; the olive upper surface of the bodies of brook Fishes; the steel gray above and white below of sea Birds that harmonize with sea and sky when viewed from above and below respectively — the number of such cases is legion. Gazelles living on the lava fields of volcanic regions are dark gray, while those of the great stretches of sand plains are white — the same species exhibiting regional variations in color which blend with the surroundings. Furthermore, the same individual may vary in color with the seasonal changes in its environment, or present different color schemes in different localities. Thus the summer coat colors of the Arctic Fox and the Weasel harmonize with the browns of rocks; and the winter coat of white, with snow-clad nature. And the Chameleons are by no means unique in their ability to change color very rapidly in response to that of their immediate surroundings.

But confusion is worse confounded when to harmonizing color is added harmonizing form, striking examples of which are the Dead-leaf Butterflies of the East Indian region, the familiar Walking-sticks, and the caterpillars ('inch-worms') of Geometrid Moths. (Fig. 216.)

Although the general tendency in nature is for *sympathetic* coloration — indeed, it is frequently possible to infer from the color

FIG. 215.—Underwing Moth. A, wings expanded, exposing the highly colored hind-wings; B, resting on bark. (From Folsom.)

of an animal its habitat — there are numerous cases in which the colors and color schemes seem to be in striking contrast with the animal's usual background. Sometimes, however, the contrast which is so striking with the bird in the hand, proves to be *obliterative* with the bird in the bush — a conspicuous color pattern, expressing gradations of light and shadow, and counter shading, fuses with a background of light and shadow afforded by foliage.

But examples of color patterns which by the most liberal stretch of the imagination cannot be interpreted as harmonious with the animal's usual surroundings are not far to seek. Brilliant yellows

FIG. 216. — *A*, Walking-stick Insect, on a twig. *B*, larva of a Geometrid Moth resting extended from a twig. (After Jordan and Kellogg.)

and reds render, for instance, many Wasps, Bees, Butterflies, and various species of Snakes actually conspicuous. And it is suggestive that very many of these forms are provided with special means of defense, such as poison glands and formidable jaws, or special secretions which render them unpalatable. Moreover, what is still

more interesting, many animals possessing this *protective conspicuousness* which renders them easily identified and advertises that they are to be avoided by their foes, are frequently '*mimicked*' in color pattern and form by defenseless creatures. Thus commonly

FIG. 217. — 'Protective mimicry.' A, drone Honey Bee; B, a Bee-fly, *Eristalis tenax*. (From Folsom.)

associating with the various species of Bees hovering about flowers are defenseless Flies which are so bee-like in appearance that they are usually mistaken for Bees, and avoided accordingly by human, and presumably by other enemies also. (Fig. 217.)

Now, what is the significance of such phenomena of animal coloration and form? This problem has attracted much attention and appears by no means so simple to-day as it did a generation

FIG. 218. — The Honey Bee, *Apis mellifica*. (From Bureau of Entomology.)

ago. Biologists to-day are not so ready to interpret individual cases as 'protective,' 'aggressive,' 'alluring,' 'confusing,' or 'mimetic.' But it is beyond dispute that nowhere else is the plasticity — adaptability — of organisms better illustrated, and that, taken by and large, such adaptations are of crucial importance in the life and strife of species. Whatever may be the origin of such adaptive

variations, natural selection apparently is responsible for their accumulation and preservation.

THE LEGS OF THE HONEY BEE. From time immemorial the Honey Bee (*Apis mellifica*) has been the subject of wonder and study, and to-day there is no more interesting and instructive example of adaptation than that exhibited by the Bee in relation to the highly specialized community life of the hive. (Fig. 218.)

An average hive comprises some 65,000 Bees of which one is a **QUEEN**, several hundred are **DRONES**, and the rest **WORKERS**. The queen is the only fertile female and accordingly she is the mother of nearly all the other members of the hive. Throughout her life of about three years she is tended and fed by her numerous offspring. The drones, or males, contribute nothing to the work of the hive but, after the old queen departs at the *swarming*, one of them mates with a virgin queen which then becomes the new queen of the hive. Thus the queen and the drones represent an adaptation of the colony to communal life — a physiological division of labor in the hive which involves a specialization of a class solely for reproduction, while the daily work and strife of the colony devolves upon the workers. The latter are sexually undeveloped females

FIG. 219. — Head of a worker Honey Bee.

which do not lay eggs but spend their time carrying water, collecting nectar and pollen, secreting wax, building the comb, preparing food, tending the young, and cleaning, airing, and defending the hive.

The worker is a 'bundle of adaptations' for its varied duties. Indeed, when we take away the adaptations there is little left! The primitive insect appendages have become specialized in the worker Bee, so that collectively they constitute a battery of tools adapted with great nicety to the uses for which they are employed. This applies to all of the appendages of the insect's body, but we shall neglect those of the head and consider only the specializations

MESOTHORACIC LEG

METATHORACIC LEG

Fig. 220. — Legs of the worker Honey Bee.

of the three pairs of legs. These, as in all Insects, arise from the THORAX; the anterior pair from the first segment of the thorax (prothorax); the second, or middle, pair from the second thoracic segment (mesothorax); and the posterior pair from the third, or last, thoracic segment (metathorax). A typical insect leg consists of several parts: the COXA, which forms the junction with the body, followed in order by the TROCHANTER, FEMUR, TIBIA, and five-jointed TARSUS, or foot. (Figs. 219, 220.)

The worker Bee's PROTHORACIC LEGS show the following specializations. The femur and tibia are covered with long, branched FEATHERY HAIRS which aid in gathering pollen when the Bee visits flowers: the tibia, near its junction with the tarsus, bears a group of stiff bristles (POLLEN BRUSH) which is used to brush together the pollen grains that have been dislodged by the hairs of the upper

FIG. 221. — Foot of the Honey Bee in the act of climbing, showing the 'automatic' action of the pulvillus. *A*, position of foot on a slippery surface. *fh*, tactile hairs; *pv*, pulvillus; *t*, last segment of tarsus; *an*, claw. *B*, position of foot in climbing on a rough surface. *an*, *c*, claw. *C*, section of a pulvillus just touching a flat surface; *cr*, curved rod. *D*, the same applied to the surface. (From Packard, after Cheshire.)

leg-segments. On the opposite side of the leg is a composite structure, the ANTENNA CLEANER, formed by a movable plate-like process (VELUM) of the tibia which fits over a circular notch in the upper end of the tarsus. The notch is provided with a series of bristles which form the teeth of the ANTENNA COMB. The antennae, or 'feelers,' which are important sense organs of the head, are cleaned by being placed in the toothed notch and, after the velum is closed down, drawn between the bristles and the edge of the velum. On the anterior face of the first segment of the tarsus is a series of bristles (EYE BRUSH) which is used to remove pollen and other particles adhering to the hairs on the head about the large compound eyes and interfering with their operation.

The terminal segment of the tarsus of each leg is provided with a pair of notched CLAWS, a sticky pad (PULVILLUS) and TACTILE HAIRS. (Fig. 221.) When the Bee is walking up a rough surface, the

points of the claws catch and the pulvillus does not touch, but when the surface is smooth, so that the claws do not grip, they are drawn beneath the foot. This change of position applies the pulvillus, and it clings to the smooth surface. Thus the character of the surface automatically determines whether claw or pulvillus shall be used.

FIG. 222. — Sting of worker Honey Bee. (From Hegner, after Cheshire.)

But there is another adaptation equally remarkable. "The pulvillus is carried folded in the middle, but opens out when applied to a surface; for it has at its upper part an elastic and curved rod, which straightens as the pulvillus is pressed down. The flattened-out pulvillus thus holds strongly while pulled along the surface by the weight of the Bee, but comes up at once if lifted and rolled off from its opposite sides, just as we should pull a wet postage stamp from an envelope. The Bee, then, is held securely till it

attempts to lift the leg, when it is freed at once; and, by this exquisite yet simple plan, it can fix and release each foot at least twenty times per second." (Cheshire.)

The characteristic structures of the middle (MESOTHORACIC) legs of the Bee are a small POLLEN BRUSH and a long spine, or SPUR,

FIG. 223. — Pollination of an Orchid (*Cypripedium*) by a Bumble Bee. A, Bee forcing its way into the flower; B, Bee obtaining nectar in the flower; C, Bee starting to escape brushes pollen upon the stigma of the flower; D, before finally escaping the Bee receives another load of pollen from the anther.

which is employed in removing flakes of wax from the WAX POCKETS on the ventral surface of the abdomen.

The METATHORACIC LEGS exhibit four remarkable adaptations to the needs of the insect, known as the POLLEN COMBS, PECTEN, AURICLE, and POLLEN BASKET. The pollen combs comprise a series of rows of bristle-like hairs on the inner surface of the first segment of the tarsus: the pecten is a series of spines on the distal end of the tibia which is opposed by a concavity, the auricle, on the proximal end of the tarsal segment; while the pollen basket is formed by a

depression on the outer surface of the tibia which is arched over by rows of long curved bristles arising from its edges.

Thus the worker is fully equipped. Flying from flower to flower for nectar, the Bee brushes against the anthers laden with pollen, some of which adheres to the hairs on its body and legs. While still in the field, the pollen combs are first brought into play to comb the pollen from the hairs, while the pectens scrape the pollen from the combs. Then the auricles are manipulated so that the accumulating mass of pollen is pushed up into the bristle-covered pollen baskets. This process is repeated until the baskets are full and then the insect returns to the hive, where the contents of the pollen baskets are removed by the aid of the tarsi of the mesothoracic legs.

Moreover, the structural adaptations of the worker Bee are but one aspect of a reciprocal fitness. Many of the flowers which the Bee visits show remarkable adaptations for the reception of the Bee and for dusting it with pollen, because Bees are effective agents in transferring pollen from flower to flower and thus insuring cross-fertilization. And so the Bee which has been given as our final example of adaptation to the physical environment, serves also as an introduction to the consideration of adaptation to the living environment. No better proof could be asked of the futility of attempting to classify the adaptations of organisms — the organism is a unit: a 'bundle of adaptations' to any and all of its surroundings, inanimate and animate, otherwise it could not exist.

B. ADAPTATIONS TO THE LIVING ENVIRONMENT

We now turn more specifically to some striking interrelations of organism with organism, in order to make possible an appreciation of the devious means to which they have recourse — to what extent the strands of the web of life become entangled — in the competition for a livelihood.

The mutual biological interdependence of organisms is, in the final analysis, the result of the primary demands of all creatures — proper food, habitat, reproduction, defense against enemies and the forces of nature. The web of life is an expression of the coöperation, jostling, and strife of individual with individual, and species with species for these primary needs; and the activities which follow from them form the foundations of life in the lowest as well as the highest. A little patch of meadow soil two feet square has revealed,

within about an inch from the surface, over a thousand animals and three thousand plants. There is a *struggle for existence*.

Take a single example. A common food Fish, the Squeteague, captures the Butter-fish or the Squid, which in turn have fed on young Fish, which in their turn have fed on small Crustacea, which themselves have utilized microscopic Algae and Protozoa as food. Thus the food of the Squeteague is actually a complex of all these factors, and such a *nutritional chain* is no stronger than its single links. Circumstances which modify or suppress the food and thereby reduce the abundance of the Algae and Protozoa of the

FIG. 224. — Diagram of the web of life and the equilibrium of nature, as illustrated by the food relations in a pond community. Arrows point from the organisms eaten to those doing the eating. (From Shelford.)

sea are reflected in correlative changes in the abundance of economically important food Fishes. And this same principle is true throughout living nature, though only occasionally is it possible to trace it. "Nature is a vast assemblage of linkages." (Fig. 224.)

1. Communal Associations

Perhaps the simplest associations of organisms are represented by GREGARIOUS animals, such as Wolves which hunt in packs, and Buffaloes and Horses which herd for protection. Here the association is more or less temporary and there is no division of labor between the members, other than leadership by one animal.

COMMUNAL animals, however, exhibit highly complex associations

in which the members merge, as it were, their individuality in that of the community. This is well exhibited, for example, among the Ants, in which all of the various species, about 5000 in number, are communal, and in the Wasps and Bees in which all gradations exist from solitary to hive-dwelling species. And, as has been mentioned in the case of the Bees, the division of labor has developed to the extent that structural differentiations have given rise to classes of individuals specially adapted for the performance of certain functions in the economy of the hive.

But the differentiations of various members of a colony of Ants or Bees are limited to their bodies and are practically fixed and irreversible, while in human society, differentiations are no longer confined to the bodies of individuals. Man's ingenuity has devised what are to all intents and purposes artificial, accessory organs — tools and machines. Accordingly it is in Man that we find the highest expression of communal coöperation, because increased intelligence, in particular, makes flexible the stereotyped life as exhibited in the lower forms — the human individual is adaptable to the various community tasks.

2. *Symbiosis*

Associations are not confined to members of the same species, nor are all an expression of coöperative adaptations. All gradations occur from those which are mutually beneficial to the parties in the pact, to those in which one member secures all the advantage at the expense of the other.

The most intimate associations in which the organisms involved are mutually benefited, if not absolutely necessary for each other's existence, are termed SYMBIOTIC. A familiar illustration is the common green Hydra (*Hydra viridis*) which owes its characteristic color to the presence of a large number of unicellular green plants which live in its endoderm cells. The products of the photosynthetic activity of the plant cells are at the disposal of the Hydra, and the latter in return affords a favorable abode and the material necessary for the life of the plants.

A far more striking example of symbiosis is afforded by Lichens which represent intimate combinations of various species of Fungi and Algae. In each case the Fungus supplies attachment, protection, and the raw materials of food, while the green Alga performs photosynthesis. Each can live independently under favorable

conditions, but in partnership they are superior to hardships with which many other plants cannot cope, and thus some Lichens become the vanguard of vegetation in repopulating rocky, devastated areas. (Fig. 225.)

From the practical standpoint of agriculture the symbiotic nitrogen-fixing Bacteria are of first importance. It will be recalled that these Bacteria form small tubercles on the rootlets of higher plants and make atmospheric nitrogen available to the latter.

FIG. 225. — The formation of a Lichen, *Phycia paratina*, by the combination of an Alga and a Fungus. A, germination of a Fungus spore (*sp*), whose filaments are surrounding two cells (*a*) of the unicellular Alga, *Cystococcus humicola*. B, later stage in which spores have formed a web of filaments (mycelium), enveloping many algal cells. Magnified about 400 times. (From Bonnier.)

Thus in return for an abode and certain food elements, such nitrogen-fixing Bacteria render their symbiotic associate largely independent of soil nitrogen. Again in the higher animals, including Man, evidence is accumulating which indicates that certain kinds of Bacteria find their normal habitat in the digestive tract, where, incidental to getting their own living, they bring about chemical changes in the food which is an important factor in the digestive processes of the animal. (Fig. 24.)

Still another type of association in which both partners profit is represented by the relation that occurs between Ants and Plant Lice, or Aphids. The defenseless Aphids are protected, herded, and

'milked' by the Ants to supply their demand for honeydew, a secretion of the Aphids which the Ants greedily devour. (Fig. 226.)

3. *Parasitism*

But associations in which one organism, the PARASITE, secures the sole advantage, and in most cases at the expense of the helpless second party, the HOST, are far more numerous — it has been estimated that nearly half the animal kingdom are parasites. And

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FIG. 226. — Rose Aphids visited by Ants.

these justly receive considerable notoriety because many human diseases are the result of Man's unwilling partnership in such associations. Indeed, PARASITOLOGY has become an important subdivision of biology, both practical and theoretical. Practical, as a cornerstone of public health; and theoretical, because many of the most remarkable functional and structural adaptations are exhibited by parasites in becoming fitted for this apparently highly successful method of gaining a livelihood, and by the hosts in bear-

ing the burden with the least outlay. Generally speaking, the effect on the parasite consists in a simplification of the various organs of the body devoted to food-getting, locomotion, etc., since their duties are performed by the host; while the organs and methods of reproduction are highly specialized and elaborated, owing to the necessity of producing enough offspring to compensate for the hazards involved in reaching a proper host. For in the majority of cases a parasite is adapted to live in a specific host, and death ensues if this is not attained at the proper time. (Figs. 251, 252, 267.)

Probably the most generally interesting example of parasitism is the cause of the disease known as MALARIA. Man is subject to at least three types of malaria, each the result of infection by a different malarial organism. The malarial parasites are all unicellular animals, Protozoa, with complicated life histories which are adaptations to the specific demands of their parasitic existence. One part of the life history, the asexual, is passed in the red blood corpuscles of Man; while the other, the sexual, occurs in the digestive tract of certain species of Mosquitoes. A single parasite inoculated into the human vascular system by the bite of an infected Mosquito enters a red blood corpuscle and multiplies. The progeny, liberated from the destroyed corpuscle, similarly attack other corpuscles and multiply until a very large number of blood corpuscles are destroyed. And poisonous products of the life processes of the parasites provoke the chills and fevers characteristic of the disease. (Fig. 227.)

But the parasites must make their escape before the human host successfully combats the toxic substances, kills the parasites by taking quinine, or succumbs to them. The getaway is accomplished, if at all, by a Mosquito biting the host and taking with the blood certain sexual stages of the parasite which can develop in the cold-blooded insect. And now the Mosquito is the host. In its stomach the sexual phase of the life history of the malarial parasite takes place, fertilization occurs, and finally the numerous products of the zygote work their way to the mouth parts of the Mosquito, where they await an opportunity to enter the human blood.

The life history of malarial parasites exhibits a continuous series of adaptations to parasitic life: the nicety of the adjustment being especially well illustrated at the transfer from Man to Mosquito, since all the parasites which enter the stomach of the latter are

FIG. 227. — Life history of a Malarial Parasite. Stages above the line occur in human blood; those below, in body of Mosquito. I-V and 6-10, asexual multiplication (schizogony) in human red blood corpuscle following introduction of parasite (XIX) by a Mosquito. This may continue by parasites (10) entering other corpuscles until a large number of the latter are destroyed. Soon sexual forms arise (VI-XIII). Male (♂) and female (♀) gametes unite (XI) to form a zygote (XII). This is motile (XIII), penetrates wall of stomach of Mosquito, and encysts (XIV). Within cyst small cells (XVI, *sp.bl.*) arise by division, and these give rise to motile cells (XVIII) termed sporozoites. These are liberated (XIX) from the cyst, migrate to salivary glands of Mosquito and await inoculation into the human body to enter a red blood corpuscle (I). *n*, nucleus of parasite; *p*, pigment and waste products of the parasites; *fl*, male gametes. (From Minchin.)

digested except those sexual forms which are ready to initiate the sexual part of the cycle in the new host. (Figs. 246, 247.)

But the acme of parasitic associations is only attained when the adaptations of parasite and host have become so complete that

FIG. 228. — Life history of the Trypanosome (*Trypanosoma gambiense*) that produces African sleeping sickness in Man. Magnified about 1500 times. (From Chandler, after Robertson.)

the latter 'pays the price' without any ill effects. Thus the Antelopes and similar Mammals of certain regions of Africa harbor in their blood various species of Protozoan parasites, known as

TRYPANOSOMES, without any apparent discomfort. But if the intermediate hosts, which are biting Flies, transfer certain species of Trypanosomes to the blood of imported Horses or Cattle, or of Man, serious diseases result which are usually fatal. Indeed, the opening up of large regions of Africa has been greatly retarded by the ravages of Trypanosomes in new hosts to which they are not adapted. Generally speaking, pathogenic species may be regarded as aberrant forms which are not yet adapted to their hosts or are not in their normal hosts. And these are the parasites which are especially forced upon our attention, though there are few organisms without their specially adapted parasites — the parasites themselves not excepted. (Figs. 228, 245.)

4. *Immunity*

At best, however, the part played by the host cannot be regarded as ideal, and devious types of adaptations against parasites exist which, in so far as they are effective, bring about IMMUNITY. Usually among the higher animals, including Man, immunity to pathogenic organisms seems to have its foundations in specific chemical substances in the blood, termed ANTIBODIES. These either modify the activities of certain cells of the body, chiefly the white blood corpuscles, or act directly upon the invaders themselves and the poisons (TOXINS) which they produce. The white blood corpuscles have been called the 'policemen of the body' because, under the influence of invading organisms and of certain antibodies called OPSONINS, some of them make their way through the walls of the capillaries in the region of the infection and, in amoeboid fashion, engulf and digest the intruders. When acting in this capacity the corpuscles are referred to as PHAGOCYTES.

Among the various classes of antibodies are also the ANTITOXINS which neutralize the poisonous products of Bacteria, and the LYSINS which actually destroy foreign cells. Various specific antibodies may be naturally present in the blood — a part of the heritage — so that an individual is immune to certain diseases due to pathogenic organisms. Or the antibodies may be produced in response to the parasites themselves, and the individual acquires immunity only after undergoing the disease. Again, immunity may be artificially acquired by various means, such as VACCINATION, which stimulate the production of antibodies so that the individual is duly prepared in the event of an infection.

Finally, it has recently been discovered that Bacteria have to combat a mysterious something called the BACTERIOPHAGE. Whether this is a hitherto unknown group of organisms still smaller than the Bacteria, or a unique enzyme-like substance, has not yet been determined. At all events a specific bacteriophage seems to exist for each kind of Bacteria and to be ever ready to destroy it.

Indeed, the subject of immunity has become a science in itself (IMMUNOLOGY) within the past few years — a science which has as its fundamental basis the investigation of the marvellous power of adaptation of protoplasm as exemplified in coping with disease-producing parasites, and with ultramicroscopic agents of disease — the so-called FILTERABLE VIRUSES — such as produce smallpox, measles, and rabies. Immunology is the “chemical warfare of existence.”

C. INDIVIDUAL ADAPTABILITY

We may now turn to a survey of the highest expression of adaptation evolved by Nature, which is revealed in relatively simple form in the BEHAVIOR of the lower organisms, gains definiteness and content as we ascend the animal series, and becomes the basis of INTELLIGENCE and all that the mental life of Man involves. It is the adaptation which renders Man essentially superior to adaptation — enables him to a large extent to control, instead of being controlled by his environment. “It seems that Nature, after elaborating mechanisms to meet particular vicissitudes, has lumped all other vicissitudes into one and made a means of meeting them all” — the nervous mechanism.

That organisms respond to environmental changes, we are well aware. Life itself is the result of — in fact, is — a continuous flow of physico-chemical actions, interactions, and reactions with the surroundings. But by the behavior of the organism we refer specifically to the reactions of the organism as a unit, rather than to the internal processes in the economy of its life. And surveyed from a broad viewpoint, there is discernible in the behavior of animals, just as in their structure in general and in their nervous system in particular, from the lowest to the highest, a gradual increase in the complexity of behavior. The behavior of Amoeba or Paramecium is an expression of the primary attributes of protoplasm — irritability, conductivity, and contractility. So is the behavior of Hydra

and Earthworm in which special cells constitute a definite coordinating, or nervous system. And so is the complex behavior of the higher animals, including Man, with their elaborate series of sense organs and highly developed sensorium, or brain.

"Let us now try to form a picture of the behavior of *Paramecium* in its daily life under natural conditions. An individual is swimming freely in a pool, parallel with the surface and some distance below it. No other stimulus acting, it begins to respond to the changes in distribution of its internal contents due to the fact that it is not in line with gravity. It tries various new positions until its anterior end is directed upward, and continues in that direction. It thus reaches the surface film. To this it responds by the avoiding

FIG. 229. — Diagram to illustrate the avoiding reaction of *Paramecium*. A, a solid object or other source of stimulation. 1-6, successive positions taken by the animal. The rotation on its long axis is not indicated. (From Jennings.)

reaction (Fig. 229), finding a new position and swimming along near the surface of the water. . . . Swimming forward here, it approaches a region where the sun has been shining strongly into the pool, heating the water. The *Paramecium* receives some of this heated water in the current passing from the anterior end down the oral groove. (Fig. 230.) Thereupon it pauses, swings its anterior end about in a circle, and finding that the water coming from one of the directions thus tried is not heated, it proceeds forward in that direction. This course leads it perhaps into the region of a fresh plant stem which has lately been crushed and has fallen into the water. The plant juice, oozing out, alters markedly the chemical constitution of the water. The *Paramecium* soon receives some of this altered water in its ciliary current. Again it pauses, or if the chemical was strong, swims backward a distance. Then it again

swings the anterior end around in a circle till it finds a direction from which it receives no more of this chemical; in this direction it swims forward. . . .

"In this way the daily life of the animal continues. It constantly feels its way about, trying in a systematic way all sorts of conditions, and retiring from those that are harmful. Its behavior is in principle much like that of a blind and deaf person, or one that feels his way about in the dark. It is a continual process of proving all things and holding to that which is good." (Jennings.)

The behavior of *Paramecium* leaves one with the impression that the animal is largely at the mercy of its surroundings — that the environment rather than the organism itself is the dominant factor, but this is true only to a limited degree. *Paramecium* is not merely an automaton. Its behavior is modifiable and, in the long run, is adapted to the usual changes of its surroundings. That the reactions are adequate for the simple life and methods of reproduction of *Paramecium* is attested by its success — it is one of the most common and widely distributed animals.

In such simple beginnings, then, must be sought the largely automatic responses of animals to the changes in external conditions, known as REFLEXES and INSTINCTS. Both are the result of inherited nervous structure and therefore may be regarded as inherited behavior — just as truly characteristics of the organism as form of body or method of reproduction. And increase in the complexity of life processes has involved at the same time an increase in the number and complexity of instincts. The primitive reflexes and instincts of *Hydra* lead it to seize with its tentacles small organisms within reach

FIG. 230. — Diagram to show the rotation on the long axis, and the spiral path of *Paramecium*. 1-4, successive positions assumed. The dotted areas with small arrows represent the currents of water drawn from in front. (From Jennings.)

and pass them to its mouth: the Earthworm, to swallow decaying leaves as it burrows through the soil: the Crayfish, to grasp its prey with its large claws, tear it into pieces by means of certain appendages about the mouth which are adapted just for the purpose — and so on to the higher Vertebrates where the feeding instincts reach their maximum of complexity. The marvellous behavior of Ants and Bees is essentially a complex of instincts. Turn the hive around and the homing instinct of the Bees fails — they cannot find the entrance. Moreover, instincts of fear, self-defense, play, care of the young, etc., render a considerable part of the behavior of even the higher organisms more automatic than is perhaps, at first thought, apparent. (Fig. 144.)

But just as the behavior of *Paramecium* and its allies is modifiable, so instincts which seem the most fixed show at least a slight degree of adaptability to unusual conditions. And it is this ever-present power of modifiability, which is in Man called 'choice,' that leavens the whole and becomes the dominant factor in the behavior of the highest animals; while reflex action and instinct are relegated to a subsidiary though by no means unimportant rôle.

The power of such more or less conscious choice of responses to external conditions affords a gradual and ill-defined transition from instincts to intellectual processes, or REASON. The foundations of both are to be sought in simple reflex actions and oft-repeated voluntary actions which gradually become HABITS — relegated to the level of reflex actions. Indeed a large part of the education of Man consists in establishing adaptive reflexes which relieve the conscious life of innumerable simple factors of behavior, and leave it more or less free for the higher intellectual processes. Although it is necessary to emphasize that mind and intelligence, in the biological sense, are expressions for that integration of nervous states and actions which makes possible a nicety of adaptation of behavior to environmental conditions that otherwise would be impossible — that it is our chief means of adaptation; it is a serious mistake to minimize the importance of the vast gulf between Man's nature and that of the most highly developed lower animals. In no respect are these differences more marked than in the various forms of learning that collectively form the means of education. Indeed, when in its highest reaches life blossoms into CONSCIOUSNESS — our own consciousness — we personally appreciate that it is able to form strange conceptions; that it has not only memory of the past, but

anticipation of the future also. We can brood and meditate and understand in part. We are guided by the past, present, and future in making adaptations.

Thus it is clear that, with all the variations in structure and function, organisms all possess irritability in common: they all exhibit adaptive responses which enable them to exist in spite of surrounding changes. "Adaptability appears to be the touchstone with which nature has tested each kind of organism evolved; it has been the yard-stick with which she has measured each animal type; it has been the counterweight against which she had balanced each of her productions . . . the general course of evolution has been always in the direction of increasing adaptability or increasing perfection of irritability." The individual's heritage affords the cumulative result of the adaptations of the race — including adaptability.

CHAPTER XXIV

THE ORIGIN OF SPECIES

Thoughtful men will find in the lowly stock whence Man has sprung, the best evidence of the splendor of his capacities; and will discern in his long progress through the past, a reasonable ground of faith in his attainment of a nobler future. — *Huxley*.

FROM the time of the Greek natural philosophers there always have been men who have sought a naturalistic explanation of the origin of the diverse forms of animals and plants, and who have suggested that the present ones arose from earlier forms by a long process of descent with change, or *EVOLUTION*. But with the revival of natural history studies after the Middle Ages, the prevailing ideas in regard to creation led the majority, perhaps almost unconsciously, to assume that there are as many kinds of organisms as issued from the Ark. And this is not so strange, as might at first glance appear, when one considers that all of the important facts which we have reviewed in the preceding pages were then absolutely unknown, and that the number of known kinds of animals totalled but a thousand or so instead of upward of a million as to-day.

The pioneer work of the early Renaissance naturalists consisted principally of collecting and describing animals and plants. This involved making a catalog of the different kinds — classifying them in some way — and consequently some basis of *CLASSIFICATION* was sought. Thus attention was focussed on the kinds, or *SPECIES*, and for practical, if for no other reasons, the species assumed a prominence which overshadowed the individuals which composed it.

Indeed, to-day biologists are hard put to it to define a species. Of course everyone recognizes not only that there are many kinds of animals and plants, but also that many individuals are essentially the same. Groups may be formed of individuals which differ less among themselves in the sum of their characters than they do from the members of any other group of individuals. And further, the members of a group produce other individuals which are essentially similar. It is such a group of similar individuals that is regarded by

the biologist as a species. But it will be noted that a species is largely a concept of the human mind — the real unit in nature is the individual animal or plant, and an understanding of the differences between individuals should give us the key to the differences between species. So, in the final analysis, the problem of the origin of species is a problem in genetics.

This seemingly obvious point of view has but relatively recently been clearly grasped by biologists, and the species rather than the individual has loomed large in the discussions of how plants and animals came to be what they are to-day. As a matter of fact, during the eighteenth century the greatest student of plant and animal classification, Linnaeus, emphasized the idea that each species represents a distinct thought of the Creator, and that the object of classification is to arrange species in the order of the Creator's consecutive thoughts. This viewpoint is somewhat whimsically expressed by the old naturalist who, finding a beetle which did not seem to agree exactly with any species in his collection, solved the difficulty by crushing the unorthodox individual under his foot. His credulity surely would have been strained by the estimate of modern entomologists that if all the species of Insects were known they would total upward of five million. (Fig. 280.)

We may consider, then, that the consensus of opinion up to the middle of the last century was overwhelmingly on the side of SPECIAL CREATION and FIXITY OF SPECIES, and therefore against the idea occasionally advanced by men, as it now appears, ahead of their times, that DESCENT WITH CHANGE is the true explanation of the origin of the diverse forms of plants and animals. But, as nearly everyone knows, a complete reversal of opinion has occurred since 1860 — to-day professional scientists and most educated laymen accept ORGANIC EVOLUTION. And we have accepted it in the preceding sections of this work; but if this appears to have been prejudging the question, the explanation is that the genetic connection of organisms is the guiding principle of all modern biology. The mere fact that an unbiased presentation of the data seems to prejudice the question is the most cogent presumptive evidence for evolution. It is true that there are wide differences of opinion among biologists in regard to the *factors* which have brought about the evolutionary change — but there are none in regard to the *fact* of evolution itself. It will be convenient, therefore, first to

summarize a few of the *evidences* of evolution and then to present certain modern views in regard to the *methods* of evolution.

A. EVIDENCES OF ORGANIC EVOLUTION

To one who has thoughtfully followed the preceding pages there must immediately occur many facts which are readily and reasonably interpreted from the point of view of descent of one species from another, but which are entirely obscure from that of the special creation of species. For instance, one will recall the cellular structure of all organisms; the method of origin and the fate of the germ layers in animals; the interrelationship of the urinary and reproductive systems in the Vertebrates; the comparative anatomy of the vascular and skeletal systems of Vertebrates; the similarity of the physical basis of inheritance in animals and plants; the gradual dominance of the sporophyte over the gametophyte from the lower to the highest plants; and so on. (Figs. 70, 82, 122, 129, 142, 231.)

In general, such is the nature of the data which support the evolution theory. Although the evidence, from the nature of the case, must be indirect, it is none the less impressive, chiefly because the facts for evolution are from such diverse sources and all converge toward the same conclusion. The theory of evolution reaches the highest degree of probability, since in every branch of botany and zoölogy all the data are most simply and reasonably explained on the basis of descent with change. It is a cardinal principle of science to accept the simplest conceptions which will embrace all the facts.

Assuming the reader's familiarity with the contents of this volume up to the present point, it is now necessary to summarize some of the most important evidence from various subdivisions of biology. But, as will soon appear, it is impossible to arrange the facts in natural groups because the evidence from one merges into that from another — the evidence interlocks.

1. *Classification*

When the serious study of biological classification was well under way, biologists found increasing evidence of the similarity, or affinity, of various SPECIES of animals and plants. Not only is it possible to arrange animals, for example, in an ascending series of increasingly complex forms, but also in many cases it is difficult or impossible to decide just where one species ends and the next

begins. That is, the most divergent individuals within a given species frequently approach those of a closely similar species. There are *intergrades*.

Furthermore it is found that species themselves can be naturally arranged in more comprehensive groups to which the name GENUS is applied. For example, the common Gray Squirrel represents the species *carolinensis*, and the Red Squirrel, the species *hudsonicus*. Both are obviously Squirrels, and therefore both species are grouped under the genus *Sciurus*. Accordingly, each animal is given a name composed of two words: the first, generic and the second, specific. The Gray Squirrel is *Sciurus carolinensis* and the Red Squirrel is *Sciurus hudsonicus*. Thus to give a scientific name to an animal or plant is really to classify it, because the first word of the name indicates that it possesses some fundamental characteristics in common with the other species of the genus — in fact, is more like them than it is like any other group of organisms.

But again, the members of the genus *Sciurus* have many characteristics in common with other animals which obviously are not true squirrels. The Chipmunks or Ground Squirrels, for instance, differ not only in certain obvious features, but in the possession of internal cheek pouches, etc. This dissimilarity and similarity is expressed by placing them in a different genus, *Tamias*, but in the same FAMILY, *Sciuridae*. The familiar eastern Chipmunk is *Tamias striatus*.

Moreover, while the Beaver (*Castor americana*) differs still more from the Squirrels than do the Chipmunks, and therefore is placed in a distinct family, the *Castoridae*, it nevertheless agrees with both in many fundamental ways so that it is placed in the ORDER *Rodentia*, which also includes the Squirrels and Chipmunks, as well as many other families and genera. Other orders, such as the *Ungulata* (Horses, Cattle, etc.), the *Carnivora* (Cats, Dogs, Bears, etc.), and the *Primates* (Monkeys, Apes, etc.), while they differ widely from the Rodents, still agree with them in possessing hair, and milk glands for suckling the young. This basic likeness is expressed by including all under the CLASS *Mammalia*.

The Mammals in turn are readily distinguished from Birds, Reptiles, Amphibians, and Fishes (each of which forms a separate class), but nevertheless are constructed on the same basic plan, comprising a dorsal central nervous system surrounded by skeletal elements forming the skull and spinal column. Therefore, all are

comprehended in the larger group *Vertebrata* which, with certain minor groups, comprises the *Chordata* and stands in contrast with the Invertebrate groups which include Hydra, Earthworm, Crayfish, etc. The classification of the Gray Squirrel, *Sciurus carolinensis* (Fig. 108), may be outlined as follows:

- KINGDOM — Animalia
- SUBKINGDOM — Metazoa
- PHYLUM — Chordata
- SUBPHYLUM — Vertebrata
- CLASS — Mammalia
- ORDER — Rodentia
- FAMILY — Sciuridae
- GENUS — *Sciurus*
- SPECIES — *Sciurus carolinensis*.

This classification of the Gray Squirrel, although it incidentally serves to illustrate the general method of classification of all organisms, is important because it places concretely before us the fact that organisms show such fundamental similarities with obvious dissimilarities. In short, the mere fact that animals and plants naturally arrange themselves, as it were, in classes, orders, families, genera, species, etc., raises the question of the origin of species. Is special creation implying fixity of species, or is descent with change the more plausible explanation? (See Appendix: Classification.)

The unavoidable answer is descent with change — evolution — because the principle in accordance with which the groups of increasing comprehensiveness are formed is solely the greater or less similarity in the structural features of the organisms. It is much more reasonable to assume that the thread of fundamental similarity which runs through all the Vertebrates, for instance, is the result of inheritance, while the differences of orders, families, genera, etc., are due to changes brought about under different unknown conditions, than it is to assume that each is the result of a special creative act. Especially so when we realize that in a very large number of cases it is difficult or impossible to decide the limits of a species, owing to variations among the individuals comprising it, and it is necessary to resort to SUBSPECIES and VARIETIES in classification. (Fig. 240.) Again, among genera, intergrading forms demand SUBGENERA; among orders, SUBORDERS; among classes, SUBCLASSES; and so on. If we admit the origin by

Fig. 231. — Vertebrate fore limbs to show homologous skeletal structures. A, left wing of a Bird (Raven); B, right wing of a Bat; C, left flipper of a Whale; D, right fore leg of Ox; E, right arm of Man. C, carpals; H, humerus; Mc, metacarpals; R, radius; U, ulna; I-V, digits. (From Scott.)

descent with change of the subspecies and varieties, there is no logical reason for denying the same origin of species, orders, and higher groups. The difference is one of degree and not of kind. Before the recognition of evolution, classification was a groping after an elusive ideal arrangement which naturalists felt but were unable to express except in artificial form and in transcendental terms. Under the influence of the evolution theory, classification became the natural expression of biological pedigrees. (Fig. 297.)

2. *Comparative Anatomy*

The evidence from taxonomy is, as has just been seen, really evidence from comparative anatomy, since modern classifications are based chiefly on anatomical characters. The various groups — classes, orders, families, genera, species, etc. — are founded not on a single difference, nor on several differences, but on a large number of *similarities*. For instance, the differences exhibited throughout the five classes of the Vertebrates are relatively slight in comparison with the basic resemblances. This similarity in dissimilarity is brought out by the science of comparative anatomy. A few concrete examples, some of which we are already familiar with, will serve to bring the main facts clearly before us.

The fore legs of Frogs and Lizards, the wings of Birds, the fore legs of the Horse, and the arms of Man are built on the same basic plan. (Figs. 102–105, 231, 232.) The same is true of the hind limbs. Clearly all are homologous structures, such variations as exist being brought about chiefly by the transformation or absence of one part or another. In short, all the chief parts of both the fore limbs and the hind limbs are HOMOLOGOUS throughout the series. All are composed of the same fundamental materials disposed in practically the same way—nearly all the bones, muscles, blood vessels, and nerves are homologous. Or compare the digestive systems of the same forms, or the excretory and reproductive systems. One has but to recall that, on an earlier page, it was possible to describe in general terms these systems as they exist throughout the Vertebrate series—in forms as obviously different as Fish and Man. They are all fundamentally the same. (Figs. 106–110, 121, 129, 142.)

Turning to the Invertebrates, we may remind the reader that all the appendages of the Crayfish are built on the same simple plan as exhibited in the swimming legs (swimmerets) of the abdomen. The

highly specialized walking legs, great claws, jaws, and feelers (antennae and antennules) are all reducible to modifications of the simple swimmeret type. (Fig. 91.) In short, all are homologous structures, though differing widely in function. This is a most striking example of SERIAL HOMOLOGY, though we have seen the same principle exhibited in the Vertebrates where the fore limbs and the hind limbs of each animal are homologous. Moreover, the

FIG. 232. — Skeletons of Man and of Gorilla. (From Lull.)

appendages of the Crayfish are not only serially homologous among themselves, but are also homologous with the appendages of all the other members of the class Crustacea—just as the limbs of one Vertebrate are homologous with those of all other Vertebrates.

Another class of facts presented by comparative anatomy is derived from the so-called VESTIGIAL organs. In Man there are nearly a hundred structures which apparently are useless and sometimes are harmful. One thinks at once of the VERMIFORM APPENDIX of the large intestine, but equally suggestive are the muscles of the ear,

which in some individuals are sufficiently developed to move the external ear; or the so-called third eyelid at the inner angle of the eye which corresponds to the lid (NICTITATING MEMBRANE) that moves laterally across the eye in Dog, Bird, and Frog; or the terminal vertebrae (COCCYX) of the human spinal column which are remnants of the tail of lower Vertebrates. (Figs. 109, 233.)

FIG. 233. — The third eyelid in Man (A) and Bird (a). (From Thomson.)

Other animals likewise possess many such structures. Porpoises have vestiges of hind limbs enclosed within the body, and certain species of Snakes bear tiny useless hind legs. The 'splint bones' of the Horse are remnants of lost toes. Among plants, it will suffice to mention the functionless remnant of the pistil which sometimes is present in 'male' (staminate) flowers. (Figs. 210, 234, 238.)

In another class of cases, the organs, or remnants of organs of a lower form are altered or completely made over, as it were, into new organs of the higher form. The milk glands of Mammals are transformed sweat glands of the skin, while the poison glands of Snakes are specialized salivary glands of the mouth. During the embryonic life of all Vertebrates there are gill slits, all of which soon vanish except one, which remains as an opening (EUSTACHIAN TUBE) connecting the middle ear with the pharynx. Gill arches, which function as supports for the gills in the aquatic Vertebrates, persist in highly modified form as skeletal structures associated with the tongue and entrance to the lungs (LARYNX) in terrestrial forms. Finally, in this connection the reader will recall the transformations of the blood vessels in the Vertebrates which occur with the substitution of lungs for gills, and also the variations and interrelationships of the excretory and reproductive systems in the ascending series of Vertebrate classes. (Figs. 121, 122, 129, 148, 235.)

FIG. 234. — Vestigial hind limbs of a Snake, *Python*. *f*, femur or thigh bone; *il*, ilium or hip bone. (From Romanes.)

One may, of course, conclude from all these facts that Fish, Frog, Lizard, Bird, and Man have each been independently created

according to the same preconceived plan—and likewise all the great numbers of orders, families, genera, species, etc., of each of the five classes that these forms represent. Or one may conclude that all have arisen by descent with change from a primitive Vertebrate organism which possessed the fundamental similarities

FIG. 235. — Head of a Rattlesnake, with the skin and part of the muscles removed. The long oval mass in the upper jaw which is connected by a duct with the curved tooth, the fang, is the poison gland. (From Smallwood.)

exhibited from Fish to Man. The latter is the conclusion accepted unreservedly by biologists to-day.

3. *Paleontology*

Huxley once said that if zoölogists and embryologists had not put forward the theory of evolution, it would have been necessary for paleontologists to invent it. What then are the main facts offered by PALEONTOLOGY, the study of the FOSSIL remains of extinct animals and plants?

In the first place it must be made clear that geologists are able to determine, with remarkable accuracy in most cases, the sequence in time, or CHRONOLOGICAL SUCCESSION, of the rock strata composing the Earth's surface. The main outline of this scheme of geological chronology was understood long before the evolution of organisms was a crucial question; so that we may consider the evidence which it affords of the chronological succession of the fossil remains exhibited by the various strata, as impartial testimony to the order of appearance on the Earth of the different types of animals and plants. (Fig. 236.)

The following geological time-table summarizes the panoramic succession of life as it is seen by the paleontologist. It is useless to attempt to state the absolute duration of geologic time, because we have little more than guesses to depend on, though there are fairly reliable data in regard to the relative length of the various eras.

Perhaps the conservative estimate of 500,000,000 years — at least half of which was before the Cambrian period — will serve to spell the Earth's unfathomable past.

THE GEOLOGICAL TIME-TABLE

PRESENT TIME.

PSYCHOZOIC ERA: AGE OF MAN OR AGE OF REASON.

The present or 'Recent time,' and the time during which Man attained his highest civilization; estimated to be less than 10,000 years.

GEOLOGIC TIME.

CENOZOIC OR MODERN ERA: AGE OF MAMMAL AND SEED PLANT DOMINANCE.

Glacial or Pleistocene epoch. Last great ice age. Rise of communal Man.

Pliocene epoch. Rise of Man.

Miocene and Oligocene epochs. Rise of Apes.

Eocene epoch. Rise of higher Mammals.

MESOZOIC OR MEDIEVAL ERA: AGE OF REPTILE DOMINANCE.

Cretaceous period. Rise of primitive Mammals, and Seed Plants.

Jurassic period. Rise of Birds and flying Reptiles.

Triassic period. Rise of Dinosaurs, and Mammalian stock.

PALEOZOIC OR ANCIENT ERA: AGE OF PRIMITIVE ANIMALS AND PLANTS.

Permian period. Rise of Reptiles and Conifer forests. Another great ice age.

Carboniferous period. Age of Amphibia. Rise of Insects. Marked coal accumulation.

Devonian period. Age of Fishes. First known marine Fishes, and Amphibians.

Silurian period. First known land floras.

Ordovician period. First fresh-water Fishes.

Cambrian period. First shell-bearing marine animals, and dominance of Trilobites.

PROTEROZOIC ERA: AGE OF INVERTEBRATE DOMINANCE.

An early and a late ice age.

ARCHEOZOIC ERA: ORIGIN OF PROTOPLASM AND OF SIMPLEST ORGANISMS.

COSMIC TIME.

FORMATIVE ERA: BIRTH AND GROWTH OF THE EARTH OUT OF THE SPIRAL-LIKE NEBULA OF THE SUN.

Beginnings of the atmosphere and hydrosphere, and of continental platforms and oceanic basins. No known geological record.

Even a casual survey of this history—natural history—of the Earth and its inhabitants cannot but impress one with the fact

that, taken all in all, there has been a continuous, though not always a uniform, advance in the complexity of organisms from the most ancient times, and that the older types seem gradually to melt into modern forms as the remoter geological eras merge into the more recent. "Only the shortness of human life allows us to speak of species as permanent entities." Invertebrates appear in the Proterozoic Era; Fishes, Amphibians, and Reptiles in the

FIG. 236. — Chart showing the origin and degree of development of the chief groups of Vertebrates, correlated with the geological time-table. (From Lindsey, after Osborn.)

Paleozoic; Birds and primitive Mammals in the Mesozoic; higher Mammals and Man in the Cenozoic. Mosses and Ferns arise before Conifers and the latter before the familiar Seed Plants. Just in proportion to the completeness of the geological record is the unequivocal character of its testimony to the truth of the evolution theory. For the sake of concreteness we may select two examples from the wealth of material offered by the paleontologist.

At first glance there seems to be little but contrasts between a typical Reptile and a typical Bird; between a cold-blooded, scaly-

skinned Lizard, let us say, and a warm-blooded, feathered Pigeon. And yet the zoölogist is convinced that Birds have evolved from a reptilian stock, because, in spite of superficial dissimilarities, there are fundamental structural resemblances not only between adult Reptiles and Birds, but also between their embryological stages. And further, because the fossil remains of a very primitive Bird, *Archaeopteryx*, have been found which form, in many ways, a

FIG. 237. — Reptilian Bird, *Archaeopteryx* (A), compared with Pigeon, *Columba livia* (B). (From Lull.)

connecting link between the Reptiles and Birds as we know them to-day. (Fig. 237.)

Archaeopteryx was undoubtedly a bird about the size of a Pigeon, but one with jaws supplied with many small teeth; with a long lizard-like tail formed of many vertebrae, each bearing a pair of quill feathers; with a four-fingered reptilian hand; and so on. In brief, just such a creature as the imagination of an evolutionist would picture for a primitive Bird has been actually discovered in the lithographic stone quarries of Bavaria, representing the later Jurassic period.

The ancestry of the modern Horse has been the most impressive 'fossil pedigree,' ever since Professor Marsh collected the famous series of fossil skeletons from the western United States and arranged them in the Yale University Museum. They have been referred to as the "first documentary record of the evolution of a race." Huxley studied this collection and regarded it as conclusive evidence of evolution.

The essential facts of the evolution of the Horse are these. Horse-like animals probably arose from an extinct group known as the *Condylarthra* which had five toes on each foot and a large part of the sole resting on the ground. However, the first unquestionable horse-like forms found in North America are little animals about a foot in height, known as *Eohippus*, from rocks of the Eocene epoch. The fore foot of *Eohippus* has four complete toes (digits 2, 3, 4, and 5) but no trace of the inner digit, or thumb, while the hind foot has three complete digits (2, 3, and 4) with vestigial remains, or *splints*, of the first and fifth. Later in the Eocene appears *Orohippus* showing a somewhat larger central digit in the fore foot and the disappearance of the splints in the hind foot. Passing up to the OLIGOCENE epoch, *Mesohippus*, an animal about the size of a wolf, occurs with fore and hind feet three-toed, but with the side toes much smaller than the central one, and just a trace of the fifth digit in the fore foot as a splint. Then *Merychippus* appears in the MIOCENE epoch, with still shorter side toes (digits 2 and 4) so that they do not reach the ground and the weight is borne solely on the hoofed tip of the third digit. This same general reduction of the lateral digits and advance in size and functional importance of the middle digit is carried further during the PLIOCENE epoch in *Pliohippus*, which is usually regarded as the first type of 'one-toed' Horse, and leads finally to the genus *Equus* which has continued from the PLEISTOCENE epoch to the present. This genus includes the modern Horse, *Equus caballus*, with one functional digit on each foot and vestiges of two more (digits 2 and 4) as the splint bones. (Fig. 238.)

In this outline of what must be interpreted as the fossil ancestors of the Horse of to-day, we have merely selected several representative forms to emphasize changes in foot structure. But the reader will realize that many other equally significant changes were involved in the transformation of an *Eohippus* type into that of *Equus*. This much appears certain to the biologist: "In early

THE EVOLUTION OF THE HORSE.

Fig. 238. — Graphic presentation of the evolution of the Horse. (From Matthew, 1926.)

Eocene times there lived small five-toed hoofed quadrupeds of generalized type, that the descendants of these were gradually specialized throughout long ages along similar but by and by divergent lines, that they lost toe after toe till only the third remained, that they became taller and swifter, that they gained longer necks, more complex teeth, and larger brains. So from the short-legged splay-footed plodders of the Eocene marshes there were evolved light-footed horses running on tiptoe on the dry plains." (Thomson.)

4. *Embryology*

If evolution is a fact, one would expect to find evidences of the genetic relationships of organisms in their embryological development from egg to adult. Under former headings we have incidentally mentioned embryological data which point toward evolution, so that now attention may be confined to an attempt to make clear a fact of first importance—the history of the individual frequently corresponds in broad outlines to the history of the race as indicated by evidence from comparative anatomy, etc. If we have in mind the earlier discussion of Vertebrate anatomy, just a few examples will suffice to suggest the type of evidence which supports this so-called RECAPITULATION THEORY, or BIOGENETIC LAW.

Lower Vertebrates, such as the Fishes, have a heart composed of two chief chambers: an auricle which receives blood from the body as a whole and a ventricle which pumps it to the gills on its way to supply all parts of the body. Among the members of the next higher group, the Amphibia (Frogs, Toads, etc.), the auricle is divided into two parts, while the ventricle remains as before. Thus these forms have a three-chambered heart. Passing to the Reptiles, we find that most of the Lizards, Snakes, and Turtles have the ventricle partially divided into two chambers, while the more specialized Crocodiles and Alligators have a complete partition and therefore a four-chambered heart. This is the condition in all adult Birds and Mammals, but the significant fact is that, in the development of the heart of the individual Bird and Mammal, embryonic stages succeed each other which parallel in a general though remarkable way this sequence from a two-chambered to a four-chambered condition as exhibited in the adults of the lower Vertebrates. (Figs. 120, 121.)

Or take the development of the brain in the Vertebrate series. Even in the human embryo the fundament of the brain arises by

simple transformations of the anterior end of the neural tube, which at first are nearly indistinguishable from the conditions which exist in the lowest Vertebrates. Then the changes become progressively more complex along lines broadly similar to those occurring from Fish to Mammal, until finally the complex human brain is formed. (Figs. 141, 142.)

The same picture is presented by a study of the development of the excretory system, the reproductive system, the skull, and so on.

FIG. 239. — Embryos in corresponding stages of development. A, Fish (Shark); B, Bird; C, Man. *g*, gill slits. (From Scott.)

One cannot avoid the fact that the organs of higher animals during development pass through stages which correspond with the adult condition of similar organs in lower forms. The correspondence is not exact, to be sure, but it is not an exaggeration to say that embryological development is parallel to that which anatomical study leads us to expect. A knowledge of the anatomy of an animal actually gives a sound basis of facts from which to predict in broad outlines its embryological development. (Figs. 129, 239.)

What are the bearings of these facts on the evolution theory? It is perfectly logical to conclude that it is an 'architectural necessity,' let us say, for the four-chambered heart to arise from a two- and three-chambered condition—and undoubtedly if this were the only example of 'ontogeny repeating phylogeny' the conclusion might be justified. But when one considers the widespread general correspondence of the developmental stages in higher forms with conditions as they exist in the adults of lower forms, the facts almost overwhelmingly force us to go further and conclude that the similarity has its basis in inheritance, in actual blood relationship between the higher and lower forms, in descent with change—evolution.

5. *Physiology*

Fundamental structural similarities throughout a series of organisms implies fundamental physiological similarities—structure and function go hand in hand, each being an expression of the other—and this is strikingly corroborated by the data accumulated. But this physiological evidence of the relationships of organisms is less readily presented in brief form, so we may confine attention to a couple of striking examples on the border line.

It will be recalled that chemical control by hormones plays an important part in the coördination of the multicellular animal into a working unit, especially in the case of such functions as digestion, growth, and reproduction. Now it is significant that the hormones seem to be largely if not completely interchangeable from one species of Vertebrate to another. Thus a deficiency in the insulin hormone in Man may be supplied from the pancreas of a Fish or a Sheep. Certainly this strongly suggests that at least certain of the chemical regulators have been common factors from a remote ancestral period.

Again, it has been known for a long time that there are certain important chemical differences—not determinable by ordinary chemical analysis—between the blood even of closely related species, because the TRANSFUSION of the blood of one species into another is usually attended by physiological disturbances and often by death. It has been found by innumerable transfusions and also by so-called PRECIPITATION TESTS of the blood *in vitro*, that is outside the body, that the degree of the reaction is in many cases proportional to the degree of relationship of the species involved, as indicated by their classification on the basis of anatomical structure.

Thus, as one would expect, human blood shows closer chemical relationships with the blood of the Man-like Apes than it does with that of the Old World Monkeys; closer relationships with the blood of the latter than it does with that of the New World Monkeys; and closer with the blood of these than with that of the Lemurs; and so on. Or, descending to the Reptiles: paleontology indicates that there is a close relationship between Lizards and Snakes and also between Turtles and Crocodiles, while the reptilian ancestor of the Birds was probably more closely allied with the latter than the former groups. These same relationships are indicated by blood tests.

Thus aside from a few startling exceptions, which further study perhaps may bring into line, all the data warrant the conclusion that the chemical similarities of the blood are almost as constant as structural similarities of the blood vessels, or, in evolutionary terms, "a common property has persisted in the bloods of certain groups of animals throughout the ages which have elapsed during their evolution from a common ancestor." Blood relationship is a fact.

6. *Distribution*

Everyone recognizes that the fauna and flora are not the same in all regions of the Earth. There is a characteristic life on mountain, plain, and seashore, and in the sea — as well as in pond and puddle — and also in the Arctic, Temperate, and Torrid zones. But the problem of animal and plant distribution is by no means so simple as this statement might seem to imply, because the study involves the investigation of both the relations of the various organisms to the general environing conditions, and the interrelations of the species with each other. It forms a part of the sciences of plant and animal ECOLOGY. (Fig. 224.)

Confining attention merely to the geographical distribution of animals — which forms the science of ZOÖGEOGRAPHY — let us take a couple of clear-cut examples and see whether special creation or evolution is the more reasonable explanation of the facts.

At the present time a characteristic genus of Mammals, known as the Tapirs, is represented by distinct species in two widely separated regions, Central and South America and Southern Asia and adjacent islands. But paleontological studies show that in the Pliocene epoch Tapirs were distributed over nearly all of North America, Europe, and Northern Asia, and thereafter gradually

FIG. 240. — Geographical distribution of Song Sparrows. Each different number indicates habitat of a *subspecies*. "We find complete integradation in color and in size. Nowhere can one draw the line. As the climatic conditions under which the birds live change, the birds keep pace. Here we have a species in flower, as it were, a single Song Sparrow stalk with its twenty-three blossoms, any one of which might make an independent growth as a species if it were separated from the parent stem. Doubtless some day the separation will come, when we shall have several species, each with its groups of races, but at present we have only one species, divided into some twenty-three subspecies, or species in process of formation." (Chapman.)

FIG. 242. — Evolution of the head and molar teeth of Elephants. A, A', *Elephas*, Pleistocene; B, *Stegodon*, Pliocene; C, C', *Mastodon*, Pleistocene; D, D', *Trilophodon*, Miocene; E, E', *Palaeomastodon*, Oligocene; F, F', *Moeritherium*, Eocene. (From Lull.)

became extinct so that by the close of the Pleistocene epoch the remnants were distributed as we find them to-day. In brief, the present *discontinuous* distribution represents the remnants of a world-wide Tapir population, and the differences between the existing species are such as one might expect to find among the members of a genus long isolated in different environments by geographical barriers. We know, for example, that a litter of European Rabbits was introduced on the small island of Porto Santo during the fifteenth century and by the middle of the last century its descendants had become so distinct from the parent form that it was described as a new species.

As a matter of fact the characteristic fauna of islands was what impressed Darwin with the need of some interpretation of their origin other than by special creation. During his famous three years' voyage around the world on the "Beagle," he stopped at the Galapagos Islands, situated about 600 miles off the west coast of South America, and was astonished to find that although the fauna as a whole resembled fairly closely that of the mainland, nevertheless the species for the most part not only were different, but even those of the separate islands were distinct — the islands nearest to each other having species most similar. Darwin wrote, "My attention was first thoroughly aroused by comparing together the numerous specimens, shot by myself and several others on board, of Mocking Thrushes, when, to my astonishment, I discovered that all those from Charles Island belonged to one species (*Mimus trifasciatus*); all from Albemarle Island to *M. parvulus*; and all from James and Chatham Islands (between which two other islands are situated as connecting links) belonged to *M. melanotis*."

Darwin's observations of such facts as these have been corroborated in the Galapagos and extended to isolated island faunas and floras all over the world. And further, his explanation of the phenomena is the most plausible extant. *Continental* islands secure their life from the mainland before they are cut off, and *Oceanic* islands after their formation by volcanic action alone or aided by coral growth. In either event the organisms inhabiting islands are isolated from the main stock of the species, and they diverge, in proportion to the length of time and the degree of isolation, until they constitute separate races and species. Each species peculiar to each isolated island has not arisen by a special act of creation but by descent with change.

FIG. 243. — A few varieties of domestic Pigeons. Over one hundred and fifty different breeds have been derived by selection from the wild Blue-rock Pigeon, some of which "differ fully as much from each other in external characters as do the most distinct natural genera." (Darwin.) 1, Blue-rock Pigeon, *Columba livia*, ancestral form; 2, homing; 3, common mongrel; 4, archangel; 5, tumbler; 6, bald-headed tumbler; 7, barb; 8, pouter; 9, Russian trumpeter; 10, fairy swallow; 11, black-winged swallow; 12, fantail; 13, carrier; 14, 15, bluetts; bird between 14 and 15, a tailed turbit. (From photograph of an exhibit in the United States National Museum.)

We have now summarized a few concrete examples of the chief types of evidence that organisms — species — have come to be what they are to-day through a long process of descent with change. This evidence, taken with that presented, so to speak, on and between the lines throughout this work, should place the reader in a position to form a more or less independent judgment of the question. It is only necessary to remind him again that, since the evidence, from the nature of the case, must inevitably be indirect, its force is tremendously increased by its amount. And the overwhelming impressiveness of all the concordant evidence for organic evolution, the reader, with only a very limited amount of the data before him, cannot appreciate.

B. FACTORS OF ORGANIC EVOLUTION

Taking for granted the fact of evolution, what are the factors which have brought evolution about? That is quite a different question, but one which has often brought confusion to the popular mind. Biologists are not so sure to-day as they were a generation ago that they know just what the factors are. And the layman has mistaken their questioning of one factor or another for a questioning of the fact.

No purpose will be served by a long historical account of the origin of the present-day point of view. Suffice it to say that the evolution idea is a generalization which has crept from science to science — from astronomy to geology, from geology to biology, thereupon becoming ORGANIC evolution. The idea in one form or another is as old as history, but for all practical purposes the biologist Lamarck, during the early part of the nineteenth century, formulated the first consistently worked out theory of organic evolution. (Fig. 293.)

1. *Lamarckism*

The evidence for organic evolution offered by Lamarck was in many cases neither happily selected nor convincingly presented, and it was laughed out of court by biologists and laymen alike. His evolution factor was essentially the change of the organism through the use and disuse of parts; the physiological response of the organism to new needs offered by new conditions of life. And these changes, somatic in origin, he believed were transmitted to the progeny. His own first statement in 1809 may be quoted:

“First Law: In every animal which has not exceeded the term of its development, the more frequent and sustained use of any organ gradually strengthens this organ, develops, and enlarges it, and gives it a strength proportioned to the length of time of such use, while the constant lack of use of such an organ imperceptibly weakens it, causing it to become reduced, progressively diminishes its faculties, and ends in its disappearance.

“Second Law: Everything which nature has caused individuals to acquire or lose by the influence of the circumstances to which their race may be for a long time exposed, and consequently by the influence of the predominant use of such an organ, or by that of the constant lack of use of such part, it preserves by heredity and passes on to the new individuals which descend from it, provided that the changes thus acquired are common to both sexes, or to those which have given origin to these new individuals.”

Lamarck's first law is apparently sound, but the second — the inheritance of acquired characters — is highly questionable to say the least, because, as we have seen, there is no evidence that modifications are heritable. But this weak point was not the one which caused the rejection of the theory by Lamarck's contemporaries. The various antagonistic influences can be summed up by saying: the time was not ripe for evolution.

2. *Darwinism*

Then a generation later appeared Charles Darwin in England. With a better background prepared for him through the headway being made by the evolution theory in geology, he did two things in his *Origin of Species* which was published in 1859. He presented an overwhelming mass of *facts* which could be explained most reasonably by assuming the origin of existing species by descent with change from other species. And he offered as an explanation of the origin of species the *theory* of “NATURAL SELECTION, or the preservation of favoured races in the struggle for life.” It was the *combination* of the facts and the theory to account for the facts that won the thinking world to organic evolution. (Fig 296.)

What, in brief, was the theory? In the first place, without discussing the cause of variations, Darwin showed the great amount of VARIATION in nature. And any and all kinds of heritable variations were, broadly speaking, important—though he questioned the

Lamarckian idea of the inheritance of acquired characters. But there are variations enough and to spare without them.

The universality of variations established, Darwin emphasized the fact that the POWER OF REPRODUCTION of organisms far exceeds space for the offspring to live in and food for them to eat. Some recent data will illustrate this point. A microscopic *Paramecium* possesses the power to eat, grow, and reproduce — to transform the materials of its environment into *Paramecium* protoplasm — at the rate of 3000 generations in five years. And all the descendants (if they actually existed) would equal 2 raised to the 3000th power, or a volume of protoplasm approximately equal to 10^{1000} times the volume of the Earth! The Plant Lice, or Aphids, may produce a dozen generations in a year. The final brood, assuming the average number of young produced by each female to be one hundred and that every individual produced its full complement of young, would consist of ten sextillion individuals — a procession, if it could be marshalled, that would extend from the Earth out into space far beyond the furthest star that has ever been discerned by the telescope. And the all too familiar Mosquito may have nearly two hundred billion descendants during one summer. Such facts are appalling, though true, and serve to afford an appreciation of the enormous unrealized potentialities of living matter to make more living matter — to reproduce.

Something must — does — suppress the inherent power of each species to overpopulate the Earth, and Darwin emphasized the STRUGGLE FOR EXISTENCE between the individuals of species. Since the struggle is so keen, a variation, however slight, which fits — adapts — an individual better to its surroundings than its neighbors are adapted, will, more often than not, give its possessor an advantage in the struggle, and accordingly the latter will tend to survive and to pass on the favorable variation to its progeny. Thus is brought about THE SURVIVAL OF THE FITTEST — the survival of those individuals, and therefore species, which are best adapted to the peculiar conditions of their environment and mode of life. And note, this offers an explanation of the fact of *adaptation* itself — the most striking phenomenon which organisms exhibit.

This is all so simple from one point of view and so confusingly complex from others that it may well be restated in a couple of sentences by Darwin himself: "As many more individuals of each species are born than can possibly survive, and as, consequently,

there is frequently recurring struggle for existence, it follows that any being, if it vary however slightly in any manner profitable to itself, under the complex and sometimes varying conditions of life, will have a better chance of surviving, and thus be naturally selected. From the strong principle of inheritance any selected variety will tend to propagate its new and modified form."

Nothing succeeds like success, and once started Darwin's theory gradually swept nearly all opposition away. Indeed, some of its advocates in their enthusiasm extended Darwin's theory to a point not justified by his own conservative statements. Then, as was to be expected, the reaction came. Acquired characters are not inheritable; variations are swamped by interbreeding; large variations and not small fluctuating variations are crucial; and so on. But it is unnecessary to obscure the main issue by entering into these controversies. What is the status of the theory of natural selection to-day? The answer must be sought in the light of genetics.

3. *Genetics and Evolution*

Evolution is not a closed book — an event which has been completed in the past — but a process which is actively going on now. "Nothing endures save the flow of energy and the rational order that pervades it." And there is every reason to believe that the factors involved in present evolution are the same as those which have operated in the past. This UNIFORMITARIAN doctrine has proved productive in explaining the evolution of the Earth, and all the available evidence indicates that this viewpoint will prove — is proving — equally valuable in understanding the origin of the diverse inhabitants of the Earth. We have come to realize that evolution is a bird's-eye view of the results of heredity since the origin of life — the facts of inheritance hold the key to the factors of evolution. Therefore in a previous chapter we discussed the relations of recent discoveries in genetics to the evolution problem, some of which may be restated now with special reference to the origin of the fitness of organisms. (Pp. 301–308.)

In the first place, we have seen that though variations are the rule and not the exception, some are of importance for evolution and some are not. All the evidence indicates that the effective variations are germinal and not somatic. Changes arising in the soma — modifications — are unable to attain representation in the germ so that they are 'born again' and evolution must be brought

about by the evolution of the germ itself. Accordingly selection must operate to eliminate the 'unfit' germ plasm rather than the unfit soma, though as a matter of fact the fitness of an individual is determined largely by its somatic characters. This apparently is the crux of the matter and presents a complication of the mental picture of the operations of selection which did not exist when we thought of soma producing germ and germ producing soma again. Since individuals frequently belie their germinal condition — what they will pass on to their progeny — natural selection has, so to speak, a more devious though not less sure path.

Secondly, how does the germ plasm change? Developed characters are the result of the activities of the genes. Of course, a gene is not a character. It is not even an undeveloped character. Characters in most cases arise from the interaction of many, perhaps all the genes, though for practical purposes it is customary to refer to one gene as the determining factor — for example, the so-called sex gene on the so-called sex chromosome. Such being the case, characters may be changed by alterations of the gene complex. This may be from the influence of changes within the soma itself or from the environment of the organism acting directly on the germ cells. But in general it may be said that mutations — germinal changes other than those arising from recombination or crossing-over — seem to be infrequent compared with non-heritable changes of somatic origin. However, it must be borne in mind not only that somatic changes are more readily apparent, but also that the majority of the mutations which occur lead to a decrease in vitality or even to death. This is to be expected, for a random change in a highly complicated mechanism such as a living organism is far more apt to upset than to improve the nicety of its internal and external adaptation, unless a changing environment is presenting new conditions to be met.

These facts from genetics, taken in connection with the data from geographical distribution, the succession of types in the geologic past, and the great diversities in 'breeds' in nature, etc., give us the modern background for attempting to form an opinion of the method of evolution. The consensus of opinion is that natural selection in general is the guiding principle underlying the establishment of the 'adaptive complexes' of organisms. Evolution is the result of mutations, germinal variations, largely, though not entirely, independent of environing conditions. Many of these

variations give rise to characters which neither increase nor decrease the adaptation of the organism, and consequently are neutral from the standpoint of its survival. With regard to such characters natural selection is essentially inoperative. Other germinal variations arise which produce adaptive structures and here natural selection is effective — it sifts them out, as it were, from the unadaptive and neutral variations and in this way makes possible their survival value in the struggle for existence.

So, it will be noted, this is essentially a clarified Darwinism. Instead of all variations being heritable — some are inherited and some are not. Instead of all heritable variations being important — some are and some are not. The important ones are the heritable adaptive variations and these form the raw materials for natural selection. Natural selection is still the only natural explanation of that coördinated adaptation which pervades every form of life, but it is probable — indeed, positive — that there are more factors involved than are dreamt of in our biology.

In the words of Thomson: "The process of evolution from invisible animalcules has a magnificence that cannot be exaggerated. It has been a process in which the time required has been, as it were, of no consideration, in which for many millions of years there has been neither rest nor haste, in which broad foundations have been laid so that a splendid superstructure has been secure, in which, in spite of the disappearance of many masterpieces, there has been a conservation of great gains. It has its outcome in personalities who have discerned its magnificent sweep, who are seeking to understand its factors, who are learning some of its lessons, who cannot cease trying to interpret it. It looks as if Nature were Nature for a purpose" — but this thought carries us beyond the accepted sphere of science into the great fields of philosophy and theology.

CHAPTER XXV

BIOLOGY AND HUMAN WELFARE

Man is part of a web of life which he continues to fashion, and the success of his weaving depends upon his understanding. — *Thomson*.

Now that we have made a general survey of the foundations of biology, it is important to consider some of the outstanding contributions of biology to human welfare — contributions made, for the most part, within a century, but already so interwoven with our everyday life that they have become indispensable.

Strange as it may at first glance appear, usefulness is not the basic standard of value adopted by most scientific men: the discovery of truth is their aim, lead where it will. Although their controlling motive is increase of knowledge and enlargement of our outlook on nature, it is nevertheless a fact that the practical application of their discoveries is responsible for most of the conditions which constitute the environment of modern life. "Science brings back new seeds from the regions it explores, and these seem to be nothing but trivial curiosities to the people who look for profit from research, yet from these seeds come the mighty trees under which civilized man has his tent, while from the fruit he gains comfort and riches."

One of the most surprising illustrations of the way in which seemingly useless biological research often reveals itself almost overnight as of the greatest utility to business, is afforded by the present interest of the oil industry in certain Protozoa known as FORAMINIFERA: not living Foraminifera but fossil forms from the geological past. A short time ago oil companies were wasting large sums in sinking holes from which no oil came: frequently such a drilling cost as high as sixty thousand dollars, eventually to be paid chiefly by the motor-car owner. Then it was noted that Foraminifera were brought to the surface with the drilling, and the problem was to determine whether the species found in material from oil-bearing drills could be distinguished from those from dry drills. Accordingly the companies turned to the secluded research workers in the laboratories of the United States National Museum

which has made a practice of gathering and preserving samples of microscopic life from all parts of the world: material which the layman would undoubtedly regard as refuse and throw away. Thanks to a lifetime spent in studying Foraminifera, one expert

FIG. 244. — Shells of several species of Foraminifera, considerably magnified. 1, *Cyclammina pauciloculata*, two views; 2, *Globotextularia anceps*; 3, *Marginulina ensis*; 4, *Vagulina spinigera*; 5, *Nodosaria filiformis*; 6, *Rhabdammina abyssorum*; 7, *Chilostomella grandis*.

was able to make the necessary determination, and his knowledge when applied in the oil fields resulted in saving the industry many millions of dollars. Whereas the small governmental appropriations for this biologist's work had been considered by many an economic waste, to-day it is reported that the annual income tax on the salary his services command from the oil industry repays many-

fold to the Government the annual grants that formerly were made to him. (Fig. 244.)

Hence it is far from true that so-called pure science and applied science are distinct and independent activities. There is only one kind of science — science aspiring for truth and knowledge, and there could be no application of science unless that knowledge previously existed. Great innovations are chiefly facile applications of truths which their authors have pursued for their own sake, and in our most theoretical moods we are frequently nearest to the most practical applications.

Indeed, some of the great biological generalizations with which we have become familiar on previous pages have in everyday affairs a profound practical significance which is easily overlooked. For example, the cellular structure of all living things — implying the existence of a fundamental similarity in organization throughout the living world. Again, the basically similar life-stuff, protoplasm — demonstrating that all living nature is united by a common bond not only of cellular organization but also of protoplasmic basis to which all life phenomena are referable. Still again, the transformation by protoplasm of non-living material into living material — proving that living matter is ordinary matter peculiarly organized. And finally, organic evolution. All nature is one.

These and other great biological truths have a far-reaching import to everyone, because collectively they unmistakably lead to the grand conclusion that human life must be interpreted in terms of all life. Man must conform to the general order of living nature of which he is an integral but dominant part. Human welfare, therefore, demands that Man must 'control' nature by consciously adapting himself to it. Indeed, the chief purpose of education is the adaptation of the individual and the promotion of adaptability — adjustment to the basic internal and external conditions of life without a loss of plasticity. Thus biology affords the natural foundation of the science and art of right living which human welfare demands.

A. MEDICINE

Health — the adaptation supreme — is a priceless possession whether it be estimated from the standpoint of the well-being of the individual or in terms of national wealth. Accordingly, medi-

cine, in the broadest sense of the word, is without doubt the most important aspect of applied biology. Human anatomy and physiology, on which the foundations of medicine rest, are merely special parts of the general sciences of anatomy and physiology of all organisms. In fact the interpretation of human anatomy is impossible except in the light of the comparative anatomy of Vertebrates, while human physiology owes its present state of development to the fundamental principles derived from experimentation on the lower animals. And hope for further advance is chiefly dependent upon similar investigations on animals which have been

FIG. 245. — *Entamoeba histolytica*, a parasitic Amoeba of the human intestine, which gives rise to amoebic dysentery. A, active Amoeba showing nucleus and three ingested human red blood corpuscles; B, encysted Amoeba with four nuclei preparatory to division into four individuals. (After Dobell.)

rendered insensible to pain by anesthetics. To mention one example: experimental surgery practiced on animals has demonstrated the possibility of innumerable operations which no conscientious surgeon would have ventured to perform for the first time on Man. In the words of Darwin who gave up the sport of hunting on account of his great sympathy with the suffering of animals: "Physiology can make no progress if experiments on living animals are suppressed, and I have an intimate conviction that to retard the progress of physiology is to commit a crime against humanity."

1. *Microorganisms and Disease*

No one will gainsay that discoveries in preventive and curative medicine rank amongst the most important contributions of sci-

entific research to civilization, and nearly all have as their foundation, studies by generations of biologists. Though Pasteur's first investigations were in chemistry, his subsequent work, which pointed out the way of preventing and eradicating diseases due to microorganisms, followed naturally from his discovery that the souring of wine and milk is the result of the activities of organisms from the air which induce chemical changes. Injure the skin of a grape, and organisms from the atmosphere enter and fermentation

COMMON EPIDEMIC DISEASES

Note Recent Years When Microbic Causes Were Established

<p>Anthrax (<i>Splenic Fever</i>) 1876</p> <p>Asiatic Cholera 1883</p> <p>Bubonic Plague 1894</p> <p>Diphtheria 1884</p> <p>(<i>Antitoxin discovered 1890</i>)</p> <p>Dysentery 1898</p> <p>Glanders 1882</p> <p>Gonorrhea 1879</p> <p>Infantile Paralysis 1909</p> <p>Influenza 1892</p> <p>Leprosy 1892</p> <p>Malaria 1880</p> <p>(<i>Transmission by Mosquitoes established 1897</i>)</p>	<p>Malta Fever 1887</p> <p>Meningitis 1887</p> <p>Pneumonia 1884</p> <p>Relapsing Fever 1873</p> <p>Syphilis 1905</p> <p>Tetanus (<i>Lockjaw</i>) 1889</p> <p>Tuberculosis 1884</p> <p>Typhoid Fever 1884</p> <p>(<i>Immunizing Vaccine established 1896</i>)</p> <p>Yellow Fever 1918</p> <p>(<i>Transmission by Mosquitoes established 1900</i>)</p>
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Several fevers are transmitted by lice or other insects — bubonic plague by rats, and sleeping sickness by the tsetse fly. This knowledge has shown how to prevent the spread of these diseases.

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begins. Exclude air or sterilize it, and fermentation is prevented. Lister immediately saw the importance of this for surgery, and modern antiseptic surgery — one of the greatest blessings of mankind — was born. (Figs. 152, 278.)

Proceeding on the theory that since fermentation is the result of the activities of microorganisms, certain diseases of plants and animals are likewise caused by the invasion of the body by similar germs, Pasteur's early success in preventive medicine came from the study of cholera in French fowls and anthrax in Sheep and Cattle. The treatment he employed reduced the death rate of the

animals from about ten per cent to less than one per cent, and saved the French nation in twenty years not less than the amount of the war indemnity of 1871. Then Pasteur devised the treatment for rabies. The human fatalities from this disease, usually arising by infection from the bite of a 'mad' Dog, fell almost at once from nearly one hundred per cent to less than one per cent.

During the past half-century a host of investigators, following the lead of Pasteur, have secured undreamed-of results in preventive and curative treatments of a long series of diseases of Man, domestic animals, and plants. One thinks immediately of diphtheria, spinal meningitis, tuberculosis, bubonic plague, typhus fever, malaria, yellow fever, syphilis, amoebic dysentery, and African sleeping sickness — all the results of the infection of Man by Bacteria or Protozoa. It is hard to realize that so recently as 1884, Koch, probably the greatest successor of Pasteur, proved that tuberculosis is caused by a specific type of Bacteria, and thereby revolutionized the treatment of this disease which has been estimated to cause about one-seventh of all the deaths in the world each year.

Only second in importance to the prevention of diseases of Man that are due to microorganisms, is the suppression of diseases of domestic animals. For example, the Chief of the Bureau of Animal Industry estimates that the Bacteria which produce infectious abortion in Cattle are responsible for an animal loss of approximately fifty million dollars each year in the United States. And the study of this disease is proving of increasing significance from the recognition that undulant fever in Man is caused by a member of the same group of Bacteria — an excellent instance of how knowledge leads to further knowledge.

Indeed, the way interlocking data from several biological fields are frequently necessary to determine the causative agent of a disease can, perhaps, be best illustrated by a brief outline of the development of our knowledge of malaria, yellow fever, and syphilis.

MALARIA. From ancient times malaria, as the name indicates, was supposed to be due to foul air, especially from swampy regions, but the first step toward the correct explanation was made in 1880 when Laveran found certain microscopic parasites always present in the blood of malarial patients. Nearly two decades later Ross demonstrated similar parasites in the body of a Mosquito, and

FIG. 246. — Mosquito life histories. Mosquitoes of the genus *Anopheles*, which transmit malarial parasites, differ from the common *Culex* in every stage. When at rest the adult *Culex* holds its body parallel to the surface, whereas *Anopheles* holds it nearly perpendicular.

FIG. 247. — Map used in anti-malaria campaign in Louisiana. Each dot represents a death from malaria. The public health importance of malaria, however, is more accurately measured by the sickness rate and the loss of efficiency than by the loss of life. It has been estimated that for each death 2,000 to 4,000 days of sickness must be included in the total burden of loss and suffering. (From Rockefeller Institute.)

then a long series of studies by various investigators, among whom Grassi stands foremost, showed that when a mosquito of the genus *Anopheles* bites a malarial patient, it secures with the blood some of the parasites such as Laveran had discovered, and thereupon the mosquito becomes the host of the Malarial organism. Within the mosquito, the parasite undergoes a complicated series of changes, including rapid reproduction. This finally results in myriads of parasites located in the salivary glands of the insect, ready to be injected into the blood of the next individual bitten and to begin the other phase of its life history in Man. (Fig. 227.)

So stated, it appears simple enough, but years of study by specialists on Insects (ENTOMOLOGISTS), by specialists on Protozoa (PROTOZOÖLOGISTS), and by physicians highly trained in general medical zoölogy are behind the scenes in making clear the way to eradicate a disease which, it is estimated, each year costs the United States not less than one hundred million dollars and the British Empire three times that amount. In India alone it is responsible for a death list of more than a million people annually. (Figs. 246, 247.)

YELLOW FEVER. Proof that malaria is due to a Protozoön

which can only be transmitted to Man by members of a certain genus of Mosquitoes, was largely the work of English, French, and Italian biologists; but the demonstration that another kind of mosquito, *Aedes*, is responsible for the transmission of the parasite which causes yellow fever is due to Reed, Lazear, and other members of the United States Yellow Fever Commission working in Cuba in 1900. Eighteen years later Noguchi at the Rockefeller Institute actually discovered the unicellular parasite and shortly after prepared a vaccine to prevent the disease. (Fig. 248.)

It might be written of Noguchi and many others, as it has of Lazear: "With more than the courage and devotion of a soldier,

FIG. 248. — Yellow fever organisms photographed alive through ultramicroscope; magnified about 3000 times. (From Noguchi.)

he risked and lost his life to show how a fearful pestilence is communicated and how its ravages may be prevented." Most inspiring is the long story of heroism and hard work which has made it possible to cope with yellow fever; made possible the building of the Panama Canal, since the earlier attempt by France was unsuccessful largely on account of the ravages of these invisible foes; made probable the banishment of yellow fever from the earth for only its smoldering fires remain under the watchful eye of biologists.

FIG. 249. — Results of a quarter century of yellow fever control.
(From Rockefeller Foundation.)

We even have to be reminded that half a million cases occurred in the United States during the past century: the epidemic of 1793 took a total of one-tenth of the population of Philadelphia, and that of 1878 killed more than thirteen thousand in the Mississippi Valley alone. (Fig. 249.)

SYPHILIS. That the tangled strands of the web of life lead us into most remarkable mazes is brought convincingly to mind by the recently developed treatment for a type of general paralysis, or paresis, a disease which has been dreaded for centuries, as a culmination of syphilis — “war and syphilis are the two greatest

enemies of mankind." A few years ago syphilis was shown to be due to a unicellular parasite, *Treponema pallidum*, whose activities often produce a gradual loss of the mental faculties, dementia, and finally death within a few months or many years. Although the use of a specific chemical substance has proved of considerable therapeutic value, the inoculation of patients with malarial organisms has, in early stages of the disease, frequently resulted in recovery and, in later stages, has stayed the progress of the paralysis and prevented death. Patients are allowed to undergo several malarial paroxysms, then treated with quinine to check the ma-

FIG. 250. — *Treponema pallidum* (the spiral bodies) in liver of child with congenital syphilis. Highly magnified.

laria, and finally with neosalvarsan. The exact mechanism of the alleviation and cure of the disease is not understood, but it is supposed that malarial immune bodies are produced which activate the protective powers of the human body against the syphilitic organism's ravages. At all events the combined series of biological and chemical studies on the malarial and syphilitic organisms are marshalled in the most intricate and unexpected manner — knowledge has made possible the playing of one parasite against another to combat the scourge, much of which in the world to-day is due to the infection of infants before or at the time of birth. The malarial organism apparently has at least one redeeming feature. (Fig. 250.)

2. *Parasitic Worms*

Thus far we have been considering causative agents of disease which are popularly called microbes, and we must now turn from this "world of the infinitely little" to somewhat larger organisms which form a most important part of medical zoölogy. This field may be illustrated by the various kinds of parasitic worms.

TREMATODES. There are many parasitic Flatworms, somewhat closely related to the free-living *Planaria*, that comprise the group **TREMATODA**. Parasitic species exhibit, for the most part, complicated life histories which have taxed the patience and ingenuity of biologists to unravel. Among the numerous species, the Liver Fluke is perhaps of most interest. (Figs. 157, 161, 163, 251.)

The adult **LIVER FLUKE** is a worm about an inch long which lives in the bile ducts of the liver of Sheep, Cattle, Pigs, etc., and occasionally in Man. It is hermaphroditic, each individual possessing both male and female reproductive organs, and in its isolated position is almost continually producing fertilized eggs. In fact, one Fluke may liberate over five hundred thousand eggs which pass down the bile ducts of the host (sheep) into the intestine and finally leave the body with the feces. An egg that happens to reach moisture develops into a ciliated larva, or **MIRACIDIUM**, which escapes from the egg-shell and swims about. For further development to occur the larva must encounter within a few hours a certain species of fresh-water Snail, otherwise death results. But once it has bored into a snail's body, the parasite receives a new lease of life involving a series of changes. After about two weeks it has become a sac-like creature, or **SPOROCYST**, which in turn proceeds to develop within itself a brood of another larval stage, the **REDIA**. Each redia liberated from a ruptured sporocyst usually gives rise to one or more generations of redia, and the final generation of these produces a third kind of larva, known as a **CERCARIA**.

All these stages have been arising in the snail's body, but now the swarm of cercariae emerges from the snail, and each swims about in the water and finally encysts on a blade of grass. Here again the life of the parasite hangs in the balance, for death follows unless the grass with the cyst is eaten by a sheep, and the cyst reaches the animal's intestine. This location successfully attained, the cercaria escapes from the cyst, and makes its way to the bile

FIG. 251. — Life history of the Liver Fluke, *Fasciola hepatica*. A, 'egg'; B, miracidium; C, sporocyst; D, E, rediae; F, cercaria; G, encysted stage; H, adult (nervous and reproductive systems omitted). (From Hegner, after Kerr.)

ducts where it soon develops into a mature Liver Fluke, the cause of liver-rot in sheep. The life history is completed.

The large number of eggs produced by a single Fluke increases the chances of a ciliated larva meeting the proper kind of snail, while the various generations within the snail multiplies many-fold the number of cercariae from a single egg, and just to that extent

increases the opportunities for at least one to reach another sheep. This life history, while remarkable, is by no means unique, and is presented as a type which is broadly representative of a large group of parasitic Flatworms. No wonder that years of study are required by specialists in different branches of zoölogy to discover the various stages of the different species and determine their relationships.

CESTODES. The group of Flatworms known as the CESTODA comprises the numerous species of TAPEWORMS which infest the lower animals and Man. The best known species are *Taenia solium* and *Taenia saginata*, both living as adults in the human digestive tract, while the larvae of the former infest Pigs, and those of the latter, Cattle.

Taenia is a long ribbon-like worm comprising a small knob-like head, or **SCOLEX**, which is an organ for attachment to the lining of the human digestive tract, and a large number of similar

FIG. 252. — A Tapeworm.
(From Shipley and MacBride.)

segments, or **PROGLOTTIDES**. These are formed by growth just behind the scolex so that the oldest and largest proglottides are at the posterior end of the animal. A worm may attain a length of nearly ten feet and comprise nearly a thousand proglottides. (Fig. 252.)

The adult Tapeworm is hermaphroditic and each of the older proglottides contains both male and female reproductive organs, while the terminal 'ripe' ones are almost completely filled with eggs which have already developed into embryos. One by one the ripe proglottides become detached from the worm and pass from the

host with the feces. For development to proceed further an embryo must be swallowed by a pig, whereupon it bores through the walls of the animal's intestine, passes to the voluntary muscles and there encysts. In this position it develops into the **BLADDERWORM**, or **CYSTICERCUS**, stage. To complete the life history, infected meat, insufficiently cooked, must be eaten by Man. If this transfer is successfully accomplished, upon attaining the human digestive tract the parasite gradually assumes the adult form, the scolex becomes attached, and a series of proglottides begins to develop. (Fig. 253.)

Since Tapeworms which live as adults in Man and the higher animals secure their food by absorbing that of their host, they seriously interfere with nutrition, but larval stages are still more

FIG. 253. — Stages in the development of a Tapeworm. *a*, egg with embryo; *b*, free embryo; *c*, bladder worm (cysticercus) before head is protruded; *d*, same after protrusion of head. (From Sedgwick.)

dangerous. Thus, the larva of *Taenia echinococcus*, which lives as an adult in Pigs, may form in Man large vesicles, known as **HYDATIDES**, which frequently rupture with fatal results to the human host. The larva of *Taenia coenurus* of the Dog becomes lodged in the brain and spinal cord of Sheep and produces a disease known as "staggers." It was such larvae in the brains of sheep that produced a stumbling-block for the early exponents of biogenesis, since, with the life history unknown, they could not account for the presence of the larvae except on the theory of spontaneous generation. (P. 208.)

NEMATODES. Passing now to the **NEMATODA**, or **ROUNDWORMS**, we come to a group which, from the standpoint of medical zoölogy, is of as much importance as the Flatworms. Free-living forms are found literally everywhere in water, soil, and air, and blown about by the wind. Most of these are harmless, but some are of great eco-

nomic interest because of their destructive action on the roots and other parts of plants. Among the species parasitic in Man and the higher animals, *Trichina* and the Hookworm will serve as examples.

TRICHINA is the cause of the serious disease in Man, Pigs, and Rats known as TRICHINOSIS. Man becomes parasitized by eating infected pork, insufficiently cooked, and pigs contract the disease by eating offal or infected rats. The larvae from the meat quickly mature in the human intestine, and each female worm produces nearly ten thousand larvae which bore through the intestinal wall

FIG. 254. — *Trichina*, *Trichinella spiralis*. A, larvae free among muscle fibers; B, a single larva encysted among fibers; C, piece of pork containing many encysted worms, natural size; D, adult worm, highly magnified. (From Leuckart.)

migrate throughout the voluntary muscles and encyst there to await a possible getaway from the body at death. Since thousands of resistant cysts may occur in a single gram of muscle, the riddling of the tissues is not only very serious, but incurable. (Fig. 254.)

The widespread distribution of the several species of Hookworms and their insidious effects make them also of great practical importance. Biological studies have demonstrated the process by which the tiny worms, just visible to the naked eye as whitish threads, are hatched in a warm moist soil, make their way through the skin of the human foot, enter the circulatory system, are carried to the lungs, and finally work to the intestine. Here, as adults, they become attached, feed upon the blood of their host and liber-

ate eggs. These pass out with the host's feces to become the source of infection for others. The spread of knowledge of the essential facts and of vermifuges to expel the parasites has been an important contribution of the International Health Board which has carried on a campaign in over fifty countries. It has been estimated that not less than two million persons are afflicted with the disease,

FIG. 255. — The American Hookworm, *Necator americanus*, highly magnified.

but the recently acquired facts in regard to the parasite should result eventually in its almost complete eradication. (Fig. 255.)

3. Health and Wealth

This glance which we have taken at some examples of the contributions of biological research to health affords at least an indication of the service of science in this field to human welfare. The young medical interne — even the intelligent layman — with this torch handed to him by indefatigable investigators, now has the path illumined so that he can go directly to the source and stamp out many of the diseases which a century — yes, even a quarter-century — ago were shrouded in absolute darkness.

It has been aptly said that health and wealth are essentially synonymous, and this is amply shown by the fact that medical progress is reputed to have added at least twenty years to the average life span of Man during the past century — mainly years of the highest efficiency from the age of thirty-five to fifty-five years. It is conservative to say that the increase in longevity has effected a saving of more money than has ever been expended in support of every kind of scientific investigation, and this without taking into account the economic value of the lives or the immensely greater factor of human happiness which follows from healthful and unbroken family life.

The same can also be said for the leading rôle which medical zoölogy has played in rendering vast regions of the tropics almost as safe for human habitation as the temperate regions of the Earth — regions which must offer an outlet for the rapidly increasing human population. Statistics make clear that the population of the world has more than doubled during the last century: what

it will do during the next century experts in vital statistics are actively computing. But this much is certain: it is merely a matter of time before regions now untenanted by civilized Man must be encroached upon more and more, not only for food and other materials but also for a place of abode; and the first step necessary to make this possible is the survey of the innumerable biological competitors in the form of parasites, etc., which Man must encounter in adjusting himself to this environment.

Again, knowledge is power — the best investment from the standpoint of health and wealth is in support of research. It is easy to forget that combined studies on the life history of Bacteria, Fleas, Rats, and the rest have made impossible to-day such epidemics as have many times in the past swept over the world. During the Christian era more people have succumbed to the Plague than constitute the total population of the Earth to-day. It is easy to forget that the biological forces of disease are costing the United States nearly four billion dollars annually — a loss largely preventable by an efficient dissemination of knowledge and an efficient application of biological principles already well established. Civilizations in the past have succumbed to the onslaughts of pestilences, and the hope of our immensely more complex community life depends upon the development of knowledge of these living agents of disease.

B. BIOLOGY AND AGRICULTURE

True it is that Man cannot live by bread alone, but it is equally true that the fundamental urge of all living things to secure food and to multiply is, in the final analysis, at the basis of human endeavor. Modern agriculture represents the body of knowledge accumulated by mankind during its slow progress toward civilization, involving increasingly exacting food demands as community life became more and more complex. But agriculture is dependent upon so many fundamental biological sciences — indeed, agriculture is one aspect of applied biology — that merely a few examples must suffice to bring the chief points before us.

1. *Plant and Animal Food*

As we know, all animals, including Man, are absolutely dependent for their food upon the photosynthetic activities of plants. Green plants must manufacture enough food for themselves, and

to spare for the rest of the living world as well. Animals must have ready-made food which, after they have used it, is useless both for animals and for green plants. Here, it will be recalled, the Bacteria and other colorless plants come in and make possible the completion of the biological cycle of the elements in nature: put the materials in a condition in which they are again available to green plants. (Figs. 22, 23.)

This intimate food interrelationship of all living organisms, which has been demonstrated by interlocking data accumulated by thousands of biochemical studies, is not only of profound theoretical interest, but also of incalculable practical importance in all problems of soil fertility, including soil composition and maintenance, crop rotation, etc. How to coax greater productivity from the soil is one of the major questions facing mankind. "Civilization rests upon the soil." Its very existence, even on the present standard of living, depends on the creation of a larger food supply which, in turn, demands economical production of food for plants themselves. This problem has been recently commanding the attention of the National Academy of Sciences. (Fig. 271.)

One natural source of nitrogenous plant food is, of course, the nitrogen of the atmosphere, trapped by Nitrogen-fixing Bacteria; but the artificial conversion of this gaseous element into solid forms suitable for fertilizers has taxed to the utmost the ingenuity of chemists. Finally after years of intensive laboratory study and experimentation, the so-called theoretical chemists have succeeded in developing industrial processes for accomplishing this result, which have created an enormous industry of world-wide extent and supplied agriculture with a cheaper source of this indispensable nitrogenous food for plants.

Soil investigations involving the coöperation of chemist and biologist lay the foundations for studies on seed planting, germination, and growth, which in turn lead to others on transplanting, grafting, and pruning, and on pollination, hybridizing, and developing new varieties of plants. Nearly every cultivated plant that is important for food or other purposes has been improved. The great body of practical information which the human race has accumulated from centuries of toil has been multiplied a hundred fold within merely the past generation, through the intensive work of investigators at Agricultural Experiment Stations, Colleges, and Universities throughout the world. (P. 270.)

But this indispensable work is only a small part of all that must be accomplished. Man's conquest of the plant kingdom has hardly begun, because the number of species already brought into his service is insignificant in comparison with the wealth of available kinds. Less than ten per cent of nearly half a million known species of higher plants are cultivated, and most of these in merely an incidental way. There is every reason to believe that many plants not as yet employed possess intrinsic value at least equal to those under cultivation—"some neglected weed in the hands of a skilled botanist may one day revolutionize agriculture." Furthermore, the botanist must develop varieties of important plants which not only afford the largest yield, but also are most resistant to unfavorable climatic conditions and to disease; the forester must develop timberland both for the materials it supplies and the indirect effect it has on soil erosion and on water conservation for agricultural and other purposes; the entomologist and plant pathologist must devise means for holding in check destructive insects, as well as bacterial and related microscopic parasites of plants. For what does it profit us if we are robbed of our crops? Much, to be sure, is being realized but all too slowly to meet the rapidly increasing need. (Fig. 268.)

2. *Insects Injurious to Animals*

The former Chief of the United States Bureau of Entomology informs us that Insects alone in this country continually nullify the labor of a million men, in spite of the annual expenditure of between two and three hundred million dollars in fighting insects, and if human beings are to continue to exist they must first win the war. This can only be accomplished by the labors of an army of patient and skilled investigators, and will occupy very many years, possibly all time to come. This is not only because the insect complex is enormous—there are probably five millions of species of which only about six hundred thousand have been described—but also because insects achieved an important place on this globe many millions of years before Man came into existence and to-day are probably the most perfectly adapted of all creatures to live under all sorts of environmental conditions. If this statement appears extreme, the following examples will serve to make clear some of the cardinal facts which are necessary for an appreciation of the stupendous problems involved.

Among this teeming insect population, probably the Botflies, Fleas, and Lice stand preëminent as parasites of Man and beast. Botflies of various kinds infest domesticated animals but rarely human beings. The HORSE BOTFLY attaches its eggs to the Horse's hair in a position where the eggs can be licked off and swallowed. Then the larvae spend nearly a year attached to the lining of the stomach, and if present in considerable numbers cause irritation and serious digestive disturbances. When fullgrown the larvae pass out with the feces, pupate in the ground and emerge as adult botflies.

FIG. 256. — Ox Botfly, *Hypoderma lineata*. A, adult; B, eggs attached to hair; C, larva; D, larva just beneath air-hole in skin of an Ox. (From Ransom.)

Again, the common Ox BOTFLY deposits its eggs chiefly on the legs of Cattle, but when the larvae emerge, they penetrate the hide, and then wander through the tissues until the following spring. Finally they come to rest just under the hide of their host, which they puncture to get air. When the larvae are ready to assume the pupal state they burrow out, drop to the ground and there complete their life history. It is estimated that the monetary loss from the Ox Botfly alone in the United States is about one hundred million dollars annually. (Fig. 256.)

Fleas and Lice of various species are common parasites of the higher animals throughout most of the world. The JIGGER FLEA of warmer climates is frequently a serious human pest because the female flea burrows into the skin when ready to deposit eggs. The

Cat Flea, Dog Flea, and House Flea we usually consider merely a nuisance, but they are potential carriers of disease-producing microorganisms. One might think that a life devoted to the study of fleas and lice could be more profitably spent, until we recall that expert knowledge of these animals was essential to discover that Trench fever in the World War was transmitted by lice; was essential to make clear that Bubonic plague, or 'Black Death,' is carried by fleas. (Fig. 257.)

It was long known that rats die in great numbers during a plague epidemic, and accordingly biologists set out to determine whether

FIG. 257. — Jigger Flea, *Tunga penetrans*. A, larva; B, adult; C, side view of adult after a meal. (After Karsten and Guyon.)

there is any relation between the disease of the Rat and of Man, and found that Man is infected with the plague bacillus, *Bacillus pestis*, by being bitten by a Flea from an infected rat. Extermination of rats and fleas means the practical eradication of the disease, but in California the Ground Squirrels have become infected with the bacillus so the problem has become somewhat greater. Bubonic plague is doomed, though it has already taken an incalculable toll of human lives: even during the first four years of the present century it destroyed about two million people in India. Still more recently San Francisco has been fighting an outbreak of the plague that not long ago would have been a national calamity; but it was immediately stamped out with the loss of comparatively few lives.

In brief, numerous parasitic Insects not only actually develop at the expense of animal tissue, but others act as the transmitting agents of Bacteria and Protozoa which are the actual parasites, as we have already seen in the case of malaria, yellow fever, and African sleeping sickness. And last, but not least, we know that HOUSE FLIES, which we tolerate as uninvited guests at our tables, have

FIG. 258. — Life history of the House Fly, *Musca domestica*.

been shown to carry the germs of typhoid fever, tuberculosis, dysentery, and several other scourges. (Figs. 228, 258.)

3. *Insects Injurious to Plants*

It has been stated, and truly, that it costs the American farmer more to feed his Insect foes than to educate his children: in fact, more than is expended for all the educational institutions in the United States, nearly twice as much as for our military and naval forces, and more than twice the loss by fire. And we all pay the bill. Every kind of plant supports many species of insects, although usually certain ones are especially destructive. Thus Oak trees are attacked by no less than a thousand kinds of insect pests; Apple trees by about four hundred, and Clover and Corn by some two hundred insect enemies. A few random examples obviously must suffice for our view of the field.

The ARMY WORM is the larva of a brown Moth which sometimes becomes so numerous in regions east of the Rocky Mountains that the caterpillars have to migrate in search of food. Immense armies crawl along totally destroying the crops over large areas. Fortunately, the pest has its own insect enemies, the chief being certain Tachina Flies which lay their eggs on the caterpillars, and the larvae of the flies burrow into their bodies and finally destroy them. (Fig. 265.)

Of equal interest is the CABBAGE BUTTERFLY which was accidentally introduced from Europe into Canada in 1868, and has gradually made the whole of the United States its field, even ousting a related native species. Many of the caterpillars of the Cabbage Butterfly are destroyed by parasites; one being a Brachonid Fly

FIG. 259. — Cabbage Butterfly, *Pieris rapae*.

which was imported from its old home in Europe by entomologists for this special purpose. (Fig. 259.)

The POTATO BEETLE first began to attract attention about fifty years ago when it transferred its activities from certain weeds in the Colorado region to the recently introduced Potato plant, and since that time it has spread all over the United States and has emigrated to Europe to become one of the serious insect pests. Large masses of yellow eggs are deposited by the beetles on the under surface of Potato leaves which serve as food for the caterpillars until they are full grown and ready to pupate in the ground. Two broods of adults are usually produced annually to carry on the depredation.

Among the most destructive parasites of Wheat, Rye, and Barley, nearly the world over, is the HESSIAN FLY which was introduced into America toward the end of the eighteenth century. The life

history is especially adapted to the growth of wheat, and two or three broods of the insect developed in one year. Fortunately, it has numerous parasites of its own and these are the chief factor in holding it somewhat in check.

The EUROPEAN CORN BORER has long been distributed over a large part of the Old World but only recently has reached America. Starting here in New England, it is rapidly moving westward and bids fair before long to infest the entire corn-raising area of the continent. The destructive stage, of course, is the caterpillar which, throughout most of the insect's range, spends the winter in the stem of its food plant and gives rise to the adult moth early the following summer. Unfortunately, however, in New England there are two generations annually, one of which winters in the larval state.

The JAPANESE BEETLE was accidentally introduced into New Jersey from Japan about fifteen years ago and since has spread rapidly through many of the eastern States, destroying lawns and golf greens. The larva spends the winter underground and the adult emerges the following summer.

It seems safe to say that the destruction wrought by the COTTON BOLL WEEVIL exceeds even its notoriety. During the first thirty-five years after its invasion of the United States from Mexico, it had to its account a wastage of upward of three billion dollars, not to mention other immense financial losses due to depreciated land values, etc. Probably each person in the United States pays annually ten dollars more for cotton fabrics than he would if this weevil did not exist. The injury to the Cotton plant is caused both by the adults and larvae: the former by feeding and boring holes for their eggs, and the latter by injuring the developing flowers so that they either fail to bloom, or produce seeds with few cotton fibers. (Fig. 260.)

While SCALE-INSECTS are so small and obscure that they are only a name to all except specialists, they constitute economically the most important group of the entire insect world. Scale-insects infest almost all kinds of trees and shrubs; in some cases doing merely temporary damage and in others actually killing the hosts. Among the myriads of species, the SAN JOSÉ SCALE is probably the most important, and since being brought to California from China has spread all over the United States. The adult female insect lies permanently attached by its beak to the bark, underneath a tiny

waxy scale which it secretes. Here eyes, legs, and antennae are lost and the sac-like creature sucks the plant sap and reproduces. It is estimated that the progeny of a single individual during one season would number several billion if all were to survive. (Fig. 264.)

FIG. 260. — The Cotton Boll Weevil, *Anthonomus grandis*. On the right, a Cotton plant attacked by the Weevil, showing *a*, a dry infested 'square'; *b*, a 'flared square' with punctures; *c*, a cotton boll sectioned to show attacking Weevil and larva in its cell; *g*, adult female with wings spread as in flight; *d*, adult viewed from the side; *h*, pupa, ventral view; *e*, larva. (From Metcalf and Flint, after U. S. Department of Agriculture.)

About forty years ago the vineyards of France, and later those of California, appeared to be doomed to destruction by the attacks of a species of minute plant lice, or APHIDS. The French government offered a large reward for an effective remedy, and many entomologists and botanists devoted all their time to the study of the problem. Eventually it was discovered that certain American wild Grapes were naturally immune to the pest. Accordingly by

grafting the cultivated grape upon the resistant wild stock a combination was effected which saved the vineyards of both countries. (Fig. 226.)

And now the MEDITERRANEAN FRUIT FLY, long the bane of fruit growers in many parts of the world, has appeared in certain Florida orchards in spite of unceasing vigilance of the United States Bureau of Entomology. It is the larvae of the fly that are the mischief makers, because when they develop from eggs deposited in the fruit they soon render it unfit for human food. When we realize that the annual fruit and vegetable crop of Florida amounts to well over a hundred million dollars, it is no wonder that this fly is one of our most notorious foreign emigrants. But

FIG. 261. — Mediterranean Fruit Fly, *Ceratitis capitata*.
(From U. S. Department of Agriculture.)

we maintain a defense on the Rio Grande against the Mexican Fruit Fly, and others throughout the country against our many native species of Fruit Flies, though the latter are held in check to a considerable extent by their own insect enemies. (Fig. 261.)

Another great problem is the preservation of forest and shade trees from native and also imported pests. The enormity of the loss attributed to this army of silent tree-killers is staggering. They destroy two-thirds as much of the nation's wealth each year as do forest fires — timber equal to one-fifth of the wood produced annually in the United States.

At the present time these destructive insects recognize neither limits nor boundaries, for their march has received relatively little

resistance. The PINE BEETLE, not content with its invasion of the vast forests of the Northwest, now is threatening those of the Yellowstone National Park. The GYPSY MOTH, accidentally introduced near Boston, has spread throughout a large part of

FIG. 262. — Gypsy Moth, *Porthetria dispar*. A, adult female; B, larva; C, pupa. (From Howard.)

southern New England and is besieging the New York state line. Entomologists have made intensive studies of its European enemies; left behind when it came to America, and the introduction of some of these into New England gives hopes that it may eventually be conquered. In one year alone nearly three million enemies, repre-

FIG. 263. — A, Carpet Beetle, *Anthrenus scrophulariae*; a, larva of Carpet Beetle; B, Clothes Moth, *Tinea pellionella*; b, larva of Clothes Moth. (From Riley.)

senting eight species, were liberated. The BROWN-TAIL MOTH is another importation from Europe whose activities thus far have been confined to New England as the result of strenuous control measures. These three examples may stand as representative of the legions of destructive forest insects. (Fig. 262.)

Finally we should be reminded, if necessary, that our households are not immune to insect marauders that take an immense aggregate toll each year. CARPET BEETLES, popularly called Buffalo Moths, and CLOTHES MOTHS are all too familiar examples. (Fig. 263.)

4. Beneficial Insects

Although we have mentioned incidentally the part played by certain insects in suppressing other noxious kinds, it would be unfair to the insect world not to emphasize, in passing, the existence of members which are serviceable to Man: those thousands which prey upon our enemies or supply us with materials. It has been well said that "if insects would quit fighting among themselves, they would overwhelm all Vertebrate animals"; though sometimes

FIG. 264. — Australian Ladybird Beetle, *Rodolia cardinalis*, and Fluted Scale-insect, *Icerya purchasi*. a, larvae of beetle feeding on scale; b, pupa of beetle; c, adult beetle; d, Orange twig showing scales and beetles. (From Marlatt.)

long biological investigations are necessary to keep them fighting when we have upset the natural conditions; e.g., moved them to a new environment away from their natural enemies. Thus Orange trees brought from Australia introduced the FLUTED SCALE-INSECT which soon spread to the great California orange and lemon groves, and entailed enormous losses. The fruit growers finally sent, at their own expense, an expert entomologist to study in Australia the native enemies of the Scale-insect. As a result some Ladybird Beetles were eventually discovered which offered hope of meeting the needs, and these were sent to California and carefully reared

until they could be colonized in the infected groves. Here they multiplied and ever since have held the Fluted Scale in check. (Fig. 264.)

Furthermore we must not forget that such insects as the SILK-WORM MOTH and the HONEY BEE are really domesticated animals:

FIG. 265. — A, Ichneumon Fly laying eggs in the cocoon of a Tent Caterpillar; B, parasitic Tachina Fly; C, part of an Army Worm with Tachina Fly eggs attached to it. (From Fiske.)

each are at the basis of an enormous world industry. One of Pasteur's most important studies was on the PEBRINE disease of Silkworms, and not only saved the silk industry of France, but also paved the way for the study of infectious diseases in higher animals

FIG. 266. — Silkworm Moth, *Bombyx mori*. A, caterpillar; B, cocoon; C, adult female moth. (From Shipley and MacBride.)

and Man. The cause of pebrine proved to be a Protozoan parasite, *Nosema bombycis*. (Figs. 218, 266.)

The dependence of many plants upon insects for pollination is well illustrated by the difficulties in establishing the SMYRNA FIG in California. The fruit would not mature, and studies by botanists and entomologists showed that in the plant's native land pollina-

tion was effected by a certain tiny insect. Importation and establishment of the insect carrier in California created there the immense fig-growing industry. (Fig. 223.)

5. *Plants Injurious to Plants*

Plants would seem to have enough animal enemies without having to contend with parasitic plants, but as a matter of fact the science of plant diseases, PHYTOPATHOLOGY, is largely devoted to the destructive activities of colorless plants, the Bacteria and higher Fungi. The life histories of many of the SMUTS, RUSTS, and related parasitic Fungi are so complicated that hundreds of specialists are continually employed in ferreting them out in order to preserve the products of farm and forest. Perhaps the WHITE PINE BLISTER RUST is sufficiently typical to present some of the difficulties involved. (Figs. 19, 267.)

This species lives during one stage of its life on the White Pine and during another on the leaves of Currant or Gooseberry bushes. In common with most of the Fungi, it produces spores which are distributed by the wind. When the spores of a certain stage in the life history fall upon White Pine leaves, they enter the stomata, develop, and grow through the tissues. Finally, after several years, the bark swells at the points of infection and sporangia are protruded which liberate myriads of spores in the form of a bright yellow powder. For further development, one or more of these PERIDERMIIUM SPORES must be carried by the wind to the leaf of a Currant or Gooseberry bush. Established here the spore germinates, grows down into the leaf tissue, and in a couple of weeks this new stage in the life history is itself forming spores. Masses of these UREDOSPORES appear as tiny specks of orange powder on the leaf surface.

This second type of spore also develops on the Currant or Gooseberry and soon another lot of similar spores are produced. Such repeating infection may continue every two weeks until autumn when the leaves fall. Then a third type of spore, TELIOSPORE, appears which can develop only on a White Pine. If this transfer is successfully accomplished, the life cycle is completed. Since either the Currant or Gooseberry acts as the intermediate host, they afford a hazard for White Pine forests in the vicinity. This life history involving two hosts recalls that of certain animal parasites, such as the Malarial organism.

FIG. 267. — Diagram of the life history of the White Pine Blister Rust. *a*, blisters on Pine in spring, from which the disease spreads to Currant or Gooseberry leaves and produces the early summer stage, *b*, thence it may spread to another Currant leaf and produce there a second crop of the early summer stage, *c*, or it may produce the late summer stage, *d*, in this stage; in the fall it infects the neighboring White Pines. (From Smallwood, after Spaulding.)

Enough, perhaps, has been said to indicate the struggle for knowledge which Man must maintain in order to cope with the biological forces that would rob him, are robbing him, of what he considers his heritage. But it is only fair to add that biologists who have given the most thought to the problem are by no means certain that the struggle will eventually be successfully terminated; it is possible that Insects and allied enemies will gain the upper hand in the warfare for food when the human population has increased beyond a certain limit. This seems incredible, though it is a conservative statement by men who are specialists and not pessimists. In any event, it is clear that the most urgent need to-day is more knowledge of the life habits of Insects and other destructive organisms. Generous Federal and State appropriations must be made so that through research effective methods of control may be developed. Experience has shown that the research dollar is not only invested in a gilt-edge security, but one at the same time producing a national dividend almost beyond computation.

C. CONSERVATION OF NATURAL RESOURCES

We are slowly awakening to the fact that we have been very shortsighted. Conservation of natural resources has, until recently, given very little concern, although it is one of the greatest problems which biologists of the present generation face, and it must be solved now or it will be too late. What happened in America is being repeated in many other parts of the world. Our forefathers came to a land of fertile soil covered with primeval forests, abounding with large and small Birds and Mammals, and with waters richly supplied with Fish. These they necessarily and rightly drew upon for their livelihood. It was their wealth — Nature's generous bonus.

But the apparently inexhaustible supply has already become alarmingly reduced and conservation must be the watchword, as was recognized a quarter of a century ago by President Roosevelt who considered it "the weightiest problem now before the nation, as nobody can deny the fact that the natural resources of the United States are in danger of exhaustion, if the old wasteful methods of exploiting them are permitted longer to continue." Yet in spite of this, as recently as 1929 the conditions were still such that Vice President Dawes was justified in stating that "it is time that the national conscience be awakened to the necessity of preserving

what is left of the outdoor heritage of our fathers, and of restoring some of that which has been destroyed and defiled."

Only about one-eighth of the virgin forest of the United States remains to-day. It seems incredible for a civilized nation — but is only too true. Approximately one-half of this is held by the Government but the rest is being destroyed far more rapidly than unaided

FIG. 268. — Soil erosion due to removal of all the trees.
(From U. S. Forest Service.)

nature can restore it. And there is nowhere in the world a sufficient supply of the kinds of timber we use to take their place. We have continuously treated our forests, except those under public control, not as a farm on which to produce crops, but as a mine whose useful product is to be gathered once for all. The axe holds almost unregulated sway. Scientific forestry is crucial for our future. (Fig. 268.)

Many of the larger animals have been exterminated and some of the smaller ones are fast approaching the same fate. The Bison is

extinct in the United States except for the few hundreds preserved in reservations; the Elk is restricted in numbers and range; the Elephant Seal remains only in one small colony; the Bowhead Whale and Right Whale are threatened with extermination; and the Beaver has disappeared from most of its former haunts. The demand for furs is estimated to be responsible for the destruction of thirty million Mammals throughout the world each year, and this number is nearly doubled if all the wild Mammals destroyed for commercial purposes are included. While there is life there is hope, but unless immediate steps are taken to reduce the slaughter, the fur-bearing animals of the world at large are doomed.

Birds are now faring somewhat better owing to the heroic efforts started a generation ago by the Audubon Societies, so that a partial restoration of our former bird population seems probable. Of what use are the Birds? Even if usefulness were the only question involved, the answer would still be clear. Experts tell us that without the services of insect-eating and seed-eating Birds, successful agriculture would soon be impossible, and the destruction of the greater part of our vegetation would also result. One caterpillar during its lifetime of less than two months can consume three-quarters of a pound of leaves, or nearly ninety thousand times its original weight. Birds are "the winged wardens of our farms." Their help is needed in the struggle.

In truth, it is dangerous for Man to upset the intricate balance of the economy of nature by the reckless destruction of plant or animal without taking thought for the morrow — without intensive study of the far-reaching consequences which may follow from the breaking of one link in the chain of the interrelationships of organisms. The destruction even of certain Protozoa and other microscopic life may seal the fate of Fish valuable for food. (P. 329.)

D. CONSTRUCTIVE BIOLOGY

The great living heritage which we have received will be permanently impaired for posterity even though useless waste is stopped, unless the highly complex problem of conservation is attacked constructively in the light of modern biological knowledge. Merely to hold Nature's bonus unimpaired, crucial as that is, will not adequately meet the requirements of increasing populations with the attendant demands of complex civilized life. Few seem to realize that the whole of our business life takes root in nature. All

of our progress and prosperity is predicated on the abundance of our natural resources and the manner in which we develop them for Man's use. Methods of raising crops and domestic animals which were sufficient for primitive communities are entirely inadequate to satisfy modern conditions.

Indeed, the state of civilization of a people is closely related to its success in developing plants and animals for particular needs. One hears of new 'creations,' but often fails to recall that Man can merely direct the laws of inheritance, and this he can do only by intensive investigations of the principles underlying heredity. Certainly the most important recent contribution of biology is the discovery of the general method of transmission of characters from generation to generation, common to all living things, which has established the new biological science, genetics. To-day, as we have seen, biologists the world over are developing and applying these principles in plant and animal breeding. What was impossible a few years ago is now being accomplished almost as a mere matter of routine work in many biological laboratories.

Important as the application of these principles is in the mastery of agricultural problems, a far more profound power remains to be realized when, as nations, mankind becomes awake to the fact that these same basic principles apply equally to human inheritance. If it be true that the human race has not improved in bodily and mental characteristics since the time of the ancient Greeks, the responsibility rests with Man himself. He has studied and applied selective breeding of animals and plants. He has in general kept the best for his purposes that nature offered and eliminated the rest. He has depended chiefly on the stock and only secondarily on the environment for permanent improvement. But it has been otherwise with himself. Much of the worst human stock has continued to survive and multiply, and disproportionately so as civilization has advanced. Reliance has been placed almost solely on the improvement of the conditions of life and not on breeding from the best. We may fairly say that humanity is what it is to-day in spite of the continual violation of many of the biological principles which would improve the race. (Fig. 269.)

This, of course, is merely a statement of fact: not a reproach. Man could not have done otherwise until it had been demonstrated by biological investigation that he is a part of, and not apart from

FIG. 269. — The Kallikak family.

Of the 480 descendants of this branch of the family 143 (21%) were feeble-minded; only 46 (9%) were normal; of the rest 189 (68%) are still undetermined. 24 were confirmed alcoholics; 3 were criminals; 3 were epileptics; 82 died in infancy; 41 were degenerate.

Of the 496 descendants of this branch of the family, none were feeble-minded, and all were good citizens. Among them were educators, physicians, lawyers, judges, traders, landowners — men and women prominent in every phase of social life. Only 2 were alcoholics. (From Goddard.)

the rest of living nature — the most profoundly important fact that biology has contributed to human welfare. With this fully grasped, new import is given to the study of general biological principles and no plant or animal is too insignificant to throw light on life problems. And this has been the chief source of the stupendous potential for biological control which has within less than a century come to mankind. Potential for control, we say, because years of research by generations of investigators is still necessary before we shall be prepared to solve the problems we now face and which

FIG. 270. — The Marine Biological Laboratory, Woods Hole, Massachusetts. One of the many laboratories where biologists each year spend their "vacations" in research covering all branches of the science.

the saturation point of human population will immensely augment. (Figs. 270, 271; p. 5.)

The natural method of securing a healthy — adapted — race is, of course, the gradual process of adjustment throughout the ages by response to environmental stimuli. But mankind has the power, which we believe is denied to the lower animate beings, of conscious response — of choice. Human volition and action can retard or accelerate nature's response. Human volition may not only decide, within limits, the response to surrounding conditions, but also not infrequently may directly change the conditions so as to render unnecessary individual or racial adaptation to them. Thoughts such as these make plain the enormous complexity of the situation and reveal the possibility of danger lurking where it may be least expected — danger lest in acting as we think humane from the

point of view of particular individuals, we may be rendering a dis-service to the race.

The complex problems of eugenics, the science of being well-born, are problems in genetics so intricately interwoven with those of all the other sciences of human life and relationships, in particular sociology and psychology, that propaganda in eugenics not fundamentally grounded in basic interlocking data from these sciences is not only premature, but fraught with insidious possibilities. Eugenics seeks improvement through nature, euthenics seeks im-

FIG. 271. — The National Academy of Sciences and the National Research Council of the United States, Washington, D. C. The focus of American scientific research.

provement through nurture. Each is a partial view and before significant progress can be made the proper balance between these two aspects of one problem must be grasped. Organism and environment are one and inseparable. (P. 300.)

The crying need of the present is for more and still more knowledge which is secured in the laboratory rather than on the lecture platform. When we realize that if the infants Darwin and Lincoln, who were both born on the same day, had been exchanged by their parents, almost certainly neither would have produced epoch-making contributions to science or civilization, it gives us pause. The Danes have a proverb that it does no harm to be born in a

duckyard if you are laid in a Swan's egg — thus emphasizing heredity, though heredity implies not a repetition in kind, but in possibilities. We cannot hope to be born equal, but we may ask to be born with an equal opportunity to develop what is in us. At least we can say at present, without fear of contradiction, that Man owes it to himself not to be less mindful of his own stock than he is of that of his domestic animals.

From every standpoint the mere pittance Man casts to biological research returns to him many-fold in health and wealth, in comfort and power, and most of all in a broader and more appreciative outlook on a congenial world. Far from depriving life of its mystery, biology affords a sublime picture of the interrelatedness of living things and still more inextricably interweaves human life with that of all Nature.

CHAPTER XXVI

EPOCHS IN BIOLOGICAL HISTORY

History must convey the sense not only of succession but also of evolution. — *New York Times*.

THE story of Man's slow emergence from a condition in which he was completely at the mercy of his environment, to his relatively masterful position as exhibited in our present civilization is the inspiring history of science — the intellectual development of the race. Indeed, as we have seen, knowledge spells power — power to direct and become adapted to the forces of nature, and this knowledge Man has acquired after much labor and safely treasured with great pains as a result of scientific study. Truly "the succession of men during the course of many centuries should be considered as one and the same man who exists always and learns continuously"; but we, for the most part, forget the past whose heirs we are. Let us for the moment "look to the mountains whence cometh our strength" in biology.

Some knowledge of hunting, agriculture, and husbandry was one of the early acquirements of prehistoric Man, and at the dawn of history, nearly 5000 years ago, systems of medicine apparently found a place in Egyptian and Babylonian civilizations. So, on the practical side, biology has a very ancient beginning. But biology as the science of life in which emphasis is placed on the study of vital phenomena for their own sake really begins with the Greeks.

A. GREEK AND ROMAN SCIENCE

Science reaching Greece from the South and East fell upon fertile soil, and in the hands of the Hellenic natural philosophers was transformed into coherent systems through the realization that nature works by fixed laws — a conception foreign to the Oriental mind and the corner-stone of all future scientific investigation. It is not an exaggeration to say that to all intents and purposes the Greeks laid the foundations of the chief subdivisions of natural science and, specifically, created biology.

ARISTOTLE (384–322 B.C.), the most famous pupil of Plato and dissenter from his School, represents the highwater mark of the Greek students of nature and is justly called the Father of Natural History. Although Aristotle's contributions to biology are numerous, perhaps of most significance is the fact that he took a broad survey of the existing data and welded them into a science. He did this by relying, to a considerable extent, on the direct study of organisms and by insisting that the only true path of advance lies in accurate observation and description. The observational method and its very modern development, the laboratory method of biolog-

FIG. 272. — Aristotle.

ical study, find their first great exponent in Aristotle. But mere observation without interpretation is not science. Aristotle's generalizations based on the facts accumulated and his elaboration of broad philosophical conceptions of organisms give to his biological works their lasting significance. (Fig. 272.)

While Aristotle's biological investigations were devoted chiefly to animals, his pupil and co-worker, THEOPHRASTUS (370–286 B.C.), made profound studies on plants. Theophrastus not only laid the foundations but also gave suggestions of much of the superstructure of botany; an achievement which entitles him to rank as the first great student of plant science. (Fig. 273.)

Before leaving the Greeks we must mention HIPPOCRATES

(460–370 B.C.), the Father of Medicine. Writing a generation before Aristotle, at the height of the Age of Pericles, Hippocrates crystallized the knowledge of medicine into a science and gave to physicians a high moral inspiration.

The history of medicine and of biology as a so-called pure science are so closely interwoven that consideration of the one involves that of the other. Indeed the physicians form the only bond of continuity in biological history between Greece and Rome. The chief interest of the Romans lay in technology, and it is but natural that the practical advantages to be gained from medicine should

FIG. 273. — Theophrastus of Eresus.

ensure its advance. As it happens, however, two Greek physicians were destined to have the most influence: Dioscorides, an army surgeon under Nero, and Galen, physician to the Emperor Marcus Aurelius.

DIOSCORIDES wrote the first important treatise on applied botany. This was really a work on the identification of plants for medicinal purposes but, gaining authority with age, it became the standard 'botany' for fifteen centuries.

GALEN (131–201) was the most famous physician of the Roman Empire and his voluminous works represent both a depository for the anatomical and physiological knowledge of his predecessors,

improved and worked over into a system, and also a large amount of original investigation. Galen was at once a practical anatomist and also an experimental physiologist, inasmuch as he described from dissections and insisted on the importance of vivisection and experiment. Galen gave to medicine its standard 'anatomy' and 'physiology' for fifteen centuries.

Any consideration of the biological science of Rome would be incomplete without a reference to the vast compilation of mingled fact and fancy made by PLINY the Elder (23-79). It was aside from the path of biological advance, but long the recognized *Natural History*, passing through some eighty editions after the invention of printing.

B. MEDIEVAL AND RENAISSANCE SCIENCE

For all practical purposes we may consider that biology at the decline of the Roman Empire was represented by the works of Aristotle, Theophrastus, Dioscorides, Galen, and Pliny. Even these exerted little influence during the Middle Ages. Dioscorides, Galen, and Pliny were in the hands of the scholars, but in so far as science reached the people in general it was chiefly by collections of quotations from corrupt texts of these authors interspersed with anecdotes and fables. Under theological influence there arose the oft-quoted *PHYSIOLOGUS*, found in many forms and languages, which is at once a collection of natural history stories, and a treatise on symbolism and the medicinal use of animals. Here, for instance, the mythical centaur and phoenix take their place with the Frog and Crow in affording illustrations of theological texts and in pointing out more or less evident morals.

Indeed, science was submerged to such an extent that the scientific Renaissance owes its origin largely to the revival of classical learning: in particular to the translation of Aristotle and Theophrastus, and renewed study of Dioscorides and Galen. Their works were so superior to the current science that, in accord with the spirit of the times, to question their authority became almost sacrilegious. The first studies were merely commentaries on the writings of these authors, but as time went on more and more new observations were interspersed with the old. In short, the climax of the scientific Renaissance involved a turning away from the authority of Aristotle and the past, and an adoption of the Aristotelian method of observation and induction.

Botany was the first to give visible signs of the awakening, probably because of the dependence of medicine on plant products. "All physicians professed to be botanists and every botanist was thought fit to practice medicine." In the HERBALS published in Germany during the sixteenth century we can trace the growth of plant description and classification from mere annotations on the text of Dioscorides to well-illustrated manuals of the plants of western Europe.

Meanwhile zoölogy began to emerge as a distinct science, but the less obvious immediate utility of the subject, combined with

FIG. 274. — Andreas Vesalius.

the greater difficulty of collecting and preserving animals and therefore the necessity of more dependence on travelers' tales, contributed to retard its advance. One group of naturalists, the ENCYCLOPAEDISTS, so-called from their endeavor to gather all the available information about living things, attempted the impossible. However, this gleaning from the ancients and adding such material as could be gathered led to the publication of huge volumes of fact and fiction, which in the case of the best — Gesner's *History of Animals* — served to popularize zoölogy and afforded the necessary survey which must precede constructive work.

Although GESNER (1516–1565) of Switzerland was without doubt the most learned naturalist of the period and probably the best zoölogist who had appeared since Aristotle, the direct path to progress was blazed by men whose plans were less ambitious. Contemporaries of Gesner, who confined their treatises to special groups of organisms which they themselves investigated, really instituted the biological MONOGRAPH which has proved to be an effective method of scientific publication.

While the HERBALISTS, ENCYCLOPAEDISTS, and MONOGRAPHERS at work in natural history were making earnest endeavors to

FIG. 275. — William Harvey.

develop the powers of independent judgment, long suppressed during the Middle Ages, the emancipator of biology from the traditions of the past appeared in the Belgian anatomist, VESALIUS (1514–1564). Not content with the anatomy of the time, which consisted almost solely in interpreting the works of Galen by reference to crude dissections made by barbers' assistants, Vesalius attempted to place human anatomy on the firm basis of exact observation. The publication of his great work *On the Structure of the Human Body* made the year 1543 the dividing line between ancient and modern anatomy, and thenceforth anatomical as well as biological investigation in general broke away from the yoke of authority, and men began to trust and use their own powers of observation. (Fig. 274.)

The work of Vesalius was on anatomy, and physiology was treated somewhat incidentally. The complementary work on the functional side came in 1628 with the publication of the epoch-making monograph *On the Motion of the Heart and Blood in Animals* by HARVEY (1578–1657) of London. No rational conception of the economy of the animal organism was possible under the influence of Galenic physiology, and it remained for Harvey to demonstrate by a series of experiments, logically planned and ingeniously executed, that the blood flows in a circle from heart back to heart again, and thus to supply the background for a proper understanding of the physiology of the organism as a whole. With the work of Vesalius and Harvey, biologists had again laid hold of the great scientific tools — observation, experiment, and induction — which since then have not slipped from their grasp. (Fig. 275.)

C. THE MICROSCOPISTS

During this revival period, when collections and accurate descriptions of plants and animals were being made and the study of anatomy and physiology was going rapidly forward, optical inventions occurred which were destined to make possible modern biology. First came the development of the SIMPLE MICROSCOPE, through an adaptation of the principles of spectacles, apparently by Roger Bacon; then the combination of lenses to form the COMPOUND MICROSCOPE first effectively employed by Galileo in 1609; and by the middle of the century simple and compound microscopes were being made by opticians in the leading centers of Europe. Significant of the times is the clear appreciation of the importance of studying nature with instruments which increase the powers of the senses in general and of vision in particular expressed by HOOKE (1635–1703) of London, in a remarkable book, the *Micrographia*, published in 1665. Using his improved compound microscope, Hooke clearly observed and figured for the first time the “little boxes or cells” of organic structure, and his use of the word cell is responsible for its application to the protoplasmic units of modern biology.

Microscopical work was a mere incident among the varied interests of Hooke, while LEEUWENHOEK (1632–1723) of Holland spent a long life studying nearly everything which he could bring within the scope of his simple lenses. With an unexplored field before him,

all of his observations were discoveries. Bacteria, Protozoa, Hydra, and many other organisms were first revealed by his lenses. But Leeuwenhoek's discovery of the sperm of animals created the most astonishment. His imagination, however, outstripped his observations for he thought he saw evidence of the organism preformed within the sperm and so regarded it as the complete germ which had only to be hatched by the female. (Fig. 276.)

The patience of Leeuwenhoek would have been strained to the breaking point by the studies on insect anatomy made by SWAMMERDAM (1637-1680) of Holland. Inspired largely by the desire to

FIG. 276. — Antony van Leeuwenhoek.

refute the current notion that Insects and similar lower animals are without complicated internal organs, Swammerdam spent his life in studies on their structure and life histories. Revealing, as he did, by the most delicate technique in dissection, the finest details observable with his lenses, Swammerdam not only set a standard for minute anatomy which was unsurpassed for a century, but also dissipated for all time the conception of simplicity of structure in the lower animals. He thus, quite naturally, added one more argument to those of the Italian REDI (1626-1698) and others against spontaneous generation — an erroneous theory that survived until the work of Pasteur (1822-1895) in the nineteenth century. (Figs. 152, 278.)

Malpighi of Bologna and Grew of London, contemporaries of Hooke, Leeuwenhoek, and Swammerdam, may be considered as the pioneer histologists. GREW (1641-1712) devoted all his attention to plant structure, while MALPIGHI (1628-1694), in addition to botanical studies which paralleled Grew's, made elaborate investigations on animals. The versatility as well as the genius of Malpighi is shown by his studies on the anatomy of plants, the function of leaves, the development of the plant embryo, the embryology of the chick, the anatomy of the Silkworm, and the structure of glands. Skilled in anatomy but with prime interest in

FIG. 277. — Marcello Malpighi.

physiology, his lasting contribution lies in his dependence upon the microscope for the solution of problems where structure and function, so to speak, merge. This is well illustrated by his ocular demonstration of the capillary circulation in the lungs, which is not only his greatest discovery but also the first of prime importance ever made with a microscope, since it completed Harvey's work on the circulation of the blood. (Fig. 277.)

D. DEVELOPMENT OF THE SUBDIVISIONS OF BIOLOGY

The microscopists taken collectively created an epoch in the history of biology, so important is the lens for the advancement of the science. Broadly speaking, we find that its development along many lines during the eighteenth and particularly the nineteenth

century went hand in hand with improvements in the compound microscope itself and in microscopical technique. Again, the microscopists in general and Malpighi in particular opened up so many new paths of advance that from this period on it is not possible, even in the most general survey, to discuss the development of biology as a whole. The composite picture must be formed by emphasizing and piecing together various lines of work, such as

FIG. 278. — Louis Pasteur.

classification, comparative anatomy of animals, embryology, physiology of plants and animals, genetics, and evolution.

1. *Classification*

Classification has as its object the bringing together of organisms which are alike and the separating of those which are unlike; a problem of no mean proportions when a conservative estimate to-day shows upward of a million known species of animals and plants — leaving out of account the myriads of forms represented only by fossil remains. (Pp. 443-447.)

Naturally the earliest classifications were utilitarian or more or less physiological — fowl of the air, beasts of the field; edible, poisonous, etc. But as knowledge increased emphasis was shifted

to the anatomical criterion of specific differences, and thenceforth classification became an important aspect of natural history — a central thread both practical and theoretical. Practical, in that it involved the arranging of living forms so that a working catalog was made which required nice anatomical discrimination, and therefore the amassing of a large body of facts concerning animals and plants. Theoretical, because in this process botanists and zoölogists were impressed, almost unconsciously at first, with the 'affinities' of various types of animals and plants, and so were led to problems of their origin.

FIG. 279. — John Ray.

From Aristotle, who emphasized the grouping of organisms on the basis of structural similarities, we must pass over some seventeen centuries, in which the only work of interest was done by the herbalists and encyclopaedists, to the time of RAY (1628–1705) of England and LINNAEUS (1707–1778) of Sweden. Previous to Ray the term species was used somewhat indefinitely, and his chief contribution was to make the word more concrete by applying it solely to groups of similar individuals which seem to exhibit constant characters from generation to generation. This paved the way for the great taxonomist, Linnaeus. (Figs. 279, 280.)

First and foremost a botanist, Linnaeus published a practical classification of the Seed Plants which afforded a great impetus to plant study, particularly because he insisted on brief descriptions

and the scheme of giving each species a name of two words, generic and specific, thereby establishing the system of BINOMIAL NOMENCLATURE. Linnaeus' success with botanical taxonomy led him to extend the principles to animals and even to the so-called mineral kingdom: the latter showing at a glance his lack of appreciation of any genetic relationship between species. Although Linnaeus believed that species, genera, and even higher groups represented distinct acts of creation, nevertheless his greatest works, the *Species Plantarum* and *Systema Naturae*, are of outstanding importance in

FIG. 280. — Carolus Linnaeus.

biological history and by common consent the base line of priority in botanical and zoölogical nomenclature. (Fig. 281; p. 346.)

2. Comparative Anatomy

Owing to the less marked structural differentiation of plants in comparison with animals, plant anatomy lends itself less readily to descriptive analysis, so that an epoch in the study of comparative anatomy is not so well defined in botany as in the sister science, zoölogy. Therefore we shall confine our attention to the comparative anatomy of animals.

Comparative anatomy as a really important aspect of zoölogical work, in fact as a science in itself, was the result of the life-work of CUVIER (1769–1832) of Paris. It is true that some of his predecessors had reached a broad viewpoint in anatomical study but

Cuvier's claim to fame rests on the remarkable breadth of his investigations — his survey of the comparative anatomy of the whole series of animal forms. And not content merely with the living, he made himself the first real master of the anatomy of fossil Vertebrates, as his contemporary LAMARCK was of fossil Invertebrates. (Fig. 282.)

Cuvier's grasp of anatomy was due to his emphasizing, as Aristotle had done before him, the functional unity of the organism: that the interdependence of organs results from the interdependence

FIG. 281. — Asa Gray (1810–1888).
The founder of American systematic botany.

of function: that structure and function are two aspects of the living machine which go hand in hand. Cuvier's famous principle of correlation — "Give me a tooth," said he, "and I will construct the whole animal" — is really an outcome of this viewpoint. Every change of function involves a change in structure and, therefore, given extensive knowledge of function and of the interdependence of function and structure, it is possible to infer from the form of one organ that of most of the other organs of an animal. But Cuvier undoubtedly allowed himself to exaggerate his guiding principle until it exceeded the bounds of facts.

Among Cuvier's immediate successors, OWEN (1804-1892) of London perhaps demands special mention. Owen spent a long life dissecting with untiring patience and skill a remarkable series of animal types, as well as reconstructing extinct forms from fossil remains. Aside from the facts accumulated, probably his greatest contribution was making concrete the distinction between homologous and analogous structures. This has been of the first importance in working out the pedigrees of plants as well as of animals; though Owen himself took an enigmatical position in regard to

FIG. 282. — Georges Cuvier.

organic evolution — quite different from that of HUXLEY (1825-1895), his great English contemporary comparative anatomist. (Figs. 283, 284; p. 121.)

3. *Physiology*

The functions of organisms were discussed by Aristotle with his usual insight, though, as might be expected since physiology is more dependent than anatomy upon progress in other branches of science, with less happy results. Similarly Galen was hampered in his attempt to make physiology a distinct department of learning, based on a thorough study of anatomy, and the corner-stone of medicine; though fate foisted upon uncritical generations through fifteen centuries his system of human physiology.

Neither Vesalius nor Harvey made an attempt to explain the workings of the body by appeal to so-called physical and chemical laws; and for good reason. Chemistry had not yet thrown off the shackles of alchemy and taken its legitimate place among the elect sciences, while during Harvey's lifetime, under the influence of Galileo, the new physics was born. But by the end of the seventeenth century both physics and chemistry had forced their way into physiology and split it into two schools. The physical school was founded by BORELLI (1608-1679) of Italy, who, employing inci-

FIG. 283. — Thomas Henry Huxley.

sive physical methods, attacked a series of problems with brilliant results; while the chemical school developed from the influence of FRANCISCUS SYLVIVS (1614-1672) of Holland as a teacher rather than as an investigator.

This awakening brought a host of workers into the field and the harvest of the century was garnered and enriched by HALLER (1708-1777) of Geneva. In a comprehensive treatise which at once indicated the breadth of view and critical judgment of its author, Haller established physiology as a distinct and important branch of biological science. It was no longer a mere adjunct of medicine. Perhaps the most significant advance in Haller's century consisted

in setting the physiology of nutrition and of respiration — both of which awaited the work of the chemists — well upon the way toward their modern form.

REAUMUR (1683–1757) of Paris and SPALLANZANI (1729–1799) of Pavia may be singled out for their exact studies of gastric digestion, which showed ‘solution’ of the food to be the main factor in digestion; although it was not clear how these changes differ from ordinary chemical ones. It was left for nineteenth-century investigators to establish the fact that food in passing along the digestive tract

FIG. 284. — Louis Agassiz (1807–1873).
Founder of American zoölogy and comparative anatomy.

runs the gauntlet of a series of complex chemical substances, each of which has its part to play in putting the various constituents of the food into such a form that they can pass to the various cells of the body where they are actually used. (Fig. 113.)

On the side of respiration, a closer approach was made toward a true understanding of the process. In France LAVOISIER (1743–1794) demonstrated that the chemical changes taking place in respiration involve essentially a process of combustion, and it chiefly remained for later work to show that this takes place in the tissues rather than in the lungs. (P. 151.)

Most of the firm foundation on which the physiology of animals rests to-day has been built up by the work on Vertebrates. But

since the middle of the nineteenth century, when the versatile MÜLLER (1801–1858) of Germany emphasized the value of studying the physiology of higher and lower animals alike, there has been an ever-increasing tendency to focus evidence, in so far as possible, from all forms of life on general problems of function. This has culminated in the science of COMPARATIVE PHYSIOLOGY.

The less obvious structural and functional differentiation of plants retarded progress in plant physiology as it did in plant anatomy. Probably of most historical, and certainly of most gen-

FIG. 285. — Stephen Hales.

eral interest is the development of our knowledge of the nutrition of green plants. Aristotle's notion that the plant's food is prepared for it in the ground was still prevalent during the seventeenth century when Malpighi, from his studies on plant histology, gave the first hint of supreme importance — the crude 'sap' enters by the roots and is carried to the leaves where, by the action of sunlight, evaporation, and some sort of a 'fermentation,' it is elaborated and distributed as food to the plant as a whole. (Fig. 58.)

It is HALES (1677–1761) of England, however, to whom the botanist looks as the Harvey of plant physiology, because in his *Vegetable Staticks* (1727) he laid the foundations of the physiology of plants by making "plants speak for themselves" through his incisive experiments. For the first time it became clear that green plants derive a considerable part of their food from the atmosphere, and also that the leaves play an active rôle in the movements of

fluids up the stem and in eliminating superfluous water by evaporation. Still the picture was incomplete, and so remained until the biologist had recourse to further data from the chemist. (Fig. 285.)

In 1779, PRIESTLEY (1733–1804) of England, the discoverer of oxygen, showed that this gas under certain conditions is liberated by plants. This fact was seized upon by a native of Holland, INGENHOUSZ (1730–1799), who demonstrated that carbon dioxide from the air is reduced to its component elements in the leaf during exposure to sunlight. The plant retains the carbon and returns the oxygen — this process of carbon-getting being quite distinct from that of respiration in which carbon dioxide is eliminated. It remained then for DE SAUSSURE (1767–1845) in Geneva to show that, in addition to the fixation of carbon, the elements of water are also employed, while from the soil various salts, including combinations of nitrogen, are obtained. But it was nearly the middle of the last century before the influence and work of LIEBIG (1803–1873) at Giessen led to a clear realization of the fundamental part played by the chlorophyll of the green leaf in making certain chemical elements available to animals. The establishment of the cosmical function of green plants — the link they supply in the circulation of the elements in nature — is an epoch in biological progress.

Enough perhaps has been said to indicate the trend of physiology away from the maze of Galenic “spirits” in which science lost itself, toward the modern viewpoint of science which assumes as its *working hypothesis* that life phenomena are an expression of a complex interaction of physico-chemical laws which do not differ fundamentally from the so-called laws operating in the inorganic world, and that the economy of the organism is in accord with the law of the *conservation of energy* — probably the most far-reaching generalization attained by science during the past century.

However, it is important to emphasize that VITALISM — the conception that life phenomena are, in part at least, the resultant of manifestations of matter and energy which transcend and differ intrinsically in kind from those displayed in the inorganic world: a denial, as it were, in the organism of the full sufficiency of known fundamental laws of matter and energy — has arisen many times in the development of biological thought. This has been either as a reaction against premature conclusions of the rapidly growing science, or from an overwhelming appreciation of the staggering complexity of life phenomena. (P. 24.)

Vitalism attained perhaps its most concrete formulation as a doctrine during the early part of the eighteenth century, in opposition to the obviously inadequate explanations which chemistry and physics could offer for the phenomena of irritability of living matter then prominently engaging the attention of biologists. The vitalists of that period abandoned almost completely all attempts to explain life processes on a physico-chemical basis, and assumed that an all-controlling, unknown, mystical, hyper-mechanical force was responsible for all living processes. It is apparent that such an assumption in such a form is a negation of the scientific method, and at once removes the problem from the realm of scientific investigation.

Of course, no biologist at the present time subscribes to vitalism in this form; some uphold vitalism — if it must still be called vitalism — in its considerably limited modern form; while all will undoubtedly admit that we are at the present time utterly unable to give an adequate explanation of the fundamental life processes in term of physics and chemistry. Whether we shall ever be able to do so is unprofitable to speculate about, though certainly the twentieth century finds few scientists who really expect a scientific explanation of life ever to be attained or who expect that protoplasm will ever be synthesized. However that may be, this much is positive: during the past fifty years some biologists have now and then thought they were on the verge of artificially creating life in the test tube, only to leave the problem, like the alchemists of old, with more respect for the complexities of protoplasmic organization and the enormous gap which separates even the simplest forms of life from the inorganic world.

4. *Histology*

Studies on the physiology of plants and animals naturally involved the progressive analysis of the physical basis of the phenomena under consideration, but the Aristotelian classification of the materials of the body as unorganized substance, homogeneous parts or tissues, and heterogeneous parts or organs, practically represented the level of analysis until the beginning of the eighteenth century. In fact it was not until the revival of interest in embryology early in the last century that the cell became a particular object of study, and attention began gradually to shift from more or less superficial details to cell organization. This culminated

in the classic investigations of two German biologists, the botanist SCHLEIDEN (1804–1881) and the zoölogist SCHWANN (1810–1882), published in 1838 and 1839. Together these studies clearly showed that all organisms are composed of units, or cells, which are at once structural entities and the centers of physiological activities. And further that the development of animals and plants consists in the multiplication of an initial cell to form the multitude of different kinds which constitute the adult. (Figs. 286, 287.)

Unquestionably the cell concept represents one of the greatest generalizations in biology, and it only needed for its consummation

FIG. 286. — Matthias Jacob Schleiden.

the full realization that the viscid, jelly-like material which zoölogists interpreted as the true living matter of animals, and the quite similar material which botanists considered the true living part of plants are practically identical. This viewpoint was crystallized in the early sixties by SCHULTZE (1825–1874) of Germany in the formulation of the protoplasm concept and thenceforth not only morphological elements—cells—but also the material of which they are composed—protoplasm—were recognized as fundamentally the same in all living beings. Indeed, the realization of a common physical basis of life in both plants and animals—a common

denominator to which all vital phenomena are reducible — gave content to the term biology and created the science of life in its modern form. (Fig. 9.)

5. *Embryology*

The cell theory resulted, as we have seen, from combined studies on the adult structure and on the development of plants and animals, and accordingly implies that the science of embryology has a history of its own. As a matter of fact, Aristotle discussed the wonder of the beating heart in the hen's egg after three days'

FIG. 287. — Theodor Schwann.

incubation, but there the subject practically rested until FABRICIUS (1537–1619) at Padua, early in the seventeenth century, published a treatise which illustrated the obvious sequence of events within the hen's egg to the time of hatching. This beginning was built upon by a pupil of Fabricius, the celebrated Harvey, who added many details of interest, though little progress in embryology was possible without the microscope.

The microscope was first turned on embryological problems by the versatile MALPIGHI in two treatises published in 1672, and at one step animal development was placed upon a plane so ad-

vanced that for over a century it was unappreciated. One conclusion of Malpighi, however, was seized upon by contemporary biologists. Apparently, unbeknown to him, some of the eggs which he studied were slightly incubated, so that he thought traces of the future organism were preformed in the egg. This error contributed to the formulation of the preformation theory, which gradually became the dominant question in embryology. (P. 262.)

As a matter of fact the time was not ripe for theories of development. The preformationists were wrong, but so were Aristotle, Harvey, and later supporters of epigenesis who went to the opposite

FIG. 288. — Karl Ernst von Baer.

extreme and denied all egg organization and therefore tried to get something out of nothing. It remained, as we know, for the present generation of embryologists to work out many of the details of the origin and organization of the germ cells, and to reach a level of analysis deep enough to suggest how "the whole future organism is potentially and materially implicit in the fertilized egg cell" and thus that "the preformationist doctrine had a well-concealed kernel of truth within its thick husk of error."

The next great advance came in the accurate and comprehensive studies of the Russian, VON BAER (1792-1876), published in the

thirties of the last century. Taking his material from all the chief groups of higher animals, von Baer founded COMPARATIVE EMBRYOLOGY. Among his achievements may be mentioned: the clear discrimination of the chief developmental stages, such as cleavage of the egg, germ layer formation, tissue and organ differentiation; the insistence on the importance of the facts of development for classification; and the discovery of the egg of Mammals. His observations on the origin and development of the germ layers, which afforded the key to many general problems of the origin of the body form, and his emphasis on the resemblance of certain embryonic stages of higher animals to the adult stages of lower forms, were crystallized by his successors, under the influence of the evolution theory, as the GERM LAYER THEORY and the RECAPITULATION THEORY. (Figs. 239, 288.)

From every point of view von Baer created an epoch in embryology just when the cell theory began to exert its influence on biological research, and thenceforth it became the problem of the embryologist to interpret development in terms of the cell. It is unnecessary to follow historically the establishment of the fact that the egg and the sperm are really single nucleated cells; that fertilization consists in the fusion of egg and sperm and the orderly arrangement of their chief nuclear contents, or chromosomes; that the new generation is the fertilized egg, since every cell of the body as well as every chromosome in every cell is a lineal descendant by division from the zygote, and so from the gametes which united at fertilization to form it. Such, however, are the chief results of cytological study since von Baer. But embryologists have not been content to employ merely the descriptive method, and the dominant note of the most modern research is physiological — the experimental study of the significance of fertilization, the dynamics of cell division, the basis of differentiation, the influence of environmental stimuli, and so on.

6. *Genetics*

The study of inheritance could be little more than a groping in the dark until embryology, under the influence of the cell theory, afforded a body of facts which clearly indicated that typically the fertilized egg is the sole bridge of continuity between successive generations. Indeed, the present science of genetics has a history largely confined to this century.

Although clearly intimated by a number of workers, the conception of the continuity of the germ plasm was first forced upon the attention of biologists and given greater precision by WEISMANN (1834–1914) of Germany in a series of essays culminating in 1892 in his volume entitled *The Germ Plasm*. He identified the chromatin material which constitutes the chromosomes of the cell nucleus as the specific bearer of hereditary characters, and emphasized a sharp distinction between germ cells and somatic cells. (Figs. 181, 289.)

While this viewpoint had been gradually gaining content and precision, the science of genetics had been advancing not only by

FIG. 289. — August Weismann.

exact studies on the structure and physiology of the germ cells, but also by statistical studies of the results of heredity — the various characters of animals and plants as exhibited in parents and offspring. The studies of this type which first attracted the attention of biologists were made by GALTON (1822–1911) of England. In the eighties and nineties of the last century, he amassed a great volume of data in regard to, for example, the stature of children with reference to that of their parents, and derived his well-known ‘laws’ of inheritance. (Fig. 182.)

But the work which eventually created the science of genetics was that of MENDEL (1822–1884) of Austria. In his studies Men-

del combined in a masterly manner the experimental breeding of pedigree strains of plants and the statistical treatment of the data thus secured in regard to the inheritance of certain characters, such as the form and color of the seeds in Peas. His work was published in 1863 in an obscure natural history periodical, and he abandoned teaching and research to become the Abbot of his monastery. Thus terminated prematurely the productive work of one of the epoch-makers of biology, and the now famous Mendelian laws of inheritance were unknown to science until 1900, when other biologists,

FIG. 290. — Gregor Johann Mendel.

coming to similar results, unearthed his forty-year-old paper. (Fig. 290.)

We have already seen that the fundamental principle of the segregation of the genes during the development of the gametes, which Mendel's work indicated, has been extended to other plants and to animals, and that instead of being, as at first thought, a principle of rather limited application, appears to be the key to all inheritance. And the present results are extremely convincing because cytological studies on the architecture of the chromosome complex of the germ cells keep pace with, and afford a picture of the physical basis of inheritance — the mechanism by which the segregation and distribution of characters by the Mendelian

formula takes place. Such is the deeply hidden kernel of truth in the old preformation theories! (Fig. 191.)

7. *Organic Evolution*

A question which has interested and perplexed thinking men of all times is how things came to be as they are to-day. The historian of human affairs attempts to trace the sequence and relationship of events from the remote past to the present. Similarly, the geologist endeavors to formulate the history of the Earth; and the biologist, the history of plants and animals on the Earth. All recognize that

FIG. 291. — Comte de Buffon.

the present is the child of the past and the parent of the future, and that past, present, and future, though causally related, are never the same. It was the Greek natural philosophers who introduced this idea of history into science and attempted to give a naturalistic explanation of the Earth and its inhabitants, and thus started the uniformitarian trend of thought which culminated in the establishment of organic evolution during the past century. (P. 342.)

Aristotle held substantially the modern idea of the evolution of life from a primordial mass of living matter to the higher forms, and placed Man at the head of animal creation. "To him belongs the God-like nature. He is preëminent by thought and volition. But although all are dwarf-like and incomplete in comparison with Man, he is only the highest point of one continuous ascent." And

evolution is still going on — the highest has not yet been attained. In looking for the effective cause of evolution Aristotle rejected the hypothesis of EMPEDOCLES (495–435 B.C.), which embodied in crude form the idea of the survival of the fittest, and substituted secondary natural laws to account for the apparent design in nature. This was a sound induction by Aristotle from his necessarily limited knowledge of nature, but had he accepted the idea of the survival of the fittest to account for adaptations in organisms, he would have been “the literal prophet of Darwinism.”

FIG. 292. — Erasmus Darwin.

The thread of continuity in evolutionary thought is not broken from Aristotle to the present, but from the strictly biological viewpoint two Frenchmen, Buffon and Lamarck, and two Englishmen, Erasmus Darwin and his grandson, Charles Darwin, stand pre-eminent.

BUFFON (1707–1788) was a peculiarly happy combination of entertainer and scientist who found expression in each new volume of his great *Natural History*. And it was largely, so to speak, between the lines of this work that Buffon's evolutionary ideas were displayed; beyond the reach, he hoped, of the censor and dilettante. It is not strange, therefore, that it is often difficult to decide just how much weight is to be placed on some of his statements; though

certainly it is not exaggerating to ascribe to him not only the recognition of the factors of geographical isolation, struggle for existence, artificial and natural selection in the origin of species, but also the propounding of a theory of the origin of variations — that the *direct* action of the environment brings about modifications in the structure of animals and plants and these are transmitted to the offspring. (Fig. 291.)

When Buffon's influence had passed its height, ERASMUS DARWIN (1731–1802) expressed consistent views on the evolution of organ-

FIG. 293. — Jean-Baptiste Lamarck.

isms, in several volumes of prose and poetry, which lead biologists to-day to recognize him as the anticipator of the Lamarckian doctrine that somatic variations arise through the reaction of the organism to environmental conditions. "All animals undergo transformations which are in part by their own exertions, in response to pleasures, and pain, and many of these acquired forms or propensities are transmitted to their posterity." (Fig. 292.)

LAMARCK (1744–1829) developed with great care the first complete and logical theory of organic evolution and is the one outstanding figure in biological uniformitarian thought between Aristotle and Charles Darwin. "For nature," he writes, "time is nothing. For all the evolution of the Earth and of living beings,

nature needs but three elements, space, time, and matter." In regard to the factors of evolution, Lamarck put emphasis on the *indirect* action of the environment in the case of animals, and the *direct* action in the case of plants. The former are induced to react and so adapt themselves, as it were; while the latter, without a nervous system, are molded directly by their surroundings. And, so Lamarck believed, such changes, somatic in origin — acquired characters — are transmitted to the next generation and bring about the evolution of organisms. (Fig. 293; p. 366.)

FIG. 294. — Charles Lyell.

Through the relative weakness of Lamarck's successors the French school of evolutionists dwindled to practical extinction; while in Germany, GOETHE (1749–1832), the greatest poet of evolution, and TREVIRANUS (1776–1837) "brilliantly carried the argument without carrying conviction," for the man and the moment must agree. Then in England the uniformitarian ideas elaborated by LYELL (1797–1875) in his *Principles of Geology* established evolution in geology and the way was paved for CHARLES DARWIN (1809–1882) to do the same for the organic world. (Figs. 294, 296; p. 367.)

True, "the idea of development saturated the intellectual atmosphere — nevertheless the elaborate and toilsome labor of thinking it through for the endless realm of nature was to be done" and Darwin did it in his *Origin of Species* which appeared in 1859. By

his brilliant, scholarly, open-minded, and cautious marshalling of the facts pointing toward the universality of variations and the mutability of species; and by the theory of natural selection on the basis of slight adaptive variations resulting in the survival of the fittest in the struggle for existence — which, strange to say, Darwin and WALLACE (1822–1913) reached simultaneously and independently — Darwin “made the old idea current intellectual coin.” (Fig. 295.)

To-day, as we know, no representative biologist questions the fact of evolution — “evolution knows only one heresy, the denial of

FIG. 295. — Alfred Russel Wallace.

continuity” — though in regard to the factors involved, there is much difference of opinion. It may well be that we shall have reason to depart widely from Darwin’s interpretation of the effective principles at work in the origin of species, but withal this will have little influence on his position in the history of biology. The great value which he placed upon facts was exceeded only by his demonstration that this “value is due to their power of guiding the mind to a further discovery of principles.” The *Origin of Species* brought biology into line with the other inductive sciences, recast practically all of its problems, and instituted new ones. Darwin beautifully and conservatively expressed this new outlook on nature in the historically important concluding paragraph of his epoch-making work:

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“It is interesting to contemplate a tangled bank, clothed with many plants of many kinds, with birds singing on the bushes, with various insects flitting about, and with worms crawling through the damp earth, and to reflect that these elaborately constructed forms, so different from each other, and dependent upon each other in so complex a manner, have all been produced by laws acting around us. These laws, taken in the largest sense, being Growth with Reproduction; Inheritance which is almost implied by reproduction; Variability from the indirect and direct action of the conditions of life, and from use and disuse: a Ratio of Increase so

FIG. 296. — Charles Darwin.

high as to lead to a Struggle for Life, and as a consequence to Natural Selection, entailing Divergence of Character and the Extinction of less-improved forms. Thus, from the war of nature, from famine and death, the most exalted object which we are capable of conceiving, namely, the production of the higher animals, directly follows. There is a grandeur in this view of life, with its several powers, having been originally breathed by the Creator into a few forms or into one; and that, whilst this planet has gone cycling on according to the fixed law of gravity, from so simple a beginning endless forms most beautiful and most wonderful have been, and are being evolved.”

APPENDIX

I. A BRIEF SYNOPTIC CLASSIFICATION OF PLANTS AND ANIMALS

A. PLANTS

Phylum 1. THALLOPHYTA: Thallus plants.

Series of the *ALGAE*. (20,000 species.)

Class I. CYANOPHYCEAE: Blue-green Algae. Oscillatoria.

Class II. CHLOROPHYCEAE: Green Algae.

Order 1. *Protococcales*: Unicellular Green Algae. Pleurococcus, Sphaerella, (Volvox). (Figs. 12, 27, 61.)

Order 2. *Confervales*: Confervas and Sea Lettuces. Ulothrix, Oedogonium, Ulva. (Figs. 62, 64, 65.)

Order 3. *Conjugales*: Pond Scums, Desmids, and Diatoms. Spirogyra, Closterium, Navicula. (Figs. 31, 63.)

Order 4. *Siphonales*: Tubular Algae. Vaucheria.

Order 5. *Charales*: Stoneworts. Chara.

Class III. PHAEOPHYCEAE: Brown Algae. Kelps and Rock-Weeds. Laminaria, Fucus, Ectocarpus, Sargassum. (Figs. 32-34, 66.)

Class IV. RHODOPHYCEAE: Red Algae. Rhodomela.

Series of the *FUNGI*. (100,000 species.)

Class V. SCHIZOMYCETES: Bacteria. (Figs. 18, 203, 204.)

Class VI. PHYCOMYCETES: Alga-like Fungi. Molds. (Fig. 20.)

Class VII. ASCOMYCETES: Sac Fungi. Mildews, Morels, Truffles, Yeasts, (Lichens). (Figs. 21, 225.)

Class VIII. BASIDIOMYCETES: Basidia Fungi. Smuts, Rusts, Mushrooms. (Figs. 19, 267.)

Phylum 2. BRYOPHYTA: Liverworts and Mosses. (20,000 species.)

Class I. HEPATICAE: Liverworts. Marchantia.

Class II. MUSCI: Mosses.

Order 1. *Sphagnales*: Peat Mosses. Sphagnum.

Order 2. *Bryales*: Common Mosses. Polytrichum. (Fig. 67.)

Phylum 3. PTERIDOPHYTA: Ferns and their allies. (5000 species.)

Class I. FILICINEAE: Common Ferns and Water Ferns. Aspidium, Marsilia. (Figs. 51, 68, 69, 71.)

Class II. EQUISETINEAE: Horsetails. Equisetum.

Class III. LYCOPODINEAE: Lycopods. Selaginella. (Fig. 72.)

Phylum 4. SPERMATOPHYTA: Seed Plants. Flowering Plants.

Subdivision 1. *GYMNOSPERMAE*: Cycads and Conifers. Pines. (600 species.)

Subdivision 2. *ANGIOSPERMAE*: The familiar flowering plants.

Class I. MONOCOTYLEDONEAE: Grasses, Palms, Lilies, Orchids. (30,000 species.) (Figs. 43, 44, 55, 81.)

Class II. DICOTYLEDONEAE: Elms, Buttercups, Pitcher Plants, Roses, Beans, Flax, Cacti, Daisies. (120,000 species.) (Figs. 37, 38, 56, 59, 60, 76.)

B. ANIMALS

Phylum 1. PROTOZOA. (15,000 species.) (Figs. 13, 25.)

Class I. SARCODINA: Amoeba, the Foraminifera. (Figs. 6, 8, 11, 244, 245.)

Class II. MASTIGOPHORA: Flagellates. Monads, Trypanosomes, Euglena, (Volvox). (Figs. 25-27, 228, 250.)

Class III. SPOROZOA: Plasmodium malariae. (Fig. 227.)

Class IV. INFUSORIA: Ciliates. Paramecium, Vorticella, Stentor. (Figs. 13, 14, 25, 229, 230.)

Phylum 2. PORIFERA: Sponges. Grantia. (2500 species.)

Phylum 3. COELENTERATA. (4500 species.)

Class I. HYDROZOA: Hydra, Obelia, Gonionemus. (Figs. 83, 158, 160.)

Class II. SCYPHOZOA: Jellyfish.

Class III. ACTINOZOA: Sea Anemones, Corals.

Phylum 4. CTENOPHORA: Sea Walnuts. (100 species.)

Phylum 5. PLATYHELMINTHES: Flatworms. (5000 species.)

Class I. TURBELLARIA: Planaria. (Figs. 157, 163.)

Class II. TREMATODA: Liver Flukes. (Fig. 251.)

Class III. CESTODA: Tapeworms. (Figs. 252, 253.)

Class IV. NEMERTINEA. (Fig. 161.)

Phylum 6. NEMATHELMINTHES: Roundworms. (1500 species.)

Class I. NEMATODA: Ascaris, Trichina, Hookworm. (Figs. 254, 255.)

Class II. ACANTHOCEPHALA: Echinorhynchus.

Class III. CHAETOGNATHA: Sagitta.

Phylum 7. TROCHELMINTHES: Rotifers. (500 species.)

Phylum 8. MOLLUSCOIDA: Polyzoans and Brachiopods. (2000 species.)

Phylum 9. ECHINODERMATA: (4000 species.)

Class I. ASTEROIDEA: Starfishes.

Class II. OPHIUROIDEA: Serpent Stars.

Class III. ECHINOIDEA: Sea Urchins. (Fig. 172.)

Class IV. HOLOTHUROIDEA: Sea Cucumbers.

Class V. CRINOIDEA: Feather Stars, Sea Lilies.

Phylum 10. ANNELIDA. Segmented Worms. (4000 species.)

Class I. ARCHIANNELIDA: Polygordius.

Class II. CHAETOPODA: Earthworms, Clamworms. (Figs. 85-87, 162, 173.)

Class III. HIRUDINEA: Leeches.

Phylum 11. MOLLUSCA. (60,000 species.)

Class I. PELECYPODA: Oysters, Clams, Scallops, Shipworm. (Fig. 93.)

Class II. AMPHINEURA: Chiton.

Class III. GASTROPODA: Snails.

Class IV. SCAPHOPODA: Dentalium. (Fig. 177.)

Class V. CEPHALOPODA: Squid, Octopus, Nautilus.

Phylum 12. ARTHROPODA.

Class I. CRUSTACEA: Barnacles, Crayfishes, Lobsters, Crabs. (16,000 species.) (Figs. 89, 90.)

Class II. TRILOBITA: Trilobites (extinct).

Class III. ONYCHOPHORA: Peripatus.

Class IV. MYRIAPODA: Centipedes, Millipedes.

Class V. INSECTA. (600,000 species.)

Order 1. *Aptera*: 'Silver-fish' (*Lepisma*), Springtails (*Podura*).Order 2. *Pseudoneuroptera*: Mayflies, Dragonflies, Termites.Order 3. *Orthoptera*: Grasshoppers, Locusts, Crickets, Stick-insects, Earwigs, Cockroaches. (Figs. 214, 216.)Order 4. *Hemiptera*: Bugs, Scale-insects, Plant Lice (Aphids), Cicadas, Lice (of Mammals). (Figs. 226, 264.)Order 5. *Neuroptera*: Ant-lions, Caddice Flies.Order 6. *Lepidoptera*: Butterflies, Moths. (Figs. 215, 259, 262, 266.)Order 7. *Diptera*: Gnats, Mosquitoes, House Flies, Crane Flies, Fleas. (Figs. 217, 246, 256, 258, 261, 265.)Order 8. *Coleoptera*: Beetles. (Figs. 260, 263-265.)Order 9. *Hymenoptera*: Bees, Wasps, Ants, Gall Flies, Ichneumons. (Figs. 217-220, 226, 265.)

Class VI. ARACHNIDA: Scorpions, Spiders. (16,000 species.)

Phylum 13. CHORDATA. (60,000 species.)

Subphylum A. *HEMICHORDA*: Dolichoglossus.Subphylum B. *UROCHORDA*: Tunicates. Styela. (1500 species.)Subphylum C. *CEPHALOCHORDA*: Amphioxus (*Branchiostoma*). (Fig. 94.)Subphylum D. *VERTEBRATA*.Class I. *CYCLOSTOMATA*: Lampreys. (Fig. 168.)Class II. *ELASMOBRANCHII*: Sharks. Dogfish. (Fig. 120.)Class III. *PISCES*: Cod, Trout, Perch. (15,000 species.) (Fig. 106.)

Class IV. AMPHIBIA: Frogs, Toads, Salamanders. (2500 species.) (Fig. 107.)

Class V. REPTILIA: Lizards, Snakes, Tortoises, Turtles, Crocodiles, Dinosaurs (extinct). (5000 species.) (Figs. 234, 235.)

Class VI. AVES: Birds. (20,000 species.)

Subclass 1. *Archaeornithes*: Archaeopteryx (extinct). (Fig. 237.)

Subclass 2. *Neornithes*.

Division A. *Ratitae*: Apteryx, Ostrich.

Division B. *Carinatae*: All familiar birds. (Fig. 243.)

Class VII. MAMMALIA. (10,000 species.)

Subclass 1. *Prototheria*: Duck-bill, Echidna.

Subclass 2. *Metatheria*: Opossums, Kangaroos.

Subclass 3. *Eutheria*: Most familiar mammals.

Order 1. *Insectivora*: Moles, Shrews, Hedgehogs, Gymnura. (Figs. 205, 209, 211.)

Order 2. *Edentata*: Sloths, Anteaters, Armadillos. (Fig. 208.)

Order 3. *Chiroptera*: Bats. (Figs. 212, 231.)

Order 4. *Rodentia*: Rats, Mice, Rabbits, Squirrels, Beavers, Porcupines. (Fig. 108.)

Order 5. *Carnivora*: Cats, Dogs, Bears, Seals, Walruses. (Fig. 104.)

Order 6. *Cetacea*: Whales, Porpoises, Dolphins. (Fig. 210.)

Order 7. *Sirenia*: Manatee.

Order 8. *Ungulata*: Horses, Tapirs, Rhinoceroses, Camels, Oxen, Antelopes, Giraffes, Pigs, Hippopotami, Elephants. (Figs. 238, 242.)

Order 9. *Primates*: (Fig. 232.)

a. Lemurs, Marmosets.

b. Monkeys, Orangs, Gorillas, Chimpanzees.

c. Man (*Homo sapiens*).

FIG. 297. — Probable relationships of the chief groups of the animal kingdom. (From Newman, after Allee.)

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III. GLOSSARY

ABIOTENESIS. The abandoned idea that living matter may arise at the present time from non-living without the influence of the former. *See* Biogenesis.

ABSORPTION. The passage of nutritive and other fluids into living cells.

ACOELOMATE. Not possessing a coelom, or body cavity; *e.g.*, Hydra.

ACQUIRED CHARACTER. A modification of body structure or function which arises during individual life as a result of environmental influences.

ADAPTATION. The reciprocal fitness of organism and environment; a structure or reaction fitted for a special environment; the process by which an organism becomes fitted to its surroundings.

ADRENALS. Suprarenal bodies. Ductless glands situated near the kidneys. Secretion supplies a hormone known as adrenin.

ADVENTITIOUS. Not in the usual position, *e.g.*, aerial roots.

AEROBE. An organism requiring free oxygen. *See* Anaerobe.

AFFERENT ROOT. Dorsal, or posterior, root of certain cranial and all spinal nerves through which sensory nerve impulses enter the brain and spinal cord. *See* Efferent Root.

ALGAE. A heterogeneous group of lower plants in which the body is unicellular or consists of a thallus; *e.g.*, Pleurococcus, Sphaerella, Spirogyra, Seaweeds.

ALLANTOIS. An embryonic membrane of higher Vertebrates, chiefly respiratory in function.

ALLELOMORPHS. Genes similarly situated on homologous chromosomes which produce 'alternative' characters.

ALTERNATION OF GENERATIONS. The alternate succession of a sexual and an asexual generation in the life history; *e.g.*, Moss, Obelia.

ALTERNATIVE INHERITANCE. Typical Mendelian inheritance.

AMINO ACID. Components of proteins. Organic acids in which one hydrogen atom is replaced by the amino group (NH_2). Monoamino acids; *e.g.*, Glycine ($\text{CH}_2\text{NH}_2\text{COOH}$). Diamino acids; *e.g.*, Lysine ($\text{H}_2\text{NCH}_2\text{CH}_2\text{CH}_2\text{CHNH}_2\text{COOH}$).

AMNION. A delicate membrane enclosing the developing embryos of Reptiles, Birds, and Mammals.

AMOEBOID. Usually applied to the flowing movements of a cell, as in the Amoeba and white blood corpuscles.

AMPHIMIXIS. The mingling of the germ plasma of two gametes in the zygote.

ANABOLISM. The constructive phase of metabolism. *See* Katabolism.

- ANAEROBE.** An organism not requiring free oxygen; *e.g.*, certain Bacteria and parasitic Worms. *See* Aerobe.
- ANALOGY.** Structural resemblance, usually superficial, due to similarity of function; *e.g.*, wing of Butterfly and Bird. *See* Homology.
- ANAPHASE.** Period in mitosis during which the daughter chromosomes move toward the respective centrosomes. *See* Telophase.
- ANATOMY.** The structure of organisms, especially as revealed by dissection. *See* Morphology.
- ANTHER.** The part of the stamen which contains the pollen sacs (microsporangia) in Seed Plants.
- ANTHERIDIUM.** The organ in plants, such as the Mosses and Ferns, in which the male gametes arise.
- ANUS.** Terminal orifice of the alimentary canal. Opening of the large intestine either on the surface of the body (Man) or into the cloaca (Frog).
- AORTA.** A great trunk artery carrying blood away from the heart. *See* Dorsal Aorta.
- AORTIC ARCHES.** Arteries arising from the ventral aorta and supplying the gills in aquatic Vertebrates. Undergo many modifications in the ascending series of air-breathing Vertebrates.
- APHIDS.** Small sucking Insects; *e.g.*, the green Plant Lice of garden shrubs.
- ARCHEGONIUM.** The organ in plants, such as the Mosses and Ferns, in which the female gamete (egg) arises.
- ARTERY.** A blood vessel carrying blood away from the heart.
- ARTHROPODA.** Phylum of Invertebrates. Includes the Crustacea, Insecta, Arachnida, etc.
- ASTER.** Radiations surrounding the centrosome during cell division.
- ATAVISM.** Appearance of grandparental characters in an individual. *See* Reversion.
- AUTONOMIC SYSTEM.** System of outlying ganglia and nerves which communicates with the central nervous system *via* the roots of the spinal and cranial nerves. Innervates chiefly the involuntary muscles of blood vessels, digestive organs, etc. Sympathetic system.
- AXON.** A nerve fiber conducting impulses away from the cell body. Dendrites conduct toward the cell body. *See* Neuron.
- BAST.** The fibrous portion of the phloem.
- BIENNIAL.** A plant which completes its life history in two years, usually reproducing in the second.
- BILE DUCT.** Tube which conveys the secretions (bile) of the liver to the small intestine. Usually unites with the pancreatic duct to form a common duct which enters the intestine.
- BINARY FISSION.** The division of a cell, especially a unicellular organism, into two daughter cells; *e.g.*, in Paramecium.

BINOMIAL NOMENCLATURE. The accepted scientific method of designating organisms by two Latin or Latinized words, the first indicating the genus and the other, the species; *e.g.*, the Dog, *Canis familiaris*; Man, *Homo sapiens*.

BIOGENESIS. The established doctrine that all life arises from preëxisting living matter. *See* Abiogenesis.

BIOGENETIC LAW. *See* Recapitulation theory.

BIOLOGY. Study of matter in the living state, and its manifestations.

BIPARENTAL. Involving two progenitors, male and female.

BIRAMOUS. Comprising two branching parts; *e.g.*, abdominal appendages (swimmerets) of the Crayfish.

BLASTOCOEL. The cavity within the blastula. Segmentation cavity.

BLASTOPORE. The opening to the exterior from the enteric pouch of a gastrula.

BLASTULA. The stage following cleavage when the cells are arranged in a single layer to form a hollow sphere.

BLENDING INHERITANCE. Apparent fusion of parental characters in the offspring so that a more or less intermediate condition arises; *e.g.*, skin color of mulattoes.

BLOOD CORPUSCLES. Detached cells present in the fluid plasma of the blood. Two principal kinds, red and white.

BUCCAL CAVITY. Mouth cavity.

BUD. Growing point of shoot. An undeveloped branch. Leaf buds form stem and leaves; mixed buds, both leaves and flowers; flower buds, flowers only.

CALCIFEROUS GLANDS. Glands opening into the esophagus of the Earthworm which secrete calcium carbonate, probably to neutralize acidity of food.

CALYX. The outer whorl of modified leaves composing a typical flower. Usually green.

CAMBium. Layer of actively dividing cells which, in the dicotyledonous Seed Plants, is situated between xylem and phloem of vascular bundles, and forms a thin cylinder between wood and bark.

CARBOHYDRATES. Compounds of carbon with hydrogen and oxygen, the hydrogen and oxygen being in the same proportion as in water (H_2O).

CARPEL. One of the innermost whorl of floral leaves which bear the megasphores. A simple pistil or an element of a compound pistil. A megasporophyll.

CASTRATION. Removal of the gonads, especially of the male.

CATALYSIS. The acceleration of a chemical reaction by a substance (*e.g.*, an enzyme) which itself remains unchanged.

CELL. A structural and physiological unit mass of protoplasm, differentiated into cytoplasm and nucleus.

CELL SAP. Water, with solutes, under pressure in a large vacuole in the cytoplasm of certain types of plant cells. Effects cell turgor.

CELLULOSE. A carbohydrate which characteristically forms the walls of plant cells.

CENTROSOME. A minute body situated in the center of the aster and active during cell division.

CHELIPED. The first thoracic appendages, or walking-legs, of the Crayfish and its allies. The 'pincer.'

CHEMOTAXIS. Movements of cells (*e.g.*, sperm, Paramecium) in response to chemical stimuli. Chemotropism is a theory of chemotaxis.

CHLORENCYMA. The chlorophyll-bearing tissue of higher plants.

CHLOROGOGEN CELLS. Outer layer of intestine of Earthworm. Probably excretory in function.

CHLOROPHYLL. The characteristic green coloring matter of plants, through which photosynthesis takes place.

CHLOROPLASTID. The special cytoplasmic bodies containing chlorophyll or functionally similar pigment.

CHORDATE. An animal whose primary axial skeleton consists temporarily or permanently of a notochord. All Vertebrates are Chordates, but the lowest Chordates are not Vertebrates. *See* Appendix I.

CHORION. External embryonic membrane of Mammals.

CHROMATIN. A deeply staining substance characteristic of the nucleus, forming chromosomes, etc. *See* Germ Plasm.

CHROMOSOME. One of the deeply staining bodies into which the chromatic network of the nucleus becomes visibly resolved during mitosis. A linkage group of genes. *See* Germ Plasm.

CILIA. Delicate protoplasmic projections from a cell, which lash in unison and propel the cell in the water (*e.g.*, Paramecium), or move particles over the cell surface (*e.g.*, cells lining various tubes in multicellular forms).

CLASS. In classification, a main subdivision of a phylum. *See* Order.

CLEAVAGE. Cell divisions which transform the egg into the blastula stage during development.

CLOACA. A cavity at the posterior end of the Vertebrate body, into which the intestine, urinary, and reproductive ducts open. Not present in most Mammals.

COCHLEA. The portion of the ear, in communication with the sacculus, which is the essential organ of hearing in the higher Vertebrates.

COELOM. The body cavity, lying between the digestive tract and the body wall. Lined with mesodermal tissue.

COELOMATE. Possessing a coelom, or body cavity; as in all the chief groups of animals above the Coelenterates. The latter are acoelomate.

COELOMIC EPITHELIUM. *See* Peritoneum.

- COLLOID.** A state of matter in which a substance is finely divided into particles larger than one molecule and suspended in another substance, semifluid or fluid.
- COLONY.** An aggregation, or intimate association of several or many similar individuals to form a superior unit.
- COMBINATION.** Heritable variation due to recombinations of genes at maturation or fertilization.
- CONJUGATION.** Union (usually temporary) of two cells, resulting in sexual phenomena; *e.g.*, in *Paramecium*. *See* Endomixis.
- CONSERVATION OF ENERGY.** The 'law' that the total energy of the universe is constant, none being created or destroyed but merely transformed from one form to another. Matter, according to recent work in physics, is one of the forms that energy may assume.
- CONTRACTILE VACUOLE.** A reservoir in unicellular organisms (*e.g.*, *Paramecium*) in which water and waste products of metabolism collect and are periodically expelled to the exterior.
- CORM.** A solid bulb-like expansion of a plant stem below the surface of the ground. A bulb is an underground storage leaf bud.
- COROLLA.** The whorl of modified leaves immediately within the calyx of a flower. The petals collectively.
- CORTEX.** The cylinder between the outer and central cylinders in root and stem of the higher plants. Part of the Vertebrate brain.
- COTYLEDON.** A seed leaf. The first leaf (in Monocotyledons) or pair of leaves (in Dicotyledons) of the young sporophyte within the seed.
- CRANIAL NERVES.** Nerves which arise from the brain.
- CRANIUM.** The protective case enclosing the brain.
- CREATININE.** A nitrogenous waste product. Present in small quantity in human urine.
- CRETIN.** A defective individual, due to a deficiency of thyroid secretion.
- CROSSING-OVER.** The rearranging of linked characters as a result of the exchange of genes during synapsis of chromosomes.
- CRURA CEREBRI.** Thickenings of ventral surface of mid-brain.
- CRUSTACEA.** A group of Arthropoda, including Crayfish, Crabs, etc.
- CUTANEOUS.** Pertaining to the skin.
- CUTICLE.** The outermost lifeless layer of organisms. *See* Epidermis.
- CYST.** A resistant envelope formed about an organism (*e.g.*, many Protozoa) during unfavorable conditions or reproduction.
- CYTOLOGY.** The science of cell structure and function.
- CYTOPLASM.** Protoplasm of a cell exclusive of nucleus. Cytosome.
- DARWINISM.** Charles Darwin's theory of Natural Selection. Erroneously used as synonymous with organic evolution.
- DECAY.** Chemical decomposition involving putrefaction or other types of fermentation.
- DENDRITE.** *See* Axon.

- DENITRIFYING BACTERIA.** Types of Bacteria which break down compounds of nitrogen and set free the nitrogen to the atmosphere.
- DERMAL.** Pertaining to the skin. The dermis is the inner layer of the Vertebrate skin. *See* Epidermis.
- DICOTYLEDONS.** The higher of the two great groups of the familiar Seed Plants, a characteristic of which is the presence of two seed leaves, or cotyledons. Contrasted with the Monocotyledons having one seed leaf.
- DIFFERENTIATION.** A transformation from relative homogeneity to heterogeneity, involving the production of specific substances or parts from a general substance or part. Specialization.
- DIFFUSION.** Intermingling of two substances due to migration of their molecules. Pressure exerted by molecules in diffusion is osmotic pressure. *See* Osmosis.
- DIGESTION.** Chemical simplification of complex food substances so that absorption can take place.
- DIHYBRID.** Progeny of parents differing in two given characters.
- DIPLOID.** Maximum (duplex) number of chromosomes in the life history of a given species. *See* Haploid.
- DIVISION OF LABOR.** Allocation of special functions to special parts which coöperate toward the unity of the whole.
- DOMINANT CHARACTER.** One of a pair of alternative characters which appears to the exclusion of the other (recessive) character when both are present.
- DORSAL AORTA.** Chief artery distributing pure blood to the body. Ventral aorta carries blood from heart to gill arteries in Fishes.
- DUCTLESS GLAND.** An organ whose function is to elaborate and secrete a hormone directly into the blood. An endocrine gland.
- ECOLOGY.** The study of the relations of the organism to environing conditions, organic and inorganic.
- ECTODERM.** The primary tissue comprising the surface layer of cells in the gastrula. *See* Germ Layer.
- ECTOPLASM.** Modified surface layer of cytoplasm of a cell. *See* Endoplasm.
- EFFERENT ROOT.** Ventral, or anterior, root of certain cranial and all spinal nerves through which motor nerve impulses leave the brain and spinal cord. *See* Afferent Root.
- EMBRYOLOGY.** Study of the early developmental stages, or embryos, of individual organisms.
- EMBRYO SAC.** Megaspore of the Seed Plants.
- ENCYSTMENT.** The formation of a resistant covering, or cyst wall, about an organism; *e.g.*, Sphaerella.
- ENDOCRINE GLAND.** *See* Ductless Gland.
- ENDODERM.** The primary tissue comprising the inner layer of cells in the gastrula, and in subsequent stages forming the lining of the essential parts of the digestive tract and its derivatives. *See* Germ Layer.

- ENDOMIXIS.** A nuclear reorganization process in Protozoa, *e.g.*, Paramecium, which does not involve the coöperation of two cells (as in conjugation) and therefore is without synkaryon formation.
- ENDOPLASM.** The inner cytoplasm surrounding the nucleus; *e.g.*, in Amoeba, Paramecium. *See* Ectoplasm.
- ENDOPODITE.** The inner of the two distal parts of the typical biramous Crustacean appendage. *See* Protopodite and Exopodite.
- ENDOSKELETON.** An internal living skeleton affording support and protection, as well as levers for the attachment of muscles. Characteristic of Vertebrates.
- ENDOSPERM.** A tissue, containing reserve food materials, formed within the embryo sac.
- ENERGY.** *See* Potential Energy.
- ENTERIC CAVITY.** The digestive cavity of the gastrula stage, and of simple Metazoa, *e.g.*, Hydra. Cavity of the enteron.
- ENZYMES.** Complex chemical substances of organisms which bring about by catalytic action many of the chemical processes of the body; *e.g.*, digestion. *See* Catalysis.
- EPIDERMIS.** The outer cellular layer, *e.g.*, of skin or leaf.
- EPIGENESIS.** Development from absolute or relative simplicity to complexity. *See* Preformation.
- EPITHELIUM.** A layer of cells covering an external or internal surface, including the essential secreting cells of glands.
- EQUATION DIVISION.** A typical division of the nucleus involving division of the chromosomes. *See* Reduction Division.
- EQUATORIAL PLATE.** The equator of the spindle with its group of chromosomes during the metaphase of mitosis.
- ESOPHAGUS.** Tubular passage from pharynx to stomach.
- EUGENICS.** The system of improving the human race by breeding the best. "The science of being well born." *See* Euthenics.
- EUSTACHIAN TUBE.** Passage connecting the Vertebrate middle ear with the pharynx. Remnant of the most anterior gill slit, represented in present-day Sharks by the 'blow-hole,' or spiracle.
- EUTHENICS.** The system of improving the human race by good environment. *See* Eugenics.
- EUTHERIA.** The highest of the three subclasses of Mammals, including all the familiar forms. *See* Appendix I, Classification.
- EVOLUTION, ORGANIC.** Present-day organisms are the result of descent with change from those of the past.
- EXCRETION.** The elimination of waste products of metabolism. A waste product. *See* Secretion.
- EXOPODITE.** The outer of the two distal parts of the typical, biramous, Crustacean appendage. *See* Protopodite and Endopodite.

EXOSKELETON. A non-living external skeleton chiefly for protection. The characteristic skeleton of Invertebrates; *e.g.*, Crayfish.

EXTERNAL RECEPTORS. Sense organs upon the surface of the body. *See* Internal Receptors.

FAMILY. In classification, a main subdivision of an order. *See* Genus.

FATS. One of the chief groups of foodstuffs. Organic salts consisting of the glycerol radical (C_3H_5), the basic part, combined with a fatty acid; *e.g.*, mutton tallow is chiefly the fat stearin ($C_{57}H_{110}O_6$) = glycerin plus stearic acid. More oxidizable than carbohydrates.

FERMENTATION. The transformation of organic substances chiefly through the activity of ferments, or enzymes, derived from living organisms. *See* Putrefaction.

FERTILIZATION. The union of male and female gametes, especially their nuclei, by which the chromatin complex of each is arranged to form the composite nucleus (syngaryon) of the zygote.

FETUS. An embryo of a Vertebrate, in egg or uterus.

FLAGELLUM. A whip-like prolongation of the cytoplasm, the movements of which usually effect the locomotion of the cell; *e.g.*, Sphaerella, Volvox, Euglena.

FLOWER. A group of sporophylls and accessory structures, as in the Seed Plants.

FLUCTUATIONS. Relatively slight variations, usually forming a finely graded series, always found in organisms; may be either modifications or combinations, but usually the former.

FROND. Fern leaf, usually both vegetative and spore-producing.

FRUIT. The ripened ovule case and contents, together with any structures which by adhesion become an integral part of it.

GALL BLADDER. Receptacle near the liver for the temporary storage of bile.

GAMETANGIUM. A gamete-producing organ, especially in the lower plants.

GAMETE. A cell which unites with another at fertilization to form a zygote. Egg or sperm.

GAMETIC NUCLEI. Nuclei of gametes that unite to form the syngaryon, or nucleus of the zygote.

GAMETOPHYTE. The sexual, gamete-bearing generation in plants.

GANGLION. A group of nerve cells, chiefly the cell bodies, with supporting cells.

GASTRIC VACUOLE. A droplet of fluid enclosing ingested food, in which digestion occurs; *e.g.*, in Amoeba and Paramecium.

GASTROLITHS. Calcareous bodies found at certain times in the lateral walls of the stomach of the Crayfish. Probably represent the storage of material for the exoskeleton.

GASTRULA. A stage in animal development in which the embryo consists of a two-layered sac, ectoderm and endoderm, enclosing the enteric cavity which opens to the exterior by the blastopore.

- GENE. Independently inheritable factor or element in the chromosomes which makes possible a particular character in the organism.
- GENETICS. The science of heredity.
- GENOTYPE. The fundamental hereditary constitution of an organism or group of organisms. The gene complex of an organism. *See* Phenotype.
- GENUS. In classification, a main subdivision of a family. *See* Species.
- GERMINAL CONTINUITY. The concept of an unbroken stream of germ plasm from the beginning of life, from which each generation is derived.
- GERM LAYER. A primary tissue (ectoderm, endoderm, or mesoderm) in the embryo from which the tissues and organs of the adult animal develop.
- GERM LAYER THEORY. The doctrine that the germ layers are fundamentally similar throughout the Metazoa and that homologous structures in various animals are derived during development from the same germ layer.
- GERM PLASM. The physical basis of inheritance. The chromatin which forms the specific bond of continuity between parent and offspring. Contrasted with soma or somatoplasm.
- GILL SLITS. Paired lateral openings leading from the anterior end of the alimentary canal to the exterior for the exit of the respiratory current of water. Permanent or embryonic characters of Vertebrates. Branchial clefts.
- GLAND. One cell or a group of many epithelial cells which elaborate materials and secrete the product for the use of the organism.
- GLOTTIS. The opening from the pharynx into the tube (trachea) leading to the lungs.
- GLYCOGEN. So-called animal starch. Sugar is stored as glycogen in liver and muscle cells.
- GOLGI BODIES. Formed elements in the cytoplasm; apparently active chemically.
- GONAD. Ovary or testis.
- GRAY CRESCENT. Localized organ-forming substance in Frog's egg.
- GUSTATORY. Relating to the sense of taste.
- HAPLOID. The reduced (one-half) number (simplex group) of chromosomes. *See* Diploid.
- HEMOGLOBIN. Complex chemical compound, in the red blood corpuscles, which enters into a loose combination with oxygen, becoming oxyhemoglobin.
- HEPATIC PORTAL SYSTEM. Non-oxygenated but food-laden blood from digestive tract passes to the liver by the *hepatic portal vein*. Oxygenated blood reaches liver by the hepatic artery. All leaves by hepatic vein. Thus there is a double blood supply to liver in all Vertebrates.
- HEREDITY. The transmission of characters from parent to offspring by the germ cells.

HERMAPHRODITE. An organism bearing both male and female reproductive organs; *e.g.*, Hydra and Earthworm.

HETEROSPORY. The condition of producing two kinds of spores, megaspores and microspores, as in the higher plants.

HETEROZYGOUS. Producing gametes which fall into two numerically equal classes with respect to the genes (allelomorphs) for a pair of 'alternative' characters. Hybrid. *See* Homozygous.

HISTOLOGY. The science which treats of animal and plant tissues. Microscopic anatomy.

HOLOPHYTIC. Type of nutrition involving photosynthesis. Characteristic of green plants. *See* Holozoic and Saprophytic.

HOLOZOIC. Type of nutrition involving the ingestion of solid food. Characteristic of animals. *See* Holophytic and Saprophytic.

HOMOLOGOUS CHROMOSOMES. The members of a pair of chromosomes, of a duplex group, one paternal and the other maternal in origin, which bear the same or allelomorphic genes. *See* Synaptic Mates.

HOMOLOGOUS GENES. Genes similarly situated on homologous chromosomes. *See* Allelomorph.

HOMOLOGY. Fundamental structural similarity, regardless of function, due to descent from a common form; *e.g.*, wing of Bird and fore leg of Dog.

HOMOTHERMAL. Animals provided with a mechanism which maintains the body at a practically constant temperature, usually higher than that of the environment; *e.g.*, the 'warm-blooded' animals, or Birds and Mammals.

HOMOZYGOUS. Producing gametes, all of which bear the gene for the same one of a pair of 'alternative' characters. *See* Heterozygous.

HORMONE. An internal secretion, frequently from a ductless gland, which is distributed by the blood and influences the activities of one or more parts of the body.

HOST. An organism in, or on which a parasite subsists.

HYALOPASM. The clear ground-substance of protoplasm.

HYBRID. The progeny of parents which differ in regard to one or more characters. A heterozygote.

HYDROIDS. A group of animals (Coelenterates) exhibiting alternation of generations; *e.g.*, Obelia.

IMMUNITY. Resistance of the body to infection by disease-producing organisms. Exemption from disease.

INFUNDIBULUM. A funnel-like outgrowth from the ventral wall of the diencephalon. *See* Pituitary Body.

INTERCELLULAR DIGESTION. Digestion by the secretion of enzymes into a digestive cavity; *e.g.*, in Earthworm and Man. *See* Intracellular Digestion.

INTERNAL RECEPTORS. Sense organs within the body. *See* External Receptors.

INTERNAL SECRETION. *See* Hormone and Ductless Gland.

- INTESTINE.** Portion of the alimentary canal. In higher forms, portion from pyloric end of stomach to cloaca or anus. Usually divided into small and large intestine.
- INTRACELLULAR DIGESTION.** Digestion of food within the cell itself; *e.g.*, in Paramecium and to some extent in the endoderm cells of Hydra. *See* Intercellular Digestion.
- INTUSSUSCEPTION.** Interstitial growth by the addition of new particles throughout the whole mass of protoplasm. Contrasted with growth by accretion, or the deposition of particles on the surface as in crystals.
- INVAGINATION.** Sinking or growing in of a portion of the surface of a hollow body; *e.g.*, during transformation of blastula into gastrula.
- INVERTEBRATE.** Metazoa without a notochord or a vertebral column.
- IRRITABILITY.** The power of responding to stimuli, exhibited by all protoplasm.
- KARYOLYMPH.** The more fluid material of the nucleus in contrast with the linin and chromatin.
- KARYOSOME.** An aggregation of part of the chromatin material within the nucleus. A 'net-knot.' *See* Nucleolus.
- KATABOLISM.** The destructive phase of metabolism. *See* Anabolism.
- KINETIC ENERGY.** Energy possessed by virtue of motion; *e.g.*, union of C with O₂ transforms chemical potential energy into kinetic energy, *i.e.*, heat, etc. *See* Potential Energy.
- LACTEALS.** Lymphatic vessels of the small intestine.
- LAMARCKISM.** Essentially the doctrine of the inheritance of modifications, or acquired characters.
- LARVA.** An immature stage in the life history of certain animals, usually active and differing widely in appearance from the adult; *e.g.*, caterpillar of a Butterfly, tadpole of Frog.
- LENTICELS.** Stem structures, originating as stomata, that provide for the entrance and exit of gases more freely than other parts of the bark.
- LININ.** The reticulum of the nucleus, upon which the chromatin appears to be distributed. Sometimes regarded as a non-stainable form of chromatin.
- LINKAGE.** Tendency for certain characters to be inherited in groups, probably because the genes for the characters are closely associated on the same chromosome.
- LYMPH.** Essentially plasma and white blood corpuscles which have passed through the capillary walls to supply the milieu of the tissue cells.
- MACRONUCLEUS.** The large 'somatic' nucleus in Infusoria with dimorphic nuclei; *e.g.*, in Paramecium. *See* Micronucleus.
- MALTOSE.** A double sugar derived from starch by hydrolysis during digestion.
- MANDIBLES.** Jaws.
- MATTER.** *See* Conservation of Energy.

- MATURATION.** Final stages in the formation of the germ cells, involving chromosome reduction (meiosis).
- MAXILLIPEDS.** The three anterior pairs of appendages of the thorax of the Crayfish.
- MECHANISM.** The doctrine that the phenomena of life are interpretable in terms of the laws of matter and energy which hold in the realm of the non-living. *See* Vitalism.
- MEDUSA.** Sexual, gonad-bearing generation of hydra-like animals, the Hydroids, and some other Coelenterates.
- MEDULLARY RAYS.** *See* Pith Rays.
- MEGASPORE.** The large spore, developed in a megasporangium, which in heterosporous plants forms a female gametophyte.
- MEGASPOROPHYLL.** A modified leaf of a heterosporous sporophyte which produces megaspores. A carpel.
- MERISTEM.** Formative (embryonic) tissue with rapidly dividing cells, as in cambium and growing points of plants.
- MESODERM.** A primary tissue, or germ layer, of animals which develops between the ectoderm and endoderm. *See* Germ Layer.
- MESOGLOEA.** The non-cellular layer between ectoderm and endoderm in Hydra and other Coelenterates.
- MESOPHYLL.** Tissue of the leaf, between upper and lower epidermis, exclusive of the vascular bundles (veins).
- METABOLISM.** The sum of the physico-chemical processes in organisms, involving the building up, maintenance, and breaking down of the living matter and its constituents. *See* Anabolism and Katabolism.
- METAMORPHOSIS.** A more or less abrupt transition from one developmental stage to another; *e.g.*, transformation of larva into adult during the life history of a Butterfly or Frog.
- METAPHASE.** Climax of mitosis involving the separation of the halves of the longitudinally split chromosomes arranged in the equatorial plate. *See* Anaphase.
- METAPHYTA.** Multicellular plants.
- METAPLASM.** Lifeless inclusions in cytoplasm; *e.g.*, yolk granules, etc.
- METAZOA.** Multicellular animals.
- MICRONUCLEUS.** The small 'germinal' nucleus in Infusoria with dimorphic nuclei; *e.g.*, *Paramecium caudatum* has one, *P. aurelia* and *P. calkinsi* have two, and *P. woodruffi* and *P. polycaryum* have several micronuclei. *See* Macronucleus.
- MICROSPORANGIUM.** A sporangium which bears microspores; *e.g.*, pollen sacs in anther of stamen.
- MICROSPORE.** The small spore, of heterosporous plants, which forms a male gametophyte. A pollen grain.
- MICROSPOROPHYLL.** A modified leaf, of a heterosporous sporophyte, which produces microspores. A stamen.

- MITOCHONDRIA.** Bodies in the cytoplasm which apparently contribute to specific chemical processes.
- MITOSIS.** The typical process of cell division.
- MODIFICATIONS.** *See* Acquired Characters.
- MONOCOTYLEDON.** *See* Dicotyledon, and Appendix I.
- MONOHYBRID.** The progeny of parents differing in regard to one given character.
- MORPHOGENESIS.** The embryological development of the form and structure of an organism.
- MORPHOLOGY.** The science of the form of animals and plants.
- MOZAIC INHERITANCE.** Inheritance of a character in part from each parent but without blending.
- MUTATION.** A heritable variation due to a fundamental change in the constitution of the germ plasm, independent of the normal processes of segregation and crossing-over.
- MYOTOMES.** Muscle segments in body wall of lower Vertebrates and embryos of higher forms.
- NATURAL SELECTION.** The processes occurring in nature which result in the "survival of the fittest" individuals and the elimination of those less adapted to the conditions imposed by their environment and mode of life. Essence of the Darwinian theory of evolution.
- NEPHRIDIUM.** A tubular excretory organ; *e.g.*, in Earthworm.
- NERVE.** Essentially a group or cable of parallel nerve fibers bound together. *See* Axon.
- NEURAL CANAL.** The tube in which the brain and spinal cord lie. Formed by the neural arches and centra of the vertebrae.
- NEURAL TUBE.** A tube derived from the ectoderm and forming the brain and spinal cord in Vertebrates.
- NEURENTERIC CANAL.** Temporary passage between cavity of enteron and neural tube in Vertebrate embryos.
- NEURON.** A nerve cell, comprising cell body and cytoplasmic processes. *See* Axon.
- NITRIFYING BACTERIA.** Types of Bacteria which, in the process of their nutrition, change ammonia (NH_3) into compounds with the NO_2 radical (nitrites), and change nitrites into compounds with the NO_3 radical (nitrates.)
- NITROGEN-FIXING BACTERIA.** Types of Bacteria which take free atmospheric nitrogen and combine it with oxygen so that nitrates available for green plants are formed. Found in the soil and in tubercles on rootlets of various leguminous plants, *e.g.*, Beans, Clover, Alfalfa.
- NOTOCHORD.** An axial cord of cells about which the backbone is formed. Gradually replaced by the centra of the vertebrae in the ascending series of Vertebrates.

NUCELLUS. The megasporangium of Seed Plants. *See* Ovule and Embryo Sac.

NUCLEOLUS. A spherical body of achromatic material within the nucleus. Plasmosome. *See* Karyosome.

NUCLEUS. A specialized protoplasmic body in all typical cells. Most characteristic element is chromatin. *See* Cytoplasm.

OLFACTORY. Relating to the sense of smell.

ONTOGENY. The developmental history of the individual. *See* Phylogeny.

OÖCYTE. The ovarian egg before maturation.

OÖGENESIS. The development of the mature egg from a primordial germ cell.

OPTIC LOBES. Thickenings of the dorsal surface of the mid brain.

ORDER. In classification, a main subdivision of a class. *See* Family.

ORGAN. A complex of tissues for the performance of a certain function; *e.g.*, the heart.

OSMOSIS. Diffusion of dissolved substances through a semi-permeable membrane. Osmotic pressure may be considered as a result of the inhibited power of diffusion of a dissolved substance — inhibited because the membrane is *semi*-permeable. The physical phenomena of diffusion and osmosis are complicated in living cells by the fact that their limiting surfaces may function now as permeable and again as semi-permeable membranes, *i.e.*, permitting water but not the substance in solution to pass through. *See* Diffusion.

OSTEOLOGY. The study of the Vertebrate skeleton.

OVULE. The body which after fertilization of the egg becomes a seed. The ovule consists of protective envelopes (integument) enclosing the nucellus (megasporangium) with the embryo sac (megaspore).

OVULE CASE. The base of the pistil in which ovules arise. 'Ovary.'

OVUM. Egg. Female gamete.

OXIDATION. The combination of any substance or its constituent parts with oxygen. Combustion.

PALEONTOLOGY. The science of extinct animals and plants represented by fossil remains.

PARASITE. An organism which secures its livelihood directly at the expense of another living organism, on or in whose body it lives.

PARTHENOGENESIS. Development of an egg without fertilization.

PATHOGENIC. Disease-producing, especially in regard to the relation of a parasite to its host.

PENTADACTYL. Having five fingers or toes; typical Vertebrate limb.

PERICARDIUM. Peritoneum lining the pericardial cavity containing the heart.

PERISTALSIS. Rhythmical contractions of the wall of the alimentary canal which force the food along.

PERITONEUM. Membrane lining coelom of Vertebrates. Consists of an outer layer of connective tissue next to the muscles of body wall and an inner layer of coelomic epithelium which forms the innermost layer of body wall.

PETIOLE. A leaf stalk.

PHARYNX. Region of alimentary canal between buccal cavity, or mouth, and esophagus. Throat.

PHENOTYPE. The somatic, or expressed, characters of an organism or group of organisms irrespective of those potential in their germ cells. *See* Genotype.

PHLOEM. The outer part of a vascular bundle. 'Inner bark.'

PHOTOSYNTHESIS. Process by which complex compounds are built up from simple elements through the energy of sunlight absorbed by chlorophyll, or a functionally similar pigment.

PHYLOGENY. The ancestral history of the race. *See* Ontogeny.

PHYLUM. In classification, a main subdivision of the animal or plant kingdom. *See* Class.

PHYSIOLOGY. The study of the functions of animals and plants. The mechanical and chemical engineering of organisms.

PINEAL BODY. An outgrowth from the upper wall of the diencephalon. The vestige of an additional pair of eyes possessed by the ancestors of existing Vertebrates. Possibly functions as an endocrine gland in Mammals. Brow-spot of Frog.

PISTIL. Organ of the flower, composed of ovule case, style, and stigma. *See* Carpel.

PITH. Middle part of the central cylinder of a plant shoot. Functions largely for the storage of water and food.

PITH RAYS. Extensions of the pith which radiate between the vascular bundles to the bark. Medullary rays.

PITUITARY BODY. A gland-like body under the brain, formed of tissue from the nervous system and from the alimentary canal.

PLACENTA. A Mammalian organ adapted for the interchange of all nutritive, respiratory, and excretory materials between the embryo (fetus) and mother. It also serves as an organ of attachment. In the higher Mammals it is composed of both fetal and maternal tissues. *See* Umbilical Cord.

PLASMA. Liquid portion of the blood.

PLASMA MEMBRANE. Living cell membrane, as distinguished from the cell wall which may also be present.

PLASTID. *See* Chloroplastid.

PLEXUS. Intercommunication of fibers from one nerve with those of another to form a network; *e.g.*, sciatic plexus.

POLAR BODIES. *See* Polocytes.

- POLE CELLS. Two cells which give rise to the mesoderm in the development of the Earthworm and its allies.
- POLLEN. The microspores of Seed Plants.
- POLLINATION. The transference of pollen to the stigma of the pistil in higher Seed Plants.
- POLOCYTES. Tiny abortive cells arising by division from the egg during maturation. Polar bodies.
- POLYHYBRID. The progeny of parents which differ in regard to more than three given characters.
- POLYMORPHISM. Occurrence of several types of individuals during the life history, or composing a colony; *e.g.*, in some Hydroids.
- POME. Fleshy fruit with a core; *e.g.*, apple, pear.
- POPULATION. Entire group of individuals from which samples are taken for genetical study. Usually comprises several pure lines.
- POTENTIAL ENERGY. Energy possessed by virtue of stresses, *i.e.*, two forces in equilibrium. Criterion is work done against any restoring force; *e.g.*, kinetic energy of sunlight through agency of chlorophyll separates CO₂ into C and O₂ and thereupon is represented by an equal amount of chemical potential energy. Restoring force is here chemical affinity. Similarly a raised weight possesses gravitational potential energy in amount equal to kinetic energy expended in raising it. *See* Kinetic Energy and Conservation of Energy.
- PREFORMATION. The abandoned doctrine that development is essentially an unfolding of an individual ready-formed in the germ. *See* Epigenesis.
- PRONEPHROS. Primitive kidney of Vertebrates.
- PROPHASE. Preparatory changes during mitosis leading to the disposition of the chromosomes in the center of the cell (equatorial plate) ready for division. *See* Metaphase.
- PROSTOMIUM. A lobe which projects from the first segment of the body of the Earthworm and forms an upper lip.
- PROTEIN. A class of complex chemical molecules, containing nitrogen, which form the chief characteristic constituent of protoplasm.
- PROTHALLUS. The gametophyte of Ferns.
- PROTISTA. Protophyta and Protozoa; all unicellular organisms.
- PROTONEMA. A filamentous growth from a Moss spore which gives rise to the leafy Moss plant.
- PROTOPHYTA. Unicellular plants. *See* Protista; Protozoölogy.
- PROTOPLASM. The physical basis of life. Matter in the living state.
- PROTOPLAST. The cell exclusive of the cell wall, especially in plants.
- PROTPODITE. The basal portion of the typical Crustacean appendage from which arise the endopodite and exopodite.
- PROTOZOA. Unicellular animals. *See* Protista and Metazoa.
- PROTOZOÖLOGY. The science of unicellular animals, or Protozoa.

- PSEUDOPODIUM.** Protoplasmic projections for locomotion, feeding, etc., as in Amoeba.
- PUPATE.** Assumption of a quiescent stage (pupa), in the life history of Insects with a 'complete' metamorphosis, during which the larva is reorganized as an adult; *e.g.*, chrysalis of a Butterfly and in cocoon of a Moth.
- PURE LINE.** A group of individuals bearing identical genes, derived from a common homozygous ancestor.
- PUTREFACTION.** The simplification of nitrogenous compounds, such as proteins, chiefly through the action of enzymes of living organisms. *See* Fermentation and Decay.
- PYLORIC VALVE.** Muscular constriction between stomach and small intestine.
- PYRENOID.** Portion of chloroplastid specialized for starch formation.
- RECAPITULATION THEORY.** Doctrine that individual embryonic development repeats in abbreviated and modified form the development of the race (phylogeny). So-called biogenetic law.
- RECESSIVE CHARACTER.** *See* Dominant Character.
- REDUCTION DIVISION.** The division in spermatogenesis and oögenesis which separates synaptic mates and reduces the chromosome number one-half. Transformation of duplex into simplex group. The mechanism of segregation.
- REFLEXES.** Relatively simple and essentially automatic responses. Merge into instincts which are the most complex reactions made without learning.
- REGENERATION.** The power of replacement of parts which have been lost through mutilations or otherwise.
- RENAL PORTAL SYSTEM.** Blood ('impure') passes from posterior part of the body to kidneys by the *renal portal vein*; oxygenated blood to kidneys by the renal artery. Thus in animals with the renal portal system there is a double blood supply to the kidneys. Present in Fishes, Amphibians, and Reptiles; vestigial in Birds; absent in Mammals.
- REPRODUCTION.** The power of living matter to reproduce itself. Protoplasmic growth resulting in cell division.
- RESPIRATION.** Essentially the securing of energy from food, involving the exchange of carbon dioxide for oxygen by protoplasm.
- RESPONSE.** Any change in the activity of protoplasm, and therefore of an organism as a whole, as the result of a stimulus.
- RESTING CELL.** One which is not undergoing mitosis.
- RETINA.** Actual percipient part of the eye by virtue of a sensory layer which is stimulated by light rays.
- REVERSION.** The appearance of a distant ancestral character in an individual. *See* Atavism.
- RHIZOID.** A root-like filament in lower plants; *e.g.*, in Mosses and prothallus of Ferns.

RHIZOME. Prostrate underground stem; *e.g.*, in sporophyte of common Ferns.

ROOT HAIRS. Prolongations of epidermal cells just above the growing point of roots which afford surface for intake of water and solutes.

ROTIFERA. Microscopic, aquatic, multicellular animals. Wheel animalcules.

RUSTS. Fungi which are destructive parasites of the higher plants; *e.g.*, the Wheat Rust.

SACculus. The anterior sac of the labyrinth of the ear, a derivative of which becomes the cochlea in higher Vertebrates.

SAPROPHYTIC. Type of nutrition involving the absorption of complex products of organic decomposition; *e.g.*, in many groups of Bacteria and other Fungi, as well as various species of lower animals. *See* Holozoic and Holophytic.

SEBACEOUS GLANDS. Glands which elaborate a fatty substance (sebum) and secrete it into the hair follicles. Oil glands.

SECONDARY SEXUAL CHARACTERS. Differences between the sexes, other than those of the gonads.

SECRETION. A substance elaborated by glandular epithelium; or the process involved. *See* Gland and Excretion.

SEED. An embryo sporophyte supplied with food and protective envelopes.

SEGREGATION. The distribution of contrasting genes (allelomorphs) to separate cells during the formation of the gametes in a heterozygous individual (hybrid). The chief factor of Mendelian inheritance.

SEMICIRCULAR CANALS. Portion of the Vertebrate ear devoted to the maintenance of equilibrium.

SEMINAL RECEPTACLES. Sacs within the body cavity of certain animals (*e.g.*, Earthworm), which receive sperm from another individual and retain them until fertilization is to occur.

SEPAL. A leaf of the calyx of a flower.

SEPTA. The partitions which divide the coelom of the Earthworm into a series of chambers, or segments.

SERIAL HOMOLGY. Homology of a structure of an organism with another of the same organism; *e.g.*, appendages of the Crayfish, fore- and hindlimbs of Vertebrates.

SETAE. Bristle-like structures which protrude from the body wall of the Earthworm and aid in locomotion.

SEX CHROMOSOME. The chromosome which bears the differential gene for sex. The so-called X chromosome.

SEX-LINKED CHARACTERS. Characters represented by genes on the 'sex chromosome.'

SHOOT. Stem and leaves as contrasted with the root.

SIMPLEX CHARACTER. The result of a gene, or genes, from one parent only.

SOMA. Body tissue (somatoplasm) in contrast with germinal tissue.

- SPECIAL CREATION.** Doctrine that each species was specially created. Implies fixity of species. *See* Evolution.
- SPECIES.** In classification, the main subdivision of a genus. A group of individuals which do not differ from one another in excess of the limits of 'individual diversity,' actual or assumed.
- SPERM.** Male gamete. Spermatozoön.
- SPERMATID.** Male germ cells after the final maturation division but before assuming the typical form of the ripe sperm. Secondary spermatocytes.
- SPERMATOCYTES.** Cells arising from the spermatogonia. Primary spermatocyte arises by growth from the last generation of spermatogonia. Primary divides to form two secondary spermatocytes.
- SPERMATOGENESIS.** The development of the sperm from a primordial germ cell.
- SPERMATOPHYTES.** Plants bearing true seeds. Seed Plants. Flowering Plants. Phanerogams.
- SPINDLE.** The fiber-like apparatus between the centrosomes during mitosis.
- SPIREME.** The linear arrangement of the chromosomes frequently observed during mitosis.
- SPLEEN.** A vascular ductless organ of most Vertebrates, usually situated near the stomach, the function of which is not definitely established.
- SPONTANEOUS GENERATION.** *See* Abiogenesis.
- SPORANGIUM.** A spore-producing structure on a sporophyll.
- SPORE.** A cell, liberated from the parent, which gives rise without fertilization to a new individual; *e.g.*, in Mosses. Also the resistant phase assumed by certain unicellular organisms; *e.g.*, Bacteria.
- SPOROPHYLL.** A leaf which bears sporangia.
- SPOROPHYTE.** Spore-bearing (asexual) generation in plants exhibiting alternation of generations.
- SPORULATION.** Occurrence of several simultaneous divisions by which a unicellular organism is resolved into many smaller cells.
- STAMEN.** The pollen-bearing organ in Seed Plants. A microsporophyll. *See* Anther.
- STELE.** The central cylinder of root and stem, formed of united vascular bundles, in the highest Seed Plants (Dicotyledons).
- STIGMA.** The tip of the pistil adapted to receive the pollen and provide for its germination. The 'eye spot' of Euglena.
- STIMULUS.** Any condition which calls forth a response from living matter.
- STOMATA.** Openings through the epidermis of a leaf for the interchange of gases and exit of water vapor. The stomatic apparatus comprises the stoma and its guard cells. *See* Lenticel.
- SUBZONAL MEMBRANE.** Embryonic membrane immediately internal to zona radiata of Mammalian egg.

- SYMBIOSIS.** The association of two species in a practically obligatory and mutually advantageous partnership; *e.g.*, Lichens.
- SYMPATHETIC NERVOUS SYSTEM.** *See* Autonomic Nervous System.
- SYNAPSE.** The contact of one nerve cell with another, which makes possible the conduction of a nervous impulse from cell to cell.
- SYNAPSIS.** The pairing of homologous chromosomes during maturation of the germ cells.
- SYNAPTIC MATES.** Homologous chromosomes of maternal and paternal origin that pair during synapsis.
- SYNKARYON.** The composite nucleus formed by the union of the nuclei of two gametes. Male and female gametic nuclei united to form the fertilization nucleus. *See* Zygote.
- TAPIR.** A large herbivorous Mammal, having short stout limbs and flexible proboscis with the nostrils near the end. New World species are brownish-black, those of the Old World are black and white.
- TAXONOMY.** The science of classification.
- TELOPHASE.** Final phase of mitosis during which the two daughter nuclei are reformed and cytoplasmic division is completed. *See* Prophase.
- THALLUS.** A relatively simple plant body, not differentiated into root, stem, and leaf; *e.g.*, in Seaweeds and other multicellular Algae.
- THORAX.** The anterior chamber of the coelom in Mammals, containing esophagus, lungs, and heart. The middle portion of the body in the Arthropoda; *e.g.*, in all Insects. In the Crayfish the head and thorax are fused to form the cephalothorax.
- THYMUS.** A glandular structure in the pharyngeal region of Vertebrates. Disappears during early life in Man. Function unknown.
- THYROID.** An endocrine, or ductless gland in the pharyngeal region of Vertebrates. Supplies an important hormone.
- TISSUE.** An aggregation of similar cells for the performance of a certain function. *See* Organ.
- TRACHEIDS.** Elongated cells which form water-conducting vessels in the vascular bundles of higher plants.
- TRANSPIRATION.** The exhalation of water vapor, particularly through the stomata of higher (vascular) plants.
- TRICHOCYSTS.** Minute bodies, arranged in the outer part of the ectoplasm of certain Infusoria (*e.g.*, Paramecium), each of which upon proper stimulation is transformed into a thread-like process protruding from the cell surface. Apparently defensive structures.
- TRIHYBRID.** The progeny of parents differing in regard to three given characters.
- TRILOBITES.** Crustacea dominant during the early Paleozoic era. Extinct.
- TURGOR.** Outward pressure of the cell, largely due to the absorption of water which distends or holds rigid the cell wall.

- TYPHLOSOLE.** A median dorsal invagination along the entire length of the intestine of the Earthworm which increases the area of the digestive and absorptive surface.
- UMBILICAL CORD.** A Mammalian structure, commonly known as the navel cord, by which the embryo is attached to the placenta. The blood vessels from the embryo to the placenta pass through it. *See* Placenta.
- UNGUICULATE.** Provided with claws.
- UNIFORMITARIAN DOCTRINE.** An interpretation of the present condition of the Earth on the assumption of similarity of factors at work during past ages and to-day.
- UNIPARENTAL.** Derived from a single progenitor; *e.g.*, in asexual reproduction. *See* Biparental.
- UREA.** Nitrogenous waste product of animal metabolism. Formed as such in the liver, removed from the blood by the kidneys and eliminated from the body chiefly in urine. $\text{CO}(\text{NH}_2)_2$. A major part of the nitrogen is excreted in this form in human urine. *See* Creatinine and Uric Acid.
- URETER.** A tube carrying urine from kidney to the cloaca or to the urinary bladder.
- URIC ACID.** A nitrogenous waste product. Present in small quantity in the urine of Man.
- UROGENITAL.** Relating to the urinary and reproductive systems.
- UTERUS.** Lower portion of the oviduct (or oviducts) modified for the temporary retention of the eggs.
- UTRICULUS.** The posterior sac of the labyrinth of the ear into which the semicircular canals open.
- VAGINA.** Passage leading from the uterus to the exterior.
- VASCULAR BUNDLE.** Composite of xylem, cambium, phloem, and bundle sheath. Except for the cambium, essentially a system of tubes for conducting water and food. A fibro-vascular bundle. Characteristic of Vascular Plants, or Ferns and Seed Plants. *See* Stele.
- VASO-MOTOR NERVES.** Nerves which regulate the caliber of small arteries by bringing about relaxation or contraction of the muscular layer of their walls.
- VERMIFORM APPENDIX.** Blind outpocketing of the large intestine near its origin from the small intestine. Vestigial end of the caecum. Found only in Apes and Man.
- VERTEBRA.** One of the series of elements forming the backbone, or vertebral column.
- VERTEBRATE.** An animal with a backbone, or vertebral column. *See* Chordate.
- VITALISM.** The doctrine which attributes at least some of the phenomena of life to an interplay of matter and energy which transcends the so-called laws operable in the inorganic world. *See* Mechanism.

VITAMINE3. Indispensable accessory food substances whose importance has but recently been realized. Chemical composition is as yet practically unknown.

WORKING HYPOTHESIS. A basic assumption to guide the study of a subject, and to be proved or disproved by facts accumulated.

X CHROMOSOME. The 'accessory' or 'sex-chromosome.'

XYLEM. The inner woody part of a vascular bundle.

Y CHROMOSOME. The synaptic mate of the X chromosome, when present in males.

YEAST. A group of unicellular colorless plants (Fungi) which are chiefly responsible for alcoholic fermentation.

YOLK. Food material stored within the cytoplasm of an egg. *See* Metaplasm.

YOLK SAC. When a great quantity of yolk is present in an egg, the endoderm gradually grows over it to form the yolk sac which is usually of enormous size in comparison with the embryo proper.

ZONA RADIATA. Temporary external covering of Mammalian egg in very early stage.

ZOÖGEOGRAPHY. The science of the geographical distribution of animals.

ZYGOTE. The composite cell formed by the union of male and female gametes. *See* Synkaryon.

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