# ORGANIC ADAPTATION TO ENVIRONMENT

PUBLISHED ON THE FOUNDATION
ESTABLISHED IN MEMORY OF
AMASA STONE MATHER
OF THE CLASS OF 1907, YALE COLLEGE

# Organic Adaptation to Environment

*By*

*George Elwood Nichols*
*Lorande Loss Woodruff*
*Alexander Petrunkevitch*
*Wesley Roswell Coe*
*George Reber Wieland*
*Carl Owen Dunbar*
*Richard Swann Lull*
*Ellsworth Huntington*

*Edited by Malcolm Rutherford Thorpe*

NEW HAVEN
YALE UNIVERSITY PRESS
*London : Humphrey Milford : Oxford University Press*
MCMXXIV

*Printed in the United States of America*

# THE AMASA STONE MATHER MEMORIAL PUBLICATION FUND

The present volume is the sixth work published by the Yale University Press on the Amasa Stone Mather Memorial Publication Fund. This Foundation was established August 25, 1922, by a gift to Yale University from Samuel Mather, Esq., of Cleveland, Ohio, in pursuance of a pledge made in June, 1922, on the fifteenth anniversary of the graduation of his son, Amasa Stone Mather, who was born in Cleveland on August 20, 1884, and was graduated from Yale College in the Class of 1907. Subsequently, after traveling abroad, he returned to Cleveland, where he soon won a recognized position in the business life of the city and where he actively interested himself also in the work of many organizations devoted to the betterment of the community and to the welfare of the nation. His death from pneumonia on February 9, 1920, was undoubtedly hastened by his characteristic unwillingness ever to spare himself, even when ill, in the discharge of his duties or in his efforts to protect and further the interests committed to his care by his associates.

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# INTRODUCTION

THOMSON and Geddes have said that "Every creature is a bundle of adaptations. Indeed, when we take away the adaptations, what have we left?" And it can not be denied that there is and must be an exceedingly intimate relationship between any plant or animal and its environment. Adaptability means life for the species as well as for the individual; the absence of it, death. Adaptation may even go so far that certain more or less defenseless organisms exhibiting the coloration and external character of other forms, are better able to care for themselves in the struggle for existence. The influence of the environment may affect the form, habits, size, and mode of reproduction of a species, as well as its external coloration and its physical structure.

It was with a view to obtain exact data on the problem of Organic Adaptation, that a symposium was proposed to consider the subject from the standpoint of biological and geological evidence, a combination novel in attacking this subject. As a consequence the following series of lectures was delivered before the Paleontology Club of Yale University during the academic year 1922-1923.

In order to understand the meaning of the term environment, it is first necessary to know just what comprises the complex series of conditions which surround both plants and animals. Professor Nichols' paper is, therefore, given over to a consideration of the environment itself in its broadest aspects, discussing the different agencies determining its character and outlining the effect of various individual conditions upon the organisms, using plant forms primarily to illustrate the results of environmental conditions.

After the discussion of the surrounding influences, we next turn to the problem of adaptation of the more mobile forms, beginning with Professor Woodruff's paper on the Protozoa, or unicelled animals. This presents a synoptic survey of racial and individual adaptations to the physical and living environments, as seen by a protozoölogist.

Proceeding with our problem, Professor Petrunkevitch takes up the metazoan parasites, tracing their life histories from inception, through intermediary hosts, to final hosts, in both animals and man. It has been estimated that nearly one-half of the animal kingdom are parasites during some part of their career and a study of these forms is highly essential, for the adaptations, both functional and structural, shown by the internal parasites, are truly remarkable, trending mainly to a simplification of structure, with a concomitant high specialization of certain parts. It will be seen that the environment here is most equable and subject to the fewest changes. The principle is set forth that natural selection has only a very limited application and that some organisms owe their distinctive characters to the stabilizing influence of the environment.

After these general surveys, we are in a position to consider some of the phenomena underlying the origin of new varieties of organisms. Professor Coe describes the mechanism involved and the reaction to environment of both the seemingly stable and the new forms, drawing illustrations from the various classes comprising the organic world.

In the next three papers, the subject of Organic Adaptation is considered from the paleontologic standpoint. The previous lectures have dealt with facts derived from the present living world, and now we turn our attention to some of the fossil evidence bearing on the problem. Doctor Wieland gives a summary of what is known of plant life of the geologic past. His studies take on a somewhat numerical aspect and tend to show that plant evolution has been an exceedingly slow process. Fossil plants appear to have resisted their environments rather than to have been easily moulded to any great extent by them.

With Professor Dunbar's paper we come to an aquatic environment, and to the discussion of a great invertebrate group. He traces the development of the Cephalopoda through millions of years, from the beginning of the Ordovician to the present, and shows their remarkable reactions to external forces. More than 7,500 species of cephalopods are known, and their evolutionary history is exceedingly interesting. There are two main divisions of this class, the one armored, sluggish, and more or less primitive, represented today by the *Nautilus;* the other unarmored, and yet swift, aggressive, and modern, as seen in the living squid. Competition is keen in the seas and adaptation imperative. That the cephalopods have survived from such remote times is ample testimony of their ability to adapt themselves to the changing conditions of marine life through the ages.

In the seventh paper, Professor Lull traces the adaptations of the dinosaurs, the dominant form of animal life during the Mesozoic, or Age of Reptiles. This great group, long wholly extinct, has, however, living relatives, represented by the crocodiles on the one hand, and by the birds on the other. The dinosaurs were of world-wide distribution, and their habitats varied from semi-aquatic to wholly terrestrial. Some were carnivorous, others herbivorous; some small, others huge; some bipedal, others quadrupedal; some armored, others unarmored—in fact, few, if any, ancient or modern groups, have ever shown so great a diversity in structure, in habits, and in adaptations. In the latter days of their racial history, the dinosaurs developed some of the most grotesque forms known in the whole realm of life.

The final paper treats of the most adaptable of all organisms, Man. Professor Huntington discusses how the environment moulds the racial character in human beings. Man is subject to the same laws as the plants and the animals, and yet, through his intelligence, he has the potentiality of adaptability far in excess of any other organism. Indeed, that is why man, in a sense, is culminant in the evolutionary process.

The normal, or obvious, attracts the least attention, whereas the abnormal and unusual often receive undue consideration. So it is with environment. The average person takes for granted the surroundings of animals and plants, without giving much thought to the methods and mechanics which have brought about the adaptations of organisms to them. Indeed, in many instances, very significant adaptations seem not to have received their full share of scientific consideration.

From the above brief statement of the papers comprising this volume, it will be readily seen that there are a great many fields of adaptation untouched in the present work. We should remember that there is hardly a niche on the globe which does not have its own peculiar form or forms of life. We must also consider the remarkable plasticity of organisms, which has permitted the various animals and plants to become adapted to extremes of heat and cold, to the great oceanic depths, to subterranean regions, to lofty peaks, and even to the upper air.

In this volume then, for apparently the first time, are considered together adaptations from the evidence of both living and fossil forms. Students of present-day animals and plants are necessarily limited to a horizontal survey of life, but it is only through their work that paleontologists can interpret the true record of past life. On the other hand, only through a consideration of the vast periods of time which have elapsed since life began on this earth, and only by going back to its beginning and tracing its development onward, can we get a glimpse into the meaning of the riddle of life.

The thickness of the sedimentary formations of the earth reaches a total of approximately eighty miles, throughout nearly the whole of which are remains of organisms. Even bacteria are found in the Devonian rocks and disease germs are of great antiquity. It is now a fairly well-established fact that life has been present on this planet for more than three hundred million years. Here in the geologic record, in the *vertical* distribution of life, we have the sources, the beginnings of adaptations, knowledge of which is absolutely essential to a true understanding of the facts as brought out by the scientists dealing with present-day organisms, whose studies have to do with the present *horizontal* distribution of life. To give a clearer conception of this time element, a quotation from the late Professor Barrell will help: "Let a year be represented by a foot; the average length of human life is measured then by the breadth of a dwelling house, and human history is limited approximately to a mile; but the duration of geologic time is measured in terms of the circumference of the globe."

By such means, then, have we tried to obtain a larger understanding of environment and environmental problems. The story is incomplete unless we bring to bear on this question the evidence derived from Zoölogy, Botany, Paleontology, and Geology. These sciences are coëqual in importance for any true conception of the fundamentals of Organic Adaptation.

In conclusion, as secretary of the Club and as editor of this volume, I wish to express my deep gratitude to the authors for their willingness to prepare the lectures, which are based on original research and which required time and careful thought; to my colleagues who have given their active support in many ways to bring this work to fruition; and, finally, to the Yale University Press for the great consideration shown in all matters connected with the publication of this volume.

MALCOLM RUTHERFORD THORPE,
*Secretary, Paleontology Club, 1922-1923.*

Yale University,
March, 1924.

# CHAPTER I

# THE TERRESTRIAL ENVIRONMENT IN ITS RELATION TO PLANT LIFE

GEORGE ELWOOD NICHOLS
ASSOCIATE PROFESSOR OF BOTANY
IN YALE UNIVERSITY

## INTRODUCTION

IN a series of papers dealing with the environmental relations of organisms, it seems but appropriate that the first should be devoted to the consideration of the environment itself. What is the nature of the agencies which determine the character of the environment? What is the effect of various individual conditions of the environment upon organisms? How are these different individual influences coördinated in their relation to the influence of the environment as a whole? It is to this phase of the subject, more particularly, that attention is directed in the present chapter, and plant life is used primarily as a background to illustrate the effects of environment upon the organism.

*The Plant an Indispensable Element in the Environment of the Animal.*—In thus using plants to illustrate the effects of environment upon organisms in general, it can not be too strongly emphasized, not only that the majority of the environmental conditions which affect plant life are directly important in their effect on animal life as well, but that the plant itself constitutes an indispensable element in the environment of the animal. The very existence of animals, in fact, would be impossible in the absence of green plants.

This dependence of animals upon plants is manifest most clearly in their nutritive relations. All animals require organic foods. They require them as building materials, since it is from organic foods that all the tissues of the animal body are elaborated, including the living protoplasm. They require them as sources of energy, since it is only through the breaking down of organic foods in respiration that life and activity in the animal body are made possible. And, directly or indirectly, all organic food comes from plants. Green plants alone, of all living organisms, are able to build up organic food from the relatively simple raw materials of the inorganic world. This they do primarily through the process known as photosynthesis (*i.e.*, building up by means of light), whereby the energy of sunlight is utilized to manufacture grape sugar from carbon dioxid and water; and the formation of grape sugar (or some closely related carbohydrate) is a prerequisite step to the formation of organic compounds of any description.*

The animal is further indebted to plants, directly or indirectly, for its amino-acids (substances which form the basic constituent of all proteins), since plants alone have the power of building up certain fundamental nitrogenous compounds of this description. It is indebted to plants for its vitamines, whether or not these substances be regarded as foods. And, finally, there seems to be little question that the animal is also dependent upon plant life for its oxygen. Free atmospheric oxygen is essential for respiration in the vast majority of both plants and animals; but while it is universally recognized that green plants give off large quantities of oxygen as a by-product of photosynthesis, the idea has not been so generally appreciated that all the free oxygen of the atmosphere has probably originated in this way. And yet, in the words of

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* The chemical formula commonly given for this reaction is 6 $CO_2$ (carbon dioxid) $+$ 6 $H_2O$ (water) $=$ $C_6H_{12}O_6$ (grape sugar) $+$ 6 $O_2$ (oxygen).

Vernadsky,* "We know of not a single reaction in the earth crust which would liberate free oxygen except its production by organisms containing chlorophyll in the synthesis of their organic substances. At the same time, we know thousands of chemical reactions in the earth crust which consume oxygen. If there were no chlorophyll-bearing organisms," he concludes, "free oxygen in the atmosphere would long ago have ceased to exist."

The facts to which I have just called attention have a significant bearing on many biological problems. They have a bearing, for example, on the conditions of environment under which life must have originated on the earth and on the nature of the first living organisms. In the present connection their chief point of interest is simply this: that the very existence of the animal is contingent upon the preëxistence of environmental conditions which are favorable to plant life. In discussing the nature of the environment in its relation to the plant world, then, we are dealing with conditions which are quite as important in their relation to the animal world.

*General Nature of the Environment.*—The environment of any organism may be described as the sum total, or, perhaps better, the resultant of all the external conditions which act upon it. Representing as it does a complex of conditions, it is only by analyzing the environment into its various components that we can hope to understand its nature and to interpret the nature of its influence. In the last analysis, the effect upon the organism of the conditions which go to make up the environment is expressed through the medium of various physical or chemical agencies, and from this point of view it is quite possible to classify all environmental influences into two cate-

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* Quoted through the courtesy of Professor Alexander Petrunkevitch, from the manuscript (in Russian) of a lecture delivered by Professor W. Vernadsky at the Bohemian University of Prague, on June 22, 1922.

gories, namely, those that are physical and those that are chemical. It is not my intention here, however, to discuss the nature of these ultimate effects of environment in their relation to the organism; it is my purpose, rather, to outline in a broad way those larger environmental features of the earth's surface which are so readily susceptible to observation and study and which are of such manifest importance, either directly or indirectly, in their relation to the form, structure, behavior, and distribution of both plants and animals.

## PHYSIOLOGICAL CLASSIFICATION OF ENVIRONMENTAL AGENCIES

*The Conditions Outlined.*—Considered with reference to their inherent characteristics, the conditions which go to make up every terrestrial environment fall more or less naturally into five groups, *viz.,* moisture conditions, temperature conditions, light conditions, chemical conditions, and mechanical conditions. These five groups will now be taken up in order.

*Moisture Conditions of the Environment.*—The importance of water to the plant is apparent when account is taken of the various uses the plant makes of it. Water forms an essential constituent in the manufacture of organic food from inorganic materials, and it constitutes a large proportion of the composition of all parts of the plant. It is water which gives firmness to leaves and other tender plant organs, as becomes evident when plants wilt from lack of water. Water is necessary for plant growth. It is necessary as a medium in which various substances in solution can be absorbed into the plant from the outside world and in which they can be transported from one part of the plant to another. It is necessary as a medium for various chemical reactions which take place within the plant. So obvious, indeed, is the paramount importance of water in its influence on their form, structure, and distribution that the classification of plants into hydrophytes, mesophytes, and xerophytes, based on this criterion, is universally recognized as the most fundamental of all ecological classifications.

Plants which require a maximum water supply—typically, plants that actually grow in the water—are termed *hydrophytes*. Plants which require a minimum water supply, notably desert perennials, are termed *xerophytes*. Plants which are intermediate in their water requirements between hydrophytes and xerophytes are termed *mesophytes:* these include the plants of ordinary moist soils.

The soil moisture conditions influence the amount of water which the plant is in position to absorb from the outside world, while the atmospheric moisture conditions influence the amount it is liable to lose through the phenomenon of transpiration,* the water actually available to the plant for carrying on its various activities being represented, of course, by the balance between what is absorbed and what is lost. When the amount of available water falls below a certain point, the plant wilts, and two of the greatest sources of danger the plant has to face are insufficient absorption and excessive transpiration. The ordinary land plant absorbs water through its root system. The roots are adapted to this function by their position in the soil where they ramify in all directions, by their hydrotropic reactions which cause them to grow toward soil moisture, and by the minute hair-like outgrowths near their extremities, which are the only regions where absorption takes place. These so-called root hairs greatly enlarge the absorbing surface of the roots and thus facilitate the rapid intake of water and substances in solution. The plant loses water by transpiration chiefly through its leaves. These latter (and also young stems) are protected against excessive loss of water primarily through the presence of a cutinized and waterproof epidermal layer which forms an essentially continuous covering over the

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* The phenomenon whereby leaves and stems give off water in the form of vapor.

entire surface, being interrupted only by the minute epidermal pores known as stomata, the presence of which is essential to the adequate absorption of carbon dioxid. In woody plants the loss of water from older parts of the stem and branches is efficiently prevented by layers of cork.

We will restrict our attention, for the moment, to the moisture relations of plants which grow in places that are either very wet or very dry.

Many plants live in situations where they are permanently submerged in water. This of course is true of the majority of seaweeds and other algæ; but it is also true of not a few seed plants. Submerged seed plants differ from ordinary terrestrial plants in having thinner leaves which are never cutinized, large intercellular air spaces, and poorly developed root systems. Water in such plants is absorbed mainly through the leaves; root hairs are commonly lacking, and sometimes even the roots.

At the opposite extreme from submerged hydrophytes are desert xerophytes which maintain their existence in regions where both the soil and the atmosphere are very dry. Many desert plants are active only during periods of moist weather, and plants of this description may differ little in their vegetative characters from ordinary mesophytes. Such are the desert annuals, which spring up at the beginning of the moist season, develop flowers and fruit, and then are carried over the dry season in the form of seeds. But the plants which we ordinarily associate with deserts are the desert perennials, and these exhibit various more or less striking features which adapt them to carry on vegetative activity at practically all seasons. The root system in such plants is very extensive, commonly reaching down to considerable depths, where the water supply is more constant than near the surface; but in many cases the roots spread out just underneath the surface of the ground, being here in position to absorb the water from light showers, which never penetrates far into the ground. This superficial type of root system is particularly characteristic of succulents—forms such as the century plant and the cactus, which tend to store up water in fleshy leaves or stems. It is highly advantageous to these plants that they be in position to absorb water rapidly at seasons when it is present, and their ability to subsist during dry periods upon the water stored in their tissues obviates the necessity of a deeply penetrating root system. Generally speaking, the leaves in desert plants are the antithesis of the leaves in submerged aquatics: in particular, they exhibit various peculiarities of form and structure which tend to reduce to a minimum the loss of water through transpiration. In addition to being relatively thick in proportion to their bulk, a condition which reaches its culmination in succulent species (*e.g.,* the century plant), the leaves of desert plants may be very strongly cutinized (a common condition); they may be coated with wax (*e.g.,* the century plant), or with gum (*e.g.,* the creosote bush); they may be covered with a dense growth of hair (*e.g.,* the sage brush); or the leaves may be very small, and in extreme cases lacking altogether (*e.g.,* various cacti).

But xerophytic plants are by no means restricted to desert regions. They occur also in regions of abundant precipitation, growing here in situations where soil moisture is scarce over long periods, or where the evaporating power of the air is intense, as on sand dunes, on bare rocks, and on the trunks of trees. Xerophytes of this description exhibit various of the characteristics possessed by desert plants.

Xerophytic conditions may even prevail in places where the ground is saturated with water. Ordinary swamp plants, for example, would die of thirst in a salt marsh. There is plenty of water here, but they are unable to absorb it because of its high salt content. It is interesting to note that many of the plants which do grow in salt marshes develop the structural peculiarities found in desert xerophytes, particularly succulence. Indeed, they are xerophytes, albeit xerophytes of a very special type. They are called physiological xerophytes: that is to say, they are capable of living in soils which, while they may be physically wet, are physiologically dry, inasmuch as the plant is unable to extract water from them.

Strictly speaking, all perennial plants of temperate regions are to be looked upon as physiological xerophytes during winter: during the season when soil water is unavailable by reason of low temperatures. The majority of our native woody plants meet the conditions which prevail in winter by shedding their leaves, all parts of the shoot system which hibernate above the ground being covered over with cork or scales which effectually prevent the loss of water. In the case of evergreen plants, in temperate regions, the leaves commonly exhibit features which tend to reduce transpiration at all seasons. The majority of our herbaceous perennials are carried through the winter by roots or stems which are situated underground, and therefore are protected from transpiration. Even annual plants in temperate regions might be regarded, in a sense, as physiological xerophytes during the winter months: they are present only in the form of seeds, and a seed, without question, is the most perfectly protected of all plant organs. While, then, we are accustomed to refer to the plants of temperate regions as being either mesophytic or xerophytic, in doing so we are speaking in relative terms only, or with reference to the conditions which prevail during the growing season. True mesophytes are found only in the humid tropics, in situations where temperature and moisture conditions are favorable to vegetative activity throughout the year.

In concluding our consideration of the moisture relations of plants, it need only be stated that plant life without water is inconceivable; and yet there is practically no land area on the face of the earth where water is not present in sufficient amount to permit the development of some forms of plant life.

*Temperature Conditions of the Environment.*—The life of a plant has been described as being made up of thousands of separate reactions, each of which is carried on within a more or less specific range of temperatures. For each separate reaction, there exists a more or less definite optimum temperature, *i.e.*, a temperature intensity which is most favorable to that particular reaction. For the organism as a whole, at any given period of its existence, the most favorable temperature is the one which conduces to the harmonious interaction of all its manifold reactions. This so-called harmonic optimum temperature varies greatly at different periods of the plant's activity. In a seed plant, for example, the harmonic optimum temperature for germination is much lower than that for full vegetative activity; and this in turn is different from that for the production of flowers or the ripening of seed. For every plant, then, there exists a more or less definite range of temperature conditions within which its various activities are best carried on, and it is hardly necessary to more than state that for different plants this range differs widely. Generally speaking, a plant can survive in the struggle for existence only where its various functions are in a more or less constant state of equilibrium, so to speak, in their relation to the temperature conditions of the environment.

For every plant there are certain minimum and maximum conditions of temperature beyond which it can not exist, and between different plants these critical temperatures vary very widely. Thus it is that while many tropical plants perish from cold at temperatures which are several degrees above freezing, many plants in the far North thrive in situations where the temperature may fall below freezing every night during the growing season. With respect to the extremes of temperature at which plants can carry on their vegetative activities, we find at the one extreme the blue green algæ of hot springs, which flourish in waters having a temperature around 140°F., and various lichens which grow on the bare faces of exposed rocks whose temperature at midday frequently rises to 140°F., or even higher. At the other extreme are various arctic seaweeds which grow and fructify vigorously at temperatures of 32°F., or lower, and large numbers of minute algæ which live out their entire life cycles on the surface of the snow in arctic regions and on high mountains. In fact, it may safely be asserted that there are few areas on the face of the earth where temperature conditions alone are responsible for the complete exclusion of plant life.

As with optimum temperatures, so in its relation to extreme temperatures the plant varies greatly at different periods of its existence. In temperate regions, for example, trees during the winter season can withstand temperatures which would be disastrous during the vegetative season. The effects of frost out of season are a familiar demonstration of this fact. Hibernating flower buds and other living plant organs may become frozen solid during the winter months without injury. Many dried seeds retain their vitality when subjected to temperatures of more than 300°F. below freezing, and they can also endure much higher temperatures than the plants that bore them. This latter fact is well exemplified by the prolific reproduction of lodge-pole pine which may follow a forest fire in many parts of the West, through the germination of seeds which passed uninjured through the catastrophe that destroyed the trees.

Proceeding further, with regard to the plants of temperate regions it is significant, not only that they are adapted, as a class, to pass through a cold season uninjured, but that, in many cases at any rate, exposure for a more or less protracted period to low temperatures seems to be actually essential to the normal course of development. Thus it is that the twigs of many deciduous trees, if brought indoors late in winter, will develop leaves or flowers within ten days, whereas it takes them a month or more to do so (if they develop at all) when brought indoors shortly after the leaves have been shed in autumn. Again, the seeds in many plants of temperate regions refuse to germinate unless they have been thoroughly chilled.[1] These and other considerations clearly suggest the significance of temperature conditions in their bearing on various phenomena of geographical plant distribution. Indeed, Merriam[2] goes so far as to state that, "Apart from obvious mechanical barriers, such as oceans, temperature is the most important single factor in fixing the limits beyond which particular species of animals and plants can not go."

There is little doubt as to the importance of temperature in its general relation to plant distribution, plant development, and plant behavior. When it comes, however, to the question of the precise physiological effects of temperature on the plant, the situation is somewhat complicated. For example, plant physiologists are in substantial agreement that the ability of any plant tissue to withstand cold is correlated with its ability to retain water. When a plant organ freezes, the water contained in the living cells tends to be drawn out into the intercellular spaces, where crystals of ice are formed. No ice is formed within the cells themselves, but, if too much water is withdrawn from the cells, they die of desiccation. Generally speaking, then, the resistance of plant organs to cold is dependent on their ability to retain water in their cells.

Without going into further details on this point,* it need only be stated that the importance of temperature, *per se,* in its relation to various peculiarities of plant form and structure in particular, is much less important than is commonly assumed. For example, the deciduous habit of trees and other woody plants in temperate regions is popularly associated

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* For further discussion see [3].

with the influence of low temperatures; yet precisely this same phenomenon is exhibited by trees in tropical regions where it is never cold, but where there are alternate wet and dry seasons. The absence of leaves here during the dry season is obviously of advantage in checking loss of water through transpiration; and the same advantage holds for temperate regions where winter is a period of physiological drought.

Again, the failure of trees to thrive in arctic regions is frequently ascribed to low temperature; yet the most extensive treeless tracts on the face of the earth, namely, the prairies, are in temperate regions, while some of the lowest temperatures known (temperatures as low as –94°F.) have been recorded within the Siberian forest district. The failure of trees to thrive in arctic regions seems due primarily, not to cold, but to the effect of high transpiration during the long arctic winter. The effect of this factor, supplemented by that of certain mechanical agencies, is strikingly illustrated by the scrubby, flat-topped habit frequently acquired by trees growing in exposed situations in the far North, all parts of the plant which are not covered over by a blanket of snow in winter being killed. As a matter of fact, except in places where the ground is covered with ice and snow or is otherwise unfavorable throughout the year, trees are not wholly lacking in arctic regions; but they are well developed only in protected situations. It is indeed doubtful if any region on the face of the earth is too cold to permit the growth of certain trees, provided they are adequately protected from transpiration.*

Illustrations might be multiplied indefinitely. The chief point which I wish to emphasize with regard to the temperature conditions of the environment is simply this, that while their influence on the physiological activities of plants and on the geographical distribution of different species is unquestioned, they are much less important in their influence on plant

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* For further discussion, see [4], p. 717.

form and plant structure than the moisture conditions of the environment.

*Light Conditions of the Environment.*—Light is essential to the life of all green plants for the reason that light, and light alone, can supply the energy which enables the plant to build up organic compounds out of inorganic materials (*i.e.*, to perform photosynthesis). The chlorophyll pigment itself, to which the green color of plants is due and in the absence of which photosynthesis can not be carried on, seldom develops except in the light. The general importance of light in relation to plant growth and behavior is familiarly illustrated by the fact that house plants invariably turn their leaves toward a window, this behavior being made possible by differential growth in the stems and in the petioles of the leaves.

The intensity of the light to which a plant is exposed may have a marked influence on its form and structure. Potatoes sprouting in the dark, for example, develop long slender shoots, with small scale-like leaves, devoid of green color,—shoots which are in marked contrast to those developed in the light. Trees growing in the open tend to develop broad, spreading crowns, the trunk often branching clear down to the ground. Growing in the forest, on the other hand, through a process of natural pruning they develop long, slender trunks which may be entirely bare of branches except toward the top. The leaves of plants growing in the shade are relatively broad and thin, as compared with leaves of the same species growing in the open. Differences in form and structure such as these may be due to the direct effect of differences in illumination upon plant growth, or they may be correlated, in part, with the fact that plants transpire more freely at high light intensities than at low.

The amount of light required by plants varies greatly in different species and at different stages in the development of the same individual. Some trees, for example, can grow only in the open sunlight (*e.g.*, the aspens), while others will thrive in the shade (*e.g.*, the hemlock). The flowers in some plants open only in the light, while others open only in the dark. Certain seeds will germinate only in the light, and others only in the dark. The seedlings of many trees are capable of growing for a long time in poorly lighted situations, as on the floor of a forest, where an older individual would perish for lack of light.

But it is not merely the intensity of the light that is important: its duration and quality must also be taken into account. Under the same conditions of moisture and temperature, and with the same conditions of light intensity, plants develop most rapidly in situations where the illumination lasts the longest. Thus it is that in southern Sweden grain takes 100 days to ripen, while in northern Norway, with its greater duration of light, it ripens in 90 days, and this in spite of less favorable temperature conditions. Recent experiments[5] have demonstrated that in the seed plants the relative length of day is a factor of the first importance in its influence, more especially, on the sexual processes; that normally a plant "can attain the flowering and fruiting stages only when the length of day falls within certain limits," which are definite for each species; and that, "consequently, these stages of development ordinarily are reached only during certain seasons of the year." It was found that "In the absence of the favorable length of day for bringing into expression the reproductive processes in certain species, vegetative development may continue more or less indefinitely, thus leading to the phenomenon of gigantism. On the other hand, under the influence of a suitable length of day, precocious flowering and fruiting may be induced. Thus, certain varieties or species may act as early- or late-maturing, depending simply on the length of day to which they happen to be exposed." The bearing of these facts on various problems of plant distribution is obvious.

With regard to the quality of the light it need only be noted that practically the only portions of the spectrum which are effective in photosynthesis are certain red and blue rays. Insufficiency of these rays, rather than mere deficiency of light intensity, may well be responsible for the inability of a plant to grow on the floor of a forest, where the only illumination available comes from the light that has filtered down through the green foliage canopy overhead. The color peculiarities of marine algæ growing at different depths have been interpreted by some as being in the nature of an adaptation to differences in the quality of the light. In general, however, it is safe to assert that, except for the depths of the ocean and dark caves, there is no area on the surface of the globe where autotrophic plants are completely excluded by lack of light.

*Chemical Conditions of the Environment.*—The close relationship which exists between plant life and the chemical conditions of the environment need only be suggested. Water, carbon dioxid, and oxygen, together with certain inorganic salts (*viz.*, salts of nitrogen, sulphur, phosphorus, magnesium, iron, potassium, and calcium), are essential to the growth of every plant; while, on the other hand, the presence of certain chemical conditions is inimical to plant life. It is thought by many that a larger proportion of carbon dioxid present in the air during certain past geological ages may have been responsible for the greater luxuriance of vegetation which then prevailed; but it is certain that the amount of neither carbon dioxid nor oxygen in the air at the present day varies sufficiently from place to place to exercise any appreciable modifying effect upon plant life. So far as chemical conditions are responsible for present-day differences in environment, their effect is expressed chiefly through the medium of the soil.

The diversity in the chemical conditions below the surface of the ground stands in marked contrast to the comparative uniformity which prevails above, and the recognized importance of this diversity is attested by the position which soil chemistry occupies in modern agricultural science. Two soils scarcely exist which are chemically identical. Differences in oxygen content alone may be responsible for marked differences in the character of the plant population, since deficiency of oxygen in the soil retards the growth and activity of roots, to say nothing of the various indirect effects which it produces. Differences in the active acidity or alkalinity of the soil are likewise the cause of striking differences in vegetation, many plants being more or less definitely restricted in their occurrence to either acid or alkaline substrata. Differences in the abundance of various soluble salts may be another factor of importance. The rejuvenation of worn-out fields through the application of phosphate and nitrate fertilizers affords a familiar demonstration of the necessity of certain salts for plant nutrition, while the detrimental effect of any salt, when present in sufficient concentration, is illustrated by the inadaptability of salt marshes and alkali lands to agriculture. Finally, differences in the kinds or amounts of organic matter present in the soil may be of vast significance, chiefly because it is upon this that the teeming population of bacteria and fungi in the soil (see further remarks on p. 28) depends for its existence.

*Mechanical Conditions of the Environment.*—All environmental conditions which represent the direct influence on the organism of any external force may be classed as mechanical. Under this head come the effect of climatic agencies such as heavy wind, hail and sleet, ice storms, and drifting snow; the effect of physiographic agencies such as water currents, waves and spray, ice, and landslides; together with various effects of animal and human activity.

## ECOLOGICAL CLASSIFICATION OF ENVIRONMENTAL AGENCIES

*The Physiological and Ecological Points of View Compared.*—Up to this point the various conditions which go to make up the environment have been considered, primarily, with reference to their inherent characteristics. They have been accepted at their face value, so to speak, with but little regard to their origin or to the cause of their occurrence. This point of view is essentially physiological, and a physiological diagnosis of the conditions of the environment in their relation to various peculiarities of plant form and structure, of plant development and behavior, is a fundamental precursor to the consideration of these conditions from any other point of view. But when it comes to the study of plants as inhabitants of a real world, and of the relationship between various features of the plant world and its terrestrial environment,—when, in other words, it comes to the ecological* study of plants and of the vegetation which plants go to build up, such a point of view, in itself, falls far short of giving a complete picture. The environmental conditions found in nature are grouped in more or less definite relation to certain more or less well defined geographic or other causes (Figure 1), and their ecological significance can be fully appreciated only when their distribution or occurrence is properly coördinated in relation to origin or source. Classifying the conditions of the environment from this ecological point of view, then, they may advantageously be grouped into five categories, which I shall consider in order, *viz.*, climatic, physiographic, biotic, anthropeic, and pyric conditions.

*Climatic Environmental Conditions.*—These may be taken to include essentially all environmental influences which are of atmospheric origin, especially conditions of temperature and moisture. Differences in temperature, for example, determine the generally recognized division of the earth's surface into torrid, temperate, and frigid zones. Within the temperate zone, to select the region with which we are most familiar, still further climatic subdivisions can be distinguished with

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* Ecology is the study of organisms in relation to environment.

reference to the length of the growing season, the hotness of the summers and the coldness of the winters, and the "sum of the positive temperatures for the entire season of growth and reproduction,"[2] with reference to the annual amount of precipitation and its seasonal distribution, with reference to the evaporating power of the air, and with reference to various combinations of these different individual conditions. The distribution of these and other climatic conditions is determined by geographic position in relation chiefly to latitude and elevation, prevailing winds and cyclonic storm tracks, oceans and mountain barriers.

The earth's surface as an environment for living organisms.

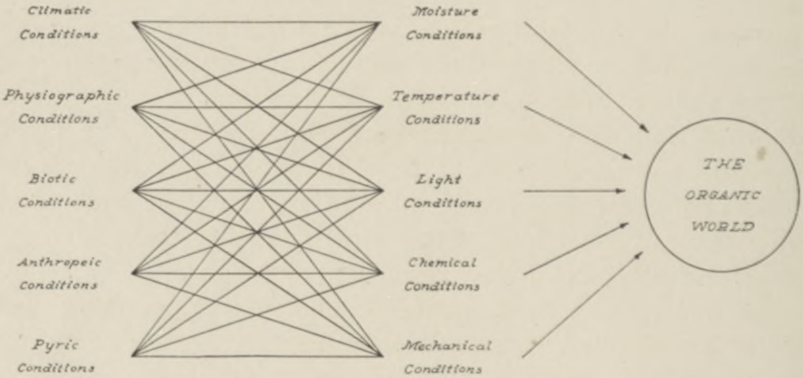

Fig. 1.—Diagrammatic scheme to suggest the nature of the terrestrial environment in its relation to the organic world, together with the ecological sources (first column) of the various physiological conditions (second column) which influence the form and structure, the development and behavior, and the geographical distribution of living organisms.

It is climate, in the main, which determines the general aspect of the plant life in any region. The explanation for this fact is somewhat as follows. It is evident, to begin with, that, in any given area, only those plants can grow which find themselves adapted to the climatic conditions of environment which prevail there. Thus it is that trees are mostly excluded from desert regions by reason of climatic aridity, while annual plants are unable to thrive in arctic regions because the short growing season prevents them from maturing their seeds.

Generally speaking, the adaptiveness of a plant to environment is manifested outwardly in what is termed its life form (or growth form). Under the head of life form are included peculiarities in size and habit of growth, in the duration of the plant as a whole and of the stem (both above and below ground), in the duration and structure of the leaves, in the position and structure of the resting buds, in the extent and other features of the root system, in the methods of vegetative reproduction, and so on: in short, the life form of a plant comprises all peculiarities in its form and structure which have a bearing on the relationship between the plant as a whole and environment. It is in terms of life form that the ecological aspect of the plants in any region is to be judged.

In this connection it should be pointed out, further, that there is a marked difference, with respect to cause, between the ecological aspect of the vegetation in any region, as determined by life form, and its floristic aspect, as determined by the species of plants which enter into its composition. The floristic affinities of the plants in different parts of the world are determined chiefly by the presence or absence of barriers, either past or present, which hinder or facilitate plant migration from one region to another—barriers in the form of oceans, mountains, or climate. Regions between which such barriers do not exist tend to have various plants in common, and *vice versa.* Thus it is that while many species of plants range throughout most of the eastern United States, very few species from this region are to be found in the Rocky Mountain region, the comparatively arid climate of the Great Plains, which lies between, forming an impassable barrier to migration from one area to the other.

When it comes, however, to the ecological character of the vegetation in different parts of the world, the presence or absence of barriers is of little import, for the reason that essentially the same life form may be developed by species which, floristically speaking, are totally unrelated. Thus it is that the deciduous tree life form, in the eastern United States, is exhibited by scores of different species belonging to dozens of different genera. In other words, it is the climatic conditions of the present which are of fundamental importance in determining the presence or absence of any particular life form in any particular region. It follows, naturally, that in different parts of the world, regardless of geographic continuity, and quite apart from floristic affinities, regions having similar climates tend to exhibit similar life forms. A striking illustration of this fact is furnished by the cacti, characteristic plants of American desert regions, and the euphorbias, which are equally characteristic in many arid sections of Africa. So closely do certain euphorbias (PLATE I) resemble certain cacti in their life form that upon superficial examination they might well be referred to the same genus, when, as a matter of fact, they are floristically far apart.

Proceeding further, it is the character and abundance of the predominant life forms which determines the mass effects of vegetation taken as a whole,—what is termed its physiognomy. The differences in the superficial appearance of plant communities which distinguish forests from thickets or meadows, deciduous forests from evergreen forests, and so forth, are differences in physiognomy. In any particular climatic region, many different kinds of life form may be represented, all of which, in varying ways and in varying degrees, are adapted to the existent climatic conditions; and, depending on the way these life forms are grouped in relation, primarily, to en-

Plate I.—A species of *Euphorbia* (*E. canariensis* L.), native to the Canary Islands, which shows a marked resemblance in life form to various North American cacti. Photograph by Bohny, from Rikli's *Lebensbedingungen und Vegetationsverhältnisse* (Verlag G. Fischer).

vironmental conditions other than those of climate, there may be many different kinds of plant communities. But in every climatic region there are certain particular kinds of life form (and commonly only one) which stand out as predominant; and there is a certain particular type of plant community which predominates over all others. Thus, in the eastern United States the predominant life form is the deciduous, broad-leaf tree; in the Great Plains it is grass; and the predominant plant communities in these two regions are deciduous forest and grassland, respectively. It follows, further, that regions which are climatically alike tend to resemble one another, not only in the character of their predominant life forms, but in the physiognomy of the vegetation, taken as a whole. Thus it is that the vegetation of arctic regions resembles that of antarctic regions in its general physiognomy, notwithstanding the fact that the two areas have practically no species in common. In the same way, the world over, luxuriant forests are characteristic of temperate regions having abundant winter precipitation, grasslands of temperate regions having moderate rainfall coming mostly in summer, and so on.

Differences in climate are commonly associated with areas which are geographically distant one from another; but even between areas which are relatively adjacent there may exist more or less marked climatic dissimilarity. In ascending high mountains, for example, differences in climate are encountered at different elevations which are accompanied by differences in vegetation quite as pronounced and of precisely the same sort as those associated with very considerable differences in latitude on the level; and even within areas of generally uniform elevation there may be local modifications in climate, due to variations in topography and in the relative position of land and water bodies. Familiar examples of the effect which these local modifications in climate may have on plant life are seen in comparing the vegetation of north-facing slopes with that of south-facing slopes, the vegetation of ravines with that of level or rounded uplands, and the vegetation of exposed headlands along the seacoast with that of near-by protected situations. The effect of localized climatic conditions on plant life, generally speaking, is most pronounced in regions of varied topography and where the character of the climate as a whole is relatively unfavorable to plant life; but strictly speaking no two spots on the face of the earth have exactly the same kind of climate.

Proceeding further, climate varies not only in point of space but also in point of time. Such a thing as absolute climatic stability does not exist. In every region, rhythmically recurrent atmospheric changes mark the passage from day to night and from one season to another; irregular fluctuations of climate occur from day to day and from year to year; while relatively progressive alterations in the character of one or more atmospheric conditions, extending over a period of years, may result in far-reaching climatic transformations. The devastation caused by frost out of season (or in regions where freezing temperatures ordinarily are absent) and by severe drought in ordinarily well-watered regions illustrate the extreme effects which irregular fluctuations in climate may have upon plant life. The petrified remains of giant trees in the now arid regions of the Southwest (PLATE II) bear mute testimony to extreme progressive changes in climate which have ensued in the course of geologic time. Evidence of marked climatic change within historic time is furnished by the ruins of formerly populous towns and villages in the Syrian desert, in arid portions of the southwestern United States, and elsewhere—in areas where today there is scarcely enough water to support even the scantiest of populations; it is furnished by the dead remains of former woodlands, still standing, which cover hundreds of square miles in the desert region of eastern Turkestan; and so on.* Incidentally, in this connection, it may be remarked that, while climate is all-important in determining the character of the vegetation, the converse relation (which is often assumed), *viz.*, that vegetation has an appreciable effect on the nature of the climate, especially on moisture conditions, is practically without basis in fact.

*Physiographic Environmental Conditions.*—Peculiarities in the form, structure, or behavior of the earth's crust, or of its superincumbent water, may play a highly important part in determining the nature of plant habitats. Broadly speaking, the larger features of the earth's vegetation are associated with peculiarities of climate; the lesser features with peculiarities of physiography. The widespread occurrence of deciduous forests throughout the eastern United States, for example, is associated with the equally widespread occurrence of climatic conditions which are favorable to the development of this type of forest. Within this area, however, there are differences in vegetation between lakes and uplands, between ravines and flood plains, between fresh and saline swamps, between rock outcrops and sand plains: in other words, differences which are attributable to peculiarities of physiography. To state the situation in a few words, the nature of the environment in any particular locality is determined primarily by the combined influence of climatic and physiographic factors.

Physiographic influences are essentially of two sorts, *viz.*, topographic and edaphic. The effect of topographic conditions on the nature of the environment is directly expressed through slope; that is, the degree in which the surface of the land approaches or departs from the level. Indirectly, it is expressed in many ways. For example, the relation of ground water supplies to surface moisture conditions is determined very largely by topography, while the correlation between topographic diversity and local variations in climate has already been sug-

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* For further discussion of this general topic, see [6].

# PLATE II

a. Petrified forest at Adamana, New Mexico. Photograph by I. B. Meyers; courtesy of the University of Chicago.

b. Salt marsh along tidal creek at Momauguin, Connecticut.

gested. Edaphic influences are those due to the physical structure or chemical composition of the soil, or water, or whatever other inorganic medium plants grow in or on, other than the atmosphere. The nature of the chemical edaphic influences has already been outlined. The influence of the physical nature of the substratum on plant growth is seen in the effect of rock as compared with sand or clay, of loose as compared with compact soils, and, in a measure, of land as compared with water.

Proceeding further, the fact must be taken into account that physiography, like climate, is subject to change. Here again the changes are principally of two sorts, rhythmical and progressive. The effects of rhythmical changes in physiography on plant life are best illustrated along the seacoast, where the various seaweeds and other marine plants growing both above and below low-water mark are arranged in more or less definite layers or zones in relation to tide levels. Other familiar examples of physiographic change which might be regarded as rhythmical are seen in the annual freezing and melting of the water in lakes and streams and in the ground, and in the recurrent rise and fall of the water level in ponds and swamps at different seasons. Progressive changes in physiography are exemplified by the alterations in the topographic form of the land and in the physical structure and chemical composition of the substratum which result from erosion and deposition, from soil leaching, and from emergence and subsidence. Such changes can be regarded as being progressive in the sense that they are, so to speak, irreversible. They may take place with relative rapidity, as illustrated by the erosion of ravines and coastal bluffs in sand or clay, by the building up of flood plains along rivers and streams and of coastal swamps, by the filling in of lakes and ponds, and by the movements of sand dunes; or they may be brought about so slowly that they can be estimated only in terms of geological time, as exemplified, in general, by the erosion of solid rock along streams and coasts and by the emergence, subsidence, and base-leveling of land areas.

Progressive changes of any description in either topography or soil can not help but have a modifying effect on the nature of the environment; and, in so far as this is true, they necessarily exercise a corresponding influence on the nature of the plant population. Such changes, in fact, may bring about profound alterations in the character of the vegetation in an area, even within relatively brief periods of time. In the development of a salt marsh along the seacoast (Plate II), for example, every change in the level of the muddy substratum tends to produce a corresponding change of vegetation, and the gradual building up of the ground from below low-tide mark to the level of high tide is accompanied by a definite succession of plant communities. The eel grass, which flourishes just below low-tide level, disappears as soon as the bottom rises high enough to be uncovered between tides. A short distance above low-tide level, the coarse salt thatch becomes the character plant, forming a dense, reedy growth which extends upward to within about a foot of ordinary high-tide level; and at these higher levels the salt thatch community, in turn, gives way to a meadow-like community of smaller grasses and other plants. A similar succession of plant communities characterizes the building up of flood plains along rivers, the building up of swamps along the edges of lakes and ponds, and other similar physiographic changes. In short, successive or cyclic changes in physiography are almost inevitably accompanied by successive or cyclic changes in vegetation.

Even coastal subsidence, ordinarily regarded as taking place too slowly to be of any immediate consequence in its effect on the environment, may bring about pronounced changes in vegetation within what, geologically speaking, are very brief periods of time. Underneath the salt meadows near New

Haven (and at various other places along the Atlantic coast), for example, buried by several feet of salt marsh peat, one can find the stumps of trees that date back to a time, not so many thousand years ago, when the land on which the trees grew was considerably higher than it is now.

*Biotic Environmental Conditions.*—Under this head we may include all environmental influences which originate through the activity of plant or animal agencies. One of the most important of these influences is shade. In a forest, for example, the shade produced by the leafy canopy overhead has the effect of excluding various light-requiring species of plants from the forest floor underneath. Furthermore, the evaporating power of the air is much less in the shade than in the open, a fact which is significant in its bearing on the moisture relations both of the air and of the soil. Herein lies at least one very important reason why many plants thrive in the woods which do not succeed in more open situations. The presence of shade also affects the temperature conditions, both of the air and of the soil. The high death rate among the seedlings of certain trees when growing in open sunlight (species which exhibit very low mortality when growing in the shade) is commonly due to the heating effect of direct insolation upon the surface layers of the soil.[7]

Quite as effective as shade, in its influence on the forest environment, may be the accumulation of humus, arising through the decay of organic matter. To cite an extreme illustration, a bare rock surface is incapable of supporting anything but the most xerophytic flora, yet the accumulation here of only a few inches of humus makes possible the growth of trees. Similarly, "the Michigan dunes show that the most mesophytic of our forests can grow on a sand dune, if there is present a humus layer a few centimeters in thickness."[8] Humus accumulation (on uplands) tends to increase the water-holding capacity of the soil. It variously affects the aëration, the temperature, the acidity, and the toxicity of the soil. It favors the growth of the bacteria, fungi, and other microörganisms which inhabit the soil. The significance of this microörganic soil population, in its relation to plant life in general, is not fully understood, but enough is known to indicate that it may be of the highest importance. The beech, for example, will not grow except in the presence of a soil fungus which infests its roots, while the part played by the nitrifying and nitrogen-fixing bacteria in making nitrogen available to the higher plants has long been known.

Another biotic influence on the nature of the environment is seen in root competition, on the part of different plants. A dense growth of shrubs on the forest floor, for example, may rob the soil of its moisture to such an extent that tree seedlings are unable to germinate. Again, the migration of plants or animals from one area into another may introduce conditions in the area invaded which lead to more or less pronounced changes in vegetation. The effects of plant invasion are familiarly illustrated in the replacement of many of our native herbs by foreign weeds. The widespread destruction of our native chestnut by the chestnut blight fungus, presumably an immigrant from China, is but another example. Other biotic influences are seen in the activity of rodents which prevent forest reproduction by destroying the seed, as in the Rocky Mountains; and so on.

Perhaps nowhere in nature is the influence of plant and animal agencies, as factors of the environment, more graphically demonstrated than in the phenomenon known as biotic succession. When a Connecticut farm is abandoned, to select a concrete illustration, the grassy pastures which constant grazing has kept open soon give way to thickets and groves of sumac and low juniper, red cedar and gray birch. These pioneer trees and shrubs, through the shade and protection which they afford, tend to promote environmental conditions that are congenial to such trees as the oaks and hickories. In so doing, however, they pave the way for their own destruction; for the pioneers among the woody plants are relatively small of stature and they are unable to grow in the shade. It is only a matter of time, therefore, when the oaks and hickories, forming the advance guard of the forest, become sufficiently large to overshadow their less fortunate competitors and sufficiently numerous to form a continuous leafy canopy overhead. But the changes do not stop here. As time goes on and the shade on the forest floor becomes deeper, it becomes increasingly difficult for seedlings of oak and hickory to establish themselves; for these trees are only moderately tolerant of shade. At the same time, as the air becomes moister and as more and more humus accumulates on the forest floor, the environmental conditions are becoming ever more congenial for trees such as the beech, the maple, and the hemlock—species which not only require more moisture than the oaks and hickories but which are capable of reproducing themselves in much deeper shade. Without going into further detail, there is every reason to believe that, under favorable conditions of soil, any open grassy pasture in southern New England, if left to itself, would, in the course of time, become clothed with a luxuriant mesophytic forest of the type which formerly prevailed over vast areas in the northeastern United States, and this very largely through the influence of progressive changes in the environment instituted by biotic agencies.

*Anthropeic Environmental Conditions.*—The activities of man differ fundamentally from those of other animals and of plants in being, to a high degree at any rate, subject to rational control. Almost without exception they are associated with the artificial as compared with the natural. In their modifying effect on the natural environment, the effect of human agencies is expressed in countless ways. It is seen in lumbering and in forest management, in the clearing of the land for settlement and agriculture, in the cultivation of the soil for the production of crops, in the introduction of grazing animals and of various exotic plants. It is seen in the flooding of large areas through the construction of dams, and in the prevention of flooding in other areas by dikes. It is seen in the diversion of streams from their natural courses and in irrigation, in the laying out of roads and trails, of towns and cities, in the effects of gas and smoke, of sewage and other waste products of industrial and community life, and in many other ways. It seems hardly necessary to more than suggest, as I have done, the widespread influence which anthropeic conditions may exercise in determining the nature of the terrestrial environment.

*Pyric Environmental Conditions.*—For reasons which seem obvious, the conditions of the environment caused by fire are placed in a category by themselves. In a sense they might be regarded as climatic in origin, since from time immemorial fires have been caused by lightning. A single dry electric storm in the Pacific Northwest has been known to set twenty-seven different fires. But of course fires are also set by man, who can scarcely be classed as a climatic agency. The outstanding effect of fire on vegetation is seen in the actual annihilation of the plant population, together, if the catastrophe be complete, with the seeds, upon which depends the ability of the vegetation to rehabilitate itself. Scarcely less important, however, may be the modification in the habitat brought about by the exposure of the soil to the sunlight, which results from the removal of the vegetation, and by the destruction of the humus, since by these changes all the conditions associated with the presence of shade and humus are done away with. Generally speaking, the effect of fire is most serious on woody plants; it is least serious on herbaceous plants which live over from one year to the next by means of underground roots or stems.

Fire has been largely responsible for the practical disappearance of forests over immense areas in the West, which in former days were heavily timbered. It has been responsible for many widespread transformations in the forests of the East, such as the replacement of white pine over large parts of Michigan by inferior species,—species which are less susceptible to injury by fire. In the prairie region of the Middle West there is little question that fire has had an important influence in determining the westward limits of the forest.

## COÖRDINATION OF ENVIRONMENTAL INFLUENCES IN THEIR RELATION TO THE ORGANISM

*Introductory.*—In what I have said thus far, I have pictured, in rather broad lines, some of the conditions which go to make up the environment of the plant, and I have pointed out the relationship between various of these conditions, on the one hand, and various features of plant structure and behavior, of plant development and distribution, on the other. There remains to be considered the manner in which the environmental complex, in its entirety, acts upon the plant.

In attempting to explain the relationship between the organism and its environment, much emphasis has been placed, in times past, on the idea of environmental optima: on the idea that for each separate function of the plant there is an optimum condition of light, of temperature, of moisture, and so on; and that for every plant, therefore, there is an ecological optimum environment to which all its functions are harmoniously attuned.* For descriptive purposes this idea of the optimum is a convenient one; but as a precise explanation for the reactions of organisms in relation to environment it is losing favor somewhat in recent years. Such relationships are

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* See [9], p. 44.

much better explained in terms of limiting factors than in terms of optima.

*The Principle of Limiting Factors.*—The general idea of limiting factors, and their application in the present connection, can best be brought out by a few concrete illustrations. For example, certain mineral salts are absolutely necessary in the nutrition of all plants, and a deficiency in the soil of any one of these salts may hinder or prevent normal growth and development: that is to say, it may act as a limiting factor. The practical significance of this fact has of course long been recognized in agricultural practice. Again, seeds require certain conditions of moisture, temperature, and air in order to germinate, and an insufficiency in any one of these conditions may act as a limiting factor to hinder or prevent germination. In a similar way, insufficiency of light, of water, or of carbon dioxid may act as a limiting factor to check or prevent photosynthesis; temperature conditions act as limiting factors to prevent the spread of tropical plants into temperate regions; moisture is obviously the factor which, under natural conditions, limits plant growth in arid areas,—areas which respond so bounteously to irrigation; and so on. In short, there is scarcely any reaction between plant life and its environment which can not be explained in terms of limiting factors.

*The Law of the Minimum.*—The general principle of limiting factors is most simply expressed in what is known as the Law of the Minimum. This law states, in effect, that whenever a process or reaction is dependent upon the combined activity of several factors, the extent to which the process or reaction can be carried is limited by that one of these factors which has a minimum value, or which is present in relatively smallest amount. The law of the minimum is now generally recognized as being "a universal law, affecting . . . *all* factors that in any way influence a reaction or process. The law is applicable to physical, chemical and geological as well as biological problems."[10] This law finds popular expression in that ancient proverb: "A chain is no stronger than its weakest link."

*The Law of Physiological Limits.*—Strictly speaking, and especially in its bearing on the environmental relations of living organisms, the law of the minimum, as above stated, is open to criticism, in that it takes no account whatever of the fact that agencies having a maximum value, as well as factors having a minimum value, may have a limiting effect. To illustrate, "Starting with the optimum intensity of heat for any plant, . . . we may reduce the temperature until death ensues, thus attaining the minimum temperature limit for life." But, on the other hand, "If the temperature be increased sufficiently above the optimum, another death point is reached, the temperature maximum. The plant is thus able to retain life only under temperature conditions that fall within these temperature limits."[11] The general idea here involved is embodied in Livingston and Shreve's Law of Physiological Limits, by physiological limits being understood the extremes of intensity for any environmental condition which an organism can withstand. This law states that "Life is able to proceed in any particular plant [or other organism] only so long as the external conditions do not surpass the physiological limits for the life processes of the form considered." The law of physiological limits, it will be seen, is merely an extension of the law of the minimum; but, in so far as the life processes of plants and animals are concerned, it represents a much more complete expression of the principle of limiting factors.

*Bancroft's Law.*—Limiting factors in themselves, however, are not sufficient to explain all reactions between the plant world and its environment. The law of the minimum, for example, fails to take into account certain phenomena which, in a measure at any rate, may offset the effect of limiting factors. In the first place, plants are able to adjust or adapt themselves, in varying degree, to unfavorable conditions in the environment. Were it not for this fact, they long ago would have ceased to live, since it is extremely doubtful if an environment has ever existed anywhere which has not been in some respect and to at least some degree unfavorable to plant life. The way in which plants react to offset the effect of limiting factors may best be brought out by an illustration. A mesophytic tree, such as the beech, requires, among other things, certain conditions of moisture and light in order to live. Growing in the open, where there is plenty of light, the chief menace to its existence is insufficient moisture. In other words, insufficient moisture here is the limiting factor of the environment. Growing under these conditions, however, the beech, through its own reactivity, tends to overcome the limiting effect of insufficient moisture in two ways. In the first place it expands its root system, thereby tending to increase the amount of water absorbed from the ground. In the second place, it develops a thicker cuticle on the leaves, in this way tending to decrease the amount of water lost through transpiration. Growing in the woods, on the other hand, where there is plenty of moisture, the chief source of danger to the beech is insufficient light. Here again the plant definitely reacts in such a way that it tends to overcome the effect of the limiting factor. The leaves of plants growing in the shade tend to become broader and thinner than those of plants growing in the open, in this way bringing about an increase in the amount of leaf surface exposed to the light. Examples might be multiplied which illustrate the same general idea. The reactions of leaves and stems in relation to light, the reactions of roots in relation to water, the reactions of stems and roots in relation to gravity,—these and many other phenomena of plant behavior and plant development afford unmistakable manifestations of a tendency, on the part of the plant, through its own reactivity, to circumvent the effect of limiting factors and to establish itself in equilibrium with its environment.

The principle involved in reactions of this description is embodied in what is known as Bancroft's Law.[12] This law states simply that "A system tends to change so as to minimize an external disturbance;" or, as Adams[13] phrases it: "A condition of stress is not a permanent one, because the pressure tends to cause such changes as will equalize or relieve this pressure."

*The Law of Compensating Factors.*—The second principle which bears on the effect of limiting factors may be termed the principle of compensation. This principle can be stated, in the form of a general law, somewhat as follows. Where a process or reaction, dependent upon the combined activity of several factors, tends to be limited by some particular factor, the limiting effect of this factor may be compensated, *within certain limits,* by the relatively favorable effect of other factors.*

This idea also may best be brought out by one or two concrete illustrations. Both observation and experiment show that, within limits, the light requirements of plants diminish with increased temperature: at relatively low temperatures plants require more light, at relatively high temperatures they require less. Thus it is that the red cedar, which in New England is confined to open situations, in the South commonly grows in the woods. That is to say, in the South the limiting effect of relatively poor illumination on the growth of cedar in the woods is compensated by the effect of relatively high temperature. Again, it is generally recognized that the water requirements of plants increase with increased temperature, for the reason that more water is lost through transpiration at high temperatures than at low. Thus it is that, with essentially

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* Hooker's (l.c.) "Principle of integration" covers both this and Bancroft's Law, but does not distinguish between the two.

the same conditions of rainfall, forests prevail in northern Minnesota, where in western Texas there are dry grasslands. That is to say, in the North the limiting effect of insufficient water on tree growth is compensated by the effect of relatively low temperatures. The restriction of various plants to particular soils in certain regions and their more general distribution in other regions may very likely be capable of explanation in terms of limiting and compensating factors, and so on.

*Summary.*—To sum up in a few words the points which I have tried to make clear, the plant and its environment may be looked upon as two interacting systems, the plant system comprising a complex of organs, tissues, and cells, the environmental system a complex of activating agencies. The influence of the environment upon the plant is expressed most clearly in terms of limiting factors; but the limitations which tend to be imposed upon the plant by unfavorable factors may be offset, in a measure, either through the reactive behavior of the plant itself or through the compensating effect of certain other relatively favorable factors of the environment.

## ENVIRONMENT IN RELATION TO EVOLUTION

IN concluding this discussion of the environment in its relation to plant life, and by way of introduction to the chapters which follow, it seems appropriate that brief attention should be directed to the influence which the nature of the environment may exercise in relation to the phenomenon of organic evolution. Organic evolution consists fundamentally in the origination of new forms of plants and animals through the modification of existing structures or the development of new ones. Broadly speaking, there are two ways in which it is conceivable that environment may play a part in this process. It is possible, on the one hand, that evolutionary changes may actually arise in more or less direct response to the influence of environment. It seems certain, on the other hand, that environment may determine whether or not the structural peculiarities arising through evolution shall be perpetuated.

That environment is effective in determining the perpetuation of advantageous structures is an idea which is almost universally accepted. In no other way can it be satisfactorily accounted for that the majority of structures in existent plants and animals *are* advantageous. However they originate, only those species can survive which are structurally adapted to the conditions of the environment in which they find themselves or which are able to migrate to other, more congenial habitats. If a tree, for example, should happen to originate in the middle of a desert, it would speedily perish; and a similar fate would befall any other form of plant life which had the misfortune to come into existence in a totally unsuitable habitat. Even in habitats which are otherwise favorable, the ability of a plant to survive is conditional upon its power to compete successfully with other plants, to say nothing of animals. Thus, a light-requiring plant, should it happen to originate in the heart of a forest, could not survive there. Many more plants are constantly being born than there is space for, and habitats are continuously tending to become overcrowded. What happens is graphically suggested by the phenomenon of biotic succession, earlier described. Under natural conditions, the ultimate or climax population of any particular habitat is made up of those forms which are relatively the best adapted to cope with all the conditions of the environment, including competition with other organisms.

In the long course of geologic time, countless forms of plants and animals have become exterminated as a result of inadaptability to environment. Even within historical time many species have become extinct, unable to compete successfully with that increasingly potent factor of the environment, —man. In many cases the cause of extermination has been the possession of some distinctly disadvantageous feature of habit, form, or structure; but it must not be assumed, from this, that advantageous features are the only ones destined to perpetuation. On the contrary, many instances might be pointed out, in the successful flora and fauna of the present day, of congenital features which not only lack any apparent advantage but which may even be of disadvantage to the organisms possessing them. The important point is simply this, that the ability of any organism to survive in the struggle for existence is conditional fundamentally upon its possession of certain advantageous characteristics by which it is adapted to meet the conditions of its environment. That an organism so equipped possesses at the same time certain other characteristics which are of no advantage, and which may even be somewhat detrimental, is not necessarily a matter of great moment. To state the situation briefly, through the *phenomenon* of evolution many sorts of structures—good, bad, and indifferent—have come into existence; but the *course* of evolution has been determined primarily by structures which were advantageous. It is for this latter reason that advantageous structures so vastly preponderate over disadvantageous ones in the organic world of today.

But, while it is generally agreed that environmental influences may be all-important in determining whether or not the structures developed by evolution shall be perpetuated, there is no such agreement when it comes to the question of whether and, if at all, to what extent environment may act as a causative agency in bringing these structures into existence. The Lamarckian ideas that the retention or disappearance of the various structures possessed by plants and animals is determined by use and disuse, that organisms possess an inherent tendency to adapt themselves to changes in environment, that the development of new structures and the modification of existing ones are determined by the needs of the organism, and that the structural variations thus acquired during the life of an individual are handed down from parent to offspring have long since been discarded in most quarters as an explanation of the cause of evolution. How far the pendulum has swung in the opposite direction is indicated by the fact that most geneticists of the present day practically disregard environment as a causative factor in evolution. They maintain that, however much the somatic or vegetative parts of an organism may become modified through the action of environment, the reproductive cells, which alone are capable of transmitting characteristics from parent to offspring, are not affected. Variations, we are told, are brought about solely through spontaneous changes in the germ plasm, and these are in no way influenced by the environment.

In the chapters which follow, various views are set forth regarding the part which environment may play in evolution, and it is not my purpose here to enter into an extended discussion of this topic. Granting, however, that the Lamarckian interpretation of evolution is untenable, it is difficult to get away from the fact that, in plants particularly, countless variations in form and structure do arise in response to varying conditions of environment. Generally speaking, these so-called reaction variations are plastic and not hereditary. They may or may not be advantageous. Whether or not they have any evolutionary significance is still an open question. Certain lines of circumstantial evidence would suggest that they may have. For example, many mesophytic plants, when growing under relatively xerophytic conditions, develop as reaction structures various features which in true xerophytes are fixed and hereditary: such features as reduced leaf surface, heavily cutinized epidermis, waxy and hairy coverings, compact chlorenchyma, and spinescence. Growing in saline soils, various mesophytic species tend to become succulent, a condition characteristic of true halophytes.* Lowland plants, when grown in alpine habitats, commonly assume the dwarfed habit of true alpine plants; and so on. Direct evidence in support of the view that plastic reaction structures may become fixed and capable of inheritance is indeed rare. An apparent example is afforded by the observations of Zederbauer† on two forms of *Capsella* growing in Asia Minor. One form, occurring along an ancient highway in the mountains, at an elevation of 6,000-7,000 feet, is assumed to have been derived through the fixation of reaction structures, in relatively recent times, from another form which is common in the adjacent lowlands. The alpine form differs from the lowland form, among other things, in its dwarfed habit, its greater hairiness, and its reddish (instead of whitish) flowers. Seeds from the lowland plants, when sown at the higher elevation, were found to give rise at once to plants identical with the alpine form; but seeds from the mountain plants, when sown at the lower elevations, continued to produce the alpine form, essentially unchanged, through four generations. A similar derivation of alpine from lowland forms, with an accompanying fixation of reaction structures, is suggested by certain experimental studies now being carried on by Clements.[15]

As yet, the nature of the evidence bearing on the relationship between reaction and congenital structures in plants is not sufficient to definitely prove the case either one way or the other. Granting, however, that reaction structures may have no evolutionary significance, and that the mechanism of inheritance is contained in the germ plasm of the reproductive cells, it does not necessarily follow, even then, that evolutionary changes take place entirely irrespective of the conditions of the environment. On the contrary, it is wholly conceivable, if not highly probable, that external conditions, in

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* Plants of saline soils are termed halophytes.

† See [14], pp. 11, 12.

some way, through their influence on the physical or chemical conditions within the organism, may act to bring about certain physiological changes in the germ plasm and that through the medium of such changes the phenomenon of evolution itself may be instituted. Some such conclusion, in the words of Goodrich,[16] "is inevitable, since any closed system will reach a state of equilibrium and continue unchanged, unless affected from without."

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# CHAPTER II

# THE PROTOZOA AND THE PROBLEM OF ADAPTATION

LORANDE LOSS WOODRUFF
PROFESSOR OF PROTOZOÖLOGY
IN YALE UNIVERSITY

THE use of the newly available simple lenses by an inquiring student of nature during the late seventeenth century, revealed, as by a lightning flash, myriads of 'animalcules' below the limit of unaided vision—living things so extremely small, so numerous, so ubiquitous, that the organic seemed to merge into the inorganic in a new world of the "infinitely little." And since the days of Leeuwenhoek, the patron saint of bacteriologist and protozoölogist, this microcosm has afforded an unfathomable wealth of living beings—the Protista; some obviously plants—the Protophyta; others obviously animals—the Protozoa; and still others showing clearly that our classifications fail at the lowest level of life—all living nature is one.[1]

From the time of their discovery the Protozoa have been at once the delight of the philosopher and dilettante and the dismay of the biologist. The former gaily interpreted them either as proof positive of indestructible eternal living units of higher forms disseminated in nature at the disorganization of the body, or of the opposite—spontaneous generation of life.[2]

O. F. Müller, writing a century after Leeuwenhoek, had enough facts at his command to attempt the first broad classification of the Protozoa.[3] He regarded them as simple animals, devoid of complicated systems of organs. Ehrenberg, the greatest student of the Protozoa during the first half of the nineteenth century, took the opposite view, interpreting the structures which his keen powers of observation revealed in terms of the organ systems of higher animals.[4] And then came the recognition of the fact that higher organisms are essentially congeries of units, or cells, composed of a fundamental physical basis of life, or protoplasm, which led to the interpretation of the Protozoa as relatively simple animals consisting of a single protoplasmic unit, a free-living cell. Today we still briefly define the Protozoa as unicellular animals, thus tacitly implying that a protozoön is directly comparable to a tissue cell of multicellular animals. Though this is undoubtedly essentially correct, the great body of data which has been accumulated within recent years has revealed a complexity of organization in many Protozoa which equals if it does not

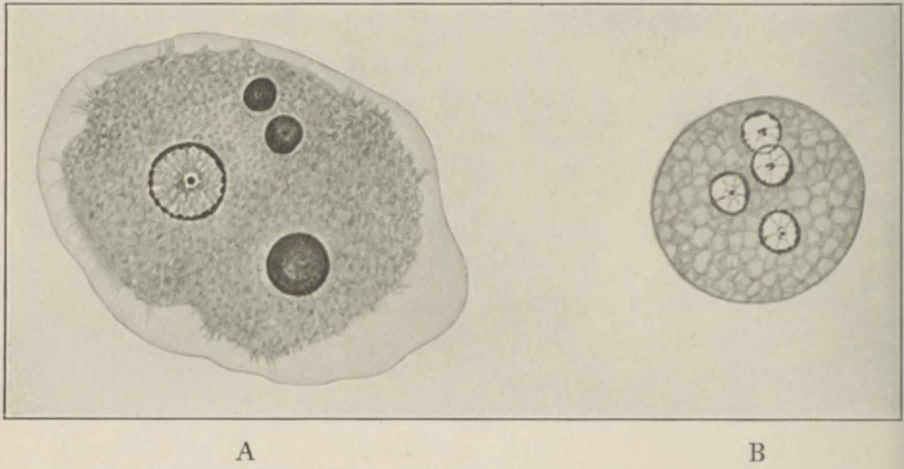

Fig. 2.—*Endamœba histolytica,* an apparently simple protozoön. A, active vegetative individual, showing the nucleus of the cell and three ingested red blood corpuscles; B, encysted individual showing the four nuclei characteristic of this stage. Magnification, about 2500 times. (After Dobell.)

transcend that of metazoan cells, and an intricacy of life history which has led protozoölogists to emphasize that the formal definition of the Protozoa as unicellular animals is highly inadequate. The Protozoa are the *simplest,* but by no means *simple* animals.

Enthusiasm for the Protozoa as simple animals early led to the belief that their study would readily yield valuable information in regard to many obscure but fundamental biological phenomena; even an approach to the riddle of the origin of life. But protozoölogists have not found them an open sesame to life secrets; and, to a certain extent, biologists in general have been disappointed as undreamed-of complexities of structure, function, and life histories have been discovered. One is prone to forget that the present-day Protozoa have enjoyed as long an evolutionary history as Man, and unquestionably are as highly specialized in the *multum in parvo* plan of organization which they typify.[5] We must get away from the Haeckelian "Amœba to Man" idea. "That happy, simple organism which just grows and divides and is called a Protozoön will have to go back some day to the place from which it came—the dominion of dreams."[6]

But with the first flush of enthusiasm faded, biologists in general appreciate that the Protozoa and the Protophyta provide the most available means of approach to many crucial questions; and that their study, in addition to supplying information in regard to the etiology of many diseases of higher plants and animals, including man, has afforded and will continue to afford data which can not be disregarded in the consideration of any broad biological problem—of which *adaptation* is one.

The mere fact that the Protozoa exist implies that they are adapted to their surroundings. "Every creature is a bundle of adaptations. Indeed, when we take away the adaptations, what have we left?" Each protozoön, like every organism, is a microcosm which exhibits a permanence and continuity of individuality correlated with specific behavior, and this it transmits to other matter which it makes part of itself and to its offspring in reproduction. In brief, the phenomena which we call life are dependent upon an exact and elaborate interplay and interchange between the highly organized protoplasmic complex and its environment. Although the protozoön is an individual, it retains its individuality—lives—solely by its powers of developing and maintaining exquisite adjustments to its surroundings. This, of course, results from the irritability of protoplasm; its inherent capacity of reacting to environmental changes by changes in the equilibrium of its matter and energy. And the reaction implies not only response, but also conduction so that the protoplasmic system as a whole is directly or indirectly influenced. It responds as a coördinated unit, an individual; it adapts itself structurally and functionally to the exigencies 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 the Protozoa from the inorganic world.[7]

In a word, the Protozoa, as all organisms, are systems dependent for their maintenance and operation upon energy liberated by chemico-physical processes in protoplasm, and therefore any and all influences which induce changes in their structure or functions must initially modify the underlying phenomena which are responsible therefor. Organic response —adaptation—is a problem of metabolism.

Since living involves a constant interplay of matter and energy between protoplasm and environment, this indicates, as has been recently emphasized by Henderson, that the fitness of organisms implies a reciprocal fitness of their milieu. "The fitness of the environment results from characteristics which constitute a series of maxima—unique or nearly unique properties of water, carbonic acid, the compounds of carbon, hydrogen, and oxygen and (for primordial life) the ocean." "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" for protoplasmic phenomena. The properties of matter and the course of cosmic evolution are intimately related to the structure of living beings and to their activities. Indeed, "the whole evolutionary process, both cosmic and organic, is one, and the biologist may now rightly regard the universe in its very essence as biocentric."[8]

The protozoön is, in its entirety, in somewhat more direct and intimate contact with its immediate environment than is the multicellular organism. The single protoplasmic unit is delimited from the outer world merely by its surface pellicle or membrane, protected, in some cases, by tests of various types. Accordingly, we have naturally looked to the Protozoa for evidences of the *direct* action of the environment in calling forth adaptive responses and, therefore, as a moulding influence in evolution. In short, that modifications, so-called acquired characters, are inherited. But research in the genetics of the Protozoa gives every evidence that the cytological

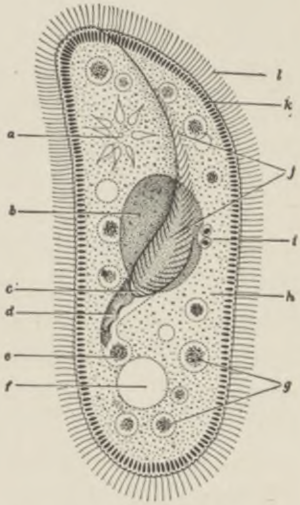

Fig. 3.—*Paramecium calkinsi*, a comparatively complex protozoön. a, contractile vacuole surrounded by radiating canals; b, macronucleus; c, mouth; d, undulating membrane in gullet; e, gastric vacuole in process of formation; f, contractile vacuole; g, gastric vacuoles; h, endoplasm; i, micronuclei; j, peristome and peristomial cilia; k, trichocysts in ectoplasm; l, cilia. Reproduced from Woodruff's "Foundations of Biology" published by The Macmillan Company.

basis—the chromosomal mechanism involved—does not differ in principle from that which is at the basis of inheritance in multicellular organisms. Accordingly, the impress of the surroundings on the protozoön has essentially as devious a path to reach the germ plasm as it has in multicellular forms. And, furthermore, there are no crucial experimental data extant from studies on the Protozoa to justify the belief that acquired characters are actually inherited, or that evolution is more rapid than in the Metazoa.[9]

Thus the zoölogist now appreciates that the problem of the origin of variations in the Protozoa is not intrinsically different from that in the Metazoa. In both it has its basis in hereditary germinal changes—mutations—how called forth he knows not. In both, natural selection is at present the only natural explanation for the accumulation and preservation of those mutations which afford variations that better fit—adapt—the organisms to the exigencies of internal and external environmental factors. However, it should be emphasized that most zoölogists recognize the potent influence of environment *directly* on the germ plasm itself, and also of the organism's reaction 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 *re*produced.

Thus a cardinal fact must be admitted: the science of biology today is not in a position to interpret the adaptation of Protozoa or of higher organisms in fundamental terms. And the protozoölogist can do little more than review some representative instances of adaptations from his field in which they are so forcibly brought to the attention.

The adaptation exhibited by the Protozoa may, for brevity of discussion, be somewhat arbitrarily grouped under general categories: (1) Racial adaptations, both structural and functional, to the physical environment; (2) racial adaptations to the living environment; and (3) individual adaptability. The first two groups comprise what may be called phyletic adaptations, that is, structural and functional adaptations which are at present a part of the racial heritage; while the last, individual adaptability, includes the immediate and *direct* responses of individuals to environmental exigencies as a result of the primary attribute of protoplasm, irritability.

Although the changes of the environment are almost inconceivably complex—uncertainty is the one certainty in nature—there are, of course, life conditions which every environment must supply if Protozoa are to live and multiply: water, food, in the general sense of the word, oxygen, and limits of temperature and pressure.

The Protozoa, as single cells, all demand for active life a more or less fluid medium, and are typically aquatic organisms. However, forms can be selected which exhibit all gradations of adaptation to variations in this regard from those which thrive in oceans and lakes, or pools and puddles, to those which find sufficient the dew on soil and grass blade, or the fluids within the tissues and cells of a host.

The majority of the Protozoa are adapted to a fairly limited temperature range, though certain forms thrive in the waters of the polar seas, and others in hot springs at temperatures certainly higher than 125°F. And in the encysted state the upper and lower limits are greatly extended.

Little is known in regard to the pressure limits which Protozoa can withstand, so all that can be said is that a fauna is present at the highest altitudes where water is not permanently in the form of ice, and almost at the greatest ocean depths which have been explored.

No organs specially devoted to respiration are found in the Protozoa, undoubtedly because the surface of the cell affords an adequate medium of exchange, aided, when present, by contractile vacuoles. Typically, oxygen is taken up from the surrounding medium by the protoplasm, the limiting membrane of which is freely permeable, and carbon dioxid is similarly eliminated. However, many Protozoa inhabiting media which are devoid of free oxygen, such as many parasitic species, are anærobic and secure the necessary oxygen by intramolecular changes in reserve materials stored in the cytoplasm. Even forms such as *Paramecium,* which normally have at their disposal free oxygen dissolved in pond water, are able to survive temporarily anærobic conditions if abundant food has been previously supplied so that a reserve is present in the cell.

Experimental variations in the milieu of the Protozoa have shown that some forms may become gradually acclimated—adapted—to conditions which before were lethal. For example, when pure races of *Paramecium* are subjected for long periods to arsenious acid, quinine, various calcium salts, and so forth, their resistance to these substances is increased and remains so for many generations after the organisms are returned to their normal culture medium. Furthermore, resistance to poisons seems sometimes, at least, to be due to the organisms acquiring the power to destroy the lethal substances. And a point of very great interest is the fact that the longer the *Paramecia* are subjected to a given substance, the longer the adaptation is transmitted after the race is placed again under normal conditions, since this raises the fundamental question whether or no permanent changes may be established in some similar way.[10]

The Protozoa probably afford the most interesting material for the study of adaptation to various nutritional conditions. Some of the lower Flagellates, which are on, if not over, the borderline between the animal and plant kingdoms, have a typical holophytic method of nutrition owing to the presence of chlorophyll or functionally similar pigments; and these forms are closely related to mixotrophic species which combine holophytic and saprophytic methods as occasion demands.

But all groups of the Protozoa, not excepting the Sporozoa which are solely parasitic, supply examples of typical holozoic nutrition, this attaining a very highly specialized state in the Infusoria. Some members of this class are herbivorous and feed practically exclusively on Bacteria; others are carnivorous, confining their food chiefly to various smaller Protozoa, or to special species of Protozoa. Thus *Didinium's* diet is practically restricted to *Paramecium,* and *Spathidium's* to *Colpidium.* It is in species adapted to such special food conditions that selection of food is most prominently displayed. Omnivorous forms are represented by the hypotrichous Ciliates which feed indiscriminately on smaller plants and animals, and even resort to cannibalism. Furthermore, certain species of Infusoria, which have become adapted to live within the bodies of higher forms, have lost all traces of a mouth and merely absorb their nourishment by diffusion through the surface of the cell in typical saprophytic manner. Finally, there is some evidence that certain Infusoria, which have been supposed to demand Bacteria as food, are able to thrive in sterile synthetic media, their carbon and nitrogen needs being satisfied by glucose and ammonium lactate. In short, it is possible to trace the adaptive radiation of various genera of Infusoria from a generalized holozoic type to types

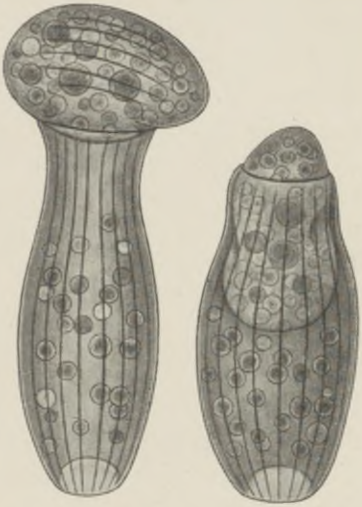

Fig. 4.—*Spathidium spathula,* capturing and swallowing a *Colpidium.* (After Woodruff and Spencer.)

specialized for fundamentally different methods of food-getting.[11]

The complex of various physical environmental factors is indirectly responsible for the phenomena of polymorphism which are illustrated by many striking instances in the Protozoa. Indeed, hardly a single species is strictly monomorphic, and many possess life histories which afford a varied pageant of dissimilar forms succeeding each other in more or less regular order, determined largely, if not entirely, by the conditions of the environment.[12] It is this multiplicity of form within the species which contributes so largely to the difficulties of the taxonomist and parasitologist, and to the pleasures of the protozoölogist interested in fundamental biological problems. In the Protozoa the complete life history is the unit which must be dealt with.

A survey of life histories would involve a consideration of the some ten thousand protozoan species. It must suffice here to state that the types of polymorphism may be classified under two chief categories, individual and racial. Individual polymorphism is essentially facultative, and the various forms are assumed as an immediate adaptation to changing surroundings. A common example is the process of encystment whereby the organism protects itself by secreting a resistant envelope, or cyst wall, around its body. Racial polymorphism, on the other hand, is an expression of adaptations which are inherent in the ontogeny of the species. In general, it must find expression, such as the periodicity of sexual phenomena, though called forth, as a rule, by either intrinsic or casual environmental conditions. Necessarily all the various adaptations to which we shall have occasion to refer as we proceed come under this general analysis.

We may turn now more specifically to a consideration of some striking interrelations of organism with organism, to illustrate the devious ways the strands of the web of life become entangled in the competition for a livelihood even among the Protozoa. Perhaps the microcosm created by adding a few wisps of hay to a beaker of water may serve as a general picture.[13] The initial period of bacterial ascendency having attained its height, another factor gradually intrudes itself almost imperceptibly—the protozoan population. The vanguard are various species of exceedingly minute Flagellates, which either absorb products of organic disintegration brought about by the Bacteria or ingest the Bacteria themselves. Then species of small Ciliates, close relatives of *Paramecium,* appear in untold numbers and feed upon the Bacteria. The dominance of these smaller Ciliates is shortly brought to an end by the ascendency of larger ones, chiefly Hypotrichs, which, though feeding upon the now greatly depleted bacterial population, obtain most of their food by eating the smaller Ciliates. And so the cycle of the Protozoa continues: saprophytic forms gradually are replaced in dominance by herbivorous, and these in turn by carnivorous, until sterility follows through exhaustion of the initial food supply—unless green plants gain access and, through the agency of their photosynthetic pigment, proceed to replenish the energy-depleted microcosm. Thus the food of carnivorous forms, indeed the life conditions to which they are adapted, is actually an integration of the organismal factors which preceded; and a glimpse is afforded of the fact that "nature is a vast assemblage of linkages" even in the world of the Protozoa.

From such associations of species in which the sequences of dominance of each is dependent upon a complex of adaptations to an environment suitably modified by all the succeeding forms, we may pass directly to mutual adjustments between individual species of Protozoa with other organisms, in which the keynote is coöperation rather than competition.

Perhaps the most familiar example of the latter is the epizoic association of *Trichodina ovata* and *Kerona pediculus* with the metazoön *Hydra.* Neither of these Ciliates is able to secure a livelihood except when creeping over the body of *Hydra* and devouring the débris from the surface. A nicety of the adaptation to this peculiar habitat has not only rendered these protozoöns immune to the nematocysts of *Hydra,* but, at least in the case of *Kerona,* exploded stinging-cells actually serve as food. And probably *Kerona* may exceed the bounds of commensal relations when occasion demands by devouring other living cells of its associate.[14]

It is only a step from such external relationships to that shown by the great assemblage of protozoan species which are specialized to live within one or another of the cavities of the bodies of higher animals. The entozoic forms, representing all of the great protozoan groups, are in most cases probably merely intestinal scavengers, though so adapted to the special conditions which there prevail that they usually succumb when introduced into a similar situation in a closely related species, or brought to the outside world.

What must be interpreted to be an effect of isolation as an evolutionary factor is more forcibly shown by some entozoic forms than by the insular distribution of higher animals, as Darwin would have attested if he could have studied, for instance, the numerous species of Opalinids which live as commensals within the rectum of various species of Amphibia. The Leptodactylidæ are the characteristic "frogs" of tropical and south-temperate America, and are found also in Australia and Tasmania, but nowhere else. This has been interpreted as indicating a former land connection between Patagonia and Australia by way of Antarctica. Some, however, have questioned this conclusion, believing the resemblance between American and Australian frogs to be due to convergent or parallel evolution. But the latter interpretation is rendered highly improbable by a study of the Opalinids inhabiting the Leptodactylidæ, which shows that similar frogs are inhabited by similar Opalinids. It is hardly conceivable that both frogs and protozoöns have evolved in parallel or convergent lines on the American and Australian continents.[15]

Commensal associations merge gradually into the truly symbiotic relationships where both members mutually contribute to the success of the partnership. Excellent examples of symbiosis are found among the Sarcodina, such as some of the Foraminifera and most of the Radiolaria, which constantly harbor unicellular holophytic Flagellates, or unicellular green Algæ. Thus Cryptomonads, symbiotic in the foraminifer *Peneroplis pertusus,* penetrate into the cell of the host, lose their flagella, and nourish themselves by their photosynthetic pigment. The carbon dioxid is obtained from the respiratory processes of the host, and the latter in turn utilizes the oxygen liberated. When the body of the host breaks up into swarm spores, the Cryptomonads develop flagella and swim off, presumably to secure a similar lodging in some other foraminifer.[16]

Another symbiotic relationship is presented by the Trichonympha which are Flagellates found solely in the digestive tract of termites, or white ants. This writhing intestinal fauna, numerous in species and numberless in individuals, has just been shown to be responsible for the digestion of wood particles which form a considerable part of the diet of termites, since 'defaunated' termites are unable to digest cellulose in the absence of commensal Trichonymphs. In brief, the protozoöns apparently act essentially as glandular cells within the digestive tract of the termites; securing in return for their enzymal action an abode somewhat aloof from the general competition in nature. And this side eddy, as it were, in the stream of protozoan evolution exhibits highly specialized structural and physiological adaptation to its peculiar life conditions.[17] So examples could be multiplied almost indefinitely, the variations on the general theme are legion. In some cases so intimate are the relations which are established that it is still debatable whether the intrusive 'symbionts' are actually distinct organisms or merely organelles of their bearer!

But associations in which one organism, the parasite, secures the sole advantage, and, in most cases, at the expense of the hapless second party, the host, afford illustrations of a nicety of adaptation only exceeded by symbiotic relations. Indeed, symbiosis is undoubtedly a further refinement, as it were, of an initial commensalism or parasitism; and it is certain, among the Protozoa at least, that many associations which we now interpret as parasitic on further study will prove to have a reciprocal aspect not now recognized. It is but natural that the associations which have been forced upon our attention are those in which the host suffers obvious inconveniences or even death. In brief, those in which the host has not become adapted to bear the burden with the least outlay.

Generally speaking, the effect on the parasite consists in a simplification of the various parts of the cell devoted to food-getting, locomotion, and so forth, since these duties are largely foisted upon 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 parasitic protozoön is adapted to live in a specific host, and death ensues if this is not attained at the proper time.

Probably the most generally interesting example of parasitism in the Protozoa is afforded by the several malarial organisms, members of the Sporozoan genus *Plasmodium*, which spend the sexual phase of their life history in the mosquito and the asexual phase in the red blood corpuscles of man. 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 digested; except the sexual forms which are ready to initiate the sexual part of the cycle in the new host. These are immune, and proceed to live and multiply.

The acme of parasitic associations is attained when the adaptations of parasite and host have become so complete that the latter 'pays the price' without ill effects. This is apparently the case with human carriers of *Endamœba histolytica*. When the normal relationship exists between the human host and the amœba, neither shows any untoward effects. The amœbæ devour the cells lining the digestive tract, though not in excess of the compensatory power of regeneration which the tissues possess. Occasionally, however, the physiological idiosyncrasies of certain individuals (*Homo* or *Endamœba*) make such mutual compatibility impossible. Chronic intestinal disturbances are set up which result in the evacuation of the amœbæ before they are able to encyst, so that many of the amœbæ are destroyed. Furthermore, lesions of the intestine allow the amœbæ to wander to liver or to brain, where again they are unable to complete their life history. In either event the serious consequences to the human host are coincident with equally serious consequences to the amœbic parasite. The human carrier, while he is a prolific source of infection, represents the ideal parasitic relationship in which reciprocal adaptation of host and parasite is practically complete.

A quite comparable relationship is illustrated by the antelopes and similar large game of certain regions of Africa which harbor in their blood without any apparent discomfort various species of Flagellates, known as Trypanosomes. But if the intermediate hosts, which are bloodsucking flies, transfer, for example, *Trypanosoma brucei* to imported horses or cattle, a serious disease results which is usually fatal.

Thus the pathogenic properties of *Trypanosoma brucei* appear to be exerted on new hosts and not on those with which it has established harmonic adaptive relations during the course of evolution. The pathogenicity of this Trypanosome, as well as similar forms, almost certainly must be interpreted as a disharmony associated with the initial stages in the origin of species. The question of the origin of trypanosome diseases merges into, if it does not become identical with, the origin of species. If this is true, the point of crucial importance is how the establishment of reciprocal relations which eventually are harmonious is attained. From the standpoint of both parasite and host the adaptations must be both individual and racial. We may safely assume that individual hosts especially susceptible to the ravages of the parasite would be gradually eliminated, and, concurrently, parasites especially lethal would contribute to their own destruction. Thus, of course, in the final analysis, we must look to mutations of parasite or host, or both, for the origin of immunity—adaptation. And here, as elsewhere in nature, the best evidences of evolution are offered when species are thrust into a new environment which affords the opportunity—the necessity, if the species is to survive—for germinal variations which happen to be adaptive to become established.[18]

Finally, we may refer briefly to the highest expression of adaptation evolved by nature, which is revealed in relatively simple form by the behavior of the Protozoa and gains definiteness and content as we ascend the animal series, to become, eventually, the basis of intelligence.

The behavior of the Protozoa which has been carefully investigated is strikingly adaptive in most cases. The organism, in general, moves and reacts in ways that are advantageous to it. If it enters an injurious chemical solution, it changes its behavior and usually escapes, if escape is possible. If it requires food, it initiates movements which tend toward securing such materials. "In innumerable details it does those things

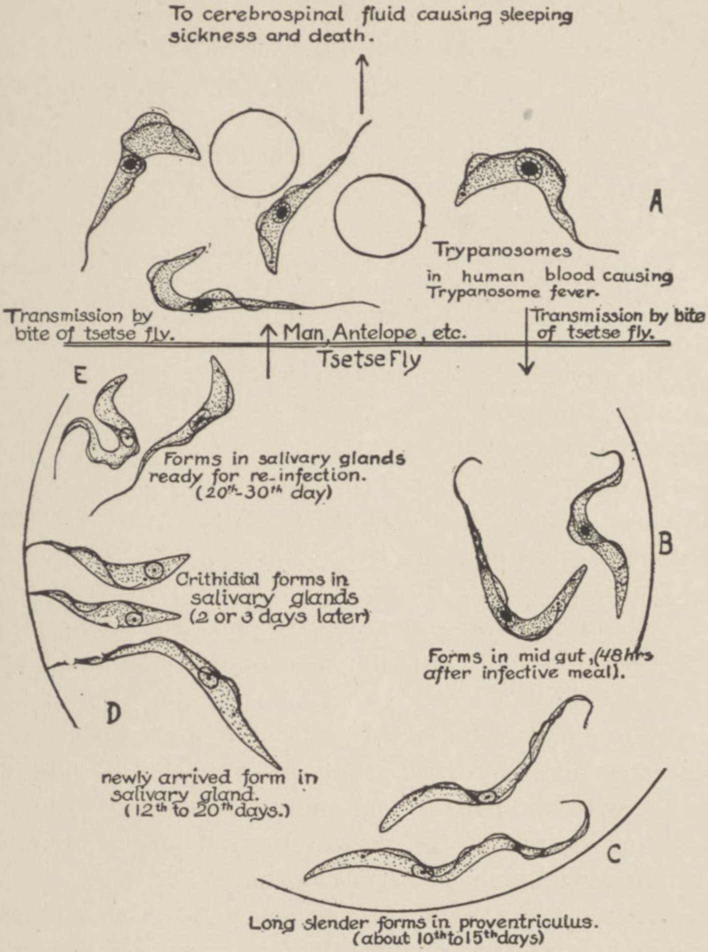

Fig. 5.—*Trypanosoma gambiense.* Diagram of the life history. Reprinted by permission from "Animal Parasites and Human Diseases," by Asa C. Chandler, published by John Wiley & Sons, Inc.

which are good for it." If this were not true, there would be no Protozoa!

In the Protozoa, however, it is possible in many cases to observe just how such adaptive responses take place. Very generally stated, conditions injurious to the animal induce changes in behavior, and these changes subject it to new conditions. Just so long as the undesirable conditions prevail, these changes continue. In other words, they cease when conditions are attained, by the so-called trial and error method, which no longer afford the unfavorable stimulus in question.

But this is only a very general statement of observations. Does it lead toward a fundamental interpretation of adaptive behavior? Our answer must be that it brings the problem down directly to the metabolism of the organism; as far down as our present knowledge of the chemical phenomena of life allows us to penetrate. True it is that, from one standpoint, the word metabolism serves to cloak our ignorance.

In the Protozoa the general processes of metabolism hold a commanding position because they are not interfered with by an "immense number of coördinated and subsidiary processes." Accordingly the organism directly changes its behavior as a result of any disturbance of its physiological processes. Granting, then, this direct influence of stimuli, how do they induce movements which are adaptive? Solely by indirect means. The animal merely reacts in all possible ways so long as it is stimulated; and the chances are that sooner or later it will attain a position which restores its previous equilibrium.

An example will serve to make this clear. When the sessile infusorian *Stentor* is first stimulated by, let us say, a flood of carmine grains which are useless to it, no reaction occurs. As the carmine continues, the animal bends over to one side. This reaction not removing the stimulus, the beat of its cilia is temporarily reversed so that the carmine momentarily does not reach the oral apparatus. But, if the stimulus still continues, the organism contracts more or less violently; and, finally, contraction being ineffectual, the *Stentor* detaches itself and swims away. Swimming away is the effectual "relieving response," but any responses in the series would have been such, if at that moment the carmine grains had ceased to reach the animal. A series of different physiological states is obviously initiated, since the animal successively responds in a different manner to the same stimulus.

Thus interference with the physiological processes initiates the changed behavior; and a cessation of interference removes the provocative cause, so that adjustment is actually reached by repeated changes of movement. The organism "selects" favorable surroundings merely by ceasing to change its behavior when such are attained. In brief, it has made an adaptive response. But an adaptive response made in this way does not demand that the purpose of the reaction bears any causal relation to the result. None of the factors necessarily include, apparently, anything different in fundamental principle from methods operating in the inorganic world.

A *Stentor* which has been subjected a few times to the experiment with carmine, just described, soon ceases to run the gamut of the series of responses. Instead, almost as soon as the carmine stimulus acts, the animal detaches itself and swims away. So it is right at this juncture that an additional factor intrudes itself. The relieving response gradually becomes established through what may be called the "law of the readier resolution of physiological states as a result of repetition." The animal after attaining several times the relieving response by repeating a succession of movements, thereupon more quickly reaches the relieving response upon a recurrence of the interfering condition. And sooner or later this reaction is made immediately to this interfering condition.

It is just at this point that we obtain a glimpse of something in the protozoön that suggests habit and memory in the objective sense. It is here that the behavior of the protozoön seems to be dominated by an end or purpose. In man, it does exist as a subjective state, an idea. Whether something elementally similar exists in the protozoön, obviously can not be determined; though there must be some transient, objective physiological state corresponding to "the objective physiological accompaniment of the idea in man." Whatever the answer, it is to such phenomena in the Protozoa that we must turn for the genesis of what in its higher reaches we call intelligence—the adaptive complex supreme.[19]

In this necessarily cursory survey of protozoan adaptations and adaptability it is evident that, looked at broadly, these phenomena are no less prominently forced on our attention by the unicellular than by the multicellular animals. However, there is one difference which has at its foundation the difference in organization between the protozoan and metazoan types. The unicellular plan has obvious inherent limitations which adaptations can not surmount, while the multicellular type of organization affords possibilities which almost transcend imagination. But the potential for evolution of the protozoan type *was* expressed when it gave rise, in the geological past, to the metazoan stock, which allowed the powers of adaptation pent up in a single cell to find expression in specialization and coöperation in the individual of another and higher order, which multicellular animals, including man, represent.

The heritage of adaptability from the Protozoa appears to be the measure by which nature has tested each kind of animal evolved, for the general course of evolution has been always in the direction of increasing adaptability, or increasing perfection of irritability. Our heritage from the Protozoa affords the cumulative results of the adaptations of the race—including adaptability.

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# CHAPTER III

# ENVIRONMENT AS A STABILIZING FACTOR

ALEXANDER PETRUNKEVITCH

PROFESSOR OF ZOÖLOGY
IN YALE UNIVERSITY

IN presenting the following thoughts concerning the relationship between the organisms and their environment for careful consideration, I was actuated by the desire to call the attention of all interested to one aspect of the problem, which under the influence of the Darwinian theory of natural selection has been most unfortunately misinterpreted. With this object in view I have subjected to critical analysis the evidence obtained from the study of parasites and gradually accumulated by numerous investigators for totally different purposes. To understand its bearing upon the broader problem of the origin of species it is, however, indispensable first to consider the relationship between the individual and its environment and then to proceed to the discussion of the true meaning of those processes which are invariably interpreted as natural selective agents, and which in my opinion have a diametrically opposite function.

The most characteristic properties of living matter are its ability to assimilate and the stability of its structure. In a way the latter property is only an attribute of the former, inasmuch as assimilation is production of like living substance from unlike chemical material. Experiments made under the most exacting laboratory conditions and covering almost every important natural factor have demonstrated beyond the possibility of any doubt that numerous of these factors constituting a normal environment are indispensable for normal development, and that a modification or elimination of some of them inevitably results in partial or complete derangement of developmental processes. But the composition of a normal environment is so complex, the singling out of the factors essential in each individual case so extremely difficult, the consequent appearance of variability of an environment so manifest, that the stability of the organism as emphasized by the similarity of every specific feature of parent and child forces itself upon our senses not only as something self-evident, but as an intrinsic quality of living protoplasm itself. What wonder that under such circumstances there should be little incentive to inquire further into the origin of this manifest stability of organisms, and greater interest in the study of the origin and behavior of their variations, using that term in its broadest sense?

It is to Weismann's everlasting credit that he was the first to show clearly what consequences have to be drawn from the assumption of an almost absolute stability of an organism. The non-inheritance of acquired characters, in the light of Weismann's theories, became a self-evident and unavoidable consequence of the continuity of a stable germ plasm. The structure of the latter, under normal conditions, was conceived as being entirely responsible for the stability as exhibited by the specific identity of progenitor and offspring through countless generations. The variations were strictly separated into somatic and germinal and the natural selection of the latter accredited with the production of new species. Later the influence of the environment was made partly, at least, responsible for both types of variations, as in the case of drugs or temperature directly affecting the germ plasm.

The Neo-Lamarckian attack on Weismann's theories, although in every respect inferior in logical perfection and harmony, possessed nevertheless such an impetus and disposed so easily of many difficulties by assumptions none too strongly based on experimental evidence, that the propositions under dispute were themselves gradually so shifted and modified as to become almost unrecognizable. In more recent years the work of geneticists has thrown new light on the entire problem and once more put on a firmer basis the idea of the germinal origin of heritable variations and with it that of the remarkable intrinsic stability of the germ plasm.

In all this reasoning on the part of those who support what may be termed Neo-Weismannian theories, there is one tacit assumption which is also accepted by their opponents as a condition *sine qua non.* I mean the "normal" environment to which the offspring is returned after the subjection of the parents to the influence of a "modified" environment. Many years ago, in my paper *Gedanken über Vererbung* I intimated the fallacy and the misleading influence of such reasoning. Let us consider this subject in greater detail as it has an important bearing upon our problem.

The heritable permanency of a character modified through the influence of a changed environment is generally tested by its behavior in subsequent generations under normal conditions. If, for instance, we have before us the case of some animal in which the color of its coat has been changed through the introduction of a new element in the food, and if that new color does not reappear in the progeny when the new element has been removed from their food, then such change would not be considered heritable. This at present will be granted without a moment's hesitation by every geneticist or biologist in general. Giving a concrete example, we may recall the case of the European bullfinch, a bird, the female of which is brown, while the male possesses brilliant red plumage on the breast. This red color, however, though normally due, as a secondary sexual character, to the internal secretion of the male glands and heritable as such, may be modified by a change in the food. A bullfinch fed for a considerable length of time on hempseed loses his red color in favor of a brown much like that of the female. But this new color is said to be non-heritable because when the young are fed on other food than hempseed they grow up to be red. Herein lies the error of such reasoning. For, barring the habit of the bird, the "normal" food may be regarded as changed environment in the case of the offspring just as much as hempseed constituted a change from the normal food in the case of the parent. We say that the bullfinch becomes brown because it eats hempseed instead of other food. But we could with equal right say that the bullfinch becomes red because it eats other than hempseed food. Whether such characters determined by some factor of the environment, in the continued presence of that factor, are subject to the Mendelian laws of inheritance or to some other as yet unknown laws, is irrelevant. For is not inheritance the transmission of characters from parent to offspring and are not all offspring in this case like their parents as long as they are bred in an environment identical for all generations?* And what but an experiment prolonged over a great many generations could decide how long it would take to establish an exclusive hempseed feeding habit?

Let us consider another and still more illuminating case, that of the European hermaphroditic fluke, *Polystomum integerrimum,* the adults of which are normally found in the bladder of frogs and toads. The reproductive organs of this fluke remain quiescent during the winter, copulation and depo-

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* We could deny the validity of such reasoning only if the color of the young which, like its parent, was fed on hempseed was nevertheless different from that of the parent, *i.e.,* if, for example, it were green or yellow. Although the identity of results is not necessarily an evidence of the identity of the causes, seeing that in nature as well as in mathematics the same result may be due to very different causes, it is more than probable that the brown color of the plumage in parent and offspring fed on the same food is caused by the presence of an identical factor in their organism.

sition of eggs beginning in spring. Yet the condition of the organs is such that if a frog parasitized by *Polystomum* is placed even in November in a warm room the parasites will begin to copulate within three or four days. In the intervals between copulation which may be repeated twenty times in one hour, fertilized eggs are laid and reach the water with the excrements of the frog. In this manner, one hundred eggs, on the average, are laid every day for ten days. They all drop to the bottom and the duration of their development is directly influenced by the temperature of the water. At room temperature it is completed in nineteen or twenty days. It may be accelerated to only fourteen days or retarded to twenty-seven days. At a temperature of 46°-50°F. the development is retarded to from six to eleven weeks. In nature the eggs are laid in spring and develop in from six to twelve weeks. The time when the larva emerges from the egg, coincides more or less with a certain stage in the development of tadpoles in the same pond. The larvæ may live up to two days in the water but are doomed to die unless they find their host within this time. Having found a tadpole the larvæ move in the manner of a geometrid caterpillar toward the external branchial aperture, pause for a few moments, then dart suddenly into the gill chamber and attach themselves to the gills. Here the metamorphosis of the larvæ is completed within eight or ten weeks, coinciding with the metamorphosis of the tadpole. The young *Polystoma* leave the branchial chamber when the gills begin to wilt, pass to the pharynx, slide down the entire alimentary canal to the rectum and enter the urinary bladder. They become sexually mature after a lapse of four or five years. The anatomical structure of *Polystoma* developed in this manner has been studied in great detail and the main features may be seen in figures 6 and 7.

Sometimes, however, the *Polystomum* larvæ attach themselves to very young tadpoles. In nature this happens only

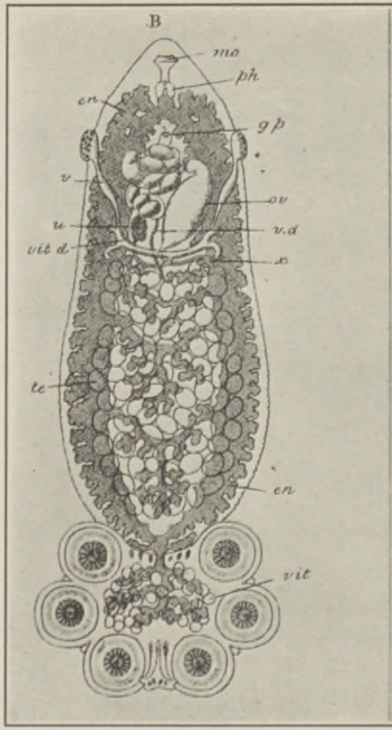

Fig. 6

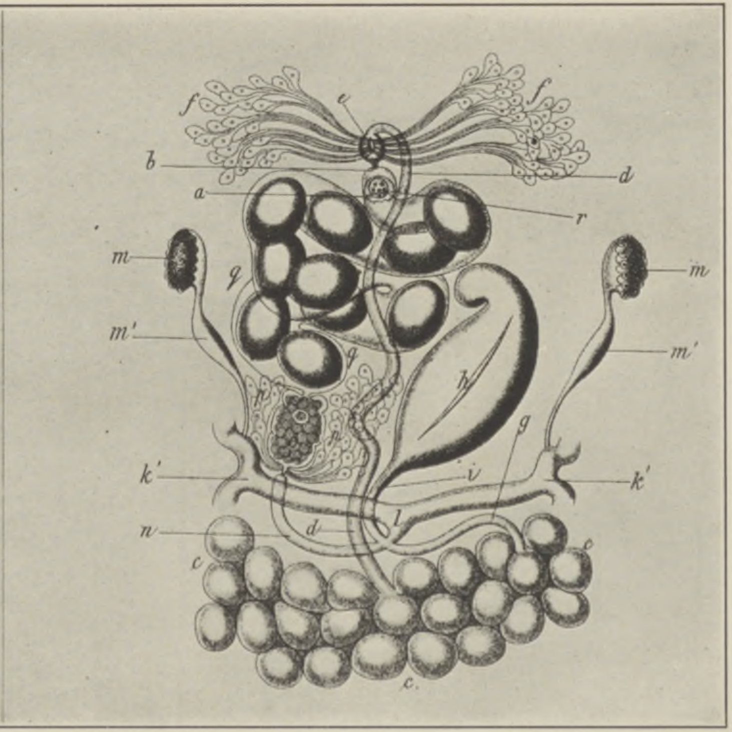

Fig. 7

Fig. 6.—*Polystomum integerrimum,* adult from the bladder of a frog. en, intestine; g.p., genital pore; mo, mouth; ph, pharynx; ov, ovary; te, testes; u, uterus; v.v.d., vas deferens; vit., vitelline glands; vit. d., vitelline ducts; x—marks the position of the genito-intestinal canal connecting the oviduct with the intestine. (After Zeller, from Parker and Haswell's *Textbook of Zoölogy.*)

Fig. 7.—*Polystomum integerrimum.* Genital apparatus of a specimen from the bladder of a frog. a, genital opening; b, genital cloaca; c, testes; d, vas deferens; e, cirrus; f, glands; g, inner sperm duct; h, ovary; i, oviduct; k′, vitelloducts; l, common vitelloduct; m, genital papilla; m′, vagina; n, second portion of oviduct; o, oötype; p, shell gland; q, uterus filled with eggs; r, sponge-like body. (After Zeller, Zeitschr. f. wiss. Zool., Vol. 27, 1876.)

extremely rarely, but in the laboratory the experiment has been repeated many times. In such cases the development is considerably accelerated, being completed in about twenty days, and the parasites mature and lay eggs in the branchial chamber. They never make an attempt to reach the urinary bladder and die during the transformation of the tadpole. What is especially interesting to us in this case is the change in the anatomical structure of the adult *Polystomum*, involving particularly the reproductive system (Figure 8). The hooks are smaller and of a different shape; and instead of numerous testes a single testis is present. The copulatory organ is modified and useless. The seminal duct which connects the testis with the oviduct serves now for the passage of the sperm to the

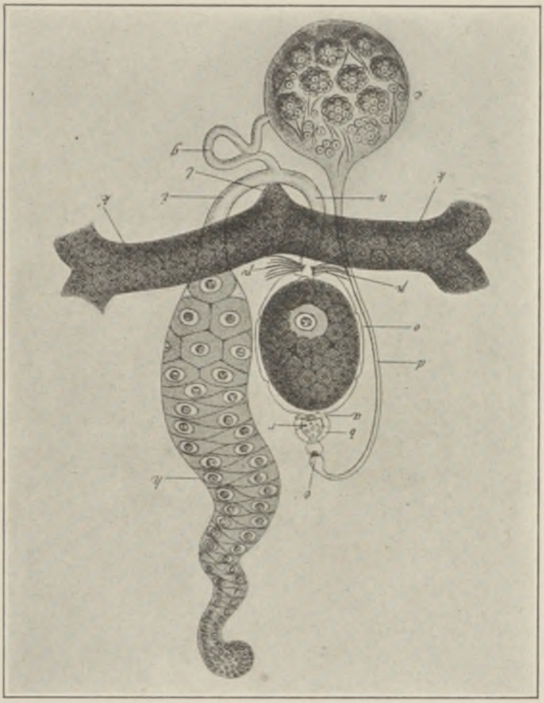

Fig. 8.—*Polystomum integerrimum.* Genital apparatus of a specimen from the branchial cavity of a young tadpole. a, genital opening; b, genital cloaca; c, testis; d, vas deferens; e, cirrus; g, inner sperm duct; h, ovary; i, oviduct; k′, vitelloducts; l, common vitelloduct; n, second portion of oviduct; o, oötype with a single egg; p, shellgland; r, sponge-like body. (After Zeller, *ibid.*)

oötype in which the eggs are fertilized. Thus cross-fertilization is impossible and self-fertilization without copulation is the rule. The spermatozoa are also modified; they have no distinct head and are slightly swollen in the middle. The female reproductive organs show still greater modification. The lateral papillæ, both vaginæ, and the uterus are absent. The yolk-glands are not greatly developed, although their ducts are filled with yolk. The oötype opens directly to the outside, a condition greatly resembling that found in another species, *Polystomum ocellatum*, found in turtles. The ovary is longer, but the eggs are normal, although fewer in number. They develop into perfectly normal larvæ which in their turn may develop into the one or the other type of *Polystomum,* depending upon the age of the tadpole which they choose for their domicile. It has been suggested that the change in the anatomical structure of *Polystomum* is due to the richer nourishment received by larvæ which attack very young tadpoles. Such an explanation, however, is quite inadequate for from observations on other animals we know that the quantity of food does not affect anatomical structures. It is much more probable that the blood of the young tadpole is chemically different from that of older ones in which the thyroid and other glands with internal secretion begin to function; and that the presence of such secretions in the blood retards the development of *Polystomum,* and is responsible for that structure which we consider to be normal because it is usually met with in nature. Yet could not the other phase be regarded just as normal? And is not the form in both cases clearly dependent upon the chemical environment?

The case of the honey-bee is similar, inasmuch as it is unquestionably true that the development of a fertilized egg into a queen or a worker is dependent upon the type of food which the adult workers offer the larva. It is in their power to change the fate of a larva destined by the mother to develop into a worker when she deposits the egg into a worker cell, and to rear a queen instead, provided that the larva is not more than three days old. Weismann tried to explain the case by an assumption of an additional set of determinants, or what now would be termed genes by geneticists, in the germinal plasm of the bee. He further postulated that food was only the releasing factor permitting the one or the other set of determinants to become dominant in development. But such an assumption is quite gratuitous seeing that the characters can not possibly be developed unless the food, *i.e.,* the chemical environment, is of a specific kind.

Let us assume for a moment that the apparent stability of morphological characters of an organism is the direct result of the wonderful stability of the germ plasm, an intrinsic attribute of the structure of the germ plasm, preserved in its function of assimilation and growth. If that were so, nothing but germ plasm could result from such assimilation and growth. Yet the very first segmentation division, or in some cases one of the closely following ones, determines the separation of the body from the germ plasm, the former merely enclosing, protecting, and nourishing the latter. Pursuing that portion of the original germ plasm which will form the body, we find that its relationship to the environment is of a most remarkable kind. For a simple calculation can show that in the adult human organism, for example, not more than one two-hundred-billionth part of it is derived from the parental germ plasm, while the rest has been assimilated from the environment. And this does not take into account the daily exchange of matter and energy in the normal processes of life during the years after the full development of the body has been reached.

But the stability of the germ plasm itself is, to say the least, of a peculiar kind. The first, or in some cases second, third, or at most the fourth segmentation division, completely changes the ability of the germ plasm either to produce directly a complete organism, or to unite without damage to itself with a male reproductive cell. The latter ability is regained only after a prolonged series of divisions inside the maturing organism which constitutes the chemical environment of the germ plasm, and from which the latter derives the material for growth. And here, if we were to calculate the bulk of all the eggs or of all the spermatozoa produced by a human being during life, we would be appalled by the infinitesimal quantity of original germ plasm in an egg or a spermatozoön.

It seems as if our conception of stability were in some respects at least an erroneous one. Indeed, if we could conceive of two identical variable systems in two identically variable environments, the changes in each system being identical, such changes would become to us quite subordinate and little noticeable as compared with the quite apparent "stability" of each system as expressed in the identity of changes. Similarly, in the case of organisms which, having the same morphological structure, may be regarded to all purposes as identical variable systems, the stability may be only an illusory one. The environment in which, for example, a mammal embryo develops, is almost identical in the case of each embryo of the same species and reaches its nearest approach to identity in the case of twins, being in the womb and nourished by the blood of the same mother. Still human identical twins if placed in totally different environments, show in after years great divergency of morphological and psychological characters not originally noticeable. Even in uniparental development, such as is never interrupted by any sexual reproduction, variations occur. Though such variations are supposed to be of a germinal origin, is it not clear that in the ultimate analysis they are due to the influence of the environment, probably of the chemical environment on the germ plasm?

"Normal" development and "normal" morphological structure can not be therefore attributed to the structure of the germ plasm alone. To be sure, there must be a certain chemo-physical structure to start with; and this structure must be very much alike in the case of all animals belonging to the same species. Nevertheless, its further fate, its mode of development and its ultimate characters, whatever their hereditary value, are dependent upon, and in a way are a function of, the environment.

As a rule it is the multiplicity of factors constituting an environment, that guarantees the "normal" development and structure of an animal. Wherever and whenever the accustomed balance of forces is upset by a considerable preponderance of a single factor, abnormalities make their appearance. That is why "normal" environment, *i.e.,* that to which the animal is attuned, may be considered to exert a stabilizing influence. But we know many cases of chemical environment in which a single factor seems to be indispensable. In such cases normal development is conditioned on the presence of this factor. Its absence means death or malformation. All the other factors either have no effect whatsoever or exert an injurious influence. But in doing this they serve as stabilizing agents. No matter how many or how advantageous the heritable variations may be, which are produced by the organism in question, all such variations are doomed to perish for lack of the single indispensable chemical factor. This means that the already existing characters alone will survive, unless the particular character will be changed, the character which makes life, without the special chemical factor, impossible. The process of elimination in this case is not selection of advantageous variations, not survival of the fittest, but a destruction of everything unusual, everything above normal, a protection of the average from the dangers of an escape from a happy mediocrity. Selection as conceived by Darwin and Wallace is a sort of favoritism manifested by nature toward the unusual. Stabilization is an aversion, as it were, shown by nature, to anything unusual. In the process of selection we usually imagine an advantageous heritable variation gradually becoming the only existing type, through the elimination of all others in the struggle for existence. But the influence of stabilization is just the reverse. It prevents the establishment of new characters; it works therefore against the formation of new species except in a single possible direction. We shall now see how this is accomplished by a detailed study of several examples. For the present we shall limit our discussion to internal parasites.

Of all internal parasites the most convenient with which to begin our inquiry are the tapeworms. They do not as a rule occur in nature outside their host in any stage except as eggs, and we shall limit ourselves entirely to such forms. Common variations in moisture, temperature, climatic conditions, and so forth, have no other influence on the development of the eggs than that of retarding or accelerating it. This is true even in such tapeworms as *Ligula avium,* in which the larva or oncosphæra emerges from the egg in the water and is then swallowed by the intermediary host. It has been shown for this species that at a temperature of 95°F. the development is completed in some four or five days after the eggs have been dropped into the water, that at a temperature of 86°-90°F. it requires seven days, at 68°-86°F., eight days, at 54°-61°F., five weeks, and at 36°-39°F., fully three months. It has been also shown that at a temperature of 54°-64°F. the oncosphæra remains alive in the water during seven to ten days. It will be seen therefore that under normal conditions the chances of the emerging larvæ to be swallowed by the intermediate host will not be diminished by a drop in temperature at the time when the eggs were deposited because this would retard the development until warmer days arrive.

In the case of tapeworms of the genera *Tænia, Multiceps,* *Echinococcus, Dipylidium,* and *Hymenolepis* the oncosphæra emerges in the alimentary canal of the intermediary host, and the eggs are deposited at a stage when the oncosphæra is fully developed and the egg shell is strong enough to withstand the influence of temperature, water, and many other fluids, without bursting. Thus the chances of the eggs being swallowed by the intermediary host are entirely dependent upon the feeding habits of the latter, as well as upon the conditions under which the eggs are scattered by the final host.

The environment of the adult tapeworm in all these cases is the most equable one imaginable, being the intestine of vertebrates. The variations of temperature are quite negligible, those of moisture are quite excluded, and the only real variations occurring are those in the chemical composition of the fluid content of the intestine of the host. Here an interesting fact must be recorded. The food of a dog, a cat, a man, may vary in many respects; it may be more vegetable or more animal at any time, without, however, affecting the tapeworm, which once in the intestine of its normal host continues to assimilate such food as it gets, and to produce proglottids and eggs. But the number of species in which a tapeworm may live is a distinctly limited one, showing that the chemical composition of the fluid content of the intestine has a direct, though as yet not sufficiently known, bearing upon the existence of the parasite. *Tænia saginata* (Figure 9, D) occurs only in man. All attempts to have it develop in monkeys, dogs, cats, sheep, goats, pigs, and rabbits, have failed. The same is true of *T. solium* (Figure 9, B), the adult of which occurs also only in man, experiments with larvæ of which were made on apes, dogs, pigs, guinea pigs, and rabbits.

It is less certain that other species of *Tænia,* known from a single species of host, really have no other host. Such are *Tænia africana, T. bremneri, T. confusa, T. hominis,* and *T. philippina* from man; *T. brachystoma, T. brauni, T. krabbei,* and *T. ovis* from the dog; *T. monostephanos* from the lynx. Of these species we know too little to take them into consideration. *Tænia laticollis* known from *Lynx lynx* and *L. canadensis*, and *Tænia balaniceps* known from the dog and from *Lynx rufus*, as well as *Tænia macrocystis* from *Felis tigrina, F. jaguarundi, Lynx rufus* and *Galictis sp.*, can all be placed in the same group of insufficiently known species. There re-

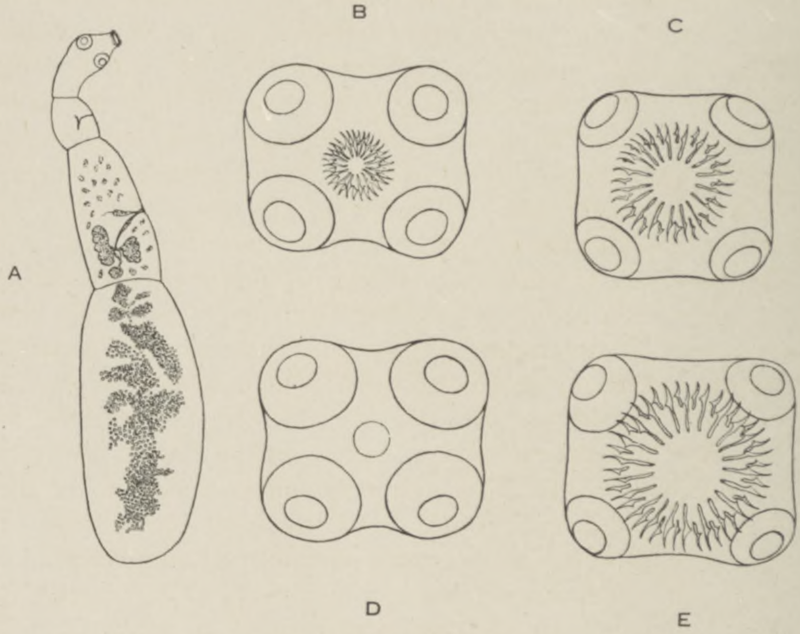

Fig. 9.—A, *Echinococcus granulosus,* complete tapeworm showing the head or scolex with a crown of hooks and two of the four suckers, the first immature proglottid with genital ducts, the second proglottid with fully developed reproductive organs, and the third proglottid with uterus filled with eggs. B-E, scolices of four species of *Tænia,* viewed from above and drawn at slightly different magnifications to bring them to the same size and thus more clearly to emphasize the specific differences of structure; B, *T. solium;* C, *T. marginata;* D, *T. saginata;* E, *T. crassicollis.* All drawings made by the author from specimens in his collection.

main three very well known species of *Tænia,* namely, *T. crassicollis* (Figure 9, E) known from ten species of *Felis,* from *Lynx,* and from *Mustela erminea; T. marginata* (Figure 9, C) from three species of *Canis;* and *T. serrata* from three species of *Canis,* two species of *Felis* and *Urocyon cinereo-argentatus* (gray fox). Experiments of Möller have shown that *T. marginata* can not develop in man, nor do we know it from any animals other than the dog, the wolf (*C. lupus*), and *C. mesomelas,* although it is undoubtedly closely related to *T. solium* of man. Nor did the experiments of Küchenmeister who fed larvæ of *T. marginata* and *T. serrata* to criminals succeed. It may be therefore stated as a fact that adult tapeworms of the genus *Tænia* either occur in a single species of host or in closely allied species. In the first case, as in *T. solium* and *T. saginata,* the slightest deviation from the chemical composition of the fluid content of the intestine, makes life for the parasite altogether impossible; in the other case such deviation, within certain limits, does not interfere either with the life or reproductive functions of the parasites. Yet this difference in the chemical composition of the environment has apparently to do only with some substance secreted by the host and used by the parasite in the process of assimilation, because the introduction of a great variety of drugs into the intestine, in the shape of medicines, seems to have very little effect on the worms (except of course a few specifics used for the removal of the tapeworms).

When we examine the series of intermediary hosts, normal for the five species of *Tænia* under discussion, we see at once that the larvæ of *Tænia* are not entirely dependent for their existence upon a single chemical factor of their environment. The conditions of moisture and temperature here also are such that variations in them may be quite safely disregarded. On the other hand, we have two different sources of variation in the chemical environment, one in the specific and even generic difference of intermediary hosts, and the other in the chemical difference of the fluids in the various infected organs of the same intermediary host. The larvæ (oncosphæræ) emerging from the eggs in the intestine soon perforate the wall and pass into the blood-stream, a change of chemical environment both considerable and sudden. Perhaps the change is made possible by the shedding of the ciliated coat of the larva in the process of penetration through the wall of the intestine, thus exposing to contact with the new chemical environment, *i.e.*, the blood, the inner cells of the embryo, which were shielded from contact with the fluid in the intestine, by the ciliated coat. In the case of *Tænia solium* the final seat of the embryo makes no difference in its further development, although there is a certain gradation of frequency of occurrence of the cysticerci (advanced larvæ capable of further development only in a new host) in the organs of the intermediary host. First place in this respect belongs to the muscular system in the case of the pig, yet even here in the following sequence: heart, tongue, abdominal wall, diaphragm, and so on; very rarely in the liver, lung, kidney, spleen, and subcutaneous tissue and fat. The sequence is, however, different in the case of man. Here the brain comes first, then the eye, the muscles, heart, subcutaneous tissue, liver, lung, abdominal cavity, and other organs. Moreover, numerous experiments have shown that the so-called *Cysticercus cellulosæ, i.e.,* the larva of *T. solium,* may be developed from eggs fed to no less than eleven widely different animals, such as man, pig, sheep, goat, rat, dog, bear, and three species of monkeys. *Cysticercus bovis* of *Tænia saginata* occurs only in the muscles, especially in the musculi pterygoides externi and interni in domesticated cattle, American pronghorn, giraffe, and llama. *Cysticercus fasciolaris* of *Tænia crassicollis* is found only in the liver, but is known from mice, rats, muskrat, moles, shrews, and bats. *Cysticercus pisiformis* of *Tænia serrata* is found in the liver, the mesenteries, and the abdominal cavity of twelve species of *Lepus* (rabbits and hares) and once each recorded even from the domestic mouse and mountain beaver. Finally *Cysticercus tenuicollis* of *Tænia marginata* occurs in the liver and abdominal cavity of probably all Ruminants (recorded from nineteen genera), in seven genera of Primates (not in man), and in several species of *Sciurus* (squirrels) among Rodents.

The geographical distribution of the two last species of *Tænia* is cosmopolitan. *Tænia crassicollis* is also probably cosmopolitan as it has been recorded from various countries in Europe, from Iceland, from Persia, Japan, and the United States. The distribution of the two human *Tæniæ,* which are also cosmopolitan, is naturally affected by feeding habits, religion (Mohammedans and Jews abstain from eating the flesh of swine), and the state of civilization, especially as to meat inspection.

The fertility of tapeworms is enormous and has often been regarded as an adaptation brought about by the danger of extinction of the species because a considerable number of scattered eggs are never swallowed; or the intermediary host, though infected, escapes being devoured by the final host. A *Tænia solium,* for example, may live from five to fifteen years and during all this time from three to five gravid proglottids are broken off daily and passed with the stool. As each proglottid contains somewhere between 20,000 and 50,000 eggs, the yearly production of eggs amounts to between 7,300,000 and 18,250,000 and the total production during the lifetime of the worm to almost a quarter of a billion (maximum). *Tænia saginata,* which is everywhere much more common than *T. solium,* produces during the same time up to 1,368,750,000 eggs! The productivity of *T. serrata* has been once placed by Dujardin at about 25,000,000 and it certainly can not be larger but is probably smaller than in *T. solium,* because the latter species has about one hundred gravid proglottids while the former has only between thirty and forty. The same applies to *T. marginata.*

The idea that great productivity is the result of adaptation could be defended only if it were possible to prove that the production of eggs may be increased and the resulting advantage inherited by the next generation. There can be no doubt whatsoever that the composition and quality of food have a direct influence on the production of eggs in some animals. Thus workers of ants may be made to lay eggs if fed for two or three weeks on animal food. It stands to reason that the same applies to tapeworms. But does it follow from this that tapeworms were originally producing fewer eggs than at present? The very fact that egg production is influenced by food supply would indicate that it is a purely physiologico-chemical process which, necessary conditions existing, will continue to capacity. As it is, the loss of eggs which will never have a chance to develop is already so appalling that one is justified in doubting the efficiency of an adaptation which would consist merely in an increase of productivity. If, of the billion eggs produced by a *Tænia saginata* during its lifetime, only one egg has to survive to assure the existence of this hermaphroditic, self-fertilizing species, and if that number were insufficient, how many more billions would have to be produced for the purpose?

But an increase in the number of eggs would mean also an increase in the number swallowed by a single animal. This would act directly against the advantage derived from an increase in the number of eggs, (1) because too great a number of larvæ perforating the intestine causes the death of the unfortunate animal which swallowed them; (2) because the organism of the intermediary host in the majority of cases so reacts even against a normal invasion of larvæ that only few of them, often only one, develop into cysticerci; and (3) because the final host can harbor only a few specimens of adult *Tæniæ* at the same time.

What happens to the eggs in nature under normal conditions? They are daily deposited with the excrement of the host. Water distributes them over the ground, numerous insects carry them on their feet to distant places. Great numbers are constantly swallowed by all kinds of animals feeding on grass, on excrement, on humus, on food to which the eggs have been accidentally transferred. For every animal in which the eggs can develop there are dozens of vertebrate and invertebrate animals, insects, snails, worms, and so forth, through whose alimentary canal the eggs will pass without developing, and others in which development may be started but not finished. To this must be added the number of animals in which the eggs may develop, but which are not used as food by the final host and in which the eggs therefore perish after all. For uncounted generations, in a number of instances passing all possibility of computation, nature performs the experiment of getting the eggs into the alimentary canal of innumerable animals and of thus increasing the number of intermediary hosts—and yet without much success. In countries like Abyssinia where *Tænia saginata* is said to occur in almost 100 per cent of the population, and where, owing to low civilization, poor sanitary conditions, and dirty habits of the people, the eggs must be scattered everywhere over the grass; every cat and every dog must be daily swallowing dozens of eggs in eating grass as they do in all countries, yet only cattle develop the cysticerci! Nor would it help the species in any way if an earthworm or a dungbeetle should have swallowed a variation of egg which should prove to be capable of developing in this strange host to the stage of a cysticercus, unless man had acquired a new taste. What a leveling force is the influence of a multiple environment!

The study of the parasites of man has a further advantage which enables us to analyze and better understand this problem. We can safely assume that man being the most recent of all animals is also the most recent host for parasites. We know parasites which occur only in man, we know such which are only occasionally infecting man while normally found in other animals. Wherever a parasite, until recently supposed to have been strictly human, has been found in nature to occur also in some other animals, as for example in the case of the *Trypanosoma gambiense,* the cause of the African sleeping sickness, we can be sure that this fact had been simply overlooked and that the true host of the supposedly human parasite is an animal. Of course, it is not impossible that a species of human parasite had developed a new mutation which would permit its existence in some other species of mammal. But such cases must be extremely rare, if indeed they occur at all, experience showing that the reverse is rather the case. Thus worms which have been hitherto known only from mice and rats were found recently to be not uncommon among soldiers in the World War. But even in these cases experiments with rearing eggs are still lacking, and it remains therefore not quite certain whether after all the specimen described from man would be capable of establishing a prolonged existence of their progeny in the new host. On the other hand, we are now almost certain that the roundworm, *Ascaris suis,* commonly found in the pig and *A. lumbricoides* found in man are two phases of the same species, the man-phase representing probably a chance-mutation of the pig-phase. It seems to be equally certain that *A. ovis* found in sheep is due to chance infection with eggs of either of the two preceding phases. But unlike *A. suis* and *A. lumbricoides, A. ovis* proves sterile and is incapable of reproduction. Such modification of its structure as is observable from comparison with the pig-*Ascaris* and the man-*Ascaris* is evidently due, not to germ-variation, but to the direct influence of the chemical environment, and owing to the sterility of the creature is not heritable at all. And yet how advantageous it might have been to the species if eggs swallowed by sheep could not only develop but produce mature individuals capable of reproduction!

But let us return to the flatworms and the genus *Tænia*. It is quite evident that the two human tapeworms, *T. solium* and *T. saginata,* can not be regarded as the progenitors of the other species but are themselves rather the latest development of a stock common in other mammals. Of the three common species the one with the greatest number of hosts is *T. serrata,* the one with the greatest number of intermediary hosts, *T. marginata.* In the case of *T. serrata* the food of the intermediary hosts is vegetal, rarely vegetal and animal (*Mus musculus*). In the case of *T. marginata* the food of the intermediary hosts is also vegetal, sometimes vegetal and animal, as in monkeys. Considering the habits of the hosts we may therefore accept as certain that in both cases the source of infection is contaminated vegetal food, presumably grass, possibly also water. If we accept, as has been done by one school of zoölogists, that the parasite was originally restricted to life in the intermediary host, then we would have to admit that in the course of time, when life in the final host became necessary, the number of hosts became more restricted. This would apply especially to the human *T. solium.* But such a restriction would be greatly disadvantageous, so much so that we might altogether dismiss the proposition. It is more likely that *Tæniæ* either originated from forms which already possessed a number of final and intermediary hosts, or later developed the necessity of spending their larval stages in an intermediary host. In either case we can understand why the human *Tænia* has only a single final host to several intermediary ones. And we can tentatively reconstruct in our mind the origin of the two human *Tæniæ* as mutants of one of the still existing dog *Tæniæ,* possibly *T. marginata,* since its intermediary hosts, at least several of them, are the same as in both *T. solium* and *T. saginata.* If this be so, and the probabilities are not against such an assumption, then we may also indicate the changes which took place, the direction in which these changes tend, and the changes which are mere accessories to chemical processes. For example, comparing *Tænia solium* (Figure 9, B) with *T. saginata* (Figure 9, D) we may at once conclude without danger of committing an error that the presence of hooks on the scolex of the former, and their absence in the latter, are not characters necessitated by the human chemical factor of their environment. For the chemical factor in both cases is the same, in fact the two species have been found on various occasions together in the same patient. Nor can the structural characters of the scolices of these two species be regarded as unavoidable sequences necessitated by the chemical or "assimilative" mutation of the germ plasm itself, when the egg became suddenly capable of assimilation in the human intestine and lost its previous ability to assimilate in the dog intestine, for then both species would be without hooks. Furthermore, the absence of hooks in *Tænia saginata* can not be explained on the assumption that it is a naturally selected advantageous mutation of a *T. solium,* because, the intermediary hosts of the two being different, such a mutation could not have been selected without another mutation, chemical in nature and synchronous in appearance, a mutation which would permit the change from one species of intermediary host to another. And herein lies the probable explanation. At least we can easily imagine two or more genes having been involved in such mutations, some of which resulted in purely structural changes accompanying the chemical, "assimilative" change. These structural mutations, without having the least selective value, would under these circumstances nevertheless become established as casual accessories, as it were, of the assimilative mutation. But the latter would be in no need of selective preference before the old stock, simply because neither would interfere with the other, having now different hosts. It also follows that any mutation involving no matter how many important but merely structural characters, such as size, shape, presence or absence or anatomical modification of organs, number of organs, and even fertility of the species, if they be mutations, would be invariably found inhabiting the intestine of the same species of host and could not be in any way responsible for an increase in the number of species inhabiting different species of host. This conclusion is unavoidable, and consequently mere structural mutants may be expected to exist only in the same host parallel with and without detriment to the original stock, while "assimilative" mutants of the same species, yet not necessarily involving structural changes, may be expected to exist in new hosts. We know some genera of tapeworms represented by several species inhabiting the same host. Whenever the intermediary host in such cases is different, if that difference is not one of chance but is permanent, the two species of parasite could not be properly considered as mutations of the same stock. But if the final host and the intermediary host are identical, then there is no escape from the necessity to recognize in the two species mere structural mutations. Unfortunately we know the life histories of only a few species and we have yet to find such species of internal parasites which have the same intermediary and final hosts. On the contrary, in all known cases, from Protozoa to Arthropods, whenever two hosts are imperative, either the intermediary or the final hosts are different. Thus *Tænia saginata* and *T. solium* both occur in man only, but the larva of the former does not occur in pig, nor the larva of the latter in cattle, even though it occurs occasionally in many other mammals. On the other hand, the larvæ of these two species occur in the same intermediary hosts with the larvæ of *T. marginata,* but the adult stage of the latter cannot live in man. Perhaps future studies will reveal purely structural mutants in internal parasites. For the present we must say that we know of no such mutants, even though we know many abnormalities or monstrosities.

The case is different with "assimilative" mutations. Here we seem to be in possession of evidence tending to affirm our contention. Such is the case, already mentioned, of *Ascaris suis* and *A. lumbricoides,* indistinguishable morphologically, yet one restricted to pig and the other to man. Such is also the case of the itch-mite, *Sarcoptes scabiei,* with its dog and cat varieties. But the species mentioned do not spend any portion of their life in intermediary hosts, and when we search for parasites with intermediary hosts then we must again admit that we know none which would show no structural difference and yet be dependent for their existence upon different species of host.

An interesting case is presented by the genus *Multiceps* with its three species, *M. multiceps, M. serialis,* and *M. gaigeri.* All three occur in the adult stage in dogs. *M. multiceps* has been described also from *Canis nebrascensis* (the coyote), at least in two authentic cases. *Multiceps* is so closely related to *Tænia* that for a long time *Multiceps multiceps* was known under the name of *Tænia cænurus,* and *Multiceps serialis* under that of *T. serialis.* The morphological differences separating *Multiceps* from *Tænia* are so insignificant—they involve only the form of the hooks and the end of the vagina—that on the basis of these differences alone the separation of *Multiceps* from *Tænia* was barely sufficient. But the so-called *"cænurus"* type of the larva of *Multiceps* is characteristic for this genus, just as the *"cysticercus"* is characteristic for *Tænia.* And yet even here the difference is not fundamental. The cysticercus produces a single scolex, while the cœnurus produces many brood pouches, each containing a scolex. But we have in *Cysticercus pisiformis* of *Tænia serrata* a first step as it were in the direction of producing more than a single cysticercus, for here the larva divides in two before the formation of the scolex, although only one of the two halves is capable of further development. The intermediary hosts in *Multiceps multiceps* are varied and include besides sheep, which are the most common, also *Bos taurus, Capra hircus, Equus caballus, Bubalis sp., Ozauna equina,* chamois, mouflon, gazelle, antelope, dromedary, and man. None of these species serve as intermediary hosts for *Multiceps serialis.* The species serving as such are all rodents, eight of them belonging to the genus *Lepus* (*L. timidus, L. californicus, L. wallawalla, L. deserticola, L. variabilis, L. texanus, L. callotis, L. cuniculus*), one to *Sciurus* (*S. vulgaris*) and one to *Myocastor* (*M. coypus*). Both species of *Multiceps* are practically cosmopolitan in their distribution. The larvæ of *M. serialis* are found in the connective tissue (intermuscular, subcutaneous, etc.). They produce both internal and external daughter bladders. The larvæ of *M. multiceps,* although occurring in many genera of ungulates, can develop only in the brain and central nervous system and produce no daughter bladders. Although this is of evidently serious disadvantage, nevertheless experiments have shown that the larvæ of *M. multiceps* perish whenever they lodge in an organ other than the central nervous system. And this naturally happens quite commonly, because when quite young the larvæ are carried by the blood to all organs, so that more larvæ perish than survive. The adults are almost indistinguishable one from another. Their size is practically the same, so are the number and shape of the hooks, the number of proglottids, the structure of the mature proglottid, and of the gravid uterus. Hall finds a difference in the shape of the proglottids, but the shape of proglottids is always subject to great variations. Moreover, the effect of temperature and of chemicals on live tapeworms is so pronounced, that under the eyes of the observer the shape of a proglottid may be rapidly changed from an elongated rectangle to one which is wider than long without any damage to the tissues. The similarity of *Multiceps* to *Tænia* suggests the possibility of the former having been once produced by the latter, perhaps by the *Tænia marginata.* If so, the type of "assimilative" mutation in this case must have been different from those discussed previously, because the adult remained capable of living only in the old host, whereas the larvæ not only became restricted to life in a certain group of animals, but also only in a certain kind of tissue. As for the ability of the larva to produce numerous scolices instead of a single one, or even to produce daughter bladders by internal and external proliferation, such ability may be entirely due to the influence of the environment being also closely related to the phenomena of asexual reproduction common in tapeworms.

The genus *Echinococcus* with its single species, *E. granulosus* (Figure 9, A), was also for a long time united with the genus *Tænia.* But the morphological differences between *Echinococcus* and any *Tænia* or even *Multiceps* are so great and so evident that not only is the separation correct but one is surprised at the conservatism of zoölogists who still place *Echinococcus* under *Tænia. Echinococcus* has never more than three proglottids and is the smallest tapeworm known, whereas *Tæniæ* possess several hundred proglottids and are a correspondingly large species. The adult *Echinococcus* occurs only in comparatively closely allied species of *Canis* (*C. familiaris, C. lupus, C. aureus, C. dingo, C. mesomelas*) and *Felis* (*F. catus domestica, F. concolor*). But the larva will develop in any mammal and any organ or tissue. As the blood-stream carries the larvæ from the intestine it is quite natural that the liver should be the organ showing the greatest percentage of infection (57.1 per cent) and that the lungs should follow with 8 per cent; next come the kidneys (6 per cent), the brain, the genital organs, the spleen, and at the end the marrow of the bones.

A comparison of the three genera, *Tænia, Multiceps,* and *Echinococcus,* should easily convince us that it is not a greater or smaller power of resistance to the chemical environment which governs the distribution of these tapeworms in different hosts, or of their larvæ in different intermediary hosts and organs, but their inability to assimilate food in absence of a certain chemical factor. The restriction is always greater in the case of the adult tapeworms than in the case of their larvæ. Therein is, however, nothing extraordinary, seeing that the structure of any animal becomes more complicated and the tissues more specialized with the progress of individual development. Is it likely that something chemically specialized, through a succession of chemical changes, should become once more chemically despecialized? We do not know enough of chemical processes in living protoplasm to make the assertion that such despecialization is possible and in absence of evidence should we not expect rather the reverse, *i.e.,* a further specialization? Should we not expect that if any new mutational change of the germ plasm should occur, such change would involve a limitation rather than an extension of the number of species capable of serving as hosts to the parasite? The life-cycle of the worms under consideration precludes any participation other than chemical of the parasite in the process of safeguarding the existence of the species. Chance, governed only by the feeding habits of the hosts, rules supreme. At first thought, increased fertility would seem to be the proper agency to counteract the heavy loss due to chance. Indeed it is quite customary to point to the correlation between parasitism and great fertility as evidence of evolution through the survival of the fittest. But more careful consideration will raise grave doubts in this respect. For we must admit that in all existing species a perfect balance has been established in which the losses are compensated by the production. Unless a species is on the increase in the number of individuals it is difficult to imagine a time when the balance was unfavorable to the species without resulting in the extermination of the latter. That fertility and nourishment are closely interrelated no one will deny. The case of *Polystomum* shows moreover that under circumstances early maturity accompanied by morphological changes may result in the reduction of fertility. How far fertility may be increased through selection is a question far from having been determined. At the same time two things are evident. First, that the life of the intermediary host is always endangered by an invasion of too great a number of larvæ, and second, that under any circumstances only few of the larvæ can develop. The rest perish even if they do not kill their host. Moreover, in many cases the entire intermediary host will be devoured by the final host and of the larvæ thus swallowed again only a limited number may develop. In the case of progressive limitation, such as we have just had under discussion, *i.e.*, in the case of a mutation suddenly not only permitting but requiring development in a new host, the balance between egg production and loss would be at once changed, and the future of the mutant would depend not upon the fertility of the parasite, but upon the chance of developing which the eggs would have. Should the mutant retain the ability to develop during its larval stage in the same intermediary hosts as the original stock, the chance of survival for the larvæ would remain exactly the same as it was for the original stock. The chance for the survival of the mutant would, in such a case, be entirely dependent upon the number of individuals in a given area, of the species of animal which serves as the new final host, and upon the feeding habits of that animal. Similarly, if the mutation should involve only the intermediary host, the chance of survival would be entirely dependent upon the number of individuals of this intermediary host and the feeding habits of the final host. In any case fertility would play no rôle whatsoever until a balance was reached on the basis of the existing fertility and the influence of the new environment, *i.e.*, new hosts and their habits. But if a balance has been reached in this manner, then why should it require an increase in fertility? Slaughterhouse records and hospital reports show that meat inspection reduced the frequency of infection quite materially. Thus previous to 1882, 0.33 per cent of pigs in Prussia were infected with *Cysticercus cellulosæ* (*T. solium*), whereas in 1899 only 0.047 per cent were infected. During the same time in Saxony the infection fell even to 0.017 per cent. Similar reduction has taken place everywhere in countries where meat inspection is rigorous. The number of cases of adult *T. solium* in man has also materially decreased during the same time. Yet though the existence of the species is thus jeopardized by the new factors—meat inspection and medical treatment—the fertility of the species has not changed during these forty years, nor has any "assimilative" mutation appeared, which would permit *Tænia* to recover the loss due to the above new factors through a timely intercession of a new host.

The researches of Morgan and his school have shown pretty definitely that mutations arise in the germ plasm. The eggs of tapeworms when deposited contain already a fully developed embryo and such changes as they may undergo under the influence of environmental factors would most likely be of a non-heritable type. Nevertheless, without further experimental evidence it would be imprudent to deny that a change may be induced in the larva by the environment, which would result in the faculty of the thus changed larva to develop into an adult tapeworm in a new host. Morgan, like all others, draws a very clear distinction between heritable mutations and non-heritable variations due to environmental influence. But here again appears the fallacy of such logic. For, if we continue our analysis of the supposed change produced in the larva by a new factor in its environment, we will be forced to come to the following conclusions. The adult, now enabled to live in a new host, will produce eggs which, in absence of the new environmental factor, will be able to develop only in the old way and as larvæ will be able to grow to the adult stage only in the old host. But in presence of the new environmental factor they will again show the new change. The problem therefore hinges on the presence or absence of a certain factor. *But in nature there is no such thing as absence of anything,* for in place of something absent there is always something else present. And it is the presence of this "something else" which we often do not even know, that is responsible for the chemo-physical reactions resulting in the outward morphological differences.

Let us now leave the tapeworms and turn our attention to other worms. Although the choice of forms is great, the detailed knowledge necessary for a careful analysis is limited to a comparatively small number of species. An interesting and important case is presented by *Trichinella spiralis.* This roundworm lives in the adult stage in the small intestine of man, the rat, the pig, and occasionally in all domesticated mammals, as well as others. Nevertheless, it shows some resistance to environment in the case of different mammals, so that rats, for example, are much more easily infected than sheep or horses, and the latter more easily than dogs or cats, a most remarkable fact considering that cats and dogs eat rats. All these animals serve also as intermediary hosts. The species is viviparous and the larvæ on being born are either carried by the lymph-stream to the heart and hence by the blood-stream to the entire body, or migrate actively through the wall of the intestine and to other organs. This latter method is, however, not so common. Further life is possible only inside the fibers of striated muscles and all larvæ which do not penetrate into such fibers, invariably perish. The frequency of infection of various organs has been very carefully studied in pigs. First comes the diaphragm, then the laryngeal muscles, the tongue, abdominal muscles, intercostal muscles, and so on. This sequence has apparently nothing to do with the course of the blood, but depends upon the properties of the muscles themselves. Once encysted, the larvæ may remain alive for years, although the duration of life of the adults is never more than seven weeks. In birds mature adults have also been reared (in ducks, chickens, and pigeons), but the larvæ are invariably expelled with the fæces. Even in salamanders infections have been successful when the animals were artificially kept at a temperature of 86°F., *i.e.*, 12.5° lower than normal human temperature. The experiments show clearly that temperature within certain limits can be a deciding factor, but the feeding habits would under any circumstances prevent many animals in nature from getting infected with *Trichinella.* The greater resistance of some mammals to artificial infection shows again that the real reason for it must be sought in the chemical composition of the food of *Trichinella.* But the ability to develop under circumstances in almost all mammals precludes the appearance of special "assimilative" mutants and so far as we know there is only one species of *Trichinella.*

A roundworm which is apparently little if at all sensitive to climatic influences in its egg-stage, and extremely sensitive to its chemical environment in its parasitic life, is *Ascaris lumbricoides,* already mentioned above. It is a cosmopolitan species and the eggs are surrounded by such a thick shell that they will continue to develop in all kinds of fluids deadly to other organisms. Recent experiments on the life history of *Ascaris* have shown that infection can be successful only when eggs are used containing fully developed larvæ. In this case the larvæ hatch in the intestine but can not remain here. They enter the capillaries, are carried to the liver, thence to the heart and the lungs, from which they migrate by way of the trachea into the œsophagus and reach the intestine some ten days after infection. It has also been shown that in rats and mice the larvæ, having thus reached the intestine, remain incapable of further development and are soon passed with the fæces. We have seen that in sheep they develop but remain sterile. Only in the pig and man, so far as we know, can the larvæ develop to maturity. Yet is it not clear that many more eggs must be regularly swallowed by all kinds of animals other than the pig or man?

There are many worms in which the eggs alone remain for some time outside of a host, while the larval stages and mature life are spent in a host without the necessity of an intermediary host. In the majority of such cases the egg shell is impermeable to fluids other than the secretions of the alimentary system of a single or of a few species of animals serving as host. In all these cases nothing but variations of temperature and perhaps prolonged excessive dryness of the soil may affect the course of development. Numerous observations and experiments have shown that the influence of these factors is here also only an accelerating or retarding one, although we are not prepared to deny definitely that it would be impossible in this manner to induce eggs to develop in other than normal hosts. In *Trichocephalus* we have, for example, several structurally different species, all found in the intestine of various mammals. Considering only species from domesticated animals and man we find *T. trichiurus* in man, various monkeys and lemurs, *T. ovis* in sheep, goats, and cattle, *T. unguiculata* in the rabbit and the hare, *i.e.,* always in more or less closely related groups of animals, while *T. depressiusculus* is known only from the dog, *T. crenatus* from the pig, *T. serratus* and *T. campanula* from the cat, *T. discolor* from the zebu, *T. cameli* and *T. globulosus* from the camel and dromedary, *T. giraffæ* from the giraffe, and *T. nodosus* from the house-mouse. The development is known for several species and is always the same, eggs containing larvæ developing directly to the adult stage in the intestine of the host. Here, too, selection of any advantageous heritable characters is unthinkable. We may easily imagine the simultaneous, parallel existence of any structural mutants in the intestine of the same host and for all we know the species *T. serratus* and *T. campanula* of the cat and *T. cameli* and *T. globulosus* of the camel may be such mutants. But the extension of the existing species of *Trichocephalus* over various species of host new to them, would have to be preceded by "assimilative" mutations and to depend entirely upon the chance of the eggs being swallowed by the right kind of possible new host at the right stage of egg development. It so happens that in all cases the eggs would be deposited with the fæces and scattered in practically the same localities. And here the probability is rather in favor of those species being the progenitors of others which were able to develop in many hosts, while those with a single host represent further specializations. Else why, in the millions of years of their existence, should not the species occurring in the dog, in the cat, and in man, have acquired the habit of developing in all three of these hosts?

In many roundworms a portion of their larval life is spent in moist soil and the method of infection varies from a passive transference to the stomach of the host, through drinking water, to an active attack on the host with subsequent complicated migration by way of the blood-stream and lungs, to the trachea and down the œsophagus. Such is the case in hookworms of which two genera, *Anchylostoma* and *Necator,* occur in man also. *Anchylostoma duodenale* occurs in man only and is cosmopolitan in its distribution, limited only by temperature and moisture. The optimum temperature for the development of the eggs lies between 77° and 86°F. A lowering of temperature retards development until at about 46°-50°F. development is suspended altogether. Yet the eggs remain alive and only the lowering of the temperature to the freezing point or its rise to 122°F. kills them. In absence of oxygen the eggs will remain inactive for about two weeks without injury, but will die if the experiment is prolonged a day or two longer. Nor can they remain for any length of time in an absolutely dry medium. The larvæ emerging from the eggs feed on fæces and grow with varying rapidity dependent upon the temperature and food. They moult twice within six to ten days, the second time without shedding their old skin, but simply by producing a new one underneath the old one. In this so-called encysted stage the larvæ may live as long as twelve months without food, being unable to eat. They can not live except in very moist soil or in water, but nevertheless they must have access to air, otherwise they drown. Thus far we understand perfectly the geographical distribution of this remarkable worm. Originally restricted to warm climates with moist atmosphere, *Anchylostoma duodenale* spread northward through the agency of workmen engaged in work in tunnels and mines, in which the temperature never drops to the freezing point while the soil and air are always moist. In this way the species became established as far north as Belgium, although it does not occur there outside of mines.

After having shed its skin the encysted larva develops a strong instinct to penetrate any porous surface with which it comes in contact. Whether, strictly speaking, this is an instinct or a simple reflex action matters not in the least. What I want to point out is that the larva enters any porous substance, regardless of its possible chemical attraction. At least it has been shown that the larvæ will not only enter the skin of man, but also aquatic plants, pith, and so forth. Yet only when they get into the skin of man can they continue to develop and on reaching the intestine in the way described above, mature and produce eggs. Man becomes infected in bathing, in wading or walking with bare feet on moist soil, and also by drinking infected water. But how much more common it must be that other animals do all this in the localities infected with *Anchylostoma duodenale* larvæ,—dogs, cattle, pigs,—yet none of these will be infected even though it is probable that thousands of larvæ attack them year after year, or are swallowed with water. Thus in this case, as in the case of *Tænia,* it is after all nothing but chance which decides the fate of each individual larva, and no matter how advantageous a heritable variation would otherwise have proven to be, no selection can take place; and the destructive agency of the environment, by not permitting the establishment of such variations, continues to exert a stabilizing influence on the existing stock, keeping it down to its proper level, from which no other escape is possible than by a combination of a chemical "assimilative" change and lucky chance.

There is a species of hookworm, *Anchylostoma caninum,* found in various wild species of *Canis* and *Felis* and occasionally also in domesticated dogs and cats. This species has also been developed in man, though normally it does not infect him. Morphologically it is different from *A. duodenale* and does not assume the specific characters of the latter even when bred in man. Its development is the same as in *A. duodenale.* Here then we have a less specialized condition with a greater chance of infection, and yet, in dogs and cats it is not nearly as common as is *A. duodenale* in man. Evidently though the number of species which may serve as hosts is greater, nevertheless for some unknown reason the chances of infection are smaller.

We now may consider those parasites in which the infection of the final host is accomplished through the feeding habits of the intermediary host exclusively. I have in mind those forms among Protozoa which produce malaria and African sleeping sickness, and *Filaria* among roundworms. In all cases it is a bloodsucking insect which serves as intermediary host. It infects itself in sucking blood containing parasites. These parasites undergo some developmental changes in the insect and are finally transferred to a new host, when the insect again sucks blood.

We know three species of malarial parasites, *Plasmodium vivax,* the cause of the tertian or spring fever, *P. malariæ,* the cause of quartan fever, and *P. falciparum* (called also *P. præcox* or *Laverania malariæ*), the cause of the æstivoautumnal or tropical malaria. All three species occur in man only and are not transmissible to other mammals, not even to monkeys. Morphologically they are quite distinct one from another; for example, *P. falciparum* is the only one which has a crescentic gametocyte instead of a spherical one, *P. malariæ,* a quadrilateral schizont instead of a circular one. Their effect on the red blood corpuscles is a different one for each species. *Plasmodium vivax* distends the corpuscle to more than its normal size and produces Schüffner's dots in it. *P. malariæ* does not produce any dots, nor does it distend the corpuscle. *Plasmodium falciparum* produces so-called Maurer's dots. The length of the asexual life-cycle is also different for each species, being 48 hours for *P. vivax,* 72 hours for *P. malariæ,* and 24-48 hours for *P. falciparum.* All three species have the same intermediary hosts whenever they occur in the same country. This host is always a species of mosquito belonging to the genus *Anopheles,* and it is likely that in cases when a species of *Anopheles* was described as the carrier of only one species of malaria, it will be found that the other species may be also carried by it. Still it may be pointed out that quartan malaria in the United States is carried only by *Anopheles quadrimaculatus,* while tertian malaria is carried by *A. quadrimaculatus* and *A. punctipennis,* as well as by *A. crucians* in Louisiana. In Europe quartan malaria is carried only by *A. maculipennis,* tertian malaria by *A. maculipennis, A. bifurcatus, A. superpictus,* and *A. turkhudi* in southern Spain. No less than twenty-six species of *Anopheles* have been found to be carriers of tertian malaria in various parts of the world and twenty-three of tropical malaria. The transmission of malaria is possible only after the completion of a complicated life-cycle within the mosquito, before which time infection is impossible. No other genus of mosquito can serve as an intermediary host. Experiments have shown that mosquitoes of the genus *Culex* may ingest malarial parasites, but the latter do not develop in them. Yet *Culex* is the carrier of a closely allied species of *Plasmodium* in birds, and is certainly a common pest of mankind all over the world. Neither can fleas, so common in hot countries and infesting particularly the homes of poor people, be infected with malarial parasites.

The parasite causing the African sleeping sickness belongs to the flagellate genus *Trypanosoma.* This genus contains a great number of species, at least three of which occur in man (*T. gambiense, T. rhodesiense,* and *T. cruzi*) and the others in various mammals, mostly in tropical countries. Recently the genus was split into several genera, but the advisability of this is not yet sufficiently demonstrated. The best known, *Trypanosoma* (*Castellanella*) *gambiense,* is transmitted by a bloodsucking fly, *Glossina palpalis,* and its variety, *G. fuscipes.* Experiments have failed to demonstrate that it can be carried by other flies of the same genus, although the parasites have been bred artificially in several species of *Glossina* to a certain stage of development. On the other hand it is definitely established that *T. gambiense* has wild mammals for its "reservoir." The Rhodesian sleeping sickness is carried by *Glossina morsitans, G. palpalis,* and *G. brevipalpis,* while *T.* (*Schizotrypanum*) *cruzi,* the cause of Chagas fever in South America, is transmitted by several bugs of the genera *Triatoma, Cimex,* and *Rhodinus* and has the armadillo for its reservoir. *Trypanosoma* (*Castellanella*) *brucei,* the cause of nagana in horses and domesticated animals in Africa, is carried by *Glos-*

*sina morsitans, brevipalpis, pallidipes, tachinoides,* and *fusca,* and may be transmitted also by some horse-flies and stable-flies, and was artificially inoculated to white mice by the bite of the common bedbug, *Cimex lectularius.* We know no less than eight distinct species of trypanosomes, ranging from man to crocodile, all carried by *Glossina palpalis,* while *G. morsitans* transmits at least five and possibly seven species of trypanosomes. None of these species is carried by fleas, although the latter are regular carriers of trypanosomes in other species, the most common of which is the *Trypanosoma* (*Trypanozoön*) *lewisi* of the rat. Moreover, cultures of trypanosomes may be reared experimentally in Agar-blood-serum.

The species of mammals which serve as "reservoirs" are less seriously affected by the disease and usually recover after a period of sickness, acquiring a more or less permanent immunity. In other species the disease is fatal, as is the case in man when he becomes infected with sleeping sickness. Man, unaided, does not acquire immunity, and the disease, if left to itself, would simply depopulate tropical Africa, reducing the chances of other human diseases, but not of *Trypanosoma gambiense,* which would continue its normal existence in the "reservoirs." The reasons for the existence of so many species of trypanosomes are not easy of analysis at the present state of our knowledge, but it is clear that no competition between species is possible, seeing that a species of trypanosome which does not produce immunity, by killing the host, diminishes not only its own chances, but also the chances of the species which does produce immunity, while both continue to exist in their respective "reservoirs."

Among the roundworms *Filaria* is not yet sufficiently delimited to allow of an extensive analysis, but we know sufficiently well *F. immitis* of the dog, *F. bancrofti* of man and the allied species, also of man, *F. loa,* now placed under the genus

*Loa,* and *F. perstans,* often referred to the genus *Acanthocheilonema.*

*Filaria immitis* inhabits the right heart and the pulmonary artery, and occasionally other arteries and veins of various carnivorous mammals, including the dog. The female is viviparous, and the larvæ remain in the blood until a mosquito draws them into its alimentary canal with the blood of the host. The species is fairly cosmopolitan, and different species of mosquitoes serve as intermediary hosts in different countries. Thus, in southern Europe we find as common carriers of *Filaria immitis, Anopheles maculipennis* and *A. bifurcatus, Mezorhynchus pseudopticus, Myzomyia superpicta,* and more rarely *Culex peniciliaris, C. malariæ,* and *C. pipiens.* In Australia it is *Culex fatigans,* and the same species seems to be the carrier in the United States. The infection is fatal to 50 per cent of the mosquitoes, because the ingested parasites perforate the wall of the midgut and invade and destroy the so-called Malpighian tubes in which they undergo some developmental changes before they can be transmitted to another dog. The disease is usually also fatal to dogs because of the heavy destruction of the red blood corpuscles. There is not a single moment in which the parasite or its larva finds itself outside of its intermediary or final host. Climatic changes, seasonal variations of temperature, moisture, and so forth, affect the parasite only inasmuch as its host is affected. The instinct of the host, too, has nothing to do with the fate of the parasite. At first thought one may be led to attribute some value to the latter factor, but we must only remember that mosquitoes do not sting infected dogs alone, but all dogs, and many other mammals besides. Therefore in the end-analysis it is again nothing but chance that brings the parasite at the right time into the right animal, *i.e.,* into its proper environment. But mosquitoes are not the only insects which suck the blood of dogs. Fleas are much more common; thousands of *Filaria* larvæ of an infected dog are daily swallowed by them, yet neither the flea, nor the louse, nor any other bloodsucking parasite of dogs is capable of transmitting the disease. The ingested *Filaria immitis* larvæ perish in the flea as they perish in deer, cattle, or man, stung by an infected mosquito.

The case of the human *Filaria bancrofti* is similar. This cosmopolitan tropical and subtropical species inhabits in its adult stage the large lymphatic vessels and lymphatic glands, but is found occasionally also in the genital organs and in abscesses. No final host other than man is known. A number of species of mosquitoes serve as intermediary hosts. None of these is an *Anopheles,* though no less than five species of intermediary hosts belong in the family Anophelinidæ. The greater number of species belongs to the family Culicinidæ, and *Culex fatigans* is the most common carrier in the southern United States. *Filaria bancrofti* has long been known under the name *nocturna* because of the regular appearance of the larvæ in the peripheral blood of the patients at night, and their disappearance during the day. The reasons for this so-called *turnus* are not yet clear, but the idea advanced by older zoölogists, that in this case we have a most remarkable example of adaptation, is entirely untenable. The appearance of the larvæ at night was commonly correlated with the habit of the mosquito of sucking blood at that time. The appearance of the larvæ in the peripheral blood was accounted for by the distention of blood capillaries in sleep, thus affording passage only at night, since the larvæ are too large to enter capillaries when the latter are not distended. The fact that the turnus can be reversed if the patient is kept awake at night and asleep during the day seemed only to confirm the idea. Yet, to begin with, not all the mosquitoes carrying *Filaria* sting only at night, and again the larvæ of the so-called *Filaria diurna* (*Loa loa*) appear in the peripheral blood only during the day, being small enough to pass into them even at that time. This species is transmitted by *Culex quinquefasciatus* and three species of *Chrysops* (Mangrove flies). Another allied species of *Filaria, Acanthocheilonema perstans,* is transmitted by various mosquitoes and also by the tick *Ornithodoros moubata.* None of the human *Filariæ* are transmitted either by fleas or lice, *i.e.,* the most common bloodsucking parasites of man, especially in hot countries where *Filaria* is prevalent. And the uncountable millions of *Filaria* larvæ ingested daily by these insects perish, and will continue to perish till some modification of the germ plasm will make it possible for some of them to continue their development in a chemical environment which spells death to the normal stock. Will that moment mean the disappearance of the original stock? Of course not! The survival chances of the original stock and of the mutant will not in any way collide. Mosquitoes will continue to prey upon man and dog, to get infected and to spread infection, and the original stock will continue to exist unless the human body develops immunity or the mosquitoes are exterminated.

An interesting case is presented by the strange parasite, *Linguatula rhinaria,* the systematic position of which is not clear. Originally classified with the tapeworms, *Linguatula* was removed by Leuckart into the order Acarina among the Arachnida. Later investigations have demonstrated that *Linguatula* has nothing at all in common with the Arachnida, and the Pentastomida, although still usually placed as an order among Arachnida, should be regarded, in absence of further evidence, as a class by itself. The adult *Linguatula* lives in the nasal cavity and frontal sinus of the dog and wolf, more rarely of the fox, horse, and goat, and once was found in man. The eggs are scattered in sneezing. They are swallowed with the food, possibly with water, by various herbivorous and omnivorous mammals, including man. The larvæ on leaving the eggs perforate the wall of the intestine and are carried to the liver, rarely to other organs. In the liver they become encysted, grow and moult until about half a year after infection, when they develop an instinct for migration. First, they leave their cysts, then they either return to the intestine, or migrate to the trachea. In both cases they are finally set free and sooner or later are sniffed up by the final host. It has also been shown that some larvæ on leaving the liver, instead of being set free, migrate directly to the nasal cavity by way of the trachea, and develop here to maturity. Thus the parasite may develop to maturity with or without the intercession of an intermediary host and the intermediary host may be of the same species or of another species than the final host. There seems to be no other limitation than that brought about by the feeding habits of the hosts. And it is a significant fact that only a single species of *Linguatula* is known and that species is cosmopolitan in its distribution. The allied genus, *Porocephalus,* found in the adult stage in pythons and in the larval stage in a number of mammals, seems also to be represented by a single species, *P. armillatus* (syn., *constrictus, moniliformis,* etc.).

From the foregoing considerations it seems to be clear that the formation of new species, in parasites at least, can not be due to natural selection of advantageous mutations and that the destructive influence of the environment is directed not toward the elimination of less fit individuals, but toward the stabilization of the existing stock. In his address before the American Society of Naturalists (December 22, 1922) Morgan says: "We can imagine hundreds of changes in any animal, but it is difficult to suggest one that would certainly be an improvement, when all the many sides of its existence are taken into account. Is it not clear, then, that almost every random change must be a disadvantageous one? This is what we actually observe when a new modification of an old character takes place. But note! Among the multifarious possible changes there *may be one* that is an improvement, in the sense that the new animal is better adapted to the old environment, or that it can better adjust itself to a slightly different one. This possibility suffices for natural selection" (*Scientific Monthly,* Vol. XVI, No. 3, p. 241). But does any selection at the expense of the already existing stock really take place? We know numerous mutations among useful plants which had a tremendous advantage over the original stock, inasmuch as man made use of them, tenderly took care of them, extended their geographical distribution wherever possible and yet the original stock did not show any signs of extermination. Both exist parallel. The new mutant is guarded from extinction by man, who plays the rôle of the stabilizing agent, while the stabilization of the old stock is taken care of by the natural factors of the environment. The same is true of animals useful to man. Here too the old stock exists parallel with the mutants. But where is a single mutant of plant or animal which survived while the original stock perished? We know of complete extermination of species in geologic times and more recently in the memory of men. In some cases we know even the causes which led to such extermination. But extermination of species is not a creative process, it does not produce a new species. The dodo, the great auk, the passenger pigeon have perished, but where are the mutants? There are none. The nearest relatives have existed at the time the extinct species were common. It was the sudden interference of man that upset the carefully balanced stabilizing influence of the normal environment and the result proved to be disastrous to the species.

Natural selection, if such ever takes place, must have therefore only very limited application. In the great majority of cases, perhaps even without exception, the elimination of individuals from their participation in continuance of the species is a process of stabilization. To be sure the mutations themselves must be the result of some physico-chemical change and this in the end-analysis is due to environmental factors. They are the new points of departure in the formation of species. If we knew the physico-chemical structure and reactions of each species of germ plasm we might be able to foretell the *direction* in which such changes may take place. For it is scarcely conceivable that such changes are unlimited.

Even a casual acquaintance with parasites is sufficient to reveal the general tendency of animals to lose complexity of structure under the influence of parasitism. But such return to simplicity is only affecting the outward manifestation of the more intimate, invisible structure of the material of which the animal is built up. And we have seen that the change is always that toward limitation and specialization. At the same time the simplicity of the morphological structures of parasites is in itself an evidence in favor of the assumption that the individual as we see it is not alone responsible for its characters. As the shape of a drop of oil is determined by the medium in which it is suspended, as the cloud assumes the appearance of a cirrus or cumulus under the influence of atmospheric conditions, so the living variable system which to our senses appears as an organism and the plan of whose structure we conceive as species, in the unceasing interplay of forces with its environment owes its distinctive characters to the stabilizing influence of the latter.

# CHAPTER IV

# MUTATION AND ENVIRONMENT

WESLEY ROSWELL COE

PROFESSOR OF BIOLOGY
IN YALE UNIVERSITY

IT will be the purpose of this chapter to inquire into the causes which underlie the origin of new varieties of plants and animals, and to give as complete an explanation of the mechanism involved and its reaction to the environment as the present knowledge of the science of heredity will permit. It will be obvious that the origin of new varieties which lead to the evolution of species must depend upon changes in the hereditary mechanism. And since it has been proved conclusively that the hereditary factors are resident in the chromosomes of the individual cells of which the body is composed, any change in the hereditary mechanism must involve these organs of the cells. Consequently the path of the inquiry leads directly to germ cells, for only by such cells can the heritable factors pass from generation to generation.

It has been shown that the personal characteristics, or individuality, of an organism is dependent upon the interaction of the factors of heredity and those of the environment. Hence the variability of a species is not determined exclusively by either of these groups of factors, for individuals having the same hereditary composition may show very diverse characteristics in different environments, and, conversely, those of quite different heredity may appear exactly alike in such an environment as is unsuitable for the expression of the hereditary properties in which the individuals differ.

Furthermore, there are many different hereditary strains in a species, due to heritable changes in past times, and an individual may have any one of a vast number of the possible combinations of the factors of which these many strains are composed. These various combinations of the characteristics of preëxisting strains, associated with diverse environmental conditions, are thus responsible for the variability of a stable species. But from time to time a change occurs in the hereditary complex—one of the hereditary factors itself becomes altered —frequently resulting in a more or less profound change in the characteristics of all the individuals to which it is transmitted in future generations. Such a change, whether so slight as to be discernible with difficulty in a single part of the body or so extensive as to affect the entire organism, is called a mutation. And we are now certain that such mutations are the basis for the origin of new varieties of plants and animals, and in all probability for the evolution of species.

It is possible to think of a multitude of changes which might occur without being detrimental to the organism, for of the many hereditary strains of some of the common species of plants and of animals, each appears to be as well adapted to the environment as are the others. But who can suggest an actual improvement in any species without the danger of contradiction by others whose opinions may be equally worthy of consideration? That many individuals of a species are distinctly ill adapted to their environment is a common observation, but this usually results from the failure of the individual to realize the full advantage of his heritage.

It has been shown in a preceding chapter that the normal environment of organisms acts as a stabilizing factor, in that it eliminates those individuals and those hereditary lines which depart too widely from the rigorously prescribed environmental requirements necessary for development, growth, and reproduction. A considerable degree of variability in certain directions always obtains, while in other directions even slight deviations from the normal type are fatal.

It has been assumed that these have been derived from distant ancestors by the survival of those among the vast numbers of intervening types which were the best fitted for their particular environments. And since these may be the fittest forms that have yet appeared (taking into consideration all the conditions under which each stage of the life history is passed) it is not to be expected that a form more perfectly adapted to the environment will appear except at very long intervals. For of the countless new hereditary types that are presumably frequently coming into existence an overwhelming majority will prove to be less well suited than is the normal stock, since this stock may represent the survival of the single best of the myriads of changes which the hereditary organism has undergone in its past evolution. Consequently nearly every new hereditary change gives rise to an inferior stock which is likely to be soon cut off—perhaps even before a single individual reaches maturity—through the exigencies of the environment to which every individual of the species is subjected. Thus the species is relatively stable, because only the normal stock can survive, or if hereditary changes do occur these are of such a nature that they are still in harmony with the environmental requirements.

## MECHANISM OF MUTATION

*Mutation by change in the gene.*—If it be granted that any change in the hereditary mechanism must be associated with an alteration of the chromosomal complex of the nucleus of the germ cell, then a critical examination of these chromosomes will be in order. It will be found that the nucleus of the cell contains a definite number of these rod-like or thread-like bodies, each of characteristic size and form (Figure 10).

In order to explain the working of this mechanism it has been postulated that the hereditary factors are really physicochemical entities, called genes, and that these genes occupy definite positions in the chromosomes. In sexually reproduced organisms all the genes except those in the sex-determining chromosomes occur in pairs (allelomorphs), one member of each pair being derived from each parent.

Fig. 10.—Diagram of the four pairs of chromosomes in a cell of the fruit fly, *Drosophila*. In the female the sex-determining chromosomes (*xx*) are similar, while in the male they are quite different in appearance (*xy*). By the process of non-disjunction a mutation may occur, producing a female with an additional x-chromosome, giving her a different chromosomal complex and thereby an altered heredity. (After Morgan.)

This results from the fact that in the process of maturation and fertilization of the egg from which the individual is derived one member of each pair of chromosomes in the egg is discarded, to be replaced by similar chromosomes brought into the egg by the spermatozoön. Thus each fertilized egg, and hence each cell of the body which develops from it, will have a definite number of pairs of chromosomes. One member of each pair is supplied by the egg and hence derived from the maternal parent, while the other member is furnished by the spermatozoön and represents the paternal inheritance.

In the fruit fly, *Drosophila,* for example, there are four pairs of these chromosomes in each cell, differing somewhat in size and appearance, as shown in figure 10. The two sexes are differentiated by the presence of a pair of sex-determining chromosomes, both members (*xx*) being similar in the female, while in the male one member (*x*) is of quite different appearance from its mate (*y*). It is in these four pairs of chromosomes that all the hereditary units, or genes, are situated, and since every cell receives its full complement of chromosomes and of genes, it is necessary that every gene should be divided at each cell division. Figure 11 indicates the manner in which this process may take place, with portions of two chromosomes showing the genes (*1, 2, 3,* etc.) in process of division in readiness for distribution to the two new cells resulting from each cell division (Figure 13).

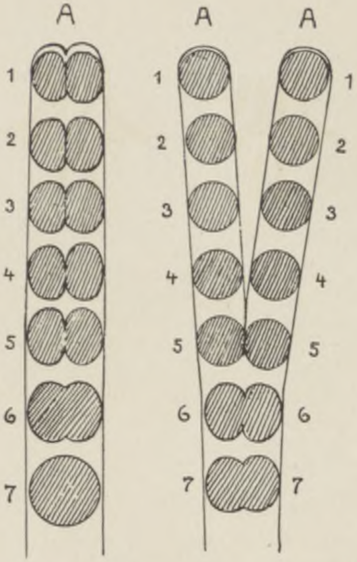

Fig. 11.—Diagram of the division of the genes (1, 2, 3, etc.) in the chromosome *A* preparatory to the division of the latter into the identical daughter chromosomes *A, A.*

Now if, as a result of any accidental or other cause, a change occurs in a single one of the vast numbers of genes which the cell contains, then some alteration of the heredity of the organism or of that part of the organism to which that cell gives rise is certain to take place. The mutation may be of a dominant nature, that is, the bodily characteristics determined by the mutant gene may appear in the presence of the normal allelomorph, or it may be recessive, not visibly affecting the body when mated with a normal gene. If the mutant gene be dominant, and in a germ cell, the new characteristic will be expected to occur in every one of the offspring to which that gene and its descendants are distributed through generation after generation as long as that hereditary line exists or until a new mutation intervenes. But if the mutation takes place in a body cell it will disappear with the death of the body, no matter how favorable it may be, unless the individual can be propagated by vegetative reproduction.

If the mutant gene be recessive, on the other hand, the changed character will appear in the offspring only when it occurs in both egg and sperm cell. And, although the genes determine the hereditary characters, it is not correct to say that each visible character of the body is determined by a single gene, for there is evidence that each organ is the result both of the interaction of many genes and of the environment. And it is furthermore probable that each gene affects more than a single part of the body.

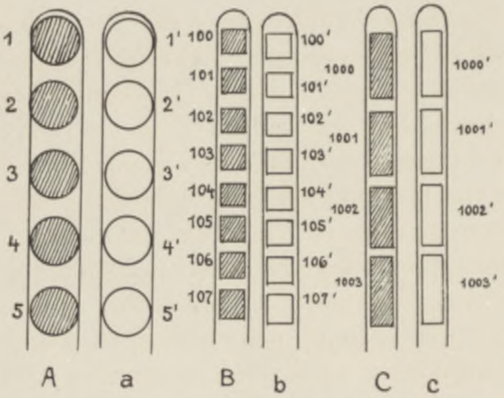

Fig. 12.—Small portions of three pairs of chromosomes, indicating the arrangement of the pairs of allelomorphic genes in each cell; those of chromosomes A, B, C having been derived from one parent and those of a, b, c from the other.

To understand more fully the processes concerned in a mutation one should have a mental picture of the hereditary mechanism of the cell with its multitude of genes arranged in definite order in the chromosomes. In figure 12 are thus represented portions of three pairs of chromosomes Aa, Bb, Cc, in which the genes 1, 2, 3, 1′, 2′, 3′, etc., are indicated as having a linear arrangement throughout the length of each chromosome. Gene 1 may now be thought of as affecting the eye color, gene 2 as one which influences the hair color, gene 100, on a separate chromosome, the character of the hair, whether straight or curly, gene 1000, in a third chromosome, a certain physiological peculiarity; another is responsible for a mental condition, and so on throughout the entire length of all the chromosomes, until we have included all the hereditary physical, physiological, and mental characteristics of the individual. In this way Morgan and his pupils have already plotted the position of over two hundred genes in the four pairs of chromosomes found in a cell of the fruit fly, *Drosophila* (Figure 10).

Now it happens that although these genes are so constituted that they are capable of self-propagation through endless generations, they nevertheless appear to be susceptible to injury and abnormal growth, just as is the cell or the body itself. But the difference between an injury to a gene and an injury to the body lies in the fact that the body eventually dies and with death the injury disappears, while the gene is immortal and retains its injured or changed condition indefinitely. But since this gene aids in determining one or another of the bodily characteristics, all the ensuing generations to which this gene is transmitted must have an altered inheritance and will usually show an altered bodily character.

A simple illustration will make this plain. To produce the colored hair on the body there must be present a certain gene which causes the cell to form an enzyme—or similar substance—which acts on a chromogen base to produce pigment, and if a sufficient amount of this pigment is produced in all the hair cells during growth the hair will be pigmented, black, brown, or yellow, according to the association of genes present. But if this enzyme-producing gene is destroyed, or lost, or for any reason is prevented from acting, then no pigment can be produced no matter how much chromogen may be present. Consequently all the hairs will be without pigment, that is, they will be white from the contained air spaces. And from such albinic animals no colored offspring will ever come if similar ones are bred together generation after generation. The color can be restored by introducing an unchanged chromogen-gene from another line, but the white, or albino, type will reappear just as soon as a pair of the altered genes come together in subsequent generations. Only by the extermination of the entire line bearing the altered gene or by an entirely new mutation can the species be freed from this aberrant type.

It sometimes happens that the mutation of a single gene may affect several organ systems of the body. If these changes are too pronounced the individual may be hereditarily feeble and short-lived or may even be unable to exist through more than the earliest stages of development. In the former case the line may become extinct in a few generations, while in the latter no hereditary line is established.

In some cases the mutation may affect the genes associated with the sex-determining mechanism, in which case we have examples of sex-linked characters, and if these characters be lethal in their nature all the offspring of that line will be of the same sex, due to the death of all individuals of the sex in which the lethal genes are not provided with normal mates. Such a line obviously can be continued only by the introduction of a normal gene from another line in each generation.

It has frequently been found that the same gene may undergo repeated mutations, giving a series of multiple allelomorphs. When the mutant gene itself mutates, a cumulative effect may result, but up to the present time the theory of orthogenesis has received but little support from geneticists. Any multiple allelomorphic series could be arranged in an apparently orthogenetic sequence, but the known history may prove that each member of the series represents merely a more or less divergent mutation of the same normal gene rather than a cumulative genetic series.

*Mutation by Non-disjunction of Chromosomes.*—But there is another type of chromosomal change which involves no alteration in the physico-chemical nature of the gene, but merely an unequal distribution of the genes. And this process will result in the loss of genes in some cells and an excess in other cells. This type of mutation is of relatively frequent occurrence in some organisms and the nature of the process can be confirmed both by genetical and cytological evidence.

When the cells of the body multiply by division, each of their chromosomes divides longitudinally in such a manner as

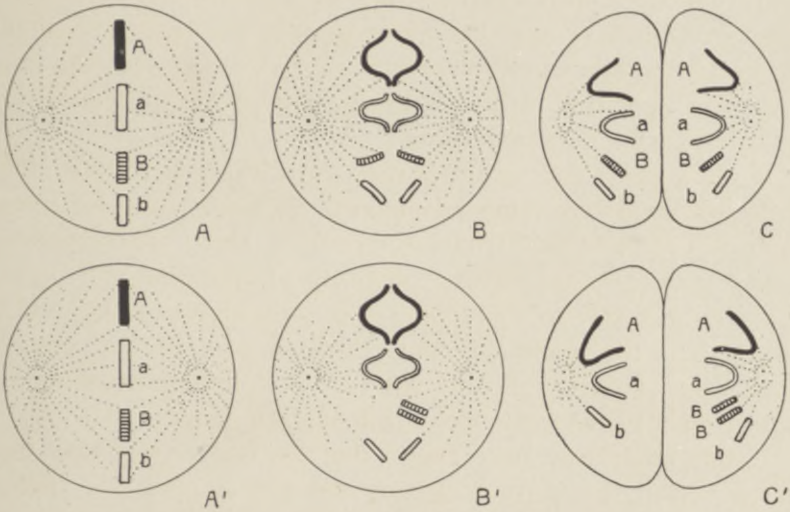

Fig. 13.—Diagrams showing the division of the chromosomes in normal cell division (A, B, C) with an equal distribution of chromosomes *A, a, B, b* to each new cell. Occasionally a mutation occurs (A′, B′, C′) in which the divided chromosomes are unequally distributed, giving one of the new cells an excess and the other a deficiency in the number of chromosomes and hence in their contained hereditary units.

to divide into two equal portions each of the genes of which the chromosome is composed (Figure 13). One-half of each chromosome, containing one representative of each of its genes, passes toward each pole of the division spindle and is thus transferred to each of the two new cells (Figure 13, A, B, C).

Occasionally, however, both members of one of the divided chromosomes pass together toward one pole of the division spindle and thus give one of the daughter cells a double representation of the genes in this chromosome, while the sister cell lacks these genes entirely (Figure 13, A′, B′, C′). The two cells will now differ in their hereditary make-up, for one will have received additional hereditary factors, while the other will be lacking in a corresponding part of its normal inheritance.

Such a process, termed non-disjunction of chromosomes, may occur at any cell division, including those which take place during the formation of the germ cells. In figure 10 is shown a well-known mutation in the fruit fly, involving the sex-determining chromosome ($x$).

If this unequal division occurs in the germ line and if both of these new types of germ cells by chance survive, and if by fertilization two similar ones form a zygote and if, further, the combinations are compatible for the development of the individual, then there would arise two divergent races, differing in chromosome numbers and in certain characters from each other as well as from the normal individuals of the species. This deficiency or excess of genes seems to be of far-reaching importance in evolution.

Large or small parts of chromosomes, instead of entire chromosomes, may be involved in a similar manner. Furthermore, an entire set of chromosomes may be thus duplicated, or even the complete double set, producing triploid or tetraploid varieties. In animals such extensive duplication is usually fatal to the cell, but in the higher plants such varieties are sometimes viable and capable of reproduction.

If any of the chromosomes are unequally distributed in the division of somatic cells abnormal parts or tissues may result. If the parts are capable of continued growth, as frequently occurs in plants and sometimes in animals, one portion of the body may be markedly different from the rest. This may form a so-called mosaic, or bud mutation, and in plants which can be propagated vegetatively, or even in some which produce seeds, may result in an endless multiplication of the mutation. Some of our improved varieties of fruits have thus arisen in recent years.

We may therefore conclude that mutations result from some unusual or abnormal change in the chromosomal constitution of a cell and that if the change is to be hereditary it must occur in a cell of the germ line. In the first type of mutation there is a change in the physico-chemical components of one or more genes and in the second type there is a change in the distribution of the genes.

## CAUSE OF MUTATION

Now inquiry may be made as to the cause of these changes. Is the external or internal environment responsible, or is it due to chance, that is, to unpredictable combinations of circumstances? If to environment then it should be possible to cause mutations experimentally. But only in a few cases have heritable changes been so produced and these are such as result from an injured germ plasm. It has long been known that prolonged exposure to x-rays results in sterility by the destruction of the germinal cells. It has been recently shown that the fruit fly can be treated with such a dosage of x-rays as will cause the sticking together of certain chromosomes of the germ cells, resulting in deficiency or excess of genes, with accompanying hereditary changes comparable to those occasionally taking place under apparently normal conditions. Mice, likewise, after treatment with a definite quantity of x-rays, show conspicuous hereditary defects in both external and internal organs of the body, persisting at least to the tenth generation. There is good reason for thinking that lead, alcohol, and other protoplasmic poisons may likewise cause defects in the germ plasm, and apparently act as racial poisons.

Finally, the work of Guyer and Smith indicates that injections of a specially prepared plasma into the bodies of pregnant rabbits lead to the production of hereditary eye defects in the young, but the subject is still open for further experimentation.

*Environmental Effects and Heredity.*—It is still a popular belief that such environmental conditions as have a specific effect upon the body of an animal or of a plant may so change the germ plasm that subsequent generations inherit this effect at least to some degree. Lamarck was a firm believer in the heredity of characters acquired during the lifetime of the individual, and so was Darwin. When subjected to the critical test of experimental breeding, however, evidence for such inheritance has never been found. Much has been written about parallel induction, whereby certain environmental influences were supposed to affect both the body and the germ plasm simultaneously, but this view likewise has failed of substantiation by any direct evidence, and there are no reasons for thinking that any such relation between environment and germ plasm exists.

Even in recent years references are sometimes made to cases in which the effects of temperature, pressure, salinity, altitude, or other changes in the environmental conditions are alleged to have exerted an hereditary influence on the germ plasm. Such reports probably always come from a mistaken interpretation of cause and effect. As an example may be mentioned one of the experimental studies of Kammerer, which has attracted considerable attention of late. By rearing yellow spotted salamanders in yellow surroundings this Austrian investigator claims to have so altered their hereditary constitution that they produce young with more extensive yellow spotting than young from individuals raised under a normal environment. At first glance this might look like a case of inheritance of the effects of environmental conditions, and such is Kammerer's interpretation, but as we shall see, such an assumption is by no means warranted by the evidence that has up to this time been produced.

Probably no one will care to deny that among the young of animals reared as stated some had more extensive yellow spots than others in the untreated stock. The question at issue is whether these larger spots appeared in the young as a result of the treatment to which their parents were subjected, and whether the heredity has been actually changed. Before one would be justified in assuming that such is the case it would be necessary to know the hereditary constitution of the parents and of this but little is known at present.

Simply because one characteristic or another fails to appear in one or more generations is not conclusive evidence that the hereditary factors for the character are not present, for it may be that the particular environment in which those generations were reared was not suitable for the development of certain factors which would have revealed their presence under other environmental conditions.

In Morgan's work on the fruit fly it has been shown that a relatively slight change in temperature or of the moisture content of the breeding jars may prevent from appearing certain truly hereditary characters which faithfully reappear when subsequent generations are bred under the proper environmental conditions. In one of the cultures appeared a mutation which causes the flies to develop supernumerary legs. It was found that when the cultures were cold the percentage of such abnormal flies was large, but in warmer cultures few or none appeared. A temperature of about 50°F. gave the highest percentage of flies with one or several legs or parts of legs duplicated, while at ordinary room temperature or higher the race could be propagated generation after generation without showing the abnormality. Nevertheless, by returning the stock to the lower temperature the factor which causes duplication of legs was again able to function and showed its presence quite unchanged by the generations during which its action was inhibited. Morgan adds: "In a hot climate there would be no evidence that such a factor was being transmitted. But if the type moved into a cold region it would show duplication in many of the legs."

A difference of a few degrees in the temperature of the environment may thus inhibit the action of hereditary factors which may be carried in the germ plasm for many generations until finally it may chance that the organism is placed, by seasonal change or by migration or by other agency, in a temperature suitable for the action of the factors present, when their influence becomes manifest.

Another case cited by Morgan, Sturtevant, Muller, and Bridges in the revised edition of their book *The Mechanism of Mendelian Heredity* illustrates the influence of moisture on the expression of hereditary factors. Flies of a mutant stock characterized by having the normal black bands of the abdomen broken into irregular spots or entirely absent appeared in one of the cultures. When reared on moist food the mutation is very conspicuous, while on dry food the individuals appear to be normal. If a moderate amount of moist food is provided the larvæ which develop first produce flies having the mutant character very distinct, but as the culture gradually dries the flies emerging later are more and more like the normal type until the last ones cannot be distinguished from the normal. But the hereditary factor remains, to reappear again in subsequent generations if its possessor is reared under moist conditions. So clear-cut are the results that the presence of the mutation can be distinguished even if heterozygous when the larvæ have moist food, and proves to be a sex-linked dominant.

Similar cases are known in the vegetable kingdom. Only in a rather definite range in the environmental complex can the hereditary factors which are present make themselves fully manifest in the organism, and only then can some of them appear at all. In the red primrose (*Primula sinensis rubra*) a moderate temperature, not above 59° to 68°F., is necessary for the production of the red color. If the plants are grown at a much higher temperature, 86° to 95°F., and in a shady place with plenty of moisture the flowers are white instead of red. Such a plant when brought to a cooler environment again produces normal red flowers. Now it should be obvious that much confusion will arise if in experimental work the environmental conditions are unconsciously changed sufficiently to interfere with the normal manifestation of the hereditary factors present. An altered inheritance is likely to be assumed when in reality it is only the environment which has been altered.

The primrose also illustrates how such confusion may arise in the absence of a full knowledge of the normal inheritance, that is, the inheritance under a normal environment. As stated, *P. sinensis rubra* has red flowers at 68°F., but there is another variety, *P. sinensis alba,* which produces only white flowers at this temperature as well as at 86°F. In the same environment of 68°F. therefore one of the varieties has red flowers and the other white. The difference in the color of the flowers of these two varieties may thus confidently be said to be the result of different hereditary factors, the one set producing red and the other white when growing side by side in a normal environment. But the red variety fails to show its normal color when the temperature is raised and might erroneously be thought to have changed to the white variety. Its real ability to produce red flowers can be tested only by bringing it into an environment where its hereditary mechanism can act. The two varieties can then be seen to differ in their inheritance.

Similarly in the coloration of animals, there are hereditary factors which control the configuration of the patterns and others which govern the hue, but both of these groups are dependent upon their internal and external environments for expression. And many strains with differing hereditary factors may breed together in the same region. Only by carefully controlled breeding can the relative effects of these hereditary factors and of the environment be determined. And until such relations are known it is unsafe to assume that a coloration differing from that of the parents is due to an altered germ plasm. If from a mixture of the two varieties of primrose mentioned above, both producing white flowers at 86°F. and therefore indistinguishable, a single specimen of the red variety should by chance be selected for experiment and grown at 68°F. it would, of course, produce red flowers as a result of the environmental change—a so-called acquired characteristic. In further breeding the red-flowered plant would breed true at 68°F., and this result might be interpreted by some as an example of the inheritance of an acquired characteristic, when, in reality, it is merely the normal expression of the plant's true inheritance. If, further, from the postulated mixture of red and white varieties growing at 86°F. a second specimen should be selected and this by chance be of the white variety it could be grown at 68°F. side by side with this alleged "new" form from the experimental culture. Then the white flowers of the former might, in the mind of the experimenter, be assumed to represent the original variety, while the red flowers of the latter might be heralded as a new proof of the inheritance of acquired characteristics.

Hence in no true sense do such results indicate the inheritance of acquired characteristics, for the hereditary factors remain unchanged and their effects become visible when the environment becomes suitable, even though they have been obscured or prevented from acting through many generations.

A very large number of somewhat similar instances of the reputed effects of environment on the germ plasm, or the "fixation of reaction systems," might be discussed, but none of them give conclusive evidence that such an interpretation is correct; all are subject to other and more reasonable explanations, and all may be brought into line with the concept that germinal changes are independent of the environment. The latter merely selects for survival or for elimination one or another of the mutations which spontaneously occur.

*Is Evolution Completed?*—If it be conceded that mutations are the basis of evolution, then there can be no doubt that evolution is taking place at the present time, for whenever any species either of plant or animal is subjected to careful observation in sufficient numbers and during a sufficient length of time, hereditary changes of a more or less profound nature have always been discovered. This is as true of wild species as of our domesticated animals and cultivated plants.

But naturally an overwhelming majority of these changes are detrimental to the species, for, as has already been stated, the present high degree of perfection has been reached only after extremely long periods of ruthless selection from the innumerable mutations that have occurred in times past. Any change is almost certain to be a defect; an actual improvement is even difficult to imagine in some species, so apparently perfect is the adaptation of each surviving organism to its surroundings. Still the adaptation of a species is not perfect until the maximum number of individuals occur in all suitable environments. The survival of the fittest means the continued existence of lines which on the whole have less serious hereditary defects than the others. Any number of mutations occur which have no survival value and several which are positively detrimental to an individual, and hence to the species, may be counterbalanced by one that is highly beneficial.

## RATE OF MUTATION

How frequently do these hereditary changes occur? In the case of the fruit fly, *Drosophila,* which has been more carefully studied genetically than any other organism, Zeleny found from 28 to 61 mutations in each hundred thousand flies. This number is vastly in excess of that found in most organisms, however, and concerns a species in which more than 200 distinct mutations have been recorded during the last few years. It is the great stability of the gene that is remarkable, rather than its occasional mutation. So relatively infrequently does a change occur that it has been estimated that even in *Drosophila* more than a thousand years of breeding at maximum rapidity would be required before every one of its component hereditary units would be affected. Muller, consequently, compares the stability of the gene with that of the radium atom, the life of which is estimated at about two thousand years.

Nevertheless, there probably are in all species certain genes more unstable than others and these may change repeatedly in a relatively few generations, giving rise to series of multiple allelomorphs. The gene controlling the striping on the kernels of maize and that affecting the number of facets in the eyes of *Drosophila* are examples of such mutations.

### DIRECTION OF MUTATION

THE vast majority of genetic changes result in physical effects on the body which are interpreted as losses. There may be, for example, the loss of color pigments in hair or eyes, the loss of horns or of the tail or of certain digits, but these changes should by no means be interpreted as actual losses of the substance of the gene involved, but rather as a change in the activity of the gene. These apparent losses may result in the production of characters which are dominant to the normal type, that is, factors which inhibit the activity of the normal allelomorph, or they may be recessive to the normal. As examples of the former may be mentioned hornless cattle, bob-tailed cats, animals with less than the normal number of digits, as well as certain white mammals and poultry. Recessive loss mutations include many white, or albinic, animals, white flowers, silky feathers, and in fact the majority of all genetic changes.

Other mutations appear on the body as additions, or accentuations of the normal characters, giving, for example, an additional number of digits, a longer tail, longer hair, or deeper coloration than the normal stock. Such mutations, also, are in some cases dominant and in others recessive to the normal stock.

*Progressive Mutation.*—In some cases a gene may undergo successive changes in the same direction, either in the accentuation or the loss of some character. There will then be produced a series of allelomorphs which the paleontologist would interpret as illustrating orthogenesis, and there is reason to believe that such mutations may be of evolutionary significance. On the other hand, it is probable that most instances which have been thought to indicate orthogenesis are merely the result of a number of independent mutations from an ancestral stock which the observer himself has arranged in such a series as to suit his theory. As examples of progressive mutations may be given the loss in the number of facets in the eyes of *Drosophila.* In some stocks of this fly a mutation occurs which reduces the normal, or full, eye, with its more than eight hundred facets, to the so-called bar eye, with about 75 facets. From this latter stock arises by a change in apparently the same gene an allelomorphic form known as ultra-bar with an average of only 23 facets in each eye (Figure 14).

From another stock has arisen a mutation entirely devoid of eyes. Now, if the systematist should have chanced to find these four types in nature he might have brought them into a graded series showing to his mind an orthogenetic series from full, through bar and ultra-bar, to eyeless. But he would have been partly in error in this assumption, for bar and eyeless are known to have had an entirely independent origin, since the gene for bar is located in the sex-chromosome, while that for eyeless is in the fourth chromosome. At the same time he would have been correct in his assumption that bar gave rise to ultra-bar, and to this extent the theory of orthogenesis would hold.

*Regressive Mutation.*—Not only does the eye of *Drosophila* show progressive mutation from full to bar and from bar to ultra-bar, but both the bar and the ultra-bar stocks are subject to regressive mutations, as indicated in figure 14, whereby there is a return to the full eye from either bar or ultra-bar. In one instance the return from ultra-bar to full occurred by a single mutation, while in other cases a first mutation leads to the bar type, and this by continued breeding gives a second mutation to produce the full eye.

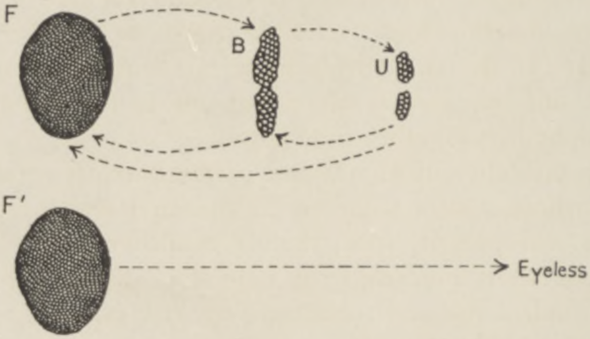

Fig. 14.—Diagram illustrating the reduction in number of facets in the eye of the fruit fly, *Drosophila*. *F*, fully faceted eye; *B*, bar-eyed mutation; *U*, ultrabar-eyed mutation. Arrows represent the directions of mutation. *F′*, fully faceted eye leading by a single mutation to an eyeless race. (After Zeleny.)

It is to be emphasized that these are true mutations, no intermediates having been found in hundreds of thousands of flies, and that there are three widely separated points about which fluctuations occur, each point correlated with the corresponding allelomorph. The bar, ultra-bar, and eyeless stocks have arisen in so far as known quite without influence of the environment, and having thus arisen each offers material for the action of natural selection.

Should the environmental conditions happen to be such that any one of these three mutants proved equal to the parent stock it would have a fair chance for survival side by side with the latter, but this does not imply that it would ever supplant the latter. If the two forms were not mutually fertile there would result two species where but one had been before, and these might live together indefinitely.

If, on the other hand, any one of the mutants should prove, on the whole, better adapted to the environment concerned than was the parent stock, then it would conceivably happen in the course of time that the new stock would supplant the old. But unless the new form were greatly superior to the old, the chances of this happening might be remote, because of the small numbers of the new mutants as compared with the ancestral stock.

## EXTENT OF MUTATION

TRUE mutations are often so minute and behave in such a similar manner to the associated environmental influences that they can be distinguished only by breeding. But their reappearance in successive generations under a variety of environmental conditions is proof that genetic changes are involved.

In its extent a mutation may be either total or partial; that is, an entire character or an entire organ may disappear or be added by a single mutation or the change may be very slight. In the former case a single mutant gene causes the entire loss of the horns in cattle or the gain of an extra pair of horns in goats; it may unite the two large toes of the pig into the median hoof of the mule-pig, or it may incompletely double the foot of the cat; it may add or subtract one digit in the hands and feet of man; it may shorten our long bones and reduce our finger joints to two, as has long been the condition of the thumb; it may prevent the formation of the cat's tail or the external ears of sheep, or it may cover the fowl's foot with feathers. These are all more or less completely dominant mutations, which have taken place in normal stocks, having appeared spontaneously and most of them without intergrading stages.

Vastly more numerous, however, are those mutations which cause but a slight visible effect on the body and which are recognizable as such only by carefully controlled breeding. Such genetic changes presumably have little, if any, effect on the existence of the species.

## TYPES OF MUTATION

It has been shown that all the organ systems of the body are subject to mutation and that the change of a single gene may have a visible effect on several different organs. Not only do mutations result in trivial changes in the external and visible parts of the body, but they may cause such profound alteration in the essential organs at any stage of embryonic development that normal growth and metabolism are rendered impossible and an early death inevitable.

*Physiological Mutations.*—Probably many more mutations affect the physiological properties and the internal organs of the body than are visible on the surface and therefore recognizable as such. And just as the majority of visible mutations render the organism less well fitted to its environment than is the parent stock, so physiological mutations are probably nearly always deleterious. Such mutations may affect the fundamental processes of development or may so interfere with the metabolism in early life that the individual may be unable to survive. Many such lethal factors are known both in animals and in plants. If the lethal be recessive to the normal gene the mortality will usually affect only the homozygotes and thus eliminate only one-fourth of the offspring of heterozygous parents.

Such physiological mutations are sometimes associated with visible physical characteristics. In the mouse the gene for yellow hair color is associated with a factor that causes the death of all embryos homozygous for this gene. Hence yellow mice never breed true, because only heterozygous yellows are born. It thus happens that the offspring from yellow mice will average 25 per cent fewer in number than those of most other varieties and will be found to occur in the ratio of two heterozygous yellow to one of some other color, according to the nature of the recessive allelomorph. A similar lethal occurs in black-eyed white mice, causing the death of all embryos homozygous for this factor.

*Sex-linked Lethal Mutations.*—All recessive mutations occurring in the sex-chromosome will appear only in the heterozygous sex unless individuals of the homozygous sex receive the same affected gene from both parents. In the case of lethal mutations appearing in the sex-chromosome, and many such are known, all individuals of the heterozygous sex receiving the lethal gene will be eliminated, resulting in a wide departure from the normal sex ratio.

*Color Mutations.*—In all groups of organisms certain groups of genes are more liable to mutation than others, and therefore changes can be predicted in any given species by knowing the mutations in more or less closely related species. The genes for pigment formation are especially liable to mutation, so that we find black, brown, yellow, white, and spotted individuals appearing occasionally as sudden mutations in many species of mammals, and less frequently in birds, amphibia, and fishes. In nature, obviously, conspicuous color mutations are seldom observed, for such individuals are usually destroyed, either by their own kind or by enemies, before reaching maturity. But where protection is provided, color mutations immediately appear.

The colors of many of the mammals depend upon the interaction of at least seven pairs of genes, *C, E, A, B, S, D, I,* the mutation of any one of which changes materially the color of the hair.

| *Dominant allelomorph* | *Recessive allelomorph* |
|---|---|
| *C,* color enzyme. Mutation gives: | *c,* albino. |
| *E,* extension factor; agouti, black, or brown. | *e,* red or yellow. |
|  | *e′,* spotted red or yellow (triple allelomorphs). |
| *A,* banding (agouti). | *a,* even pigmentation. |
| *B,* black. | *b,* brown. |
| *S,* self color. | *s,* spotted white. |
| *D,* dark eyes. | *d,* pink eyes (no pigment in iris). |
| *I,* intense color. | *i,* dilute color. |

With these seven pairs of genes $2^7$ or 128 different color varieties may be secured, and if e′ is included the number is 256. All these can be secured from the offspring of a single pair of animals heterozygous for all the eight factors, and all the 256 varieties will breed perfectly true until a new mutation of one of the color genes intervenes.

The pigments are further complicated by an inhibiting factor which prevents any of these colors developing except in the eyes even when all their genes are present. This factor, *W,* gives a dominant black-eyed animal with white hair. Curiously enough, when such a white animal, if homozygous for *C,* is bred with an albino all the offspring will be fully colored, and from such a white pair, if the albino is suitably selected for the necessary genes, all the 256 varieties of colored young may be secured. In poultry there are three different white mutations, two of which are recessive to color and the other dominant. Hence a white cock of one variety mated to a white hen of another breed may produce chickens all of which are highly colored like the ancestral jungle fowl.

There is also a darkening, or melanic, mutation which produces a black or nearly black animal from an agouti. And finally there is a time factor which determines the age at which the color appears. In a certain breed of horses the glossy black colts become permanently gray at the age of a few months. In man gray heads rarely occur before the age of 30, but in some families gray hairs appear in the teens. On the other hand the young seal is white and the adults are dark in color. Still other factors control the sequence of changes in animals with seasonal color phases.

Now, in such cases, it is not the environment which determines which colors the young shall have, but it *is* the environment which determines which shall survive under natural conditions, and consequently it is the environment which selects the best-adapted line, if any, for survival as a race.

There is no intergrading; there are no intermediate steps; the animal has the colors determined by its genes and in so far as ascertained by experimental evidence all its other characters likewise. If a mutation chances to produce characters adaptive to survival, the line may persist either side by side with the parent stock or, by the action of rigid natural selection, it may supplant the parent stock. But if, on the other hand, the mutation produces something less fit than the ancestral stock, as it nearly always does, then elimination occurs and no record is left. In other words, neither natural selection nor artificial selection can originate any hereditary change; selection merely determines which of an endless series of spontaneous mutations are to continue.

*Polydactyly.*—Some of the most interesting mutations in man and domesticated animals concern the increase or decrease in the number of digits. Polydactylism is of wide occurrence in man and in cats, behaving in heredity as an imperfect Mendelian dominant. An additional number of toes invariably occurs in several breeds of poultry and of guinea pigs, and is occasionally found in cattle. In all these cases polydactylism is more or less perfectly dominant to the normal condition.

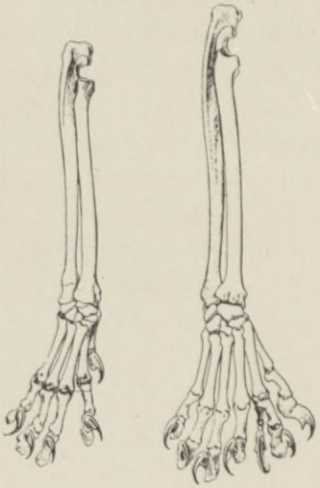

Fig. 15

Fig. 16

Fig. 15.—Skeleton of fore foot of a normal cat and of a polydactylous or "double-pawed" mutation. The latter is the result of an imperfectly dominant hereditary factor for twinning.

Fig. 16.—External appearance and skeleton of the foot of a syndactylous mutation of the domestic pig, the so-called mule-footed pig. The hoofs of the two large toes are fused together, but the bones remain separate except for the fusion of the terminal phalanges.

In those animals having less than the full complement of digits of the primitive pentadactyl limb, the appearance of additional digits has been generally looked upon as an atavistic return to or toward the ancestral type. But in the case of polydactylism in pentadactyl limbs, such as those of man or of the cat, the supernumerary digits can only be attributed to a factor for reduplication or twinning. The latter interpretation is probably correct in all cases, and if a foot such as that of the cow comes to have in its inheritance three instead of the normal two large toes, it is pretty certain that the additional toe is due to a gene which causes a duplication of one of the toes already present. Further indication that this explanation is correct is shown by the fact that the same polydactylous stock is said to have produced one individual which had three toes on each front foot, four on one hind foot and five on the other, involving a duplication of one or more of the metatarsal bones.

Here again the mutation appears suddenly in a normal stock, producing a line in which polydactylism is dominant to the normal type and hence immediately subjected to environmental tests as to its fitness. It is not improbable that continued breeding and artificial selection might yield a stable stock with at least two additional toes.

Polydactyly reaches an unusual degree in cats (Figure 15), where seven or eight digits, instead of the normal five, occur in so-called double-pawed breeds. This imperfectly dominant mutation comes from an hereditary factor for the duplication of the embryonic rudiment of one or more digits.

*Syndactyly.*—Less common mutations result in a fusion of two digits or a reduction in number through failure of one or more digits to develop. A striking example of syndactyly is found in the so-called mule-footed pig (Figure 16). In this mutation of the domestic pig the fusion of the two large toes is so complete as to form a single median hoof. The bony skeleton shows that the fusion involves only the most distal phalanges of the second and third toes, the proximal phalanges and metatarsals being separate (Figure 16).

Again the mutation is dominant in heredity and is at once ready for environmental tests as to its survival. Should the fused hoof render its possessor distinctly superior to the ancestral type with the cleft hoof, and should this mutation be unassociated with any other physiological or physical changes markedly deleterious, then the new race has a good chance to supplant the old in the course of time.

But if the fused hoof should make little difference in the animal's welfare the chances of the new type being continued depend upon an endless number of accidental conditions. The probabilities are that both stocks might live together for a long time, finally reaching proportional numbers of the population according to the law of Mendelian segregation.

If the fused hoof seriously interfered with the normal activities of the animal, on the other hand, or if it were associated with other characters which did, the mutant race would be marked for speedy extermination in spite of the dominance of the mutation, unless migration to a more favorable environment were possible.

*Zygodactyly.*—In the early embryonic life of mammals the digits are united by a continuous growth of skin to form a more or less complete web. An occasional dominant mutation occurs in which the interdigital web continues throughout life in one or both pairs of limbs. Sometimes all the digits of the limb are involved and in other cases only two. It has long been known that the web between the second and third digits of the human foot persisted longer than that between any two of the other digits. In several groups of marsupials and in one or more species of the gibbon, *Hylobates,* the second and third toes are thus united throughout life as far as the last joint. A perfectly similar mutation occurs in some families of the human race and is inherited as a dominant factor.

### ORIGIN OF ADAPTATIONS

Is it possible that all the marvelous adaptations to the environment which every plant and animal shows could have thus arisen either by chance mutations of the genes or by a chance redistribution of stable genes? It seems not unreasonable to grant that they may have done so. Taking into account the vast number of individuals of a species and the number of generations which must have occurred since its ancestral stock originated from some preëxisting form of life we need not be surprised to find such great diversity. To produce even this long sequence of forms would require but a single mutation in many millions of the population.

Some forms are relatively stable in spite of great changes in environment, and some appear to have changed but slightly since early geologic times. But even such forms may have been the progenitors of countless other hereditary stocks, more progressive in their nature because more versatile in their genetic changes, and hence more successful in the establishment of new forms. The old stock still remains because it, too, continues to be sufficiently well adapted to its surroundings to reproduce itself at a rate approximately equal to its death rate.

It has been believed that a new mutation is relatively unstable and that it can be predicted to give rise to a succession of new forms more rapidly than does the ancestral stock. This may prove to be true, but the success of Morgan's work on the fruit fly was possible because he chose a form which breeds rapidly under artificial conditions, which is provided with external features, such as eyes, wings, legs, bristles, and other organs so sharply marked and with parts so definitely arranged and colored that even minute aberrations from the normal type can be readily detected. This species has been found to mutate so frequently that some hundreds of new mutations have been recorded in the course of a few years. Yet the numberless millions of wild flies of this same species have probably formed a thousand times as many mutations in the same period. Very few, if any, of these new varieties either in the experimental cultures or in nature can successfully compete with the wild stock in its natural environment.

The majority of gene mutations are recessive to the normal type and therefore as a rule will not be manifest even if present until there comes a chance meeting of two similar mutant gametes. And so it doubtless frequently happens in nature that a mutation of a greatly superior character occurs, but later disappears because it has no survival value until it appears in an individual in homozygous form. If, for example, a group of snowy owls or of polar bears should find themselves permanently separated from their natural environments there is every reason to think that each would face extermination within a few generations. And yet it is possible that certain members of both groups may be heterozygous for a mutation which, if homozygous, would release them from their now unadaptive white coats. But as they mate generation after generation, even if both parents bear the recessive gene, there are probably three chances to one that any given individual will retain the white coat of its parents. And thus a species which already bears in its germ plasm exactly that mutation necessary for its survival, becomes extinct for the simple reason that in the random mating of gametes chance did not favor the one union which would have led to the establishment of the new and fitter line. Millions of such recessive mutations presumably exist in the animals and plants about us, and unless a chance meeting occurs between two similar heterozygotes they may continue powerless to affect the body which bears them for a thousand generations more. On the other hand, brother and sister mating may occur in the first filial generation and give immediate expression to the recessive mutation in one-fourth of their offspring.

It is no longer necessary to follow Darwin in his assumption that new characters arise by a succession of minute heritable changes. The mutation of a single gene may give rise to such profound changes as to affect not only the entire color pattern but other characteristics as well.

*Mimicry.*—Perhaps the most remarkable adaptations of animals to their environment are shown in cases of so-called protective mimicry. As examples of such may be mentioned the numerous instances in which the individuals of a defenseless species assume the form, habits, and conspicuous coloration of some other species living in the same locality and protected from enemies by defensive weapons or by secretions which are extremely unpalatable. The latter species—the model—will naturally secure immunity from foes which would devour it except for its means of defense, while the mimic likewise secures a certain degree of immunity by being mistaken for the inedible model. Thus many edible flies resemble so closely certain species of stinging bees and wasps in their neighborhood that only careful scrutiny will enable even the naturalist to distinguish between them. The flies are therefore supposed to masquerade in the garb of their protected models, the bees or wasps, as the case may be, and thus escape attack from the birds and other animals which would otherwise feed upon them.

Such impostors are found in other groups of animals, but are most common in insects and other arthropods. Spiders, bugs, and beetles may assume the guise of ants, which are generally avoided either because of the stings which many of the latter possess or because of their secretion of an unpalatable formic acid.

But it is among the butterflies that the cases of mimicry have been most fully studied. In all parts of the world are to be found species of unpalatable butterflies which are faithfully mimicked by edible species living in the same regions. So close is the resemblance between model and mimic that the collector may be unable to distinguish between them until he has them in his net. In North America the common milkweed, or monarch, butterfly (*Anosia plexippus*), as is well known, is said to be mimicked by the viceroy (*Basilarchia archippus*), both species being often found together in the fields. There is some evidence that the monarch is unpalatable to birds, while the viceroy is edible. The Batesian explanation would be that so long as the monarch is more abundant than the viceroy the latter is protected by the inedible qualities of the former, but should the viceory become more abundant than the monarch this protection would cease and both species would be destroyed until the mimic becomes less numerous in the region than is the model.

In other parts of the world, and particularly in Asia and Africa, are species which are doubly or trebly protected, in that the species has two or three different color patterns, each of which resembles that of an unpalatable species in the vicinity.

A classic example is found in the genus *Amauris* of Africa, consisting of a number of species which seem to be unpalatable to birds because of noxious internal secretions. In the same regions occur edible species of the genus *Euralia* resembling those of *Amauris* in almost every detail of form and color pattern. In one of these species, *Euralia wahlbergi,* shown on the accompanying plate (page 143) the female occurs in two distinct forms, one of which (variety *mima,* figure 3) resembles *Amauris echeria* (figure 1), while the other (variety *wahlbergi,* figure 4) is closely similar to *A. dominicanus* (figure 2). There are no intermediates between the two forms of female, and experimental breeding has shown that the variety *wahlbergi* produces both forms and is a simple Mendelian

MODELS MIMICS

Plate III.—Mimicry in butterflies.

Fig. 1.—*Amauris echeria,* alleged model for number 3; reputed to be avoided by birds and lizards.

Fig. 2.—*Amauris dominicanus,* alleged model for number 4; unpalatable.

Figs. 3 and 4.—Two forms of female of *Euralia wahlbergi,* an edible species supposed to mimic numbers 1 and 2 respectively. The natural color is black, with yellow and white spots of similar pattern, in both model and mimic.

Figs. 5, 6, 7.—Three forms of female of the edible *Papilio polytes.* Number 5 is similar to the male, while numbers 6 and 7 are supposed to mimic respectively *Papilio aristolochiæ* and *Papilio hector,* having color patterns of brown and red almost identical with those of their alleged unpalatable models. (After Punnett.)

dominant to *mima*. Thus it is proved that the difference in the two color patterns depends upon a single Mendelian factor and that one form has arisen as a mutation from the other. There is no evidence of any intermediate steps in the process, the original form was protected from its natural enemies by its resemblance to an inedible species of *Amauris*. Mutations may have happened frequently, producing new forms which lacked such protection and were soon weeded out. A new mutation produced a form which by chance resembled another inedible species living in the neighborhood and this survives side by side with the ancestral variety. Both the original and the mutant form can survive as long as both model species are abundant in the locality, but the protection would immediately cease for either form if the respective model should disappear.

The evidence from these studies is that color patterns in both models and mimics are controlled by similar hereditary factors and that the latter does not gradually come to resemble the former but that the resemblance is complete with a single chance mutation.

Another case of mimicry in butterflies has also been extensively studied and proves to rest similarly upon Mendelian heredity. In India and Ceylon there is a common species of butterfly, *Papilio polytes,* in which the females show three distinct color patterns, as indicated in Plate III, figures 5, 6, and 7. All three varieties are readily eaten by birds. One form of the female (figure 5) is black with a row of light spots on the border of both pairs of wings and another row across the middle of the hind wings. This form is quite similar to the male of the same species. The second form (figure 6) has lighter fore wings and a row of red crescents on the hind wings. Now this second form is strikingly different from the male and from the first form of female, but is almost exactly like another species (*Papilio aristolochiæ*), found in the same region, but the latter feeds upon the poisonous pipe-vine and is consequently inedible. The third form of female of *Papilio polytes* (figure 7) has parallel oblique bars of light color on the fore wings and red spots in addition to the red crescents on the hind wings. This form is also strikingly different from both the others, but is so very like another inedible species of the region (*Papilio hector*) that the two might easily be mistaken by a good observer. But *Papilio hector,* like *Papilio aristolochiæ,* feeds on the pipe-vine and is avoided by birds.

It is not at all unlikely that both the two mimicking forms of *Papilio polytes* enjoy a large degree of immunity from attack because of the presence of the two corresponding inedible species, and if so, natural selection would favor the continuation of both. By the Darwinian explanation it might be supposed that these three forms of females had originated by gradual changes leading in different directions from an original type toward the two models. But breeding experiments have shown that such was not the case, but that both have arisen as mutations from an ancestral stock. For it is known from breeding experiments that the three forms differ by only two Mendelian factors, a single gene controlling the color pattern of one form, a second gene that of the second form and a combination of the two genes giving the third. These three forms, then, must have originated as single mutations of the original stock, and these mutations by chance were parallel to the previously existing mutations which had produced the patterns of their respective models. No one knows how vast a number of mutations of *Papilio polytes* have occurred which have not survived because of the absence of a suitable model to give them survival value.

The evidence of mutation is convincing whether or not one is inclined to put credence in the protective value of mimicry.

The presence of the model can have no influence on the *origin* of these mimicking varieties; it can only become a deciding factor as to which, if any, of the countless mutations of the defenseless species will be able to exist in its vicinity. As previously stated, the environmental conditions, of which the model is one, are powerless to originate new forms, but only determine which can survive.

The model may to some extent guide the course of evolution of its associated species, just as its own mutations are guided by the environment, but it can do this only by the action of natural selection in favoring "the survival of the fittest among the many new forms produced."

There are reasons for believing that in a great many of the cases reported as examples of mimicry the so-called model exercises no influence whatever on the form which is thought to mimic it, both happening by chance or by a similarity of genetic constitution to show similar characteristics. Color patterns are particularly misleading, and the survival value of a particular coloration may be quite different to a nocturnal animal than it would be in similar surroundings in the daylight. One of the commonest mutations in all groups of vertebrates is albinism, but no one would call this mimicry.

It is only when there is good evidence that the mimic actually secures protection by the presence of the model which it resembles that the term mimicry is appropriate.

*Artificial Selection.*—If mutation is the basis upon which natural selection operates, such is equally true of artificial selection. Every one of the many varieties of our domesticated animals and cultivated plants owes its existence to mutation or hybridization, or both. The selection of suitable mutations, together with hybridization of varieties or species in order to secure favorable combinations of mutant characters, and the establishment of the best pure lines of these characters have produced wonderful results in the past and warrant the expectation of still greater success in the future.

*Origin of Species.*—And thus it is that mutations come and go in all directions, and their origin is quite without the directing influence of the environment. If more suitable than the ancestral stock they survive, frequently wiping out the older stock itself in their keen competition. If of no survival value and of no serious detriment to the organism they may still persist indefinitely, until possibly by interaction with subsequent mutations they may ultimately exert some influence for good or ill. If less suitable they lead a rapid decline to extinction.

And yet the most profound mutations that have thus far been observed have produced only new breeds or new varieties—no unquestionably new species has been created under human observation. Do species also originate from mutations, and if so what kind of genetic changes are involved? The best criterion of a species is continued fertility through successive generations, for many species interbreed and produce young, but such offspring are usually sterile. This sterility has been found to be due to incompatibility of the chromosomes. The first generation hybrid, as in the case of the mule, may be superior to either parent species in hardiness, but yet it forms no germ cells because the homologous chromosomes of the two species fail to unite in normal synapsis. Hence it may be concluded that species are created by changes so fundamental as to interfere with the compatibility of the chromosomes of the new and of the parent stocks. But it seems not unreasonable to assume that the same principles are involved as in varietal mutations; there is a different effect and the process seldom occurs or is slowly cumulative, but the theory of chance mutation is quite sufficient to account for *all* organic evolution under such environmental conditions as select now one, now another of the countless mutations for survival.

"Environment permits and directs evolution but does not cause it."

# CHAPTER V

# FOSSIL PLANTS AS EVIDENCE FOR RESISTANCE TO ENVIRONMENT

GEORGE REBER WIELAND

ASSOCIATE OF THE CARNEGIE INSTITUTION OF WASHINGTON

> Where Alph, the sacred river, ran
> Through caverns measureless to man
> Down to a sunless sea,
>
> . . . . .
>
> there were gardens bright with
> sinuous rills
> Where blossomed many an incense-bearing tree;
> And here were forests ancient as the hills,
> Enfolding sunny spots of greenery.
>
> *Coleridge.*

INQUIRY into the reaction of the plants of the ancient world to their environments must include and at the same time pass far beyond the more local fossil floras. Such, with the partial exception of certain Cretaceous and Tertiary floras, and the coal swamp floras, or forests fringing the continents of Carboniferous time, are generally very incomplete. Comparison of one incomplete flora with a preceding or a succeeding flora even more incomplete or local, and a scant knowledge of distribution may, indeed, suffice to show the main course of climatic change for the periods represented, although little can be averred of the final factors producing change. Certain results appear, but seldom either cause or intervening step.

If, however, the evidence from the fossil floras be broadly examined in the light of planetary rather than local environments, some of the rates of change hitherto obscure come into a clearer view. Obviously, causes of change can not be very well understood if rates and amounts of change in geologic time remain without analysis. And yet this is an almost untouched topic in evolutionary research. The brief initial studies of the following pages are made from this more quantitative point of view, and indicate that plant evolution is on the average an exceedingly slow process. Environments appear to be resisted rather than easily yielded to.

Coördinated paleobotanic or ancient plant research now celebrates its first centenary, dating from Brongniart's essay of 1822 on the classification and the distribution of fossil plants in general. Especially the past twenty-five years have witnessed an immense extension of the paleobotanic domain. Knowledge of the dicotyl, monocotyl, and gymnosperm development and distribution has been fully doubled; the Devonian petrified peats of Rhynie, Scotland, have been made to yield singularly complete restorations of the most primitive vascular land plants known; the anatomical studies of the English coal plants begun by Joseph Dalton Hooker nearly seventy years ago, still go on; the prediction of the existence of seed-bearing quasiferns has been fully justified, and remarkable reconstitutions of these singular generalized plants have been made; carbonized imprints are studied histologically by means of the chemical methods introduced by Nathorst; and in turn, the long-concealed structures of the lignites of many horizons are visualized by new methods of thin section technique mainly perfected by American students; while here at Yale a far-spread group of cycadeoid adumbrants of the higher types of flowering plants has been brought to light. Surely these extensions of knowledge, as marked by great improvement in the methods of research employed, during so short a period as this last quarter of the paleobotanic century, must come to rank amongst the great paleontologic accomplishments of all time.

Moreover, with the development in the past ten or fifteen years of paleogeography into fairly dependable form and the approximate mapping of the ancient continental outlines, some idea of the superficies covered from age to age by the wholly unknown floras can now be formed, while the lapse of geologic time has been only recently found so enormous as to demand revision of all earlier ideas of evolutionary change. Bettered determinations of rates and amounts of change mean much in estimating the effects of environment.

As just observed, Adolphe Théodore Brongniart (1801-1876), son of the well-known geologist, Alexandre Brongniart, has the great distinction of being the first to align the fossil and existent plants in a rational system. The elder Brongniart had successfully divided the unwieldy group then known under the name of Reptilia, into Saurians, Batrachians, Chelonians, and Ophidians. While the younger Brongniart, inheriting his distinguished father's talent, was favored with a more or less close association with the immortal Cuvier, then at the acme of fame. In that highly stimulant atmosphere of rigid inquiry and research, he, in 1822, at the age of 21, brought out the remarkable treatise on the classification and distribution of fossil plants.

The view of life held by Cuvier, as shared in by the younger Brongniart, and later amplified so notably by him, can be simply stated. Cuvier in his discourse on the revolutions suffered by the globe and the changes produced thereby in the animal kingdom, was only willing to admit that many forms have disappeared in time, and their ancestors likewise. He held that ancient life had been often interrupted by catastrophes, found little evidence of origins unless simultaneous after great catastrophes, and saw only the most stubborn persistence of type. He believed in much migration, held specific features constant even in domesticated breeds, and thus denied that the present life could be derived from the observed past. Yet Cuvier saw the need of a bettered chronology, and said: "The present state of the theory of the earth somewhat resembles that of the period when certain philosophers believed heaven to be formed of polished freestone, and the moon in size like the Peloponnesus; but, after Anaxagoras arose Copernicus and Kepler who paved the way for Newton; and why should not natural history one day also boast her Newton?"

The mantle of Cuvier primarily fell on the English vertebrate paleontologist, Richard Owen, and in his work many striking passages on lines of development and change are found; although man was still held to have been in his origin exempt from the operation of otherwise universal laws. Then after the lapse of about thirty years, there blazed in splendor on the horizon of the biologic world the genius of Darwin, none other than Cuvier's Newton!

Yet those were really rational interpretations of ancient life and its origins, as held by Cuvier and Brongniart one hundred years ago. On rereading, nothing is truly narrow, or disappointing, in the methods and energy of this dawn of the paleontologic day; though in retrospect one may regret that Goethe's poetic idea of a metamorphosis from simple elements into a flowering plant was not elaborated and shaped in the light of Lamarck's views of all-powerful environmental factors. But only time is the balance and more evidence the means of weighing and evaluating great ideas. A concourse about the year 1830 of Goethe, Lamarck, Cuvier, and the young Brongniart was not to be.

It is not known that Goethe ever heard of Lamarck, and Cuvier with his remarkable powers of presentation and great knowledge of detail bore down all opponents. The idea of fixed species prevailed.

In the reaction to the earlier ideas of persistence and stubbornness of species and types on which Lamarck's clearer views from the invertebrate world of environment had at first made so little impression, opinion then swept to the opposite extreme. Any scientific disbelief in a more or less gradual evolution of animals and plants gave way completely; and despite certain difficulties encountered by students of genetics in their attempts to visualize the actual genesis of species, paleontologists, with time in their favor, observe so much change in species that an opposed difficulty seems to be injected into the current conception of the evolutionary course. One new fossil type after another so demands and fixes the attention that nothing but change comes to be the theme. In the midst of these many investigations of origins, the counter-phenomenon of extinction has received little attention; and the persistence of many of the more highly organized plants in defiance of environmental changes during exceedingly long periods of time, has been scarcely considered at all.

Moreover, with the knowledge that there has been a far more intense parallelism than was earlier conceivable and that types have persisted far longer than was a short while since supposed, environments appear less immediate in their effects. In reality, many facts appear which prove that plants have offered a stubborn resistance to environments instead of ever yielding to them. And some day it may be necessary to answer the question whether plant evolution, aside from the specialized types which perish, has not been partly bathmic or inherent.

## SOURCES OF MATERIAL

BEFORE going on to separate topics let it be noted that compared with the other two divisions of the paleontologic trio, namely, vertebrate and invertebrate paleontology, the data of paleobotany have had a rather scant elaboration, due to the small number of workers in the field, and to a certain dearth of criticism. During the entire paleobotanic century hundreds of well-equipped men studied the countless invertebrates of marine strata of immense extent compared with the fresh-water beds yielding plants; while the vertebrates have also had the continuous attention of a considerable body of students. Yet, because of the great extent of histologic features, derived from the lignitic and the petrified plants, the plant record as a whole possesses a significance in evolutionary study not second to either the vertebrates or the invertebrates. All the way from near the beginning of the fossil record down, there is found in the various fresh-water strata of the globe first one and then another plant with its structure preserved. The cone of some Carboniferous lycopod may be as fresh and clear as if shed but yesterday instead of perhaps 300,000,000 years ago. Again, a vastly older trunk of some tree from the world's first forests may afford the thin sections for critical microscopic study of the essential stem characters and organization. A great and growing record of petrified seeds is known, extending to the very base of the coal period.

In several commercially unprofitable English coal mines are found the remarkable "coal balls," or petrified parts of coal seams, in which the plants making up the coal are present in great numbers. The petrifying agent is calcium carbonate, so that the balls are far easier to cut than most of the French and American quartz petrifications. The leaves, seeds, or stems of the various types of coal plants are usually preserved in great perfection in the balls, and many of the sections cut from them prove of surpassing beauty and interest. Nor is there any likelihood that discoveries of new forms or features of the English coal ball plants will cease for several generations. The great mass of this evidence causes regret that similar coal balls of Austria carrying equally well-conserved structures, and found many years since, were not freely collected and studied. Until late in 1923 such parts of coal seams had seemed relatively rare; but coal balls which must rival in interest those of Europe are at last reported from the American

Carboniferous of Indiana, Illinois, Kentucky, and Texas. This material is abundant, and, it is even not too much to say, of imposing significance.

Fully as important as the coal balls to the science of paleobotany, are the lignitic forests. Lignites are vastly more abundant in the stratified deposits than is generally appreciated, and these masses of logs and stems from great forests of the past await study. Such woody tissues retain their original structure, and more or less their form, but require chemical treatment before they can be thin-sectioned. This is now successfully accomplished by clarifying and imbedding by the so-called nitro-cellulose method. Also, due to replacement of the lignitic cellulose by silica from alkaline solutions, through a slow process not yet demonstrated in laboratories, the conversion of such lignite into coal, or its loss by erosion, is prevented, and the more permanent "petrified" record is left behind, often of grand proportions. (Note PLATE II.)

Continuing this glimpse, there are then, in many terranes, vast petrified forests, usually quartzose or silicified, extending far back in geologic time. In fact, such may be expected in most sandy fresh-water strata from recent back to lower Carboniferous and Devonian rocks. Not merely lesser groups of trees occur, but there may be tens of thousands of stems reaching gigantic size. The petrified forests of the Yellowstone are one of the wonders of the world. In the Hocking Valley, near Athens, Ohio, there was in the late sixties of the last century a marvelous petrified forest of the coal period mainly of stems of an old tree-fern type known as *Psaronius,* but most of this forest outcrop, said to contain a thousand specimens, was carried away and more or less lost to view. The trunk segments were, in many instances, polished into ornamental table tops.

Fortunately the outstanding interest of such occurrences is now recognized. The petrified forests of the Arizona Shinarump are protected for all time in their colorful desert setting as a National Monument of imperishable and fadeless interest. So also, the greatest of the petrified cycad localities of the Black Hills, at Minnekahta, South Dakota, has been formally set aside as the "Cycad National Monument." There, in addition to the trunks from the greater coniferous forests, occur numerous cycad trunks with the flower-buds, fruits, and young crowns of fronds, all silicified in such perfection that polished surfaces and thin sections cut from them, have, added to their rare scientific interest, all the beauty of semi-precious stones.

Summed up in a few words, the bulk of the fossil plant record consists in leaf imprints and casts, the structural key to which is afforded by the petrified and lignitic series. And thus botany and paleobotany come to overlap very far. Only from the two subjects combined may a more ultimate knowledge of the final effects of plant environment be had. For the petrified and lignitic record of the main course of histologic change, taken as the key to the cast and imprint testimony to former distribution, extends from the Cambrian, or "Age of Algæ," and from the simplest of fungi to the ancient seed-bearing, and finally the modern flowering plants. The invertebrate paleontologist deals much in forms clad in an easily enduring shelly outer covering, and the vertebrate paleontologist has progressed far in the restoration, and in establishing the natural classification of the extinct skeletal types which outline the course and extent of ancient vertebrate life. But no evidence for the inherent nature of evolutionary change, and especially of the lines along which life takes its majestic way through the course of geologic time, is clearer than that afforded by the data of paleobotany.

It is in the Permian that modernity in plant life largely takes its beginnings, accelerated by extensive deserts, by cold and aridity, and influenced by the glaciation which at least in the southern hemisphere cut off much archaic plant life. Let

Plate IV.—A Permo-Carboniferous landscape; from the original by Samuel Wendell Williston.
(Adapted from Neumayr.)

the eye rest for a moment on that landscape of Plate IV. The drawing pictures the banks of a sluggish stream or inlet in Texas or New Mexico in lower Permian time. There is a varied amphibian and early reptilian life; great dragon flies and other insects of not unfamiliar aspect are seen; the plants of the Coal Period are still present in vast development and variety. But this single riparian view only typifies one among many landscapes of ever varying detail, rising at last into those with very different plateau and mountain forests. Strange as such life at first appears, it yet includes the immediate ancestry of modern types; and some of even the higher types present are destined in the next 300,000,000 years to changes no greater than separate the groups of genera called families.

### THE TERM "FOSSIL SPECIES"—ITS USE

A PRACTICAL standard by which species so-called, or in a more extended sense specific units, may be measured, defined, recorded, and successfully used in evolutionary argument, can not be entirely uniform for both fossil remains and existent forms of life. Especially is this true of fossil plant species, which even more than fossil animal species are very generally based on imperfect or dissociated parts. If the entire structure and especially the organism of reproduction could be fully known, many fossil species would be accorded generic rather than specific rank. Fossil plant species are, if well founded, relatively large units, often widely separated from each other geographically and chronologically; while lesser variations of form comparable to those denoting "varieties" as known to botanists, are either hidden or exceedingly difficult to define. Occasionally, great masses of fossil material may illustrate some plant species so fully as to give it exactly the value of the living type with the true range of form variation. But however abundant the fossil material, the species are only seen from afar, and only emerge to view in virtual isolation. Very different is the study of species under direct observation or experimental control, and undergoing those relatively instantaneous changes which form the special province of genetics.*

Defining further, the paleontologist deals only with the final, the tangible, results of change in time. Species so-called are all purely form entities ("types"), constituting form genera based on either the acquisition or the loss of outlines or parts, or even of organs. Greater anatomic separations denote families and finally new orders. As the ancient forms are sought out and classified, structural gaps are measured, "missing links" hypothesized. The ultimate goal is that natural classification which begins with the original elements of life, the beginnings of faunas and floras, and successfully fixes the upward course of change into the complex, the specialized, or back into the reduced, with respect to both geologic time and the actual lines of descent.

Obviously this super-purpose or ideal, this whole of philosophic truth, can never be attained in any but the most ap-

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* It is well worth while to turn aside for a moment to see how species look from the near, the almost microscopic, viewpoint of the geneticist. Variations are observed from generation to generation, and for convenience described as *positive* or *negative,* that is, toward or away from some given feature or function. The great mass of variation is, of course, negative (not producing new species), and the positive variations are very generally confined to those tending merely to fix more or less established species. Most variation seen at the origin is in the loss of something.

Bateson, an outstanding genius amongst geneticists, refers to the evidence within the set limits of genetics as merely leading to "evolutionary faith." There can be no "acceptable knowledge" of species "until an unquestionably sterile hybrid is produced by completely fertile parents!" Variations in domesticated animals and cultivated plants are held to have nothing to do with the origin of species. Indeed, as the geneticist views the phenomena of variation, he cannot see those slow changes in assimilation and function which alone are the more adequate basis of outer or visible change, and to which only time may give permanence. Observation is never final.

proximate and always very uneven sense. And yet paleontologists do not admit a lingering doubt as to the reality of the change, from the remote protoplasmic condition into protozoan and all of metazoan life, species by species. The origin of faunas and floras becomes an engraved page of eternal writ. Time and climate have magnified all, and the ordinary operation of natural law, with a continuously resistant and stubborn unity of life, is the only explanation sufficing. Any other is beset by overwhelming difficulties of the disconnected, the uncoördinated, the inchoate. The world will never need another Leonardo da Vinci to tell that fossil shells of the high mountains once lived in ancient seas. Modern art may turn with an ever surer knowledge and steadier brush to the depiction of extinct ancestral and specialized life. Paleontology knows no "faith," in the interpretation of the fossil record, although fortified by both the science of genetics and embryology.

## PARALLELISM

In attempting to reach a true conception of species as a response to, or measure of, environment, it is convenient to define casually what is now commonly termed *parallelism.* It is seen that the forest canopy has always been numerous in species, subject to much the same conditions of growth as now. Two conceptions of the course of change are possible. In the first, origins are mainly local and confined. The second conception, here regarded as the rational one, is that in which all forms supposedly occupy their environments stubbornly. Plants tend to undergo and tend to resist change equally. As a consequence, origin is more simultaneous in various tribes and races, more ancient, more widespread than in the first view, migration being less called into requisition. Graphically, plant descent is more truly shown by slowly convergent lines. These are not represented in actual contact, as the chance of exactly tracing the fossil ancestry for the given line is slight.

Every searching examination of the ancient floras shows an extreme persistence of the main types. Nearly all the elemental vegetative and reproductive organs go back to the Paleozoic. The variation of old stem structures into modern types must follow simple lines. It is seen how foliage of later seed plants changed or suffered reduction from the antecedent simpler forms. How the cycadeoids and pines, standing at the very opposite extremes of the gymnosperm world, yet show astonishing likeness in their seeds, becomes apparent. Even the perfect or strobiloid flowers of the one, and the cones of the other are found to be of no utterly variant genesis. In fact both, and perhaps angiospermous flowers too, may arise from apical whorls of fertile leaves or short branches of limited growth bearing such. Discussion of this point has much centered about the remarkable old floral type of Plate V.

Parallelism with great persistence of type is not a new idea, nor even a new term. Facing the severity of far more limited fossil evidence, Hugh Miller used with a certain logical felicity both the term and the idea in the *Testimony of the Rocks* seventy years ago. Later Huxley, with an intensely well-ordered knowledge of structure, noted as a most astonishing thing the fact that the proportion of extinct ordinal types is so exceedingly small. Type after type is found in older and older geologic strata as discovery goes on.

Evidently, change in plants and animals which often occurs along broad fronts and in entire groups, is due to interdependent factors, and must partly transcend and defy the local environment,—perhaps all environment taken in the ordinary sense. The theory of a persistent and never ending migration has been a convenient one, but a heavy burden of proof is put upon it by the similarity seen in remote floras from age to age. Homoplasy, or the development of similar features independently, is the opposed principle. That which strikes the observer as fossil evidence increases is not so much abrupt change or "saltation" as the persistence and directivity of change in great groups. Change often seems to extend beyond the ordinary environmental limits, very far regionally and geographically. In fact, less of order in observed change might well be expected. But however much the forms of life may seem to yield to environmental change for the time being, a course of resistance follows, and long persistence of type is the tendency.

### KNOWN NUMBERS OF FOSSIL PLANTS

SIXTY years ago, Hugh Miller said: "The fossil botanist on leaving the lower Carboniferous beds quits the dry land and puts out to sea." While not meant to be taken too literally, this was true then and is, in a lesser sense, still true. But certainly it can not be long before 500 types of Devonian plants may be enumerated. Carboniferous landscapes unfold before the paleobotanist up to 3,000 or 4,000 known types, often well conserved structurally, and as a whole more satisfactorily studied than has been the vegetation of any other greater division of geologic time. Permian plants denote the great evolutionary turning point from the ancient into the more modern cast of vegetation, but are preserved in considerably less numbers. While the Triasso-Jurassic record, which must indubitably cover the main period of origin for the modern flowering plants, can not rise much beyond 2,000 valid species. With the appearance of vegetation of a strictly recent cast in the Cretaceous, fossil plant species again become abundant, and from North America more than 3,000 Cretaceous-Tertiary plants have been described. From Europe and the polar regions there must be as many more.

Today there are at least 12,000 well-described and illustrated species of extinct plants. While doubtless many thou-

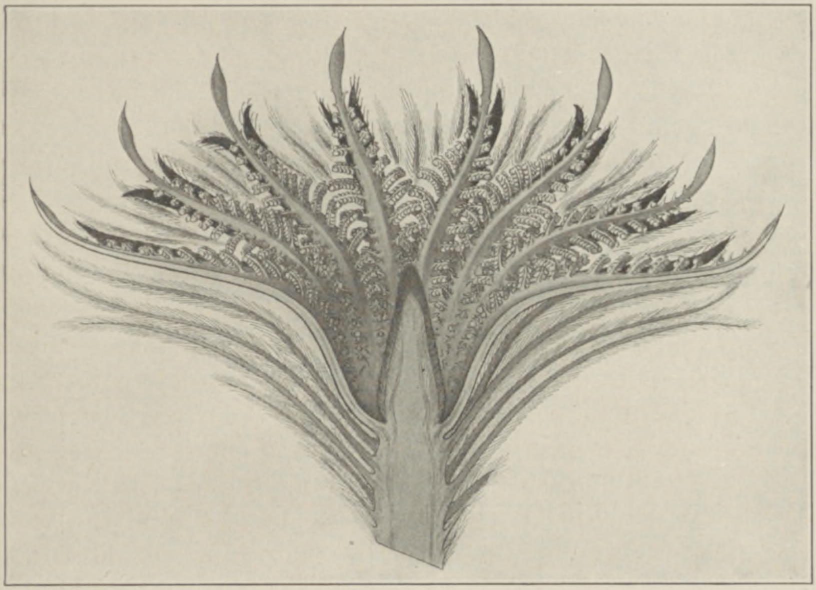

Plate V.—Plan of flower of *Cycadeoidea ingens* of the Lakota Cretaceous of the Black Hills, as determined from the silicified buds. About half natural size. The petrified stem of Plate VI bore similar flowers, the species being quite different.

sand more plants have been seen and listed, even as described forms; although in the case of fossil plants, because of dissociation, the stem, leaf, and fruit must often bear distinct names. The actual or absolute numbers of species are somewhat indeterminate. E. W. Berry says that in his catalog there are listed over 20,000 specific names of post-Paleozoic plants. These are of course subject to continual revision.

In Unger's *Genera et species Plantarum Fossilium* of 1850, just about 2,500 species of extinct plants are enumerated, of which some 2,000 had been described within the preceding twenty-five years; and this is very nearly the unit rate for the century, though somewhat accelerated of late. Noting that North America, the Arctic lands, and Europe have contributed over 90 per cent of known forms, it becomes certain that during the course of the next twenty-five to fifty years the number of well-defined extinct species must reach over 20,000. Even so, many thousands of valid species will probably escape observation.

## POSSIBLE NUMBERS OF ANCIENT SPECIES

THE algal forms of the Pre-Cambrian, Cambrian, and Ordovician have only in very recent years come to be understood as representing a true Age of Algæ. Indeed, it is said that no dominant organisms of later ages, whether plant or animal, ever exceeded these older seaweeds as rock-forming agents, or left a bulkier record. The algæ are essentially immortal types, and those of today an average representation. Thus even the fresh-water "stonewort" goes back to the Devonian *Chara devonica*.

Variation in slime-moulds is not recorded by fossils; although the bacteria were a feature of the life of the remote past, and may now be more numerous in accordance with the life forms invaded. The same might be said of fungi, both in their ærial growth and in their existence as organisms of decay.

But certainly the fungi are of aristocratic lineage. Time is little to them, whether found invading the tissues of the lower Devonian peat bog plants of Rhynie, Scotland, the Jurassic coniferous stems of Spitzbergen, or the palm stems of the Pierre Cretaceous of the Black Hills. They were the same tens of millions of years ago as today.

The liverworts, lichens, and mosses may be regarded as simple long-persistent types with an almost negligible fossil record. But consonant with the far more varied forest canopy of today, their present 8,000 species may number several times greater than their pre-Jurassic forerunners of the pro-angiospermous environments.

The club mosses and equisetes of the Paleozoic which find such great extent, and reach such gigantic size and variety in the swamps of the coal period, some nearly attaining the seed habit, afford a nearly complete picture of the dominant life preceding the rise successively of the conifers, cycadeoids, and angiosperms. The dwarf descendants of today are a mere shadow of past bulk and numbers.

The ferns are hypothesized as reaching variation with establishment of their place in the earliest forest, about the same time that certain fern allies led into the early seed fern lines, perhaps in mid-Devonian time. One of the most interesting events in the long history of the ferns is the slight recrudescence of the foliage type in the mid- and later-Mesozoic. The ordinary or true fern foliage being so much like that of the seed ferns it is safe to assume that as seed ferns disappeared in the Jurassic, true ferns took their place in many forests, with some incidental increase of species of late type, as the record appears to indicate. Furthermore, as the seed ferns gave way the vegetative basis of the later pro-angiospermous forests, that is, the forest types more or less antecedent to the present flowering plants were undergoing profound changes. This, in fact, is the great Jurassic turning point in the plant world, preceding the main course of mammalian development. And with this immense change in the forest canopy, certainly marked by great numbers of new species, the fern types entered at last the very varied conditions of the modern net-veined forests of lower Cretaceous time. The richer stores of humus, and more varied shade conditions could scarcely fail to result in many changes in fern vegetation, with probably the final differentiation into the present estimated 6,200 species.

Whatever form speculation as to the variations in number in the plants of the past may fairly take, no types traverse the varied climates of geologic time more successfully than the true ferns. They show little instability of feature vegetative or reproductive, and through full three hundred million years, they remain the same simple generalized plants, intensely resistant to environmental change.

Turning to the seed-bearing plants, now numbering over half of all existing plant species, the very long record and very varied forms encountered must some day permit rational estimates as to ancient numbers, and the main events of past change must be revealed. But as yet there are many gaps in the history of the orders. Primordial seed vegetation must have reached a somewhat varied structure and type, by early Devonian time. Certainly this early plant front was numerous in species, despite simplicity in structure. From the mid-Devonian down there must have been a steady increase in total numbers of seed plant species.

By the close of the Carboniferous the seed plants were well established and well advanced toward modern types, seemingly not excepting the early angiosperms. By Jurassic time, with replacement of the old Cordaite stock, the cone-bearing gymnosperms or evergreens of purely modern type come into view, as a very numerous group compared with present-day evergreens, although still including many relatives of rather ancient aspect. Pines, araucarias, and many types of ginkgos of leafy and varied foliage were then features of great forests of cosmopolitan range. While vast stretches of cycad-leafed plants of old, rather than archaic, aspect girdled the globe as an immensely varied group capable of living in every clime, and probably including thirty thousand to forty thousand species. These are in paleobotany somewhat comprehensively termed the "cycadophytes," which include the so-called cycadeoids, or hemicycads, as a great group related to the present cycads or "sago palms." Moreover toward the close of the Jurassic the cycadeoids, or, to be exact, the flowering cycadophytes, decline somewhat in the visible numbers toward their later total extinction at the verge of Tertiary time. It would seem that at the close of the Jurassic, however, the cycadeoids could still have numbered 10,000 species. Whatever the number, the decline of the cycadeoids covered the later Jurassic and all of Cretaceous time, and nothing is surer in paleobotany than that this decline foreshadowed the advance of the true flowering plants. (Plate VI.)

Probably the opening of Cretaceous time saw in all the world fully 40,000 species of non-flowering plants, and many thousand seed-bearing plants representative of all the modern orders. Both monocotyls, including the typical palms, and dicotyls, or net-veined types, are modern in form and widely distributed, although the known species of these higher types do not become numerous until the mid-Cretaceous. Since then, the main course of plant evolution can be summed up as a rapid disappearance of naked seeded types, or gymnosperms, to 600 species of relatively limited distribution, with the steady increase of the flowering plants or the angiosperms to their present numbers, about 120,000 species. E. W. Berry insists that there has been much recent evolution within the dicotyls. But it would not be absurd to hypothesize for the dicotyls of early Cretaceous time fully half as many species as now exist.

There is an unverified impression that insect evolution permitting active cross pollination, played a marked rôle in later floral development. And similarly in the tropics the humming birds may have had a lesser effect. Flowers had probably reached marked variation of form before any of the true birds appeared, and must also have antedated the bees, which are recognized as early as the Jurassic. Just when an abundant nectar secretion was followed by the appearance of varied types of bees can only be surmised. But that this date was crucial, environmentally speaking, may be visualized from the fact that a ton to a ton and a half of honey is yearly gathered or consumed by a group of six ordinary hives of bees, of which only about 5 per cent to 20 per cent is safely available to the apiarist. The bees in gathering one pound of honey are estimated to visit as many as 6,000,000 clover flowers.

Any idea that sweets, the nectars, were scarce in the past must fall short of the truth. The sugar pine secretes an edible sweet, and conifers may produce a globule of sweet at the time of fertilization. Even beekeepers themselves are unfamiliar with the extent of the extra-floral nectaries, naturally the lower and primitive ones. But from these, or indirectly through the aphids in drier seasons, the bees gather great amounts of the so-called honeydew honey. In this as compared with the finer table honey of the apple and the blackberry, unfortunately very rarely on the table, the sugars are the same, and about the only difference is in the higher percentage of gums.

Emphasizing, it is unlikely that the total number of species of all plant life in the world, at present round 200,000 distinct species, has been fewer than from ten to thirty thousand at any time since the older Paleozoic. The Ordovician, Silurian, and Devonian witnessed the development of Archaic land plants and the first forests. Ancient plant life then followed in the Carboniferous and Permian. All later time is that of relatively advanced and modern types. *Transition* from ancient to modern types was marked in the Triassic and Jura; while Cretaceous and later time is that of *dispersal* of modern types as bound up with bipolar glaciation.

From the facts briefly stated, it is seen that bearing in mind a reasonable diversity of type in the ancient plant world, there is no necessity for hypothesizing less than some great number of plant species, as 100,000 at the base of the Cretaceous, when the defined transition into strictly modern types begins. It is evident then, that a plant front numerous in species, a

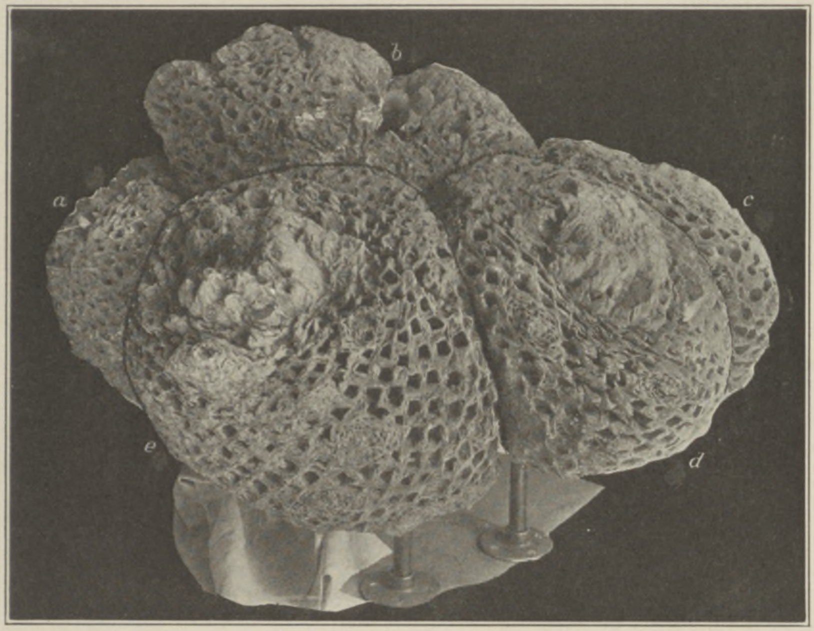

Plate VI.—*Cycadeoidea superba,* one of the cycadeoids. Lower Cretaceous arid type of the southern Black Hills. Petrified trunk with five large low set subglobular branches, 75 cm. across. Each in life bore a crown of pinnate fronds. Various of the sparsely set flower buds in a young stage of growth are indicated by areoles of bract scars. See Plate V.

front running into a certain constancy in or homogeneity of character, has existed from far back in the Paleozoic; although the exigencies of preservation in the fossil condition must from age to age lead to imperfect ideas of what were precisely the ascendant types, as they appeared in all the older continental interiors.

But behind the veil in that less visible plant world of the past, there lie persistence of the simple and generalized types and long courses of parallel development. It is this obscure phase of evolution that is emphasized rather than either the reduction, specialization, or extinction which follow when life yields more sharply to environmental influences.

### DURATION OF SPECIES

ESTIMATES of the trend of specific change and the duration of species are within the bounds of possibility. A number of fossil gymnosperms could be examined in this connection, but a more general statement based on one or two will suffice.

Great and satisfactory discoveries of the range of structure within the Ginkgo or "maidenhair tree" alliance are a promise of the near future. This group is scarcely separable from Cordaites and is presumably composed of the little changed descendants of old Cordaite stocks. It spread over the globe in Jurassic times, and Ginkgo-like foliage then had a particularly luxuriant circumarctic distribution. The sole remaining form, *Ginkgo biloba,* now so exactly on the verge of extinction that not one undoubted occurrence "in the wild" has ever been recorded, has even been called a "living Cordaite," and by Darwin a "living fossil." The species is Chinese, and it is possible that its preservation is due entirely to frequent planting in temple gardens, the habitus being both unique and beautiful. Be this as it may, various close relatives persisted into Tertiary time as types of cosmopolitan distribution at least in all but the torrid climates. Evidently the type could not compete with other forest types, and has reached some hidden limit to further environmental adaptation. *Ginkgo,* indeed, appears to have undergone few specific changes since the Permian. A few stamen, seed, and leaf changes of no more than species value, added to stem change in the pith, wood rays, and tracheids, amounting to little more than generic distinction, are all of the changes needed to carry the "maidenhair tree" into agreement with its ancestry at the base of the Permian. A simple series of ten species may well bridge that gap of two hundred million years. And the fact can not be gainsaid that on the average those *Ginkgo* species thus lasted from twenty to thirty million years each. Ten million years would here be a very low estimate for the average appearance of specific change.

And these must be real enough values which the geneticist may consider in explaining hybridism and the return to type. For certainly tree species which on the average last ten million years, or the equivalent of 500,000 generations, have a profound resistance to final change. But no great number of end-to-end specific changes would be required to bridge the gap between the Permian and early Carboniferous or perhaps late Devonian Cordaites. The seed-leaf-stem variation is not profound. Especially the seed change would be easily accomplished by reduction. Perhaps, then, thirty species would carry *Ginkgo* back to the typical Cordaites, and twenty species more would measure change into some of the simplest of early Devonian seed plants. That is, fifty distinct gradations or steps such as are sufficiently clear to define fossil species might well carry *Ginkgo* to the base of the Devonian. And however these values may accord with species of existent plants, it is at least readable as from the pages of an open book that the Cordaite-Ginkgoid vegetation which underwent the climatic changes of full 300,000,000 years and lived during the deposition of nearly 200,000 feet of sedimentary rocks, showed throughout a marked adherence to type.

Or take the yew, in its seed structures and shoots also markedly reminiscent of the Cordaites, as noted by Mrs. Newell-Arber. Begin with the exact study of the structure of the features of the yew under the microscope. Consider feature by feature those slighter changes which, if taken consecutively, would carry the yew in its entire organization back into agreement with its early Cordaite-like antecedents. How many minor or approximately specific changes would be required to bridge that structural hiatus? Perhaps forty, with an average duration of nearly ten million years each.

It is true that a quantitative study of a course of change based on adequate comparative material ranged before the microscope, like that just suggested, can not be extended to many types or made finally accurate, because the exact ancestry is difficult to assign. But at least in the evergreens and in fact in all the naked seeded plants, there was a prevailing cast of change from age to age, and whether comparisons are searching or more general there results an impression of great stability. The sequoia and pine are further instances of persistence, being recognizable in the Jurassic. Amongst types held by some as very specialized, *Araucaria,* the Norfolk Island pine type, may be mentioned as old and also clearly defined in the Jurassic.

The course of change in the plant world looks unduly complex because the specialized types were often the more readily conserved and now have a bulk in the fossil record, as recovered and known, quite disproportionate to true importance in the evolutionary sequence. Only long years of research can somewhat segregate the odd and the specialized, from the ancestral lines leading down toward the modern floras. But the facts already touched upon indicate an average persistence of species often so long, and frequent lateral distribution so wide, that lesser or local environments seem to have produced comparatively insignificant results. The stubborn persistence which becomes evident when the average of longevity is considered from any numerical viewpoint certainly suggests that beyond the more demonstrable environmental factors must lie yet other still more profound or "bathmic" change-compelling forces.*

The subject of average duration of species has had less attention than it deserves. About twenty years ago the botanist De Vries, taking specific duration in excess of 4,000 years, a length of time extending back into Egyptian records, reasoned that if 6,000 specific changes led from the beginning of plant life into the primrose, *Œnothera,* the course of biologic time would be 24,000,000 years,—a result quite in harmony with estimates of the age of the earth then reached by such physicists as Kelvin. In the De Vries equation,

$$M \times L = BZ$$

M being the number of mutants, L species duration, and BZ an expression for biologic time. Supplying the estimated values,

$$BZ = 6{,}000 \times 4{,}000 = 24{,}000{,}000 \text{ years}$$

But with the biological age of the earth now held far in excess of a billion years, it is possible to derive a closer approximation to the value of L, thus:

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* Involved views of relationship gained from the study of existent plants should be carefully guarded against in all study of fossil evidence for lines of descent. Roundabout courses of change are not to be implied where direct steps may lead to the same result. For instance, the disposition of some botanists to regard *Araucaria* as decidedly primitive, and of others to hold that *Araucaria* is one of the most highly specialized of all conifers, appears somewhat academic to any one intent on scanning the broader fossil horizon. With time so long, and former gymnosperm vegetation so cosmopolitan and numerically far greater than now, the simple, the direct course of change in long-persisting parallel lines, is of course the more probable.

$$BZ \div M = L, \text{ or,}$$
$$1{,}000{,}000{,}000 \div 6{,}000 = 166{,}666 \text{ years}$$

That is to say, even assuming 6,000 as the value for M, although admitted by De Vries himself as probably too high, L, or the average species duration for the sequence ending in one of the higher types of flowering plants, appears to be very much in excess of 100,000 years.

It must be practicable to picture change within the time and structure limits of the fossil land plant record, and as was seen above many species may and do endure for even millions of years. The four great facts which must be accounted are,—parallelism, simple end-to-end change, deep-seated slow histologic change, and extension of geologic time. Approximated, or estimated numbers of ancient species must also measure approximately the gross environmental effect, and may next be considered.

## MAXIMA OF SPECIFIC CHANGE

Actual rates of specific change in geologic time can never be closely determined for even those more limited periods where the recoverable record rises to an appreciable percentage of the contemporary forms. Moreover, there must be exceedingly long periods of little change, and other shorter times of rapid change. And yet there is here a competent method of attack. An answer within rational bounds can be given to the question how many species of all plants have existed in the past, and what was the average rate at which new species of plants appeared. For certainly the lack of evidence is less overwhelming if faced fairly from end to end of a record which is being augmented continually.

The numbers of plant species which formed the successive plant fronts or "canopies" of the past must measure the evolutionary forces. These numbers are approximable, as suggested in the preceding paragraphs. Nor are such numbers lacking in value, although there are more or less notable variations from the more ordinary or even course of development. Doubtless at several times, in the past and especially during Permian time, there was some great shrinkage in both faunal and floral numbers; and precedent to the more recent glacial stages, somewhere in pre-Pliocene time, it is quite possible there were more seed plants in existence than now. Plant evolution appears to go on considerably in advance of animal evolution, providing for the latter the greatest of all environmental factors—the food supply. Hence it is more than an unreasoned guess that the dicotyls and grasses reached their maximum numbers for all time precedent to the culmination of the mammalian phylum in the Pliocene. Suggestive, however, as such variations from some theoretic mean may be, the totality of species in existence has always borne some numerical relation to complexity in structure.

It would mean scant treatment of an interesting subject to say that because full accuracy can not be reached it is not worth while to set down and try out the meaning of the more obvious numerical limits to species of plants in the past. For several methods or means of computation are available. Geologists have long been accustomed to present schemes to show the rise, culmination in abundance, and decline of the principal plant phyla. This method is probably not any more accurate than that of direct averages, taking as a base the assumed total numbers of species about the beginning of the first well-attested land plant record in the early Devonian, and ending with the present total numbers of species. But either method must permit some further study of limits by the use of the ordinary arithmetic and geometric formulæ.

(a) *Geologic Tabulation.*—Taking first the old-time geologic method of tabulating the plant life of the past, but using instead of a diagram, fairly well-considered numerical limits, probably the lower ones, the plants which have existed from the Devonian down may be arranged somewhat as follows:

| | Recent | Lower Cretaceous | Jurassic | Permo-Triassic | Carbon-iferous | Devonian |
|---|---|---|---|---|---|---|
| MYXOPHYTA (slime-moulds) | 400 | 300? | ? | ? | ? | ? |
| THALLOPHYTA (bacteria, algæ, fungi, lichens) | 59,000 | 30,000 | 15,000 | 10,000 | 10,000 | 5,000 |
| BRYOPHYTA (liverworts, mosses) | 8,000 | 6,000 | 4,000 | 3,000 | 2,000 | 1,000 |
| PTERIDOPHYTA (ferns, equisetes, lycopods) | 6,000 | 6,000 | 5,000 | 10,000 | 10,000 | 3,000 |
| SPERMOPHYTA (flowering plants): | | | | | | |
| I Gymnosperms | 600 | 10,000 | 20,000 | 10,000 | 5,000 | 3,000 |
| II Angiosperms | 120,000 | 50,000 | 15,000 | 10,000 | ? | — |
| Assumed totals | [194,000] | 102,300 | 59,000 | 43,000 | 27,000 | 12,000 |
| Uniform totals | [194,000] | 118,000 | 95,000 | 60,000 | | 12,000 |

The above table expresses the belief that with due regard to the fossil record there may have been in existence at the base of the Cretaceous about a round hundred thousand species of plants; in Jurassic forests 60,000; in the Permo-Triassic, 43,000; in the Carboniferous, 27,000; and in Devonian time a possible 12,000 species. And it is pointed out that if some rational number of species be assumed for the Devonian, such as 12,000, then by ordinary proportion to the geologic time scale, the *uniform totals* are found to be more or less in agreement. That is, these latter, or plotted, numbers are merely in direct ratio to an estimated duration for the Carboniferous of 85 million years, for the Permo-Triassic, 60 million years, for the Jurassic about 40 million years, for Cretaceous time down to now, 120 million years, taking an assumed Devonian base of 12,000 species. As these uniform numbers may very well exceed the limits of change in the primeval floras of simpler and simpler structure, they have a certain control value. Indeed, such methods of control in these estimates rise above the simply curious, and should not be too quickly dismissed.

(b) *Geometric Method of Estimate.*—The bettered approximations of the age of the earth afford a fairly trustworthy chronology for biologic time. Of the several methods of measurement the most noteworthy is that based on the lead-uranium ratio in certain radioactive minerals obtained from successively older geologic horizons. As time goes on there is a slow transmutation of uranium into lead, at a rate determinable by laboratory experiment. Also a certain check to the lead-uranium data for the age of the earth is afforded by the ratio of the total salt content of the sea, to the estimated accession from the slowly eroding rocks.

Surely such data lend their dignity to empiric calculations of the limits or possible range of numbers of species in the ancient floras. For the biologist, time values are crucial,—especially such as, for example, the minimum lead-uranium age of about 340,000,000 years for Hugh Miller's famous "coniferous tree" and the associated *Osteolepis* of the "Middle Old Red" of Cromarty. The minimum duration of the geologic ages as calculated from the uranium minerals by Barrell, with the maximum thickness of the sedimentary rocks, follows:

| | Duration in years | Thickness in feet |
|---|---|---|
| Pleistocene | 1,500,000 | 4,000 |
| Cenozoic | 55,000,000 | 63,000 |
| Mesozoic | 135,000,000 | 84,000 |
| Neopaleozoic | 200,000,000 | 78,000 |
| Eopaleozoic | 160,000,000 | 43,000 |
| Total | 551,500,000 | 272,000 |

Now, assuming an average uniformity of the evolutionary course, several methods of interpolation may be used in setting theoretic numerical limits to the ancient floras. The great stream and course of all life for all time may well be, and can be, conveniently pictured in the form of some giant inverted cone or more accurately modified conoid, with the apex at the origin of life, an altitude equivalent to the lapse of biologic time, and a base numerically that of the totality of present species. Dismissing conoidal representation and here using the cone, the base then has an area of 190,000 equal to the present number of all plant species, and an altitude of 500 corresponding to 500,000,000 years. This time-period is somewhat arbitrarily taken, being about the age of the lower Ordovician rocks, perhaps a usable point in geologic time where life is clearly and fairly begun, both in the sea and on the land. A simplification is next reached if each of the present totality of species is taken as a tridimensional unit, binding all of its average of history and descent within itself. Then, the cone representing the average and totality of the history of plant life as it stands with its apex on the Ordovician rocks with an altitude of 500, has for its volume 190,000 in agreement with present species numbers. While comparison with similar cones for the plant life of the successive geologic ages is made direct from the geometric formula:

$$v = \frac{Va^3}{A^3}$$

in which V and A, and v and a stand for the volumes and altitudes of the larger and smaller cones respectively. The altitudes are in proportion to geologic age, and the volumes to total numbers of species corresponding. Taking for an example the upper limits of the Devonian: these limits are about 300 million years back, or 200 million years above the base of the Ordovician; whence $A = 500$, $a = 200$, $V = 190,000$; and on substituting these values in the formula, v is found to equal 12,000± or the probable number of all plant species in existence near the close of Devonian time.

Such a value as that just derived by methods of proportion needs few words of defense. The results of substitution are rational, are within the bounds of plant structure; and variations from them due to excessive eras of specialization, to widespread extinction, or to other causes, can not seriously detract from the value of the general results.

It was, however, suggested above that some form of conoid might more nearly express reality, and a word on that point may serve to bring out one qualifying fact of importance, without the introduction of higher mathematical calculation. The estimates of old floras leave the impression that they are rather high. Thus there is known in the Carboniferous that great and varied group of calamites, already old in the fossil record, cosmopolitan, and presenting an imposing array of evidence covering both stem structure and fruiting, and now most elaborately monographed. The recovered species for certain parts of the Carboniferous may even represent a majority of all the contemporaneous species, running into the hundreds. But even were the data scantier, the calamites at their climax could be understood to fall far short of the numbers of species in later landscape groups of comparable importance, such as are seen in the grasses, or in the orchids. They might at most, at the very extreme, reach such numbers as occur in more stereotyped vegetation like the cactus group, with 1,200 species (according to a recent estimate by Rose).

Or putting this idea still more simply. Take the very old and simple Devonian plant known as *Psilophyton,* isolated, highly characteristic for its time. The Psilophytons are the simplest vascular plants ever discovered. Found abundantly in Europe and North America, it is known that they formed mats of vegetation like certain aquatic plants or like swamp grasses, probably often of vast extent. In the case of plants organized so simply it may even be that most of all the species for some given period will be recovered. In going back therefore to the plant fronts of simpler and simpler structure, species were fewer, change formal; whereas after plants reach that elaborate development of stem, leaf, and flower seen in some great and isolated group like the orchids with their 7,000 species, the possibilities of variation, and finally specialization, must reach a maximum.

## POSSIBLE NUMBERS OF SPECIES FOR ALL TIME

WITH the present types of plants and their great capacity for variation under daily record and experiment, the naturalist, if asked how many species have lived in the past, taking all those that became utterly extinct, and all those that left their changed descendants, might unguardedly think of some untold number, perhaps a billion! And so the effects of environment and all those hidden causes which have brought about the plant succession from ancient times down might readily be magnified to an all but immeasurable degree.

There are two distinct categories into which all plant change, or species origin, seems divisible. In the one, action is slow, comprehensive, and pertinent to the main course of ascent to higher plant types. In the other, change at some point in the line of descent becomes comparatively rapid or accelerated, and so is more intimately concerned with narrow environments. Progression then takes the form of specialization, tending by sudden check to extinction. In the first category extinction is only relative, the changed descendants being left, but in the second it is absolute. Moreover, it is a fact that many of the absolutely extinct forms are the more likely to be left behind as fossils, exactly because of those exaggerated features which brought them to an end. Size and spines seem the two greatest items in specialization. The most ancient of all forests on the North American continent, indicated by the huge Medullosan trees of Gilboa, New York, are an example of specialized and extinct giant forms; the stately araucaroids of the painted deserts of the Arizona Shinarump are another; and the columns of Mariposa and Tuolumne will follow in the records of gigantism. Amongst animals, the dinosaurs are notorious examples of the specialization that leads to early extinction and an undue bulk in the fossil record, out of all proportion to their importance compared with types that prevailed. It is even unfortunate that the attention of investigators has been so much centered on the effort to make these absolutely extinct types outstanding examples of progressive evolution. Such have a definite value, it is true; but only as evidence of the causes of extinction, and of change within themselves, rather than of anything they may teach of the main course of evolution.

Opposed to the specialized types which appear from age to age in various ascendant races are the many lower forms of life, and the so-called "immortal types" which change little or not at all. The great body of change appears, however, to go on in that series of more generalized plastic forms which constitutes the greater stream of life. For from age to age there is a more or less discernible prevailing cast, or average expression of development. In considering the ancestral course for all present plant species from some given period in the past, obviously, then, some forms have suffered few specific mutations,—others, like orchids, many. Hence from the close of the Devonian, when there were about twelve thousand species in existence, there must be some general average number of specific mutations which leads into the present totality of living plants; and there must be in addition the changes, the rapid mutations which led into the specialized forms that were cut off. Both listed together measure the total effects of environment; although only the forms concerned in descent are a final index of evolutionary progress.

From the foregoing statements it is seen that that which prevents the determination of the total number of specific mutations from the upper Devonian plants, for instance, until now, within very close limits, is the inability to know what the approximate average of change for all forms has been for this given stretch of time. For with this factor known, the formulæ of ordinary arithmetic progression may be applied. Taking this given problem of the amount of specific change from the Devonian down, by assuming, therefore, some average number of mutations within rational bounds, such as 100, certainly not a very low factor, an approximate result may be had from the formula:

$$S = \left(\frac{l + a}{2}\right) n$$

The first term of the progression here, $l = 192{,}000$, the last term $a = 12{,}000$, the assumed number of Devonian plants, and $n = 100$. Substituting, $(192{,}000 + 12{,}000)\ 100/2 =$

10,200,000 = S. That is, if the number of Devonian plants when put at twelve thousand allows sufficiently for specialization, and if 100 mutations is a fair average for post-Devonian change into present plant life, then the sum total of plant species for the past 300,000,000 years would only reach a little over 10,000,000. This is a number at least sufficiently well defined to indicate that specialization can never have resulted in excessive or unrealizable numbers of species.

Now one more word, and a rational and safe conclusion about relative numbers of species in the past may be reached. It can well be imagined that change in such a group as the generalized and ancient ginkgo relatives was long widespread and steady. But on the contrary an isolated group like the orchids may be due to recent expansion of some old line, for long rather few in numbers; so that the actual number of changes required to bring this modern group into being might be low. It is even conceivable that some number of post-Devonian end-to-end changes under 200,000 was all that was needed to produce the entire facies of present-day orchidian structure, amounting to 6 per cent of the spermophyta.

Considering these general facts, and bearing in mind the many thousands of simple or archaic plants, all of post-Devonian plant evolution may be accounted for by some fraction of the above totality of 10,000,000 changes, perhaps a half or a third. And as that change covers the lapse of over 300,000,000 years, it follows that to some all-seeing eye, scanning the plant life of the globe continuously, one single well-marked new species of moss, fern, shrub, or tree, might appear in something like eighty years. And then it would take ten thousand years more to know that the change was not a mere fluctuation.

Considerably more attention has been given the subject of limits to the environmental effects than the text may appear to imply. The end-to-end change resulting in the evolution of an orchid, *Cypripedium,* for instance, from its absolute Carboniferous ancestry, must be of two kinds, physiologic and structural, with both subject in some degree to minute or differential change. Hence it is perhaps somewhat of an academic guess as to whether 200, or 1,000 changes produced the *Cypripedium.* Inferential, moreover, must remain the number of forms which were cut off along the line of *Cypripedium* descent, or those which became extinct for any cause without sharing in descent. Nevertheless it becomes a rational process to define the types and limits of change, and then treat the known facts with exactitude, calling to aid arithmetic, and finally algebraic analysis. It is rational to define the upper limits of parallelism, homoplasy, and specialization, beyond which numbers can not go. With limits set, the results of interpolation are suggestive and valuable.

These results, though admittedly empiric, show indisputably that only in the absence of arithmetic analysis can the unverified impression of immensity in the numbers of extinct species persist. In no case were the ancient numbers of species "infinitely numerous," "infinitely great," as Darwin at least implied, and as anyone must infer without numerical study. The actual numbers of new species have been limited throughout geologic time, and that fact must temper all ideas of the final or quantitative effects of the purely environmental factors, whether considered for shorter or for longer periods.

Definitions of environment, if made expansive enough, may include all planetary conditions, even the slow change which the chemical elements undergo. Then well-nigh the totality of organic change may be ascribed to environment. But whether or not a more circumscribed definition be given, it is seen from the average excessively slow appearance of new species, and the limited numbers of such in geologic time, that life sets up or bears an attitude of continuous resistance to all lesser environmental changes. Such unquestionably tend to hold the species in unstable equilibrium, to set the organism in vibration. Although, after change there must forever be some intrinsic tendency to return to the older condition, perhaps even to some profoundly primitive estate.

# CHAPTER VI

# PHASES OF CEPHALOPOD ADAPTATION

CARL OWEN DUNBAR

ASSISTANT PROFESSOR OF HISTORICAL GEOLOGY
IN YALE UNIVERSITY

## INTRODUCTION

IN a study of the manner in which organisms respond to environment the inductive method is most natural to students of the living world, since from the evident relations which the creatures reveal to a definite and obvious environment the principles of adaptation may be drawn. The paleobiologist, on the other hand, must often reverse the process, for in teeth or claws or bones or shells may be recorded the adaptations to an environment that has long since vanished. By deductive processes he may attempt to rediscover many of its unknown elements and to see again in the mind's eye glimpses of the home life and habits of the creatures of other days.

Some will deprecate the method because of its indirectness; for circumstantial evidence is always less appealing than direct observation, and conclusions thus reached have so often been amended in the light of subsequent discoveries. But the soundness of the hypothetical interpretation becomes more certain as it is found to fit a larger and larger array of unrelated facts. And this has ever been the path of progress and of growth in natural science, from hypothesis to theory to fact. The science of paleobiology is young because the facts and principles of modern biology had to be amassed before it was possible to interpret the mode of life and environment of extinct creatures. Nor can its first attempts hope to be without errors, for how many of the possible, significant facts in the lives of existing plants and animals are yet to be perceived, and what single student can command the use of all those which are already recorded? Only by the crisscross and interplay of the contribution of many students will all the facts be made to focus their light upon these interesting problems. It is thus with the hope that it may add some bit of detail or correct the accent of lights and shades in our picture of the lives of the ancient cephalopods that the following paragraphs are offered.

Cousins, so to speak, of the clams and snails, the cephalopods comprise one of the five great classes of the Mollusca—and the most interesting of them all. Theirs is an ancient lineage and not without a golden past. There was a time, before the fishes came to dominate the seas, when cephalopods were the largest and most powerful creatures upon the earth. Nor is their glory all of the past, for their continual pursuit of an active and independent life has led to a development of alertness and keenness of senses that mark them today the highest culmination of molluscan evolution.

Of all the living cephalopods there is one genus, *Nautilus,* which bears an external chambered shell and, among other peculiarities, possesses two pairs of plumose gills; all the others, including squids, cuttles, and octopi, are lacking in armor and possess but a single pair of gills. Two great subclasses are thus indicated, the four-gilled Tetrabranchiata (or better Ectocochlia), and the two-gilled Dibranchiata (or Endocochlia). The first group includes, besides living *Nautilus,* a host of extinct nautiloids and ammonoids of Paleozoic and Mesozoic seas, while the second embraces the belemnites of the Mesozoic, but is not recorded in more ancient times. Notwithstanding sharp points of contrast, however, the modern naked cephalopods are lineal descendants of the ancient armored tetrabranchs, and the two subclasses show a community of structure and organization more significant than their differences.

It is the tetrabranchs which particularly challenge our interest, for only the Pearly Nautilus remains, a straggling survivor of these armored rulers of the ancient seas, and thus our hope of reconstructing their life and habits must be largely in the use of deductions from their structures and adaptations. Fortunately they lend themselves particularly to this treatment, not only because so vast an array of their shells is faithfully preserved in the rocks, but also because the many chambers of each shell, like outgrown clothes, keep record of the growth and development at every stage from infancy to old age. Certainly no other group of animals has left a longer and more complete history in the rocks.

In spite of their great interest, however, the question of their mode of life has led to the widest divergence of opinion. To cite but a single illustration, the extinct ammonites have been regarded by some writers as free swimmers of the open high seas, by others as dwellers near the bottom, and by still others as crawling benthos. There are few facts to be cited in direct proof, but the circumstantial evidence of the correspondence between form and function may shed light upon these mooted questions.

## TRENDS OF EVOLUTION

In the long view of earth history one may often discern on the part of a group of organisms great trends of development. And whether it be the reduction of digits among the hoofed mammals of the plains, or the development of horns by the ruminants, or the progressive coiling of the shell of the cephalopods, the significant feature of the trend is that it becomes the vogue for a geologic while, followed simultaneously by the most distantly related members of the race concerned. The independence and spontaneity with which it often manifests itself here and there among isolated branches of the group rule out the possibility of any inherited tendency to direct its bent; the explanation must be sought rather in a common factor—the response to a common environment. Among the cephalopods, at least three such great trends of development are displayed.

### EVOLUTION OF SHELL FORM

*Progressive coiling.*—The first of these was the evolution of shell form, perhaps the most striking phase of which is to be seen in the progressive coiling of the shell. The earliest cephalopods had straight, or gently curved, shells. Curved, and then loosely coiled ones followed, and much later the deeply involute nautilicones were developed. Although straight forms persisted for ages alongside the coiled, the proportion gradually increased in favor of the latter until the last straggling *Orthoceras* vanished and all were coiled. During the Ordovician fully 50 per cent of these shells were orthocones, less than 15 per cent being coiled and none involute. Half remain straight during Devonian times, but 25 per cent were then coiled and several of these deeply involute. By Carboniferous times the percentage of straight shells had fallen to 20, while that of coiled arose to 70, and with the Triassic the last orthocone was gone.

The inclination to enrollment affected all the orders and many families of the tetrabranchs, each of which accordingly embraces straight, curved, and coiled shells. The geologic succession, no less clearly than ontogeny, shows that the coiling and involution were slowly and gradually acquired and that the cyrtocone and ophiocone were intermediate evolutionary steps between orthocone and nautilicone.

The progressive coiling of the shell, thus strikingly manifested, could not have failed to attract the attention of students of the cephalopods and to lead to the search for an underlying cause. The explanation currently given is that natural selection favored the more compact, coiled shell. It is obvious that if the creature swam backward, as living cephalopods do, the enrolled shell would have many advantages over the long, straight one, since it escapes many of the dangers of breakage and is less cumbersome to guide through the water. But while it is clear that the nautilicone would thus be favored by natural selection over the orthocone (provided the animal swam backward), it is quite improbable that a curved shell would possess any of these advantages. Indeed, it would be more awkward than a straight shell to direct through the water—and this stage, it must be remembered, preceded the coiled form. If the curvature, then, had no selective value until coiling had been completed, it is clear that some other factor was involved during the geologic ages while the cyrtoceran stage was being passed.

This factor may have been the increasing buoyancy of the shell. *Orthoceras,* as Ruedemann was first to prove,[1] lived in a horizontal position. The cameræ of its shell can not, therefore, have been filled with buoyant gas as they are in *Nautilus,* since buoyant chambers posterior to the body would tip the animal head downward as they do in the living *Spirula.* The shells of the long straight nautiloids must have been fairly balanced so as to be neither a burden of weight nor yet a float. They doubtless dwelt near the sea floor. Ruedemann considers them to have been creepers[1] but this habit is hardly to be reconciled with the shape of their apertures. The shells of creeping molluscs, like gastropods, are carried obliquely over the back and unless carried in an almost vertical position the aperture of the shell thus becomes oblique to its axis. The aperture of the early orthocones, on the contrary, is at right angles to the shell. Moreover, the shells never show wear on the ventral side as though dragged along over the bottom.

These features speak strongly for independence of the bottom and we may picture *Orthoceras* rather as a free swimmer, like the living devil-fish, dwelling near or upon the sea floor, resting perhaps much of the time upon the bottom but able to dash away in search of prey or in escape from enemies, swimming by means of its hyponomic funnel. The presence of this swimming organ is suggested, indeed, by the slight emargination of the ventral edge of the aperture. Some of these straight-shelled cephalopods, as *Orthoceras,* lingered on for geologic ages without a tendency to coil, and these retained their pristine orientation in the water. The preservation of color markings in these ancient fossils well illustrates the possibilities of the deductive methods employed by paleobiologists. Ruedemann has observed specimens of two genera of orthocones in which the color pattern is retained, the first, *Geisonoceras tenuitextum,* from the middle Ordovician, and the second, *Orthoceras trusitum*, from the middle Silurian. In both these cases the color bands become obsolete on one side of the shell. In existing pigmented animals of the seas the side directed upward toward the light is colored, and that toward the bottom light. The relation is never reversed and it is quite independent of the anatomical orientation of the organism. Thus the broad belly of the depressed ray-fish is white, but in the flounder, which lies on one side, the entire downward side is lacking in pigment and the whole upper side is plentifully colored. Therefore, applying a generalization well established for the living world, it is quite certain that these differentially colored cephalopod shells were carried in a horizontal position during life and that the uncolored side was downward. Other similarly colored shells have come to the writer's attention. Several finely preserved specimens of *Orthoceras anguliferum* in the Yale Collections from the middle Devonian of Paffrath, Germany, are marked by a geometrical pattern of zigzag bands which are in every case confined to the one side of the shell.

One of these specimens is illustrated in figure 17. Yet another case, that of *Orthoceras* sp., from the Pennsylvanian formations of Oklahoma, shows differential coloring. In this instance the color bands are transverse, running around the shell but all becoming obsolete in the one side. These several instances from as many different periods, each showing a different type of color pattern, point most strongly to the conclusion that the straight-shelled cephalopods retained their early benthonic habits and their horizontal orientation. Their shells, therefore, were not buoyant.

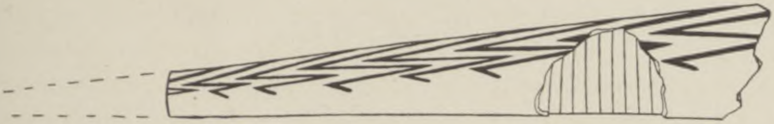

Fig. 17.—Color bands confined to the upper side of *Orthoceras anguliferum* from the Middle Devonian at Paffrath, Germany, which indicate that the animal lived in a horizontal position.

On the other hand, *Nautilus,* the only coiled tetrabranch still living, is able to float at ease in the water because the cameræ of its shell are filled with gas. Moreover, there is much evidence that the extinct coiled cephalopods likewise generally possessed buoyant shells.

When *Nautilus* is at rest with the head and tentacles retracted, it hovers over the bottom with the aperture of the shell directed obliquely upward, the center of gravity suspended directly beneath the center of buoyancy of the chambered coils of the shell. This is a position of perfect equilibrium, retained as well after death, until the decaying body drops out and the shell rises to float at the surface, as the following incident recounted by Dean[2] bears witness:

> I soon found that it was difficult to know just when the animal did die, for it retains a very lifelike position. This I discovered as follows:

> with a view to finding whether at any time the movements became more active, I caused my helper to watch a specimen throughout the night, the man to call me in case it showed a change in position or any peculiar behavior. In the early morning I was told that the animal had shown no movements, a statement I soon had little reason to doubt, for I found my *Nautilus* dead. On returning it to the water I observed that it floated, retaining, however, its customary position; and so it stayed in spite of my efforts to cause it to sink. (P. 827.)

As Willey[3] and others have explained, the shell owes its buoyancy to the fact that the cameræ are filled with a nitrogenous gas. Since the shell contains gas when the creature is brought to the surface, the majority of students have accepted that fact as proof that the gas was also present when the animal was in its normal habitat near the sea bottom. Verrill's widely quoted statement to the contrary seems to be due to an erroneous observation of Sir Richard Owen,[4] who in 1832 (p. 27) reported that there was indirect communication through the axial canal of the siphon between the mantle cavity and the empty cameræ whereby sea water could be introduced to the latter. Accepting this observation, Verrill argued that,

> The chambers were unquestionably filled with fluid under normal conditions. But living as the animal does under pressure at considerable depths, the fluid in the chamber is saturated with gases in solution. When the *Nautilus* is rapidly brought to the surface some of the gas is liberated in consequence of the diminished pressure, and must occupy part of the space within the chambers by forcing out some of the fluid. (Zittel,[5] p. 589, quoted by Hyatt.)

Willey[3] has since demonstrated, however, that the axial cavity of the siphon does *not* communicate with the exterior, but is simply a vein. Far from being capable of introducing water into the chambers, the venous system of the *Nautilus,* on the contrary, was found to be remarkable for its propensity to form nitrogenous gas, so that, as Willey recounts, his knowledge of the pallial veins "was chiefly due to their automatic injection with gas after removal of the animals from the shell." After his elaborate researches on *Nautilus,* Willey entertains no doubt that the cameræ of the shell normally contain gas. Regarding this matter he says:

> The buoyancy of the shell is due to the series of air-chambers which have long excited the admiration of poets and philosophers. . . . It is, I am convinced, an error to suppose that variations of pressure of the air in the chambers enable *Nautilus* to rise or sink as the case may be. The air simply renders the shell buoyant once for all. (P. 747.)

The orientation of the shell in the water as it hovers above the bottom clearly indicates its buoyance, and the orientation seen when the animal is in the aquarium is the normal one, as shown by the coloration of the shell. In this position the upper half of the shell is striped with yellowish brown color bands, which run entirely across the venter of the whorl above. On the lower side, however, the bands fade out and the shell is almost white. Relying again upon the unsymmetrical coloration, we may feel certain that *Nautilus,* at whatever depth it lives, has the body neatly balanced beneath the chambered portion of the shell, so that the unpigmented side is down.

There is but one other living cephalopod with a chambered shell, the rarely seen little squid known as *Spirula.* Although its shells float to shore in vast numbers, the animal itself was little known until the recent voyage of the *Michael Sars,* in the course of which ninety-five specimens were taken alive and an opportunity was afforded to study them in an aquarium. Schmidt's[6] account of them is of unusual interest because it is the first to give an adequate idea of their mode of life and it serves to correct very erroneous conceptions derived from the study of the few previously known specimens. He found, for example, that instead of being attached to the bottom, *Spirula* floats head downward, when at rest, where it is wont to hover in the intermediate depths far from the bottom. To quote from him:

> The movement of *Spirula* is characterized throughout by the presence of the interior chambered shell, which is situated at the posterior end of the body, and tends to lift this portion in the water. A specimen recently dead, or a live one not inclined to active movement, will therefore, if placed in an aquarium with sea-water, rise to the surface, and remain suspended there head downward, with the lighter, posterior part uppermost. If moved from this position, it will immediately swing back to it again, like a weighted tumbling figure.

In other words, the buoyancy of its shell is so great that it is impossible for it to attain a horizontal position when at rest.

Like *Nautilus,* the host of extinct coiled cephalopods, with few exceptions, had buoyant shells, if we may judge by their perfect bilateral symmetry and the lightness of their construction. Since these features are further discussed below, it may be permissible to proceed here upon this assumption. They may not, as in the case of *Spirula,* have prevented the animal from descending to the bottom without an active effort, but at least they tended to float rather than to be a dead weight upon their bearers.

We have noted that the earliest cephalopods were dominantly straight and, further, that the straight shells were not buoyant. The later development of the tendency to float can hardly have failed to enforce adjustments, since the inevitable tendency would be to turn the creatures head downward. On the other hand, the tendency of the animal to maintain the body in a horizontal position was doubtless a strong and very general one among the cephalopods, as it is on the part of most active aquatic animals. Floaters or sluggish benthonic creatures have habituated themselves to every possible orientation, some with heads up and others down; but the active, aggressive animals, characterized by distinct heads and elongated and bilaterally symmetrical bodies, exhibit a remarkable proneness to keep the axis of the body normally in the horizontal plane, whether they be mollusc, fish, reptile, or mammal. If we may judge from living examples, most cephalopods were not an exception to this generalization. Thus the squid, although it can ascend or descend, swimming in all directions as does a fish, nevertheless comes back to the horizontal plane to rest as typically as the fish. The same is true of the cuttles and even of the octopus. *Spirula,* however, is exceptional and shows that it is possible for the cephalopod to adapt itself to living head downward in the water. *Nautilus,* on the other hand, notwithstanding its coiled shell, has the body balanced so that the longer axis is almost exactly in the horizontal plane.

Let us consider therefore the situation of a primitively straight-shelled cephalopod, prone to keep an "even keel" but gradually acquiring more gas in the abandoned cameræ posterior to the body. The center of gravity is thereby shifted further forward and the creature tends to "go down by the head." Upward curvature of the camerated portion, however, would effectively shorten the shell and thus reduce the advancement of the center of gravity. A cephalopod could, therefore, more easily keep its even balance with a curved than with a straight buoyant shell, while a coiled shell like that of *Nautilus* is in perfect equilibrium with the animal at rest in approximately the horizontal plane. The coiled form is thus the adjusted one for a buoyant shell.

Curvature in any other direction than upward in the vertical plane would, of course, be counter to adjustment for a swimming or floating animal. Downward bending would tend the more to tilt the body forward, while curvature to one side would rotate the body onto the opposite side. Possibly selection will, therefore, account for the progressive tendency in the direction of coiling.

At the same time there would come into play, under the conditions postulated, a lifelong and agelong mechanical factor working to the same end. Assuming that the animal strove to maintain a horizontal position either while swimming or while resting on the bottom, the lightening of the camerated part of the shell would exert an upward torsion of the shell from behind. The resulting tension at the line of attachment of the shell on the ventral side of the body would favor a slightly more rapid advancement of the body on this side during growth, with resultant larger increments to the shell on the venter than elsewhere. The result would be a curved and finally a coiled shell. Even after the first volution is attained, the stimulus to coiling still operates, because each new chamber is larger, and hence more buoyant, than the one before, so that the last formed, at the posterior end of the body, has more lifting power than the initial one at the apex, now in contact with the creature's head. Equilibrium is attained only in a deeply involute shell, such as *Nautilus,* or an ophiocone, like *Tarphyceras,* in which there are many volutions, with the body occupying a relatively small portion. If, during the ages, such a modification of form becomes inheritable, the struggle to maintain an even keel in spite of a buoyant shell would seem to be a potent cause for enrollment.

Balance was apparently attained in a different manner by the enigmatic Mixochoanites such as *Ascoceras.* After starting their growth with the cameration posterior to the body and a curving tip to the shell, these cephalopods later begin to form incomplete "saddle-like" septa, cutting off a series of chambers along the dorsal side of the shell, the last of which reaches forward almost to the aperture. Their form in such species as *Ascoceras bohemicus* should give an almost ideal balance to the shell, removing the stimulus to coiling.

*Gerontic uncoiling.*—Thus far but half the cycle of coiling has been considered, for, having attained complete enrollment, several stocks of the cephalopods evince, toward the end of their racial careers, a tendency to revert to the earlier and simpler stages. Among the nautiloids we see *Ophidioceras* of the Ordovician beginning to uncoil and *Lituites* ending entirely straight except for the small initial portion which proves its coiled ancestry. During the Triassic a few of the ceratites parallel these vastly older nautiloids, giving rise to the loose-coiled *Choristoceras* and the straight *Rhabdoceras.* Finally, during the late Cretaceous the gerontic ammonites are represented by the loose-coiled *Ancyloceras* and the straight *Baculites.* In these cases the bilateral symmetry of the shell is maintained as the shell uncoils, but there are a few remarkable cases wherein a spiral form is assumed (*Trochoceras, Turrilites*) or the growth becomes altogether irregular and unsymmetrical (*Nipponites*). In the reversion toward the straight shell, however, the steps in coiling are not exactly retraced, as the ontogeny of the shell clearly shows. In the primitive forms, undergoing enrollment, the earliest part of the shell is least coiled, the volutions become more and more tightly wound with growth, and the umbilicus is wide and even perforate. Moreover, if a deeply involute nautilicone be broken back to its apex, the early stages of growth show progressively less involution, and it may be seen that the individual in its youth was an ophiocone. Thus ontogeny bears silent witness to the racial history of progressive involution. But in the uncoiling, it is the outer whorl which first begins to loosen. In other words, the coiling is normal and tight until the old age of the individual. With the progress of time, however, the loosening comes earlier and earlier in life, and more and more of the shell is uncoiled, but even to the very last the initial whorls in all the genera are tightly wound and bear record of the coiled ancestry of the "degenerating" form. Because these abnormal forms so often shortly preceded the decline and extinction of the particular stock concerned, they have been attributed to racial senility and are seen, in the picturesque phrase of Barrell, "writhing in the death agony of their race." But just how does racial old age induce the abnormal form? If it be through the medium of a change in life habits or environment as they approach their old age, we may be able to trace the chain of cause and effect one link nearer to its source. Such is the opinion of Diener,[7] who concludes a paragraph on the uncoiling ceratites with this sentence:

> I consequently find in the development of uncoiled shapes in the family Ceratitidæ, which begins with *Choristoceras* in the upper Carnic and reaches its climax in the lower Noric substage, a sign of increased adaptability to new modes of life, not of degeneration. (P. 126.)

Just as the horizontal orientation explains the coiling of a buoyant shell, so the habits of the living *Spirula* suggest a cause for these gerontic forms. It will be recalled that *Spirula* lives head downward, being unable to balance itself in another position because of its buoyant shell at the posterior end of the body. As described by Schmidt:[6]

> It may often be seen in the aquarium moving vertically downward from the surface, head first. During the descent the fins are held vertical and move with a rapid waving or fluttering motion which, in conjunction with the current of water from the funnel, now facing upward (to the rear), carries the animal down toward the bottom. Sometimes it will come to a standstill in mid-water, at others it will not stop until it has reached the bottom, but so long as it remains below the surface the fins are kept in motion as described and the funnel is pointed upward. It may rise again slowly to the surface without altering its vertical position: the fins are then sometimes seen in motion, sometimes pressed in close to the hinder end.

Upon the removal of one of its fins the creature was unable to remain still under water, but invariably arose again to the surface, except when it discovered the bottom or sides of the aquarium, when it would spread its arms out and cling tenaciously to the same.

In this vertical position the external coiled shell would meet exactly the reverse of the stimulus that favored its enrollment, for, being beside the center of gravity, the buoyant coils tend to rotate backward, leading to more rapid growth on the inner side of the coil. This would make for the loosening of the coil, and equilibrium would be attained when the shell finally becomes straight and the buoyant pull vertically upward from the center of gravity of the creature's body. The uncoiling would, of course, be slowly and gradually attained, because the accumulated inheritance of coiling acquired during the geologic ages would have to be overcome. A slight and gradual response should result in a loose spiral, as *Crioceras,* but a more complete and rapid response would lead at once to such forms as *Baculites.* The initial portion would remain coiled till the last, because of the inertia of inheritance and probably also because the juvenile stages would long continue to be passed in the ancestral nectonic habits.

All these uncoiling forms being extinct, there is no direct evidence that they lived head downward in the water. A reason why they may have done so, however, is not far to seek. Suppose that an enrolled cephalopod with buoyant shell should come to outgrow its living chamber, the front of the body protruding some distance beyond the aperture. The balance which *Nautilus* enjoys would thereby be upset, the buoyant chambers again being shifted behind the center of gravity. In some regards its circumstance would then resemble that of the primitive orthocone whose growing buoyancy favored coiling, but there would also exist a critical difference. The primitive cephalopod with a slightly buoyant shell probably rested on the bottom when not actively swimming, and thus was able to retain a horizontal position; the gerontic cephalopod with a fully buoyant shell and independent of the bottom could only rest head downward. The former became enrolled, the latter unrolled.

The ancestors of all the dibranchs lost their shell by first outgrowing and then enveloping it in the posterior end of the body, but as they descended from orthocones which they weighted down by the developing guard, they retained a horizontal position. It is little surprising if from time to time coiled tetrabranchs also tended to outgrow their buoyant shells. The outcome in these cases being a maladjustment, they did not long endure and hence appear as gerontic types.

The correlation of life habits with shell form as here conceived may thus be summed up as indicated in figure 18. In many ways this interpretation is the antithesis of one recently proposed by Dollo.[8] This great student of vertebrate paleontology pictured the enrollment as an adaptation to benthonic life and the uncoiling as a result of a return to a pelagic floating existence wherein the animal's head was uppermost. He offered no explanation, however, as to why the assumed life habits should lead to these shell forms. Possibly his explanation of the uncoiling forms was suggested by analogy with living *Spirula,* in which the internal shell is loosely coiled, for he cites this form as floating head uppermost. As the work of Schmidt has now made clear, the orientation of *Spirula* is quite the reverse of that supposed by Dollo. Nor could the orientation he postulates be possible if the shells of the ancient cephalopods were buoyant.*

*Symmetry of coiling.*—There are two great classes of the molluscs which possess coiled, univalved shells, and although they spring undoubtedly from a common ancestral stock, the hypothetical creeping *Archimollusc* of authors, there has been the most persistent and striking contrast in their methods of coiling. The cephalopods, with rare and sporadic exceptions, exhibit a coil of perfect bilateral symmetry; the gastropod shell is proverbially spiral. The occasional exceptions in each case are interesting because they show that there is nothing

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* It should be added that the loose spiral of *Spirula* is not believed by the present writer to have arisen as those of the ectocochlia did and that the above arguments are not based upon its shell form. The history of *Spirula,* as suggested by the geologic chronology of belemnites, *Spirulirostra,* and *Spirula,* has been one of coiling of an internal shell, a situation in which entirely different factors come into play to mould its form.

about either class of molluscs which intrinsically makes impossible the other type of coiling.

Among the cephalopods the spiral shell was developed in the early nautiloid genus *Trochoceras;* it is seen in the case of *Cochloceras* among the Triassic ceratites; and it appeared again in *Turrilites* of the late Cretaceous ammonites. There can, of course, be no connection whatever between these three examples drawn from different families and orders and belonging to widely separated geologic ages.

Analogy with living forms could not avoid suggesting a relation between the shell form and mode of life, since the gastropods, with their spiral shells, are crawlers, whereas the cephalopods are swimmers. The inference would follow that those aberrant cephalopods, with spiral shells, had forsaken the swimming for the creeping mode of life.[9] Unfortunately there is not a living example of a cephalopod, with a spiral shell, to serve as a criterion. But, conversely, one may note that the pelagic gastropods, the pteropods, are all bilaterally symmetrical and that the genus *Atlanta,* which has forsaken the crawling habit and become adapted to a pelagic existence, is coiled very nearly in one plane.

But if the suggested relation of symmetry to mode of life is real, there must be an underlying *cause* why the crawling habit should lead to a spiral coil and the swimming or floating to a bilaterally symmetrical shell. A lifelong mechanical stimulus is not far to seek, if the shell of the coiled cephalopods is buoyant. For the stimulus to coiling, pointed out above, is exactly calculated to mould the shell into a single vertical plane. The buoyancy being directed vertically, the tension at the line of attachment and at the line of growth is constantly on the same ventral side of the body and symmetrical growth occurs. The shell of the gastropod, on the contrary, is not a floating organ, but a burden to be carried by its possessor, and as a result of its weight, there is a tendency to lop over. Here is a cause that would not only tend toward enrollment itself, but also, and at the same time, due to the lop, would favor the more rapid advancement of the shell along the opposite and forward quarter, and thus stimulate a spiral growth. It must be supposed, according to this conception, that each of the several cases of spirally coiled shells among the cephalopods denotes a return to the bottom of an animal whose shell was losing its buoyancy.

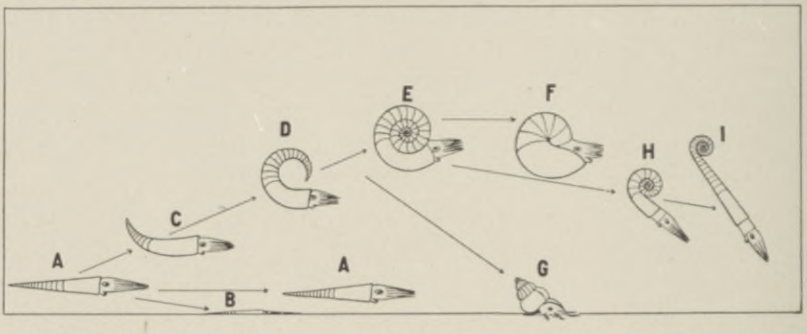

Fig. 18.—Evolution of shell form and its relation to mode of life. The primitive orthocone, A, was not a buoyant shell. Its bearer could swim but rested upon the sea floor when inactive. B represents one of the few grovelers which developed very depressed shells. C, a cyrtocone, has begun to develop a buoyancy due to the secretion of gas into the cameræ behind the body. This gives a little more independence of the bottom and tends to tip the animal forward. Still resting on the substratum when not actively swimming, it strives to keep a horizontal attitude and its shell grows more rapidly on the venter and becomes curved. This leads to the gyroceran stage, D, and culminates in the ophiocone, E, or the nautilicone, F, in which the animal is balanced beneath the spacious gas tanks of its fully buoyant shell. Such forms probably became independent of the bottom, even though, like *Nautilus,* some of them preferred to hover near it. A few forms descended again to the bottom and adopted a creeping habit, developing thereby a spiral coil, the torticone, G. Certain others outgrew their living chambers, whereupon their buoyant shells suspended them head downward until the shell finally uncoiled, H and I.

*Specializations for benthonic life.*—Although the vast majority of the shelled cephalopods were measurably independent of the bottom, swimming or floating at ease because of their gas-filled shells, there are many others which display specializations to obviate or counterbalance the buoyancy of the shell, and these we must regard as adaptations to a life on or near the floor of the sea. This does not imply necessarily the loss of ability to swim, but more probably a mode of life similar to that of the living *Octopus,* which spends much of its time resting or hiding on the bottom, but is able to dash away through the water in flight from enemies or in search of prey, swimming by means of its ambulatory funnel, settling back to the bottom, however, as soon as its activity ceases.

One expression of this adaptation for benthonic life is to be seen in the secondary limy deposits, along the siphuncle, which weight the shell down. Such deposits are common in some groups of the early nautiloids, particularly of the Ordovician and Silurian (*Actinoceras, Ormoceras, Gonioceras*), but they are uncommon in the late Paleozoic and are never seen among the ammonoids. In the Holochoanites the deposits take the form of invaginated conical sheaths, which solidly fill the large siphuncle and make a structure heavier and more durable than the rest of the shell. In such genera as *Endoceras* this structure attains a diameter as much as half that of the shell.

In the Cyrtochoanites the deposits have an entirely different structure, taking the form of bead-like expansions between the septa. They are developed only in certain genera of a few families, but are especially characteristic of the Actinoceratidæ.

The suborder Orthochoanites scarcely shows any development of siphuncular deposits, but Girty[10] has described a different form of ballast in *Pseudorthoceras* in which "the chambers themselves are about half filled by a testaceous deposit which accumulated about the walls instead of about the funnels" (p. 230). According to Frech[11] (p. 596), the chambers of *Orthoceras luxum* and *O. opeletum* are also filled with organic deposits.

If buoyancy led to the coiling of the shell, one would anticipate that those groups, which from the first had their shells heavily ballasted, would not reflect the tendency to progressive coiling so strikingly shown by cephalopods in general, though there is the possibility that such deposits might be developed secondarily in a swimming, coiled shell as an adaptation for a return to benthonic life. This expectation is verified in the most striking way by the facts. The Holochoanites, characterized by heavy endosiphuncles, are almost a suborder of straight shells, *Piloceras* alone being slightly curved, and the little known *Cyrtendoceras* of Remele being a gyracone, with the siphuncle sometimes filled with organic deposits. In this case, however, the deposits are abnormal in their structure, and endocones are absent or obscure. The heavy, beaded siphuncles likewise are characteristic of straight shells, as *Actinoceras, Ormoceras,* and *Huronia.*

While some cephalopods thus weighted down their shells with limy ballast, others showed their adaptation by periodically shedding the terminal chambers. Barrande[12] (p. 573) long ago demonstrated through a study of the common Bohemian species, *Orthoceras truncatum,* that this truncation of the air chambers in certain species was no accidental mutilation, but a habit regularly practiced throughout the entire period of growth. In this species the cameræ were regularly shed in groups of four and the wound to the shell then patched by a characteristic plug, which was secreted from without, apparently by means of specialized arms, such as those which in *Argonauta* aid in the secretion of the shell. Barrande states that during the life of a normal, mature individual the truncation of the shell and patching of the wound must have occurred some fifty times. This remarkable habit, moreover, is not confined to a single species or genus, but was noted by Barrande in five species of *Orthoceras,* two of *Gomphoceras,* and seventeen of *Ascoceras,* and Frech[11] has described still another fine example in *Discoceras antiquissimum.* The last, being a curved shell, gives evidence, in this truncation, of a return from free-swimming to benthonic life, as pointed out by Frech.

In these several cases enumerated above, the adaptation to escape the buoyant pull of the shell is clearly evident, but if, instead, a fluid ballast had been employed, no tangible evidence of the same might be preserved. Such evidently was the case for those straight shells like *Orthoceras* which permanently retained a horizontal orientation without change of shell form.

*Constricted apertures.*—There is another interesting modification of shell form exhibited in several unrelated cases. The aperture of the shell is normally uncontracted, so that the animal could freely extend its head and arms, but in a few groups and at widely separated times there have developed forms wherein the aperture became constricted at maturity. This is seen in such Silurian nautiloids as *Phragmoceras* and *Gomphoceras* and appears again among some of the Mesozoic ammonites, reaching a climax in *Morphoceras pseudo-anceps* (Figure 19). We are indebted to Abel[13] for the suggestion that the forms with constricted apertures used only microscopic food and hence had no need to thrust out the head. This supposed change in feeding habits finds a parallel among the living Dibranchiata, for although these cephalopods are predominantly macrophagous, there are genera belonging to four different families which subsist upon microscopic food. These cases among the dibranchiates are marked by a reduction of the fleshy arms.

*Conclusions from shell form as to varied modes of life.*—In so vast a group of animals as the cephalopods, with their immensely long geologic career, it would be most surprising if life habits did not vary widely and if, from time to time, there were not specializations away from the normal mode of life. In fact, this is clearly evident in the living Dibranchiata, some of which, as the *Octopus*, live more or less isolated lives, hiding in some hole on the rocky sea floor, while others, as the squids, swim in vast shoals through the upper waters, rivaling the fish in their activities, and *Spirula* floats in the intermediate depths. The diversity of form of the shells of the ancient tetrabranchs undoubtedly indicates the diversity of their life habits, if we can but interpret their significance aright.

Thus we may picture the primitive straight-shelled forms as benthonic, coming to rest on the sea floor, but also able to swim near the bottom, with their horizontally disposed shells neatly balanced by ballast of liquid or limy deposits, and neither a burden of weight nor yet buoyant. Ruedemann, who first gave us proof of this horizontal position, suggested a crawling instead of a swimming habit for *Orthoceras*, reasoning that the long, straight shells would have been difficult to carry in a horizontal position while swimming backward, and that in so progressing there would have been frequent collisions and fracturing of the shell. However, it must be remembered that the chances for a solid impact and breakage would be greatly lessened, because the creatures lived upon soft, yielding mud bottoms, and then, too, we have no assurance that the slender apex of the shells usually did escape injury, since it is the rarest thing to find a fossil specimen of mature size retaining the apex. As for swimming backward, the arms which trail in the wake of a moving squid serve as a very good rudder to steer its course in any desired direction.

*Gonioceras* and *Tripteroceras*, the veritable flat fish of all the cephalopods, with their extremely depressed shells, the former having a heavy siphuncle, show an extreme of specialization, and, from analogy with other creatures possessing such a form, must be regarded as grovelers which probably lived half buried in the mud.

In contrast with these straight-shelled forms, there were others with shells tending to float, because they contained more of gases. These developed curved or coiled shells, became more independent of the bottom, even though they preferred to live as *Nautilus* does, hovering not far above, or coming to rest upon, the sea floor. Many undoubtedly floated to higher levels. From time to time there was an attempt to return to benthonic life, which, if accomplished *in spite of* a buoyant shell, led to the uncoiling of the same, but, if preceded by a lessening of the buoyancy so that the shell would settle voluntarily, gave rise to the spiral coil so characteristic of crawling molluscs.

The few forms that appeared late in the Cretaceous, forsaking all regularity and symmetry of shell form, present a difficult problem upon which little light seems to be shed by analogy with living animals. Frech[11] (p. 93) has suggested that such forms lived more or less completely imbedded in the soft oozy bottom muds, where they were relieved of the stresses that would have demanded some symmetry of coiling. As an analogy he points to the irregularly coiled gastropod, *Siliquaria,* which he found living within a sponge. The irregular growth so often seen among certain of the rugose corals may suggest a more probable explanation of such unsymmetrical cephalopods. Such a coral as *Campophyllum torquium* lived on muddy bottoms where its anchorage was often insecure. As a result, after growth had reached two or three inches of height, the coral usually fell over. In attempting to keep its mouth above the mud, the polyp bent itself upward and new growth ensued in this direction, so that the corallum thereafter had a sharp bend. In this species, which tended to form a long and nearly cylindrical corallum, it is not uncommon to find specimens with three or four such pronounced angulations, recording as many times of overturning.

It may be that these irregularly coiled ammonites did not live buried in the mud, but that they attempted to keep above the somewhat soft muddy bottom. Then, since they had no attachment to keep them oriented, they would come to rest with the body prostrate on the mud, or even head downward if the camerated part of the shell contained gases. If in endeavoring to keep the head above the suffocating mud the forward part of the slender body were bent upward, the growth of the shell would follow in this direction. But as the body moved upward, with growth, its position would become unstable and it would topple over. The head must then have been bent in a new direction to keep it above the mud. Occasional disturbance by the waves of the heavier storms would prevent the eventual establishment of any stable form. Such irregular shells are found, it may be noted, only in stocks that had elongated and very slender, almost serpent-like, bodies.

### EVOLUTION OF SUTURES

THE second great trend of cephalopod evolution is that from simple to complex sutures. In all the early cephalopods the septa were simple, saucer-shaped partitions of the shell fitted to the bluntly rounded posterior end of the body. Beginning with the Devonian, the septa in certain stocks came to be plaited toward the margins like radially-corrugated discs and the sutures accordingly show angular bends. Thus arose the goniatites, most primitive of the ammonites. As the simple-sutured nautiloids waned almost to extinction toward the end of the Paleozoic, the ammonites flourished, expanded, and developed ever more complicated suture lines. Once started, the trend toward complexity manifested itself in endless variety of pattern, giving rise to family after family of the expanding race, but in every case the final complexity was slowly and gradually attained.

The chronogenetic succession in the rocks shows this fact with striking clearness, but no more so than the ontogeny revealed in every ammonite shell, for, however complicated the suture line of the adult, they become simpler and simpler, if we break the shell back toward the original chamber. And while here, again, some of the ancestral type persisted unchanged, the new vogue at once became immensely successful, and the ammonites became the dominant shellfish of the Mesozoic seas, outnumbering the nautiloids beyond comparison.

The explanation currently given for this specialization is that it enabled the animal more easily and securely to hold its shell. The complex suture is merely a result of the fluting of the septum. Further, since each septum in turn was secreted by the posterior surface of the body, the fleshy tissue was interlocked into all its irregularities, so that with the least muscular effort the animal could cling tightly to its shell. Thus Hyatt supposed that "the progressive complication of ammonoid sutures took place because of their utility in helping to carry and balance the shell above the extruded parts when the animal was crawling." It has also been suggested that in a rapidly moving, swimming form this secure anchorage of the shell to the body would be a real advantage. *Argonauta* has been seen to lose its shell by a sudden start and later to return to it, as a hermit crab might do. Of course the shell of the Tetrabranchiata is more firmly attached, but since the body must constantly move forward in the shell with growth, the attachment in any case is very slight. It would be a particularly critical mishap if the creature should thus inadvertently lose its armor by a sudden movement at time of danger. However, in most of the ammonites the complexity of the sutures is carried altogether beyond its need as a means of anchorage to the shell.

A more vital need for the complex sutures may have been the adaptation to rapid changes of depth in the water. Pressure under water increases at the rate of about .4 pound per square inch for each foot of depth. A change of depth of one hundred feet therefore results in a change of pressure of about forty pounds per square inch, so that for a rigid, chambered shell a sudden rise or descent would be dangerous, unless the shell were strong; even though the chambers were partly or even largely filled with liquid, such gases as were present, even in solution, would tend to burst the shell upon rising, just as the increased pressure, without, would tend to crush it upon sinking. Moreover, as a corrugated iron pipe is stronger than a plain one, so the complicated septa of the ammonite shells, buttressed by their inflections, are immensely strong, even though thin and light. The extreme lightness of such shells has been commented upon. It appears, as Walther has put it, that everything about the ammonite shell has been concentrated for lightness and strength. It is not the kind of strength, however, that would be of avail against the sharp teeth of the fish, as he supposed. In the jaws of a large fish or reptile the thin walls of the shell would have been like paper, but against the even pressure of the water such a shell as *Anarcestes* must have been a miracle of strength and lightness. *Nautilus,* with its simple sutures, shows a tendency to keep near the bottom, and, though it may be found throughout a range of many fathoms, apparently only changes depth gradually. The ammonites, with their strong, light shells, may have been more independent of the bottom, descending considerable distances to congregate upon their feeding grounds, and dispersing again to greater safety in the higher waters upon the pursuit of powerful piscine or reptilian enemies. The increasing complexity of the sutures reflects the degree of their adaptation to vertical range in the seas.*

This explanation involves, of course, the assumption that the ammonites were really swimming animals, a belief which appears to be thoroughly warranted by such recent works as those of Diener and of Frech. Nevertheless, it was for a long time a mooted question. The living *Nautilus* has a notch, the so-called hyponomic sinus, at the lower side of the aperture to

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* After this paper was written the writer has discovered that this idea was clearly set forth by Abel in 1920.[13]

give play to the swimming funnel, and the presence of such a sinus among the nautiloids has generally been conceded to indicate the possession of the power to swim. The earliest ammonites also had a deep hyponomic sinus and this was, in fact, a characteristic feature of most of the Paleozoic genera, but by Triassic time the sinus had gradually become shallower and in most of the stocks ceased to exist. Its gradual disappearance has led some students to believe that the ammonites without the hyponomic sinus had accordingly lost the ambulatory funnel and must, therefore, have been crawling benthonic animals. Their shells, however, show an array of features that speak strongly for a free-swimming life, and thus there have arisen two opposed schools of thought. Hyatt, Walther, Haug, Phillips, and Pompeckj have argued for a crawling habit; but the more recent works by Diener, Frech, and others seem to have established the fact that the ammonites were chiefly swimmers.

In favor of the crawling habit, Hyatt mentioned, in addition to the gradual loss of the hyponomic sinus, the fact that their occurrence as fossils in the rocks seems to indicate for some of them a gregarious tendency, but his conclusion does not necessarily follow, since *Nautilus,* though decidedly gregarious, moves almost exclusively by swimming and in so doing exhibits surprising agility.[2] Nor does the disappearance of the ventral sinus necessarily prove the loss of the power to swim. The emargination of the ventral side of the aperture is of use when the head is only partly protruded, since it allows more rapid and unobstructed ebb and flow of the water to and from the hyponome, but in case the elongate, muscular body be protruded a little further from the shell while swimming, the sinus is needless. For a free-swimming cephalopod adapted to considerable changes of *depth,* it would be a most advantageous specialization to be able to thrust the head well out of the shell in swimming, for in so doing it displaces more

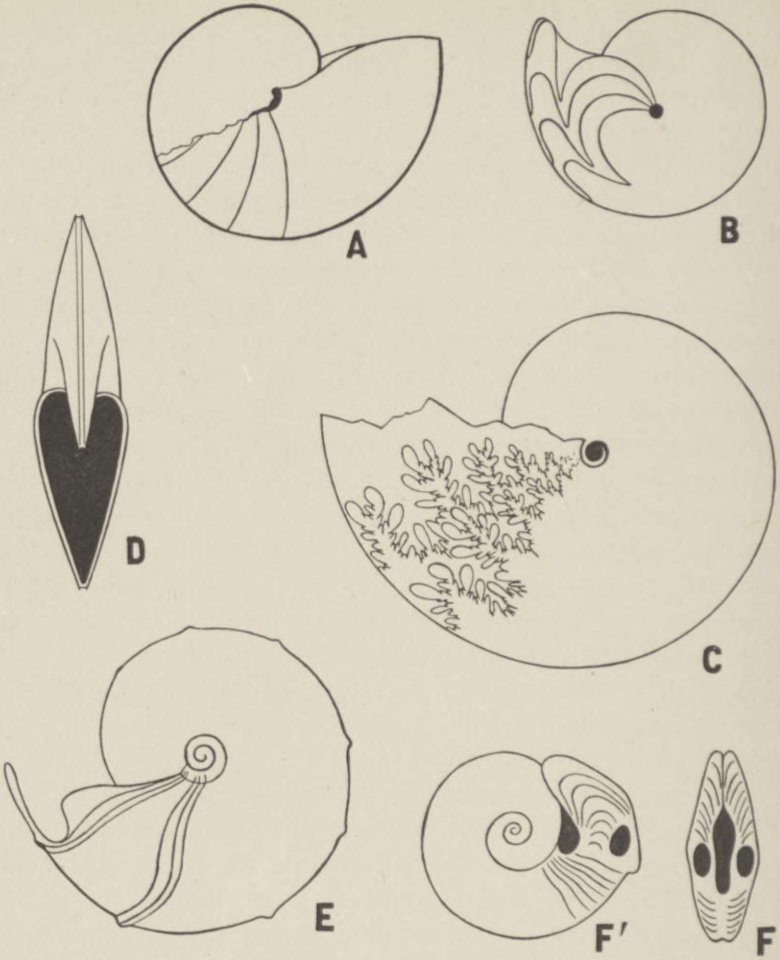

Fig. 19.—Sutures and apertures. A-C, three stages of sutural development: A, simple sutures of a nautiloid such as characterized all cephalopods of the earlier Paleozoic era; B, *Brancoceras,* an early ammonite of the late Paleozoic (Mississippian); C, *Phylloceras,* a fully developed ammonite of middle Mesozoic (Jurassic) time. D-F, types of ammonite apertures that indicate swimming habits; D, *Placenticeras,* representing the many ammonites with thinly compressed shells; E, *Phylloceras mediterraneum,* a rostrate shell with deep ventro-lateral sinuses probably related to a strongly developed hyponomic funnel; F-F′, lateral and ventral views of *Morphoceras pseudo-anceps* with its aperture almost closed at maturity but leaving a deep opening for the swimming funnel and for the eyes. (E and F after A. M. Davies.)

water, and, as a result of this greater displacement, the animal, adjusted to perfect equilibrium when at rest, becomes buoyant the moment it starts to swim. Having the proper balance, it might therefore withdraw as completely as possible into its shell and automatically settle to feeding grounds on the bottom, but in case of danger quickly rise some fathoms in the water by extruding its head and forcing out a few strong jets of water from the hyponomic funnel, directing its movements meanwhile by the trailing arms which serve as a rudder. Far from proving the loss of the hyponomic funnel, the disappearance of the ventral sinus may, on the other hand, be correlated with more perfect adaptation to a swimming life and greater independence of the bottom. The rostrum which replaces the lost sinus on the venter of many ammonites, it may be noted, is usually confined to those with narrow or thinly compressed volutions, and in this type of shell the water has such free access to the mantle cavity along the sides that the rostrum is really no impediment to the hyponome. Perna regards the rostrum as a support for a greatly developed hyponomic funnel and considers rostrate shells to be evidence of strong swimming powers.[14]

On the other side of the question there are many features of the ammonites' shells that are more difficult to reconcile with a crawling habit. One of these is the delicacy and thinness of the shells. They are almost invariably "paper thin"—nodes, spines, ribs, or other surface ornamentation being hollow—so that a filling of the interior gives a faithful representation of the outside, lacking only the lines of growth. Such delicacy of shell is characteristic of pelagic or swimming animals, rather than of the creeping benthos.

Furthermore, there is a complete lack among the ammonites of secondary limy deposits, such as those which in many nautiloids served to ballast down the shell.

The ammonites, even more than the nautiloids, are coiled shells, the only straight ones being the primitive *Bactrites* of the Devonian and a very few gerontic forms, such as *Baculites* of the late Cretaceous. The significance of the perfect bilateral symmetry of the overwhelming majority of them has previously been pointed out. It is incredible that so vast a horde of creeping molluscs would persistently have generated bilaterally coiled shells.

Then, too, many of the ammonites developed deeply involute and greatly compressed volutions, with keeled venters. It is difficult to conceive of such a form as *Placenticeras* creeping on a body so narrow and acute at the venter and carrying the shell vertically above its back. The difficulty is greatly increased when there is a protruding rostrum at the keel. If the rostrum, as Hyatt argued, would be an obstacle to swimming, how much more insurmountable an impediment to a crawling habit, for it projected beneath the supposed contact of the body with the substratum and, as dragged forward, would have caught upon every possible obstacle in its way, at least suffering abrasion, if not frequent breakage?

But in these same compressed shells there is often quite clear evidence of the presence of the hyponomic funnel, not in a ventral but in a pair of ventro-lateral sinuses just above the rostrum, a feature strikingly shown by *Phylloceras mediterraneum* (Figure 19E) and usually more or less clearly developed in compressed and rostrate shells. Finally, in those cases where at maturity the aperture becomes largely closed by converging lateral crests there is even more certain evidence of the hyponome in the deep ventral sinus of the constricted aperture. Thus, in the remarkable case of *Morphoceras pseudo-anceps* (Figure 19F) there is no suggestion of the hyponomic sinus during the earlier stages of growth when the front part of the body could be freely protruded from the shell in swimming, but with the constriction of the aperture a deep hyponomic sinus is again evident. Growth lines on the immature part of the shell, like the apertures of less specialized forms, fail to show evidence of the swimming funnel, and its unexpected revelation with the last growth stages of such a shell as *Morphoceras* leaves little room to doubt that it was present during the earlier stages of development in this species and likewise in other species, which even at maturity do not show a ventral sinus. All in all, therefore, the balance of the evidence strongly favors a swimming habit for most ammonites.

### ENVELOPMENT AND LOSS OF THE SHELL

THE last and perhaps most significant great trend of cephalopod evolution was the loss of the shell whereby the modern dibranchs emerged from out their ancient armored forebears. This was clearly a response to the biotic factor in their environment. The cephalopods are carnivorous animals and voracious feeders. In turn they have been preyed upon by greater and more agile enemies, including fishes, reptiles, and mammals. *Nautilus* is fed upon by the sharks, the conger eel, and probably other fishes,[2] and the fondness of fish for certain species of the naked dibranchs has given them the common appellation of "bait squid." Bartsch quotes this significant paragraph from *Commercial Products of the Sea:*

> The squids form an important element in the North American fisheries. The Common Loligo is the favorite food of the Cod, and is therefore itself fished for bait. One half of all the Cod taken on the banks of Newfoundland are said to be caught by it. When the vast shoals of this mollusc approach the coast hundreds of vessels are ready to capture them, forming an extensive cuttle fishery, engaging 500 sail of French, English, and American ships.

Not only are they subject to the attack of fishes, but the worst enemy of the giant squid is the great sperm whale, in whose stomach its remains are usually found by whalers. (Bartsch,[15] p. 371.) During the times of reptilian dominance in the Mesozoic, cephalopods were likewise hunted by the great marine reptiles, for as many as two hundred guards of the belemnite have been found within the carcass of a single ichthyosaur, mute evidence of a feast before the creature's death. If the belemnites suffered such inroads, how much more may the less agile, paper-shelled ammonites have suffered! We have, however, less direct evidence that they were thus fed upon, because at the first snap of such hungry jaws the ammonite would have fallen free of its crushed shell and there would remain in the enemy's carcass no recordable evidence of its fate.

During their long geological career the cephalopods have been witnesses of the rise and fall of dynasty after dynasty in the seas. In Ordovician times the great *Endoceras* vastly exceeded in size any other type of animal upon the earth. As in stature, probably also in alertness and keenness of sense, there was none to compare with these early cephalopods, whose chambered shells were an impregnable fortress against feeble creatures, such as trilobites and the more sluggish clams and snails. But Devonian times witnessed the ascendency of the fishes, and during the Mississippian the "oyster crusher" sharks dominated the seas, with their tooth-paved jaws adapted particularly for the crushing of the armor of "shell-fish." By the beginning of the Mesozoic the return of the reptiles to the sea was under way, and from the Triassic to the Cretaceous, ichthyosaurs, plesiosaurs, and finally mososaurs roved the seas with none to dispute their sway. Even before the close of the Age of Reptiles and of Ammonites the spectacular rise and expansion of the horde of modern bony fishes had begun, and with the vanishing of the great marine saurians came the upwelling of the whales and porpoises to usurp the marine kingdom. Such great changes in the biotic complex of their environment could hardly have failed to exert a profound influence upon the long-enduring cephalopods. Throughout the early periods, their pearly shells were safe refuge from the attacks of feebly armed adversaries; but against the later great enemies they were of no avail. At the best, armor, of any sort, is a handicap, whose advantages are to be balanced against the loss of free and alert movement. Faced by enemies powerful enough to crush the armor, the only safety lay in escape from attack. The ammonites' adaptation to rapid ascent from the crowded bottoms at time of danger may be looked upon as one attempt to find such refuge. But in the escape from fast-swimming enemies speed in flight is imperative, and the bulky shell of the cephalopods was worse than useless. The successful response which certain of the tetrabranchs made to this situation was the reduction and loss of the shell. These now thrive in countless shoals in all the seas; but those which were unable to make the adaptation have almost vanished from the earth.

The shell was not quickly abandoned, however, for the inheritance of ages could not be readily cast off. Its loss was gradual and by the roundabout way of envelopment and subsequent degeneracy. The course of this evolution is most clearly recorded by the fossil belemnites, but it is also suggested by the living *Spirula,* which can only be regarded as a static type halted halfway in the process of losing its shell.

The first step in its loss was a diminution in the size of the shell. The body outgrew the living chamber and came to project permanently beyond it. As it also expanded to greater diameter in front of the dwindling shell, a reflexed fold of the mantle grew backward over the outside of the shell, ever increasing as the shell gradually degenerated, until the shell was entirely enveloped in flesh. Along with its envelopment a limy deposit came to be secreted about it which would serve the purpose of counterbalancing this posterior gas tank and preventing the animal being tipped head downward. At the same time a thin, shelly growth pushed forward from the dorsal side of the aperture to form an axial stiffening along the dorsal side of the muscular body which reached almost to the head, and, behold, out of the ancient armor had been forged a makeshift backbone for these aspiring creatures! This change had transpired by early Triassic time.

In the belemnites of the Mesozoic these structures are well preserved, the delicate, degenerating, chambered shell, the phragmocone, being protected by the enveloping guard. The radiating, fibrous structure of the guard shows that it grew from without and hence was embedded in the flesh, and there is also direct paleontologic proof of this, for traces of the fleshy tissue, and even of the arms, have been discovered in the Jurassic formations of Europe. In the majority of the belemnoids the guard was relatively large and heavy, and we may regard these ancient squids as adapted to a life near the bottom of the sea. But there is an allied and parallel line, represented by *Phragmoteuthis* of the Triassic, *Belemnoteuthis* of the Jurassic, and *Conoteuthis* of the Lower Cretaceous, in which the guard is only a thin investment of the phragmocone, and these lightly ballasted forms were apparently more independent of the bottom.

As the enveloped shell degenerated to a smaller and more fragile structure, its counterbalance, the guard, again decreased in size, but the proöstracum, serving as a pseudo-backbone, was retained still longer. Thus in the modern squids the horny pen along the back is the remnant of the proöstracum, last vestige of the disappearing shell. In the cuttles, on the other hand, the porous "cuttle bone" represents the undifferentiated guard and proöstracum, as shown by intermediate fossil ancestors such as *Belosepia,* in which both can be distinguished. The octopus, most highly specialized of cephalopods, has lost all traces of the shell.

Concomitant with the gradual loss of the shell, there were other changes impossible to trace in the fossil record. Some of the more important of these were the development of the ink sac, first evidences of which are clearly shown in the Jurassic limestones at Solenhofen, Bavaria; the perfection of the highly complicated eye and of the complete ambulatory funnel; and

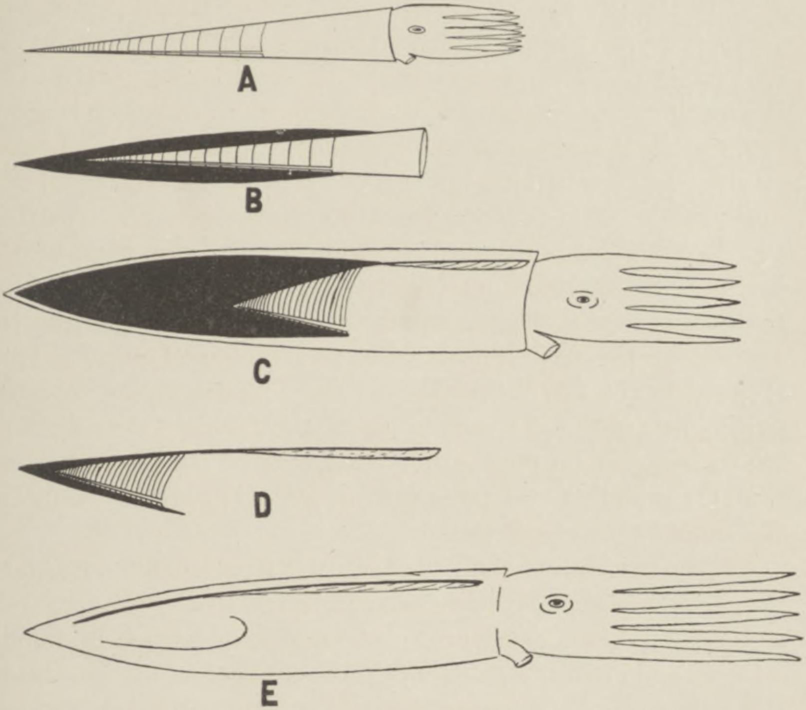

Fig. 20.—Evolution of the naked dibranchs from the shelled tetrabranchs. A, an orthocerid of the late Paleozoic with its body enclosed in the living chamber of the shell. B, *Atractites,* one of the earliest of the belemnids from the Triassic. Here the body had outgrown its shell, which was now covered by a reflexed growth of the mantle. The guard secreted over the chambered shell is thin. C, a typical Jurassic belemnite. The relation of the fleshy body to the shell is shown in fossil specimens. The guard has thickened, the chambered phragmocone has shortened and a spatula-shaped projection of its upper side, the proöstracum, reaches forward almost to the animal's head. D, *Belemnoteuthis,* another belemnid from the Jurassic in which guard and phragmocone are reduced as the proöstracum expands. E, a modern squid, *Loligo,* in which the proöstracum alone remains, forming the "pen."

the development of suckers upon the arms. The gross result has been that out of the relatively stupid and slow-moving armored tetrabranchs there has emerged one of the highest types of invertebrate life, powerful, alert, and aggressive, armed for attack with powerful beaks and prepared to elude unequal enemies behind "smoke screens" of inky fluid. Thus by heroic adaptations they have kept abreast of the changing biotic environment, still able to meet on fair terms of equality the higher marine vertebrates, for fishes form a part of their food and even the sperm whale often bears scars of battle with the giant squid, hugest invertebrate of all time.

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# CHAPTER VII

# DINOSAURIAN CLIMATIC RESPONSE

RICHARD SWANN LULL

PROFESSOR OF PALEONTOLOGY IN YALE UNIVERSITY

## INTRODUCTORY

THE climatic response on the part of any animal may be both direct and indirect—direct in adaptation to temperature or degree of moisture, extremes of which may affect not only habits of hibernation or æstivation, but the attainment of constant blood temperatures and of body clothing, and also changes in bodily activity with a consequent alteration of the motor mechanism. Indirectly the climatic response is largely a dietary adaptation due to the induced alteration of the vegetative world with its consequent influence on plant-living forms and the elimination of the inadaptable. Not all of these responses are possible, or at least probable, in the reptilian class, as, for instance, the attainment of warm blood and body clothing, for we have no reason to believe that a constant temperature characterized a dinosaur any more than a modern crocodile, although such ideas have been advanced.

*Place in Nature.*—The reptilian character of the dinosaurs of the Mesozoic is abundantly attested by their skeletal conformity to type, hence their inclusion in that group. To the student of paleontology this seems scarcely in need of emphasis, but to the lay observer of the many restorations which we have of these long-vanished forms, tinged perhaps in part

Figures 23, 24, 26, 27, 28, 29, 31, and 32 first appeared in Pirsson and Schuchert, "A Text-Book of Geology," Part II, published by John Wiley & Son, Inc., and later in Lull, "Organic Evolution," published by The Macmillan Company. Figures 22 and 25 are also reproduced from "Organic Evolution."

by the artist's knowledge of existing types, they do in frequent instances correspond so closely with existing mammals, notably *Triceratops* with the rhinoceroses, that knowledge of their true place in nature can not be assumed as understood. As reptiles they must have possessed the diagnostic traits of lung-breathing, with a scaly or armored hide, for reptilian nakedness is, as with the whales, an adaptation to a greater degree of aquatic life, such as in the ichthyosaurs, than the dinosaurs possessed. Whether bipedal or quadrupedal in their gait, they walked with the body well clear of the ground, as do the bipedal lizards of today, or even, on occasion, the usually crawling crocodiles. That their activity, which implies increased metabolism, raised the bodily temperature during the time of such activity, it is, I think, safe to assume,—an analogy is seen in the tuna* among the bony fishes today,—but that they possessed a mechanism for the maintenance of a constant bodily temperature irrespective of external conditions, as with birds and mammals, is sustained by no evidence thus far offered. In fact, their entire lack of heat-retaining clothing, such as the feathers of the bird or the hair of the mammal, negatives such possibility. While fossil hair is not known, feathers are; but hair when present leaves its imprint on the skin, and in none of the several impressions of dinosaur skin which have come to light is there trace of such imprint. With such bulk as the greater of the dinosaurs possessed, with its relatively small radiating surface, which increases with the square of the diameter while the bulk increases with the cube, the retention of the heat accompanying muscular activity would probably be somewhat prolonged. One can, however, visualize

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* Boulenger, *Cambr. Nat. Hist.*, Vol. VII, 1910, p. 679: "The Tunnies are the only fish known to be warm-blooded." Is this a maintained temperature, or merely the result of increased metabolism due to the fish's violent efforts to escape the angler? Presumably the latter, which might readily apply to certain of the more active dinosaurs as well.

long periods of utter quiescence, as in modern reptiles, when no impulse stirred to animation and during which the temperature would fall to that of the external medium. That they were egg-laying was doubtless the rule, and that the eggs must have been laid on land is a necessary conclusion, for the allantoic egg of reptile or bird would surely drown, if laid in the water. The retention of the egg within the maternal body until it hatched may well have been a specific adaptation to definite life conditions, as with certain of the modern lizards and snakes, but no evidence of a contained embryo has ever been met with, except possibly in the type of *Compsognathus* (see beyond), and here Nopčsa[1] considers the apparent young to be merely the remains of ingested prey. The skull characteristics, with the complex jaw, the quadrate, and other skeletal elements, are distinctly reptilian. It is reasonable to suppose that the internal organs followed the reptilian plan, with probably a more perfect isolation of systemic and pulmonary circulations than with reptiles in general, an outcome of, or contributory to, greater apparent activity. That the dinosaurs were diapsid or two-arch reptiles (Williston,[2] Osborn[3]) is at once evident from the skull, and as such they were remote from the mammalian ancestral stock; on the other hand, their lineage lies close to that of the crocodiles and the birds among living forms.

*Diphylogeny.*—Huene advanced the hypothesis of racial separateness of the two main dinosaurian phyla from the very beginning of their evolutionary career. This very reasonable belief has been accepted by Matthew and has much to commend it, though with certain qualifications of the proposed relationships with non-dinosaurian ancestral forms.

If this hypothesis be maintained, the Dinosauria as an order lose their entity—rather are there two dinosaurian orders and the name itself becomes merely a convenient group name comparable to the Pachydermata of Cuvier, which included the "elephant, hippopotamus, tapir, horse, and hog," representatives of orders unrelated genetically but having the common character of a more or less thickened hide. It is unfortunate that the subordinal names proposed by Seeley[4] of Saurischia for the carnivores and sauropods, and Ornithischia for the plant-feeding forms should be so unwieldy that neither lends itself to a convenient anglicizing for ordinary use, as they are based on the character of the pelves, and not on the more strikingly distinguishing features which the animals show.

The appended chart, which is in part from that of the writer,[5] modified in the light of our more recent knowledge, expresses the present conception of dinosaurian relationships.

## SYSTEMATIC REVIEW OF MAJOR FORMS

*Order Saurischia.*—The Saurischia may be thus defined: dinosaurs with triradiate pelvis resembling that of crocodiles, except that the pubis forms part of acetabular boundary; skull small, with preorbital fenestra, carried at right angles to neck; large vacuity through mandible, as in crocodiles; marginal socketed teeth compressed and either knife-like, with serrated margins, or spoon- or pencil-like, present in anterior portion of mouth and generally along its sides as well; no predentary bone; no calcified (ossified) tendons preserved in vertebral column.

The Saurischia make their first appearance in rocks of Lower Triassic (Bunter) time and are divided into three main phyla, at least two of which persist until the close of the Mesozoic. There is some doubt of the survival of the third beyond Comanchian (Lakota) time. To these three main phyla, which are of subordinal rank, Huene adds another, the suborder Pachypodosauria, ancestral, at least in part, to the others and confined entirely to the Trias. The suborder Pachypodosauria is not recognized by Zittel,[6] the several families included therein being placed under the Theropoda.

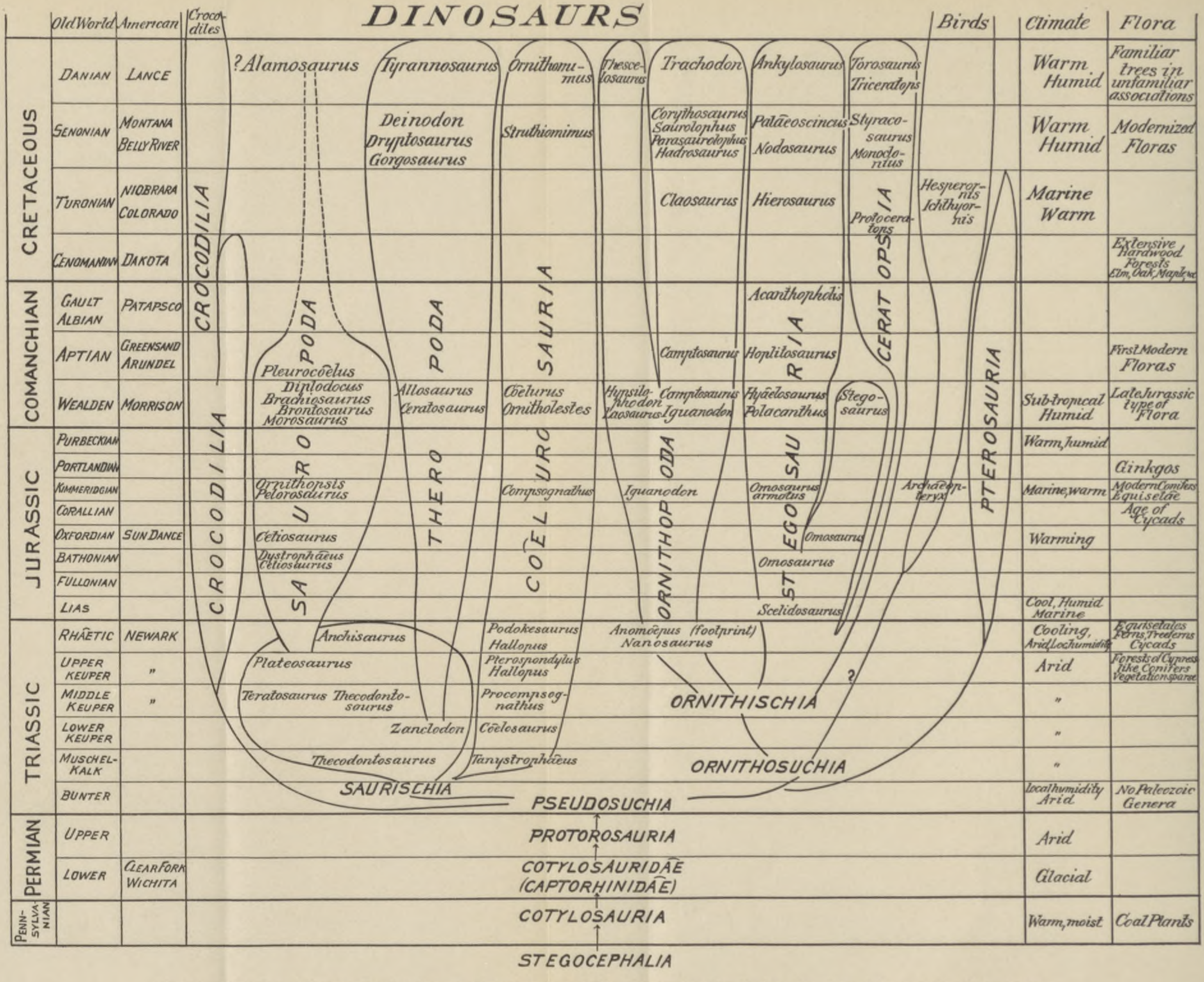

Fig. 21.—Diagram of dinosaurian diphylogeny. (Based on R. S. Lull, *Dinosaurian Distribution*, Am. Jour. Sci., 29, 1910, and on recent publications by W. D. Matthew and F. von Huene.)

*Suborder Theropoda.*—Bipedal dinosaurs, with bird-like raptorial feet, the clawed fore limbs becoming proportionately smaller as their evolution progressed; teeth laterally compressed, often serrate; pubis having foot-like expansion at symphysis in forms above the Trias, those without it being included in Huene's Pachypodosauria. The most characteristic families are:

*I. Plateosauridæ.*—Triassic forms of medium to large size; bones generally hollow, with abdominal ribs; pubis broad, elongated, distally coössified, but without expanded foot-like symphysis; femur S-shaped and longer than tibia; astragalus without ascending process; manus with backwardly directed digits iv and v; pes with first and fifth digits reduced; Trias, Keuper, and Rhætic. *Plateosaurus* is the best known genus, for several skeletons, some of which are entire and measure at least nineteen feet in length, have been found in the Keuper and Rhætic of France and Germany. Others are *Gressylosaurus* and *Pachysaurus.* It is out of the Plateosauridæ, specifically *Plateosaurus* or *Pachysaurus,* that Huene would derive the Sauropoda. This evidence will be reviewed later.

*II. Zanclodontidæ.*—Skull large, containing knife-like teeth, bending backward but not possessing marginal serrations; anterior dorsals having small centra, but high, strong spines. *Zanclodon* is from the German Lettenkohl.

*III. Anchisauridæ.*—Small, lightly built, with hollow bones, but strong limbs; ilium broadened behind the acetabulum; teeth partly rudimentary; astragalus without ascending process; Triassic. *Anchisaurus* and *Ammosaurus* from the Connecticut Valley Rhætic, *Thecodontosaurus* from the Muschelkalk to the Rhætic, and *Massospondylus* from South Africa show the wide range of this family.

*IV. Megalosauridæ.*—Moderate to large carnivorous dinosaurs, with sharp, serrated teeth; ilium broadened anteriorly with long pubic peduncle; pubis slender with a symphyseal foot-like expansion; femur longer than tibia; astragalus with ascending process.

Matthew's definition of the "megalosaurid group" limits these forms to the Jurassic (and the Morrison, here included in the Comanchian or Lower Cretaceous), and embraces such forms as *Allosaurus* (*Antrodemus*), *Ceratosaurus,* and possibly *Megalosaurus.* The last genus, however, is relatively ill-defined, and quite probably covers what would prove to be a number of distinct genera. *Allosaurus* is known from the fine, mounted skeleton from the Morrison of Wyoming in the American Museum of Natural History, while a mounted skeleton of the quite different, but contemporaneous, *Ceratosaurus* is in the United States National Museum at Washington.

Fig. 22.—Restoration of *Allosaurus,* based upon the specimen in the American Museum of Natural History. Length, 34 feet. Comanchian, Wyoming, Colorado, and Maryland.

*V. Deinodontidæ.*—The gigantic carnivores of the Cretaceous have a deeper and more massive skull than do the megalosaurs. These latter show that a certain movement was possible between some of the bones of the skull (fronto-parietal and jugo-quadrato-jugal). This is absent in the deinodonts. The V-shaped cross section of the anterior teeth, so

Fig. 23.—Restoration of Tyrannosaurus, based upon a specimen in the American Museum of Natural History. Length, 47 feet. Upper Cretaceous, western North America.

marked in the deinodonts, is merely a tendency in the megalosaurs, and the fore limbs are relatively much more reduced, with an extremely specialized manus. Principal genera are *Deinodon, Dryptosaurus,* and *Tyrannosaurus.*

*VI. Spinosauridæ.*—Teeth straight, conical, pointed; posterior neural spines strikingly high, reminding one of those of *Dimetrodon;* represented by the genus *Spinosaurus* (*Ægypticus*) from the Cenomanian of Egypt (Stromer).[7] (Matthew and Brown are authority for the statement that certain of the European megalosaurs represent an earlier stage in the evolution of this remarkable aberrant group.)

*Suborder Cælurosauria.*—Small to middle-sized, slenderly built, bipedal dinosaurs, with cavernous vertebræ and limb bones; hind limbs, pubis, and ischium very slender, as are three fingers of hand; metatarsus elongated, bones being closely appressed, but without fusion; teeth of carnivorous type, but entirely lacking in late Cretaceous forms, *Struthiomimus* and also probably *Ornithomimus.*

*I. Hallopididæ.*—Very small animals, possessing backwardly projecting calcaneum, as though adapted for leaping (*Hallopus* Marsh, Trias of Colorado; *Procompsognathus* E. Fraas, Middle Keuper of Württemberg); skull with triangular preorbital fenestra and large, round orbit; teeth pointed, somewhat recurved; pubis as long as much-curved femur (3¾ inches); fifth metatarsals strongly reduced; digits ii, iii, iv, and v of pes with claws, fourth very short; hind limbs three and a half times as long as fore.

*II. Podokesauridæ.*—*Podokesaurus,* from the Trias (Rhætic) of Massachusetts, is typical of the family, with an extremely long tail and rod-like pubis.

*III. Cæluridæ.*—Dinosaurs of small size, with relatively small skull and long, slender neck; fore limbs relatively large, having specialized manus with long, slim phalanges, except for short, divergent first digit; claws strongly curved; tibia a little longer than femur; foot long and slender, with three functional digits; claws of pes moderately curved. *Cælurus,* from the Morrison of North America, Gilmore considers synonymous with Osborn's *Ornitholestes,* which is much more completely known. *Ornitholestes* was about seven feet long, although the tail is not entirely preserved.

*IV. Compsognathidæ.*—*Compsognathus* is known from a very perfect skeleton from the Solenhofen limestone of Kelheim in Bavaria, Upper Jurassic, and preserved in the Munich Museum. But two and a half feet long; neck long; pubis strong, longer than slender ischium; femur shorter than tibia; astragalus bearing long ascending process in close contact with tibia; metatarsals long and slender; both hands and feet possessing but three functional digits.

*V. Ornithomimidæ.*—The relatively small skull, with its large orbit, borne upon very long, slender cervicals, is one of the most characteristic features of this group. Limbs long and slender, with specialized manus, bearing three digits, the elongated claws of which are not strongly curved; pubic bones possessing foot-like symphysis, ischia being curved; tibia longer than femur; metatarsals elongated and closely appressed, but remainder of foot of moderate size, with short, rather straight unguals; tail long, with distal caudals interlocked by prolonged zygapophyses. Three closely allied, if not in part identical, genera belong in this family, all Comanchian or Cretaceous in distribution. They are *Cœlosaurus, Struthiomimus,* and *Ornithomimus.*

Fig. 24.—Restoration of the small carnivorous dinosaur, *Ornitholestes,* based upon a specimen in the American Museum of Natural History. Length, 7 feet. Comanchian, Wyoming.

*Suborder Sauropoda.*—Amphibious, plant-feeding dinosaurs, with relatively very small head, bearing one, rarely two, preorbital fenestræ; jaws partially or wholly beset with spatulate or styliform teeth; most of presacral vertebræ opisthocœlous, posterior dorsals and caudals being as a rule amphicœlous or amphiplatyan, rarely procœlous; vertebræ generally cavernous or with lateral cavities, pleurocœles, in centra; neural canal greatly enlarged in sacrum, somewhat as in *Stegosaurus* (see below); limb bones massive, probably without medullary cavity; fore limbs generally shorter, but sometimes fully equaling or even exceeding hind in length; feet semi-plantigrade, five-toed, but with reduced phalanges on external side; unguals strongly compressed, but massive.

The Sauropoda range from the Jurassic to the close of the Comanchian, possibly Cretaceous, time (see p. 275). They were secondarily quadrupedal, relatively short of body, but with long and slender neck and tail, the latter sometimes (*Diplodocus*) terminating in a ten-foot whiplash-like appendage, used probably as a weapon. These creatures, while ranging greatly in size, were probably the greatest land animals which have ever lived. Four families are recognized, the most primitive being:

*I. Cetiosauridæ.*—With opisthocœlous cervicals, and anterior dorsals; posterior presacral vertebræ being, on the other hand, amphicœlous; presacrals all possessing lateral pleurocœles, but dorsal spines not forked; sacrals and caudals solid, and sternal plate unpaired; pubis flattened, with large obturator foramen; scapula broadened at each extremity; fore limbs almost as large as, or somewhat larger than, hind; Jurassic

Fig. 25.—Restoration of *Brachiosaurus,* the most ponderous sauropod. Length, about 80 feet. Comanchian, North America and East Africa.

to Lower Cretaceous. *Cetiosaurus,* humerus and femur as a rule about equal in length; ischium feebler than pubis and tapering distally; Dogger to Lower Malm, England; not completely known, but the British Museum contains a mounted hinder half of *Cetiosaurus leedsi. Brachiosaurus,* both humerus and femur exceeding 6½ feet in length; centra of dorsals not elongated, but extra articulations, hyposphene, and hypantrum strongly developed. This genus was described from material collected in the Morrison beds of Western North America. To it have been referred dinosaurs from the Tendaguru beds of Tanganyika Territory, East Africa. *Barosaurus,* a huge dinosaur recently redescribed by the writer, possessing the extremely long cervicals (39 inches) of the African brachiosaurs. Otherwise it is more *Diplodocus*-like. The limbs seem ponderous, but their relative length may not as yet be determined, because of defective material. *Haplocanthosaurus* has the centra of fourteen dorsals elongated and their transverse processes directed upward and outward. The two last-mentioned genera are known from single specimens from the Morrison of South Dakota. The ill-defined genus *Distrophæus* is the oldest American sauropod, as it comes from the red beds of Painted Cañon, southeastern Utah, which are variously estimated as of Bathonian (Jurassic) age, or even Triassic.

*II. Atlantosauridæ.*—Neck and anterior dorsal vertebræ opisthocœlous; hinder dorsals amphicœlous; presacrals, sacrals, and anterior caudals cavernous; cervicals and anterior dorsals with paired and divergent dorsal spines; cervical ribs with very long capitulum and tuberculum; bony sternal plates paired; scapula not broadened distally; Comanchian. *Apatosaurus* or *Brontosaurus* is perhaps the most perfectly and widely known sauropod, especially under its second name, from its great size, long neck, comparatively short back, and long tail. The posterior caudals have large pleurocœles; the ischium is much slenderer than the pubis, the latter having broadened extremities. *Brontosaurus* is known from an abundance of material from the Morrison of Wyoming and Utah.

*III. Morosauridæ* (*Camarasauridæ*).—Cervical and dorsal vertebræ opisthocœlous and cavernous, with paired neural spines; sacral and caudal vertebræ solid; scapula having proximal end strongly broadened and distal end less so; fore limbs substantially shorter than hind; Upper Jurassic to Comanchian. *Camarasaurus* Cope=? *Morosaurus* Marsh, characterized by short, high skull, with very large orbit, nasal openings, and upper and lower temporal fenestræ; a very massive quadrate. Teeth, about 48 in number, large and spatulate, crowned somewhat as in

*Brontosaurus;* about 13 cervicals, 10 or 11 dorsals, 4 or 5 sacrals, and 53 caudals; neural spines of cervicals bifid; dorsals with hyposphene-hypantrum articulations; ischium slender; Morrison, from many localities in Wyoming and Colorado, also from the Trinity Sands (Aptian) of Oklahoma and possibly from the Wealden of Cuckfield, Sussex, England; a large, massive form, up to 55½ feet long. *Pleurocœlus,* a smaller form known from the Morrison of Western North America and from the Potomac beds in Maryland, also from the Wealden and Aptian of England, France, and Spain. A number of genera of sauropod dinosaurs, in many cases ill-defined, have been included in this family; thus, *Pelorosaurus,* ranging from the Oxfordian through the Jurassic to the Wealden of England, France, Portugal, and Madagascar. Among more remarkable forms are the *Gigantosaurus,* described by Fraas (non Marsh), from the Tendaguru, which has also produced *Dikræosaurus,*

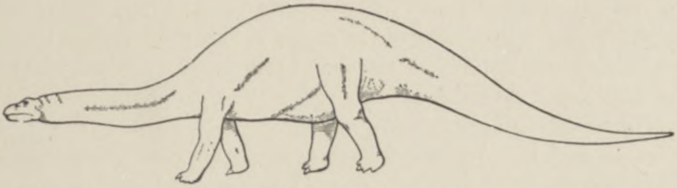

Fig. 26.—Restoration of *Brontosaurus,* based upon a specimen in the Peabody Museum of Natural History, Yale University, and the American Museum of Natural History. Length, about 65 feet. Comanchian, western North America.

Fig. 27.—Restoration of the sauropod dinosaur, *Diplodocus,* based upon the mounted specimen in the Carnegie Museum. Length, 87 feet. Comanchian, Wyoming.

with long neck and enormously high, bifid neural spines in the cervical and dorsal vertebræ. *Ornithopsis* (*Pelorosaurus*), from the Uppermost Jura and Wealden of England, as well as in Western Europe and Madagascar.

*IV. Diplodocidæ.*—The most distinguishing feature of the dinosaurs of this family is the relative slenderness, coupled with length up to 87 feet (24 metres). Skull long and somewhat horse-like in contour, with two antorbital fenestræ and nares at apex; teeth, borne in the front of jaws, slender and cylindrical, with slightly flattened crowns; presacral vertebræ all opisthocœlous, those of the neck and anterior part of back bearing bifid neural spines; presacral and anterior caudal vertebræ cavernous; sternal plates paired; tail very long, with terminal "whiplash"; pubis and ischium distally thickened; scapula broadened at extremities, especially the proximal one. *Diplodocus* Marsh, of the Morrison of Wyoming, Colorado, and Utah, is perfectly known. *Barosaurus* resembles it in some respects, but has a relatively much heavier neck.

*Order Ornithischia—Orthopoda Cope, Predentata Marsh.*—The distinguishing feature of this order of predentate or beaked dinosaurs lies in the tetraradiate pelvis, in which the pubis has two branches, a forwardly directed prepubis, and a slender postpubis, varying in its development in the different families, but lying approximately parallel with the ischium. A further distinction is the direct outcome of their herbivorous mode of life, in that the teeth are confined almost entirely to the posterior part of the mouth, maxillaries and dentaries, while with but two* known exceptions (*Hypsilophodon* and *Protoceratops*, see below) the premaxillæ are toothless. The two rami of the mandible are united by a toothless symphyseal bone, the predentary. The Ceratopsia have in addition a rostral bone above in front of the premaxillaries. The anterior or prehensile part of the mouth was sheathed by a leathery or horny beak. The crowns of the teeth are generally more or less leaf-shaped, and the cutting surface faced inward in the upper jaws and outward in the lower. The anterior nares are

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* A third exception, *Troödon,* has just been described by Gilmore. See p. 238.

very large and lateral in position, while the antorbital fenestræ are small, sometimes wanting; vertebral centra generally solid, opistho-, amphi- to platycœlous; limb bones hollow or solid; digitigrade or semiplantigrade feet, generally depressed unguals, sometimes hoof-like; astragalus without ascending process; dermal skeleton sometimes very strongly developed, sometimes lacking; Upper Trias to Uppermost Cretaceous.

Three phyla of predentate dinosaurs are recognized: the unarmored *Ornithopoda,* the armored *Stegosauria,* and the horned *Ceratopsia,* all of which have subordinal rank.

*Suborder Ornithopoda.*—Bipedal, unarmored dinosaurs, with small head borne at right angles to neck; premaxilla as a rule toothless, the leaf-shaped maxillary and mandibular teeth having midrib-like keel and sharp, generally serrated, cutting border; dorsal vertebræ opisthocœlous; fore limbs much shorter than hind; feet digitigrade, with depressed claw or hoof-like unguals; pelvis with long, slender postpubis; dermal skeleton as a rule absent. These creatures, while bipedal, were not so exclusively, as were the Theropoda, for they occasionally rested the hands on the ground, while the latter probably did not. Numerous footprints pertaining to each group impressed upon the Triassic rocks of the Connecticut Valley bear this out. Otherwise there is a curious parallel in the evolution of the Orthopoda and Theropoda, the contrast of feeding habit being apparently responsible for most of the divergence. In each case, if one considers the Theropoda and the Cœlurosauria as one group compared with the Ornithopoda, there is a division into a phylum of greater, slower-moving, forms, and one of lesser and more agile dinosaurs, the Hypsilophodontidæ among the latter corresponding to the Cœlurosauria among the former. Whether the divergence of the Hypsilophodontidæ was as remote in time is not yet clear, for the Triassic reveals as yet but few ornithopods. That they existed in several genera and species, with decided differentiation of size, by

Rhætic time is amply attested by the footprints before alluded to (Lull[8]).

*I. Hypsilophodontidæ.*—This family contains what are apparently the most primitive members of the Ornithopoda, especially as regards the teeth, which are in a single row as compared with the multiple rows in most of the other groups. They also possess premaxillary teeth. Anterior vertebræ platy- or opisthocœlous; sacrals coössified, and posterior ribs single-headed; hand five-fingered, fourth and fifth generally reduced; foot with four functional digits and vestigial fifth metatarsal. These are the lesser ornithopods, ranging apparently from the Upper Trias to the close of the Age of Reptiles. Whether or not future discovery will divide them into more than one family is not yet known, but the time seems excessive for the duration of a single family.

The known genera are:—*Nanosaurus,* the oldest in point of time, known from a single imperfect skeleton from the Upper Trias of Colorado, and preserved in the Yale Museum. The skull is unknown, but not the mandible. (See p. 260.) *Hypsilophodon,* about 39 inches long; premaxillæ with thecodont teeth; dermal ossicles; ossified tendons in dorso-caudal region; Wealden of England. Heilmann[9] (figure 78) conceives of this form as arboreal. *Thescelosaurus* Gilmore, a form similar to *Hypsilophodon,* except that the femur is shorter than the tibia. Gilmore has restored it, with a similar skull and premaxillary teeth. Of the latter there is as yet no evidence. *Geranosaurus* Broom, from the Uppermost Trias (Stormberg beds) of South Africa.

*II. Troödontidæ.*—Aberrant Orthopoda with premaxillary teeth, dome-like, thickened skull, and abdominal ribs. A single genus, *Troödon,* is known from the Belly River of Alberta and the equivalent Judith River of Montana. It presents a curious admixture of characters previously noted in widely separated groups of dinosaurs. It seems to lie nearest to *Hypsilophodon* of any known form.

*III. Camptosauridæ.*—Toothless premaxillary; teeth in more than one functional row; anterior vertebræ opisthocœlous; sacrals not coössified; ilium with long preacetabular process; postpubis slender and equaling ischium in length; femur longer than tibia; five-fingered hand; four-toed foot; Jurassic and Comanchian. *Camptosaurus,* varying from about ten to thirty feet long, with the characteristics of the subfamily; fourth and fifth fingers reduced, as in *Plateosaurus;* maxillary teeth large and irregular; well-developed pubis, with broad prepubis; femur curved; about 25 presacrals and 4 or 5 sacrals, not coössified, each sacral centrum having posterior notch into which process of succeeding one fits. *Camptosaurus* has been reported from the Oxfordian and Kimmeridgian of England, the Purbeckian of Boulogne-sur-Mer, and the Morrison of Wyoming, Colorado, and South Dakota; also from the Lakota of South Dakota, and from the Wealden of the Isle of Wight. *Laosaurus* and *Dryosaurus* are slenderer forms, described by Marsh, from the Morrison of Wyoming.

*IV. Iguanodontidæ.*—Toothless premaxillæ; anterior vertebræ opisthocœlous; sacrals coössified; postpubis very slender and shorter than ischium; sternum bony; femur longer than tibia; hand five-fingered, with spike-like pollex; foot four-toed, only ii, iii, and iv functional, as shown by associated footprints; Comanchian. The genera *Iguanodon* and *Craspedodon* have been assigned to this family. They are extremely local in distribution and restricted in time, being found only in the Lower Greensand and Wealden of Southern England and the Isle of Wight, and in Belgium. *Iguanodon,* so-called from the similarity of the teeth to those of the modern lizard, *Iguana,* is known from material discovered years ago by Mantell and Owen and more recently by a remarkable find of 23 skeletons in a coal mine at Bernissart, Belgium, and now preserved in the Brussels Museum. These have been the subject of a number of short, but highly significant, papers by Dollo. A forthcoming memoir is expected.

Fig. 28.—Restoration of the predentate dinosaur, *Camptosaurus.* Average length, about 10 feet. Comanchian, North America.

*V. Trachodontidæ.*—Premaxillaries toothless; teeth with several rows simultaneously functional; anterior vertebræ opisthocœlous; femur generally longer than the tibia; hand four-fingered; foot four-toed, with hoof-like unguals. The tooth battery reaches its maximum development in the members of this family, there being as many as from 45 to 60 vertical and from 10 to 14 horizontal rows of teeth, making at least 2000 in both jaws, a very perfect adaptation to a harsh plant diet. (See pp. 262-263.)

The trachodonts also possessed a powerful, laterally compressed tail suitable for swimming, and the hands and probably the feet were webbed, the skin in the hand extending paddle-like beyond the ends of the digits, as we know from the mummified specimens which have been preserved to us. There was no defensive armor, as the skin is covered everywhere with small, raised, roughly pentagonal scales, somewhat similar to those of the Gila monster, *Heloderma,* and never overlapping, as are those of most lizards and snakes and the fishes. *Trachodon* itself is known from several mounted skeletons, including a splendid one in the Yale Museum. It has a curious, depressed head, with a broad, duck-like beak. Others of the family, however, notably those of the Judith River stage of the Red Deer region of Canada, have a most curiously modified skull, notably in the rear part. They are known as the helmeted

Fig. 29.—Restoration of *Trachodon,* based upon the mounted skeleton in the Peabody Museum of Natural History, Yale University. Length, 29 feet. Cretaceous of North America.

or crested dinosaurs. The principal genera of the latter are *Corythosaurus, Saurolophus, Kritosaurus,* and *Parasaurolophus,* to which allusion will be made later.

The oldest member of the family is *Claosaurus,* from the marine Niobrara Cretaceous of Smoky Hill Valley, Kansas. *Hadrosaurus,* probably congeneric with *Trachodon,* comes from the Senonian of New Jersey. A partial skeleton was described in 1858 by Leidy as being "restored and mounted in the Museum of the Philadelphia Academy of Natural Sciences." It has also been found in North Carolina and Georgia in the East. In the West trachodonts range from Alberta to New Mexico in Senonian, Judith, and Belly rivers, and Danian (Lance) formations.

*Suborder Stegosauria.*—Armored quadrupedal dinosaurs; skull small, with anterior part of mouth toothless; functional teeth in single row; large, forwardly placed, anterior nares, but small infraorbital fenestræ; upper temporal fenestra lacking in the Nodosauridæ (Ankylosauridæ), with their broad, heavily armored skull; vertebræ amphicœlous or platycœlous and, together with extremities, very massive; fore limbs shorter than hind; feet semi-plantigrade, digits three to five, with short, hoof-like unguals; dermal armor very strongly developed, which has compelled the assumption of the quadrupedal posture as a secondary adaptation for the carrying of the great weight of the armor. Their ancestors were doubtless bipedal, with less developed armor. Geological range from the Lower Lias of Dorset, England, to the close of the Cretaceous. They are found mainly in the Northern Hemisphere, with the probable exception of the Tendaguru region of Africa.

*I. Scelidosauridæ.*—Teeth spatulate, triangular in cross section, with coarsely serrated margins; skull with single supratemporal fenestra; vertebræ all amphicœlous; neural canal not expanded in sacrum; limb bones hollow; hand with four, foot with three, functional digits, hallux reduced, and outermost absent; armor consisting of dorsal, longitudinal rows of dermal ossicles, together with small tubercles. *Scelidosaurus,* from the Lias of Charmouth, Dorset, England, about 13 feet long, based on a nearly perfect skeleton preserved in the British Museum of Natural History.

*II. Stegosauridæ.*—Small, elongated skull having no antorbital fenestra; nares large, anteriorly placed; toothless premaxillary; teeth small, spatulate, with coarsely serrated margins; vertebræ amphicœlous or amphiplatyan, solid throughout, as are limb bones; postpubis not slender, nearly as long as ischium; neural canal greatly enlarged in sacrum, less so in brachial region of back; hind limbs much the larger, with straight, somewhat flattened femur; fore limbs robust and angulated; semi-plantigrade feet, pentadactyl, with first digits somewhat reduced, phalanges hoof-like; armor strongly developed into huge dermal plates and spines. *Stegosaurus,* an aberrant type, with the two rows of immense, upstanding dorsal plates, and caudal spines. This genus, known from a number of species, is from the Morrison of Wyoming. A nearly allied type, *Omosaurus durobrivensis* comes from the Oxfordian of Felton, England. *Omosaurus armatus,* on the other hand, does not show the upstanding armor, and may be a different genus from the above, or even a different family.

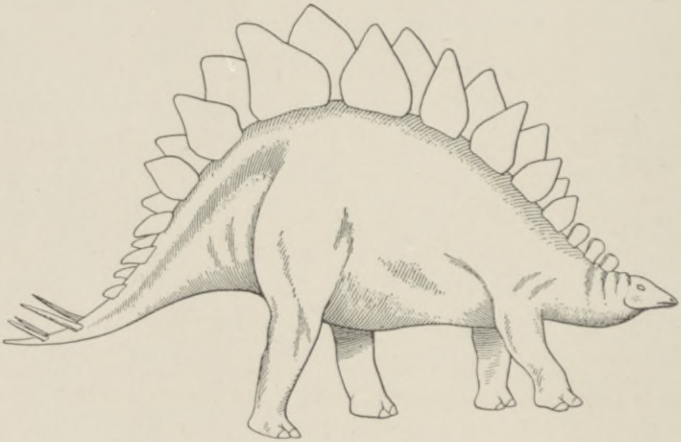

Fig. 30.—Restoration of the armored dinosaur, *Stegosaurus,* based upon the mounted skeleton in the Peabody Museum of Natural History, Yale University. Length, about 20 feet. Comanchian, Wyoming, and Colorado.

*III. Acanthopholidæ.*—Skull without upper temporal fenestra; small, quadrate shoulder spines; armor of the region of the pelvis coalesced into a *Glyptodon*-like rump-shield. The best known genus is perhaps *Polacanthus,* redescribed and restored by Nopčsa. The rump-shield is highly developed and coalesced entirely with the ilia, but the position of the spine-like plates seems highly conjectural. *Polacanthus* is from the English Wealden.

*IV. Nodosauridæ (Ankylosauridæ).*—Skull broad, depressed, triangular, with heavy beak and coalesced dermal armor; teeth small; vertebræ platycœlous or somewhat amphicœlous; three sacrals coalesced, with four presacrals and two sacro-caudals; limb bones massive; sacral region armored with rump-shield, sometimes coössified with ilia; posterior ribs ankylosed with vertebræ; dermal armor plates oval, with median keel, sometimes spine-like;—ponderous armored dinosaurs of the Upper Cretaceous of North America. Some of the genera are: *Nodosaurus,* Senonian of Wyoming; *Palæoscincus* and *Ankylosaurus,* Senonian (Belly River formation), Red Deer River, Alberta, and of the Danian (Lance) of Hell Creek, Wyoming.

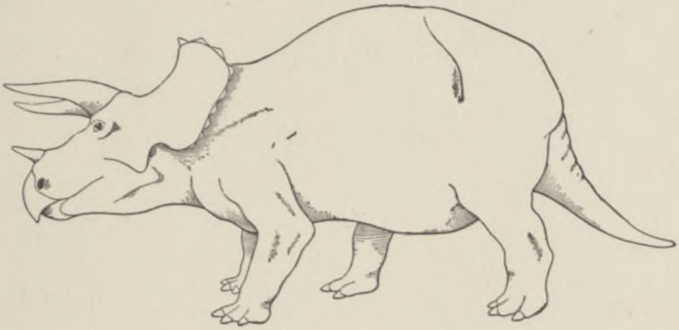

Fig. 31.—Restoration of the horned dinosaur, *Triceratops*. Length, 20-25 feet. Upper Cretaceous (Lance), western North America.

*Suborder Ceratopsia.*—Horned dinosaurs with huge skull, upwards of one-third the entire length of the animal, with one to three horns on the facial region and a backwardly projecting crest or frill formed of the squamosals and postparietals (dermosupra-occipitals, Huene); upper and lower temporal openings present; no preorbital fenestra; toothless premaxillaries, in front of which is an unpaired rostral element, which bore the turtle-like cutting beak and met the corresponding toothless predentary of the lower jaw; teeth in deep groove and with divided roots, unique among reptiles; vertebræ amphiplatyan, with four anterior cervicals fused; both vertebræ and limb bones solid; fore limbs somewhat shorter than hind and with heavy rugosities; femur longer than tibia; hoof-like phalanges, five in front and four behind; integument covered with thick, mosaic-like squamation; Senonian (Judith and Belly rivers of Montana and Red Deer River, Alberta); also Danian (Lance) from Montana to New Mexico. Principal genera: *Triceratops* and *Diceratops* of the Lance, with complete frill and three or two horns; *Torosaurus* of like age, with perforate

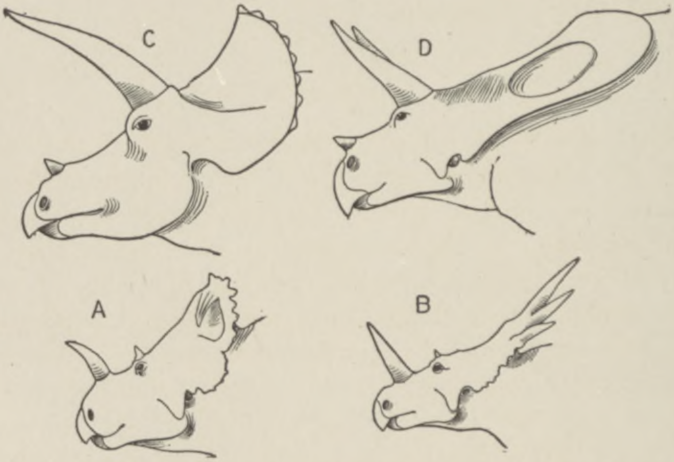

Fig. 32.—Heads of horned dinosaurs, Ceratopsia. A, *Monoclonius*, Upper Cretaceous (Belly River); B, *Styracosaurus*, Belly River; C, *Triceratops*, uppermost Cretaceous (Lance); and D, *Torosaurus*, Lance. Drawn to scale. *Torosaurus* skull 8½ feet long.

frill and three horns; *Monoclonius* (*Centrosaurus*), with a single large nasal horn and varying supraorbital ones; *Ceratops* similar; *Styracosaurus* with horn-like processes around the periphery of the frill; *Brachyceratops,* evidently immature, with very small horns. These are from the Judith-Belly River formations. The discovery of an ancestral ceratopsian* without horns has been announced by the American Museum party in Southeastern Mongolia.

### HABITATS

TRIASSIC dinosaurs, which naturally are the oldest that we know, are apt to be preserved in the prevailing red sandstone indicative of climatic aridity. It would seem as though the initial evolution of the dinosaurs, as manifest in their bipedality in both phyla, is a partial response to aridity of climate, which, among other things, enforces cursorial adaptation in many animate forms as a condition of survival. Perhaps the environmental conditions of the Connecticut Valley during most of the time when it was tenanted by the dinosaurian hordes are typical. Barrell[10] has likened it to the semi-arid valleys of California of today, as the deposits are manifestly terrestrial and, changing as they do from fine-grained shales to coarse conglomerate, indicate varying precipitation and consequent rate and character of deposition. If Triassic dinosaurs occupied other habitat conditions than these, which is of course entirely possible, they are apparently as yet undiscovered, for the contemporary reptiles of North Carolina, for example, are phytosaurs and were denizens of a coal-producing habitat, hence humid, swampy areas. So far no

* *Protoceratops andrewsi* Granger and Gregory,[11] known from a splendid series of skulls from China, collected by the third Mongolian expedition of the American Museum of Natural History, is an undoubted ceratopsian, although the horns had not yet appeared. It is at least structurally ancestral to the American horned dinosaurs.

trace of dinosaurian remains has been discovered in such localities.

Above the Triassic, dinosaurian remains are at first extremely rare, in fact almost none* are known from America, if one excludes the Morrison from the Jura and includes it in the Lower Cretaceous (Comanchian), as is the best American practice. We have, however, practically no continental Jura in North America, and the rare inclusion of dinosaurian remains in marine strata has not thus far betrayed their existence. In Europe, on the other hand, the record of Jurassic dinosaurian life is more complete, as dinosaurs appear from time to time throughout the period.

The Liassic of Charmouth, near Lyme Regis, has produced *Scelidosaurus,* the oldest armored dinosaur known, and at Lyme Regis, *Megalosaurus.* These rocks are marine, and the inclusion is probably accidental, the carcasses having drifted down a stream and out to sea for burial along the coast. The Lias contains, nevertheless, so many land plants, as well as numerous insect remains, that the deposits, while chiefly marine, were laid down not far from shore. The molluscs associated with the insects are sometimes marine, sometimes brackish water forms. The inclusion of dinosaurian remains is not therefore so remarkable, but it points to a range of habitat commencing not far from the sea. The many black shales of the Liassic are considered evidence for cool and non-tropical conditions. The presence of coal, however, points to a humid, rather than an arid or semi-arid, climate. We can with difficulty visualize the dinosaurian habitat of that day, but indications of the coming of conditions which typify the amphibious-aquatic environment of the Sauropoda and late Ornithischia are manifest.

In Europe each principal formation of the Jurassic has produced carnivorous dinosaurs, provisionally called *Megalo-*

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* See *Distrophæus,* Painted Cañon, Utah.

*saurus*. The record in England is complete, while in France but two, the Fullonian and Corallian, have been non-productive; the latter is also true of Germany. Spain has the genus in the Lias, and Portugal in the Corallian and Portlandian. Sauropoda, represented by the genera *Cetiosaurus* and *Pelorosaurus* (*Ornithopsis*), are found in England in all continental Jurassic deposits, being absent only in such marine horizons as the Lias, Fullonian, and Corallian. The first recorded sauropod is Bathonian. It is, nevertheless, a fully evolved member of the phylum, and, as such, implies a sauropodous ancestry of considerable length. The Bathonian strata were deposited under a variety of geographical conditions, for they include not only land plants and insects as well as reptiles, but marine brachiopods and molluscs and also ganoid and shark-like fishes. There has likewise been found in the Stonesfield slate from this horizon a number of mammal jaws, some of marvelous perfection. The cetiosaurs were widespread, as they are found at Oxford, Stonesfield, Bilsworth, Bilbury, Enslow, and Cogenhoe. The implied habitat is clearly in low-lying lands along the coast. The Oxford clay is the next dinosaur-bearing horizon. It ranges through Oxford County from the Dorsetshire to the Yorkshire coast and consists of layers of blue and brown clay and some earthy limestone. There are many marine forms, lamellibranchs and ammonites, and they also contain a number of genera of ganoid fishes. Dinosaurs are numerous, at least seven genera being represented, including theropod, sauropod, and ornithopod forms, but with these are also crocodiles, which may have been estuarine, and the strictly marine ichthyosaurs and plesiosaurs as well. Once more the dinosaur habitat seems to imply coastal swamps and lagoons where the water was none too clear and where supporting plant life was sufficiently abundant.

The Corallian is not only entirely marine, but clearer seas with no great influx of sediment-bearing fresh waters are indicated. It is therefore natural that the dinosaurs should be rare in these deposits and these entirely megalosaurs, except one sauropod, *Pelorosaurus,* from Ourem, Portugal. They must have existed, however, in their normal habitat, but the record is either undiscovered or obliterated.

In the Kimmeridgian, dinosaurian remains again become more numerous, some half dozen genera being recorded. These deposits in the typical locality are clays to paper shales and bituminous shales. The shells are few as to species, but extremely numerous in individuals, and all are marine. There are also plesiosaurs and ichthyosaurs, sea-turtles, and crocodiles. The dinosaurs again must have been inhabiting the low-lying coastal lands with more abundant drainage to the sea than in the Corallian, hence there was a greater opportunity for their carcasses to drift out of the rivers and be buried along the coast. The Kimmeridgian adds to the other phyla a stegosaurian dinosaur, *Omosaurus.* The Portlandian is also somewhat productive of dinosaurian forms, chiefly *Megalosaurus* and *Pelorosaurus* (*Ornithopsis*). The beds are marine, flint and limestone, indicating sandy and marshy conditions. The most abundant fossils are lamellibranchs, while corals are represented by a single species. The implied conditions do not aid us in our investigation, as the dinosaurs are again accidental inclusions and out of their native haunts.

The Purbeckian is threefold, two fresh-water divisions, with a marine group interpolated between them. The fresh-water strata contain lake and river shells pertaining to living genera; also the remains of insects and of mammals. The dinosaurs belong to four phyla, including the stegosaurs, and are again probably in their normal habitat, the low-lying coastal swamps and lagoons. Crocodiles are associated, as are numerous turtles and the plesiosaur *Cimoliosaurus,* the latter evidently in the marine layers. The German Purbeck group contains not only an abundance of fresh-water shells, *Corbula, Viviparus,* and

*Cyclas,* but these are separated by beds of gypsum and salt, pointing to semi-aridity of climate. The only German dinosaur of Jurassic time is *Compsognathus* of the Kimmeridgian. (See p. 232.)

*Jurassic climate.*—Schuchert tells us of clearly marked temperature zones in the Jurassic, a very wide medial warm water area embracing the present tropical and temperate zones, with cooler, but not cold, areas to north and south. The dinosaurian habitats, as one would suppose, lie entirely within the warmer area, though they ranged beyond 50°N. in England, which is their northernmost recorded outpost. The plant life points to a warm, moist climate, for the luxuriant tree and other ferns of that period are now found only in subtropical lands. The large and abundant insects also indicate warmth of climate. The climate of late Trias and Lias, on the other hand, was markedly cooler.

*Lower Cretaceous or Comanchian.*—This period is ushered in by continental emergence, which occurred at the close of the Upper Jurassic. One result was the accumulation of extensive fresh-water deposits, known in Europe as the Wealden, with, as a homotaxial equivalent, the American Morrison of the Rocky Mountain region of the West and possibly, at least in part, the Potomac or Arundel formation on the Atlantic seaboard. It was in these widespread, low-lying areas, fringing the Atlantic and the western shores of the interior Cretaceous sea, that the ideal habitat of the dinosaurs developed. This has been likened to the lower reaches of the Amazon today, where there are extensive areas of backwater with little or no current, like the Mississippian bayous or the cypress swamps of the southern Atlantic coasts, with some dry land, interspersed with numerous waterways, both land and water supporting a more or less abundant vegetation, which in turn gave sustenance to the sauropods, stegosaurs, and camptosaurs, while the carnivores preyed upon these.

Knowlton concludes from the character of the flora that the climate was "certainly much milder than at the present time" and "was at least what one would now call warm temperate." The presence of bayous, if fresh water, and there is no evidence to the contrary, would imply a humid, or at least subhumid, climate. The dinosaurs, other than the Sauropoda, are adapted for terrestrial life, but the vast bulk of certain of the former, to be supported, according to Marsh, upon not more than four square yards of foot area, together with the very imperfect character of the articular ends of their massive limb bones, implies that they rarely, if ever, came ashore. This of course puts certain difficulties in the way of egg-laying, but this is so readily met in recent reptiles by the condition of ovivi-parity, that is, the retention of the thin-shelled eggs within the oviducts of the mother until they hatch, that the assumption may be made that similar conditions prevailed with the Sauropoda.

Wealden-Morrison time gives us one of the most complete vistas of dinosaurian life we possess, due in part of course to the ease of adequate burial of the defunct animals and the extent of the deposits.* It may well have been that among certain types, at least, such as the Sauropoda under discussion, the summit of their evolutionary career was attained, for their size and number, both of kinds and individuals, were never equaled before or since. Apparently, except for lingering lines in the rather remote places of the globe, the phylum dwindled, until few, if any, were left. (See p. 275.) The American Morrison has proved more productive than the European Wealden in bringing to light the vast assemblage of dinosaurian fauna of this period.

*Middle Comanchian.*—The Aptian of the Old World and in America the Trinity Sands of Oklahoma and the Lakota of

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* See Lull,[5] or appended chart, for dinosaurian geologic distribution.

Buffalo Gap, South Dakota, may be considered of equivalent age.

*Upper Comanchian.*—The Albian, being marine, has yet to disclose the presence of dinosaurian remains, none thus far having been brought to light, either in the Old World, or in the Dakota, the time equivalent in the New. Such dinosaurs, if found, would give no insight into the habitat conditions under which they had lived. In the Wichita (Gault-Albian) the plants show a great change over those which have gone before, for while the flora of the Trinity is decidedly Jurassic in character, now it partakes of the nature of the Cretaceous.

Sauropoda from Patagonia, which have heretofore been referred to the Danian, may be of earlier age, as they are not as yet surely dated, and one hardly looks for sauropod survival for so long a time. (See p. 275.) The Turonian has no recorded dinosaurs in the Old World. The American Niobrara formation of Kansas, however, has been highly productive of marine vertebrate life, and in addition several dinosaurs have been found.

The Old World Senonian is a more productive zone, but no Sauropoda are now known. The North American Senonian has produced a remarkable fauna, especially from the Red Deer region in Alberta (Belly River formation) and the Judith River of Montana; also in the East, in North Carolina, Georgia, and New Jersey. The Danian again is highly productive of dinosaurian life. In North America the Danian has had various titles, the Ceratops and Converse County Beds, the Laramie, and lastly the Lance, from a notable locality in Niobrara County, formerly a part of Converse County, Wyoming. This formation is distributed along the west coast of the interior Cretaceous sea from New Mexico to Montana. Gilmore reports from the Ojo Alamo beds of New Mexico a huge sauropod, *Alamosaurus,* a most unexpected survival. (See p. 275.)

*Cretaceous habitat conditions.*—Schuchert[12] (p. 890), speaking of the Coloradoan sea, says that the Comanchian sea had disappeared and that after an unknown period of time the Mexican gulf again began to invade the continent. This, the greatest extension during the Mesozoic, he calls the Coloradoan sea and says that the deposits which were made therein pass unbroken into the overlying Montana series, the deposits of a somewhat smaller sea. The Coloradoan deposits vary much locally, but it is especially in the West where the materials came from the periodically rising Rocky Mountains that brackish and occasional fresh-water deposits are most frequent, as compared with its eastern part. A great deal of bituminous and lignitic coal is found in this western area, indicating that, while coal marshes were more abundant toward the close of the Cretaceous, they also existed in various places throughout the period. Evidence goes to show that "the sea was shallow, with bars and marshy islands, ever changing from place to place, due to shifting sea currents, the unloading of rivers, and the crustal warpings."

It was on the landward side of the strand that the known dinosaurs had their home. It is not remarkable that they show evidence of semi-aquatic adaptation, notably the trachodonts, and that occasional unfortunates were actually carried out and buried in the marine sediments along the seaward side. It is a curious thing too that so many of the known armored dinosaurs are found entombed in marine strata, from *Scelidosaurus* of the Lias on. Possibly their lack of celerity of movement rendered them more readily caught by rising floods and drowned, while the more active, or the semi-aquatic, either of which could readily escape from dangerous waters, survived.

*Cretaceous climate.*—Knowlton calls attention to the widespread condition of very similar Cretaceous plants from Argentina to Greenland and Alaska, including such as the palms and figs, indicating a climate somewhat warmer than at present, and a mild, humid one in the Rocky Mountain area during Coloradoan time. Schuchert thinks that climatic zones also existed then, but were less marked than at present. The expectation of cold as an accompaniment of the Laramide revolution, which marked the close of the Cretaceous, is not borne out. There may have been Alpine glaciers, but nothing like a widespread glacial climate. A temperature drop sufficient to react upon the rather sensitive reptilian fauna may, however, have occurred and have been one of the several contributory causes of dinosaurian extinction. (See p. 276.)

*Summary of habitat conditions, climatic, and vegetative. Early Triassic.*—Climatic indications are that the dinosaur habitat was arid, a condition which, except locally, prevailed throughout the Trias. There are local areas where coal swamps prevailed, sometimes simultaneously with aridity elsewhere and with a consequent faunal differentiation. Even in the Connecticut Valley there are occasional black shale bands, which indicate lake-like standing waters of no short duration, with an abundance of vegetation and fishes therein. Plants of the Trias are conifers, cycads, rushes, and ferns, varying greatly in form and habit of growth, but not at all in the monotonous, somber greens. Little is known of the early Triassic flora, which must have been in part transitional with the Paleozoic. During the Upper Trias the Paleozoic genera had, with few exceptions, disappeared. As Knowlton says (Schuchert,[12] pp. 825-826), the Upper Triassic flora consisted essentially of rushes, many of large size. Ferns, both tree and herbaceous, existed, as did many genera of cycads, some of which were as tall as are those of today. The vegetation therefore, while not abundant, was not stunted, which is so often the case in semi-arid regions of today. The trees show no annual growth rings, from which is inferred a uniformity of the warm subtropical climate, without change of seasons.

*Jurassic.*—The climate of the Lias seems to have been cooler and more humid than that of late Triassic time. Insects which are abundant are all smaller by far than those of the later Jurassic. This Handlirsch interprets as indicative of cooling, comparable to that of northern Europe of today and as compared with that of either Mid-Trias or Upper Jurassic. Indications are that this climatic reduction was rather widespread and not local.

In the Late Jura the temperature zones, comparable to our temperate and torrid, became more marked, but the plants are widespread and such as would live in a warm and moist climate, comparable to those of the subtropical regions of the globe today.

The land floras were very extensive, for, according to Knowlton, nearly half of the North American species other than cycads also occur in the Old World,—England, Scandinavia, across Siberia, Manchuria, and Japan to Alaska. Also the plants collected by Shackleton south of Cape Horn are essentially the same as those of Yorkshire, England.

The Jurassic has been called the Age of Cycads from the abundance and variety of these sago palms. Otherwise it resembles the Triassic very largely, embracing the scouring rushes, herb and tree ferns, ginkgos or maidenhair trees, and modern cypress-like conifers, although it does take upon itself a yet more modern aspect, and many of the plants are represented by direct descendants in the existing flora of the warmer regions of the earth. The vegetation is as yet unrelieved by color, as flowering plants do not make their appearance until Cretaceous times.

The *Comanchian* is a time of great dinosaurian expansion, if one may judge by the known material, but just how largely this is due to favorable conditions of preservation is not known. The extensive, low-lying plains, with their interlacing network of streams and bayous, formed a habitat that was ideal, and at the same time the opportunity of preserving burial in the abundant sediments was very great. The older Comanchian floras, those of Morrison and Wealden times, still bear the character of those of the Jurassic. The rushes are diminishing in numbers, and the ferns of the older age are undergoing modernizing. In late Comanchian, on the other hand, the flora begins a marked change, for the cycads are undergoing gradual replacement by modern hardwood trees, sassafras and the poplars. By the end of Comanchian time oaks, elms, and magnolias had been added and had extended so far that by the earliest Cretaceous they had spread over the whole world.

*Cretaceous.*—This was a period of coal formation in local swamps along the borders of the inland epicontinental seas and provided the habitat of the known Cretaceous dinosaurs, some of which are as thoroughly aquatic in their adaptation as are the modern Crocodilia and must have lived much as do the latter today in our southern bayous and cypress swamps. The draining of these low-lying lands during the time of the Laramide revolution was certainly a contributory cause of dinosaurian extinction.

Of the flora of the close of the Cretaceous, Schuchert emphasizes the extreme Tertiary character: "It was almost wholly an angiosperm forest flora, of which three species are still living, a condition unknown in the floras of earlier times. Further, it abounded in poplars (thirteen species) and planes (eight), and of the significantly warm climate trees it had figs (three), magnolias (one), and palms (four). Of this flora about 13 per cent was derived from the Cretaceous, while 81 per cent was Tertiary in character and continued into later times."

## FEEDING AND TOOTH ADAPTATION

It has been claimed that we have no direct knowledge of the feeding habits of extinct forms, but can only *infer* what they may have been. This is true, so far as actual observation of the living creatures is concerned, but when tooth and claw are each preserved to us, with all of their adaptive characters, so comparable to those of creatures now alive, our inference, especially in its broader interpretation, amounts to a practical certainty. We are therefore justified in speaking of the Theropoda, with their curved, dagger-like teeth, with sharp, serrated edges, and powerful grasping claws, as sanguinary beasts of prey, but whether certain of them slew their victims, or like the hyæna, fed upon carrion, we have no direct means of knowing. The mounted specimen of *Allosaurus fragilis* in the American Museum is shown above the partial skeleton of a sauropod. The neural spines of the latter's vertebræ are grooved and bitten, the grooves corresponding with the spacing of the *Allosaurus* teeth, broken fragments of which were found with the sauropod.

The assumption is evidently safe that the Theropoda, at all events, were carnivorous and served to keep in check the relatively more abundant herbivorous dinosaurs. It is hardly to be supposed, however, that they were at all exclusive in their diet, but, wolf-like, occasionally devoured their more unfortunate fellows, even of their own species.

The feeding habits of the Cœlurosauria are more conjectural. They were always of much less physical prowess than were their greater brethren, and their fingers were often long and slender, the claws sometimes extremely curved and of great grasping powers. That the large majority of them was carnivorous there is little doubt, but of their diet, whether fish, flesh, or fowl, one can not be so sure. Osborn has depicted *Ornithomimus* of the Morrison in the act of capturing a bird, although the artist of the picture, Charles R. Knight, expressed the opinion, in a conversation with the writer years ago, that it might well have used those slender fingers for the capture of fish. Certain Cœlurosauria may have fed upon the smaller reptiles—aëtosaurs, lizards, any whose lack of prowess would make them possible victims. They show no recognizable adaptation to mammalian destruction, as do the broad-snouted crocodiles, but the mammals of their day were so small that they may readily have been captured and destroyed with no more effect on the structural modification of the dinosaur than in the case of modern birds of prey.

With *Ornithomimus* and *Struthiomimus* an interesting problem has arisen. The latter was toothless, with an ostrich-like beak, as the name (ostrich mimic) implies. The skull of *Ornithomimus* is as yet unknown, but was quite probably similar, if indeed the two forms are not actually congeneric. Several ideas have been advanced to explain this edentulous condition. They have been summarized by Osborn as follows: that its long claws were used to break into the hills of ants which were then devoured, possibly by aid of a prehensile tongue; that they were used to collect molluscs on the shore, which were crushed between horny pads borne on the jaws in place of teeth; that the creature had become herbivorous, browsing on more succulent herbage, which it dragged within its reach; and lastly, that its habits were omnivorous, as with the ostrich of today. With the latter the variety of food is amazing—lizards, small mammals, fruits, berries, and seed grasses.

Nopčsa,[13] in a paper received recently, discusses the probable habits of *Struthiomimus,* reviewing the work of the American paleontologists. He speaks of the adaptation to swift running, either as one pursued or pursuing. The latter is not considered probable; the former highly so. *Struthiomimus* was therefore an inhabitant of the open country, avoiding the marshy ground or that covered with dense vegetation, thus resembling the ostrich more nearly than the moa. The structure of the arm shows no evidence of adaptation for struggling with opponents or with prey, nor are the arms suitable for pulling. There are, however, three fingers of equal length, with an opposable pollex. Nopčsa's inference is, therefore, that the creature robbed the nests of reptilian forms, lifting the eggs in its hands to be pierced by the sharp, pincer-like beak, the swallowing of the fluid contents necessitating the jerking to and fro movement of the neck, to which Osborn has already called attention. The nests it found along the sandy shore, and frequently had to make good use of its cursorial powers in escaping from the wrath of the despoiled parents. Among the Varanidæ and the snake, *Dasypeltis,* to-day are similar nest-robbing habits found.[13] Smith Woodward[14] speaks of the dinosaur *Genyodectes* from Patagonia as being completely destitute of successional teeth. It therefore constitutes a similar problem to *Struthiomimus.*

*Sauropoda.*—The great bulk of the majority of Sauropoda, together with the character of their skeleton, has been taken as evidence for an amphibious habitat. Their teeth are peculiar in having lost the serrate-edged, trenchant character of those of the Theropoda, such as *Plateosaurus,* the group's presumptive ancestor. The teeth are confined largely to the anterior part of the jaws and are either spatulate, or, in *Diplodocus,* almost pencil-like in character, but with a fairly efficient method of tooth succession. The teeth generally show wear on their distal margins, though not always, and are neither fitted for the rending of flesh nor the holding of slippery prey, such as fishes that have been suggested by Tornier as food. Add to this the occasional presence of highly polished pebbles, called gastroliths by Wieland, within the ribs of certain specimens, notably the type of *Barosaurus lentus* in the Yale Museum, which imply a powerful, muscular, gizzard-like stomach, and the evidence for some sort of plant diet seems complete. There is generally but a single huge claw on the hand, with which some free-growing aquatic plant could have been dislodged to be sucked down the capacious gullet, after having been taken into the mouth by the rake-like teeth. The gastroliths would then function to reduce such a mass to proper consistency for its ultimate digestion. What these plants could have been we do not know, as there is little evidence of an abundant vegetation in the actual strata which include the dinosaurian remains. Holland has suggested a plant like the alga *Chara,* the seeds of which have been reported from the sauropod quarries. Holland also suggests the possibility of the interior of the cycad or sago palm trunks, which, as in the modern sago palms, must have contained a store of nutritious food, if the creature could tear away either the thin outer bark of the stem or the terminal end and thus expose the soft inner pulp.

That all Sauropoda fed upon the same plant species is hardly probable, if one may judge by the varying character of their teeth, but that they were fitted only for plant food seems abundantly proved. What constituted the transitional diet, however, from that of their carnivorous ancestors is highly conjectural. More intensive study of *Plateosaurus* may aid in the solution of this problem. A cast of *P. trossingensis,* just received from the Museum at Stuttgart, shows numerous teeth of nearly uniform size, borne the entire length of premaxillary and maxillary and at least one-half the length of the mandible. These are set vertically in the jaw, are somewhat laterally compressed, and were well adapted for the holding of slippery prey. The backward prolongation of the angle of the jaw gives evidence of ability to open the mouth forcibly for a quick snap. This form might have been piscivorous in part as a transitional adaptation to the herbivorous diet of the sauropod. In itself, however, it could hardly have been plant-feeding.

*Ornithischia.*—The ornithischian dinosaurs are markedly different from their saurischian allies in their dental armature in that, while varying in apparent efficiency, there is in every known instance a dental battery of successional teeth in the maxillaries and dentaries and, with the exceptions of *Hyp-*

*silophodon, Troödon,* and the Mongolian *Protoceratops,* absent from the anterior part of the mouth. The last have a few teeth in the premaxillaries, but none in the opposing predentary. The remaining genera referred to the Hypsilophodontidæ are too imperfectly represented to determine this feature. Normally, therefore, the anterior or prehensile part of the mouth is edentulous, and, while it varies in shape from the turtle-like, trenchant, cutting beak of the Ceratopsia to the broad, spatulate mouth of the duck-billed trachodonts, nevertheless it seems always to have been sheathed with horn or a leathery skin and to serve very adequately for the prehension of food. Posteriorly the teeth are clearly masticatory in function, hence there arises a division of labor between the anterior and posterior parts of the mouth, comparable to that seen in many mammals.

The basic diet of the predentate dinosaurs was quite evidently from the vegetable kingdom. That some were omnivorous in their habits it were futile to deny. None, however, show a specialization which would make a phytophagous habit impossible.

*Ornithopoda.*—The presence of ornithopod dinosaurs in the Trias has been proved by the finding of *Nanosaurus* in Colorado, and their footprints, not otherwise interpretable, in the Connecticut Valley,—*Anomœpus* and others, as demonstrated by Lull[8] (pp. 207-208). Here on occasion the five-fingered hand is impressed, and it is *not* that of a theropod dinosaur, which would be unmistakable. The dental adaptation is of course unknown, but in *Nanosaurus* and the South African *Geranosaurus,* described by Broom[15] from the Stormberg beds (Trias or Lower Jura), the mandibular teeth are in a single row and show no special adaptation to a plant diet.

*Hypsilophodon.*—This form is remarkable and almost unique in the possession of premaxillary teeth. This may be interpreted, however, as a primitive character and may well have been true of the predentates already mentioned, in which this element is not known. The portion of the premaxilla which bore the teeth is smooth of surface, but anteriorly the bone becomes very rugose and pitted and ends in a short, downwardly turned, beak-like process, as though sheathed in the usual horny beak of the order. The premaxillary teeth, five in number, have lanceolate, acuminate crowns; the preserved portion of the maxillary, on the other hand, bears ten teeth set in alveoli in a single row and resembling in a general way those of *Iguanodon,* but with very marked generic distinction, as the margin is not serrated, but, as Huxley says, sinuated by the termination of strong ridges of enamel on their outer surface.

The dental adaptation is clearly for an herbaceous diet, but not of so harsh or abrasive a sort as with many of the later ornithopods, trachodonts and others.

*Camptosaurus.*—The teeth of *Camptosaurus* are confined to the maxillæ and mandibles. They are individually similar to those of *Hypsilophodon* and are in a single functional series, with the crowns of successional teeth appearing at their base on the inner side in the lower jaw and apparently the outer side above. The alveoli appear to be confluent. As with the other ornithopods, the lower teeth bite within the upper, the worn face being directed outward and upward to meet the downward and inward face of the upper teeth in a chopping shear.

The premaxillaries, together with the predentary bone, are rugose, showing the presence of the prehensile beak. The lower jaw outside of the tooth row is of such form as to imply the presence of considerable space within the muscles of the cheeks. This is varyingly true of all Predentata, and Hatcher has suggested the presence of cheek pouches in *Triceratops* into which the chopped food that would fall outside the teeth could be retained. That there were spaces and that that was their function seem probable, but not necessarily in the sense of distensible cheek pouches, such as those of certain primates and rodents. The teeth of *Camptosaurus* and its allies are fairly efficient. It seems likely that cycad pulp would better serve their purpose than that of the Sauropoda.

Fig. 33.—Tooth occlusion of a predentate dinosaur. (Modfied from Lambe.)

*Iguanodon* is a much larger form than *Camptosaurus,* although the several species of the latter differ markedly in size. Its teeth are of the same general character, though larger, heavier, and with decidedly serrated edges. These animals, with their efficient dental battery and prehensile beak and hands, must have been very well-adapted browsing types, feeding on the herbaceous vegetation of their time. So much of this vegetation, save possibly the sago palms, is shunned by browsing mammals today in view of other less harsh food that it is difficult to hazard a guess as to just what among the known flora the actual food may have been. There is every probability of dietary distinction between the species and genera of contemporary ornithopods.

*Trachodontidæ.*—It is with the trachodonts that the battery of teeth reaches its highest perfection, there being, as we have seen, as many as 45 to 60 rows, each containing 10 to 14 successional teeth in each half of each jaw, making more than 2,000 all told in the actual possession of the animal at the time of death, to which must be added the unknown number worn out through use. The diagram from Lambe shows the method of tooth succession and the manner in which those of the upper and nether series occluded. The perfection of this dentition is mechanically comparable to that of the horse, an adaptation to a harsh, abrasive food. Abundant Equisetæ, which contain a high silica content, have been found associated with the trachodont remains. It is possible that the broad, duck-like beak aided in dislodging these and their underground stems and that the teeth then chopped them into short lengths suitable for swallowing. In my own restorations of these animals, in contrast to those of Gilmore, I am inclined to limit the gape of the mouth to the prehensile portion, for some sort of muscular cheeks must have been present in the region of the teeth to retain the food in the mouth. Were the head armored, however, or even protected by an inflexible covering, there must have been a crease to the hinder limit of the movable portion of the jaws, the contractile muscles being continuous over the gap within. The rear portion of the mouth of a crocodile is thus formed, although here the prehensile part, and hence the gape of the mouth, is proportionately very much longer.

*Stegosauria.*—The stegosaurs are also beaked dinosaurs, with teeth of a peculiar sort, having a long, cylindrical root and a widely spatulate crown, usually about as broad as long, generally subtriangular, serrated of margin, and grooved on the outer and inner aspect. The most remarkable single feature about these teeth seems to be their relatively small size and apparent inefficiency, as compared with the bulk of their possessor. The teeth of *Stegosaurus* are placed in distinct sockets, about 23 to the jaw, the germinal teeth forming within the alveoli of their predecessors. The number is thus vastly fewer than in *Trachodon,* for Gilmore counts but 184 functional teeth in the complete series of the skull. Their wear is oblique, indicating a shearing bite. The peculiar, spout-like symphysis of the lower jaw of *Stegosaurus,* and of *Camptosaurus* as well, would seem to imply a prehensile tongue, which would aid in gathering in the food on which they lived, which, especially in the case of *Stegosaurus,* must have been of a yielding character. The teeth are invisible from without when the jaws are closed and may have had rather less than their usual value to the animal, being replaced in function by the horny margins of the jaws.

*Scelidosaurus.*—This is the first armored dinosaur and indeed one of the oldest of the Ornithischia of which we have record. Unfortunately the anterior part of the head is missing, so that the presence of premaxillary teeth is not determined. It is perhaps safe to assume that they may well have been present in so primitive a form. The teeth which are present are rather small, but relatively larger than in the later stegosaurs. They possess the usual cylindrical fang and a peculiar flaring crown, having three divergent ridges and a deeply denticulate border, and are closely set in separate sockets. They must have formed a fairly efficient dental battery, the teeth of the upper jaw overlapping and concealing those of the lower when the mouth was closed. Owen speaks of the teeth as being adapted for the division of vegetable substances, but says that they would be equally effective in piercing and cutting or tearing through animal textures.

*Scelidosaurus,* as we have seen, was found in the marine Lias. Hence Owen says of it: "If this dinosaur occasionally went to sea in quest of food, it may be expected to be present in the fore part of the jaws, wanting in the present specimen, laniariform teeth . . . for the prehension and retention of living prey. Should these prove to be absent, and the dental series to begin as it ends, it will incline the balance of probability to the phytophagous nature of the food." The conformation of the jaws gives evidence of the "cheek pouches" comparable to those mentioned above, which are unnecessary in a carnivorous type.

*Stegosauridæ.*—The true stegosaurs, with the erect armor-plates along the back, are an aberrant side line, known first from the Jurassic Kimmeridgian (or Oxfordian) of the Old World, for the form known as *Omosaurus durobrivensis* from

Felton, England, and preserved in the Cambridge Museum, has the same peculiar type of vertebræ, with a heightened neural arch, and the same sort of dermal armor-plate, as have the American Morrison types. The degree of specialization of the neural arch is naturally not so extreme as in the later American forms.

*Stegosaurus ungulatus* was tall and lank of body,—*Stegosaurus stenops* less so,—but to what specific environment it was adapted, with the above-mentioned feeble teeth, one can not say. At all events, while contemporaneous with the giant Sauropoda, they are rarely found entombed in the same quarry, which seems to imply a certain local differentiation of habitat. It is difficult to imagine *Stegosaurus,* with its low-carried head and rather rigid back, being even semi-aquatic, and yet the limb bones have massiveness and rugosity of articular ends comparable to those of the Sauropoda. The general environmental conditions of low-lying, more or less swampy, lands must have been characteristic of their home. True stegosaurs do not apparently survive the Morrison, so that their contemporaneity is with the host of the Sauropoda, and the habitat restriction which the geological record indicates may have been a contributory cause in the extinction of both groups. Both are also highly specialized, showing characters—huge bulk, or spinescence—generally recognized as those of racial senility, which in themselves would seem to foreshadow the doom of their possessors. (See p. 275.)

*Nodosauridæ.*—The nodosaurs, or ankylosaurs, are the plated dinosaurs, the armor of which tends to coalesce into a carapace-like protective shield, especially over the rump. In these forms the skull is known in but few, such as *Ankylosaurus* and *Palæoscincus* of the American Upper Cretaceous. The head is depressed, broadly triangular, and armored with bony plates, which have coalesced with the skull. There was a powerful, cutting beak, but the teeth were small and inefficient, as in *Stegosaurus*. They had the usual sub-cylindrical root, with a compressed lanceolate crown, with crenelated margins. *Palæoscincus* has forward and outwardly projecting, spine-like plates on the shoulders, which would very effectively retard its passage through a forest. It seems hardly possible that it could have been aquatic. The inference is therefore that it lived on the open savannas, browsing on the low shrubbery. These ankylosaurs simulated in a very curious way the mammalian glyptodonts of the Pliocene and Pleistocene, even, in *Ankylosaurus,* to the development of a club-like caudal armament, like a medieval battle mace, which is also characteristic of the glyptodont *Dædicurus*. While we do not know by actual observation the habits of the glyptodonts, we do know that they probably lived on the pampas, where their remains have been frequently found, and, as their teeth were unfitted for the pampas grasses, they, too, must have been browsing types.

*Ceratopsia.*—The horned dinosaurs are a short-lived race, exclusively North American, except for the conjectural ancestor *Stenopelix,* from the Wealden of Brickenberg, and *Protoceratops,* undoubtedly ancestral, discovered by the American Museum in southeastern Mongolia. (See p. 245.) The head was huge, from one-fourth to one-third the total length of the animal, bearing, as a rule, the one to three or more horns and the protective posterior crest. There is an additional bone, the rostral, corresponding to the predentary of the lower jaw, in front of the paired premaxillaries. It was compressed, turtle-like, and bore the upper horny beak, which opposed that of the lower jaw. The premaxillaries were edentulous, except in *Protoceratops,* but the teeth of the maxillaries and dentaries were very efficient, with a triangular crown and a fang divided into an external and internal root by the closely pressed crowns of the next series, which alternated in position with their predecessors. The teeth were formed in an open channel, the former alveoli being represented by vertical grooves in its walls. The teeth were so loosely held in place after decay had removed the soft parts that they are almost invariably missing from the upper jaws. The skull has large sinuses above the brain case, wherein gases must have generated during the disintegration of the animal. The skull, therefore, had great powers of flotation, but must have drifted in its normal position, hence the loss of the teeth, some of which are occasionally found in the enveloping matrix. *Triceratops,* which is typical of the group, was a huge, unwieldy beast, carrying the head rather low, though there is evidence of very free mobility of the head on the neck in wielding the horns. With its shearing beak and efficient teeth, it must have been a browsing type that could readily find subsistence in the everglade-like region which was its home. It must be remembered that its time was late Cretaceous, after the flora had become entirely modernized. Its habits might have been quite comparable to those of the African black rhinoceros, which it resembled in appearance in a very general way.

*Origin of cursorial types.*—I believe the origin of cursorial types among the dinosaurs to have been largely the outcome of Triassic aridity, which gives rise to occasional temporary bipedality on the part of certain modern lizards. The Sauropoda, on the other hand, are the outcome of the reverse climatic type, humidity with abundant, interlacing water courses and stagnant bayous, much like the habitat of the crocodiles and alligator snapping-turtles of the present. It is possible that greatly increased size over that of their more normal contemporaries preceded the assumption of the amphibious habits for greater ease of supporting a huge weight and of finding food, and that the diverting of the energy needed to overcome gravity into growth force completed a vicious circle, which ultimately gave rise to the most ponderous creatures the world has ever seen, with the exception of the modern whales. Again in the Cretaceous there was a similar adaptation to the semi-aquatic habitat; this time, however, the animals, the trachodonts, were swimmers rather than waders. The Sauropoda probably could and did swim at times, but not very efficiently. There is no evidence of webbed feet, nor of a laterally compressed swimming tail, both of which we know were present in the trachodonts. One can well imagine that, except for their greater average bulk, the trachodonts were as active as crocodiles in the water and probably much more so ashore, for their adaptation is a double one, as they had not lost entirely their cursorial habits, with the resultant structural modification.

*Size and grotesqueness.*—Size has already been mentioned in connection with the Sauropoda, and even in the late Trias certain possibly ancestral theropods, notably *Pachysaurus,* had reached an overall length, according to Huene, of about 29 feet, while *Gressylosaurus plieningeri* was nearly 32, measured on the curve. Some of the Connecticut Valley dinosaur tracks are huge, that of *Eubrontes giganteus* measuring 14½ inches overall, *E. approximatus* 16 inches, *Gigandipus caudatus* 18 inches, and *Otozoum moodii* 19¼ inches. Lull has compared the foot of *Gigandipus* with that of *Allosaurus fragilis* of the Morrison, which must have been about 28½ inches long to 34 feet of overall length. If the ratios held, it would give to the dinosaur that made the *Gigandipus* track a length of approximately 21 feet. None of these Triassic forms, however, was as large in total length as are occasional modern Crocodilia, such, for instance, as a 30-foot gavial. Ditmars gives the following measurements for certain crocodilians: *Gavialis gangeticus,* 30 feet; *Crocodilus porosus,* the salt water crocodile, 20 feet; *Crocodilus robustus,* that of Madagascar, 30 feet; *Caiman niger,* of South America, 20 feet; while Gadow is responsible for the statement that in the Sivalic Pliocene of India a gavial, *Rhamphosuchus crassidens,* attained "the gigantic length of about 50 feet!"

Of Jurassic dinosaurs the largest recorded seems to be the sauropod *Cetiosaurus,* which makes its appearance in rocks of Bathonian age. *Cetiosaurus leedsi,* of the Oxfordian, now preserved in the British Museum, would have an estimated length of between 40 and 50 feet. So little is known of the other Jurassic types, Theropoda and others, that a length estimate is difficult to secure. With the Comanchian, with its wealth of completely known forms, very accurate figures are obtainable.

*Allosaurus,* above mentioned, 34 feet 2 inches long, is the largest accurately known theropod. The camptosaurs range from 9 feet 11 inches, in *Camptosaurus nanus,* up to 17 feet in *C. browni* Gilmore; *C. dispar* Marsh about 21 feet; while *C. amplus* was possibly upward of 30 feet, and thus compared with its approximate contemporary, *Iguanodon,* of the Wealden of England and Belgium, the length of which is about 34 feet. The stegosaurs of the Morrison are not much over 21 feet between perpendiculars, more of course when measured on the curve. It is in the Sauropoda that indications of actual giantism occur, although even here some of the estimates of overall length have doubtless been much exaggerated.

*Brontosaurus* measures 65 feet. The mounted specimen of *Diplodocus* in the Carnegie Museum at Pittsburgh, with its greater slenderness, measures 87 feet. The total bulk of *Diplodocus* and *Brontosaurus* was about the same, and Gregory, after a very carefully wrought experiment, based upon Knight's model of *Brontosaurus,* which in turn was most carefully checked up with the mounted American Museum specimen which the present writer helped to collect in 1899, came to the conclusion that the weight of the animal in the flesh was not far from 37 tons, or about one-half that of a modern whale of approximately equal length.

It is from the Tendaguru region of Tanganyika Territory that the largest reported dinosaurs are found, but the estimated length of 125 feet is based upon a comparison of individual bones, such as cervical vertebræ, with those of *Diplodocus*. We now know that these Tendaguru brachiosaurs were long of neck and short of tail, and, while their bulk was probably the greatest known, exceeding that of *Brontosaurus,* their proportions were such, especially in the giraffe-like neck and immense fore limbs, that their overall length was probably less than that of *Diplodocus*—Matthew says about 80 feet. Gilmore has just described a form, which he calls *Alamosaurus,* from the Ojo Alamo beds of New Mexico, an undoubted sauropod, but in inexplicable association with Lance forms, long after the *general* extinction of the race.

He compares measurements with those of *Brontosaurus;* the scapula of *Alamosaurus* was 65 inches long to 45 inches for that of *Brontosaurus;* the ischia, on the other hand, were more nearly equal, showing again a brachiosaur-like beast, with huge fore quarters, but one which otherwise might not have exceeded the Tendaguru forms in length.*

Cretaceous dinosaurs are mighty, as compared with their lineal Comanchian predecessors. Thus *Allosaurus* is replaced by *Tyrannosaurus* of 45 to 47 feet, but the trachodonts are not proportionately large, as the Yale specimen of *Trachodon annectens,* of the Lance, is 29 feet 3 inches on the curve. The ankylosaurs are immensely bulky, being in *Ankylosaurus* itself 6 feet wide across the ankylosed ribs, with an overarmor diameter greater yet; but their length was rarely more than 20 feet; *Triceratops* and its allies were also huge of bulk, and at least two of the several skulls in the Yale collection are 8 feet or more in length. The entire animal, however, was probably

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* An associated press dispatch from Buenos Aires, December 18, 1922, speaks of dinosaur thigh bones from Neuquen, Patagonia, measuring 270 cm. (nearly 9 feet) long—apparently a late survivor of gigantic size. If the bone ratios of *Diplodocus* held in this instance, which is improbable, the creature would be 140 feet long!

not greater than 25 feet long, but with a weight of 10 or more tons.

Another strange feature, especially of the later dinosaurs, was their grotesqueness, their *bizarrerie* being manifest in spines and crests and protuberances of one sort or another, borne on the skull or armor. Magnification of a number of our modern lizards, notably *Phrynosoma,* the horned "toad" of our own Southwest, *Zonurus* of Africa, *Trachysaurus* of Australia, the basilisks, and others, to the size of a dinosaur, gives us a creature in every way as grotesque as were their Mesozoic predecessors.

As a rule the Theropoda are comparatively conservative in their evolution, and while, as in *Tyrannosaurus*, they attain huge bulk, and in *Struthiomimus* toothlessness, the changes, as a rule, are entirely predictable,—just what the evolutionary trend would normally give rise to. A remarkable exception, however, is the theropod *Spinosaurus,* described by Stromer,[7] from the Cenomanian-Albian, of the Baharieh Oasis of Egypt, which in its way is a remarkable grotesque. (See p. 231.)

The Sauropoda specialized in bulk, though they differed markedly in bodily proportions. The long whiplash-like appendage, some ten feet or so in length, at the end of the tail of *Diplodocus* and possibly other genera, is the most unexpected feature.

It is among the Ornithischia that the *bizarrerie* is most marked, not alone the armored dinosaurs, but in the ornithopods, especially of Judith (Belly) River age. From this level, especially in the Red Deer region of Alberta, come the strange, helmeted dinosaurs, allied to *Trachodon,* but, unlike this comparatively conservative form, exhibiting most remarkable skull modifications. Of these *Saurolophus* has a high, bony spine, projecting upward and backward from the roof of the skull; *Corythosaurus* has a high, thin crest on top of the skull, which, together with a small facial region, gives a peculiar appearance to the head, not unlike that of the living cassowary; *Kritosaurus* has a highly arched profile, due to development in the nasal region; while in the most remarkable of all, *Parasaurolophus,* recently described by Parks, the posterior part of the cranium has a remarkable, curved prolongation, fully as long again as the entire skull. A unique feature connected with this animal is a corresponding modification of the mid-dorsal spines, of which the sixth is unusually wide and straight; the fifth is pointed and inclined backward, so as almost to touch

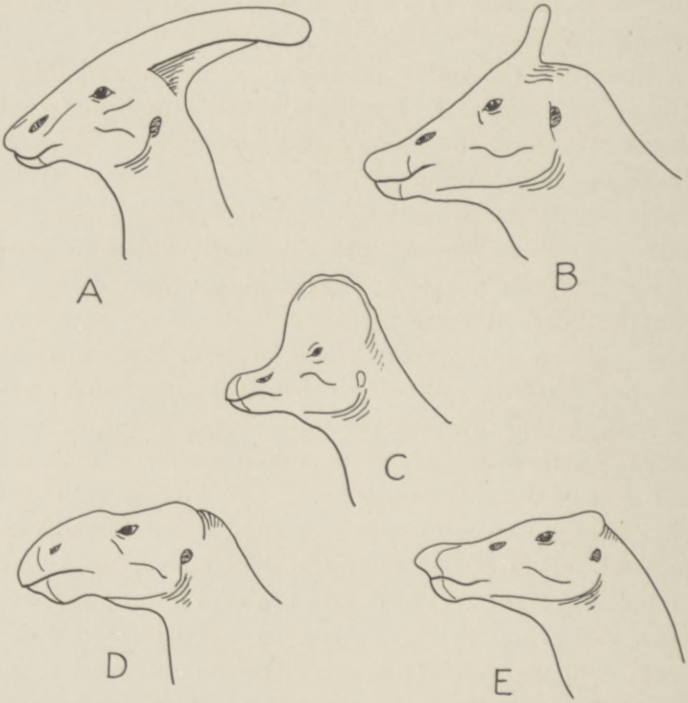

Fig. 34.—Heads of trachodont dinosaurs. A, *Parasaurolophus;* B, *Saurolophus;* C, *Corythosaurus;* D, *Gryposaurus;* E, *Trachodon.* (Lull restorations, modified from figures by Matthew, and Parks.)

the sixth; the seventh, on the contrary, is inclined forward and apparently was in actual contact with the sixth. The sixth, and to a lesser extent the seventh, spines are capped by a remarkable, originally separate, though now coössified, rugose ossicle, about 4 inches in diameter by ¾ inch thick, which seems to have been the point of insertion of a ligament which originated at the extremity of the crest. As the articulated skeleton now lies, with the neck sharply flexed backward, the result of post mortem muscular shrinkage, the crest and backwardly bent eighth spine are almost in contact with one another, but a definite articulation during life is inconceivable.

The thick skulled *Troödon,* just described by Gilmore, is another Belly River grotesque. (See p. 238.)

*Palæoscincus,* the most spinescent of the plated dinosaurs, is also of this age and place, while the contemporary Ceratopsia likewise have their share of bizarre types. *Monoclonius,* which seems to be the equivalent of *Centrosaurus* of Lambe and because of its priority to be the accepted name, shows curious, curved and forwardly directed, spine-like processes from the posterior portion of the frill, partly overlapping the large apertures. But the strangest of all is *Styracosaurus* Lambe, with a single erect facial horn on the nose and no fewer than six long spike-like processes, outwardly and backwardly projecting, around the posterior portion of the crest. Other lesser processes are abundant on the crest and over the hinder part of the cranium proper. (See Figure 32, B.)

The most noteworthy thing is that these Red Deer grotesques are replaced by comparatively conservative types in the Lance formation. Thus *Trachodon* alone apparently survives of the group that gave rise to the helmeted dinosaurs, and, while the supraorbital horns grow to immense size in some of the later Ceratopsia, the nasal horns diminish, and the excrescences around the frill (the epoccipitals of Marsh), become very conservative and sometimes are apparently entirely lacking. Why it is that the Sauropoda are gigantic, and that the contemporaneous *Stegosaurus* has developed its remarkable upstanding plates and caudal spines, and that the Red Deer creatures are so bizarre, is understandable either as evidence of racial senility (phylogeronty) or racial disease.

I have suggested the influence of endocrine glands, particularly the pituitary body, which alone of these structures impresses the bone, and therefore comes within the scope of the paleontologist's observation, as reacting on the growth of these creatures, especially the riotous growth of the spinescent types. To what extent the endocrines may in their turn have reacted to environmental condition it is difficult to say, but experiment has shown the result of the paucity of certain chemicals, such as iodine, upon endocrine growth, and one is strongly led to suspect such influences in the dinosaurian environment, especially when such things occur so locally, both as to time and place, as in the Red Deer fauna, and affect not alone one phylum, but several distantly related phyla, giving rise to superficial convergence of result.

The modern huge reptiles, such as the crocodilians, are all confined to the subtropical to tropical waters, both fresh and estuarine, and, in the case of *Crocodilus porosus,* to the high seas. The larger snakes and lizards are also tropical, but the spinescent forms are generally found in arid to semi-arid regions and seem to be a direct response to such climatic conditions. *Phrynosoma,* for instance, which is represented by several species, varying, among other things, in the length of their horns, is said to be spiniest where the climate is dryest, as toward the Southwest, the spines diminishing as one goes toward the more humid regions.

There seems to be a direct relationship between size and temperature on the part of the poikilothermous, air-breathing forms, for the turtles also bear out the rule which has already been applied to lizards, snakes, and crocodilians. Thus the great marine turtles, Sphargidæ and Chelonidæ, do not range beyond the isotherm of 50° mean annual temperature. The huge alligator snappers are found in our Southern States, while the great land tortoises, *Testudo,* survive in certain oceanic islands, Galápagos, Seychelles, and Mauritius, within the tropical zone. The warm-blooded mammals, on the other hand, are apparently not so limited, for, while many today, like the rhinoceroses, hippopotami, and elephants, conform to the rule, there are others which do not, such as the Kadiak, the largest of bears, the Greenland and Southern right whales, and the great Alaskan moose. The proboscidians and rhinos were represented by subarctic, though not especially large, types during the Pleistocene, *Elephas primigenius* and *Rhinoceros tichorhinus.*

*Extinctions.*—The extinction of the Sauropoda has already been discussed. Few survived the Comanchian, although individual species are reported from rocks as high as the Lance. It is hardly conceivable that a few stragglers should survive, even in the more remote portions of the globe, for millions of years after the general extinction of the group, yet this is precisely what our records seem to show, unless there has been a misinterpretation of an extremely local remnant of older strata, as in the Ojo Alamo specimen described by Gilmore, or the lack of recognition of true age, possibly of the lower members of an apparently continuous formation, as in Patagonia. One strongly suspects that one or both of these explanations may prove true and that the Sauropoda did not actually survive the Comanchian by any considerable time. *Stegosaurus* is another outstanding instance of abrupt extinction—a highly specialized, phylogerontic type. The true camptosaurs, which are frequently found associated with *Stegosaurus* and which apparently lived under much the same climatic conditions, do not survive as such, though whether they are racially extinct or merely transmuted into trachodonts is not clear to me. The

Red Deer grotesques, like *Stegosaurus,* were from their very nature doomed to speedy extinction as a result of the mortal outcome of a racial disease. The end of the era survivors are in every case the logical culmination of long, more or less conservative, but widely divergent, racial lines. They were magnificent creatures, each after its kind, and there is little about them prophetic of their fate.

There have been many theories set forth to explain their sudden and dramatic end, no one of which will in itself suffice. That the Laramide revolution lies back of it all as a basic cause I have not the least doubt; in what way it reacted upon the dinosaurs is not at all clear. Vegetative change from the Mesozoic to the Tertiary type, which occurred during Comanchian time, was readily survived by the dinosaurs, their powers of adaptation proving superior to such a change. Nor does an alteration in degree of humidity suffice, although the readaptation of the later types to semi-arid conditions seems doubtful. An unrecorded or unrecognized temperature drop, which affected both land and sea, would be effective, as would a change in the terrain of the dinosaur habitat, resulting in a sharp reduction of its extent and suitability. That they had run a biotic cycle as a whole is conceivable, yet the lineage of the separate phyla was old enough to justify the belief that this cause could hardly have affected so many lines simultaneously after so many thousands of years of blood isolation.

That their extinction, as their inception and general evolutionary trend, was the result of climatic response seems by far the most plausible view.

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## CHAPTER VIII

# ENVIRONMENT AND RACIAL CHARACTER*

ELLSWORTH HUNTINGTON
RESEARCH ASSOCIATE IN GEOGRAPHY
IN YALE UNIVERSITY

ONE of the great triumphs of modern science is the widespread recognition that man is subject to the same laws as plants and animals. The application of this principle, however, is still far from complete. In the study of the character of races it has scarcely been applied. Yet when so applied it may go far toward solving some of the most important historical problems.

In paleontology and biology it is universally recognized that evolution depends upon two great factors. One is the mutations or variations which every group of living beings seems to undergo under certain conditions. How these mutations arise, or whether they are directed along special lines and toward special ends, we do not know, but the fact of their occurrence and the probability that they give rise to new species are generally recognized.

The other foundation of evolution is environment. This, in the broadest sense, seems to determine whether variations shall perish, or persist, and perhaps become new species. Among the environmental factors the form and altitude of the lands, the form of the sea bottom, and the depth and movement of the water hold an important place. Still more important are food

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* A summary of the first part of a volume entitled *The Character of Races,* Charles Scribner's Sons, New York, 1924. The remainder of the volume applies to modern nations the principles here discussed in reference to human origins.

and the enemies, large or small, which prey upon a species or compete with it. Most important of all is climate, which not only has a direct effect in determining the limits within which a species can thrive, but indirectly plays a large part in determining the nature of the food, the migrations, the enemies, and the rivals which are such important factors in natural selection. Moreover, the effects of relief and of the depth and movement of the water depend largely upon the temperature, moisture, light, and movement of air and water which prevail at different levels.

If the general principle here laid down is accepted for plants and animals, it should also be accepted for man. If it is accepted for man it should apply to his mental character as well as to his physical structure. The most variable part of man is his brain. Not only does it differ in size from race to race and from individual to individual, but it differs vastly more in sensitiveness and activity. Moreover, its activity is probably affected more quickly than that of almost any other organ by changes in the environment. At present man's mental activity and capacity as measured by progress in civilization show a remarkable relation to climate. In *Civilization and Climate* I have published a map of climatic energy and a map of the distribution of human progress. The two are almost identical except where very recent migrations have occurred, as in northern Australia and Alaska, or where the constant supervision of people from better climates raises the standards of less favorable regions, as in Egypt and the Philippines. The agreement between human progress and climate is so close that man's mental activity appears to correspond to climatic conditions as closely as, and perhaps more closely than, to any other condition, including even race. In fact, a thorough analysis suggests that much of what we call racial character is the result of past and present environments. This by no means indicates that race and inheritance are unimportant, but merely that they are so closely interwoven with environment that the two can scarcely be separated. Race may be a major factor in determining the lines along which man's higher activities are directed, whereas climate is probably a main determinant of the degree of activity with which he works along these chosen lines. But the lower activities, and the kind of work by which the great masses of mankind make a living, appear to depend upon climate even more than upon race or other conditions of environment. Even such a specialized form of work as manufacturing, in spite of the prevailing opinion to the contrary, is much less likely to be located where coal or raw material is abundant than where the climate makes people healthy and active.

The close relation which we now see between climate and human activity has presumably prevailed in even greater degree in the past, for the more primitive man is, the more closely he depends upon environment. These past effects of environment become, through heredity, an indispensable part of what man is today. Taylor seems to be right when he says "that environment is a more important determinant than heredity. As the environment changes, so does civilization wax and wane, and so different races rise to eminence and then sink to oblivion."*

Let us apply this conclusion to human history, by tracing in broad outlines some of the first steps by which the character of races has been determined. To go back to the very beginning, we may inquire under what environment man first became definitely separated from his anthropoid ancestors. The general region where this occurred was almost certainly Asia. That continent appears to have been the original home of the majority of the great families of mammals. Thence the more primitive types seem again and again to have been driven outward, while new types have developed in its central portions.

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* *Geographical Review:* 11, 1921.

Today the most primitive mammals are generally found far from their place of origin, in mild environments, or on the remote outskirts of the continents, such as the ends of peninsulas or other places of refuge. Thither they appear to have migrated, sometimes because they found mild climatic conditions which they could easily endure, sometimes because they found uninhabited areas, and sometimes because they found places of refuge. Man seems to have followed the same course. His most primitive types are found in tropical regions, mountain refuges, or remote peninsulas like Patagonia. His highest types, biologically not culturally, appear to be located in Central Asia, or to have migrated from there in relatively recent times.

These statements can be understood only by recalling that the general tendency of human evolution has been to develop a nearly spherical head. In the more primitive types an enlarged space for the brain was obtained through a simple elongation of the head from front to back. In later types height was added to length, thus giving a high forehead and narrow face. The last step seems to have been to add breadth to length and height, thus giving a maximum capacity in the upper parts of the head. Judged by this criterion the potentially highest races, or those that are biologically highest and most specialized, are not the long-headed, high-headed races which are now dominant, but types which have originated in Asia more recently and whose skulls are broad, high, and round. Thus with man, as with the majority of mammalian families, we find in Asia the most specialized types so far as head form is concerned; and from that region, according to the usually accepted opinion, has come the vast majority of migrations into all the other continents.

As to the part of Asia where man originated, almost our only means of judging seem thus far to be climatic relationships. The absence of hair on man's back and its presence on legs and chest, as Matthew well points out,* seem to indicate that the hair was lost because man learned to cover himself with skins. Among the animals, on the contrary, the legs, belly, and axillæ are always the parts where it disappears first, for those are the parts that least need protection. Moreover, when animals lose their hair in tropical countries, as has happened to many like the elephant and rhinoceros, the skin invariably becomes thickened as a protection against insects and bushes. In man the skin has become more and more delicate as if in response to a protective covering of furs or other clothing. Hence it appears that man presumably lost his hairy covering in a climate which at certain seasons was cool enough so that even in his original hairy condition he enjoyed throwing the skin of a slain beast over his shoulders. Another reason for thinking that man did not originate in the tropics is the fact that practically all races from the Eskimos and Finns in the North to the Cubans and even Negroes on the South seem to have the best health and the most energy at temperatures averaging between 60° and 70°F. for night and day together. Thousands or even tens of thousands of years in the heat of Africa do not seem to have fully acclimatized the Negro to a temperature averaging above 80°F. The same is true among northern races in respect to cold, although they protect themselves by means of clothing, fire, and houses so that they are not really exposed to such low temperatures as might be supposed. All this seems to mean that an adaptation to a climate averaging between 60° and 70°F. is a very primitive trait and presumably belongs to the earliest type of humanity. Therefore we conclude that man probably did not originate in the tropical parts of Asia, but somewhat farther north, presumably in the general region extending from Persia or Mesopotamia eastward to southwestern China. This accords with the region

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* W. D. Matthew: *Evolution and Climate.*

from which the most numerous migrations are known to have come.

The picture of man's early environment is completed by considering that his anthropoid ancestors must have lived in the forest, for there is abundant evidence that real hands were first evolved as a means of swinging from tree to tree. It has been plausibly suggested that the descent from the trees was one of the main steps in man's upward evolution. This descent is supposed to have occurred during Miocene or Pliocene times. In the Miocene, central Asia stood far lower than now. Some of the greatest mountain ranges such as the Himalayas, Hindu Kush, and Tian Shan had scarcely begun their last great upheaval. In their place were low, gentle ranges such as those whose maturely dissected remnants and rounded hills may now be seen on the top of the Tibetan and Tian Shan plateaus. Many of what are now the great inland basins were occupied by arms of the sea, and the same was true of certain regions where lofty mountains like the Himalayas now rise. Because of this physiography and because of abundant evidences of mild climatic conditions elsewhere, we infer that the climate of man's supposed early home was mild and equable, and that great forests presumably covered the lands. Then, during the course of hundreds of thousands of years, the continent gradually rose and the mountains were upheaved. This in itself would have been enough to cause deserts to replace the earlier forests, but it is possible that other causes which later brought on the glacial period also coöperated in the same direction. At any rate it appears that little by little the forests began to disappear.

At first, disappearance of the forest was presumably confined to isolated open patches. If man's anthropoid ancestors lived in such a forest many would doubtless venture into these patches. The more brainy animals and also those which had some special peculiarity—some mutation perhaps—which enabled them to walk erect would have an advantage. For all the anthropoids the danger of being caught by flesh-eating animals would be unusually great in the open spaces, but those who were clever enough to protect themselves by using clubs, and especially those which walked upright and hence could use their hands for defense would have a great advantage. As time went on and the climate grew drier, the open glades must have increased until the country was largely covered with savannas, or broad grassy plains with trees scattered here and there. The anthropoids which could not walk erect, which were not alert and bold, and which were not clever enough to use sticks and stones as weapons, would be at a great disadvantage. So it is supposed that the less competent anthropoids gradually disappeared, and there remained only the erect form whose hands were free and which had an inventive brain so that it could use tools. Thus man's separation from his anthropoid ancestors appears to have been closely conditioned by the changes of climate which went on for hundreds of thousands of years in the Miocene and Pliocene eras.

With his assumption of the erect form it became possible for man's head to enlarge and develop. So long as his head hung forward, as it does in the apes, and so long as the teeth were used for rending and carrying prey, a large head was probably a disadvantage because it imposed so great a strain upon the muscles of the neck. But when the head was mainly supported by the bony spinal column instead of by muscles, and when the hands assumed the work of rending and carrying prey, each increase in the size of the head was presumably an advantage, as it gave more space for the brain.

In the early development of man's racial character the glacial period seems to have occupied a large place. It will be remembered that there were at least four glacial epochs. In each the climate appears first to have become not only colder than now but more stormy in high latitudes, and drier in middle latitudes and in the interior of the continents. The increased storminess and low temperature in high latitudes caused the development of great ice sheets especially in North America and Europe. Little by little these sheets expanded, and each, to judge by the present ice sheets of Greenland and Antarctica, must have become an area of high barometric pressure. Hence the storms were presumably obliged to skirt their edges and therefore the stormy area was pushed south, so that at the height of the glacial period the main area of storms probably formed a belt one or two thousand miles wide to the equatorward of the ice sheets, or along their lower border. In America this belt presumably covered the southern United States and the Mexican and Caribbean areas; in Europe and Asia it must have covered the Mediterranean region and its borders on either side, together with the present desert regions farther east where man appears to have originated. Consider what probably happened to primitive man each time that such a change of climate swept over the world, imposing new conditions which lasted for tens of thousands of years. Each glacial epoch must have exerted a strong selective effect in certain regions, but very little effect in others. It must also have caused great migrations and a great mixture of races. From this selection and these migrations arose the people who now inhabit the earth.

Let us trace some of the probable steps in this process of migration and natural selection. Before the coming of the first glacial epoch Asia, as we have seen, appears gradually to have been growing drier and drier. The savannas must have given place to steppes and the steppes to deserts in the central parts of the continent. Meanwhile the forest was pushed gradually outward and formed a peripheral belt. The savannas and then the steppes were pushed outward in the same way. Under such conditions the anthropoids whose lack of mental cleverness and of the proper physical structure made it impossible for them to take to the ground must have retreated with the forest. They probably could not retreat far northward for they may not have been adapted to a cold climate. To the east and the west, the forests ultimately disappeared almost completely in the dry belt extending from the Sahara to northern China. Therefore the main retreat of the anthropoids must have been southward, where they either evolved into some form of apes, or else, as is more likely, were extinguished.

Just as the anthropoids who did not evolve into men presumably followed the retreating forests, so some of the most primitive types of man probably followed the savanna belt as it was pushed outward in all directions by the gradual growth of the Asiatic deserts. Let us consider the primeval men who went southward. Some of them may have remained in the savannas and some may have pushed on into the tropical forests. But whether they lived in warm savannas or forests they were not subjected to very strong new types of natural selection. Of course they still had to struggle for existence as do all forms of life; and those who fell below certain standards of mentality, fleetness, strength, or other qualities, were killed off. But the point is that there would be no very severe *new* factors. The environment would not change for they would migrate with it, or if it changed when they entered the tropical forests they would merely be going back to the environment from which their ancestors originally came. Thus those who were more or less arboreal in habit would have certain advantages. That is perhaps why some of the most primitive peoples, like certain Negroid Pygmies and some of the Australoid people of southeastern Asia and the East Indies, live largely among the trees.

Moreover, these southern migrants would go into a climate less stimulating than that where they became of human form. They would find that great exertion heated them there much more than in their old habitat. Whenever they became thus heated they would unconsciously have a mild and perhaps harmless fever, for the temperature of the body rises under such conditions. The inevitable result is a feeling of lassitude and a tendency to be idle for a long time before making further exertion. In fact those who were not thus idle would be at a disadvantage, for they would give themselves so much fever that probably their health would suffer and in the course of hundreds of generations their type would be eliminated. In addition to this, the search for food would be easier among those who migrated into the forest than among those who remained in the savannas. There would be more edible fruits, nuts, and roots, and it would not be so necessary to make great efforts both physically and mentally in order to capture game. Thus the net result of going back into the forests of low latitudes would presumably be to retard evolution and possibly in some cases to reverse its direction.

Among the people who migrated in other directions under the stress of growing deserts, the conditions would be quite different. Those who went east or west would presumably remain indefinitely in the savanna belt unless that belt disappeared and the deserts reached the sea, as they do in northern Africa. Among the people who went north or who remained in the areas which became drier and were converted into steppes or deserts, the struggle for existence must have been much harder than among any others. Moreover, they were confronted by new conditions and therefore the people who had ingenuity and adaptability presumably had a great advantage. In the deserts, as in more northern regions, the extremes of temperature in winter are great. Therefore there is a premium on the kind of ability which enables people to provide clothing, shelter, and fire. Game is scarcer than in the savannas because there is less vegetation. Again, in the deserts it is often necessary to go long distances to procure water as well as game. Hence there is a great premium on powers of endurance and on ingenuity in devising traps and other methods of catching game. There is likewise a premium on the taming of wild animals, although presumably that was a relatively late stage. In addition to all this those who remained in the desert or who went north must have felt the pinch of the seasons in a way unknown to earlier men or to those who went south, east, or west. The seasons seem to be one of the greatest factors in promoting the evolution of the human brain. Of course the seasons can be met by migration, as in the case of the birds, or by hibernation, as in the case of bears, or merely by the development of thick fur and of the ability to subsist a long time without food, as in the case of the fox. But man did not happen to adopt any of these lines. His line of adaptation was in forestalling cold weather by hoarding clothing, food, and even fuel while the weather was still warm.

Such a method of adaptation put a tremendous premium on foresight and the power to think intelligently. Therefore it appears that the migrants who went north from their ancestral home or who remained in the parts which became deserts, although they seemed unfortunate at the time, were really the most fortunate. Among them mental ability was especially necessary to enable themselves and their children to live. Thus when mutants arose with unusual mental ability they tended to survive while others perished, and new types of man presumably arose more rapidly than elsewhere.

Thus far we have been considering the effect of increasing aridity. Now assume that a glacial period comes on. Early man, we have supposed, has migrated into all parts of the Old World and perhaps the New, although that need not now concern us. What type and degree of natural selection did the glacial period involve? In tropical countries it presumably had relatively little effect. The mean temperature at such times may be lowered from above 80°F. to perhaps 70°F. To that extent the climate becomes more healthful and invigorating, but this may not involve any great natural selection. It does not materially reduce the supply of either vegetable or animal food and does not cause any appreciable alteration in the mode of life. Nor does it require much more than formerly in the way of clothing, shelter, and the use of fire. The change to the lower temperature of course occurred gradually, so that no single individual was conscious of it during his lifetime. Thus the net effect in tropical countries was presumably little more than to give man a somewhat greater degree of energy and thereby make it easier to get a living, but it does not seem as though this would cause any strenuous natural selection.

This, it appears to me, is one of the most important points in understanding the true character of tropical people. Of course migrants from other regions have come into the tropics and have brought abilities acquired elsewhere, but so far as the tropics themselves are concerned they are the refuges, so to speak, where primitive man has been most able to preserve the qualities of his earliest days. Evolution has there stagnated, because during all the hundreds of thousands of years of man's existence there have been few great changes, few *new* types of selection whereby mental specialization has been accelerated. Thus the people of the tropics are in reality the children of the human race. They represent our primitive ancestors. Their characteristics are those which unspecialized man first showed when he separated from the apes and came down from the trees. It is not to be expected that such people should ever rise very high in the scale of civilization. Such a conclusion seems to be inevitable if we apply to man the ordinary principles of paleontology and ecology. It accords with the conclusions of the majority of unprejudiced scientific observers, but conflicts strongly with many of the ideas fostered by religion, philanthropy, and sociology. It seems to me that tropical races are bound to be inefficient in close proportion to the degree to which they are unmixed with people from higher latitudes. The converse is presumably equally true, namely, that every mixture of people from higher latitudes with tropical races tends to carry the higher type back toward the primitive type from which it evolved perhaps a million years ago.

Turn now to the desert areas in north Africa and western and central Asia. There the main effect of a glacial epoch was to produce a climate somewhat colder than now and also marked by greater storminess and rainfall with frequent changes of weather. Such conditions would greatly increase the amount of vegetation and game. They would stimulate activity among the desert people, for they would make the climate almost ideal. But they would have relatively little evolutionary effect so far as new types were concerned. They would merely permit the types which had been previously selected by the desert environment to expand and multiply. The new environment might be so favorable that the prevailing types of people might become very numerous, according to the standards of density of population prevailing among nomadic hunters. When the next interglacial period arrived and deserts once more prevailed in these regions, this large body of people would be subjected to a fierce selective process. Thus in the central deserts we should expect that each of the dry periods would cause a rapid evolution of new types, while the moist periods would permit the expansion and invigoration of these types. Moreover, during the change from moist to dry periods the people of the deserts, especially those of the center of Asia, would be driven out in all directions. That is what we know has happened. Human races of more and more specialized types have repeatedly come from that region. The long-headed, high-headed, broad-headed Alpine type of the latest migrations from Asia is the most specialized along the line of man's peculiar progress. As yet, to be sure, that race has not become dominant, but it would be rash to infer that it is biologically inferior to the long-headed Nordic and Mediterranean types.

The evolution of the modern European types of men is especially interesting. In that continent we have a peculiar condition because of the alternate expansion and retreat of the ice. Suppose that primitive men were spread over much of Europe previous to the first glacial epoch, as we infer to have been the case because of the Foxhall flints. The advent of a glacial period must have subjected those ancient men to a tremendous strain. Little by little the climate became colder and stormier, the trees of the forest diminished in size, game became scarce, and the animals which had once been common disappeared. All this presumably happened so slowly that early man was not conscious of it except perhaps through traditions handed down from mouth to mouth. Under such conditions a population inevitably falls into three groups. First, under the pinch of cold and hunger, some of the bolder, stronger, and more adventurous are finally impelled to migrate. Some go in one direction, some in another. A migration, especially in primitive times, always exercises a severe selective effect. The migrants may come in contact not only with new physical conditions, but with other people with whom they must fight. Moreover, until they become established in a new home, they are subjected to the rigors of the elements and of hunger to an unusual degree, because they do not thoroughly know the region where they happen to be and can not easily make provision for the future. Thus the survivors of such migrations are almost sure to be a highly picked group of unusual physical strength and mental ability as well as of more than the usual originality and power of initiative.

A second group among the primitive Europeans who lived where the climate became unfavorable presumably consisted of those who merely died. This does not mean that there was any manifest destruction of people. It simply means that among the more inefficient, more stupid, less energetic, and less thrifty, the death rate is bound to rise as a glacial period approaches. This is especially true among children. Thus in the course of generations these less effective types are weeded out.

The third group is intermediate in character between the other two. Its special characteristic is the ability to endure privation, cold, hunger, and all the other troubles that come as the environment grows worse. Among such people the arts degenerate. Everyone is so engrossed with the burden of maintaining life that no one has time or energy for improvements. Moreover, such people lack leaders; and initiative grows less and less among them as more and more of the adventurous and ingenious group move away. In a large part of Europe, however, this group, like the others, completely disappeared. When the ice was most extensive it came as far south as England, Holland, central Germany, and central Russia. Another great ice sheet spread out from the Alps into the lowlands. Practically all the country north of the Alps, Pyrenees, and Carpathians, and even southern Russia, Hungary, and Rumania, must have been so cold and raw that only a very few people survived.

Thus it seems safe to say that all the preglacial and interglacial inhabitants of Europe were driven out of the northern parts where the ice prevailed. Almost all except a few with unusual tenacity and ability to resist an adverse environment were killed off in the central parts. On the other hand, a considerable number of the more competent, progressive, and sturdy doubtless succeeded in pushing their way into the southern peninsulas or across into southwestern Asia or northern Africa. Thus we may think of each snowy *glacial* epoch as squeezing out into the Mediterranean regions and southwestern Asia the best of the people of Europe. But we must also think of each dry *interglacial* epoch as driving into those same regions the best of the sifted people of the deserts of north Africa and central Asia. Here then, it seems to me, we have perhaps an explanation of the fact that civilization first arose in southwestern Asia and northern Africa. It sprang up there not merely because the climate ten thousand years or so ago was relatively favorable, being halfway between that which prevailed during the glacial period and that which prevails today. It also sprang up because just in those areas, as we infer, the selected portions of one race after another—from Europe and from Asia—came together and fused to form new races of uncommon ability. Then as the climate ameliorated, essentially these same racial elements, although differing slightly in tribal names, gradually pushed into Europe, attracted by the new lands which slowly emerged from the reign of ice and storms, and driven from behind by pressure from the growing deserts. In northern India and in China somewhat the same occurrence took place but to nothing like so great a degree. Europe, because of its alternate glaciation and de-glaciation, and central Asia and north Africa, because they have alternately been highly habitable and desert, have acted like great winnowing machines. In each a vast amount of chaff has been discarded while the good grain of first one and then the other has been thrown into western Asia and the lands around the Mediterranean. From these lands Europe received its people. To the inheritance thus received we may attribute much of European supremacy.

In America a very different process has taken place. It is almost universally agreed that the ancestors of the primitive Americans came from Asia. Just when they came is not known, for we are not yet sure that man existed in America before the last glacial epoch. Probably he was here, for it seems hardly credible that fifty-five linguistic stocks and a far greater number of languages should have been evolved in the comparatively short time since the postglacial climate was mild enough to allow man to migrate by way of Siberia and Alaska. Moreover, although Bering Strait is only fifty-six miles wide, it is a very real barrier to migration, as is proved by the fact that only a few American Eskimos have crossed into Asia while practically no aboriginal Asiatics have come to America so recently that traces of them are still apparent. In earlier times, however, there was a land connection across Bering Strait and passage from one continent to the other was relatively easy.

Regardless of the time when man came to America or whether he crossed by land or water, each set of migrants must have passed through essentially the same experiences on its way from Asia to America, for all presumably came by way of Alaska. That there were several such migrations appears probable, for the racial types of America, as indicated by the heads of the American Indians, are as diverse as those of the Old World and of essentially the same kind. At the beginning of each migration it seems probable that the migrants were driven northward and northeastward in Asia by the expansion of the central deserts. Those migrants who reached America were forced to go through what is now the coldest part of the whole world except perhaps the centers of the great ice sheets of Greenland and Antarctica. There they must have been subjected to a repressive evolution such as we have described for the small remnant of people who remained in central Europe during the ice ages. But the conditions in Siberia may have been even worse than in central Europe. Suppose that during the height of an interglacial epoch the primitive Amerinds, as they are often called, had reached northeastern Siberia and spread into the Yukon Valley of Alaska which would be their normal line of migration. Even if the climate were as mild as now they would have had to dwell in a place where the temperature in January averages anywhere from 10°F. to 50°F. below zero. Not till they had migrated almost two thousand miles could they get out of such a region unless some unusual chance led them to skirt the Alaskan coast southward. Since primitive migrations usually take place very slowly, it was presumably many generations before they left this cold region. If a glacial period came on while they were there, they were perhaps driven out more rapidly than otherwise, but they were likewise exposed to still greater extremes of cold and storminess.

Few people have any idea of the rigorous natural selection which goes on in northeastern Siberia. Stefánsson has lately emphasized the habitability of many Arctic regions, and there is doubtless much truth in what he says. On the other hand, the actual fact is that the primitive people of northern Siberia live a most miserable existence and are not only again and again on the brink of starvation, but frequently suffer many deaths from that cause. Some years the fish fail to come at the expected season, or the reindeer fail to migrate in the usual way. Then the people face the long cruel winter with absolutely nothing stored up against its hardships. They try to hunt, but game is scarce; ice and snow cover everything; and even the boldest hunter is not likely to get much when the thermometer is 40°F. or 50°F. below zero and there is almost no daylight.

In addition to all this there are certain highly significant diseases among the aboriginal Siberians. One of the most important is Arctic or Siberian hysteria. According to good authorities, nervous diseases are more common in Siberia than in any other part of the world. Moreover, these diseases increase in intensity as one approaches the region of lowest temperature. The center of Arctic hysteria, a kind of madness to which women are especially prone and which sometimes seizes most of the people in an entire encampment, is in the coldest part of Siberia. This disease leads people to do all sorts of foolish things such as going out unprotected into the cold where they freeze to death, or jumping into the river in summer. It is especially harmful because it prevents the birth of children or else causes the children to be defective. Such nervous diseases are apparently more likely to prevail among the intelligent, wide-awake people of a community, among those who have the power of ingenuity and leadership, than among those who are relatively phlegmatic. The natural selection due to this disease together with the great premium which the Arctic environment places upon passive endurance may have been an important factor in moulding the mental quality of most of the people of America. If we compare the Amerinds with European races, one of the most striking differences is not only a lower degree of originality and initiative, but a certain passivity. The emotional types have been eliminated. A comparison with the Negroes shows the same thing. The Indians may and perhaps do have better minds on an average than the Negroes, but they have little of the quick, alert temperament which makes the Negro so fond of humor, so affectionate, and so demonstrative.

Farther than this we can not now trace the effect of environment on character. We have merely sketched certain broad outlines. The principles here illustrated apply to all races. In their application lies one of the great steps toward an understanding of the philosophy of history. The geographer and ecologist insist that history must be interpreted in terms of environment; the historian insists that it must be interpreted in terms of events and personalities; the anthropologist insists on an interpretation in terms of races. All are right, for what is needed is a synthesis of the various points of view. The character of any race, its ability to produce genius, and hence its history, are functions partly of the present environment, and partly of countless past environments which have selected first one type and then another for preservation, and thus have played a large part in moulding racial character.

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** indicates on which page illustration occurs.*