EVOLUTION IN OUTLINE

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EVOLUTION IN OUTLINE

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CHAPTER I

FACT AND THEORY

EVOLUTION is a theory to explain the nature and history of the vast array of animal and plant species that inhabit the Earth It is concerned with origins, and accounts for the present diversity of organisms by reference to past events of organic development Its central doctrine is one of change with descent, and, in opposition to belief in the fixity of species, it asserts that there have been profound and continuing modifications in the forms of life as generation has followed generation over the millions of years of geological time In its descriptive content it is a generalization now almost universally accepted, but in its principles it is still an imperfect synthesis, and remains a field of debate and wide difference of opinion.

Evolution is a modern concept in biology A hundred years ago theories of organic change were regarded by a majority of biologists as mere conjecture having little actual relevance either to the kinds or to the vital processes of the living animals and plants with which they were acquainted It is true that a few outstanding scientists, notably the Frenchmen Buffon and Lamarck, had already imagined the possibility of marked changes in structure and habits in succeeding generations of organisms They had even suggested means by which the changes might have come about. But the evidence which they put forward in support of their views was for the most part so inadequate and unconvincing, not to say fanciful, that it was disregarded or dismissed by their less speculative colleagues

The "climate of opinion" in biology during the first half of the nineteenth century was one in which large-scale time-effects had no significant place In part this was because it was permeated by assumptions going back to medieval days that the universe had always been much as it appeared Moreover, there was quasi-Biblical support for the belief that the Earth had been in existence for only a few thousand years—a time-span scarcely allowing the possibility that radical change in organic form had taken place

Men's minds, in consequence, were not deeply curious about problems of organic change, and only rarely were the right questions being asked, the appropriate evidence being looked for, to permit the problems to be clearly recognized, still less to be solved A reflection of this attitude is seen in the weight of interest of the pre-Darwinians in form and structure rather than in function and process, the dynamic factors in organic development being relatively ignored or neglected

Nevertheless, during this same period (the first half of the nineteenth century) oblique light from various sources, which in due course was to be focused on the central fact of evolution, was beginning to reveal the interconnections between seemingly unrelated scientific discoveries, some of them within the field of biology itself, others in fields of borderland sciences. Since evolution is a historical process needing time for its accomplishment, a major stimulus to evolutionary thought came from the science of geology The record of the rocks recast altogether the time-scale of organic history, and revealed whole new worlds of organisms inhabiting the Earth in past ages

Already by 1788 James Hutton of Edinburgh (the "Founder of Modern Geology") had shown that major revolutions of the Earth's surface, marked by widespread changes in sea-level, by periodic volcanic action, and by the piling-up and wearing-down of folded mountain chains, had occurred at several stages of Earth-history and pointed to a time-scale vastly longer than any previously imagined (" with no vestige of a beginning, no prospect of an end ").

He was followed by William Smith, who between 1799 and 1817 established a technique for dating and correlating strata of past ages by means of the fossils they contain, and who thus incidentally demonstrated that there have been orderly changes in the kinds of animals and plants inhabiting the Earth during geological time

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Approximate measurements of geological intervals in terms of years may nowadays be made from the evidence of radioactive changes in the rocks. The Earth is as a planet probably rather more than 3000 million years old The oldest known rocks were formed about 2000 million years ago, the oldest richly fossiliferous rocks—the Cambrian rocks—about 500 million years ago. The date of the first appearance of life on the Earth is unknown, but already by Cambrian times animals had become greatly diversified and elaborate in structure. (*See* page 120.)

With continued increase in geological knowledge it soon became manifest that whole groups of organisms had at various times emerged from insignificant beginnings, increased in abundance and variety, and then

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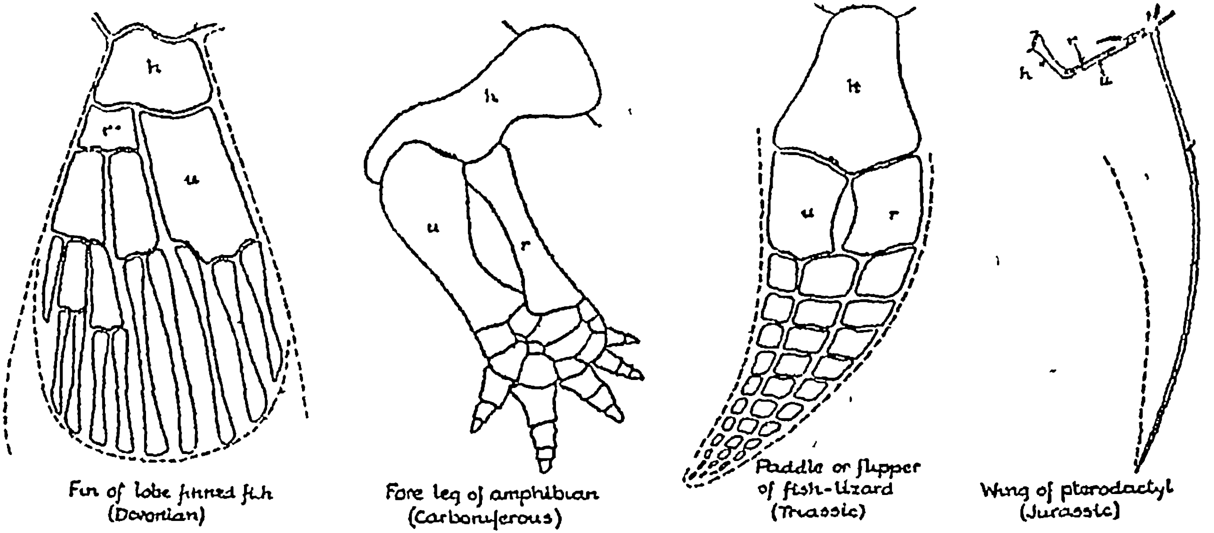
attaches to those basic similarities of structure which exist even in organisms or organs displaying marked contrasts in function Among the vertebrate animals, for instance, the walking limb of the newt or the dog, the swimming limb of the fish-lizard or the seal, the flying limb of the pterodactyl or the bird, have very different superficial appearances, but the bony supports of all three kinds of organ display similarities revealing the essential relationship, although it is masked by the different modes of life (Fig 1)

Equally, vestigial and rudimentary structures take on a meaning they would not otherwise possess when their usefulness is seen in the light of ancestral rather than immediate need The reduced tail (the coccyx) in man, the buried hind limbs in whales, the minute shell-remnant in slugs, the splint-bone side toes of the horses are functionless (at least in their primary nature) at the present day, but as degenerate relics of organs which formerly were well developed and functional they are signs of a process of change that cast doubt on a static persistence of structure in organic species

The deviations, otherwise incomprehensible, from straightforward development often seen in individual life-histories may likewise be recognized as throwing some light on ancestry and descent Thus gill-slits in the neck of the mammalian fœtus (which receives oxygen through the maternal blood-stream) are never furnished with functional gills The adult barnacle is an attached form adhering by the head region, but during growth after hatching from the egg it passes through free-swimming larval stages in which it has an appearance very like that of normal crustaceans Conversely, the floating adult feather-star *Antedon* has attached young stages The asymmetrical flat-fishes like the plaice and flounder, lying on their side when adult, are upright



Fin of lobe finned fish
(Devonian)

Fore leg of amphibian
(Carboniferous)

Paddle or flipper
of fish-lizard
(Triassic)

Wing of pterodactyl
(Jurassic)

FIG 1—Homologous bones in the limbs of various vertebrate animals, illustrating unity of structural plan in organs having very different functions The bones lettered are humerus (*h*), radius (*r*), and ulna (*u*) and symmetrical normal fishes when they are young The hint in such growth is that individual development is in some degree, at least, a reflection of steps in racial history

During the early nineteenth century much was also added to biological knowledge by voyages of exploration, on one of which (that of the *Beagle*) Darwin himself obtained his first insight into evolutionary processes In particular, a great deal of information was gathered about the animal and plant life of distant and little-known countries This new knowledge was partly of strange kinds of creatures (like the kangaroos and koala-bears of Australia and the sloths and armadillos of South America), partly of the distribution of various kinds of organisms

It was soon realized that the distribution is systematic and not haphazard, and that the Earth's surface may be partitioned into biogeographical realms, each with its own distinctive animals and plants Moreover, the localized animal and plant associations at the present day are often found to reflect associations of similar kinds of fossils, and the evidence suggests that groups tend to establish themselves in selected areas, to which they are more or less restricted over long intervals of time

Thus the pouched marsupials have been almost the only mammals in Australia for at least 60 million years, and the sloths (including extinct giant ground sloths) have occupied South America for a similar period The birds of the Galapagos Islands in the Pacific Ocean, though differing in detail and belonging to different species from those of the mainland, are of South American type, while those of the Cape Verde Islands in the Atlantic are in total contrast, being comparable with those of the African mainland this, despite the close similarity in general geographical conditions between the two groups of islands

On the other hand, it is no less significant that groups of animals and plants which nowadays display discontinuous distribution, like the tapirs of Malaya and South America, and the fresh-water lung-fishes of Australia, Africa, and South America, were formerly (as their fossils show) much more widespread and have become fragmented in their geographical ranges through local extinction

By the middle of the nineteenth century these diverse items of evidence had accumulated in such abundance that a recognition of their mutual relations was sooner or later inevitable They were welded into a coherent theory in Darwin's *The Origin of Species* (1859), which, like Newton's *Principia*, has a primary importance in the history of science as a synthesis of vast fields of observation in a manner at once comprehensive and convincing.

Darwin found the clue to organic variety in evolution, just as Newton found the clue to mechanical movement in gravitation He marshalled the arguments in its favour so cogently, and spread the net of his explanation so widely (bringing in facts of fossil succession, geographical distribution, comparative anatomy, individual life-history), that after the first shock of novelty had worn off his theory became generally accepted. It is by now so firmly established that in a scientific sense it has a certainty that effectively makes it fact

This is not to say that the theory lays claim to an eternal infallibility, or that it will never be refuted by future biological discovery But it is to assert that all biological phenomena as they are now understood find their place within its framework, and that the manner of the present-day approach to biological problems and the techniques devised for solving them are based on evolutionary principles that are virtually taken for granted In this sense, the theory of evolution as a highly successful and symmetrical normal fishes when they are young The hint in such growth is that individual development is in some degree, at least, a reflection of steps in racial history

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Darwin's supreme achievement was to make com pelling the inference that evolution has in fact taken plac and so to give to organic kinds a long and compl history. It caused a replacement of the view of th static immutability of species by one which envisage a never ending transformation of organisms over th generations. It applied a dynamic to explanations organic development and descent that made biology [illegible] [illegible] truly natural history In its practical effec it gave coherence to the disparate elements that pr viously had constituted the more or less independe branches of zoology and botany It directed fruitf research along new lines of knowledge—in palaeontolog in embryology, in physiology, in genetics Mo powerfully it recast the attitude of scientists (and in short time of laymen) to organic process, and in pro viding a basis for mechanistic interpretation it helped t free biology of animistic influence and brought it int line with physics and chemistry as a science self-contained in its ordered body of knowledge

At the same time, only in the limited sense that it entails conviction of the fact of evolution is Darwinian doctrine generally acceptable at the present day Darwin was not satisfied merely to collect evidence, but supplemented his presentation of the case for evolution with theories concerning the mode of spent much time in studying the causes of the variations between individual organisms, he was never able to distinguish clearly between those aspects of outward form which are the accidental effects of circumstance and those which are the expression of innate hereditary factors. Most of his labours in the field of genetics were fruitless and futile, in part because he was not able to ask the right questions, and he vacillated between a Lamarckian acceptance of the inheritance of acquired characters and a frank confession of ignorance. The work of Mendel on heredity in plants was unknown to him, and his conception of the relations between the germ-cells (which carry the heritable qualities) and the body-cells appears nowadays to be fantastic He carries a strong weight of support at the present time only in his deductions concerning the operation of natural selection, and even from these there are powerful voices of dissent

A sharp distinction must therefore be made between the two aspects of Darwinism. As an alternative word for biological evolution, or as an expression of the fact that evolution enters into the ancestral history of animals and plants, it is unexceptionable, and is indeed the central theme of current biology But as implying a particular kind of evolutionary mechanism which Darwin favoured, it is by some scientists regarded as erroneous and by many others as inadequate During the present century its deficiencies in genetics have been met by Mendelian theory, the synthesis of Darwinian natural selection and Mendelism being known as Neo-Darwinism.

Some biologists, however, find a thoroughly satisfactory explanation of evolution in Mendelian process alone Others, the Neo-Lamarckians, maintain that some truth still adheres to the speculations of Lamarck, who supposed that evolutionary organic change can be brought about by individual functional—and inherited—

response to the demands of the environment (though the Neo-Lamarckians usually go far beyond Lamarck in attributing evolution to the direct influence of the environment in evoking heritable adaptations) Yet others, believing that a mechanical explanation of process in living things must necessarily be partial and inadequate, hold that some sort of vital principle is the source of evolutionary change

Evolution may be summarized as change with descent In the course of generations offspring come to differ from their ancestors to a degree that prohibits their being classed in the same group (which may be a closely defined group like a species, or a broader group like a genus or a family) Thus rhinoceroses are descended from small, slender, lightly-built running forms not very different from ancestral horses Hippopotamuses are modified swine, and through a series of intermediate types can be traced back to ancestors not very different in essential structure from living pigs The earliest known birds have a reptilian-like true bony tail, but their modern successors have a tail only of feathers Such changes involve constant and cumulative variation in the members of a species, the descendants successively departing from the norms of earlier generations The process is possible only when individual variants arise and pass on their novelties and differences to succeeding generations

At the same time, the only agent of transmission of characters is heredity The manner in which the individual grows in the likeness of its parents—so that a tadpole grows into a frog, an acorn into an oak—shows that heredity is powerful as a conservative force tending indefinitely to maintain uniformity of type, and if heredity were the only force operative, evolutionary effects could not be maintained for any length of time, but would gradually die down to insignificance

A satisfactory theory of the mechanism of evolution must therefore take into account a number of separate factors of organic process, some of which appear to be mutually opposed These factors include the means whereby like begets like, the emergence of variant individuals to allow progressive change to take place, the selection ensuring survival of at least some of the variants, and the incorporation of variant characters in the hereditary stream The theory must also explain the courses taken by the lines of evolution, the diverse products of evolutionary process in different parts of the Earth, the recurrence of similar evolutionary trends at different periods of Earth-history, and the periodic extinction of previously successful lines of evolution.

All the factors are not equally or identically expressed in every organic group For instance, inheritance in organisms which reproduce by buds or shoots (such as corals and sea-mats among animals, potatoes and blackberries among plants) is not identical with inheritance in sexually reproductive organisms (which comprise the great majority of animals, and most plants). The mode of evolution is thus not readily stated in a single formula It may differ in kind, or may display a differential emphasis, in different groups of organisms or in contrasted circumstances. Sweeping generalizations are ceasing to be acceptable as summaries of evolutionary theory; and the problems of evolution become more intricate the greater the detail in which they are studied.

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The other regards the materials of inheritance to be independent particles or elements which remain discrete and unblended as they are passed from one generation to the next.

A theory of blending was particularly favoured by Darwin himself As a thorough mixing of inherited ingredients, and a mutual annulling of any parental differences, blending implies that the individual in its general form lies midway between its parents In successive generations it should thus cause a pervading sameness to spread through the members of an interbreeding population. To counteract this increasing uniformity, which manifestly does not occur, Darwin supposed that a corresponding measure of variability was restored partly through the incidence of mysteriously arising " sports " (what would now be called mutations), partly through differences in individual habits. A difference in habits is reflected in a difference in form (the muscular development of a blacksmith is not that of a postman), and Darwin followed Lamarck in thinking that the effects of individual use and disuse could be transmitted to the germ-cells, and so be carried into succeeding generations

These assumptions have not survived practical tests True and complete blending, as Mendel first showed in 1866 and as experiment has since amply demonstrated, does not occur, and when attempts are made to induce heritable Lamarckian effects in pure stocks they are almost invariably unsuccessful, or the results are ambiguous. The doctrine of the Russian Michurin-Lysenko school that nurture is of supreme importance in evolution is based on inadequately reported experimental evidence, the value of which cannot at present be assessed.

In any event, it is difficult to imagine, even as hypothetical possibility, any mechanism by which environmentally induced change in the gross structure of an individual can be genetically transmitted to its offspring Thus the nearly constant self-regulating internal environment of warm-blooded vertebrates is virtually unaffected by even strongly marked changes (say in temperature or humidity or food-supply) in the external environment, and the germ-cells which live in the internal environment could provide for an adaptive structural change in the next generation only through prophetic intuition

Sufficiently violent and penetrating environmental stimuli may, of course, reach the germ-cells in the ovaries or the sperm-sacs It is now a usual experimental practice to induce heritable changes by means of X-rays and certain poisonous chemicals But the ensuing alteration in the nature of the hereditary materials (and consequently of the offspring) is "random," and bears no necessary functional relationship to the nature of the stimulus

Blending inheritance, and gross bodily response to use and disuse, are thus rejected as means of accounting for heredity and evolution They are replaced by a theory, now generally accepted, that has its roots in the experiments of Mendel on inheritance in garden peas It explains the transmission of hereditary qualities in terms of the constitution and activities of the elements of the germ-cells These elements are chiefly the visible thread-like chromosomes, and the genes which the chromosomes are inferred to carry

In the germ-cell of any one kind of organism each chromosome is highly individual in both the number and the kinds of genes it carries, and differs not only from neighbouring chromosomes in the same cell, but also from the chromosomes of cells in other kinds of organisms The genes appear to be the primary stimuli of growth, and frequently (if not as yet invariably) the nature of particular organs and characters in the growing body may be attributed to the influence of particular genes That is, there is a very close correlation between maturing body-form and the inherited system of chromosomes and genes assembled in the initial fertilized egg. Correspondingly each specific kind of organism has its standard complement of specific chromosomes: for instance, there are twenty-four chromosomes in a full set in man, four in the banana-fly, seven in the sweet-pea

The process of formation of the germ-cells is highly elaborate and is not completely understood, but in essentials it ensures that by fission and subdivision of the parental chromosomes and genes a full set of each is normally given to every germ-cell. That is, the chromosomes and the genes reproduce themselves, and recur as discrete entities at successive stages of cell-structure and cell-division, retaining their individuality as they are transmitted from one generation to the next

When an ovum is fertilized by a sperm, the resultant first cell of the newly conceived offspring thus contains a double set of hereditary elements · twin pairs of chromosomes and twin pairs of genes, the members of each pair being derived the one from the male, the other from the female parent. Each parent thus contributes roughly half of the determinants of growth to the offspring.

When the two chromosome sets are identical—which sometimes happens in self-fertilized organisms—the hereditary line is said to be pure, and all members of the line have the same hereditary constitution. When, as is usually the case (since the two parents are very rarely identical), there are differences between the chromosomal or genic contents of egg and fertilizing sperm, the hereditary product is hybrid The hybrid form then contains, or may contain, aggregates or associations of genes different from those of either its parents or its fellows, and thus as it grows may reveal a variability that is strictly the expression of a unique constitution

The chromosomes and genes in the fertilized egg, derived from different parents, associate but do not fuse. They may be looked upon as a board of directors working more or less harmoniously together in the organization of individual growth, but each maintaining a physical distinctness that is not destroyed by their association In succeeding generations they may go their more or less independent ways, separating and recombining in ever-increasing complexity as the number of ancestors increases

This independent assortment, reflecting sharp segregation and particulate behaviour of the genes, was Mendel's essential discovery It explains much of the variation that occurs in organisms of the same species, even in brothers and sisters in the same family As the genes are ultramicroscopic in size, proof of the assortment cannot be obtained through direct observation. it lies in statistical deductions based on the mathematics of probability when a sufficiently large number of instances are examined Nevertheless, whatever the nature of a single gene may be, the results of Mendelian experiment are not to be controverted when the populations dealt with are large enough to smooth out any irregularities arising from incidental " random " effects

Reshufflings of a finite number of genes cannot, however, promote indefinitely continued evolution they can only alter the arrangement of the units of basically similar organic forms Mendelian assortment thus gives rise to only a limited (though wide) variability For major evolutionary progress to persist it must be supplemented by other means of hereditary change. These arise when the steady transmission of chromosome-sets and gene-sets from ancestors to descendants is periodically broken by abrupt modifications in the regularity of the process or in the nature of the genes Such alterations in genetic constitution are called mutations They take place in two principal ways. as chromosome-mutations and as gene-mutations.

Not infrequently the splitting of the twin pairs of chromosomes in the formation of the germ-cells may be incomplete, and cells then become overstocked (or under-stocked) with chromosomal material This commonly happens in plants, when the succeeding generation, grown from seeds with an abnormal endowment of growth-stimulus, departs markedly from the parental type The spectacular contrasts brought about by such means in the evening primrose offered the Dutchman de Vries his chief evidence of mutation in the early years of the twentieth century.

Rearrangement of the chromosomal elements may also result (commonly in both plants and animals) from breakages occurring in the chromosomes during the separation of the members of twin pairs there may be simple exchange of corresponding segments between the twins, or inversion of the chromosomes by a twisting of the twins, or gains or losses on the part of one or other twin

Since the chromosomes carry the genes, the genic pattern in the germ-cell is affected by such chromosome-mutations Nevertheless, regroupings of chromosome-segments, since they do not cause alteration in the intrinsic nature of the hereditary units, have the same shortcomings as gene-recombinations in their inability to sustain radical evolutionary advance for any considerable length of time, and in the frame of the geological time-scale their effects are minor in comparison with those of gene-mutation

Mendelian assortment is statistically a fact of experiment Chromosome-mutations are facts of observation. Gene-mutation, the third type of alteration in the nature of the germ-cell, is not so directly known This is because the genes cannot yet be isolated and examined as separate physical entities Nevertheless, through their effects they can be located in specific parts of specific chromosomes, and they are carried in chromosome-mutations with those segments of the chromosomes to which they are inferred to belong They have an existence no less real than that of chemical molecules, and in their reactions suggest that they consist of complex proteins operating in a matrix of nucleic acid Their mutations may well be due to changes in the composition of the protein molecules In any event, each gene has a highly specific control on growth, whatever is its fundamental nature, and in terms of hereditary effects gene-mutation is an alteration in this specificity of control It is revealed in an alteration in the form or function of the bodily character whose growth in the maturing organism is controlled by the mutant gene Such mutations are known to occur repeatedly, and over extended intervals of time their cumulative effects may lead to profound transformations of bodily structure

All or nearly all the evidence points to the conclusion that the inherent determinants of growth reside very largely in the chromosomes and the genes, the nature of which is reflected in the structure of the growing organism Except in the rare cases of pure strains, the individual therefore usually displays variation from the parental type through Mendelian assortment and through the " accidents " of chromosome- and gene-mutation Even under conditions as nearly uniform as possible the members of a single population will consequently respond differently to environmental stimuli because of differences in genic composition, because of inherent differences in potentialities of growth.

Nevertheless, the organism is at all stages of growth organized in its structure and activities, and a view of heredity that regards the genes to be simply additive in their influence is misleading. Thus in simple chromosome-exchange and inversion the mutation involves no net addition or subtraction of germ-cell material, and the total number and kinds of genes remain constant the only recognizable alteration lies in a re-arrangement of segments of the chromosomes. The modified growth processes to which such a mutation gives rise cannot therefore be attributed to the influence of new genic substance, but must follow solely from position-effects, from changes in the locations of the genes, from a reconstitution of the whole genetic system That is, the chromosome-exchange causes some or all of the displaced genes to find themselves in novel environments of other genes

It is consequently an over-simplification to regard the individual genes as wholly isolated agents operating in utter disregard of surrounding circumstance, each separately determining some particular structural feature in the growing body. On the contrary, the position effects show that each gene is itself influenced by neighbouring genes, and the whole association of chromosomes may be looked upon as a complex gene-environment itself controlling the specific behaviour and effects of individual genes—though, as Mendel's work showed, there is a crude division of genic labour.

A chromosome-association in a cell is thus a highly elaborate and integrated mechanism, each part of which is in a stimulating and controlling environment of all the other parts Any sort of mutation, though in one sense physically localized, is in reaction more or less pervasive It is therefore a misleading simplification to equate a particular character in an organism (like pigmentation in man, or rose-comb in fowls, or wrinkled skin in peas) with the influence of a specific gene or a few specific genes The gene is not the character, not even the character in embryo, not even the point of origin of the character—though it may be the primary catalyst of character-expression, of organ-differentiation, as the body grows In a sense, all the genes, as active participants in the promotion of growth, contribute to each and every character that arises in the process of growth Indeed, it may be shown experimentally that combined genic operations in the control of character-expression are widespread thus eye-colour in the banana-fly is directly controlled by more than a score of genes Conversely, a single gene may have multiple effects and control the growth of a number of " separate " organs and characters thus the gene " stubbloid " in the banana-fly demonstrably promotes the growth of crumpled wings as well as of shorter bristles

Every mutation disturbs the equilibrium of the whole organized gene-complex, which in turn acts as the constraining environment of each new mutation Since the intricate machinery of the gene-complex (with thousands of genes integrated in their activities throughout a constantly changing life-history) rests in a delicate balance of mutually affective gene-reactions, any upset, however slight, of that balance is more likely to be disadvantageous than beneficial Most mutations are consequently harmful, many of them lethal This is another way of saying that the individual genotype—the whole organized association of genes in the germ-cell—can survive only when its own internal environment allows.

Furthermore, the chromosomes and the genes form only a comparatively small part of the total cell, whereas growth of the body as the cells divide involves the elaboration of a great variety of materials organized in complex chemical and physical ways If the genes control this process of growth they must do so not so much by direct participation (the gene does not itself become the crumpled fly-wing or the serrate tomato-leaf) as by stimulation. The stimulus is chemical, and the genes function as activators, organizers, and determinants probably through the agency of catalytic ferments like hormones and enzymes

Direct evidence of the functional controls on growth exercised by genes is afforded in the case of those gene-mutations which are outwardly recognizable only through differences in behaviour of the mutants, and not through differences in anatomical structure. Thus the normal form of the water-flea *Daphnia longispina* enjoys an optimum temperature of growth of 20° C., with limits of survival ranging from 11° to 28° C. A warmth-loving mutant, outwardly indistinguishable from the normal form, has its optimum at 27° C, with survival limits ranging from 20° to 32° C

In summary, Mendelian theory at once illuminates the manner in which individual growth is controlled by inherited factors, provides reasons why offspring resemble their parents in some respects and differ from them in others, and explains the emergence of variants with heritable qualities providing the material for evolutionary advance.

CHAPTER III

VARIABILITY

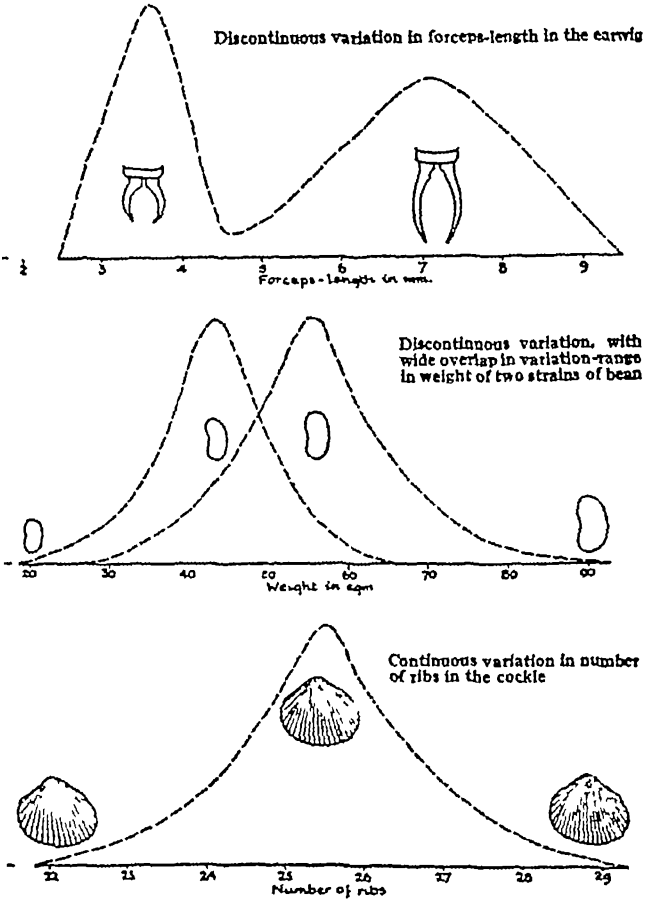
GENOTYPIC variability, the range of potential differences between the structure and habits of members of a species that may arise through differences in genetic constitution, is not the only kind of variability

Organisms do not grow in a vacuum They react to the stimulus of the environment, and although the determinants of heredity reside in the material substance and the arrangement of the elements of the germ-cells, it is naïve to look upon the chromosome and gene content of the egg as the embryonic structural content of the developing individual Preformation, with each separate structure in the adult having its material equivalent in the egg, is no longer an acceptable assumption (though at one time biologists imagined they could see the diminutive man, the homunculus, in the human sperm) Development is not a simple Chinese-box emergence of what is already there An organism is what it becomes

In heredity characters as such are not handed on the egg carries developmental potentialities only The potentialities are composite They derive from what is given in the inherited genotype, and they are limited by what the organism can tolerate at every stage of growth They become actualities only when there is continuous adjustment of separate parts in an integrated whole, when there is always appropriate function to satisfy changing organic need But within the limits set by the necessity to survive, relatively wide differences in structure and form are possible on any given genotypic basis, and reveal themselves when growth takes place in contrasted environments. No organism is compelled to grow to precise strait-jacket specification, or to travel a single-track route to some predestined end

The effects of abnormal environments in modifying "normal" growth are sometimes spectacular Thus a mere change in temperature or in relative humidity may cause delay in the metamorphosis of certain salamanders from the tadpole stage, so that gill-bearing individuals, still "larval" in not having acquired lungs, are senile in other respects, and die of old age. Conversely, thyroid extract induces the premature metamorphosis of tadpoles into frogs The addition of minute amounts of lithium to the water in which certain fishes grow causes them to develop a single central cyclopean eye In amphibian grafts and chimeras thoroughly healthy monsters with two heads or two tails or displaced organs are common products of laboratory experiment Sponges may be fragmented to powder and sieved, and the particles induced to reorganize themselves into complete sponges again. Hydra-headed planarian worms may be manufactured by snipping the single head of a normal worm

These are gross examples of "mutilation," but what is abnormal about them is no more than what is unusual. The abnormalities reside only in the wide deviations of growth from what has come to be expected, and not in the violation of any intrinsic property of living matter. They merely illustrate in startling fashion the pervasive relation between organic form and conditioning environment. In daily experience, a man may be thin because he belongs to a slender race or because he needs food, a deficiency of iodine in the diet may lead to cretinism; trees lean away from the wind, plaice take their colour



G. 2 —Kinds of variation in four population samples The graphs show the proportionate abundance of the different variants, and the inset diagrams the forms of the normal and extreme variants

variants about a norm or average. That is, the variation is continuous. For instance, pure-bred self-fertilized broad beans (genetically uniform therefore), grown in a garden under slightly differing environmental conditions of soil-type, nutrition, insolation, humidity, distance from the ground, and position in the pod, display corresponding somatic variation a few beans may have a weight of as little as 10 cgm or as much as 80 cgm, but the vast majority (about 76 per cent) have a weight of between 50 and 60 cgm, and there is a rapid falling-away in numbers on either side of the mean. Similar continuous variation is displayed in the number of ribs on cockle-shells collected on a beach over an area of a few square yards; but it is not certain in this instance that all the variation is free of genetic influence (*See* Fig. 2)

Nevertheless, although there is thus a convenient analytical distinction in kind between genetic or mutational variation and somatic variation—the one being heritable, the other not—it is difficult to resolve the two components in the individual phenotype. Since no two organisms, even if genetically identical, find themselves in precisely the same environment throughout life, phenotypic variation is universal. Usually it embraces or is superimposed on genotypic variation, and as there is no abstract standard of the genotype detachable from the environment (that is, as the nature of the genotype is necessarily and invariably manifested in some environment or other), the unitary individual variant is a composite product of two independent variables

The individual fertilized egg has a wide range of potential phenotypic variability. It could survive, and might grow, in any one of a great many possible environments. These are, however, initial possibilities only. From the moment of its conception—once it begins, in fact, to grow—it is, of course, affected by only one specific environment (or only one sequence of environments) that in which it finds itself of the many it might have met Its potentialities of form are narrowed down as it matures, and its resultant growth comes to be directed along a defined channel · in its adult state it cannot be both fat and thin, stunted and well set It thus matures into a merely incidental individual variant differing partly by chance from the norm of its species in more or less degree

Similarly, the variability of a community of freely interbreeding members embraces the whole field of possible variants that might arise with growth This is a more extended variability than that of the single individual, since (except in pure lines of descent) there is usually an indefinitely large number of genotypic patterns in the germ-cells of a community of fair size, permuting all the genes and gene-mutations of its members But any one community, however large, cannot meet all possible environments permitting survival, and the range of variation actually expressed in its adult members is always more limited than the inherent range of variability

Certain significant results follow from these facts, for different interbreeding communities of a given species never find themselves in precisely the same environments Thus communities of trout inhabiting neighbouring streams, or of flowers growing on neighbouring soils, or of gulls nesting on neighbouring islands, no doubt live under broadly similar conditions, but in detail they meet appreciable disparities in food-supply or exposure or temperature or crowding, and so tend to become phenotypically divergent

The fresh-water mussels are very susceptible to environmental control on the form of the shell In them obesity tends to increase with increase in streamvelocity, and shell-thickness with increase in the calcium content of the surrounding water. In the still hard water of a pond, therefore, a community of mussels may display fluctuating variation in the shape of its members, but on the whole it is likely to be typically represented by forms which are relatively slender and thick-shelled A neighbouring stream of fresh water, on the other hand, may contain mussels of similar inherent constitution · some of these may be as slender and as thick-shelled as those of the pond, but most will be relatively stout and thin-shelled

When there is an abrupt separation of communities by physical barriers, as of mussels of unconnected streams, the differences may be so marked that little variational overlap occurs between the separate communities, which then appear to belong to different species Thus in France over 250 so-called "species" of the mussel *Anodonta* have been reported Reciprocal transfer and cross-breeding between the forms from different localities have revealed, however, that environmentally induced differences (habitat differences) are mainly responsible for the community-contrasts and have been mistaken for gross genetic differences, and it is, in fact, probable that no more than two or three distinct species of mussel are represented

In America, on the other hand, it has been shown that the mussels of a large, continuous water-body like the Mississippi river, in which there are notable environmental contrasts in different parts of the course, display a systematic change in the form of the shell as they are traced along its length

Variation is thus manifold. It has a central importance for evolution in providing a diversity of phenotypic forms without which there could be no continued change. Sustained evolution obviously rests in the recurrence of genetical variation—the only kind that inheres in the essential constitution of successive communities For this reason some of the early Mendelians considered evolution to be simply and adequately explained by ascribing it to a single important factor, the accumulation of a succession of mutations This clearly is an over-simplification The actual individuals forming the sundry communities upon which the evolutionary process operates are phenotypes always reflecting a component of environmental variation, and since the process is one of the continued selection of certain actual forms and types and the extermination of other actual forms and types, the influence of the environment cannot be ignored.

CHAPTER IV

ADAPTATION AND NATURAL SELECTION

IN the vast majority of their characters all organisms are adapted to live in the environment in which they find themselves The alternative to not being sufficiently adapted is not to live. This is a trite statement of fact It confers on adaptation a meaning that implies no more than a close correlation between structure and mode of life Birds have wings, and fly. Razor-shells have tubular siphons, and eat food-fragments carried by the channelled water-currents. Sturgeons are toothless, and grub in mud Fishes have gills, and breathe in water Heart-urchins have slender, hair-like spines, and burrow. Geese have webbed feet, and swim.

The organism's ability to function is clearly dependent on the availability of a suitable environment: a fish out of water or a man in it soon dies. The adaptation is always more or less specific and contingent, and is the expression of a relation. The closer the adaptation to a given environment, the more the organism is "specialized," the more narrowly defined is the relation If the relation is rigid (as when the giant panda must have bamboo-shoots, the koala eucalyptus-leaves, or starve), the adaptation may be so delicately balanced that survival is likely to be precarious and short.

In a great many cases the cruder sorts of adaptation are obvious, especially the mechanical devices for locomotion and feeding. Thus the horse has the slender build of the fast long-distance runner, not only in the general form of its hooved long legs and streamlined over long periods, and the same result is achieved by greatly elongated roots which may descend scores of feet to reach deep-seated water. The sharp ribs and spines on the shell of the piddock are instruments useful in filing away soft rock as the mollusc bores the hole in which it lives The "line-and-bait," sometimes luminescent, on the head of the angler-fish is an effective device for enticing prey. The most spectacular of such adaptations are perhaps illustrated in the phenomena of mimicry—not only the warning likenesses between one animal and another (harmless fly and stinging wasp, palatable and inedible butterfly), but also protective and aggressive likenesses between organism and background (stick-insect and leaf-insect resembling twig-structures for defence, spiders simulating oak-galls for attack)

Rather less obvious than large modifications of structure are adaptations most clearly expressed in functional and physiological behaviour The desert-inhabiting camel stores food temporarily in its hump. The lung-fish, living in streams which may periodically dry up, secretes a protective gelatinous cover to reduce body-evaporation to a minimum when it buries itself in the mud. Lactation-intervals in the grassland horse, constantly on the move, are short, but in the relatively sedentary ruminant cow, naturally inhabiting mixed woodland, they are long The ability to shed part of the body, as when a crab sheds its claw or a lizard its tail, allows escape from danger Colour-patterns, warning in the wasp and coral-snake, cryptic in the leopard and arctic fox and plaice, illustrate certain kinds of mimicry

The general occurrence of adaptation, in the sense of this correlation between certain characters of the organism and the environment in which it lives, has misled some biologists into supposing that all structural contour, but also in the details of muscular attachment and bone-joint in almost every part of its skeleton It expects to escape from enemies by never being caught, and in open grassland (its natural home) its expectations are mostly justified As a prairie herbivore it has a long battery of deep-crowned grinding cheek-teeth of intricate structure, admirably suited to the mastication of harsh grasses

In contrast, such a large carnivore as the lion, which preys upon the horse and other fast runners, must be powerfully built for attack its body is consequently relatively well-knit, massive, and muscular, with short legs and clawed toes, and it cannot maintain the speed of its prey for any length of time it thus compensates in agility for loss of fleetness, and achieves its ends by surprise Its food, being flesh, requires little mastication, and its teeth are short-crowned and relatively simple in structure, but with elongated stabbing canines and shearing back teeth

Among fishes " normal " forms like cod and mackerel are almost continual swimmers, with torpedo-shaped bodies and small, sharply pointed teeth for hunting prey They differ markedly from such bottom-dwellers as skates and rays—forms swimming by horizontal undulations of the laterally expanded flat body and feeding mostly on shellfish by means of teeth arranged in a mosaic pavement to function as crushing mills Significantly, the secondarily aquatic mammals like the porpoises and dolphins, and reptiles like the extinct fish-lizards, bear close structural and mechanical analogies to predator-fishes like the cod

Such adaptations of structure are so common and widespread among animals and plants that they need only be indicated to be recognized The swollen leaves and stems of many desert plants enable them to store water over long periods, and the same result is achieved by greatly elongated roots which may descend scores of feet to reach deep-seated water. The sharp ribs and spines on the shell of the piddock are instruments useful in filing away soft rock as the mollusc bores the hole in which it lives. The "line-and-bait," sometimes luminescent, on the head of the angler-fish is an effective device for enticing prey. The most spectacular of such adaptations are perhaps illustrated in the phenomena of mimicry—not only the warning likenesses between one animal and another (harmless fly and stinging wasp, palatable and inedible butterfly), but also protective and aggressive likenesses between organism and background (stick-insect and leaf-insect resembling twig-structures for defence, spiders simulating oak-galls for attack)

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The general occurrence of adaptation, in the sense of this correlation between certain characters of the organism and the environment in which it lives, has misled some biologists into supposing that all structural elements and functional responses must necessarily be adaptive, and much effort has been expended in attempts to prove the usefulness of sundry organic features Some of the explanations given have been so unconvincing that other workers have repudiated the universality of adaptation, and have quoted instances seemingly opposed to its occurrence These include the fantastic ornament seen in some mollusc shells, the enormous antlers of the (now extinct) Irish elk, the grotesque bony outgrowths of some of the dinosaurs, the incoiled cheek-penetrating canine teeth of the hog *Barbirusa*, the helmet and beak of the hornbill

In less bizarre organisms it is clear that many characters and habits are without directly recognizable adaptive value This is notably so with vestigial and rudimentary organs which, on an evolutionary interpretation of their significance, are relics of ancestral conditions no longer persisting It is difficult to imagine any appropriate use for the wings of the kiwi, or the minute hidden hind limbs in whales, or the splint-bone toe-relics of the horse, or the teeth of the infantile duck-billed platypus Some of these vestiges are not merely useless, but may be positively disadvantageous or harmful, like the human appendix and wisdom-teeth, and all of them divert energy of growth Some vestigial structures may be converted to uses other than their original ones, but such secondary adaptation is no explanation of essential structural form human toes, relics of grasping organs, make poor balancers, and as a paddle the penguin-wing is contrived with unnecessary elaboration

In any event, structural and functional adaptation can rarely if ever be specific and precise, but must generally be a compromise. The environment occupied by the members of any given species is not absolutely uniform over the whole range of the species, and individuals must be resilient enough to accommodate themselves to more or less marked departures from optimum conditions Indeed, except perhaps in the almost unvarying conditions of the very deep sea, the organism must expect to meet day-to-day and season-to-season changes in environmental circumstances, and may need to make relatively large-scale adjustment to the changes

The seasonal effects upon many birds, upon mammals like the reindeer and the bison, upon fishes like the salmon, evoke the response of migration Some animals meet unfavourable environmental conditions by becoming torpid during cold winters or hot dry summers Seasonal cycles also involve changes in food-supply, and resident temperate birds eat seeds in summer, berries in winter, caribou eat shoots, leaves, and grasses in summer, lichens and mosses in winter, many carnivores supplement flesh by vegetable foods during periods of dearth—some of them, like bears and men, becoming more or less undiscriminating and omnivorous Seasonal change of appearance, as in a loss of winter wool by the sheep, in the coloration of the stoat and the arctic fox, and in the conspicuous courting feathers of many birds, is a further instance of the same systematic controls The yearly cycle among flowering plants in temperate lands is an outstanding example of seasonal effects

A comparable lack of environmental uniformity is experienced by all organisms as they grow from infancy to maturity Thus adaptations of the fœtus in mammals, of swimming larval stages in crabs and lobsters, of caterpillars of moths and butterflies, are useless in the adults, and are partly discarded as maturity is reached In most groups there is often significant (though usually not large-scale) migration from one environment to another at various stages of growth.

Influenced by these complex variables, the individual cannot be closely and comprehensively adapted throughout its life to any single static environment, but must exhibit a generalized over-all response to the fluctuations of events, and must be prepared (if it is to survive) to accommodate itself to the conflicting or successive demands of the different and changeful elements in its total environment Some of its structures and potential functions are at times dormant, and may become obsolete and cease to have adaptive significance if the environment should suffer continuing change—as in fact geological evidence shows all environments to have done

Adaptation is thus not a simple conception, and is not always revealed by inspection Since it reflects a balanced relationship between organism and environment, an empirical measure of its occurrence and its effectiveness is given not by equating single characters or functions with specific uses, but by the success with which members of a species manage to overcome the disabilities of existence The proof of that success can only be in terms of the survival of a sufficient number of individuals to reproductive maturity, and thus of a maintenance of the numerical size of the species from generation to generation If numbers are maintained or increase, the species is well adapted, if they diminish, ill adapted An objective definition of adaptation is thus a reflection of this relationship between organism and environment what is adapted is what survives

The physical environment is indifferent to organic survival, and is not itself adapted to the organism The best it can do for the adapted form is not to change In fact it always changes If the changes are too rapid or too radical, as during the onset of an ice age, adaptation cannot keep pace, and widespread extinction follows This happened in the northern hemisphere in the relatively recent geological past, when a great many kinds of organisms were either killed off or were restricted in their geographical range When the changes are long-term, the more fortunate animals and plants may survive if in successive generations they make appropriate adjustments of structure and function—that is, if they evolve along the right lines The environment therefore is always hostile in more or less degree to the individual organism or species, and there is a never-ending struggle for survival in the teeth of this hostility.

To the single species, however, the environment is not simply represented by climate and geography It also includes all the other species of organisms with which there might be contact. Indeed, the mouse sees the hostility of the cat or the hawk more immediately than the constraints of weather or food-supply Competition between species includes not only the obvious interdependence of prey and predator (so that the fast zebra escapes the lion, the agile lion captures the zebra), but the much more devious chain of food-relations involving both plants and animals, fluctuations in any link of which immediately affect the survival of all the other links. It also includes the direct competition between species for the supply of a limited good, as of birds for territory or for much the same food. Any adaptive advantage then confers a transitory survival-value on the species possessing it, and in succeeding generations there arise corresponding changes in the balance of species-populations.

Finally, within the single species (including such slow-growing species as elephants) the reproduction-rate is enormous, far more individuals being born than can possibly survive. Thus the individual oyster may lay six to nine million eggs, the ling twenty to thirty million eggs, at a single spawning. A high reproduction-rate is an adaptive insurance for the species, but if the adaptation is too successful, if too many individuals survive, the end is defeated, and the survivors overstock their province to the point of starvation To restore equilibrium a great number must necessarily be killed off before maturity, and then take no part in evolution

Many of the premature deaths are no doubt "accidental" and random, but those individuals which survive continue to be subjected to competition with their fellows This may well be more intense than the competition between species, since all of the one kind are concerned to get the same good things (especially food, but also shelter and mates) The direct interspecific struggle may be virtually non-existent for the single island species like the dodo of Mauritius (before man appeared), and among some of the larger mammals, like the elephant, polar bear, tiger, it may be negligible, except in infancy But competition within the species is universal it may even penetrate the uniform protective environment of the mammalian womb, where the faster-growing fœtus may out-race and obliterate its weaker sib or twin.

Compounded of physical and organic factors, the struggle for survival is thus an extremely complex process, not readily resolved Its results are net results, success in the struggle being judged solely by the fact of survival to maturity Except in very small populations in which chance and random effects may achieve a special significance, there is a probability that the struggle will give some net relative advantage to those species or individual variants which on the whole are better adapted to the environment than their neighbours (This probability, being no more than a probability, an average expectation, does not necessarily ensure the survival of any single individual however well adapted it may be Survival-value attaches only to samples in bulk, and as between different varieties and species it is measured by the relative proportions of those which do in fact survive) In the result, there is a differential selection of kinds of organisms, and a consequent endlessly changing balance of numbers with advancing time.

This was the fundamental theoretical inference made by Darwin in his explanation of the evolutionary process —an inference confirmed by all subsequent work. No matter how evolution proceeds, natural selection is an operative factor that cannot be neglected. In its mechanism it is a passive filter, though in its results it has a more constructive role It eliminates the " unfit," those organisms insufficiently adapted, and then shows a preferred bias towards those surviving But it cannot induce structural novelties for future selection, and thus cannot initiate evolutionary lines.

In any species the novelties arise only when mutation occurs, and sustained evolution is the cumulative product of a succession of mutations expressed in a selectively preferred series of mutants Most mutations are harmful or lethal (which is to say that they find the environment discouraging) But when the advantageously adapted mutant arises and stands a better chance of selection and reproduction than its fellows, it gradually permeates the species, replacing the " old " type at a rate depending on its proportionate superiority and the periodicity of its occurrence (provided the size of the population in which it occurs is large enough to allow the laws of probability to apply)

This picture of the action of natural selection on mutations, however, needs to be filled out by reference to the real conditions in large populations. A mutation is usually change in a single gene Each individual gene-association contains thousands of genes, every one of which may (presumably) undergo mutation. The number of genes in the germ-cells of a whole population may amount to billions Many mutations occurring in a great number of genes thus certainly happen in every generation, even though mutation-rate may be low Each mutation is not solely a change in a solitary gene it influences and is itself influenced by the whole gene-complex in which it occurs Free interbreeding between the members of a large population ensures endless change in the combinations and proportions of genetic factors in successive generations A single community is consequently made up of a great variety of individual types, differing in slight and often subtle ways from one another, and meeting not precisely the same circumstances throughout all their lives

Natural selection is thus not offered in any one species a simple clean-cut choice between the " fit " and the " unfit," but must discriminate (in large populations) between a host of variants displaying mixed phenotypy through the interaction of a great number of genes and their mutations Its results are expressed in the changing proportions of mutants in successive populations In so far as selection determines the frequencies with which different mutants survive, it limits the random distribution of genes through a population, and so gives a preferred direction to the line of succession. In this sense it may be looked upon as an active participant in the evolutionary process—indeed, as the agent which decrees the course of evolution once the mutant types are provided

The results of systematic selection are statistical, and ensue only if the process operates in a sufficiently large breeding population (For instance, one of the effects of changing the social environment during the past hundred years has been to increase the average expectation of life in Britain from about forty-seven to rather more than sixty years. This, of course, is a statement true only for a large enough sample of the population: it does not follow that a score of men may not by chance all die before reaching thirty, or all live to be eighty) The more intense the pressure of natural selection, the smaller is the minimum size of population-sample in which its effects are significant and systematic, since the less is the environmental tolerance of variants departing widely from the mean

There are a few species which exist in very small numbers (for instance, the Chatham Island robin in twenty to forty pairs, the lizard *Lacerta simoni* in perhaps sixty to eighty individuals on a rock 100 yards square in the Canary Islands, the primrose *Œnothera organensis* in perhaps 500 plants in a few valleys in New Mexico), and in them selection may not be systematic, and random evolutionary " drift " may occur But the populations of most kinds of organisms are very much larger than the minimum for effective selection and directed evolution, which may then be looked upon as the normal process.

CHAPTER V

EVOLUTION IN TIME THE FOSSIL RECORD

GENETICS is an essential part of evolutionary theory the analysis of the mechanism of heredity is foundational to a proper understanding of the material with which evolution works But the few brief generations of banana-flies and guinea-pigs and garden-peas that have been studied during the past half-century have disclosed no great evolutionary advances the amount of genetical divergence as yet obtained by artificial selection and cross-breeding lies wholly within the confines of the single species, and is merely an indication, not a demonstration, of what may be inferred to have happened over many thousands of years Evolution involves a prolonged time-sequence of forms Geology provides such a sequence covering hundreds of millions of years during which organisms now fossil were continuously evolving It thus sets in true perspective the results of genetical study

Fossils, on the other hand, are dead, and although under very exceptional conditions of preservation they reveal intimate cell structures—chromosomes are said to have been identified in the cell-nuclei of some early-Tertiary[1] fossil plants—they are not amenable to laboratory experiment on growth and development, and virtually nothing is directly known of their genetic relations In compensation they provide a great number of instances of lines of evolution in which the change in structure is not merely within the single species or from

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[1] A table of the geological eras and formations is given on page 120

species to species, but covers an extended range from genus to genus, family to family, even order to order, and occasionally class to class For instance, the transition from goniatites to ammonites, from fishes to amphibians, from reptiles to mammals, is known in fair detail Fossils thus provide evidence of the course of evolution. Genetics provides evidence on how it is to be interpreted.

The details of the evolutionary succession, however, are fragmentary. It is usually impossible for organisms lacking a hard and durable skeleton to be preserved as fossils. Except as occasional impressions in very fine-grained mud, whole orders of invertebrate animals are thus missing from the fossil record—for instance, amœboid unicellular animals, sea-anemones, jelly-fishes, worms Most plants also perish before fossilization is possible, and only when they are buried under the relatively exceptional airless conditions of peat-formation are they found abundantly in the rocks. Thus few plant-remains of any kind have been discovered in the oldest fossiliferous rocks, though clearly an abundance of trilobites, molluscs, and other marine animals in the same rocks implies a corresponding abundance of plant-food at the time of rock-formation.

A lack of skeletal hard parts may supply a reason why no evidence has yet been discovered of the origin of the major groups of animals and plants. The fossil representatives of each group are already fully differentiated when they first appear in the record, and the implication is that they must have had a long antecedent history. On the other hand, the negative evidence of absence has been taken by some Mendelians to indicate a major break in evolutionary continuity, and they have postulated the occurrence of " large " mutations to explain the leaps from forms without to forms with a skeleton

Discontinuity in the evolutionary succession may also

CHAPTER V

EVOLUTION IN TIME THE FOSSIL RECORD

GENETICS is an essential part of evolutionary theory the analysis of the mechanism of heredity is foundational to a proper understanding of the material with which evolution works But the few brief generations of banana-flies and guinea-pigs and garden-peas that have been studied during the past half-century have disclosed no great evolutionary advances the amount of genetical divergence as yet obtained by artificial selection and cross-breeding lies wholly within the confines of the single species, and is merely an indication, not a demonstration, of what may be inferred to have happened over many thousands of years Evolution involves a prolonged time-sequence of forms Geology provides such a sequence covering hundreds of millions of years during which organisms now fossil were continuously evolving It thus sets in true perspective the results of genetical study

Fossils, on the other hand, are dead, and although under very exceptional conditions of preservation they reveal intimate cell structures—chromosomes are said to have been identified in the cell-nuclei of some early-Tertiary [1] fossil plants—they are not amenable to laboratory experiment on growth and development, and virtually nothing is directly known of their genetic relations In compensation they provide a great number of instances of lines of evolution in which the change in structure is not merely within the single species or from

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[1] A table of the geological eras and formations is given on page 120

species to species, but covers an extended range from genus to genus, family to family, even order to order, and occasionally class to class. For instance, the transition from goniatites to ammonites, from fishes to amphibians, from reptiles to mammals, is known in fair detail. Fossils thus provide evidence of the course of evolution. Genetics provides evidence on how it is to be interpreted.

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Discontinuity in the evolutionary succession ma than the younger geologically recent evolutionary series are consequently more amply documented than geologically ancient Since plants are fossilized in abundance only when they are protected from complete decay on death, they are preserved most often under the conditions of peat-formation ancient peats are not widely represented in the geological record, except in the group of strata known as the Coal Measures it therefore happens that fossil plants of Carboniferous age are on the whole more completely known than any before or since The western part of North America was an area of accumulation of widespread lake and river deposits during the Tertiary era (the last sixty million years or so) the evolution of mammals is consequently far better known (as yet) from the fossils of that continent than of any other part of the world

Nevertheless, the incompleteness and bias in the fossil record are daily being reduced, and the course of evolution is now broadly known for most groups of animals and for a number of groups of plants In some well preserved fossil series the stages of successive change are minutely revealed in an abundance of material, and allow thorough analysis of the mode of evolution Indeed, what can at present be said with conviction on the long-term evolution of organic groups higher than the species is almost entirely based on the evidence provided by such series

A very few fossil types appear to have survived almost unchanged for several hundred million years the present-day lamp-shell *Lingula* is very like specimens of the genus found in rocks of Ordovician age (Fig 5), and typical oysters differing only trivially in shell-form from those living today are found fossil in rocks deposited 180 million years ago In most cases, however, successive generations of fossils constituting an evolutionary sequence show marked changes in form as they ascend the time-scale. For instance, the molluscan group to which the living pearly nautilus and its kin belong is a long-lived one, members of which are known from the earliest fossiliferous rocks During the Lower Palæozoic era, some 500 to 300 million years ago, it was typically represented by conical shells more or less loosely coiled into a plane spiral with internal partitions of gently concave form dividing the shell into chambers In the succeeding Upper Palæozoic era, some 300 to 200 million years ago, the typical members of the group were the goniatites, tightly coiled forms with sharply corrugated internal partitions They were succeeded in Mesozoic times, 200 to 60 million years ago, by the ammonites, which became so abundant that the era is sometimes known as the Age of Ammonites Still more elaborate than the goniatites, ammonites have a shell with ornament of ribs, nodes, and tubercles, and with complexly frilled and contorted internal partitions (Fig 3)

A very different group of animals—the graptolites—is now wholly extinct, indeed it did not survive Palæozoic times; but it illustrates comparable changes in form The group was colonial, each individual living in a small skeletal cup connected with neighbouring cups arranged in linear rows. The earliest colonies consisted of a large number of branches radiating from the initial parental individual, with a single row of simple conical cups extending along each branch. In later forms there was progressive simplification of the branching, but progressive elaboration of cup-form. The number of branches was reduced first to eight and four, and then to two, and finally to one (though there were some digressions from the line of simple reduction). In evolution the cups in some forms became square-cut, in others hooked, in others bell-shaped, in yet others elongate and tubular, there being a number of divergent lines of evolution in cup-shape which can be followed in some detail from forms with simple to forms with complex cups Over much of the record the time-sequence is very closely reflected in the fossil succession, so that the several evolutionary stages can be used for very precise dating of the rocks in which they are found (Fig 5)

A third group of animals—the sea-urchins—is nearly as long-lived as the molluscs. The earliest representatives are known from Ordovician rocks, and members of the group still exist in large numbers They possess a more or less globular skeleton, consisting of very many plates fitted together in a mosaic In modern forms the mosaic has a high degree of symmetry, with the plates arranged on a radial five-rayed plan, but the symmetry was imperfect in Palæozoic times, which may be considered a period when the group was slowly acquiring its most successful basic form In later eras, particularly during the Mesozoic, stages in progressive adaptation to different environments are clearly shown in the fossil succession Those sea-urchins which, like the present-day edible urchin, continued to live on the rocky sea-floor retained the radial symmetry and the large predatory jaws of their ancestors, and developed a great variety of long thick protective spines But those entering as sand- and mud-burrowers the novel environment of the soft sea-floor evolved by losing the radial symmetry as front end became differentiated from hind their skeletal plates became thin and delicate, and their spines hair-like, and they exchanged a predatory for a mud-eating habit, with a consequent loss of jaws. The stages of the passage from a sub-globular shape to a heart-shape are well preserved in the rocks of the Jurassic and Cretaceous formations, species showing various degrees of loss of radial symmetry and of jaw-

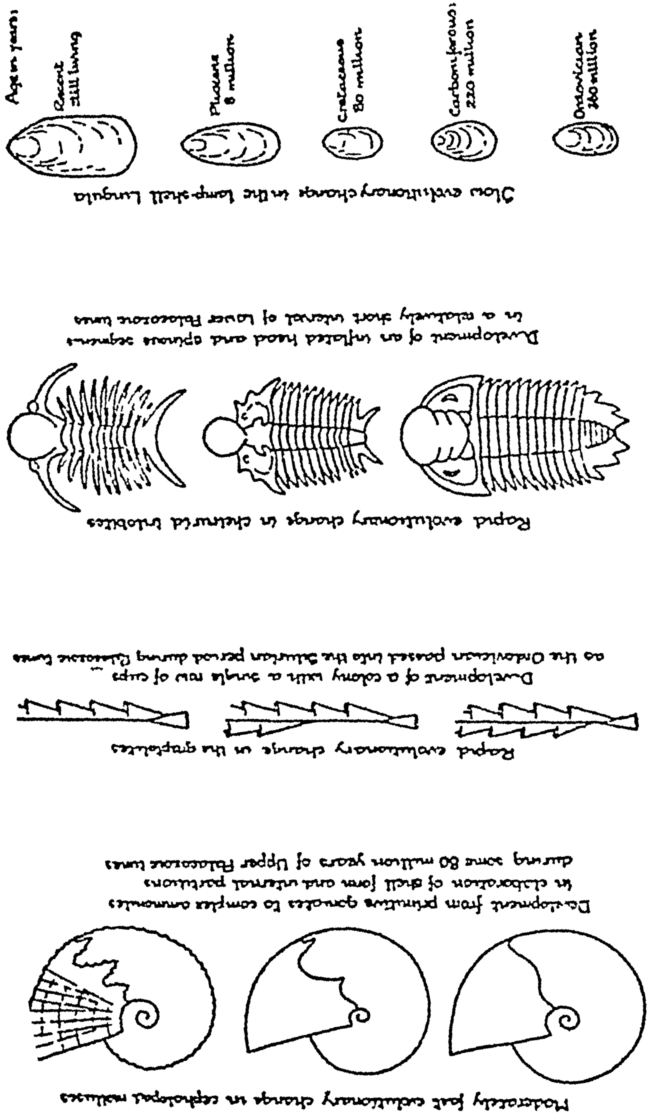

FIG. 3 —Examples of evolutionary change as revealed by fossils

structure forming connecting links between the ancestral regular and the descendant irregular forms

Among the plants, evolutionary details are not so fully known, but the primitive land-forms of the Old Red Sandstone show a progression in structure from leafless and rootless types to the large arborescent " tree-mosses " which reached their maximum development in the succeeding Carboniferous period The conifers appear to have arisen in late Carboniferous times, possibly from forms already present in the Old Red Sandstone Most Palæozoic and Mesozoic plants had naked seeds, but the Caytoniales (a small group of Jurassic forms in other respects gymnospermous and thus comparable with the conifers) possessed seeds enclosed in seed-cases they may thus represent a link with the most advanced plant group, the angiosperms or flowering plants The Tertiary era was marked by great advances in the angiosperms, particularly important to animal economy being the spread of the grasses which allowed a vast number of Tertiary herbivorous mammals to evolve and flourish

These examples of evolutionary development are not always readily related to environmental controls, partly because the skeletal adaptations and exact modes of life of fossil forms are not always determinable, partly because the full environmental context of fossil species is largely unknown Nevertheless, there is strong indirect evidence that secular geological changes are a powerful influence on the mode of evolution, and at least one major event in Earth-history of violent environmental change appears to have had immediate and drastic consequences on plant and animal life, and to have been a cause both of widespread extinction of previously " successful " " old " types and of great evolutionary stimulus to " new "

This occurred in the interval of transition between Palæozoic and Mesozoic times, when there was locally intense mountain-building, accompanied by radical changes in land-and-sea relationships. The geographical revolution was paralleled by great climatic oscillations: widespread desert and semi-desert conditions are represented in the contemporaneous strata by red beds, and glacial conditions by morainic boulder-beds The geographical revolution appears to have been worldwide, and inevitably to have had profound effects on organic life

Most groups flourishing in numbers and kinds during the Palæozoic era suffered great diminution, some being completely exterminated, and the renewed evolutionary expansion of the surviving groups during the Mesozoic occurred from nuclear stocks which in many cases had occupied insignificant positions in Palæozoic times. This crisis in evolutionary history is notably expressed in the fossil remains of trilobites, corals, sea-urchins and their kin, molluscs, lamp-shells, and sea-mats among the commoner kinds of invertebrate animals, and among the vertebrates it marks the change from the Upper Palæozoic Age of Amphibians to the Mesozoic Age of Reptiles—only two insignificant amphibian groups (frogs and newts) surviving to later times in appreciable numbers Among the plants there was a great decline in the dominant group of the seed-bearing fern-like pteridosperms, and a replacement of them by cycads and primitive conifers It is a fair interpretation that the material conditions of the environment were mainly responsible during the period for the profound evolutionary effects

Adaptation in the vertebrates is more readily ascertained from anatomical structure than in the invertebrates. Thus the rise of land animals, involving the hind paddles that could have achieved only slow speeds The fish-lizards (ichthyosaurs), on the other hand, evolved a fully developed fish form, with degenerate hind limbs, fin-like fore limbs (*see* Fig 1, page 13), and an expanded fleshy tail for sculling presumably they were open-sea, fast-swimming creatures like the present-day dolphins and porpoises

Opportunity for this evolutionary activity and wide dispersion seems to have come with the great geographical changes that took place at the end of Palæozoic times, when the reptiles found themselves with what were virtually uninhabited continents awaiting their occupation They entered most of the major adaptive niches available to them, though there is no indication in their tooth-structure that they were ever at home in grassland country

Mammal-like reptiles appeared at the end of Palæozoic times, and occasional fossils of small, marsupial-like mammals are found in the Mesozoic rocks But the reptiles remained the dominant land animals throughout Mesozoic times (that is, for some 120 million years), and under such dominance the mammals could make little evolutionary advance At the end of that era, however, most of the major families of reptiles died out, and those which persisted were greatly reduced in numbers

During the Tertiary era their place was taken by the mammals, which show improvements on reptilian structure notably in the size of brain, the mechanics of limb-formation, and the specialization of the teeth, but in broad outline they paralleled the reptiles in their adaptation to the different environments open to their occupation The whales and the dolphins are the aquatic counterparts of the fish-lizards, and display a similar atrophy of the hind limbs, encasement of the muchshortened flipper-like fore limbs in leathery skin, and expanded fleshy tail The bats (which, however, truly fly) simulate the pterodactyls in wing-form, though there are differences in strut-construction, all four fingers in the bats participating in support of the skin-fold. The rhinoceroses closely reflect the horned dinosaurs in general build, and the kangaroos have a heavy balancing tail like that of many of the bipedal dinosaurs. The parallelism is, of course, not precise, and there are no mammalian equivalents of the brontosaurs or the tyrannosaurs or the birds, and no reptilian equivalents of the horses or the cats or the primates But the broad fact of adaptive radiation is recurrent in the two vertebrate classes, and in similar environments similar forms were evolved

During Tertiary times the distribution of continents and oceans was in fundamental plan much as it is today. The Old World formed a self-contained unit more or less freely open to mammalian migration It was, however, not completely severed from North America, and there was for most of the era a wide land-bridge in the region of the Behring Straits which allowed a common range to such Old-World and New-World forms as horses, elephants, oxen, camels, deer, cats, wolves, and bears Australia, on the other hand, seems to have been isolated by a sea barrier from at least the end of Mesozoic days, and South America was only intermittently connected with North America by the narrow land-bridge of the Panama isthmus Thus three continental regions became more or less independent centres of mammalian evolutionary radiation. The marsupials of Australia are the most exceptional, but strange kinds of animals are also common (and formerly, as fossils reveal, were even more common) in South America The differences between the three regions strongly imply if they do not prove that evolution is dependent on local circumstances for the course it follows

At the same time, there are close adaptive similarities between the forms from the three major regions which are even more revealing in the light they throw on evolutionary processes In North America and the Old World the placental mammals display a broad dichotomy in descent from their late-Mesozoic ancestors carnivorous forms with powerful stabbing and shearing teeth are distinguished from herbivorous forms with cutting and grinding teeth In subsidiary detail, the carnivores show evolutionary branching into dog-like and bear-like forms, cat-like forms, stoat-like forms, whose general modes of life differ in more or less degree It is highly significant that in the absence of competition with placental mammals, one line of Australian marsupial evolution led to the thylacine (the Tasmanian wolf), which is almost the precise equivalent of the dogs, and another to the koala, which is almost the precise equivalent of the true bears, while during mid-Tertiary times in South America marsupial equivalents of the stoat family were not uncommon

Similarly, the placental herbivores (most of which are hooved) show considerable evolutionary differentiation into a great number of groups in the Old World and North America, while forms having no near relationship were evolving indigenously in Australia and South America along subparallel lines to give end-forms displaying astonishing similarities to the placental mammals in general outward build Notably, in South America some of the extinct litopterns in their three-toed and one-toed limbs were closely like the true horses to the north (*see* Fig 5, page 73), the macrauchenids were three-toed dry-grassland creatures like the two-toed camels in build, the toxodonts were massive and rhinoceros-like, and the astrapotheres had long incisor-tusks and a short trunk, giving them an appearance like that of primitive elephants

Such parallel series in independently evolving and isolated groups of mammals provide convincing evidence of the control of environmental selection on lines of evolutionary development . in similar circumstances similar forms are evolved At the same time, too sweeping conclusions should not be drawn from the similarities, for the parallelism is always inexact in detail, and the precise plan of evolutionary change is not repeated in the separate groups The adaptive response of the organisms must therefore be referred to the selection of mutants (and so of gene-associations) which were randomly different in the different areas, and not to anticipatory pre-adaptation in the various stocks

CHAPTER VI

FOSSIL SERIES

THE general sequence of fossils in the sedimentary rocks provides an outline picture of the course of evolution that is effective proof of the reality of the process The interpretation of the changes in time, particularly as they are displayed by the vertebrates, is one which ascribes a central place to the role of adaptation in promoting evolution The sequence, however, is a general one, and gives no indication of evolutionary mode, evidence of which is mainly provided by short segments of fossil series which happen to be unusually complete and well preserved

A sufficiently large collection of fossils of any one organic group may usually be arranged in series showing progressive grading in structure. But such grading is in itself no direct evidence of evolution, still less is it an indication of the mode of evolution, unless the graded series consists of forms arranged in true time-sequence and can reasonably be supposed to be made up of members related in hereditary succession. The conditions of formation and preservation of sedimentary rocks and the circumstances of organic migration usually preclude the discovery of such series, and they are in fact uncommon, but those which have been examined in sufficient detail are consistent in the conclusions they suggest, and they may be regarded as acceptable samples of the mode of evolution

The Chalk of southern England happens to be a deposit singularly uniform in lithological character, the uniformity presumably indicating a general sameness of conditions persisting during the time of its formation. It is about 1000 feet thick, and took perhaps 20 million years to accumulate. It contains fossils of certain organic groups, notably the sea-urchin *Micraster*, which found the Chalk environment congenial throughout the period of sedimentation, and are represented fairly abundantly at many levels in the sequence of strata It thus provides materials for the establishment of detailed evolutionary series Systematic collection from successive layers yields specimens, the earliest at the base, the latest at the top, which are in true time-sequence and thus represent successive generations If they are sufficiently like in structure to be regarded as belonging to a single group, they may be presumed to fall on a line of evolution and to represent a true racial or phylogenetic sequence, a lineage.

The work of collection was carried out by Rowe at the end of last century, when he showed that a series of micrasters arranged in true time-order provided a chain of what Darwin called " intermediate links " displaying complete gradation between the earliest and the latest members. There is a notable difference in shape, in ornament, in position of the mouth, in proportions, between the end-forms, and the difference (which is comparable with that occurring between some living species of sea-urchins) is usually considered to justify their being placed in different species. But the connecting series between them can be graded to any desired degree of fineness : the slightest recognizable differences between two specimens (collected perhaps only inches apart) may be bridged by the finding of an intermediate form adding another link The transition from link to link may thus be rendered so perfect that neighbouring transients are virtually indistinguishable Though the end-forms may thus belong to different species, at no point in the stratal sequence is it possible to demarcate one species from the other, referring all forms below a given level to the earlier species, and all above to the later

There is consequently nothing intrinsically natural about the recognition and naming of species in this evolutionary line On the contrary, natural divisions are wholly lacking, and the continuity of the merging transient members of the evolutionary series is complete. The transformation of "species" in time takes place without the faintest suggestion of interspecific breaks at any stage in the process, and a species in such a fossil sequence can thus only be arbitrarily defined, having no real entity

The same essential relations are displayed by numbers of other and unrelated fossil series—bivalved molluscs, snails, corals, lamp-shells Lineages of this sort, preserved in varying degrees of completeness, are probably of general occurrence at least among most groups of animals They reveal, however, only part of the course of evolution, since they are linear and successional A great number of phylogenetic lines, on the other hand, become forked and give rise to divergent off-shoots having only collateral relationship, and representation of the evolutionary connections takes the form of the customary branching tree

Among the spire-bearing lamp-shells of the Carboniferous rocks, for example, is a series (belonging to the genus *Reticularia*) showing progressive elaboration of shell-form. The most primitive members are subcircular in outline, with unfolded margins where the two valves of the shell meet More advanced members tend to become proportionately broader and to develop plications along the shell margin What may be regarded as the main line of evolution consists of forms which combine both features in the line of progress, and culminate in very broad, highly plicate forms From this main line two others diverge. One side-branch consists of forms which become very broad while remaining feebly plicate, the other side-branch of forms which become strongly plicate, while remaining narrow The evolutionary divergence is therefore not one of sharp qualitative contrast—the three branches all possess the same essential characters—but only one of relative degree of development in the different characters (Fig 4)

Divergent evolution by the forking of lineages is almost universal. Where the evidence is reasonably adequate, the transition in branching series appears to be as perfect as in the micrasters, and there is never any positive evidence of discontinuity The branching is therefore an expression of differential and independent rates of evolutionary change in individual structural characters There is no direct evidence of the influence of genetic controls on the process of divergence, but the phenotypic contrasts between the divergent forms must presumably rest in genotypic differences resulting from mutation. The mutant genes causing the differences then appear to operate by changing the relative rates of growth of different parts of the body.

Such an interpretation is in accord with what is known to have taken place in mammalian evolution during Tertiary times The adaptive radiation which characterized almost all the groups of mammals is one in which divergent branches arising in a number of central stocks differ mainly in degree of character expression, according to the nature of the environmental niches to which they became adapted. All the members of the elephant family, for example, display evolution by an increase in the length of the snout to form a trunk and of the incisor teeth to form tusks, and by elaboration of the

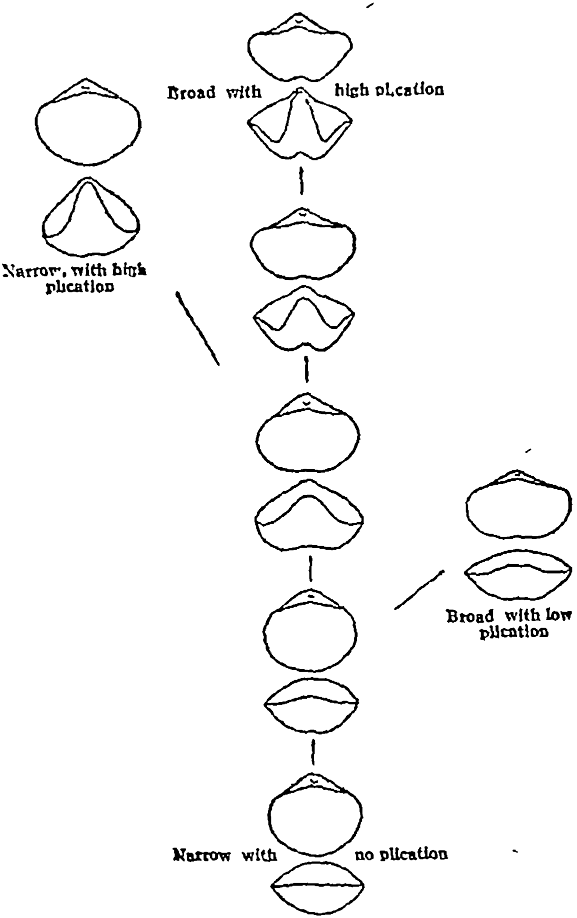

FIG 4—Divergent evolution in *Reticularia* The central series illustrates the main line of evolution. The off-shoot on the right displays an increase in the growth-rate of breadth, the off-shoot on the left increase in the growth-rate of the marginal plication, as compared with the main line

cheek-teeth for mastication. The adaptations are partly related to the assumption in early Tertiary times of a forest-dwelling habit by the ancestral elephants, the trunk being used for tearing vegetable food and carrying it to the mouth, the tusks for digging A forest diet is fairly succulent, and the cheek-teeth in such an environment remain relatively simple, with only a few cross-ridges on the grinding surface. The mastodons, which became extinct only in geologically recent days, continued to inhabit forests, and so to retain the relatively primitive molar tooth-form. The elephants proper, however, diverged in late Tertiary times by migrating into bush and savannah country, there partly to become grazers, and their molar teeth developed a complex grinding surface of a great number of deeply infolded cross-ridges. Thus while there is no fundamental structural difference between the two groups (the elephants proper indeed having had mastodon-like ancestors), the divergence is partly expressed in differential development of tooth-elements

An illuminating instance of branching evolution is provided by the primitive horses, of which several divergent lines are known It is a commonplace that during Tertiary times the horses evolved by a progressive reduction in the number of functional toes and by elaboration of the structure of the teeth In part this followed from an adaptive change in mode of life, a grassland environment demanding powers of fast locomotion and strong mastication. Some horses remained forest or woodland dwellers until a late date in the Tertiary era, however, and as three-toed browsers they were contemporaneous with the one-toed grazers. The browsers thus remained "primitive" in the pattern of their foot-structure and their molar teeth, and in at least one branch there persisted throughout the evolutionary series an almost static relationship between the growth-rates of the several bones of the foot and of some of the tooth-cusps From this series, however, there diverged at an early Tertiary date a branch leading towards grazing forms (including the modern horses), in which divergence is marked less by anatomical contrast in foot-structure and tooth-pattern (though that is achieved in the end-forms) than by a change in the relative growth-rates of the several bones and tooth-cusps The change of growth-rates was abrupt (without, however, breaking the perfect grading of the series of structural changes), and implies the occurrence of environmentally selected Mendelian mutants (Fig 5)

A line of evolution, a lineage, may be conveniently apprehended and partly analysed by supposing it to consist of a series of intergrading transients showing continuous change of structure with time. But this is an idealized simplification of the true relations between successive generations An individual transient, a single " intermediate link," is almost never wholly representative of the community of which it is a member, since it is in the highest degree improbable that any community, however narrowly localized, should consist of a number of individuals either phenotypically or genotypically identical In fact, fossil communities display the same kinds of contemporaneous variation as living (compare Fig 2, page 34), and the nature of the lineage is obscured by supposing it to consist of a succession of phenotypic forms all displaying steadily progressive development in all characters

Any one generation in a community is not usually the offspring of a single parent, or even of one kind of parent : on the whole, there are as many genotypically mixed kinds of parents as there are offspring reaching maturity Moreover, in a freely interbreeding com-

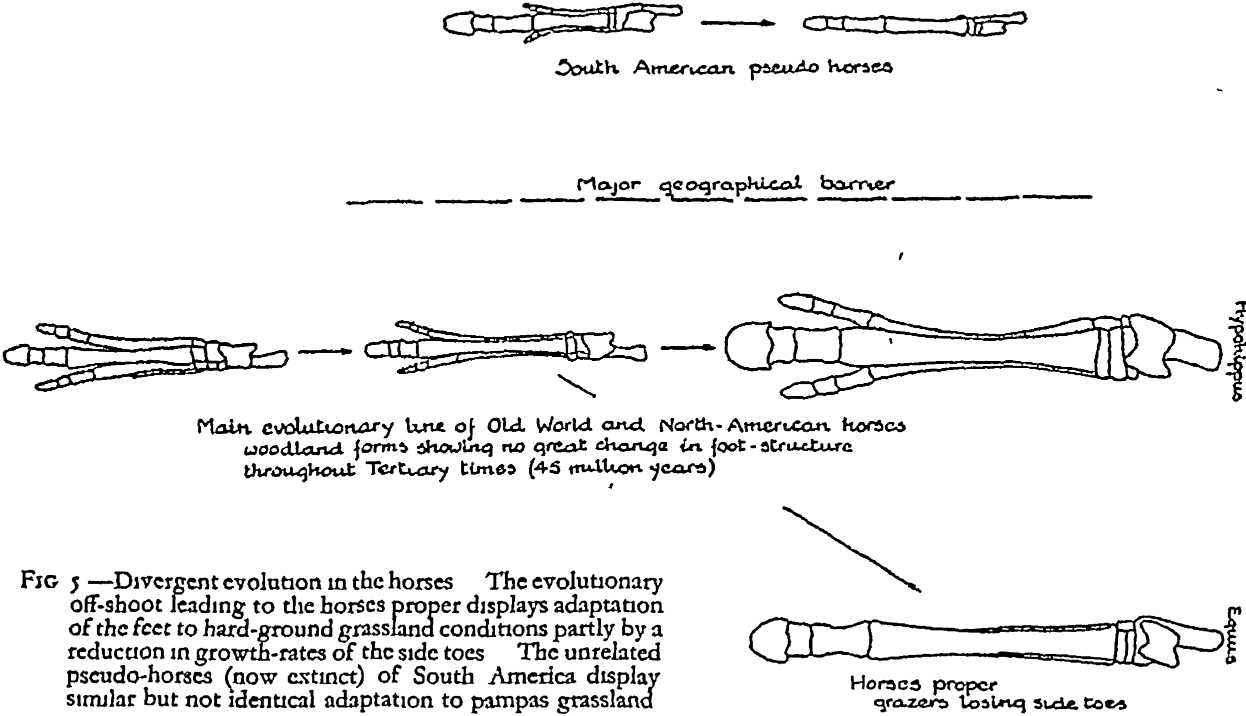

FIG 5 —Divergent evolution in the horses The evolutionary off-shoot leading to the horses proper displays adaptation of the feet to hard-ground grassland conditions partly by a reduction in growth-rates of the side toes The unrelated pseudo-horses (now extinct) of South America display similar but not identical adaptation to pampas grassland munity ancestors and descendants increase in number geometrically with distance apart (in time) of the generations, and a phylogenetic series is better represented by an intricate network, a plexus, of genealogical threads than by a single line It is quite impossible that any collection of fossils, however large in number and however strictly localized, should yield identifiable parents and offspring at best, any two specimens from such a collection are in no more than collateral relationship An analysis of kinship in fossil evolution must thus be in terms of the links between whole generation-groups That is, evolution is best regarded as bulk change in whole communities

Fossil oysters from the Jurassic rocks provide a well documented illustration of community-evolution Trueman has shown that they fall into a lineage in which there is progressive coiling of the left valve from the earliest forms, nearly flat like living oysters, to the latest, incurved through a whorl or more. The evolutionary changes are probably closely related to changes in mode of life from a rocky to a muddy environment, the flat forms usually having a large, the curved forms a small, area of attachment Evolution in these molluscs is marked (as in the Chalk sea-urchins) by the usual sequence of merging intergrades, which can be arranged as a continuous series of transients showing increasing curvature Moreover, the latest members of the series are so different in appearance from the earliest that they are considered to belong not merely to different species but to different genera (species of the flat forms being referred to the genus *Ostrea*, of the incurved forms to *Gryphæa*) As in the sea-urchins, however, the distinctions between the species (and genera) are arbitrary, defining a vague conception rather than a reality

Variation among the individuals in one stratal layer

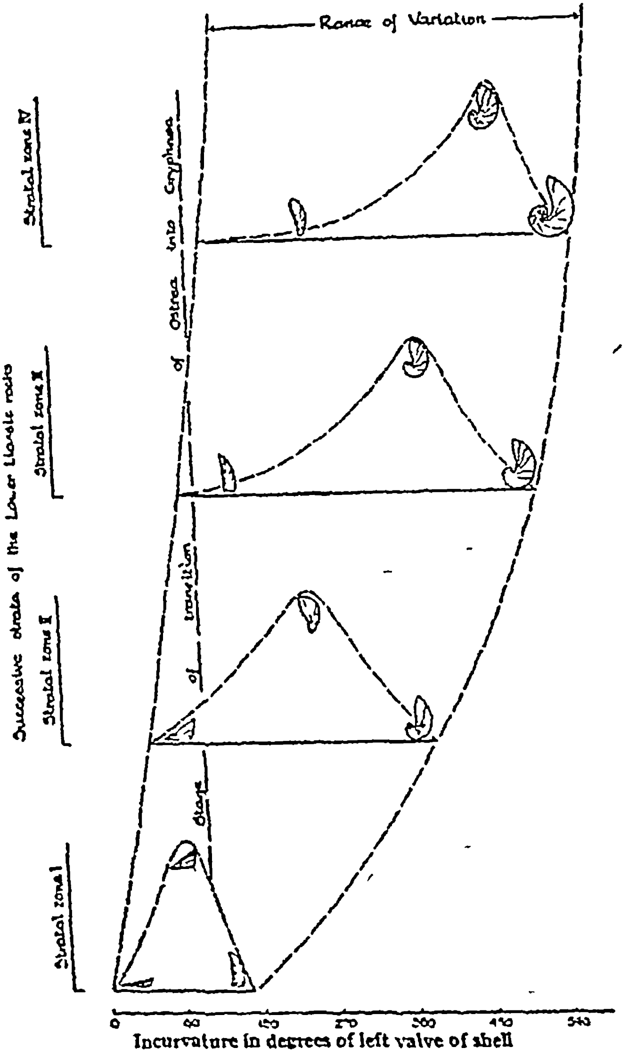

FIG 6.—Community-evolution in Jurassic (Liassic) oysters Each population-sample is represented by a variation-graph like those of Fig 2 Progressive incurving of the shell is shown by the shifting peaks of the graphs, but each community contains forms having different degrees of incurvature, as the inset-diagrams illustrate. The graph of the latest community is notably skew, and may indicate increasing selection-pressure leading to extinction

is wide, and a typical community is composed of a mixture of forms not all of which are in the same stage of evolutionary advancement The variation is continuous in kind there is a preponderance in any one community of forms of more or less the same degree of incurvature, but with them are found (in decreasing proportion towards the extremes) some almost flat forms side by side with others closely coiled It is possible to define each separate community by the average degree of coiling of its constituent members, and to represent the variation by graphical devices to illustrate the amount of departure from the average shown by variant members of the community When this is done, the evolutionary mode in the full succession of communities is revealed in a systematic shift of the norms in the direction of increased coiling, and the over-all impression is again one of continuous transition throughout the graded series (Fig 6)

Manifestly, however, this is not a series composed of a simple chain of individual " intermediate links " In any one community the solitary individual may lie near the norm, or it may be flatter than the norm, or it may be more curved than the norm In an earlier generation its direct and collateral ancestors may similarly have been mixed some near the norm of their community, some flatter, some more incurved Since the variation is continuous, presumably all the members of a particular community could freely interbreed It is highly improbable, therefore, that an unusually flat oyster in one community was consistently in direct descent from flat oysters in earlier communities, or had consistently flat descendants in later communities On the contrary, the individual oyster is no more than an incidental point of convergence in a vast plexus of lines of evolutionary relationship, every ancestor and every descendant in which are the products of almost completely random parentage, and include in their genealogy forms of various degrees of incurvature If selected ancestors were more incurved, evolution would appear to be retrogressive; if less incurved, to be progressive

An individual, moreover, does not consist of a single character, but is compounded of a host of characters integrated to form the whole organism. In any community the possible combinations of structural elements may be enormous when there is free interbreeding For instance, the rocks of the Coal Measures accumulated under fresh-water or brackish conditions in which mussels of various kinds flourished A time-sequence of the molluscs displays lines of evolution of the usual serial kind, marked by a number of changes in shell-shape. The shells may increase in length, or become deeper, or develop a prominent cross-keel, or become sharply acute at one end, or show a migration of the apex towards anterior or posterior Most of these analytically separate characters seem also to be independent in hereditary assortment, so that an individual mussel may appear to be precocious in some respects, primitive in others In like manner, its ancestors or its descendants in any given stratum may show similar contrasts in character-expression, but it is highly improbable that they will do so to the same degree in the same characters

A representation of evolution in the form of a linear graded series of individuals, even should they be in proper time-order, is thus partial and imperfect. The evolutionary stages are truly represented only in bulk samples of successive communities, and are determinable in detail only when community clusters are followed in chronological sequence. When this is done the course of evolution is revealed as being highly intricate. It is multi-dimensional, and has a weaving plasticity much like the fluctuating balance of mixed variants displayed in genetical experiment by successive generations of hybrid communities

In most of the instances of community evolution so far studied the overlap in variation-range between the earliest and the latest communities of the known series is small or nil, and the marked phenotypic contrasts between them presumably imply that the most primitive and the most advanced members could not have interbred (had they been contemporaries) Such sterility could be the product only of genetic change The mode of evolution thus appears as a succession of small gene-mutations, with phenotypic variation at any one stage having a range sufficiently wide to submerge the abruptness of intrinsic mutant differences

This analysis of the kind of evolution exhibited by fossil series emphasizes the artificiality of much biological classification The variation-ranges of two widely separated communities in an evolutionary series may indicate quite clearly that they belong to different groups, but the variation-range of an intermediate community may well overlap that of the earlier on the one hand and of the later on the other (as in the oysters illustrated in Fig. 6) Two of its variant members, therefore, mutually interfertile but at opposite peripheries of the field of variation, may be indistinguishable in outward form, the one from members of the earlier group, the other from members of the later group If the groups are considered to belong to different species, the isolated individual judged solely on its form might justifiably be ascribed to more than one species Only when it is seen in a context of its fellows is the species of which it is truly a member identifiable, for the nature of the species lies in the collective association of its constituent variants

The genus has even less claim to be regarded as objectively real than the species It is a category of convenience A theoretically complete lineage, such as that of the Jurassic oysters, displays a transformation of species that allows no natural generic subdivision Thus the genera *Ostrea* and *Gryphæa* completely intergrade, and at the stage in the series where the one supposedly gives place to the other there is a separation of scarcely distinguishable communities Nevertheless, the genus, though not a real entity, may be a real convenience, and conventional definition may set objective limits to each genus as precise as those of a calendarial century or a

CHAPTER VII

EVOLUTION IN SPACE GEOGRAPHICAL SPECIES

A SPECIES, however small in numbers, has some range in space. Environmental influences cannot therefore be precisely identical for all the separate individuals belonging to it, and they inevitably display a degree of phenotypic (including genotypic) variation. Nevertheless, so long as all its members freely interbreed, the gene-interchange arising through Mendelian assortment and recombination effectively prohibits fragmentation of the species, which continues to be a unity Over a prolonged interval of time there may then arise (through cumulative mutation) a developmental series of successional forms of the kind exhibited by fossils, but there cannot be divergent evolution

A species—especially one large in numbers or of low population density—usually, however, has an extended geographical range greatly exceeding the range of individual wandering The potential freedom of the individual members of the species to breed indiscriminately may then cease to be an actual freedom That is, continuity in space of a large population is not adequate assurance or evidence of completely random mating Thus the domestic habits and small size of the individual field-mouse scarcely allow it to roam over more than a few acres of its full-species range in a single lifetime, and the community of neighbours which it is ever likely to meet is in fact very much smaller than the total potential freely interbreeding population So a

Londoner will more probably marry a Londoner than a Glaswegian

A wide-ranging or migratory species like the bison or the locust or the cod has correspondingly greater opportunities for indiscriminate mating, but even so, there are varying probabilities of encounter between individuals in different parts of the range, and the peripheral wanderers will always remain strangers. Moreover, there are psychological and other restrictive controls on random mating that in many instances prohibit even strongly migratory species, congregating in huge flocks or herds, from full interbreeding Thus migrant birds frequently have the habit of nesting in the same locality in successive years, and are self-restrictive in the size of population in which sexual selection can operate, and this degree of inbreeding tends to bring about a measure of genotypic uniformity A comparable tendency for seals to return to favoured islands during the breeding season, and for salmon to return to the family stream for spawning, has a similar result

Among invertebrate animals, especially those living in the sea, free interbreeding is facilitated both by the enormous numbers of eggs laid and by the dispersal of the floating eggs and larvæ (and often floating adults) over vast distances by currents But the great majority of species of such organisms have a greater range than the probable dispersal range of individuals, and the chances of interbreeding are dependent on relative proximity

Because of this disparity between individual range and full species-range, there ceases to be thorough mixing of genes in successive generations, and local groups, though merging imperceptibly into one another, tend to arise through partial isolation The ensuing inbreeding and reduction of free gene-flow cause genotypic differences to be established between the groups by differential selection The greater the total range of the species in relation to the individual range of its separate members, the greater are likely to be the effective environmental differences between the remoter parts of the range Correspondingly, there are greater divergences in selective preference Even with low mutation rates, sooner or later there emerge local races (geographical races, "elementary species") differing from one another more or less radically the parental species begins to display subdivision into subspecies This is known as differentiation by distance, or subspeciation

A first stage in the process is one in which the difference between local races is revealed in the systematic replacement of a single gene by a mutation over the species range Thus the guillemot exists in two forms—the bridled with a ring of white feathers round the eye, and the non-bridled without the ring—the appearance of which is controlled by a single pair of alternative genes Part of the range of the species runs along the coasts of north-western Europe, where the proportion of the bridled forms is almost nil in southern England but increases systematically northwards to about 25 per cent in Shetland and to over 50 per cent in Iceland There is a similar progressive replacement of the grey-and-black hooded crow by the black carrion crow as the range is followed southwards from the Scottish Highlands into England

The beetle *Carabus nemoralis* offers a more complex illustration of the same sort of systematic genic replacement in apparent physiologically adaptive response to the environment The graded conditions preferred by the different geographical races of the beetle in Germany and France are as follows —

Race	*Optimum Temperature*. °C.
Dresden	26·1
Rhone mountains	27·1
Münster	27·9
Coblentz	29·3
Paris	29·4
Olargues (southern France)	29·7

—a relationship that reflects the climatic gradient in western Europe.

A later stage is one in which the differences between neighbouring communities are trifling and are limited to a few genes and their mutant forms, while more distantly removed communities differ in a more or less considerable number of genic elements. The whole species then consists of an intergrading series of local races displaying gradual change in genotype from one end of the range to the other, while still remaining a single species as judged by a willingness to interbreed among all its members. The systematic genotypic gradation is outwardly exhibited in a gradual change in structure or appearance, a character gradient or cline. It is almost universal in all species with extended range, and is illustrated by plumage in birds, striping in zebras, size in caribou, tail-length in mice, pigmentation in man.

A still later stage is one in which the clinal gradient is so steep or so prolonged that end-forms of the species range come to differ more or less radically from one another. Through functional incapacity or psychological inhibition they may then be unable or unwilling to interbreed, and thus themselves acknowledge their differences in reproductive isolation. In these circumstances complete gradation of variants throughout the species range, and complete merging of neighbouring subspecies (each conveniently grouped about a local mode) along common zones of contact, do not exclude the occurrence of end-forms which are nevertheless truly distinct species and display full speciation

Species distinction in the continuity of fossil series may be arbitrary and conceptual (*see* page 78) But among living forms (at least of nearly all animals) a species has exact meaning and is an objective reality, though it is recognized in terms less of special structural characteristics than of organic behaviour It is a community of actually or potentially freely interbreeding and interfertile individuals, separated from other species by a reproductive barrier—a barrier psychological but not always functional between near species like wolf and jackal, horse and ass, both psychological and functional between less closely related species Under natural conditions, members of distinct species show themselves to be well versed in species distinction a vixen never mistakes a dog for a fox In a number of instances, especially among birds, some of the biological significance of the colour-pattern seems to be that of recognition marks, for aid in specific identification. Natural hybrids, if not due to exceptional circumstances like captivity, are almost always hybrids within the limits of the single species

With such a criterion for the species, the occurrence of full geographical speciation is illustrated by a number of different groups of animals Thus the common herring-gull has a circum-polar chain of subspecies in the northern hemisphere that seem to have arisen by a progressive extension of range and an ensuing differentiation from an ancestral home perhaps in north-eastern Asia The extension is represented in a graded series of forms ranging eastwards across Canada to the Atlantic and to the West-European sea-board, where the typical herring-gull has pale grey wings appreciably lighter than those of the East-Asian forms Westwards it is represented in a series of no less perfectly graded forms ranging across Siberia and northern Russia to the West-European sea-board, where the typical form has wings appreciably darker than those of the East-Asian individuals, and is known as the lesser black-backed gull. In the region of overlap in Europe the two extremes differ markedly not only in appearance, but also in temperament and habits (the herring-gull being more aggressive and quarrelsome, and nesting a fortnight earlier, than the black-backed gull), and behave as distinct species.

Similarly, the deer-mouse *Peromyscus maniculatus* of western North America exists in a number of subspecies or local races differing under the influence of physical (including climatic) controls. The grassland forms include *arcticus* of the cold Canadian prairie and *osgoodi* of the rather warmer Colorado–Montana country. The woodland forms similarly include a northern race, *artemisiæ*, of the American–Canadian border, and a southern, *sonoriensis*, of Nevada–Utah–Idaho The chain of interbreeding races covers a nearly unbroken area, and the divisions between them are thoroughly arbitrary, except in the case of *artemisiæ* and *osgoodi*, which, in a zone of overlapping ranges where relatively recently the chain has closed, behave as independent species without interbreeding.

The clinal gradients are steady and continuous when the range of the geographical races of a species is fairly evenly and thickly populated and offers no local restrictions on free gene-flow between neighbouring populations The primary factors determining the form of the cline are then distance apart of the races, and systematic environmental change. Sea-birds, fishes, marine organisms generally, have such unrestricted ranges; though inshore dwellers meet a variety of contrasted coastal environments, and may have highly variable population densities, which tend to modify the regular clinal gradient On land, however, there are often sharply distinct neighbouring environments (as between alluvial plain and flanking hill-slope, Chalk down and clay vale, fenland and dune), and clinal gradients (which are a reflection of the environmental controls) may show marked steepening at the frontiers If there are positive environmental barriers interrupting the range of the species, the cline may be discontinuous

Thus a peninsular population having easy access to the mainland by a broad isthmus may show a steady gradation from the mainland forms, but if the isthmus is constricted, there is a direct limitation of individual cross-breeding between the neighbouring populations in proportion to the narrowness of the bridge If the isthmus disappears altogether, the land-dwelling insular forms become completely cut off, and the possibility of gene-flow (by cross-breeding) between the island and the mainland diminishes almost to zero Sometimes a trickle of genes manages to cross the environmental barrier, as by such accidents of transport as wind-borne seeds and insects, bird-borne mussel larvæ, raft-borne mammals, but the effects of chance dispersal in reducing reproductive isolation clearly depend partly on the distance apart of the populations, partly on the incidence of mutual gene-exchange in relation to size of populations In Britain the local races of the Bute and Skomer voles occur on islands lying only a few hundred yards from the mainland

The barrier need not be the sea Mountain or desert or river or forest may equally fragment the range of a species, and prove a more or less insurmountable obstacle to cross-migration and gene-flow between populations Each self-contained group then tends to throw up "random" mutations which undergo differential selection in the separate areas, and there are produced unique local genotypes having little or no opportunity of inter-group recombination and assortment. A group at first establishment is then perhaps closely similar to its neighbours, but prospectively it is an incipient species

The effects of selection, if not swamped by periodic immigration of related forms (as might arise, for instance, when fluctuations of the sea cause a tract of land to oscillate between peninsular and insular conditions), are progressively divergent, leading to communities reproductively no less than geographically isolated Full geographical species are then established, often with few subspecific links between them.

Indigenous island forms are a spectacular example of the process. In this respect the Australian marsupial animals and the South American sloths and marmosets are instances of organic isolation on a continental scale. Britain and Ireland are geologically part of the European continent, and geographically were part of that continent in very recent times, yet the Irish hare, the Orkney and Skomer voles, and the red grouse have all differentiated from continental types since the end of the Glacial period In the Azores about 30 per cent of the beetles, in remote St. Helena about 55 per cent of the insects and 80 per cent of the flowering plants, and in the Hawaiian Islands set in the heart of the Pacific Ocean 85 per cent of the beetles and all the land-birds and all the land-snails are indigenous

Comparable isolation and speciation are displayed by such a local and self-contained species-group, almost certainly of single evolutionary origin, as the finches of the Galapagos Islands—an example of considerable historical importance, since it was a major stimulus to

Darwin's interest in evolution Lack has shown that each single larger island appears to have its separate species or species assemblage The birds habitually are land-dwellers, flying comparatively short distances in the search for food, and there is little cross-migration from one island to another, and the diversity of environmental conditions in the islands seems to have been the principal factor in the process of speciation by differential selection of the respective mutants The structural contrasts between some of the species are not very great—sometimes, indeed, a bird needs a second look to be sure a prospective mate is of its own kind—but reproductive isolation is complete or nearly so

The complement to oceanic islands is found in isolated lakes, the organisms of which show equal peculiarities Thus nearly all the species of pond snails, sponges, bivalve molluscs, and water-fleas of Lake Baikal are confined to its waters, and the Baikal seal, a differentiated relic of a marine form cut off from the sea, finds its nearest kin in the Arctic Ocean

Disjunction of species-range by mountain barriers is illustrated in New Guinea, where speciation among upland birds-of-paradise is brought about by the limitation of localized groups to the higher and more or less isolated mountain tracts, each of which tends to have its particular subspecies In the same island the backbone of mountains also separates zones of humid lowland in which kingfishers find their home, and the birds consequently fall into a number of distinct local geographical races on the way to becoming full species (Fig 7)

Similar geographical control operates in the small Hawaiian and Sandwich Islands These reach considerable altitudes, and are drained by streams which have excavated deep radial valleys separated by steep walls and sharply crested ridges The islands have become

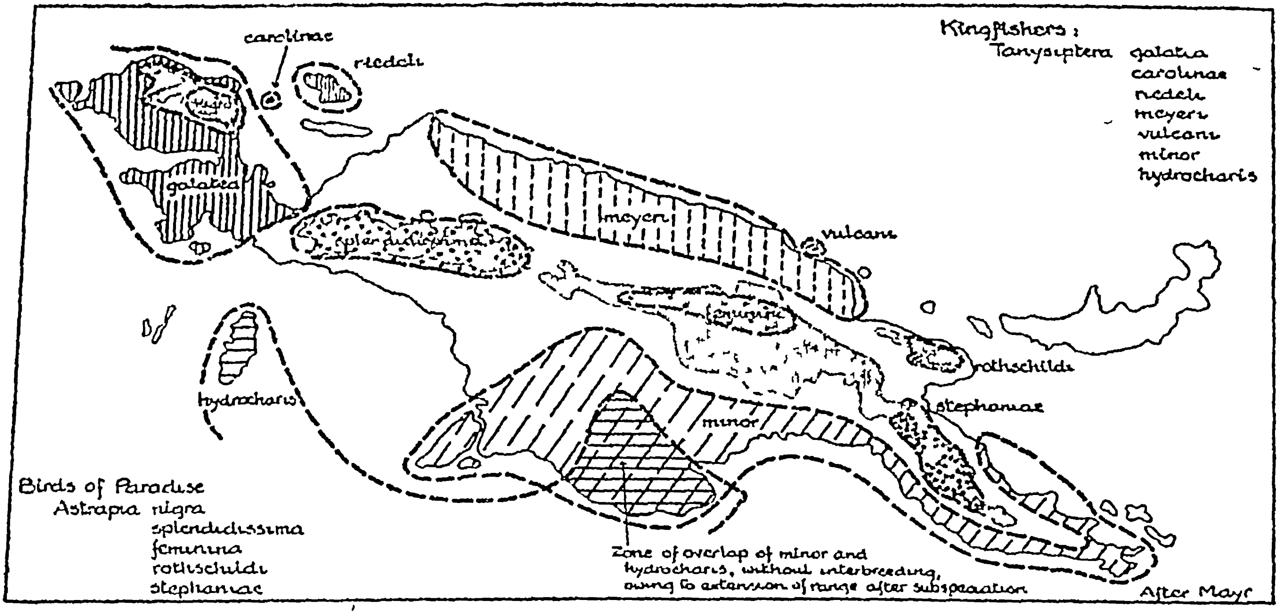

FIG 7—Speciation in New Guinea The area is geographically broken by mountains (finely stippled in the illustration) and by sea Each island or more or less isolated tract of low ground tends to have its peculiar kind of kingfisher, and of high ground its peculiar kind of bird-of-paradise The names are of the species and subspecies.

populated by land-snails which favour the humid warm environments of the valley floors, and avoid or are only thinly distributed in the uplands The isolation of the valleys and the difficulties of trans-crestal migration have imposed fairly rigorous reproductive isolation, and with the near-cessation of gene-flow almost every valley is now the home of its own separate local race, or even its own species Moreover, the narrowly linear form of many of the valleys has induced a supplementary subspeciation revealed as the snail populations are followed from the interior towards the coast.

Speciation as the breaking-up of a unitary group thus follows from localized adaptive response of members of a species to contemporary environmental differences In the continuously transitional series of forms of the simple cline, it bears analogy with fossil series, in which there are similar (but inferred) species contrasts between end-forms and an unbroken grading through the intermediate links The disruption of clines by geographical barriers, the resulting isolation of local groups, and the consequent sharp distinction between subspecies and species of common origin, have their equivalent in the fossil record when the continuity of evolving forms is interrupted by layers of unfossiliferous sediments, and the intergrading of transients is obscured

CHAPTER VIII

ADAPTATION IN EVOLUTIONARY SERIES

THE concept of geographical speciation lays emphasis on the space-factor in the divergence of groups, rather than on sequential changes in time Nevertheless, the same process must account for both geographical species and successional species, since of course every species has both geographical definition and a place in time. Adaptive response, therefore, if it is a real factor in the emergence of geographical species, must enter no less into an explanation of the transformations in fossil series

If environmental conditions remain more or less constant for long periods, there tends to be close organic specialization, particularly but not necessarily when the pressure of natural selection is high In such circumstances, variants departing in any direction from the preferred norm are relatively less closely adapted, and therefore are discouraged, either by reduction in proportionate numbers or by complete extermination The variation-range of the population is thus limited Since the variation is partly of genetic origin, selection encourages genotypic approximation to a pure line by eliminating the more aberrant mutants, and the potential variability-range is thus also limited

Under such conditions, the evolutionary process appears to be highly conservative, and its products are long-lived kinds existing in almost static optimum relations with their environment The lamp-shell *Lingula*, for instance, buried in the mud of the shallow-water sea-floor, lives under conditions which are monotonously persistent over long geological intervals, so long as lands have normal coasts Relatively minor changes, as in the nature and abundance of microscopic food or in the salinity and temperature of the surrounding water, are then the only factors likely to affect the constancy of its environment A lingula in its burrow might then find little difference between Ordovician and Recent mud, and transformation over geological eras may be so slow as to remain within the limits of the single genus (*see* Fig 3, page 57)

Though the physical environment, especially in the sea, may persist with very little modification for long periods, usually it shows change in a great many minor ways, and at times of major earth movement, as during the building of folded mountain-chains, it may undergo great transformation more particularly in its terrestrial and coastal zones In any event, the organic elements in the environment are always changing, and to them the individual species must make due response Close adaptation to a particular environment may then ensure a temporary success, but a group displaying it, particularly one of low variability, may, when conditions change, find itself at a disadvantage in comparison with a group relatively less closely adapted but of higher variability (especially genotypic variability)

A selective and systematic shift in variation-range and variation-balance is a necessary response to modified adaptive needs (with extinction as the only ultimate alternative) Adaptation being not a state but a relation, the shift is determined, within the limits of survival, by statistically expressed differential selection This is the sort of form-sequence that is displayed by the Jurassic oysters, the mussels of the Coal Measures, the horses

There is clearly a conflict between the need for close adaptation to the environment as it is, and for broad "plastic" response to the environment as it changes. High specialization, concentrated adjustment to selected features of the environment, is advantageous while it lasts, but it tends to result in an inadaptive condition when the environmental optimum shifts even slightly Thus the sabre-toothed tigers were in build and dentition very highly specialized predators, probably finding their chief food in the larger mammals like the elephants and the ground-sloths: their size and relative awkwardness probably made it difficult for them to subsist on a diet of smaller animals, if only because they could not capture a sufficient quantity of meat daily for their needs. So long as the larger mammals (in their turn dependent on a rich herbivorous diet) continued abundant, the sabre-tooths were "successful" But the deterioration of climate towards the end of Tertiary times, and the consequent reduction in numbers and final extinction of many of the herbivores, especially in North America, carried the sabre-tooths to extinction also.

Similarly among the horses the adaptation to forest and woodland of the North American *Hypohippus*, possessing short-crowned cheek-teeth suitable for browsing, was "successful" (in the sense that the form was common) for much of later Tertiary times, but with the extension of grassland prairie and the reduction in forest as the Glacial period approached, *Hypohippus* found itself disadvantageously placed in competition with the one-toed long-toothed horses proper, and became extinct (*see* Fig. 5, page 73)

If the rate of environmental change is very fast, and the variability-range cannot offer new mutants to keep pace, adaptive response may lag behind environmental requirements, and extinction then is the lot even of relatively unspecialized forms (as during the onset of glaciation).

Evolutionary specialization as the development of elaborate structure, as in the elephants, the duck-billed dinosaurs, the highly ornamented ammonites, has sometimes been taken to imply racial senility But while no doubt some lack of "plasticity," some stiffness in adaptive response, is indicated by such elaboration, the long-continued evolution of other equally "specialized" groups like the crocodiles (little changed since mid-Mesozoic times) and the king-crabs (almost unchanged since the beginning of Mesozoic times) is a warning that elaborate structure as such is no danger to survival

The history of the fish-lizards is in this respect illuminating They persisted in abundance during the greater part of the Mesozoic era as marine predators superbly specialized in structure for their fish-like mode of life, and racial senescence can scarcely be attributed to forms which were "successful" for over 100 million years Their extinction at the end of Mesozoic times is therefore probably not to be attributed to any intrinsic decline on their part (or to major changes in the continuing physical environment of the sea), but to a novel factor in the organic environment the emergence of direct competitors more responsive to selective stimulus—the first dolphin-like secondarily aquatic mammals

At any moment, therefore, there is a favoured adaptive form upon which selection-pressure centres in a given environment But as the time-factor enters, systematic environmental change involves a changing bias in selection pressure, which then becomes asymmetrical in its incidence and gives a directional component to the line of evolution. This is expressed in correlated modal shift in the variation-range of successive generations The process is well illustrated by the Jurassic oysters, which display a modal shift in successive communities while retaining a fairly wide variability-range (*see* Fig. 6, page 75)

Most broad environments have subdivisions displaying some differences, and the speciation that may ensue when an ancestral central stock sends evolutionary branches into different environmental niches is what has been called adaptive radiation Under selective bias each separate branch follows its independent line of directed evolution, until it achieves an adaptive peak of secondary specialization in the new environment as the directional component of selection-pressure diminishes At the same time the ancestral stock as a whole loses its initial unity, and breaks up into a number of separate and independent lines This is essentially geographical speciation in time, evolution by divergence, the branching phylogenetic tree

A gross alteration in the environment, as when the retreat of ice-sheets at the close of a glacial period, or widespread uplift of a sea-floor, or volcanic eruption, exposes uninhabited country for re-population, provides conditions in which interspecific competition is for a time less acute or less restrictive than in thickly populated ground; and the opportunities for divergent evolution, for adaptive radiation, are relatively great. A rapid extension of species-range is then accompanied by correspondingly rapid adjustments of structure and habits and the consequent eruption of numbers of new species (and in due course genera, families, and orders) There is a "burst" of evolution, often in the fossil record seemingly of leaps in evolution, and this explosive release of potentialities has the aspect of youthful vigour as against the apparent senility of long-established "old-fashioned" phylogenetic series

The "burst" of amphibian evolution after the mid-Palæozoic earth-movements, of ammonite and reptilian evolution after the late Palæozoic movements, of mammalian evolution in Tertiary times as the reptiles rapidly died out, has the appearance of such rejuvenescence, and has led some geneticists to assume a radically different evolutionary mechanism to explain the sudden eruption of new species and genera This they have suggested to be systematic mutation, with "hopeful monsters," novel organic types, forming the new points of origin of evolutionary lines

The attribution of a subjectively recognized renewed youth to evolutionary series is, however, not to be taken too literally as implying an inherent contrast between emergent and decadent groups Racial childhood and racial old-age are fictitious, if the terms are intended to suggest different intrinsic natures at opposite ends of evolutionary series, to suggest that inherent capacity for change has run its course and no future awaits the evolving series but extinction At any one moment all organisms are in an evolutionary sense equally young and equally old, since their ancestries go back to the beginnings of organic time Racial senility has descriptive meaning only within short segments of evolutionary series, and then only if there is prior ascription of senile qualities to such characters as elaborate ornament in shells or " excessive " spine development in crustaceans In modern view the recognition of racial old age rests on subjective judgements which contradict coherent theory and which are permeated by animistic ideas no less than by animistic terminology

It is true that some organisms may be over-specialized, not intrinsically in being extravagantly constructed or in having peculiar habits, but in possessing a variability-range too limited to allow ready accommodation to rapidly changing environmental conditions, and other organisms less rigid in adaptive response may be more tractable to the stimulus of change afforded by new environments, and then appear to be more richly endowed with evolutionary energy. But explosive evolutionary activity, notably expressed when "empty" novel environments await invasion, is always a short-lived experience for any particular group of organisms, and is sooner or later followed by a diminution of speed and a limitation of evolutionary routes as the various environmental niches become occupied. The group then remains in a state of evolutionary quiescence, until the accident of changing circumstances once again promotes a phase of renewed activity and apparent renewed youth

These relations between organisms and changing environments are well brought out by the manner in which the reptiles were replaced by the mammals as dominant land vertebrates. In numbers and variety of kinds the reptiles achieved high success in their occupation of many different environmental niches during Mesozoic times That this was not due to an inherent compulsive pressure is shown by the fact that while evolutionary branching of the principal stocks took place early in their history, there is no suggestion of a diminished evolutionary vitality in later members. For instance, the diversification of the rhinoceros-like horned dinosaurs and of the duck-billed amphibious dinosaurs in North America was the product of an adaptive burst in late Mesozoic times The reptiles maintained their dominant position without sign of decadence for some 140 million years; and the mere existence of mammals during the greater part of the period—mammals which remained small in both size and numbers and were without notable place in vertebrate economy—was clearly not in itself a challenge or a danger to continued reptilian success The replacement of the one class by the other as Mesozoic times passed into Tertiary must therefore be attributed to some factor not predetermined in the innate qualities of the animals but external to them

A major environmental stimulus to which the mammals responded but the reptiles did not was the appearance of a *new kind of food, the grasses* The *grazing habit*, however, demands considerable powers of mastication, to which the conical reptilian tooth was not readily adapted, and the extended food-range provided opportunity to the mammals whose cheek-teeth were already more complex in cusp-form than those of the reptiles The long-prevailing balance of nature was thus upset, and the new adaptive zone of grassland was rapidly occupied by herbivorous mammals which, having crossed the threshold, *soon outpaced* the reptiles in supplementary anatomical adjustment The carnivorous mammals, developments out of a stock of late Palæozoic age and waiting in retiring modesty throughout Mesozoic times upon such opportunity, were far more efficient in their battery of offensive weapons and in their locomotory agility than such reptilian carnivores as the huge clumsy tyrannosaurs, and as predators preying on the herbivores they were a correlated adaptation Together, herbivorous and carnivorous mammals came to occupy many of the old niches of the reptiles and the niches new to Earth-history.

Such "explosive" evolution, displaying antecedent threshold effects, was nevertheless highly complex in detail, and its experimental nature, marked by trial and mixed success of body-build and tooth-form, is well illustrated in the number of evolutionary lines of early Tertiary mammals which became extinct without leaving modern descendants Thus perhaps four or five separate stocks of carnivores, differing in the development of back teeth for flesh-cutting, stemmed from a central late Mesozoic ancestry, but of these only the group employing as principal shears the fourth upper premolar and the first lower molar survived—presumably because of the mechanical superiority of the jaw apparatus—into mid-Tertiary times, when the way was open to it for supplementary adaptive radiation. Similarly, a number of lines of "primitive" early Tertiary herbivores became extinct or failed to achieve notable success, and at the present day the dominant forms (judged by numbers and kinds) are limited to the even-toed hooved animals, also mainly the product of a later Tertiary secondary radiation.

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CHAPTER IX

VITALIST THEORY

It is possible among the vertebrates frequently to recognize adaptive response in structural change It is less often possible to do so among the invertebrates, whose mode of life, especially in fossils, is sometimes difficult to determine An inability to attribute significant functional use to sundry evolving structures has commonly been charged against Darwinian evolutionary theory, and has been the foundation for assuming a directive force in evolution that is independent of, and in more or less degree opposed to, environmental control This directive force has been variously conceived, and has been endowed with a variety of names, but the implication of all vitalist theory is that some measure of inevitability is a factor not to be neglected in evolution though the inner drive, the momentum, is in the less mystical versions regarded as an innate quality of living matter, and not necessarily as the instrument of special cosmic purpose

The evidence for non-adaptive evolution falls into a number of categories Chief is the indication of " disharmony " between organism and environment, revealed in grotesque and monstrous characters A particular instance, illuminating in its general application, is that of the antlers of the Irish elk The antlers sometimes reach a span of nearly 10 feet and a weight of 80 lb (on a skull weighing 7 lb), and the view that their enormous size could have been attained entirely as a result of adaptive selection certainly seems inacceptable It is difficult to suppose that they were not too cumbersome for efficient attack and defence, and not a serious disadvantage in woodland country, and they must certainly have absorbed a great deal of the energy of growth Nevertheless, increasing knowledge of the processes of growth and of the mathematics of selection makes it possible to avoid vitalist explanation of the structural enormity.

The Irish elk is a member of the deer family, one of its near relatives (judged by similarity of form) being the red deer Huxley has shown that in the latter species there is a close correlation between antler-size and body-size in individual growth, so that an absolute increase in body-size is accompanied by both an absolute and a systematic relative increase in antler-size (which in turn involves a correlated increase in branching and palmation) The genetic explanation is that of unitary genic controls on a number of apparently separate but actually correlated characters.

On the assumption that a similar linkage controlled growth in the Irish elk (as is suggested by its relationship to the red deer), the extreme size and elaboration of antler seen in the elk may thus be no more than an incidental secondary result of a primary line of evolution leading to large body-bulk Such a primary line, for which it would not be difficult to find adaptive justification, was almost universal in the whole range of deer evolution during Tertiary times So long as the advantage accruing from increased size outweighed the possible disadvantage of hypertrophied antlers the evolutionary line was "successful" But ultimately a point of nice balance was reached when whatever advantage was given by increased body-size was offset by the unwieldiness of the antlers. The slightest further evolutionary progression in body-size plus antler-size then made the organism inadaptive in net result, and extinction sooner or later was inevitable.

The principle is of wide application Thus the repeated evolution of enormous horns in such forms as the mammalian titanotheres or the reptilian horned dinosaurs is not to be explained solely by reference to the functional value of the horns as isolated structures It is a common feature in vertebrate evolutionary lines that earlier hornless forms are much smaller than later large-horned forms In any one line a threshold of size has to be crossed before horns begin to appear, and thereafter there is a fairly consistent correlation between size of body, size of skull, and size of horn Since an évolutionary trend towards large body-size is displayed in most of the series, the fact of growth-correlation makes it unnecessary to invoke any mutational change in special genes affecting horn-growth, which may be regarded as no more than an incidental feature of general growth, given a certain basic genetic constitution

The evolution of organisms under the effects of an internal momentum to stages positively out of " harmony " with their environment (that is, positively inadaptive) is, in any event, statistically impossible in large populations, if adaptation is defined in terms of survival and if the fact of environmental selection is accepted. It occurs, if it occurs at all, only in populations of smaller numbers than a few hundred at most Conceivably, random inadaptive evolutionary " drift " may have had some significance in small herds of the later titanotheres and horned dinosaurs, and of the Irish elk *in its last days; but since selection (the agent of adaptation)* does not operate on the individual as such, it becomes a relevant factor in the evolution of such small groups only when adverse selection-pressure (itself a measure of " disharmony ") becomes intense

Lack of " harmony " can by mere inspection be judged only subjectively in fossil structures, and it has meaning in living forms only in terms of survival. If in fact species continue to survive with the structures they possess, it is meaningless to talk of disharmonic relations with the environment, which is the arbiter of survival. Though a particular character in isolation might justifiably be regarded as a disability (like very large antlers), the whole organism because of its very existence must be sufficiently adapted to survive.

Vitalist explanation is also invoked to account for the evolutionary mode of an organic group seemingly compelled to follow a prescribed course until, at a peak of "disharmony," it meets extinction in the fiat of an uncompromising environment Such directed evolution has been called orthogenesis It appears to be exemplified in the extravagant antlers of the Irish elk and the horns of the titanotheres. A commonly cited instance is the close incoiling of the more advanced forms of *Gryphæa* (page 74), in which the left valve of the shell gives the impression of curving over and pressing on the right, finally to prohibit the opening of the shell. Various species of sea-mats build extremely elaborate skeletons, some of them three-storied, whose choked apertures apparently leave the individual little opportunity of obtaining food The ammonites (Fig 3, page 57) in their most "specialized" forms have the solid chamber-partitions frilled in the greatest complexity. The evolving lines ending in these products seem to lead more or less undeviatingly from "normal" forms by progressive stages to an extreme of "aberration"

It is obviously not easy to give full and acceptable reasons for the paths followed in such evolution in terms of adaptation and selection. Nevertheless, there is little genuine evidence for supposing the evolution to be enforced in indifference or opposition to adaptive needs. Straight-line "determinate" undeviating evolution in fact characterizes a lineage only over short sections of its course, and then only when the series is idealized In the actual detailed sequence of forms evolution is, on the contrary, nearly always divergent and radiating, and is marked by recurrent branching speciation. If a single ancestral stock gives rise to diverse off-shoots adapted to different environmental niches, as illustrated in the common origin of oysters and gryphæas, of nautiloids and ammonites, of mastodons and elephants, of browsing and grazing horses, of pigs and hippopotamuses, of camels and llamas, of apes and men, the implication is that no internal compulsion drives the several lines along the courses they follow

A similar attribution of perfectionist urge in evolution, the lineages being regarded as striving towards a predestined goal, is found in the view that there is an irreversibility about the process As a rule the transformation of characters in evolutionary series certainly cannot usually be undone A fin evolved into a terrestrial leg or a flying wing never reverts to true fin-structure when (as in the sea-lizards and the penguins) there is a return to an aquatic mode of life Lungs, once they replace gills in vertebrate evolution, have to serve even when (as in the whales) they are a poor instrument for breathing under water A reduction in length and strength of the fore limb in bipedal stance is stamped upon body-build when (as in a number of the dinosaurs) there is reversion to a quadrupedal stance

Nevertheless, the " law " of irreversibility is merely empirical Although it may be a true reflection of the probability that complex gene-controls on structure are not likely to be regained once they are through adverse selection lost from the collective genotype of the evolving group, the " law " is not an absolute rule of development, and is in fact contradicted in numerous exceptions

For instance, the widespread tendency, notable in the evolution of the terrestrial vertebrates, towards attaining large size has been taken to indicate irresistible urge. But the tendency is far from universal, and in a single group, as in the deer, there may be such contrasts as that between the moose, 7 feet high, and the pudu, little more than 12 inches high. Dwarf kinds of elephant, rhinoceros, pig, antelope, hippopotamus, man, also run counter to rule, some of them being found in environments (insular or semi-desert or thickly forested) suggesting the effects of "adverse" conditions. During the onset of glacial conditions in late Tertiary times, some of the lines of horse evolution show a steady reduction in size, in reversal of the trend previously followed, and collateral stocks may show opposed modes of evolution—one of increasing, another of decreasing, size

Even more significant is the manner in which characters display retrogressive (cyclical) evolution. In the adoption of a fast-running habit, the horses throughout most of their evolutionary history display a proportionate lengthening of the limbs. This was partly achieved by a relative increase in the length of the foot, marked by a high position of the hock above the ground. The change in structural proportions was progressive until late Tertiary times, and thus apparently offered confirmation of orthogenesis. But in their latest members a number of stocks began to show retrogression, and living horses have proportionately shorter feet than their pre-Glacial ancestors

Similarly, the earlier sabre-toothed tigers developed lateral flanges in the front of the lower jaw along which the huge upper canine teeth slid on jaw-closure. The later descendants, however, lost the guiding flanges, and the front of the lower jaw reverted to the form [illegible] possessed in the original ancestors of the sabre-tooths (and which it still possesses in all living cats) Such cyclical evolution refutes the suggestion that inevitability attaches to evolutionary trend

A repeated expression of similar evolutionary themes offers a stronger case for vitalist theory Parallel evolution, the sense of motif in different stocks, the suggestion of "programme" in serial pattern, all lend some weight to the view that a basic common impulse prompts the successional changes When incurving of the shell is repeated in oyster-stocks time and again, when the horned dinosaurs arise along four or five independent routes of development from ancestral hornless forms, when corals of different geological periods pass through similar evolutionary stages in colonial form and internal plate-structure, when toe-reduction is characteristic of all the branching lines of the horse family, the evidence suggests the conclusion that the similarities of structure and of evolutionary trend are due to the same internal stimuli Nevertheless, the explanation of the parallelism need not be a vitalist one and can, with a desirable economy of hypothesis, remain within the mechanist frame

The environment is passive in its control on adaptation It cannot evoke variants of the preferred kind, but must wait upon "chance" mutation for the materials of selection Mutations are (in large populations and in the course of geological time) many and varied, but they are not utterly random, and do not occur in "all" directions, and of those which arise, a great number are disadvantageous, and are likely to be discarded from the stock in the course of a few generations. Furthermore, mutations cannot be adjudged beneficial in isolation. They always work in association with all the other genes of the genotypic system, which must necessarily be in a state of harmonious functional equilibrium; and their effects are resultant effects A new mutation cannot upset the genotypic equilibrium unduly, and must pass the test of being acceptable to its fellow genes before the organism possessing it is able to grow Those kinds of mutations which have been tried and proved thus tend to receive preferential treatment and to survive. In any one major group of organisms, therefore, the field of mutation is narrowly circumscribed by the group's basic structural pattern, and within the field, because of this constraining uniformity of the ground-plan, there is a recurrent tendency to throw up repeatedly for selection the same kinds of mutants

In one sense evolution is thus predetermined, being limited in its operations by the nature of the genic mutations, and evolutionary trends are expressions, when the environment is encouraging, of latent possibilities. In successional species the appearance of rectilinear evolution is then due to the inherent conservatism of genotypic self-protection on the one hand and the necessity for some degree of adaptation on the other. In stocks belonging to the same broad organic group having a fundamental genetic unity, parallel lines of evolution occur because in a given environment similar mutants are likely to recur in he separate stocks and to be equally selectively preferred

It is significant that the parallelism need not be, and almost never is, synchronous in its expression in the different stocks, which bear every indication of waiting upon circumstance for opportunity. Significantly, too, the parallelism is rarely precise Thus the astonishing similarities displayed, for instance, by the foot-series of North American horses and South American litopterns break down in detail when the relative proportions of the various bone-lengths are measured (the toes being longer, the splints shorter, in the litopterns) or the mechanism of the ankle-hinge examined (*see* Fig 5, page 73) The selected mutants were therefore not identical in the two groups, and represent opportunist response to adaptation with whatever genic instruments were available

Vitalist theory also enters into certain interpretations of individual development It is notorious that in summing up the relation between the stages of individual growth and the stages of racial history, Haeckel in the late nineteenth century propounded the " law " that the development of the individual recapitulates the history of the race Understood literally, the " law " enforces a rigid predetermination on individual growth, and lays central emphasis on the arbitration of past events in determining the nature and the order of individual developmental stages This can scarcely be the case

As the individual at all stages of growth must be able to live, must be sufficiently adapted to survive, must make immediate response to immediate need, the prophetic control of past ancestral stages on present living ones can only be partial and coincident, not wholly instrumental and antecedent The fact that primitive ancestral vertebrates, bony fishes of Devonian times, spent their whole lives in water cannot directly control the manner of growth of a descendant reptile spending the first weeks of life inside an egg-shell before hatching out into a dry environment, and the fish-form, well adapted for aquatic swimming, cannot possibly be repeated by the fœtus growing in the womb of the descendant mammal.

Systematic modification of successive life-histories, which is evolution, is not simply brought about by each generation adding a little more to the sequence of steps passed through in parental life-history On the contrary, it depends on mutation, which is a reorganization of the activator system that controls growth A new mutation is (normally) already present in the initial fertilized egg, and it can exercise its influence at any stage of growth of the mutant form. There is no intrinsic reason, therefore, why individual growth-history should not differ and deviate from ancestral growth-histories in infancy or in youth or in maturity The conventional expectation that individual growth will pass through stages in correct order and all reflecting the forms of successive adult ancestors has no warrant in the nature of the evolutionary process or in the physiology of growth. That in fact it often (but only approximately) does so is probably due to the resistance of the whole gene-complex to radical disturbance by any single mutation, the effects of the mutation then being chiefly expressed in slightly modified growth-rates of organs and characters.

In its accommodation to changing circumstances of growth, individual life-history seems to be as opportunist as the process of evolution of which it is an incidental by-product.

CHAPTER X

PURPOSE AND PROGRESS

IN anthropocentric view it is possible to look upon the ultimate purpose of evolution as being the emergence of mankind, and its progress to be marked by the appearance of successively higher forms of life. In the light of the evidence now available, and the kind of explanatory synthesis which is scientifically acceptable, such a view invites rejection

In a biological sense, human evolution displays the same kinds of changes as those seen in the oyster and the sea-urchin, the dinosaur and the horse Man is a member of a comparatively insignificant and primitive group of mammals, the primates, which had their obscure origin, possibly in small rodent-like or insectivorous creatures, towards the end of Mesozoic times The form of the early primates shows them to have been tree-dwellers, and, with few exceptions until the appearance of man-like apes, they continued to favour a forest environment throughout their evolution Modern forms which are not very different in general structure from the ancestral primates include the tree-shrews and the lemurs, and although living lemurs cannot be links in the chain of human evolution, fossils suggest that a lemuroid stage probably occurred in the early Tertiary ancestry of most of the larger modern monkeys, apes, and men, all of which preserve some anatomical relics of arboreal adaptation

The distribution of the early primates and near-primates was wide, fossils being known from all the continents except Australia. Manifestly there have been a fragmentation and a restriction of range in more recent times, and much of the Old World is without lemurs and apes, and North America and Europe virtually without primates (except man), at the present day The fragmentation is accompanied by adaptive isolation: already in early Tertiary times there was a major differentiation of primate groups reflecting geographical location. The remote New-World forms, confined almost exclusively to South and Central America, include the marmosets and the ring-tailed monkeys: they differ, notably in having three premolar teeth, from the Old-World monkeys and apes, having only two Since this structural difference was already displayed by the forms of mid-Tertiary times, it is probable that the increase in brain-size which took place in both groups throughout the Tertiary era is an instance of parallel but independent evolution

The Old-World monkeys, living in the warm forest belt extending from Africa through southern Asia into the South Seas, look very like and have similar habits to their South American cousins. They are known in the fossil state from specimens discovered in both Africa and Eurasia, and they appear to have remained modestly successful in their adaptations until the present day—though the cold conditions drove them out of Europe during the Glacial period and they have not since returned (except to Gibraltar).

Related to the Old-World monkeys, and probably evolved out of them in early Tertiary times, the anthropoid apes differ from the other primates in brain-size (and correlated intelligence), in body-size, in the loss of the tail, and in the assumption of a ground-dwelling habit While the monkeys are little reduced in numbers or variety, and indeed (subject to competition with man) may still be progressing from their condition in former periods, the apes are certainly declining Fossil apes have been discovered in considerable numbers during recent years the earliest known lived perhaps forty million years ago, and during mid-Tertiary times, particularly in Africa, whole families of apes evolved and spread over much of the Old World (but not of the New) In later Tertiary times, for whatever reason (partly perhaps because they suffered hardship with the onset of the rigorous climate of the Glacial period), their numbers were reduced, and they now exist only in the gibbon, the orang-utan, the gorilla, the chimpanzee, and man The gorilla and the chimpanzee need to be artificially protected to be saved from likely extinction, and only man is "successful" as judged by increasing numbers

Anatomically, man is a great ape not differing in any notable feature from the other apes, and displaying particularly close resemblance to the chimpanzee and the gorilla—not that he is descended from either, since all three are contemporaries. His ancestry, like that of the other apes, is represented in the fossil record by forms which clearly show the collateral stages of transition from early Tertiary prototypes

On the whole, evolution in the apes has been relatively slow, skeletons of what seem to be typical gibbon-like and gorilla-like forms being known from mid-Tertiary rocks Man, on the other hand, shows evolutionary progression notably in two features the structure of his head, and his upright posture The former is characterized by an inflation of the brain-case and a refinement of the face, the latter by the perfection of the bipedal stance (which entails structural adaptation of the backbone and the legs) with the adoption of a permanent ground-dwelling mode of life. In these features he is "progressive," and offers the main contrasts to the "conservative" gorilla and chimpanzee.

A number of intermediate types linking man with typical apes are now fairly well known. He belongs to a divergent offshoot that stemmed from a form not unlike the mid-Tertiary *Proconsul*, a ground-dweller standing perhaps not too surely on his hind legs Shortly before the beginning of the Glacial period, whole families of ape-like forms, of which *Australopithecus* is representative, were common in South and East Africa, pointing to a local burst of evolution: they had the low skull-crown, brow-ridges, and projecting jaws of an ape-like form, but in subdued degree, in the size of their brain they were (being small) proportionately far in advance of the chimpanzee or the gorilla, though approximating to the latter in an absolute cranial volume of about 600 c c., and they appear, from the structure of their hip-bones, to have been upright walkers The more recent Java man (*Pithecanthropus*) and his near relation, Pekin man (the so-called *Sinanthropus*), lived during the Glacial period, perhaps half a million years ago. Although they show many ape-like features in their skulls (including prominent brow-ridges and projecting jaws), the volume of the brain-case in some specimens reaches 1300 c.c.—about that of a living Australian aborigine—and they were skilful and intelligent enough to make artefacts and to use fire, and imaginative enough to be ritual cannibals The English Piltdown man (*Eoanthropus*), also of Glacial age, is even more modern in appearance, with a characteristic human cranium of about 1300 c.c in volume, but with projecting simian jaws Neanderthal man (to whom Rhodesian man is very similar) is sufficiently human to be placed in the genus *Homo* (though not to be called *sapiens*) He is known in a large series of specimens from many parts of the north-western Old World—

specimens which show a gradation, particularly in refinement of face and perfection of upright stance, towards distinctly " modern " types, and which in some samples hint at direct relationship with races of men still living

The precise lines of descent of present-day man continue to be matter for argument, most of them probably not stemming directly from a neanderthaloid stock But, despite this uncertainty in detail, the fossils leave no room for doubting the essential truth that man is descended from simian ancestors Moreover, it is clear that within the species *Homo sapiens* there have been widespread regional differentiation and local evolution comparable with but not so profound as those seen in the monkeys The broad distinction between the four main kinds of men—australoids, negroids, mongoloids, and " whites "—is in a generalized way an instance of incipient geographical speciation, partly in the form of graded clines, as between Europeans, Iranians, and Indians, partly by disjunction, as between " white " North Africans and negroid tropical Africans separated by the Sahara desert barrier

It will probably remain impossible to disentangle in detail all the threads of man's ancestry, since superposed on the regional subspeciation (a product of relatively static settlement) there has been widespread migration tending to smooth out the subspecific contrasts All men are thus hybrid in more or less degree, and with the relative intensification of migrant cross-breeding in recent centuries (especially in the New World), novel gene-combinations are producing new types of men as further examples of the evolutionary process

In no single respect does the evolution of the primates differ in kind from that of any other group of organisms. As in those other groups, it is compounded of elements

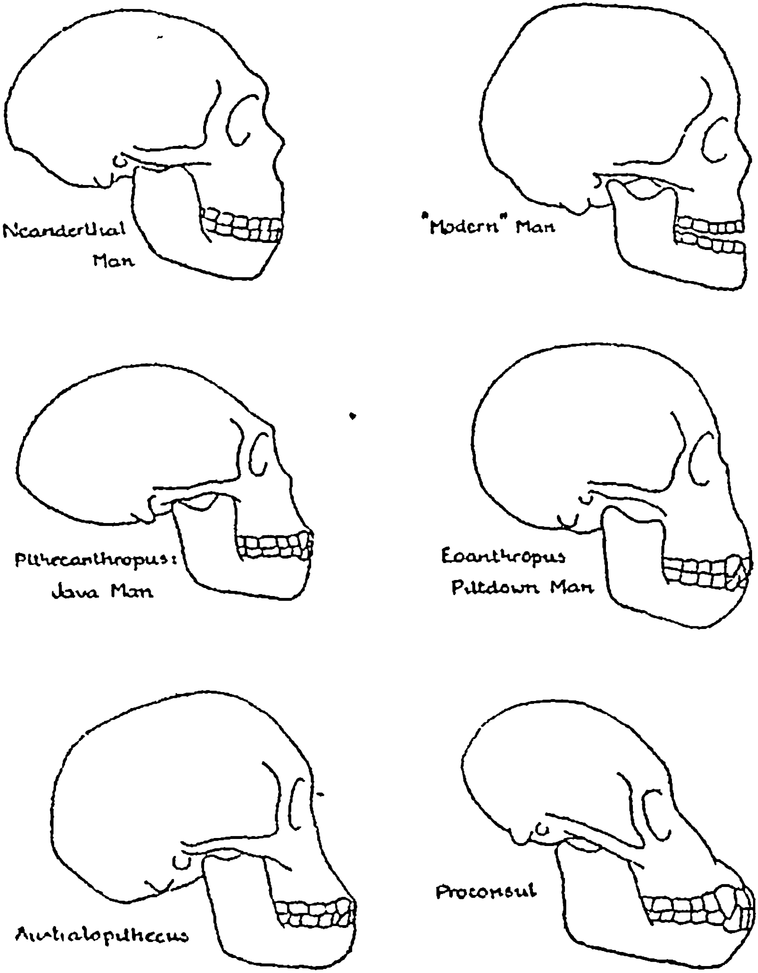

FIG 8—Fossil man-like apes and men, showing gradation in structure *Proconsul* lived about 20 million years ago, *Australopithecus* about two or three million years ago, the remainder were more or less contemporaneous during the Ice Age, and were sufficiently intelligent to manufacture implements

which are come together at random, and its products are likely to suffer the vicissitudes and fate of all organic groups Monkeys and man happen at the moment to be successful, or perhaps in the ascendant, but the lemurs are declining, most kinds being restricted in their distribution to the island sanctuary of Madagascar, and the great apes, formerly relatively abundant, varied, and widespread, are now on the way to extinction The rise and diversification of the different groups took place by a happy but quite fortuitous association of the right genes and the appropriate environment of selection It is quite impossible to " explain " primate evolution without taking both factors, which are mutually independent, into account.

In scientific aspect the evolutionary process is without obvious purpose—though, knowing how it works, man may become increasingly able to make it purposeful in his own behalf Nor does it bear the marks of what can be called progress By equating progress with size or intelligence or complexity it is, of course, possible to see progress in sundry manifestations of evolution. Reptiles may then be regarded as an advance on fishes, mammals on reptiles, man on monkeys But such partiality and over-simplification neglect the multiplicity of elements in the evolutionary process A " line " of evolution is a convenient fiction it is, in fact, never a line, but a network linking a great number of more or less related individuals which show diversification through constant radiating adaptation Some, perhaps most, of the adaptations have only a brief and modest day before their lines are exterminated Some are given the opportunity of exploring new environments, and flourish in numbers and variant kinds Some display close selection and persist as long-lived forms in an unspectacular way But none shows continued " success " (judged by numbers and kinds) over long intervals of geological time.

There is no steady march of progress. The reptiles did not evolve out of the ruling amphibians, or the mammals out of the ruling reptiles, and the primates had their origin in a mammalian group completely insignificant to the present day. The general picture is not one of continued advance (even as measured by arbitrary yard-sticks), but of replacement. This is to be expected as a reflection of the fact that successful specialization in one environment is disadvantageous in another; and only exceptionally is the closely specialized form able to retrace its steps or diverge along a novel path at a speed sufficient to prevent extinction in the struggle for survival. In a sense, the more successful a group happens to be, the more "progress" it appears to have made, the more ominous is the prospect for future evolution. Sooner or later it can expect to be replaced by another group adaptively more responsive, which in due course will undergo similar rise and decline.

Moreover, there is no single dominant reigning group of organisms at any one time references to the "Age of Trilobites," the "Age of Goniatites," the "Age of Reptiles," though proper comments on aspects of the fossil record, are partial and biased in broad view. There was no period in geological history which was dominated exclusively by trilobites or goniatites or reptiles. Different classes of organisms have tended to select different kinds of environments for colonization and consequent survival, and if the environments are very different the classes may never meet Thus competition between mammals and deep-sea fishes, or between birds and corals, is exceedingly indirect, and in their respective realms successful and abundant forms persist without coming into disastrous conflict. Thus the Age of

Trilobites was also the Age of Graptolites, and the Age of Reptiles was also the Age of Ammonites

Even within the one group of the reptiles it is only partly true to say that they gradually declined and nearly died out with the rise of the mammals (the replacement being regarded as an aspect of "progress") The statement applies only to terrestrial and aquatic reptiles It does not apply at all to that specialized reptilian offshoot, the birds, which throughout their history have been virtually untouched by mammalian competition (the bats being poor rivals, acknowledging as much in their nocturnal habits) they continue to thrive in the greatest variety and abundance at the present day, and the Tertiary era has been the Age of Birds no less than the Age of Mammals indeed, on any material measure of success the birds are at least as successful as the mammals, in most groups of which there are clear signs of decline

In the same way, invertebrates are, no doubt, in structural and functional complexity "inferior" to the vertebrates, but there manifestly has been no progressive evolutionary rise from one group to another Molluscs and crustaceans, corals and sea-urchins, are as abundant as ever they were, and within their groups they display the same sort of evolutionary expansion as the fishes or the reptiles or the mammals, and the insects have reached a peak of diversity and abundance scarcely approached by the vertebrates The single-celled animals and plants, structurally the most "primitive" of cellular organisms, may well be at their acme of development at the present day

In such a rich and varied context of evolutionary lines it is impossible to discern a single over-riding motif in evolution A scientific explanation of the course of evolution therefore avoids reference to either purpose or progress in its recognition of the factors of change. So far as it is scientific, it falls back on the empirical evidence; and to cover the phenomena it elaborates the relations of nature and nurture as its theme, which it sets in the scale of geological time.

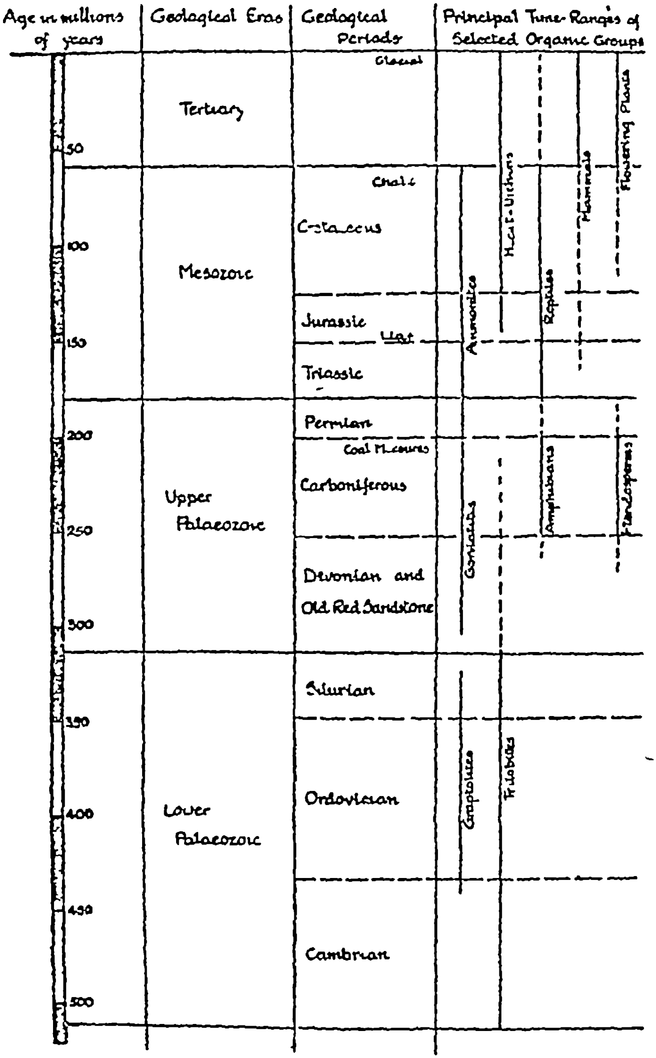

FIG 9 —Table of the fossiliferous geological formations

GLOSSARY

Adaptive radiation. The divergence from a primitive ancestral stock of lines of evolution displaying structural and functional adjustment to a variety of environments

Amphibians. A class of vertebrate animals, typified by newts and frogs, which lay eggs in water, and breathe by means of gills in the tadpole stage and lungs in the adult.

Angiosperms. Flowering plants.

Arthropods. A group of invertebrate animals, including wasps, spiders, centipedes, and crabs, which have a segmented body with a more or less large number of legs, and an external skeletal sheath of horny material.

Chromosome. A thread-like structure in the cell nucleus, usually of specific shape and represented in constant number in each species, which appears during stages of cell division and carries a complement of genes

Cline. A graded change in the structure or appearance or behaviour of members of a species or species-group which has a wide range in time or space, a character-gradient.

Cycad. A plant of general palm-like form, but differing from the true palms (which are flowering plants) in having naked seeds

Drift. The evolution that may take place for a short time in populations too small to permit the statistical laws of systematic selection to apply, and that may then not be strictly adaptive.

Fœtus. The earliest stage in the growth of a mammal, when it still lies in the womb.

Fossil. A relic of former life, most often a skeletal hard part, but sometimes an impression, usually preserved in sedimentary rocks

Gene. A unit of hereditary control, having a definite position on a particular chromosome, and probably a definite chemical composition, which is a prime stimulus of individual growth.

Gene-flow. The exchange and re-assortment of genes between genotypes on cross-breeding

Genetic system The integrated association of chromosomes and genes in a germ-cell forming the internal environment in which the single gene operates

Genotype. The association of hereditary materials in the germ-cell determining the nature of the individual

Genus. A classificatory category in which species of common origin or common basic form are placed

Habitat The normal environment of an organism living under natural conditions.

Hormone. A secretion usually of the ductless glands which has a marked effect in stimulating the processes of growth

Hybrid. The offspring of parents which differ genotypically from one another

Invertebrate. Animals, like snails, jelly-fishes, lobsters, worms, and sea-urchins, which are without a bony backbone though they may possess other kinds of skeletal supports

Larva. A young stage in individual development that is markedly different in outward form from the adult, as the chrysalis of a butterfly or the tadpole of a frog

Lethal gene A harmful gene whose possessor fails to survive beyond the early stages of growth

Lineage. A succession of forms constituting an evolutionary series, a " line " of evolution

Mammals. A class of vertebrate animals in which the young is nourished in the womb until a late stage of growth, and after birth is suckled for a time by the mother

Marsupials. A group of primitive mammals in which the young are born at a stage of extreme immaturity, and for a time are carried by the mother in the marsupial pouch

Molluscs A large group of invertebrate animals, most of which are partly protected by an external shell, single and coiled in snails and ammonites, bivalved in mussels and cockles

Mutant. An individual displaying structural or physiological differences from its fellows because of genic differences, a gene differing through mutation from equivalent genes in other individuals or cells

Mutation A change in the hereditary quality of the genotype arising through an alteration of the chromosome-arrangement or of the nature of a gene.

Orthogenesis. As description, the determinate and undeviating course of evolution apparently displayed by some groups of organisms, as theory, the ascription of inherent momentum promoting the rectilinear trend of such evolution.

Phylogeny. The path of evolution in a group of animals or plants, sometimes equivalent to a lineage, but usually with a wider connotation to include collaterals; racial history.

Placentals A group of mammals in which the young are born in a relatively advanced stage of growth (the name being derived from the placenta, a structure in the womb allowing a rich food-supply for the fœtus)

Plexus. The network of kinship between generations when evolution is seen as the historical passage from a host of individual ancestors to a host of individual descendants

Position-effect. The effect on the mode of activity of a gene following from the controls exerted on it by neighbour genes according to its position on its chromosome.

Pteridosperms. A group of plants with a general fern-like appearance and foliage, but (unlike true ferns) bearing seeds

Pure line. A succession of generations in which parents and offspring are genotypically identical

Reptiles. A class of vertebrate animals which, like the mammals, breathe by means of lungs throughout life, but, like the amphibians, lay eggs and do not suckle their young.

Speciation. The process of differentiation of a parental species into a number of distinct descendant species, usually through geographical isolation.

Species. A classificatory category subjectively defined in various ways, but objectively defined for convenience as the group of all those organisms which (actually or potentially) freely interbreed in natural conditions to produce fertile offspring

Subspecies. Usually a local subdivision of a species characterized by structural or physiological peculiarities but not separated from neighbouring subspecies by reproductive isolation, a geographical race

Transient. An individual member of an evolutionary series.

Variability. The capacity of an individual or a population to express a range of differences in form or behaviour according to the reaction between genotypic nature and possible environments of growth.

Variant. An individual differing phenotypically (for whatever reason) from its fellows or from the norm of its kind

Variation. The type or range of variability of an individual or a population actually expressed in a given environment

Vertebrate. An animal possessing an internal backbone as essential skeletal support.

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