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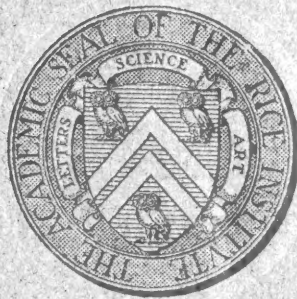


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PROBLEMS OF ORGANIC ADAPTATION¹

LECTURE I

FITNESS IN THE LIVING WORLD

ADAPTABILITY may be defined as the power of self-regulation, self-preservation, and race perpetuation, by means of which living things are enabled not only to remain alive but also to adjust themselves to varied environmental conditions and to leave offspring. From the standpoint of any species the best that can happen is to increase and multiply, the worst is to become extinct. Self-preservation and race perpetuation are the *summum bonum*; everything that makes for these is beneficial and adaptive, everything that prevents or hinders these is injurious or unfit. Adaptability is a fundamental property of living things without which life itself could not long persist, for as Herbert Spencer has said, life is "continuous adjustment of internal relations to external relations." The origin of this or of any other fundamental property of life, such as metabolism, reproduction, or irritability, is shrouded in the same mystery as the origin of life itself.

On the other hand, adaptations are special adjustments to particular conditions; they are individual examples of the general property of adaptability. As such they have arisen in the course of organic evolution, and their origin, no less than other special structures and functions, must be explained by any adequate theory of evolution.

¹A course of three public lectures delivered at the Rice Institute, March 8, 9, and 10, 1921, by Edwin Grant Conklin, Ph. D. (Johns Hopkins), Professor of Biology in Princeton University.

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Such special adaptations to particular conditions of life are very common among all organisms, but they are not universal. Some organisms have been able to adjust themselves to one kind of environment and others to another kind, and although a certain degree of adaptability is universally present, no single organism is able to adjust itself to every kind of environment. Special adaptations to particular conditions of life are examples of differentiation, which always implies limitations in certain directions in order to progress in other directions. Consequently one organism is peculiarly fitted for one environment and another for another, but no organism is universally fitted for all environments.

Again, adaptations are relative but not absolute adjustments. Even the most perfect adaptation is not absolutely perfect. For example, that marvel of adaptation, the human eye, is very far from being a perfect optical instrument; Helmholtz is reported to have said that if an optician should send him an optical instrument as imperfect as the human eye, he would send it back to him and tell him to learn his business; and yet there is probably no more perfect adaptation in nature than this. Furthermore, all gradations of adjustment occur among different organisms from the relatively imperfect to the most perfect, and these gradations indicate that fitness in the living world is relative and not absolute, and they indicate that adaptations are a product of natural evolution rather than of supernatural creation.

Adaptations to particular conditions of life are seen in almost every structure, function, and relation of organisms; in the microscopic and ultra-microscopic parts of cells, as well as in entire cells, tissues, organs, systems, biological persons, and animal states; in the chemical and physical

constitution and behavior of protoplasm and cells as well as in the morphological and physiological modifications which fit the organism to changed conditions of environment.

So general are such adaptations that it has often been asserted by naturalists and philosophers that they are universal—that all structures, functions, and relations of living things are adaptive or useful, or at least that they were adaptive at the time of their origin, and that, with regard to every vital process, we may properly ask the question, *cui bono*, being confident that it is or has been useful. This postulate of universal utility in the living world could be maintained only by assuming that many things which are now injurious had once been useful, and that many things which now seem to be useless will sometime be found to have a use. Such a postulate may be logically and hypothetically possible, but it is very improbable. While there are innumerable instances of utility in the living world, there are thousands of cases where structures, functions, or relations are in all probabilities not useful but indifferent, and some cases, though relatively few, in which they are positively injurious. Therefore it is not possible to maintain the postulate of universal utility in the living world.

Having found that general adaptability is universal in the living world but that success in making adaptations to particular conditions is never perfect and is sometimes lacking altogether, and that it is not safe to assume that every structure, function, or relation of organisms confers some known or unknown benefit upon its possessor, we may proceed to examine in detail some of the more striking and wonderful fitnesses which are found in the living world.

In this survey, we shall deal not only with the general relations of organisms to their environments but also with

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the intimate and minute adaptations found in organs, tissues, and cells, and we shall consider first, inherited adaptations, and later, acquired ones.

Our object is not to catalogue and describe the multitudes of adaptations which have been observed among animals and plants, but rather to find an explanation of their origin. However, since some recent writers have adopted the method of explaining adaptations by explaining them away and have solved the problem of their origin by denying their existence, it seems advisable to review some of the more striking fitnesses that are found among living things and especially among animals.

Let us begin by freely admitting that under the influence of the doctrine of supernatural design there has been a marked tendency to exaggerate the frequency and the perfection of organic adaptations. Many naturalists have seen adaptations where they do not exist and have invented environmental conditions to fit these fanciful adaptations, and when the usefulness of any structure or function could not be made probable even by these means, it was always possible to assume that this was due merely to our ignorance of the real functions of the part in question or the real needs of the organism. Sometimes the purely mechanistic results of necessary physical, chemical, and biological conditions have been regarded as special adaptations, and in general, the attitude of those who are looking everywhere for adaptations has not been very critical.

But when we are assured by some modern critics that all adaptations can be explained away in this manner, is it not evident that extravagant and uncritical opinion has swung to the other extreme? Adaptations may not be universal, they may not be perfect, but that they are very numerous and frequently so delicately adjusted to needs as to excite

the admiration of the thoughtful, let the following classification and illustrative examples testify:

I. RACIAL OR INHERITED ADAPTATIONS

Inherited adaptations are those which appear in the development of individuals as if in anticipation of future needs and not as a result of present ones. The eye, for example, usually develops in the entire absence of light, and its various parts are formed as if in anticipation of their future uses; the same may be said of almost every other inherited adaptation. Particular adaptations characterize certain races, species and larger groups of organisms. Among these are innumerable structures, functions, habits, and instincts; indeed, one can think of scarcely any normal structure or function, reflex or instinct, that does not illustrate such racial or inherited adaptation.

1. *The Efficiency of the Living Machine*

This is an age of machinery, and the fitness of any machine is measured by its efficiency. Let us consider the fitness of the living machine as contrasted with those of human invention.

The frame or skeleton of most vertebrates is so constructed as to give the maximum of strength with the minimum of weight. Long ages before men had thought of using tubular frames in machines such as bicycles, nature had been using them in the shafts of long bones; ages before wire wheels and tangential spokes were thought of spicules and trabeculæ of bone were laced through the ends of long bones so as to afford maximum strength with minimum weight. Long before any human being had discovered, used, or classified the different forms of levers, nature had been using them in the limbs of arthropods and vertebrates.

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The mechanical principles of the wheel and the screw are not found anywhere among organisms for the obvious reason that every portion of the animal machine must be connected by blood vessels and nerves with the central part, but the use by animals of levers of all kinds and for every conceivable purpose has never been surpassed in machines of human invention.

The motive power of the living machine is found in protoplasmic contractility whether it manifests itself in amoeboid, ciliary, or muscular movement. But since all movement of large bodies must be brought about by muscles, we may limit our consideration to this type of movement. In spite of the fact that more attention has probably been devoted to the structure and function of muscle than to any other animal tissue, the ultimate causes of muscular contraction are still problematical. Nothing comparable to this form of motion exists except among animals. It is known that the chief source of chemical energy in muscular contractility is the burning of dextrose, but the manner in which this chemical energy is transformed into mechanical energy is unknown. However, the relative efficiency of different types of engines is known, and they may fairly well be compared with the living engine. The ordinary steam engine transforms about 10% of the energy of the steam into motion; the steam turbine, about 17%; the Diessel internal combustion engine has a practical efficiency of about 30%, while muscle has a net efficiency of from 20% to 30%. The living engine is therefore more efficient than the steam engine and about as efficient as the best type of engine that has been devised by man. But in addition to this, the temperature developed in muscle is much less, and the flexibility of the living machine, as measured by the rate or extent of movement, is much greater than in any other engine. For example, the

temperature never exceeds 110° F. and is usually much less than this, while it reaches 5000° F. in a gas engine; the rate of contraction may vary from movements so slow as to be scarcely visible to a rapidity of about 24,000 contractions a minute, as in the beating of a mosquito's wings; the extent of movement may vary from a scarcely perceptible shortening to one one-hundredth part or less of the maximum expansion, as for example, in certain worms and in the tentacles of some cœlenterates.

Consider the variety, complexity, and efficiency of the means of locomotion in animals. Among the marvels of nature Solomon enumerates "The way of the serpent on the rock and the way of the eagle in the air," but the more usual forms of locomotion, such as running, jumping, climbing, digging, sailing, wading, and swimming show fitness and efficiency that are equally marvelous. Consider the manner in which unusual speed has been attained in the horse, giraffe, and antelope by the lengthening of legs and digits, the elevation of the animal upon the ends of the middle digits and the loss of the lateral ones. Consider the remarkable contrivances of the kangaroo, the jack-rabbit, the grasshopper, the flying squirrel for leaping; of the sloth, squirrel, and woodpecker for climbing; of the earthworm, mole cricket, and mole for burrowing. Among aquatic animals almost every means of propulsion which man has devised was discovered ages before by lower animals: the Portuguese man-of-war and the paper nautilus spread their purple sails to the breeze and "sail the uncharted main"; the jelly-fish and squid use hydraulic motors; fish, seals, and whales employ oars and sculls. Finally, consider the wonderful adaptations by means of which animals travel the highways of the air: the spider which spins a thread that floats out on the breeze and then, clinging to this gos-

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samer, goes "ballooning" to new lands; the tremendous power of flight of the albatross and eagle; the apparently effortless soaring of the buzzard and frigate-bird; the flight of the arctic tern and golden plover from pole to pole, or the world-wide flight of the tiny humming-bird. Long ages before man had appeared on the earth, animals had conquered the land, the water, and the air; and although by means of his machines man can now surpass them in speed and strength in these three elements, they can still teach us much in skill and efficiency of locomotion.

The heart, with its valves, is a remarkably efficient pump; the strength and thickness of the muscular walls of the auricles and ventricles are nicely adjusted to the "load"; the valves are ideally constructed for quick, simple, and efficient action; the sequence of the beats in auricles and ventricles is usually perfect. Even more remarkable are adaptations to increased "load" during violent exercise or in high altitudes. In man the resting heart pumps about five pints of blood a minute, but in violent exercise it pumps seven times as much as this. The structures of arteries, veins, and capillaries are admirably suited to the needs of efficient circulation, and the mechanism for regulating blood pressure is extraordinarily efficient.

The efficiency of the living machine in the production of light, as for example in the firefly and glowworm, is incomparably greater than in the case of any lighting system of human invention. In electric lighting from 90 to 95% of the energy is wasted in heat and only 5 to 10% produces light, whereas these proportions are reversed in living things.

The mechanism for heat regulation in warm-blooded animals is wonderfully perfect. Irrespective of extreme changes in external temperature, the internal temperature is frequently maintained for years at a time within a few

tenths of a degree. Anyone who has ever tried to maintain an incubator at constant temperature, and especially under great external changes, will be in a position to appreciate the remarkable efficiency of this living thermostat. In hibernating animals the body temperature falls during the winter sleep, and in severe weather it may continue to fall until it approaches the freezing point. The animal then wakes up, as if an automatic alarm had been set to rouse it when the danger point had been reached, and by means of muscular movements, increased respiration and oxidation, and sometimes by feeding, the temperature is raised. This safety device is found not merely in the highest warm-blooded animals, such as hibernating bears, but also among some insects, such as bees. When the temperature in the winter cluster of bees goes below 57° F. the bees become active, eat honey, oxidation increases and the temperature of the cluster rises.

The respiratory mechanisms by which oxygen is brought into contact with every particle of living substance and the exhaust gas is eliminated are far more perfect than is to be found in any other engine. In the case of insects, minute air tubes or tracheæ run to every part of the body, whereas in many other animals in which respiratory organs (gills or lungs) are limited to certain regions, the blood contains a substance, hæmoglobin, which serves as a wonderfully efficient oxygen carrier.

The mechanisms of living things for obtaining, preparing, absorbing, and utilizing substances as fuel are incomparably more complex and efficient than in any engine of human devising, and the utilization of foods for growth and repair is wholly unparalleled in any other mechanism.

The uniqueness of the living machine is nowhere more evident than in its capacity for reproduction. Imagine any

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machine of human invention which had the power not only to do the work for which it was devised but also to give rise indefinitely to other machines of the same sort! Nothing could illustrate more clearly the fundamental difference between the living and the lifeless machine than this power of reproduction. If reproduction is one of the fundamental and original properties of living things and is therefore not to be explained as a result of organic evolution, at least the innumerable adaptations for promoting reproduction have arisen in the course of evolution and demand an explanation. Among these are the differentiations of male and female sex cells and all the differences in structure, functions, and instincts between males and females; the remarkable contrivances for insuring cross fertilization in plants and animals and for preventing hybridization of species; the infinite variety and nicety of the means for the protection and nourishment of the young. Nothing in the whole world of living things is more wonderful than these adaptations for reproduction.

Consider the wonderful fitness of the nervous system for receiving and transmitting stimuli and for coördinating the multitudinous activities of animals. The timer of an automobile is no more perfect than the timing of the various contractions in the heart beat, and the timing of various muscular contractions in standing or walking and much more in talking or in playing any game such as tennis or baseball is vastly more complex and perfect than in any lifeless machine. Think of the fitness of every organ for its particular use and then consider the peculiar fitness with which these organs are coördinated into an harmonious whole.

Think of the variety and range of sensations in any higher animal and the admirable fitness of the sense organs: the

fitness of the organs of touch and taste and smell, and the complex fitnesses and coadaptations of the many parts of the ear and eye. Many instruments of human invention are more sensitive to particular kinds of stimuli than some of the sense organs. For example, a thermometer is more sensitive to temperature changes than our heat and cold organs, the photographic plate is more sensitive to light than the retina, the microphone more sensitive to vibration than the ear; but when one considers the range and variety of stimuli to which higher animals are sensitive, there is no doubt that their sense organs are much more efficient than any non-living mechanism.

Finally, consider the durability of the living organism and its power of self-regulation and self-repair as compared with any other machine. Not for one moment between birth and death does the living engine stop. The heart and respiratory muscles cannot rest for a minute at a time during the whole course of life. Engines have been built that would run for a month or two without stopping for repairs, but the heart may continue to beat without interruption every second for a hundred years, pumping during this time not less than sixty million gallons of blood. The regulatory power of an organism is incomparably more varied and perfect than in any other mechanism; not only do all the complex processes of life occur, under normal conditions, in the best possible sequence and to the most favorable extent, but when as the result of abnormal conditions these processes are disturbed, the living machine has a wholly unparalleled capacity of regulation and restoration. When the living machine undergoes wear, injury, or loses parts, it is able to a surprising extent to repair itself and to restore or compensate for lost parts. What other kind of machine has a regulatory power that is comparable with that of a living thing?

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When we consider the wonderful efficiency of the living machine in all of the respects named, is it any wonder that there have always been those who have refused to believe that it is really or only a machine? Is it any wonder that they have insisted that it must be controlled by some sort of indwelling intelligence? When we consider these remarkable characteristics, we may well say in wonder and admiration, "What a piece of work is a man!" or any other organism.

Such adaptations to general conditions of existence are so common that to most persons they do not seem remarkable, while some peculiar adaptation, such as the leaf-insect or the Venus fly-trap, seems wonderful simply because it is not common. Many of these more uncommon adaptations have played an important part in the discussion of the various theories of evolution which have been advanced during the past century. As illustrations of adaptations to peculiar conditions of life may be mentioned the fitness of horses' limbs for running, those of seals for swimming, those of birds for flight; or the adaptation of the long neck and fore legs of the giraffe to its habit of browsing on trees; of the long necks and legs of wading birds to their peculiar habits; of the small fore legs and large hind legs and tail of the kangaroo to its peculiar method of locomotion. In this connection must also be considered the absence of limbs in certain lizards, snakes, and amphibians, and the degeneration or loss of wings in the apteryx and *dinornis* among birds and in certain insects inhabiting stormy islands. Here also must be classed the cases of adaptive atrophy or hypertrophy of organs, as for example the loss of eyes by cave animals, the decreased size of the jaws and teeth of civilized man as compared with savages, the increased size and length of the middle digit, and the reduction or disappearance of the lateral digits in ungulates, etc.

2. *Adaptations for Defense and Offense*

Every principle of defense known and used by man has been employed by lower animals for uncounted millions of years. Among these are thorns, spines, and armor, camouflage, the false flag, and that most effective means of defense—a strong offense. Thorns and spines, frequently barbed and poisonous, are of wide occurrence among animals and plants. The cactus and bramble, the sea-urchin and porcupine, ward off enemies by their bristling surfaces. Mollusks, crustacea, armored fishes, dinosaurs, tortoises and armadillos are veritable armored cruisers or land tanks.

Nowhere has the principle of camouflage been carried to such extent or perfection as among certain animals. The principle of protective coloration is of very general occurrence in the animal world. The polar bear and fox, the lion and antelope, the dark upper and light under surfaces of birds, resemble the backgrounds against which they are usually seen. Even the tiger and zebra are protectively colored to match the lights and shades of their natural habitats, a thing which can be readily believed by anyone who has seen the bizarre bars and patterns on camouflaged ships. When the background changes, as from winter to summer, some animals change their colors, as in the case of the ptarmigan and arctic hare, which are white in winter and gray or brown in summer. Other animals change colors and patterns very rapidly to match corresponding changes of the background, as in the case of cephalopods and fishes (especially flounders), amphibians and reptiles (notably chameleons).

Animal camouflage includes not only colors and color patterns, like those of the background against which the animal is seen, but also shapes and outlines like those of surrounding objects. Some fishes, crustaceans, mollusks, and worms which live in sea-weed are covered with streamers,

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and ragged processes so like sea-weed that it is very difficult to distinguish them from the weed. Certain animals, such as the stick insect, dead-leaf butterfly, and bark spider are so much like the objects on which they are commonly found, both in form and color, that it is difficult to detect them even when searching for them. Other common forms of camouflage are found in "feigning death," or rather in remaining perfectly quiet to escape detection, for moving objects even though they have concealing colors or forms are much more readily seen than those that remain motionless.

The use of a "false flag," which has been so much condemned in human warfare, has apparently been resorted to by animals in certain instances. Such sailing under false colors is known in zoölogy as "mimicry." Insects that are protected by nauseous odors or by other means are sometimes mimicked in form, color, and peculiarities of posture or locomotion by other insects not closely allied to them. Snakes that are non-poisonous sometimes mimic poisonous ones in forms, colors and threatening attitudes. But in zoölogy it is almost as difficult to establish the use of a false flag as it is in naval warfare, and it may be that two different species have independently developed similar flags so that neither is "mimic" or "mimicked."

Electrical fishes, such as the electric eel and the torpedo, are able to generate a strong charge of electricity with which they can shock and stun their enemies or their prey. Of course submarines and flying machines are an old story in animal life, and even smoke screens, or what correspond to these, are used by the squid and other cephalopods which in fleeing from enemies throw out a cloud of ink which conceals them. These modern methods of human warfare have been used for millions and even hundreds of millions of years by lower animals.

In animal, as well as in human warfare, the most effective defense is a strong offense, and innumerable adaptations are found for this purpose. Among these are many ferocious modifications of teeth, such as tusks, sabers, and swords; great developments of spurs, claws, pincers, and horns; poisons and poison gases, such as the sting of the bee, the poison of serpents and scorpions, the odors of bugs and skunks. These last anticipate in many respects some of the newest methods of gas warfare. But although many animals have stings and spears, none has developed projectiles that can be discharged at a distant mark.

When one considers all these striking contrivances for defense and offense, together with the appropriate behavior by which they are accompanied, such as the well-known habits of the rattlesnake, the porcupine, the opossum and the skunk, the question inevitably arises whether lower organisms have not discovered these means of protection in a manner comparable to the way in which man has discovered methods of defense and offense.

3. Interorganismal Relations

Another class of racial adaptations is found in certain typical correlations between animals and plants, between different species of animals or plants, and between different individuals of the same species. Fifty-six years before Charles Darwin published the "Origin of Species," Konrad Sprengel (1793) published a work entitled "Das neue entdeckte Geheimniss der Natur" in which he proved that flowers exist for the purpose of attracting insects in order that the insects may carry pollen from flower to flower, thus insuring cross fertilization. The contrivances by which flowers attract insects, such as color, scent, and nectaries, reach a climax in such plants as orchids, in which the nectary

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can be reached only by a particular route and by certain species of insects, and the pollen is so located in the flower that masses of it will become attached to the proboscis or other portions of the insect, and these masses will then be deposited upon other flowers of this species visited by the insect. Both flowers and insects are benefited by this adaptive relationship. The yucca moth collects pollen from one flower of the yucca, flies to another flower and lays her eggs among the ovules, and then places pollen upon the stigma, without which fertilizing act the ovules would not develop. As the larvæ of the moth develop, they eat a part of the ovules but leave a part, so that seed is produced, and thus both species are perpetuated. This act is performed but once in the life of a moth, so that there is no opportunity of learning by experience or imitation. It is a principle in such mutual dependence that each member must conserve the other, and even in parasitism the parasite must not usually destroy the host else it will at the same time destroy itself.

Extraordinary cases of adaptation are found in the peculiar life histories of certain parasites, which must pass through one or more larval stages in intermediate hosts before they reach the adult stage in the final host. Consider, for example, the almost infernal ingenuity shown in the life history of the malarial organism, which adapts it to life in the mosquito and in man and to its transfer from one to the other; or the adaptations shown in the life history of the liver-fluke, which passes through four different larval stages in one or two intermediate hosts before reaching its final host; or the life histories of the tapeworm or hookworm or trichina, which are wonderfully adapted to securing the survival, multiplication, and distribution of these parasites. Perhaps nothing in nature exceeds in complexity and nicety of adaptation the life histories of such parasites.

The more common relationships of individuals of the same species, as for example between males and females, parents and offspring, and all the castes with their different functions among social insects, are notable instances of adaptation. What is more wonderful than the great drama of sex, in which all living things, except the very lowest plants (bacteria), are actors, in which admirable coadaptations for bringing about cross fertilization are found, all the way from the structures and functions of the egg and spermatozoon to the secondary sexual characters and the complicated instincts and behavior of males and females? Consider the very common adaptations found in the relations of parents and offspring, the various methods by which the young are protected and supplied with food, and the complicated behavior which characterizes this relationship in higher animals.

4. Adaptations of Development

To the embryologist at least, no adaptations are more striking than those of development. In the normal development of an egg or embryo every step leads to what seems to be a preconceived end. The differentiations of ontogeny are usually adaptive. The cleavage of the egg subdivides the egg substance both quantitatively and qualitatively in such manner as to determine the relative sizes and locations of future parts. Even the distribution of substances in the unsegmented egg may foreshadow the proportions and localizations of future organs. These organs develop not for immediate but for future uses and in anticipation of distant needs. For example, consider the development of the eye; the retina with its sensory rods and cones, the lens with the ciliary processes and muscles for focusing, the transparent cornea and humor—each and every portion of the organ

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develops toward the end, or shall we say "for the purpose," of vision, and yet there is no vision until after all these parts are formed and connections have been made with the central nervous system, which does not occur until late in development, sometimes, as in the case of the rat, some time after birth. Organs are sometimes developed which are used only once in the life of the individual, as, for example, the egg-tooth on the beak of a bird, which is used only for breaking its way out of the shell at hatching.

In all of its general features development is teleological, and contemplating this we may well appreciate the words of the psalmist, "I am fearfully and wonderfully made." "In thy book all my members were written which in continuance were fashioned when as yet there was none of them."

5. Adaptive Behavior

Some of the most striking of all adaptations are found in the field of behavior and instincts. Even the simplest plants and animals avoid injurious regions and substances and find beneficial ones. For example, some bacteria will aggregate in certain regions of the spectrum and avoid other regions; they move away from salt solutions, or from distilled water, and collect in nutritive substances. Paramecium and many other protozoa behave toward injurious or beneficial substances in a similar manner, and especially notable is the way in which Paramecium avoids extremes of heat and cold and remains in regions of moderate temperature. The tropisms of germ-cells, of seeds, seedlings, and embryos, are generally adaptive. In plants as well as in animals the sperm finds the egg and is received by it. The root of the seedling grows down into the soil and the shoot up into the light and air. Sensitive plants close their leaves when stroked or exposed to dry air, thus preventing injury or desiccation. Insectivo-

rous plants catch insects by sticky secretions or traps, and they then infold and digest them. The plant known as "Venus fly-trap" does not respond, by closing, to a single stimulus, such as would be produced by accidental contact with a falling object, but only when the stimulus is repeated within three minutes, as it would be if that object were an insect; incidentally, this behavior shows that this plant has a kind of memory ("organic memory") which lasts for a period of about three minutes.

The behavior of higher plants and animals is almost always adaptive, and where it is not so it can usually be explained as the result of unnatural, or at least unusual, conditions; thus the tendency of insects to fly into a flame is the result of positive phototropism, which is beneficial in a state of nature and injurious only in the artificial conditions created by man. The behavior of insects is sometimes so remarkably adaptive that it seems to be intelligent and purposive. Thus the solitary wasp, *Sphex*, digs a burrow in the ground and stores it with caterpillars which have been stung in such a way as to paralyze but not to kill them. On these caterpillars she lays her eggs, and when the larvæ hatch they find an abundance of fresh meat for food. On leaving the burrow the mother *Sphex* carefully conceals it by closing it with earth; the Peckhams and more recently several others have observed that she then takes a small stone in her mandibles and pounds the earth down with it and then smooths the earth so that all traces of the burrow are removed. The instincts of ants and bees have long been studied, but they never lose their charm and interest; the instincts of the different castes or members of the colony, and even of the same individual at different stages of its life, are very unlike, and yet all are adapted to the preservation and prosperity of the colony.

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The migratory habits of animals are no less wonderful. At the breeding season myriads of shad and salmon migrate from the sea far toward the sources of fresh-water streams where the young may grow up in comparative safety, and although very few of the adult animals ever get back to the sea, yet this same instinct for migration possesses every new generation as it did the old one. The immemorial migrations of certain birds, going north in spring and south in autumn, are equally wonderful. The value of such an instinct to the birds is easily understood; but how did it arise, what series of natural causes can explain such an instinct? These adaptive instincts are no exceptions but only striking illustrations of a universal phenomenon among organisms. How can such useful and apparently intelligent and purposive adaptations be explained? Are intelligence and purpose in man fundamentally different from this adaptive behavior of animals? Apparently many gradations exist between these two, and in the development of the human individual every intermediate step is found between mere tropisms at one extreme and intelligence at the other. If tropisms and instincts are generally adaptive, are not intelligence and purpose higher and more complicated forms of adaptation?

6. Cellular Adaptations

Adaptations are found not only in gross structures and functions but also in the most minute, not only in tissues and cells but also in the smallest parts of cells. For example, what is there in the whole world more remarkable than the complex mechanism of nuclear division? We now know that the material basis of heredity is located in certain portions of the nucleus, the chromosomes, and, if this material is to be equally distributed in development to all portions of the body, each chromosome must be divided with exact

equality and the halves separated into the two daughter cells formed at each division. This "purpose" is accomplished by the complex mechanism of mitosis, which is almost universal in occurrence and has existed at least as long as many-celled animals and plants have, but which was not discovered by man until the middle of the nineteenth century, and its significance has been appreciated only during the past forty years.

Since chromosomes are persistent structures their number would double, and the inheritance material would double, every time a spermatozoon unites with an egg, were not some provision made to prevent this. Such provision is made in a unique form of nuclear division, which takes place only once in the whole life of an individual—in man once in billions of billions of divisions. This unique division is brought about by the union of corresponding or homologous chromosomes of the father and mother at the time of the formation of the germ-cells—a process known as synapsis—and the subsequent separation of these *whole* chromosomes in mitosis, so that each germ-cell, whether egg or sperm, contains only half the normal number; then when egg and sperm unite in fertilization, the normal number is restored. Upon these processes of synapsis and reduction of chromosomes and subsequent union of egg and sperm depend all the phenomena of Mendelian inheritance.

The fact that in most species males and females occur in equal numbers has always been regarded as a remarkable adaptation—indeed, the fact that males or females, with their coadapted structures, functions, and instincts, should occur at all is a notable adaptation. It is now known that sex is determined by a certain combination of chromosomes; in the female there are usually two sex chromosomes (xx), in the male there is only one (x), or a combination (xy). In

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the process of chromosome reduction at the time of the formation of the sex cells, each egg receives one x chromosome, while one half of the spermatozoa receives one x and the other half a y chromosome or none. If then an egg is fertilized by a sperm containing an x , a female is produced, but if fertilized by a sperm containing a y or no sex chromosome, a male is produced; and since these two types of spermatozoa exist in equal numbers it results by mere chance, on the theory of probabilities, that males and females are produced in equal numbers. But there is no evidence that this remarkable mechanism of sex determination is itself the result of mere chance, and, however it may have been caused, it is a wonderful example of adaptation.

The fertilization of an egg is a very complex process, and yet every step in that process is adaptive. An egg ready for fertilization gives off substances which activate the spermatozoa, and when by its active movements a sperm comes into contact with the egg, the latter sends out a process to receive the sperm. Immediately after this the whole surface of the egg undergoes some change which usually makes it impossible for another sperm to enter. If by any means more than one sperm nucleus unites with the egg nucleus, the resulting development is very abnormal. Thus the provision for preventing multiple fertilization and pathological development is highly adaptive. Many other cases of intracellular adaptations could be cited, but the ones mentioned indicate that adaptations are found in the smallest as well as in the largest parts and functions of organisms—"Natura in minimis maxima."

7. *The Subtle Chemistry of Life*

Although chemists no longer hold that there is a great gulf fixed between organic and inorganic chemistry, and

although certain organic compounds can now be made artificially in the laboratory, every living thing performs many complicated chemical processes which the chemist can neither duplicate nor understand. In particular the power which all kinds of protoplasm have of converting food substances into their own peculiar kinds of protoplasm—the power of assimilation—is a chemical secret which the mind of man has not been able to discover, although every cell of his body knows this secret. The secret of “fixing” free nitrogen was discovered by some of the simplest bacteria hundreds of millions of years ago, and their efficiency in this respect is much greater than man can hope to attain either at Niagara Falls or Muscle Shoals. The ability of all green plants to convert water and carbon dioxide into sugar and starch in the presence of sunlight is a secret of such importance that if man could duplicate the process cheaply and efficiently it would forever solve the problem of the food supply. The chemical processes involved in fermentation and digestion may be artificially duplicated by man, but only with the aid of chemical substances known as enzymes, which are made by even the simplest kinds of protoplasm but which cannot be artificially produced by man.

Other substances known as chemical messengers, or hormones, which are produced by certain ductless glands and which circulate in the blood, profoundly influence the growth, development, and activity of many distant parts of the body—indeed, many of the most remarkable correlations of growth and form, of function and structure, of differentiation and integration, are determined by hormones. There is good reason to believe that they are the real materials of heredity, and that they determine race, sex, and type of personality; but although these hormones may be produced by chromosomes, cytoplasm, and glands, they can-

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not in general be synthesized by human intelligence. Other chemical substances of unknown composition but of the most vital importance as accessories to food are known as vitamins. They are produced only by certain cells and tissues of plants and animals, and they have never yet been analyzed or synthesized.

These are only a few of the many unique and wonderful chemical secrets which protoplasm has discovered but which are as yet largely beyond human comprehension. How did lowly plants and animals ever discover such subtle secrets of chemistry, which intelligent man is only coming to appreciate and which he cannot yet artificially duplicate?

II. INDIVIDUAL, ACQUIRED, OR CONTINGENT ADAPTATIONS

As contrasted with such racial or inherited adaptations, there is a whole class of fitnesses which may be known as individual, acquired, or contingent. These are adaptations which arise in response to particular stimuli; they are not inherited, as the structure of the eye is, for example, which develops in the dark as well as in the light, and which is fully formed before it is put to the use for which it is fitted, but they are acquired in that they arise in each individual in response to particular external conditions, and they are contingent in that they may or may not appear, depending upon whether the appropriate stimulus is present or not.

Among these individual adaptations, or useful responses to stimuli, may be listed the following classes:

<i>Stimulus</i>	<i>Beneficial Response</i>
Increased light	Increased pigmentation
Increased friction	Increased thickness of epidermis
Increased use	Increased size or strength
Unusual foods	Appropriate digestive fluids

Stimulus—Continued Beneficial Response—Continued

Unusual temperatures	Acclimatization
Poisons or toxins	Toleration or antitoxins
Injury	Regulation or regeneration

Strong light, and especially light of short wave lengths such as ultra-violet, is very injurious to protoplasm, and when the skin of white persons is exposed to such light the living cells suffer "sun-burn." But another result of such exposure is that the skin becomes more deeply pigmented or "tanned," and this screen of pigment serves to protect the living cells from the injurious rays.

Moderate friction and pressure on the skin, instead of wearing it thin, leads to the thickening of the epidermis and the formation of callosities by which the deeper lying parts are protected. A similar result follows the application of various chemicals to the skin. The epidermis of plants that are exposed to salt-water spray becomes thickened, thus protecting the protoplasm from the injurious effects of the salt.

It is a truism that in living things use strengthens a part and disuse weakens it. The used muscle grows in size and strength, and, within certain limits, it fits itself to the task required of it, while the unused muscle grows small and weak. A similar thing is true of glands, and even sense organs or brains may be improved by use.

Unusual kinds of food often lead to adaptive modifications of the digestive organs. Grain-eating birds have a tough gizzard with a hard lining, but if they are fed on soft foods the gizzard becomes soft and flabby. If animals which live largely on meat are put upon a carbohydrate diet, or *vice versa*, the character of the digestive fluids undergoes an appropriate change.

Remarkable also are the adaptations which many organisms show to extremes of temperature and to dessication. By

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gradually increasing the temperature of the water certain protozoa have been acclimatized to water so hot that other individuals of the same species that have not been so acclimatized are instantly killed and cooked when placed in it. Some animals and plants may undergo complete dessication and yet come out "as good as new" when they are again placed in water. There is a small rotifer that is found in rain gutters and cemetery urns which can be completely dried so that it contains no trace of water. When it is again placed in water, it is not only completely restored, but is found to have renewed its youth.

Even more remarkable are the adaptations that organisms show to certain poisons, if these poisons are given in graded doses so that the organism acquires a tolerance for them. Such tolerance may be acquired to a limited extent to violent mineral poisons, such as corrosive sublimate, as Davenport showed in the case of *Paramecium*. It is also known that human beings, as well as other organisms, may acquire tolerance for arsenic and arsenical compounds. One such compound is "salvarsan," and Ehrlich, its inventor, points out the importance of giving it in doses large enough to kill the syphilis organism "mit einem Schlag," since the organism will acquire a tolerance for the poison if it is given in smaller doses. But the poisons to which living things most readily become adapted are those of organic origin, such as alkaloids. It is well known that "drug fiends" may take enough morphine or cocain to kill a man, who is unaccustomed to the drug, without any very serious or immediate injury. Similarly, tolerance is gradually acquired for tobacco, alcohol and many other poisons. Among the most striking instances of this is the tolerance to serpent's venom and to bacterial toxins. If the venom of rattlesnakes or cobras is injected into guinea-pigs or rabbits in graded doses,

they may be rendered immune to the poison even when given in lethal quantities. The venom of every poisonous snake is highly specific, and the antidote for one kind of venom will not serve as an antidote for another kind. Furthermore, it is certain that the ancestors of the guinea-pig, which is a native of South America, could never have had any experience with the venom of the cobra, a native of India; and yet the guinea-pig can form an anti-body against cobra venom, and for every particular kind of venom its own peculiar anti-body. One who has had diphtheria has acquired a toleration for the diphtheria toxin, so that he is thereafter usually immune to that disease. In this way most persons have acquired immunity to certain common diseases. It is known that each kind of toxin leads to the formation of a specific anti-body which serves as an antidote for that poison. Many of these toxins are complex and highly specific substances, and yet the living organism, if given sufficient time, can make a specific antidote for each particular kind of toxin. What chemist by the use of his intelligence could do anything approaching what his unconscious cells are able to do in this respect?

Internal regulation is frequently the result of the action of certain internal secretions, or hormones: Thus the ability to "nerve oneself" for a great effort involves many correlated adjustments, such as increase of heart beat, of blood pressure, of respiration, and of muscular energy, and all of these are caused by setting free into the blood "adrenin," which is secreted by the adrenal gland; even the coagulability of the blood is increased by this hormone. The adaptive character of all these reactions can be readily appreciated when it is realized that these are just the conditions needed in fight or flight, and in life and death struggles. It is probable that many regulations of development are depen-

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dent upon a proper sequence and balance of internal secretions. Such a secretion known as "andrase," formed by the interstitial cells of the testes, leads to the development of the secondary sexual characters of the male in mammals, while a corresponding hormone, known as "gynase," is formed by the ovary and causes the development of the secondary sexual characters of the female. The great changes which accompany pregnancy and lactation in mammals are caused by hormones from the ovary and the fœtus. Other internal regulations affecting many parts of the body and the general course of development are caused by hormones from the thyroid gland, the pituitary body and many other organs of internal secretion.

But although the hormone is the chemical stimulus which leads to the adaptive reactions in each of these cases, it does not in the least explain the fact that these reactions are adaptive. Why should the reactions of so many different organs to adrenin be of such a nature that they coöperate to fit the animal for fight or flight? Why should the reactions of so many different parts of the body to andrase or gynase be of such a character that they lead to the development of all the complicated organization of the male or female, and why should the organization of the two sexes be so adapted to each other? It is evident that the stimulus which starts these adaptive reactions does not explain the fact that they are adaptive. That can be found only in the teleological nature of the mechanism which is set in motion by these hormones.

Finally, some of the most remarkable of all individual adaptations are found in the regulations and regenerations which follow injury. Many eggs, embryos, and adults have the power of restoring lost parts and in general of resuming their typical form after injury. Certain flat worms and

hydroids may be cut up into minute fragments and each piece will give rise to a typical animal. Some eggs may be broken apart in the two-cell or four-cell stages and each cell will give rise to a whole individual. Many lower animals such as newts, crayfish, and worms have this power to a very marked degree. The legs of a newt or crayfish may be cut off again and again and yet may be replaced after each amputation. In the regeneration of the legs of crabs, Morgan has shown that those legs which are least liable to injury regenerate as readily as those which are most liable to be lost. If the lens in the eye of a newt is removed, it will regenerate more or less perfectly. Such individual adaptations cannot be explained as the result of the inherited experiences of former generations, since the injuries are frequently of such a kind that they could never have occurred in nature.

Higher animals do not have such extensive power of regeneration, but every living thing has this power to a certain extent. Human beings cannot regenerate limbs or other complex parts, but they have the power of healing wounds and making repairs, otherwise cuts and other little injuries would prove fatal.

These individual adaptations are only samples of innumerable others that could be cited; indeed, individual adaptations are almost if not quite as numerous as racial ones, and they are even more mysterious and wonderful, since nothing in the world seems more inexplicable than the ability of an organism to respond in a useful and apparently purposive way to conditions which it has never experienced before and which in some instances even its ancestors could never have experienced in all their past history.

LECTURE II

THE MECHANISM OF ADAPTATION

THE wonderful adaptations of organisms to their environments, of structures to habits, of responses to needs, of means to ends, have ever been and still are the greatest problems of biology. From the time of the early Greek philosophers to the present day, the mystery of life has centered to a large extent in this great problem of how organisms came to be so marvelously adapted, in structures and functions, for their preservation and welfare. Aristotle maintained that the essence of a living thing is its fitness, and after centuries of observation, experiment, and theorizing we must still say that one of the most mysterious and inexplicable phenomena in nature is the capacity of the lowest plants and animals, as well as of the highest, to respond to external conditions and stimuli in a useful and an apparently intelligent and purposive way, although it is certain that conscious intelligence and purpose are not usually involved.

How have lowly organisms learned to utilize processes of chemistry and physics so subtle in character that intelligent man after centuries of civilization has come only to the place where he can appreciate these processes but cannot duplicate them? How have those units of living matter, the cells, come to have complex teleological mechanisms for assimilation, growth, and division, for secretion, contraction, and sensation? How can we explain the origin of multitudes of inheritance units, their location in the chromosomes, the wonderful mechanism of mitosis for the precise division and distribution of these chromosomes to all

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the cells of the body; and how explain the union of homologous maternal and paternal chromosomes in synapsis and their unique method of separation in the reduction division, upon which processes the phenomena of Mendelian inheritance depend? How is it possible to explain the adaptive mechanisms of the egg and sperm and of the processes of fertilization? How can we explain the teleological character of embryonic development, in which the end is apparently in view from the beginning? How is it possible to account for the adaptive tropisms, reactions, and instincts of animals, the complicated but delicately adjusted relationship between different individuals and species, their ingenious means of defense and offense and the surprising efficiency of the living machine? Finally, is it possible to find any natural and causal explanation of the adaptations of individuals to conditions which neither they nor their ancestors have ever before experienced?

The list of such fitnesses is well-nigh endless, and the question of their origin forms one of the most striking and fundamental problems of biology. It may be necessary for the biologist to disregard this problem for the present because he cannot deal with it, but he should never forget that it is a real problem and challenges scientific explanation. This subject is undoubtedly a dangerous one for the scientist, full of pitfalls for the unwary and with many alluring calls to metaphysical speculation; but it lies in the background of every biological problem. As Professor W. K. Brooks taught, "Life is response to the order of nature," and it is the element of useful and apparently purposive response which more than anything else distinguishes the living from the lifeless, and separates the methods and results of biology from those of chemistry and physics.

Innumerable attempts have been made by philosophers

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and biologists to find an explanation for adaptation. One need only enumerate the "supernatural design" of theologians, the "perfecting principle" of Aristotle and Nägeli, the "indwelling soul" of Plato and Bruno, the "active teleological principle" of Kant, the "unconscious purpose" of Hartmann, the "vital activity" or "vitalism" of Bunge, Wolff, and Virchow, the "will" of Schopenhauer, the "élan vital" of Bergson, the "entelechy" of Driesch, the "archæstheticism" of Cope, the "desire" or "need" of Erasmus Darwin and Lamarck, and finally Charles Darwin's "natural selection," to indicate over what a wide field these attempted explanations have ranged. All of these proposed explanations may be classified as natural or supernatural, or more accurately as mechanistic or vitalistic. The former presuppose only natural forces and processes in the regular sequence of cause and effect; the latter assume that some form of will or purpose is present as an uncaused cause which lies outside the field of scientific inquiry.

If for the present we pass over those views which attempt no casual explanation, but merely restate the mystery in terms of supernatural design, perfecting principles, or entelechies, and those which find the causes of adaptations in unknown laws of variation or of physiological response, there remain two attempted explanations of organic fitness which may be known by the general terms of Lamarckism and Darwinism, though at present neither of these systems represents accurately the views of the man whose name it bears.

1. *Lamarckism*

Lamarckism attempts to explain racial adaptations as the result of the inheritance of individual or acquired adaptations; it is assumed that the beneficial responses which are called forth in individuals by external stimuli are handed

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on to later generations by heredity, and in this way racial adaptations are supposed to have originated. Thus all racial or inherent adaptations are held to have come from individual or acquired ones. The increased pigmentation of the skin of one who is exposed to tropical light is said to be inherited by his children, and so a dark-skinned race arises; the stretching of the neck and legs of any animal that browses on trees is supposed to be inherited, and so the giraffe was evolved. Such an explanation is so simple and plausible that it has been widely accepted. Unfortunately for this attractive explanation, there is no evidence that it is true. The evidences in favor of the inheritance of any somatic modification are very unsatisfactory, and when it comes to the inheritance of acquired *adaptations*, critical evidence is lacking altogether. For years evidences of such inheritance have been earnestly sought, but no such confirmations have been found as would certainly have been the case if this kind of inheritance were at all common.

On the other hand, there seems to be no reasonable escape from the postulate that modifications of the germplasm are produced by environmental influences. The germ-cells, and more especially the chromosomes and genes, are well protected from almost every change in the external environment, but there is an internal environment of body fluids and of cytoplasmic and nuclear substances which comes into much more intimate contact with the germplasm, and it seems necessary to assume that certain changes in this internal environment may cause changes in the germplasm itself. Some experimental evidence, especially that of Guyer and Smith on inherited eye-defects in rabbits, favors this view.

However, such environmental modifications of the germplasm are not generally adaptive, and the beneficial charac-

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ter of germinal modifications must be explained in some other way. The assumption that individually acquired adaptations of parents are directly inherited by their offspring and thus become racial is not supported by any critical evidence.

Furthermore, there are many adaptations that benefit the species at the expense of the individual. For example, in many instances the reproductive instincts lead directly to the death of the individuals concerned; every male bee, every male and female salmon, goes to its certain death in perpetuating the species. Such adaptations that are for the good of the race but lead to the death or injury of the individual cannot be explained by the Lamarckian theory that racial adaptations are merely individual adaptations that have become hereditary.

Samuel Butler, Bergson, Bernard Shaw, and many others maintain that the evolution of adaptations cannot be explained except on the basis of Lamarckism. Herbert Spencer said, "If there is no inheritance of acquired characters, there is no evolution"; but it is evident that Spencer did not define with sufficient clearness what he meant by "acquired characters." In one sense random mutations are acquired characters, but they are not somatic modifications due to use or disuse. Sumner says, "The imperative demand for *directed* germinal variations can be met only by assuming the inheritance of acquired characters. . . . Adaptations have come about not because of their harmlessness but because of their utility." But in spite of theoretical necessities, it is a fact that mutations occur in many directions; they are multifarious, and in their origin they do not seem to be directed any more than "the course that the wind blows." The directing comes after their appearance and through the elimination of the less fit.

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It is a mistake to suppose that Lamarckism explains the real origin of adaptations; it maintains that individually acquired adaptations are inherited and thus become racial, but it attempts no other explanation of the origin of individual adaptations than is to be found in "desire," "need," or "will." The beneficial character of the response of an organism to changes in its environment and to use, disuse, and needs remains as much of a mystery as ever. Lamarckians who have attempted to explain acquired adaptations have generally appealed to some mysterious principle, such as unconscious purpose, entelechy, *élan vital*, or vitalism as contrasted with mechanism; thus the search for the causes of acquired adaptations is removed from the field of scientific inquiry. Lamarckism is thus fundamentally non-mechanistic, and it is not surprising that vitalists and obscurantists generally should favor the Lamarckian philosophy.

In order to explain racial adaptations, Lamarckism begins with the unproved and discredited assumption that individually acquired adaptations are inherited, and in attempting to explain the origin of individual adaptations it ends in a fog of obscurantism or in a bog of mysticism.

2. Darwinism

Darwinism, on the other hand, rejects the possibility of the inheritance of such individual or acquired adaptations and maintains that there is no *genetic* connection between racial and individual fitness. It holds that all racial adaptations are due to (1) multifarious variations (mutations) among offspring and (2) the elimination by natural selection of those that are poorly adapted. It will be seen that all adaptations that are for the good of the species rather than of the individual admit of no other natural explanation, for such adaptations could not have arisen from

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the beneficial responses of individuals, as Lamarckism assumes, since they benefit the species at the expense of the individual.

The probabilities are distinctly favorable to these two fundamental propositions of Darwinism. We know that mutations occur in many directions, and that most of them are not beneficial. We know that the more injurious they are the earlier the individuals possessing them are eliminated. There is an immense elimination of germ-cells; among mammals not one spermatozoon among billions ever fertilizes an egg, and not one egg in thousands matures and is fertilized; and while it must often happen that the fittest perish along with the most unfit, still it is highly probable that on the whole the germ-cells that are fertilized and begin to develop are among the fitter. There is a large elimination of embryos and larvæ; among many animals thousands perish for every one that survives; and again, it is most probable that on the whole and in spite of individual exceptions it is the fitter that survive. Many young and sexually immature individuals die for every one that arrives at sexual maturity, and here also the survivors are in general the fitter. There is thus an immense elimination of individuals in every generation before they reach the period of reproduction, and most of this elimination is wholly unseen and unknown by the casual observer of nature.

On the whole, much of this elimination is discriminative; there is universal elimination of the most unfit and, in general, survival of the better fitted. It is true that in many catastrophes destruction is wholly indiscriminate and the fit and unfit perish together. Even in the more usual forms of elimination, it does not happen that in every generation and in every individual instance the fitter survive and the less fit perish; but if this happens in the majority of cases, it

will in the course of time bring about the diminution of unfitness and the general prevalence of fitness. Darwin showed in masterly manner that the greater elimination of unfit individuals in each generation and the more general preservation of better fitted ones would gradually improve the standard of fitness until finally such exquisite adaptations as are found in the eye, for example, might be reached. This seems to me to be the crowning glory of Darwin's great theory; it is not so much its species-forming power which impresses one as its ability to explain on simple and natural principles very many of the wonderful adaptations of the living world.

3. *Mutation Theory*

The mutation theory has to a certain extent changed our point of view regarding adaptations as it has also regarding species formation. Neither of these phases of evolution can any longer be regarded as the result of minute variations which persist and replace ancestral forms, if they are infinitesimally better adapted, but mutations may represent relatively large changes both in form and usefulness. They occur in many directions and are usually non-adaptive and are frequently positively injurious. The latter are quickly eliminated in a state of nature, but indifferent mutations may persist, and it is no longer necessary to assume, as older Darwinians did, that every structure of an organism is of some benefit to its possessor; on the contrary, it appeared without reference to its usefulness or its uselessness, and it persists only if it is not injurious.

Preadaptations.—In applying the mutation theory to the explanation of adaptations, Cuénot has proposed a modification of the Darwinian theory which he calls "preadaptation." Mutations which are injurious or indifferent in the

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environment in which they arise may be well fitted for some other environment and will persist if they can find that other environment. Thus white insects or spiders, which probably originally appeared as sudden mutations, are badly fitted to live on a dark object, since they are so conspicuous; but they are well fitted to live on a white background—for example, white flowers. Their white color was not acquired by a long and slow process in order to fit them to live on white flowers, but white mutants appeared suddenly and then found, by a process of trial and error or by natural selection, an environment for which they were suited. Loeb has shown that fish with degenerate eyes may be produced by hybridizing two species with normal eyes or by keeping normally fertilized eggs at a temperature of 2° C. for several hours after fertilization. Such fish were not slowly adapted to life in caves or dark places, but, since they stand a very unequal chance of survival in competition with seeing forms in the light and probably an equal chance in the dark, they can survive only in dark places. Thus the blind fauna of caves was not made for life in the dark, but blind or nearly blind animals found in caves an unoccupied place in nature where seeing did not offer any advantage. In short, the adaptation was present before its fitness was discovered by its possessor; the environment did not make the adaptation but merely revealed it. This is, as I understand it, the same conception which has been called by ZurStrassen "organized seeking."

Cuénot cites as instances of such preadaptations the following cases among many others: Any beneficial change of food or habitat, such as the turning of certain butterflies or moths from particular species of flowers which they ordinarily frequent to other species; or the newly acquired habits of the ground parrot (*Nestor notabilis*) of New

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Zealand, which was originally an insect-eating and fruit-eating bird, but which has become more or less carnivorous since the introduction of sheep into that country; it was evidently well fitted, or preadapted, for this new kind of food even before the food appeared. All such fitnesses were developed without regard to their later use; they are therefore preadaptations.

Cuénot further points out that such preadaptations, or fortuitous conjunctions of favorable environment and characters preadapted to this environment, have been an important factor in progressive evolution. For example, the appearance of several great classes of the animal kingdom has followed the occupation of a place, either unoccupied or peopled by an inferior group not able to resist the invasion. Thus shallow-water fishes have given birth by mutation to amphibians capable of living in a merely humid environment, thanks to their aërial respiration and walking limbs. From these issued reptiles which occupied dry regions; their hard skin, digits armed with claws, internal fecundation and large eggs, capable of direct development, permitting the omission of an aquatic stage, were preadaptations necessary to this change of habitat. Birds, derived from reptiles, peopled the unoccupied realms of the air owing to their preadaptations for flight. Mammals derived from primitive reptiles were able to replace these because of their intra-uterine development, maternal protection of the young and constant temperature. Man has been able to prevail over preceding forms because of his superior brain—all these fitnesses being preadaptations.

This theory of preadaptation is evidently a modification and extension of the Darwinian doctrine to the origin of adaptations, as the mutation theory is an extension of that doctrine to species formation; it is merely a variant on the theme of natural selection.

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4. Individual Adaptations

But while Darwinism as thus expanded is able to explain the origin of racial or inherited adaptations, it does not, as ordinarily understood, succeed in explaining the numerous and equally remarkable individual adaptations of organisms any more than Lamarckism does; indeed, some of these individual adaptations have been held by several recent writers to be absolutely fatal to both of these theories. For example, it has been found that if the lens of the eye of a newt is removed it will be regenerated perfectly within a few weeks. Now it may be granted that such an injury as this, involving as it does a very delicate surgical operation, never took place in nature; newts may have had their heads bitten off from time immemorial, but they never had the lens removed from the eye except in an experiment directed by human intelligence; and yet Darwinism in its original form can explain this regeneration only by supposing that the loss of the lens has taken place so frequently among the ancestors of present-day newts that they have become perfectly adapted to this injury by the more frequent survival of those which were inherently capable of regenerating the lens.

Again, the eggs, embryos, or adults of many animals may be cut or broken into fragments or otherwise injured in such ways as could never have occurred in nature, and yet these fragments will, in many cases, give rise to perfect animals "as if the pattern of the whole existed in every part." This power of regeneration cannot be the result of past experience, since there is no constant correlation between its occurrence and the liability to injury. Other contingent, individual adaptations that are most difficult to explain are found in the acclimatization of certain organisms to extraordinarily high temperatures and in the toleration

that may be developed for violent poisons; such acclimatization or toleration cannot be due to the elimination on a large scale of organisms that cannot become adapted, since in well-conducted experiments few if any of the individuals perish. In the case of bacterial toxins or snake venom, the manner in which tolerance to the poison is brought about is better understood than in the case of other poisons. It is known that the body that is poisoned forms various antibodies as antidotes to these poisons, and for every toxin, or at least for every toxalbumin, its particular anti-body; but why a particular toxin causes the formation of its one appropriate antitoxin is a mystery. Many of these toxins are of such a sort that it is perfectly certain that the immediate ancestors of the individuals poisoned could never have had experience with them, as, for example, in the case of guinea-pigs inoculated with cobra venom; and yet the response is as perfect as it could be if it had been due to long experience. Many other similar cases might be cited, but these are enough to indicate how difficult it is to find a natural explanation for these individual, contingent adaptations. Indeed, it may be said that the apparently intelligent and purposive response of an organism to a stimulus or environment which it or its ancestors have never experienced before is one of the most important and mysterious problems of biology.

Both Lamarckism and Darwinism hold that *racial* adaptations are due to experience; Lamarckism, that they are the directly inherited effects of individual experience; Darwinism, that they are the indirect results of ancestral experience operating through the presentation of many variations to the action of natural selection and the survival of the better adapted. Neither of these theories explains sudden adaptations of *individuals* to conditions never experienced before.

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It has sometimes been said that while racial adaptations are due to natural selection, individual adaptations are due to the "plasticity" of the organism; but this is merely seeking refuge in a name. Plasticity is only passivity and is no explanation at all. It has also been suggested that individual adaptations are problems of development rather than of evolution, of physiology rather than of phylogeny. But this distinction also is nominal rather than real, for evolution is only one form of development, and phylogeny no less than ontogeny must be based on physiological processes. It is true that individual adaptations are things with which we can deal directly by experimental methods, whereas racial adaptations were established in the more or less distant past and are not readily submitted to experimental tests. Therefore we ought to know more about the causes of individual adaptations than of racial ones, but hitherto attention has been focussed largely upon the latter and relatively little study has been given to the former. One of the greatest needs of biology is for more detailed and accurate information regarding individual adaptations; we must know exactly what happens in each case—the physiology of the response irrespective of its usefulness—and then perhaps the latter may find an explanation.

Many of these physiological processes are in a certain balance with one another or with the environment, and when this balance is disturbed there is a compensatory regulation. For example, a muscle that is neither increasing nor decreasing in size receives a certain amount of blood; increased use of this muscle is balanced by an increased flow of blood, and decreased use leads to a decrease in the blood supply; correspondingly, the muscle increases or decreases in size. Similarly, if one kidney is removed the one that remains has to perform the functions of two, and it receives more blood

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and grows in size. If much blood is lost in hemorrhage the activity of the blood-forming organs is increased, and they send more corpuscles and plasma into the circulation; for there is a certain equilibrium between the activity of the blood-forming organs and the quantity of blood in circulation. If white corpuscles are destroyed by x-rays the lymphoid tissues are stimulated to send an excess of leucocytes into the blood, to compensate this deficiency.

This tendency to equilibrium is probably one of the most important physiological processes in the regulations and adaptations of organisms. A similar tendency is found in the inorganic world; when the osmotic pressure between two fluids separated by a permeable membrane is unequal, equilibrium is automatically restored; when the gas tension differs on two sides of a permeable membrane, diffusion occurs through the membrane until the tension is equal on both sides; when the oxygen or carbon-dioxide tension in the blood differs from that in the tissues or in the lungs, there is an exchange of gases until equilibrium is reached; a chemical reaction proceeds in the direction of equilibrium, and if an excess of products is formed in one direction the reaction may sometimes reverse and go in the other direction until equilibrium is restored. Such cases seem to be analogous with the compensatory regulations of organisms, but the balance between one physiological process and another or between the organism and the environment is not only vastly more complex than these inorganic equilibria, it is self-preservative and useful; and it is this quality of usefulness or fitness for which we are seeking an explanation.

It is possible that some of these individual adaptations belong to the fundamental and original properties of living things and as such are not to be explained by any theory of evolution; for it must not be forgotten that organic evolu-

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tion is a theory of transmutation which undertakes to explain the diversities which exist in the living world, but not the original properties of life. It undertakes to explain the various forms of adaptation found among organisms, but not organic adaptability. It may be that regulation or regeneration is one of the fundamental physiological properties of living things, and that it belongs in the same category with assimilation, growth, metabolism, reproduction, and irritability—properties which are found in the lowest organisms as well as the highest, and which can therefore be left out of the list of things which organic evolution may reasonably be expected to explain. But this would certainly not apply to peculiar, individual adaptations such as have been named. The origin of these must be explained no less than the origin of particular racial adaptations. Moreover, it is incredible that things so much alike as racial and individual adaptations should be due to wholly different causes.

It seems, therefore, that while natural selection is a fairly satisfactory explanation of racial adaptations, it does not, in the form proposed by Darwin, furnish a satisfactory explanation of individual adaptations, and this has led several biologists, notably Wolff and Driesch, to the conclusion that Darwinism "fails all along the line," while many who are not biologists have hailed with joy what they regard as the "death of Darwinism." But this conclusion is certainly unwarranted and extreme. There are many racial adaptations, as we have seen, which are beautifully explained by the Darwinian theory, and it is certainly premature to abandon hope of explaining individual adaptations by a similar principle.

5. Intra-personal Selection

Weismann recognized that natural selection as set forth by Darwin was not a satisfactory explanation of all phe-

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nomena of evolution, and especially of the degeneration and disappearance of useless parts and the concordant modification of numerous parts of the organism. In order to explain these he proposed to extend the principle of natural selection from individuals or persons ("personal selection" or "Darwinism" in the strict sense) to organs and tissues ("histonal selection" of Roux), and even to germinal units such as determinants and biophores ("germinal selection"). This hypothesis as originally proposed was open to many and serious objections. It is impossible to hold with Weismann that there is a struggle between germinal elements for food, and that the weaker ones are starved and eliminated in this struggle; but we are on safe ground when we affirm that natural selection is operative at every stage in development from the earliest steps in the formation of the germ-cells up to the adult condition. Not even the most radical critic of Darwinism doubts that animals which cannot live die. No one doubts that this is true also of individual cells as well as of persons: What reason is there to suspect that it is not also true of parts of cells, such as plastids, nuclei, chromosomes, chromomeres, and even genes? We know that many young forms perish before reaching maturity, that numerous organisms never develop beyond embryonic stages, that multitudes of germ-cells perish, and that, in general, elimination is much more severe in the earlier than in the later stages of ontogeny. We know that in the life of higher organisms many kinds of cells are continually dying and being replaced by others; so far as epithelial, glandular, and blood cells are concerned, we may say with St. Paul, "We die daily." The death of cells is frequently selective; for example, it is said by medical authorities that the leucocytes or white blood cells are destroyed in large numbers by the influenza germ, thus opening the way to infection by

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many germs, especially those affecting the respiratory tract. It is known also that x-rays kill certain cells, particularly the leucocytes, sooner than others. We know that it is possible to destroy parts of a cell and yet keep other parts alive for a time at least; whole chromosomes may be lost and yet the cell be capable of continued life and division. What reason is there for supposing that the same may not be true of the units of which chromosomes are composed, and even of the genes themselves? If this should be true, the elimination of the unfit may take place at any stage in the ontogeny, and the least viable would be those which disappear earliest and leave fewest traces. The greatest misfits in the world never become visible to the naked eye, for they never begin to develop. In this way doubtless many mutations are eliminated before they ever come to light, and so modifications which are disharmonious disappear almost as soon as they occur.

Recent work of Morgan and his pupils shows that there are inheritance factors or genes which are transmitted in Mendelian fashion and which cause death either before development begins or at some time during that process. These "lethal factors" bring about the complete elimination of certain genotypes, so that natural selection may be said to begin in such cases with the genes themselves. But it may be objected that such selection is not necessarily adaptive, that it does not represent the survival of the fittest, since these non-viable genotypes might have given rise to phenotypes which were highly adapted to conditions of life if only they could have lived; but it must not be forgotten that in order to leave offspring organisms must live, and that fitness to survive must be found not merely in adult stages but in every stage leading up to the adult. Those individuals that leave offspring must be fit *at all stages of development*

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to persist in the conditions in which they are found; those that leave no offspring may be fit to live, but they are unfit for the perpetuation of the species, and those that are incapable of beginning development are least fit of all.

6. *Trial and Error*

Such elimination of persons or cells or genes would not, however, explain individual or contingent adaptations, which are really only beneficial responses to environmental stimuli in which no elimination of individuals occurs. It seems to me that many, perhaps all, such adaptations may find a mechanistic explanation in the further extension of the selection principle to the physiological responses of organisms. Herbert Spencer explained adaptive motions on the principle of "overproduction of movements" and the persistence of those that are beneficial. Darwin suggested this method of explaining the apparently intelligent behavior of the earthworm. Lloyd Morgan applied this principle to the study of animal behavior under the designation of "trial and error." In a series of masterly works Jennings has proved that the beneficial responses shown by many lower organisms may be reduced to this simple principle of "trial and error"; in this way apparently purposive behavior which Binnet supposed to be due to the relatively complex "psychic life of micro-organisms" has been shown to be due to a few simple motor reflexes, which are repeated indefinitely until they bring the organism into a favorable environment. Many recent investigators have shown that this principle is applicable to the behavior of a large number of animals.

This principle of overproduction of movements or of "trial and error" is in reality the rejection, elimination, or cessation of unfit responses and the persistence of beneficial ones. It has hitherto been applied only to motor reactions,

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but in 1909 I suggested that it might be applicable to many other organic reactions. ZurStrassen has generalized this principle under the title "overproduction of opportunities (Gelegenheiten)." If this principle should be found applicable to physiological responses in general it would explain in equally simple manner many apparently purposive responses which are at present inexplicable. It is known, for example, that immunity to bacterial or other toxins is not acquired immediately but only after a certain lapse of time during which physiological processes are more or less disturbed; there is frequently an increase of destructive metabolism, the body temperature rises, and there are other abnormal conditions. "Fever is the process of adaptation to such toxic agencies as can be neutralized by the development of anti-bodies" (Adami and McCrea, p. 149). It is at least possible that during this period the responses to the toxin are in the nature of trial and error, that many kinds of anti-bodies are formed, and that the production of useless kinds gradually ceases while beneficial ones continue to be formed. This last might be explained as a result of the establishment of chemical equilibrium, for if many kinds of anti-bodies are formed and only one is used up in the "fixation" of a toxin, this one would continue to be formed while the other kinds would not.

If this suggested explanation of individual adaptations should prove to be true, it would mean that the living, developing, reacting organism is like a swimming Paramecium; it tries many paths, eliminating or ceasing to follow useless or injurious ones and persisting in the beneficial ones. Such an hypothesis implies in many cases the capacity on the part of organisms to distinguish between harmful and beneficial conditions, and this capacity is left unexplained. Since it is present, however, in living things generally, it may be

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considered to be one of the original properties of life, and our inability to explain its origin is not different from our inability to explain the origin of metabolism, reproduction, irritability, or of life itself. Thus the simple principle of overproduction and the elimination of the injurious or unfit, whether individuals, cells, or physiological responses, would offer a possible mechanical explanation of both racial and individual adaptations and of the almost universal occurrence of fitness in the living world.

There are, however, certain difficulties which such an explanation encounters, and there is always left an unexplained remainder which for the present at least is inexplicable on purely mechanical principles. One of the most serious of these difficulties is that the rate of adaptation does not appear to be proportional to the rate of overproduction and elimination, as it should be if these are the only causes of adaptation. The rate of adaptation can be measured by the rate of divergent evolution, that is, adaptations in different directions, or by the relative complexity and perfection of corresponding adaptations in two groups of approximately equal age. Measured in either of these ways, we find that the rate and degree of differentiation and adaptation are not always proportional to the amount of overproduction and elimination. The rate of reproduction and of elimination is lowest in some genera and classes in which adaptations are most varied and perfect. For example, compare the rate of reproduction and elimination in lower animals and plants with that in higher ones. If the variety or complexity of adaptations is dependent entirely upon these two factors, why do not bacteria and protozoa have the most numerous and complex adaptations of all organisms; or why do not mice greatly surpass elephants in these respects; or grasses, sequoias; or why is not

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man one of the least highly adapted of all animals? Certainly some animals and plants which have the lowest rate of reproduction and elimination have the highest types of differentiation and adaptation.

One answer to this argument is that one organism is as well adapted as another, and that there are no such differences in fitness as have been assumed. For example, an amœba may be as well adapted to its environment and needs as a man is to his. If one has reference only to the capacity to survive and leave descendants, this is certainly true. Every individual or species that persists must be well enough adapted to live and multiply. But adaptations differ greatly in *number* and *complexity* in higher and in lower organisms, just as differentiations do, and, since these adaptations have arisen in the course of evolution, those animals and plants that have the more numerous and the more complex adaptations must have had a longer course or a more rapid rate of evolution. However, the duration of evolution cannot have been longer in higher forms than in lower ones; if all organisms have had a common origin, all are equally old so far as ancestry and evolution are concerned, and if one considers only the different phyla, classes, genera, etc., it is evident that these are much older in the lower than in the higher forms.

It must therefore follow that the rate of evolution and of adaptation has been much more rapid in higher than in lower organisms in spite of the fact that in general the rate of reproduction and elimination of persons has been lowest in those forms in which adaptation has gone farthest and fastest. A possible explanation of this apparent contradiction of the Darwinian theory is found in the fact that higher organisms have more different kinds of genes as well as more differentiated cells and organs than the lower ones, and

even if mutations of genes occurred with equal frequency in all organisms (which seems improbable), those in which the genes were most numerous and most differentiated would furnish the largest number of mutations. If this should prove true, the rate of mutation should be greatest in the most highly differentiated organisms. Incidentally, the fact that the number of mutations is not proportional to the number of germ-cells that undergo maturation and fertilization is evidence that evolution and adaptation do not depend largely upon Mendelian segregation and recombination of genes, and it also indicates that gene mutations are not limited to the period of maturation of the germ-cells.

In view of the fact, therefore, that there is in general a much greater overproduction and elimination of individuals in lower than in higher animals, it is possible to maintain the Darwinian theory only by assuming that there is a greater production and elimination of mutants in higher forms than in lower ones; if this be true, it would explain on mechanistic grounds the more numerous and more complex adaptations of higher as compared with lower organisms.

On the other hand, the more rapid evolution and adaptation of higher animals would be easily explained by Lamarckian principles. If desire and intelligence are factors in evolution, then it should follow that with increasing intelligence there should be an increasing rate of evolution and adaptation. Certainly these two—intelligence and rapidity of evolution—seem to be associated, but whether as cause and effect we cannot say. Evolution has undoubtedly led to intelligence; has intelligence in turn affected evolution?

Finally, whether the Darwinian theory, as thus expanded, is capable of explaining all the fitnesses of organisms or not, it does succeed as no other theory does in offering a casual or mechanistic explanation of very many of these wonderful

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phenomena. The development of particular structures and functions fitted to particular conditions of life, such as organs of locomotion, sensation, respiration, digestion, offense, and defense, and all the multitudes of diverse forms and ways in which organisms are fitted to carry on the fundamental properties of life amidst the most varied conditions—these adaptations we may reasonably expect a theory of evolution to explain, and it is the crowning glory of Darwin's theory that it is, on the whole, able to explain them.

In the preface to his "Vorträge über Descendenz-theorie" Weismann says: "The selection principle controls in fact all categories of life units. It does not create the primary variations, but it does determine the paths of development which these follow from beginning to end, and therewith all differentiations, all advances of organization, and finally the general course of development of organisms on our earth, for everything in the living world rests on adaptation." I have here proposed that the selection principle is also applicable to physiological reactions as well as to vital units, that it lies at the basis of behavior as well as of bodily structure, and that even instinct, intelligence, and purpose are themselves the residuum that is left after the elimination of unfit responses. The selection principle is the only causal and intelligible explanation of all forms of adaptation, and if we reject it we can turn only to non-mechanistic explanations.

LECTURE III

MÉCHANISM, VITALISM, AND TELEOLOGY

MANY non-mechanistic explanations of organic adaptations have been proposed, but they all agree in this—that they attribute organic structures and functions, especially those that are directed to particular ends, to some sort of will which is present as an uncaused cause, either in some supernatural being or beings, in the universe as a whole, or in organisms themselves.

Primitive people have generally regarded all the activities of nature as expressions of will, and a similar view has been maintained by certain philosophers even in modern times. As the only cause of his own actions which the primitive man knew was his will, so he attributed all activities everywhere to will. Even inorganic nature was personified, not merely poetically, but actually; winds and waves, lightning and thunder, rain and snow, the regular succession of day and night, of seed-time and harvest, of life and death, were presided over by certain deities. Of course the actions of all animate things were supposed to be voluntary; their wills moved their bodies and directed their activities to desired ends.

But step by step, before advancing knowledge of nature, supernaturalism withdrew from ordinary phenomena until it dwelt only on the misty mountain tops of origins and creations. Likewise the voluntaristic conception of inorganic phenomena was gradually abandoned, though it has long persisted, and in a rather obscure form still persists, as an explanation of vital phenomena, and especially of organic adaptations.

1. Supernatural Design

It was the fitness of living things which furnished the stock argument for the doctrine of supernatural design in nature. Since these fitnesses are evidently purposive, and since it is no longer credible that intelligent purpose is to be found in the simplest plants and animals, it was argued that an intelligent Designer must have supernaturally created each and every one of these adaptations for the specific function which it now performs. This doctrine reached its climax in the Bridgewater Treatises, in which natural history became largely a study of the designs and purposes of the Creator as revealed in his creatures, and biology was made to serve as the handmaid of theology.

But although adaptations are very general they are not universal, and although they are frequently very efficient they are not divinely perfect; indeed, all gradations of fitness are found in nature from a high degree of perfection to positive unfitness, and if all of these are the products of supernatural design some of them show more than human bungling. Furthermore, one "design" is frequently pitted against another; the parasite is exquisitely, one might suspect infernally, "designed" to prey upon its host, and the beast of prey upon its victim, but on the other hand the host is fitted to resist the parasite and the victim to escape its enemy. If adaptations are supernatural designs, they must be the designs of many intelligences working at odds rather than of one, and their prevalence in the living world would indicate that there are relatively few phenomena that are natural. Finally, the "frivolities of teleology" were carried to such an extent that they rendered the doctrine of the supernatural origin of every adaptation not only incredible but even ridiculous. And then came Darwinism, which

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finally and forever put an end to this extravagant doctrine. "Bridgewaterism is dead." As Darwin says, "There seems to be no more design in the variability of organic beings and in the action of natural selection than in the course which the wind blows." The adaptations of organisms are natural and not supernatural phenomena, and their causes are to be found, not in the individual creative acts of some infinite Designer but in natural forces and conditions. It may be that these forces and conditions are at present unknown and their method of action mysterious, but at least they are natural, unless all distinctions between nature and the supernatural are to be abandoned. Certainly the fertilization of an egg, the development of an embryo, the formation of an eye, acclimatization to extreme temperatures, tolerance for poisons, repairs of injuries, etc., are natural phenomena, and neither religion nor science, poetry nor truth, are served by denying this fact.

2. *Vitalism*

At present there are few if any defenders of the dogma that each and every adaptation was supernaturally created for the purpose which it now serves, but there are many who maintain that living things contain some sort of intelligence, will, or soul which directs their activities to desired ends. The phenomena of life are so mysterious and wonderful and so different from inorganic phenomena that to the great majority of mankind it seems incredible that they should be the effects of purely mechanistic causes. Accordingly from time immemorial the activities of animals and plants have been attributed to some mysterious vital force, *anima*, *spiritus rector*, unconscious purpose, or will, which is wholly different from the causes of inorganic phenomena, which lies beyond the reach of scientific investigation,

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and which is more inexplicable than the phenomena it is supposed to explain. To account for the phenomena of life by ascribing them to *vitalism* is no more helpful or intelligible than to explain the properties of water as due to *hydrism* or of light to *photism*. These are merely names without intelligible meaning. Explanations that explain must be in terms of other and better known phenomena.

In contrasting vitalism and mechanism it should be understood that the term "mechanism" is not used in the sense of philosophical "materialism" nor of "mechanics" in its narrower physical meaning, but rather to connote the regular and invariable sequence of cause and effect, or the principle of causality. Furthermore, it is the function of science to *classify* but not to give ultimate explanations of phenomena; to explain phenomena only in the sense of reducing them to common causes, to deal only with proximate causes and never with final ones. For example, the law of gravity does not explain the ultimate causes and mysteries of falling bodies, but it reduces a thousand causes and mysteries to one. Scientific explanations of life or of anything else attempt nothing more than this.

The biologist is often asked, either naively or scornfully, "What is life?" One might as well ask, "What is matter, mind, energy?" No final and complete answer to such questions is possible; these fundamentals can be defined only in terms of their properties and proximate causes. *Life is a complex of many structures and functions associated with peculiar conditions of matter.* It is never manifested except in connection with protoplasm, "the physical basis of life," and this is an organization of many parts. The universal form of protoplasmic organization is the cell, which is the smallest unit of structure and function capable of independent existence. The most general and distinctive proper-

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ties of life are: (1) protoplasmic and cellular organization, (2) metabolism, (3) reproduction, (4) sensitivity, (5) adaptability.

Are these properties explicable in terms of physics and chemistry, and to what extent may they be duplicated in not-living matter? Does the law of cause and effect apply here as elsewhere in nature? Theoretical mechanism would answer each of these questions in the affirmative, vitalism in the negative. But practically and actually, the mechanist knows that there are many properties and phenomena of life which cannot at present be explained in terms of physics and chemistry, though he has faith that they may ultimately be so explained. On the other hand, the vitalist knows that the immediate causes of certain life processes are physical and chemical, though it is always possible to assume that the more remote causes are not.

Certain simulacra of protoplasm and of cells have been produced artificially, but they bear only a few resemblances to the real living substance. Such artificial products show that some structures and functions of living cells may be explained in terms of chemistry and physics, but the more we know of protoplasm and cells the less likely it seems that it will ever be possible to synthesize them artificially.

For the past two or three hundred years, and ever increasingly up to the present time, physiology has been dealing with the chemistry and physics of living matter, and especially of metabolism. Since the time of Lavoisier it has been known that combustion goes on in the body, oxygen being consumed and carbon dioxide given off, as in combustion outside the body. Digestion is a chemical process which can be duplicated in the laboratory. Muscular contraction and even nerve conduction are accompanied by well-known chemical and physical changes. No one now questions the

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fact that many vital processes may be explained in terms of chemistry and physics. Even the strongest adherents of vitalism must recognize the fact that neither matter nor energy is created or destroyed in an organism, but that these merely undergo transformations (metabolism). All energy of an animal comes from its food just as the energy of an engine comes from its fuel; the vital machine is as dependent upon food as the engine is on fuel. However, only the first and last steps in constructive and destructive metabolism are known; the middle step, assimilation, is still a good deal of a mystery, but it is probably a chemical process in which each of the many kinds and varieties of protoplasm is built up out of the common nutrient materials through the action of specific enzymes.

The properties of reproduction, irritability, and adaptability are more distinctive of living things and are more difficult to explain on a physico-chemical basis than is metabolism. Certain analogies to each of these processes are found in the inorganic world, and certain steps in each of them are plainly physico-chemical in origin, but it must be admitted that there is left a large residuum which cannot at present be explained on mechanistic grounds. However, much progress is being made in this direction, and this justifies the hope that many more, if not all, vital processes will ultimately be explained in this way; certainly there seems to be no justification for abandoning the search for mechanistic explanations at a time when they are being found as never before, nor for turning at once from a mechanistic philosophy of life to obscurantism or mysticism. For although mechanism may not in the last analysis explain vital phenomena, or anything else for that matter, it is evident that very much of a mechanistic nature remains to be discovered in organisms, and the great advantage of mechanism over

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vitalism is not only that it is more intelligible but also that it encourages scientific investigation, whereas a thorough-going belief in vitalism discourages research.

Of late several notable attacks have been made upon the mechanistic conception of life, particularly with reference to the causes of adaptation. Bergson, Driesch, Noll, Pauly, Reinke, Schneider, Thomson, G. Wolff and other "neo-vitalists" hold that many vital processes are indeterminate, non-predictable, non-mechanistic, and creative; they attempt to solve the riddles of life by a direct appeal to mysterious conditions or principles which are found only in living things.

Bergson's evidence for his *élan vital* is found in part in phenomena of parallel or convergent evolution. He maintains that, starting from different sources and proceeding by wholly different routes, organisms may reach the same terminus. For example, he holds that the eye of the mollusk, Pecten, and the eye of a vertebrate are practically the same in structure, though they have evolved by wholly different paths and from wholly different sources; or again, that societies of ants and of men are fundamentally alike, although they have evolved in entirely different ways. If identical results can thus come from wholly different causes, there is scientific indeterminism, and some principle other than cause and effect must be involved, some form of vitalism rather than mechanism.

But neither in the living nor the not-living world do identical results come from dissimilar causes; in short, convergent evolution does not result in identical structures. When Mivart denied that homologies are evidences of evolution and claimed that the eye of a cuttle-fish and the eye of a vertebrate were homologous, though they could not have had a common origin, Darwin replied by showing that these two types of eyes are in no sense homologous; that is, they are

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fundamentally dissimilar though superficially alike. And in reply to Bergson it may be said that although the eye of *Pecten* is in a single feature, namely, the inverted retina, like the vertebrate eye, it is in other respects fundamentally different. These eyes are not homologous and Bergson's contention is groundless.

Neither are the similarities between societies of ants and men, and many other examples of a like nature which are cited by Bergson, real homologies or examples of convergent evolution. The similarities which are present are merely such as are due to principles of universal application, such as the extension of differentiation and integration from individuals or persons to colonies and states. Practically all of Bergson's cases of convergent evolution are of this sort. They indicate only the essential unity of all living things, that certain properties are characteristic of all life and are present in the simplest as well as in the most complex organisms. They certainly do not prove that life processes are indeterminate or that identical results may follow different causes, and therefore that vital activity is non-mechanistic.

It is true that it is often impossible to predict what living things will do, but this is probably owing to the fact that the factors involved are very numerous and complex. Whenever the number of factors is large and the times and circumstances of their action numerous, it is difficult to predict results, as is seen for example in so simple a phenomenon as the weather. This is especially true of the behavior of higher animals, for here the number of factors is much greater than in many inorganic phenomena and the interactions of these factors are most complex. Professor W. K. Brooks used to comment upon the ease of predicting what would happen when you kick a stone, as compared with the difficulty of predicting the results of kicking a dog. In the

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latter case one needs to take into account many hereditary and environmental factors; one needs to know the breed and size of the dog, whether he is at home or not, whether the one who kicks is a stranger or not, etc. There is good reason to believe that when all these factors are taken into account the results in the case of the dog would be as predictable as in that of the stone. Certainly none of the cases cited by Bergson proves that the activities of animals are indeterminate and non-mechanistic.

Driesch also has maintained that adaptive responses in general cannot be explained by mechanistic science. His first proof of vitalism is that a living thing is a "harmonic, equipotential system"; that is, "the pattern of the whole exists in every part," and under suitable conditions a fragment of an egg, embryo, or adult can give rise to a typical whole. Likewise, when the cells and nuclei of segmenting eggs are forced out of their normal positions by pressure normal development may result, and Driesch holds that neither cytoplasm, nucleus, nor medium are the causes of differentiation, but that "the fate of a part is a function of its position" in the whole, and that "any part is capable of any fate." Some organisms may be cut up in the three dimensions of space and yet each fragment that is sufficiently large may give rise to a complete organism like the original one. It is inconceivable, he says, that any machine could be broken up in this way and yet the parts be capable of becoming complete. He therefore concludes that something, not mechanistic nor causal, lies in the background of development; this something he calls, in the language of Aristotle, "entelechy."

His second proof of vitalism is drawn from the genesis of this complex equipotential system. It is absurd to suppose, he says, that any machine could give rise to such a sys-

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tem, and again he invokes the aid of "entelechy." Finally, he finds a third proof of vitalism in the field of behavior, or what he calls the "individuality of correspondence between stimuli and responses." In such cases something non-mechanistic interferes when the good of the organism requires it, and this something, which resembles the "indwelling soul" of Plato, he calls "psychoid." In short, Driesch's three "proofs" of vitalism are all based upon *adaptive* responses.

However, all the parts of living things, whether eggs, embryos, or adults, are rarely, if ever, equipotential. Even parts of the embryos of the sea-urchin, upon which Driesch did much of his work and based most of his conclusions, are not equipotential in the chief axis; that is, fragments from the upper or lower poles are not capable of regenerating a whole embryo or larva. Fragments of the hydroid *Tubularia* are not equipotential so far as proportionality is concerned (Child). Regeneration in the ascidian *Clavelina* is complicated by degeneration, regeneration, and budding (ZurStrassen). The different cleavage cells of the eggs of mollusks, annelids, and ascidians are not equipotential, and when one of these cells is destroyed its function is not taken by other cells, but the embryo remains incomplete (mosaic development).

When Driesch maintains that neither cytoplasm, nucleus, nor medium is the cause of differentiation what can he mean? All of these factors are in varying ways and degrees the causes of differentiation. And when he asserts that it is inconceivable that any machine could be broken up in the three dimensions of space and the fragments still be capable of producing whole machines, or that it is absurd to suppose that any machine could give rise to an equipotential system, it is evident that his conception of a machine is

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too narrowly limited to those of human invention. The living machine is not a single one, as is an engine or a watch, but it is composed of machines within machines. Every living body is composed of cells within which are nuclei. The visible differentiations of a body are developed from the portion of the cell outside of the nucleus, but always under the influence of the nucleus. The nucleus itself rarely undergoes differentiation, so that there is in every such nucleus a complete machine which under certain conditions may be capable of developing a complete organism, as in the case of development from an egg cell. If this nuclear machine is fragmented or destroyed no regeneration is possible. Therefore the machine-theory of organization does not fail in this case; only Driesch's conception of the vital machine fails because the real organism is more complex than he supposed.

But even granting Driesch's claims that organisms are equipotential systems capable of complete regeneration after injury, that they differ greatly from machines of human invention, and that they generally respond beneficially to stimuli, it does not follow that they are in any respect removed from the field of mechanistic causality.

In the works of Bergson, Driesch, Thomson and other "neo-vitalists" hundreds of pages are devoted to labored refutations of mechanistic explanations of life and to eloquent presentations of mystical, allegorical, and unintelligible causes. In a notable contribution by Jennings' the ground is cleared of mere verbiage and the solid foundations of a mechanistic conception of life are laid in eighteen pages. Jennings shows that diversities in life phenomena are accompanied or preceded by diversities in materials, functions, and structures, and that they are not indeter-

¹"Life and Matter." Johns Hopkins Univ. Circ., 1914.

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minate or capricious. He points to the very significant fact that there is no evidence of life apart from protoplasm, and that such phenomena as development, adaptation, reason, and purpose are not annulled if they are found to be bound up with matter, for it is no more extraordinary that they should be associated with matter than that they should be separate from it.

In living as in lifeless things, mechanistic factors are not merely additive as Driesch maintains, but they are frequently creative. In chemical compounds new qualities appear which were not present in any of the elements entering the compounds. No one could predict beforehand the qualities of water from the properties of hydrogen and oxygen, and in general one cannot predict the results of combinations before they have been learned by experience. The fact that one could not predict consciousness from a knowledge of the organic or inorganic constituents of the body is not fundamentally different from these other cases in which new things are formed by new combinations. The "creative evolution" of Bergson is not different in principle from "creative synthesis," which is found everywhere in the living and the lifeless worlds; it is therefore no proof of vitalism.

The new vitalism no less than the old has failed at every point to establish its main proposition, namely, that the reactions of organisms are not causal, and that they require, in order to explain them, a special principle which is lacking in the inorganic world and which is non-mechanistic in action and wholly unrelated to the principle of cause and effect. This is not to deny that there may be a teleological principle in all nature, but rather to affirm that there is no sufficient reason for supposing that in this regard the living world differs fundamentally from the lifeless.

3. Mechanism and Purpose

The only mechanism of adaptation that has ever been suggested is the elimination of the unfit and the persistence of the fit. Inherited or racial adaptations may be explained as the result of the elimination of unfit individuals ("personal selection" or "Darwinism" in the strict sense), while acquired adaptations and useful responses to new conditions can be accounted for by the elimination of unfit structures and functions within the individual (intra-personal and reactional selection). Thus the simple mechanical principles of overproduction of varied individuals or reactions and the elimination of the less fit furnish a mechanistic explanation of all kinds of fitness in the living world.

But in man at least, and probably also in some of the higher animals, there is conscious purpose, and the behavior of many lower animals suggests that they also possess something similar to human purpose, though it is probably not accompanied by consciousness. If conscious purpose has evolved during the course of evolution, as it certainly develops during the individual development of man, do we not here find a phenomenon which cannot be explained as due to mechanistic causes? And if conscious purpose is non-mechanistic in its origin, is it not probable that "unconscious purpose," such as is manifested in the many apparently purposive responses of digestion, respiration, circulation, development, regulation, and the adaptive behavior of lower organisms, is also non-mechanistic? In short, if we approach this problem of fitness from the standpoint of human consciousness rather than from that of the physiology of the lowest organisms, from the top rather than from the bottom, do we not find that the mechanistic philosophy fails to furnish an adequate explanation? Mechanism must ac-

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count for purpose in man, as well as for fitness in lower organisms, if it is a universal principle.

It is this point of view that gives weight and force to non-mechanistic philosophy. Any system that denies will and purpose to man must be false, not only because it contradicts one of the most fundamental facts of consciousness, one of the most general experiences of men, but also because it is impractical and unlivable.

If man is the product of mere chance or accident; if as one biologist has said, "The evolution of consciousness is the greatest blunder in the universe"; if men live and die like the beasts and leave only their bones and implements behind; if life and evolution and consciousness are purposeless and lead to nothing—if this were the teaching of the mechanistic philosophy, then certainly it would be true that it debases man, and destroys the hopes of mankind. The blighting effect of such a philosophy is that it substitutes blind chance and necessity for plan and purpose, both in nature and in human life. If there is no teleology in nature, the course of evolution leading to man and to consciousness is the result of blind and blundering accident. If there is no purpose or value in human labor and suffering, life is not worth living, and the only sane and sensible thing to do is to end it all by suicide and race extinction.

But there are evidences of teleology in nature and of purpose in human life. Even struggle, suffering, and death have their value if in the long course of evolution they lead to progress. Men do not die and leave only their bones and implements, but "they rest from their labors and their *works* do follow them." "Others have labored and we have entered into their labors." Civilization is what it is today because of the labor and influence of millions of persons, most of whom are wholly unknown to us. Only a few men have achieved immortal fame, but multitudes have contributed to human progress.¹

In man at least intelligent purpose exists and must be accounted for. Here is the crucial test of universal mechanism—the purpose, consciousness, soul of man! If these psychic phenomena are not mechanistic in origin some principle other than mechanistic causality is present in man; and when

¹"Direction of Human Evolution," pp. 231, 232.

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we observe the purposive actions of animals, for example crows dropping mussels on rocks to break them open, cats turning buttons to open doors, or horses unlatching gates, it is evident that we are here dealing with the same fundamental problem that we have in human purpose. Finally, even non-conscious and purely instinctive acts, that are purposive, belong in the same category; for example, the mating, nest-building, brooding, and care of young on the part of birds, or similar reproductive habits of mammals, show instinctive, but not perceptual purpose. In man only, so far as we know, does purposive action at certain times rise into the field of consciousness, but most of his activities are non-conscious, although they are purposive. All such phenomena, from conscious purpose at one extreme to instinctive reactions and to tropisms at the other, seem to be fundamentally akin, and if mechanism fails to explain any of them it probably fails with all; if tropisms and instincts are entirely explicable on mechanistic grounds, it is probable that even perceptual purpose may be so explained.

In commenting upon the fact that adaptations are mechanisms for securing the persistence of organisms, Roux¹ says: "Persistence is not an *aim* of living things but an indispensably necessary *condition*. Life cannot suddenly arise anew, but if it exists it must be preserved, and so must before all be capable of persisting, otherwise it disappears. This is no *aim* but a direct necessity of its existence."

But after all, the real question is how living things are able to meet these necessary conditions of life. It may be granted that adaptations are not caused by conscious aims or purposes, but their results are much the same as if they were; they do attain certain desirable ends, and to this extent they are purposive. But results may be purposive while

¹Arch. Entw. Mech. Bd. 26, 1908.

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their causes are mechanistic; the contrary view is due to a false conception of purpose or of mechanism. There are good reasons for believing that purpose and will in ourselves are not uncaused but rather that they are results of antecedent causes; that they also are links in the chain of cause and effect, and hence are mechanistic in origin.

We have already found that many of the beneficial responses of protozoa and germ-cells are the residuum left after the elimination of non-beneficial responses; in these cells, however, there is little if any capacity to profit by experience. On the other hand, a cat that by random movements accidentally unlatches a door and lets itself out, as in Thorndike's experiment, gradually omits useless movements, remembers past successes, and finally learns to unlatch the door at once, thus showing intelligent purpose, developed through the mechanistic process of the elimination of useless responses. Are intelligence and purpose in man fundamentally different from this? There is every reason to believe that human beings arrive at intelligence and reason by the same process—a process of many trials and errors, a few trials and successes, a remembering of these past experiences, and an application of them to new conditions. All solving of problems, directed thinking and consecutive reasoning are accompanied by, if they do not consist in, rapid elimination of unfit ideas and mental activities. Thus intelligence and purpose in man, no less than fitness in all organisms, may be explained as results of the elimination of the unfit; they also are adaptations; and for this reason, if for no other, adaptations appear to be intelligent and purposive.

4. *Teleology*

Nevertheless, this mechanistic explanation of fitness and purpose is not complete and many things are left unex-

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plained. For example, the mechanism of trial and error by which *Paramecium* avoids extremes of heat and cold is based upon its ability to distinguish between favorable and unfavorable, or between satisfactory and unsatisfactory, conditions. In some of the simplest forms of living things as well as in the most complex this capacity exists, and for the present at least it cannot be accounted for on mechanistic grounds. Thus in our mechanistic explanation of fitness we put in at the beginning what we get out at the end, namely, a capacity to distinguish between the fit and the unfit, and a tendency to retain the one and eliminate the other. And so in all mechanistic sciences from mathematics to biology, we introduce in one form or another in our factors the qualities which we seek to explain in the end product. It is said that in some rural districts hogs are weighed by driving them on to one side of a balanced platform, throwing stones on to the other side until they equal the weight of the hogs, and then guessing at the weight of the stones. When we attempt to explain the actual origin of fundamental qualities by quantitative mechanistic methods, do we not, with much labor, perform a similar operation? It is a striking fact that at present it is impossible to explain the organization of a cell, the potencies of development or of evolution, or the elements of fitness, purpose, and consciousness on purely mechanistic grounds. "It is because living things are irritable, registrative, persistent, variable, that they have been able to evolve in adaptive ways," but we cannot explain the fact that they possess these qualities. Thus we introduce on one side of the equation the equivalents of the things on the other side which we seek to explain.

In a recent treatise on evolution in its widest aspects, Macfarlane¹ has proposed as one of the principal factors in

¹"Causes and Courses of Organic Evolution," p. 628.

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evolution and adaptation what he calls "proenvironment"; this he defines as "the capacity of any organism for perceiving and then positively growing or moving toward an environment that is the most *satisfying* for it." This capacity he holds is present in all living things and has its analogue even in chemical affinity. Certainly when one observes how almost universally organisms distinguish between beneficial and injurious environments, one is compelled to admit that some such capacity must be present in all living things, and that it must be an important factor in the adaptive or beneficial responses of organisms. Whether it is also a factor in the evolution of racial adaptations depends upon the answer to the question whether such individual or acquired adaptations can become hereditary. Macfarlane takes it for granted that they can be, and he would probably maintain, though he has not developed this thesis specifically, that all inherited adaptations were in their individual origins beneficial or satisfying responses to the environment. Against this view may be urged all the weighty objections to the doctrine of the inheritance of acquired adaptations which are familiar to all biologists. It is difficult if not impossible to explain on this ground the origin of numerous inherited adaptations which are for the good of the species only and are destructive of the individual; for example, the peculiar structures, functions, and instincts of worker and drone bees, which lead to the sacrifice of the individual for the good of the colony, cannot be explained by any form of Lamarckism, but are readily explained by Darwinism.

According to the Darwinian theory, the guiding and directing power of selection should be directly proportional to its severity. If it eliminates only those mutants that are positively injurious or non-viable, as many adherents of the

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mutation theory believe, would it be possible to explain such perfect adaptations as are found, for example, in the eye? If these be attributed to the chance occurrence of favorable mutations, do we not place upon chance a perfectly impossible burden when we load upon it not only all the wonderful adaptations in such an organ as the eye, but also all the multitudes of adaptations and coadaptations which exist in every part and function of man or one of the higher animals?

Most of all, when we turn from analysis to synthesis and consider the whole course of organic evolution from amœba to man, from the simplest motor responses to the development of an intellect capable of studying the universe and its origin, are we impressed with the idea that evolution has been guided by something other than chance. Progressive evolution consists in increasing complexity of organization and in increasing adaptation to the environment. It is probably no accident that organization, mutations, and environment have been so correlated that they have led to the perfection of organization and adaptation which we see all about us. Evolution has not been an eternal seesaw: it has led somewhere. The fact that organisms can adapt themselves to changing environment is no accident; the fact that environment has so changed as to bring about progress is no accident. Philosophically, it is difficult to avoid the conclusion that evolution has revealed a larger teleology than was ever dreamed of before—a teleology which differs from vitalism in that it takes in not only the living but also the lifeless world.

And yet science cannot deal with teleology but only with causes and effects and mechanisms; *given* matter and energy and life, with all their potentialities, science deals with the succession of events in evolution, explaining them in a purely

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mechanistic manner. In biology the desire for simple mechanical explanations is so great that it often causes us to minimize the difficulties and magnify the successes of such explanations. We may temporarily close our eyes to these difficulties, but they remain and must be reckoned with. Few persons have the intellectual honesty of Darwin, who wrote down at once the objections to his theory as they occurred to him, lest he might forget them, and who confessed that he never thought of explaining the evolution of the eye without a shudder. But even if an ultimate mechanistic explanation of adaptations is not possible, it does not follow that we must *at once* resort to an explanation which is either non-mechanistic or supernatural. Many things which were once supposed to be due to supernatural causes are now readily explained by natural ones. The earlier students of evolution proposed absurdly simple mechanical explanations of the process. Later these were replaced by more complex mechanisms, and when these latter fail to offer a satisfactory explanation the scientific solution must be sought in more and more complex mechanisms; for science deals only with mechanisms, and a scientific explanation must be mechanistic.

Some of the world's great philosophers and scientists, from Aristotle and Plato to Kant, Schopenhauer, Lamarck, Cope, Bergson, Driesch, and Henderson, have maintained that the fitness and order of nature can be explained only by assuming that there is some sort of teleological principle in nature, which lies back of or runs parallel with the principle of causality—something which acts more or less like human will or purpose, and which is itself an uncaused cause lying outside the field of scientific inquiry.

Kant has expressed this opinion in a well-known passage: "It is quite certain that we cannot become sufficiently acquainted with organized creatures and their hidden potentialities by aid of purely mechanical natural principles, much less that we can explain them; and this is so certain that we may boldly assert that it is absurd for

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man even to conceive such an idea, or to hope that a Newton may one day arise to make even the production of a blade of grass comprehensible, according to natural laws ordained by no intention."

Haeckel and other pure mechanists have hailed Darwin as Kant's impossible Newton of the living world and his theory of "natural selection" as the purely mechanical principle which accounts for the adaptations of organisms. . . . In the light of Darwin's theory we see that adaptations are the results of natural causes: the causal mechanism applies to all the fitnesses of nature as well as to other phenomena; but back of all mechanism, or running through all mechanism, is teleology or purpose.

From the standpoint of science and philosophy the origin of this order and mechanism is the great secret of the universe. Science deals only with mechanisms, and a purely scientific explanation must be mechanistic, but there is no mechanical explanation for the ultimate mechanism of the universe; mechanism cannot explain itself. The mechanism of a locomotive will explain what it does, but it will not explain its origin nor the purpose which it subserves. The organization of an animal or plant or egg is said to explain what it does, but it will not explain the teleological nature of that organization.

Biologists no longer think of any adaptation as having been directly created for the purpose which it now serves but rather as having been slowly developed in the course of evolution. Nevertheless, in tracing an adaptation to its sources we do no more than transfer the origin of fitness to earlier causes. We may explain the fitness of the eye as due to its ontogenetic development, and this as due to heredity and environment, but this does not explain how the potentialities of the eye came to be in the germ-plasm. We have merely shifted the problem to an earlier stage. And the same is true of the evolution of eyes: our explanation of the origin of eyes may be that they are due to mutation and natural selection, or to the inherited effects of use and disuse: but in either case we do not explain the fact that eyes were potentially present in these causes. We have merely shifted the problem from the fitness of results to the fitness of the causes of those results: and in spite of Darwin and his great theory, it is still true that no Newton has yet arisen "to make even the production of a blade of grass comprehensible, according to natural laws ordained by no intention."¹

In two recent books of great philosophical and scientific value, Henderson has shown that very many elements of the

¹Conklin, "Direction of Human Evolution," pp. 221-224.

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environment are chemically and physically the best possible for life phenomena. In particular, water, carbonic acid and the compounds of carbon, hydrogen, and oxygen possess many unique properties which are necessary to life, and these substances are better fitted to the life processes than any other known substances. He concludes, "Therefore the fitness of the *environment* is both real and unique." The origin of this fitness of the environment for life "lies at least as far back as the phenomena of the periodic system, at least as far back as the evolution of the elements, if they were ever evolved." And yet he holds that it "is conclusively proven that the whole process of cosmic evolution from its earliest conceivable state to the present is pure mechanism." In explanation of this fitness which runs through the whole of nature, he concludes that it is conceivable that a teleological "tendency would work parallel with mechanism without interfering with it. The effect of such a tendency working steadily through the whole process of evolution is also at least conceivable, however small its bearing upon science, provided, like time itself, it be a perfectly independent variable, making up therefore, with time the constant environment, so to speak, of the evolutionary process. This tendency must not be demonstrable either by weighing or by measuring, else it would amount to an interference with the mechanistic process, and it must not itself be liable to any kind of variation whose detection would directly reveal it. Where, then, can the origin of such a tendency be located? Why, clearly, if we accept the induction in favor of mechanism, only where Bergson¹ has shrewdly placed his vital impulse, at the very origin of things, just before mechanism begins to act. In short, our new teleology cannot have

¹Bergson places his *vital impulse* not at the origin of the universe but only at the beginnings of life. It is a form of *vitalism* rather than of general *teleology*.

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originated in or through mechanism, but it is a necessary and preëstablished associate of mechanism. Matter and energy have an original property, assuredly not by chance, which organizes the universe in space and time."¹

These important philosophical conclusions supplement but do not destroy a mechanistic interpretation of nature. If the chemical and physical characteristics of the environment had been very different from what they are, life as we know it could not have existed on the earth, just as it is probable that life does not exist on the moon because of the absence of water and of an atmosphere. It does not necessarily follow that the environment was made as it is for the purpose of supporting life, or that prospective life was a cause of antecedent environment, but it is impossible to reflect upon this fitness of the environment and indeed the whole order of nature without recognizing our inability to explain finally such phenomena on purely mechanistic grounds.

This conception of a general teleological principle running through all nature differs from vitalism in that it recognizes no world-wide distinction between the organic and the inorganic; both of these belong to the same universe; in both mechanism is universal, and so also is teleology. Here is common ground upon which mechanists, vitalists, and religionists may take their stand; for the thing which mechanists desire to prove is not the absence of teleology but the universal presence of mechanism, while the proposition which defenders of vitalism and of religion are concerned to prove is not the absence of mechanism but the presence of teleology.

Some of the most profound students of nature from the ancient Greeks to the present time have thought it necessary to assume some initial teleological principle. Weismann,

¹"The Fitness of the Environment," pp. 307, 308.

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whom Bernard Shaw counts the chief of scientific sinners because of his advocacy of a mechanistic conception of evolution, believed that extreme mechanism was consistent with extreme teleology; indeed, he maintained, "The most complete mechanism conceivable is likewise the most complete teleology conceivable. With this conception vanish all apprehensions that the new views of evolution would cause man to lose the best that he possesses—morality and purely human culture." And no less a mechanist than Huxley said, "Perhaps the most remarkable service to the philosophy of biology rendered by Mr. Darwin is the reconciliation of teleology and morphology, and the explanation of the facts of both which his views offer. The teleology which supposes that the eye, such as we see it in man or one of the higher Vertebrata, was made with the precise structure which it exhibits, for the purpose of enabling the animal which possesses it to see, has undoubtedly received its death-blow. Nevertheless it is necessary to remember that there is a wider teleology, which is not touched by the doctrine of evolution, but is actually based upon the fundamental proposition of evolution. That proposition is that the whole world, living and not living, is the result of the mutual interaction, according to definite laws, of the forces possessed by the molecules of which the primitive nebulosity of the universe was composed."¹ And Darwin confesses "the extreme difficulty or rather impossibility of conceiving this immense and wonderful universe, including man with his capacity of looking far backwards and far into futurity, as the result of blind chance or necessity. When thus reflecting I feel compelled to look to a First Cause having an intelligent mind in some degree analogous to that of man; and I deserve to be called a Theist. This conclusion was strong in

¹Huxley, *Collected Essays*, Vol. 2, p. 110.

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my mind about the time, as far as I can remember, when I wrote the 'Origin of Species'; and it is since that time that it has very gradually, with many fluctuations, become weaker. But then arises the doubt, can the mind of man, which has, as I fully believe, been developed from a mind as low as that possessed by the lowest animal, be trusted when it draws such grand conclusions?"¹

Finally, Henderson has summed up his conclusions on this subject in the following thoughtful sentences: "We may progressively lay bare the order of nature and define it with the aid of the exact sciences. Thus we may recognize it for what it is, and now at length we clearly see that it is teleological. But we shall never find the explanation of the riddle, for it concerns the origin of things. Upon this subject clear ideas and close reasoning are no longer possible, for thought has arrived at one of its natural frontiers. Nothing more remains but to admit that the riddle surpasses us and to conclude that the contrast of mechanism with teleology is the very foundation of the order of nature, which must ever be regarded from two complementary points of view, as a vast assemblage of changing systems, and as an harmonious unity of changeless laws and qualities working together in the process of evolution."²

CONCLUSION

The great problems of the methods and causes of organic evolution and adaptation are slowly being solved. We have made many false starts and have had to retrace many steps, but nevertheless much progress has been made along many lines. Many attractive theories have had their day and are now abandoned; unfortunately we do not know that many

¹Life and Letters, Vol. I, p. 282.

²"The Order of Nature," pp. 208, 209.

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current theories may not suffer a similar fate. But to certain theories in one form or another we come back again and again, and always they are more secure. This is especially true of the underlying idea in the theory of Darwin, that master of those who interpret Nature.

But whether we have reached any satisfactory solution of evolution problems or not, we know at least that these problems are being attacked in the only possible scientific way, viz., by observation, analysis, and experiment. Doubtless some of these great problems will always remain unsolved, for Nature is infinite. It is not the possession of perfect truth, but its pursuit, which falls to our lot and fills up the measure of our lives; and we would not have it otherwise, "for to travel hopefully is a better thing than to arrive, and the true success is to labor."

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