

ENVIRONMENTS AND LIFE DEVELOPMENT

Presidential Address

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The environment is both physical and living, but, in so far as the individual organism is concerned, the physical environment is the fundamental background. The physical environment is populated by living organisms and the living population is therefore adapted to the physical environment and is conditioned by it. The relations between the individuals which make up the organic population of any environment are exceedingly complex and the relations of the population to the physical environment are equally complex. The plant population of any time and any place is a flora and the animal population is a fauna. The individual species of a flora are adapted to each other and the species of a fauna are likewise adapted. Since the entire population is adapted to the physical environment, the physical environment is the stage on which life develops.

Although the major physical environments are land, water, and air, these are so complex that it is difficult to discuss them individually as physical environments or as the habitats of organic populations. The gross physical environments, continental platforms, and ocean basins are more readily treated. The continents, which form the major terrestrial environments, consist of all of the earth's surface above high tide, or, roughly speaking, above sea level. The ocean basins, which contain the deep seas, constitute all of the earth's surface below the 100 fathom line. That part of the earth's surface lying between sea level and the ocean basins is the continental shelf. The oceans thus lie on the continental platforms as epicontinental seas and in the ocean basins proper as the deep seas.

The present oceans occupy about 71 per cent, or somewhat less than three-fourths, of the surface of the earth. The deep seas occupy approximately 66 per cent of the earth's surface and of the continents, about 26 per cent. Thus, the

deep seas occupy approximately two-thirds of the earth's surface, whereas the continental platforms are about one third.

The oceans may be divided into four life zones, the littoral and the neritic zones, which occupy the bottoms of the epicontinental seas; and the bathyal and the abyssal zones, which constitute the bottom life zones of the deep seas. The littoral zone occupies the areas between high and low tide and the neritic zone occupies the remainder of the continental shelf down to the 100 fathom (600ft.) line. The bathyal zone lies between 600 and 6,000 feet. The abyssal zone lies at depths lower than 6,000 feet down to approximately 34,000 feet, the greatest known depths of the deep seas.

The continents may be divided into many more or less sharply defined environments which are modifications of aquatic and truly terrestrial or land environments. Aquatic environments are in part running water, as in streams, and standing water in lagoons, lakes, inland seas and ponds. The terrestrial environments are plains, plateaus, and mountains. Swamps, marshes, and bogs are important environments partaking in part of the characters of terrestrial and in part of aquatic environments. Latitude, altitude, and humidity modify all of these into a very considerable number of environmental variants. Thus, plains may be high or low, with consequent variations in temperature and humidity. They may be in high or low latitudes and thus subjected to great variations of climatic factors. They may be in the unobstructed pathway of prevailing winds or the prevailing winds may be modified by intervening mountain ranges. Plains may vary as physical environments from humid swamps to steppes to deserts. Variations from tropical plains to arctic tundras exist.

Whatever the environment, it is populated by living things, and these are adapted to it and to each other in so complex a relationship that separation of physical and biological environment is difficult.

For the purposes of this discussion, however, we may regard the physical environment as basic and fundamental, since individuals or populations must be first accommodated

to it. Considered as primary, physical environments are not equally favorable to organisms. Some environments, such as warm epicontinental seas, are highly favorable, as shown by the density of population of the present as well as ancient seas. Warm swamps and forested lowlands are also highly favorable to dense populations. Deserts are unfavorable, and the bottoms of the deep seas, from what is known of them, are difficult or unfavorable to dense populations of living things. Some environments, such as the steppes, are also difficult, and place stringent requirements on their organic populations. Physical environments offer biological slums, such as brackish water lagoons and stagnant bogs to the deprived organisms which are adapted to them.

Whatever the organism and wherever it lives, it is accommodated to the environment by adaptations. Of first importance are the adaptations to those essential components of the environments, without which life is impossible. These essential components are food, including carbon dioxide, water, and oxygen; and temperature, light, and pressure. Since these are absolute essentials, all organisms are adapted to them by an endless variety of organic mechanisms and structures. Although this vast array of organic structures is required to fit the organism to the primal necessities, we may consider them to be mostly functional adaptations. All organisms, both plants and animals, must obtain food; metabolism must occur; and accommodations of the organism to temperature, light, and pressure, must be made by all living protoplasm. In so far as these adaptations are functional, they will not be considered here.

Many adaptations, however, are structural adaptations to physical environments. May we consider, as illustrative, one type of structural adaptation, that of cementing the hard parts or exoskeleton to the sea bottom? There are hundreds of examples, both living and fossil, of sessile benthonic animals from every phylum, save possibly the vertebrates. For the most part, because of lack of locomotion, these live in clear waters where sedimentation is slow.

Since the requirement for this adaptation to fixed adult existence on the sea bottom is attachment, a considerable

variety of modes of attachment have been developed. Hard parts or skeletons are attached directly in some of the protozoa, both living and fossil. There are similarly attached sponges, living and extinct. Other invertebrate examples are the corals, hydroids, hydrocorallines, some fossil brachiopods, most bryozoa, some pelecypods, including the oysters and the remarkable fossil caprinids and their allies; the gasteropods, for example, the vermicularids, the tube dwelling annelids with attached and cemented tubes, many cystoids, and all blastoids, as well as a host of genera of crinoids both living and fossil. Even the arthropods have adapted this structural adaptation among the barnacles.

Burrowing animals, whether terrestrial or sub-aquatic, are structurally adapted to the environment by body forms which are strikingly similar to one another. Excellent examples are the pelecypods among the molluscs. These bivalves have developed the exoskeleton for ease in burrowing in soft mud. Burrowing pelecypods thus have shells without projections to impede progress. This adaptation is not essentially different from that of burrowing echinoderms, such as the heart urchin or the sand dollar. The chief difference is in the vertical flattening in the pelecypods and the horizontal compression of the representatives of the echinoderms. Many races of animals which are adapted to burrowing have developed similar structural devices. Among the arthropods, many of the trilobites of the Ordovician and Silurian exhibit an exoskeleton differing only slightly from the general shape of the sand dollar. The body form of some of the burrowing trilobites, which are arthropods, is remarkably similar to that of the mole, which is a vertebrate. Indeed it is of the highest class of vertebrates, the mammals.

Structural adaptation to swimming is excellently illustrated by the fish. The entire body form has become stream-lined and appendages have been developed for propulsion and stabilization in a liquid environment. This most typical natant adaptation is not monopolized by the fishes, but is equally well displayed by some amphibians, especially in the tadpole stage, by the extinct marine reptiles known as the

ichthyosaurs, by the extinct Cretaceous bird, *Hesperornis*, and even by the mammals in the whales and porpoises. The striking resemblance in body form among some of these is so striking that it results in popular misconceptions as to the classification of such animals as the whale.

Among the natant shell bearing invertebrates, the same tendency to become stream-lined is illustrated among the molluscs, where it reaches a high degree of perfection and is climaxed among the discus shaped cephalopods, the ammonites. Some protozoa with tests so closely approach this stream-lined molluscan form that early workers confused them with molluscs.

Adaptations of animals to swamps and bogs are most characteristic. This environment is conducive to the luxuriant growth of vegetation, so that food is abundant and easily procured. Animals here tend to take on weight because of easy acquisition of food. Locomotion, however, is difficult because of the shallow water and soft underfooting inherent in the environment. Heavy animals are hence of necessity structurally adapted to locomotion in this peculiar environment. Thus the stumpy, post-like legs of the hippopotamus and rhinoceros are seen also in the swamp dwelling dinosaurs. Some of these extinct reptiles approach the rhinoceros in leg and body architecture more closely than they do their own cold-blooded relatives.

These examples are only a few of the structural adaptations to environment. There are many others which illustrate adaptation equally well. They suffice to show the tendency of various organisms to adapt the same or similar structures as adaptations to the same or similar environment.

Races appear to be or have been originally adapted structurally to certain environments. Thus the fishes are fishes because they are primarily adapted to swimming in water. Most of them have held to that adaptation. The pelecypods probably were originally developed by adaptation to burrowing in the benthonic environment. By and large, they have retained that adaptation throughout their long racial his-

tory. Mammals were fundamentally adapted to quadrupedal locomotion on land.

Organisms which are structurally adapted to one environment may leave that environment to live in another. They can leave it, however, only by modifying the structure to adapt it to the new environment. The cephalopods appear to have been originally adapted structurally to crawling on the sea bottom. In the Mesozoic, some became stream-lined so beautifully and perfectly that they can be best interpreted as nectonic, structurally adapted to swimming. Others become globose and appear to have been best adapted to a floating or pelagic existence. Still others lengthened the shell, which was bent and twisted, much like a pile of rope. These were so poorly adapted to any sort of locomotion that they appear to have become sedentary or still bottom dwellers. Many other examples of departure from primary or fundamental structural adaptations are known by the biologist and the paleontologist. Such departures are adaptive radiation.

Geologic history is a history of changing environments. Rocks and fossils which record this history indicate that environments, such as we know them today, are not new. Indeed, physical environments such as those of the present have been in existence since the beginning of recorded geologic history. The continental platforms and ocean basins have long been in existence. In so far as the record can be interpreted, there is essentially no evidence that deep seas have occupied any area of the earth now occupied by continental platform except possibly some volcanic islands. Thus we may assume, with considerable confidence, that the deep seas have occupied their present positions since their origin.

The great changes of the past have been due to the relation between elevation of the continental platform and sea level. May we take the Silurian period as an example of changes which have occurred? At the beginning of the period, the shallow seas were restricted to the borders of the North American continent. The continents were, therefore, greatly expanded. As time went on, the continent was depressed and the Appalachian and Rocky Mountain regions

were gradually inundated by shallow seas, seas less than 100 fathoms deep. The subsidence continued to about the middle of the period, when possibly a third of the continent was below sea level. During the latter half of the period, the continental platform was slowly uplifted, the seas retreated, leaving the continent expanded as at the beginning.

Another typical example of periodic changes in continental and oceanic environments is that recorded for the late Cretaceous. In this period seas expanded across the western interior from the Gulf of Mexico to the Arctic Ocean and around the southern end of the Appalachians to New Jersey. This inundation was one of the greatest of all geologic history. After the maximum expansion of the Cretaceous seas, they slowly retreated, and the North American continent again returned to continental conditions.

Such vast changes in fundamental environments have recurred many times in the history of the earth. The examples illustrate a most important fact in the consideration of environmental changes. One environment, such as a shallow sea, may expand, but expansion is always at the expense of some other environment. Thus, in the Silurian and Cretaceous, as the shallow seas, over millions of years, spread over the continental platforms, the continental environments were proportionately contracted. As the seas retreated, the continental environment was expanded to include the areas formerly occupied by seas.

A population adapted to an expanding environment is in a most favorable situation, more especially since these expansions have been very great and long continued. Pressure of the physical environment due to restriction is slight, increasingly slight. The population lives under conditions of a biological boom, very slow but long continued. The tremendous expansion of the reef corals seems a natural biological accompaniment of the expanding clear shallow seas. The equally remarkable development of the chambered cephalopods or ammonites of the Cretaceous is another equally significant example. In Pennsylvanian time, swamps and bogs were possibly expanded to a greater extent than at any other time in the history of the earth. Witness the rise of the amphi-

bians, especially and peculiarly adapted to life in such a medium. Again, observe a similar expansion of the bog dwelling dinosaurs in co-ordination with the expansion of the swamp environment in the late Cretaceous.

Contracting environments produce a situation which is the reverse of expansion. The organic population must endure millions of years of progressive restriction of the environment to which each member is adapted. Biological competition must of necessity increase throughout such a time. A biological depression results. The races which make up the organic population appear to respond to the beginning of environmental contraction by extensive adaptive radiation. Near paradoxes in structural adaptations, in some races, accompany this trend. In the Cretaceous, the cephalopods, adapted primarily to crawling, became stream-lined to adapt them to the nectonic environment. They become sedentary on the sea bottom. In the seas of the Pennsylvanian, some protozoa floated, then became sedentary bottom dwellers and at last adapted a light spherical test to float them as pelagic organisms. The reptiles of the Mesozoic at two such times developed wings, by tremendous growth of the little finger, and flew. They became turtle-like and swam. Others took on an eel-like body form and swam equally well. The crowning achievement of adaptive radiation among the reptiles was the remarkable ichthyosaur, which became as streamlined as any fish, modified the hands into flippers, the feet likewise, and developed a caudal fin like that of a fish.

As contraction progresses, however, an inevitable result occurs. Species, then whole genera, and even families of organisms, fail to meet the constantly contracting environment and become extinct. Perhaps the botanist, the zoologist, or the geneticist can offer an explanation to the paleontologist for the failure of those organisms which are the result of adaptive radiation. The evidence of paleontology appears to indicate that such organisms become extinct during protracted and great contractions of environment. Thus perished the trilobites, the corals of the Silurian, the amphibians of the Pennsylvanian, and the reptiles, including those colossi of

life development, the dinosaurs. A host of other examples might be added.

Another set of environmental conditions must yet be considered. At the height of expansion of the continent, or great contraction of the epicontinental seas, elevation of the lands is a concurrent factor. Mountains have been formed at such times. Elevation of mountains, particularly in the paths of prevailing winds, results in the climax of all terrestrial environment in the steppes environment and the desert. Times such as these are physically so important that the geologist refers to them as revolutions.

Biologically, periods of revolution are most significant since they climax a period of expansion of continental environments unfavorable to dense populations. Obviously they are also the times of greatest sea restriction. Two periods of revolution in which such extreme conditions existed were the Appalachian revolution, at the close of the Paleozoic era and the Rocky Mountain revolution, at the close of the Mesozoic era. But two attendant features of the effect of these events need be cited, the termination of the rule of the amphibians at the end of the Paleozoic and the downfall of the reptiles with the Rocky Mountain revolution.

Contraction and expansion of physical environments thus appear to be directly related to the expansion of races which make up the organic population of any time. The geologic history of environments has an important relation to the history of life development.

The causes of changes of physical environment have long been subject to study by the geologist and the geological historian. They are traceable directly to the dominant geological processes; diastrophism, the movement of solid rock; gradation, the levelling process which cuts down the high places to build up the low; and vulcanism, the movement of liquid rock. Of these diastrophism, which produces elevation and depression of the continental platforms and the making of mountains, in so far as life development is concerned, is most important.