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THE METHOD OF EVOLUTION IN THE UNIONIDÆ.*

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After I had incautiously and somewhat improvidently, perhaps, accepted the invitation of the chairman to take part in the discussion this afternoon, I began to consider what there was to say upon the subject that had been assigned to me. At the outset it seemed that there was a certain element of uncertainty, what we lawyers call a latent ambiguity, as to what was meant by "method of evolution." Assuming the existence of a primitive, simple, homogeneous type of any class of animal life, which in the course of time has become changed into a series of similar, yet diverse, types of greater complexity of organization, does the "method of evolution" refer simply to the changes in the organism itself from simplicity to complexity, or does it mean those external forces, which, exerted

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upon the original innate tendency toward variation through changes in environmental conditions resulting from migration, isolation, changes in climate, food supply, and chemical constituents in the water, have, first stimulated and then by the pruning off, through natural selection, of improvident variations, guided and directed, as it were, the organism, not only to its present, greater complexity, but to its more perfect adaptation to its present surroundings. Whether the original primitive type, if there had been no changes in environmental conditions, but simply through competition and the struggle for existence, would have evolved along the same lines that it has under the changes of environment to which it has actually been subjected in the past ages, is at the best only a matter of speculation. But there can be no doubt but that the more complex organization of the recent fauna is the combined result of the innate tendency to variation and the influence of changes in the external environmental conditions. The two are coincident.

For this reason, therefore, taking the North American Unionidæ as a concrete example, I propose to discuss briefly both aspects of the question.

I. Changes in the Animal.

The Unionidæ are a very ancient family. While it is probable their precursors are to be found in the bivalves, which, both in this country and in Europe, have been discovered in the Coal Measures, the connecting links are too few, and the interval of time too great to make that a matter of profitable speculation. The first genuine Unios now known in this country have been found in the Triassic of Texas. They are all simple forms and not unlike many of the simpler forms found in the recent fauna. In the Cretaceous deposits in the western

states, extending from Texas to British America, however, are to be found in very considerable abundance what are evidently the prototypes of our recent species. These fossils show great variation, some of them are exceedingly similar to recent forms, and others are diverse types which have apparently become entirely extinct. Of course, we only know these species from their shells. There is no evidence whatever as to the peculiarities, if any, of the animal that lived inside of the shell. But comparing these fossil species with the recent fauna we find that, with one exception hereafter to be more fully considered, there has been, so far as the shell is concerned, no change of any great extent.

There being no evidence as to what were the peculiarities of the animals of these fossil species, we are forced to judge as to what was the course of evolution in the animal from the various forms of development which we find represented in the recent species. Taking the modern Unionidæ as a whole, we find that their organization is comparatively simple and, with one exception, very similar throughout the whole world. The one feature in their anatomy which is a variable one is in the adaptation of the gills as marsupia for carrying the eggs until they are hatched. Assuming that the most primitive form represented in the recent fauna is that of the genus Margaritana, and this assumption is based not only upon the peculiarity of its structure, but upon its range at the present time, which is greater than any other genus and, with the exception of the central part of British North America, extends entirely around the world, we find that all four gills are used as marsupia. The eggs, passing from the ovaries, occupy all four gills of the animal. The gills have neither water-tubes nor septa. The interlaminar connections are patch-like, irregular in shape and position, with indications of a

diagonal arrangement which does not follow the gill filaments and does not form continuous septa.

The next step apparently in the evolution of this feature of the animal was the formation of water-tubes by septa running parallel with the gill filaments, all four gills, however, being still used for carrying the eggs. The next advance was a very radical one, and resulted in the division of the Naiades into two great families; in the one (the Mutelidæ), which is not represented in our northern fauna but is confined to the southern half of the globe, only the inner gill is used for carrying the eggs, while in the Unionidæ proper, which includes the whole of the North American fauna, either all four gills or only the outer gills are used for that purpose. All the North American species of the recent fauna, which belong to the subfamily Unioninæ, which contains the more primitive types, and in which either all four gills or only the entire outer gills are used as marsupia, carry the eggs only a short time and are what are called tachytictic genera.

It would seem that, for some reason which we do not now know, the next step in the evolution of these creatures was for the purpose of enabling the female to carry the eggs in the gills for a longer period, practically through what we now call the winter season. These higher groups are called brachytictic for that reason. The development for this purpose was carried on in two different ways. In one great division, or subfamily, the Anodontinæ, the necessity was met by increasing the complexity of the water-tubes themselves. Whereas in the more primitive forms the water-tubes were filled with the eggs, and the water circulated through them, in this particular subfamily there has been developed in the water-tubes a series of longitudinal partitions which divide each tube into three parts, an inner ovisac in which the eggs

are carried, and two outer (secondary) water-tubes which permit the free circulation of the water around the eggs in their special receptacle. In this way it was possible for the animal to afford the eggs all the aëration that could be obtained. In the other group, or subfamily, the Lampsilinæ, the necessity has been met, either by restricting the marsupia to certain parts of the gill alone, usually in the posterior or central portion, or by developing an increasing number of folds, or pleatings, caused by the swelling of the water-tubes, which thus exposes the eggs to the full benefit of the circulating water. This change in many of the groups has been accompanied, also, by a greater development of the posterior flaps of the mantle, which enable the animal to expose the posterior portion of the gill, when charged with eggs, to the full current of water received from the incurrent siphon. This development of the animal, when carried to its extreme form, represents the highest stage in the present evolution of the family. In the first subfamily, the Anodontinæ, the whole of the outer gill is still used for carrying the eggs, and in these groups, as in the Unioninæ, there is no difference to be noticed between the male and female shells, except, perhaps, that sometimes the female shell is, on the whole, somewhat more inflated. But in the Lampsilinæ, where the marsupium is restricted to a particular portion of the gill, which consequently becomes greatly inflated during the breeding season, the shell of the female is changed in order to afford room for the expansion of the gill, and in these forms there is an inflation of the lower, posterior portion of the shell which is very marked and easily distinguishes the shell of the female from that of the male. Indeed, in the most advanced genus of this subfamily, Truncilla, the difference between the male and female shells is so great that in an early day, before the fact was known

that these differences were sexual, in a number of instances the male and female shells were described as distinct species. This modification of shell in the female is practically the only change, excepting, perhaps, the sculpture of the beaks,* that has taken place, so far as we know, in the structure of the shell itself.

II. Environmental Factors Affecting Evolution.

These are primarily migration and isolation, and it is necessary to briefly consider what they have been.

Migration.—The oldest land in eastern North America is what is known as the Laurentian Highlands in eastern Canada. When they first emerged from the sea they were separated from the earliest western land, the Sierra Nevada Mountains, by the sea itself. Later, as the land continued to rise, the southern Appalachians were uplifted and in the first instance, and through Carboniferous times, these, and their western extension, now known as the Cumberland Plateau, extended continuously from the eastern states southwest into Texas. This highland was the original divide between the drainage systems of that time. On the east and south the rivers flowed into the Atlantic and the Gulf of Mexico. North and west of this divide the streams flowed westerly into the Mesozoic Sea, which extended from the Gulf of Mexico to the Arctic Ocean. It was in the swamps, streams and bayous which lay along the eastern shore of this ancient sea that in Cretaceous times were evolved from the primitive forms, coming down at least from Triassic times, the prototypes of the

* There is a very considerable amount of variation in the recent fauna in the sculpture of the beaks. These differences are generally recognized as valid generic distinctions. But we have not as yet accumulated sufficient facts in regard to the development of this feature, either in recent or extinct forms, to formulate any very definite theory as to either the cause, or manner, of its evolution. The whole subject is still in the speculative stage.

present fauna. Through the migration which they were able to make up these ancient rivers, these early primitive forms were enabled to reach and establish themselves in the headwaters in the Laurentian Highlands and in the ancient Appalachian System.*

ISOLATION.—The first, and perhaps the greatest, factor of isolation which has resulted in the development of our recent fauna, occurred in early Cretaceous times, when by the sinking of a large section of the earth's crust in the Gulf region, what is known as the Mississippi Embayment was formed. This affected a triangular piece of territory extending along the line of the Gulf of Mexico from eastern Texas to the middle of Alabama, and thence northerly to a point above the present junction of the Ohio and Mississippi Rivers. The whole land between these two lines sank at least 5,000 feet, and the sea was admitted as far north as Memphis. This continued entirely through Cretaceous and Tertiary times until by the gradual uplifting of the land and the deposits of sediment brought down by the rivers on either side the depression was filled up and the present systems of drainage were established. So far as the Unionidæ are concerned, the important result of this fact was that during all this time the Unios which remained in the rivers west of the embayment were entirely separated from those, which, prior to the great landslide had been able to affect a lodgment in the headwaters of the ancient rivers flowing from the Cumberland Plateau. This created two centers of development and distribution; the one west of the Mississippi, and the other in eastern Tennessee.

* There is a large amount of evidence tending to show that there was considerable migration from the west of the Mississippi, northeastward into the Laurentian region after the Mississippi Embayment, during Tertiary times, but "that is another story" and does not in any way conflict with the general statements herein made.

The first emigrants from the West to the headwaters of the Mesozoic rivers, in the Laurentian and Appalachian Highlands, through orographic changes which caused the transference of streams, were undoubtedly able to penetrate in one way and another into the early streams which flowed easterly and southeasterly into the Atlantic Ocean, but ultimately the continued rise of the Appalachian System resulted in the entire separation of the eastern and western faunas and enabled each of them to develop under local influences, wholly independent of each other.

In the same way changes in the drainage systems of the rivers from the highlands of Tennessee, which originally had flowed southerly into the Gulf of Mexico, by which some of them—those which are now comprised in the Cumberland and Tennessee systems of drainage,—were cut off from their southern connections and established a new system of drainage toward the northwest into Ohio, resulted in the separation of the fauna in the streams south of the Tennessee Highlands from that inhabiting the streams which flowed westerly through what is now the Tennessee and Cumberland Systems, and enabled these, also, to develop under their own peculiar local influences.

Such was the situation at the beginning of the Glacial Epoch. This covered with ice to the depth of several thousand feet practically all the territory in eastern North America north of the Ohio River. The result was, so far as the Unionidæ are concerned, the absolute extermination of the whole race north of the line of glaciation. This wiped out all the connecting links, which might have then existed between the eastern, or Atlantic, fauna, and the western, or Mississippi, fauna, and left them, as represented along the southern borders of the glaciated areas, as distinct faunas, and from

these, upon the retreat of the ice and the establishment of the present systems of drainage, the waters of the glaciated area were re-peopled.

The result of all these changes in the earth's surface is shown in our present fauna by the fact that we have: 1st. East of the Appalachian Mountains a very distinct fauna which extends from Florida to New England, and thence northwesterly toward Hudson Bay. 2nd. Between the Appalachians and the arid regions of the West, occupying the Mississippi Valley and all its tributary streams and drainage systems, the characteristic American fauna, known as the Mississippian. 3rd. In the Alabama River and its tributaries, a very distinct subfauna, evidently derived from the ancient fauna of the Tennessee, but still sufficiently differentiated to be recognized as a distinct faunal element. 4th. West of the Rocky Mountains the Unione fauna is very meagre and is evidently derived from migration from Siberia. It has none of the distinctly American types characteristic of the eastern areas.

In these great faunal areas our modern species have been evolved. Separated from each other, the diverse local influences of climate, food supply and chemical elements contained in the water have all played their part in bringing about the evolution into the numerous species that now exist. This evolution has in some instances gone so far that new genera have been formed, but just when in geologic time these had their beginning, is not known, because the evidence afforded by the fossils of the Tertiary Period is as yet too imperfect to give us the connecting links. We can only imagine when and where they originated. Why they were evolved, like so many similar questions in other branches of the animal kingdom, is almost wholly a matter of speculation.

Such, then, in brief, has been the "method of evolution" of the North American Unionidæ, both in the animals themselves, and in the causes which have brought these changes about, and, in conclusion, it may be summarized somewhat as follows:

1. So far as the animals of the Unionidæ are concerned, the evolution from the most primitive forms that are known, to the most complex that now exist, has been all centered around the adaptation of the gills of the female for the care of eggs until they are hatched. Whatever changes have been brought about in the shell have been a necessary corollary to the changes in the animal itself.

2. The causes of evolution, aside from the innate tendency to variation that is present in all animal life, must be recognized in the history of the original migration brought about by the opportunities afforded by the earliest drainage system of the country and the subsequent isolation effected by changes in the earth's surface. All these have combined to affect the animal, and to intensify its innate tendency to variation.

The evolution of the species is a minor matter. It is almost wholly the result of local influences and is too complicated and, in many details, as yet too uncertain to justify any attempt to consider it at the present time.