ON THE GEOGRAPHICAL DISTRIBUTION OF CERTAIN FRESH-WATER MOLLUSKS OF NORTH AMERICA, AND THE PROBABLE CAUSES OF THEIR VARIATION.

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PART II.

Having set forth, in a previous number of this Journal, the main facts connected with the distribution of the *Unionidæ* and *Strepomatidæ*, over the region under consideration, it now becomes my task to attempt a solution of some of the problems thereby indicated; for to the careful student of this subject, several of its features are in the nature of unanswered questions, and these, it seems to me, will be found to be so intimately associated with the history of our continental development, and especially with that part relating to the evolution of the systems of drainage, as to cause continual reference to that subject, in the light of present geological knowledge.

Without stopping, at this point, to discuss the zoological relationships which possibly indicate the marine ancestry of the mollusks under consideration, it is a fair presumption that *the first fresh water forms were lacustrine.*

Of this proposition there seems to be ample evidence in the fact, that even during Archæan times, fresh water lakes were not impossibilities or even improbabilities. The processes by which salt water areas, isolated from the main ocean, pass through their various stages of approach to fresh water conditions, are familiar to all students of physical geography; nor is the fact of the existence of such bodies of water in regions of limited drainage, any less well known. High plateaus and low plains alike contribute examples of this fact. They are most typical in regions of comparative aridity from various causes; and many such bodies of water now known, have been undergoing the freshening process since the early Tertiaries.

It can not, I think, be doubted that there have been, throughout the geological ages, depressions of this description; and when we consider the fossil shells found in lacustrine deposits, and the forms now inhabiting such bodies of water as Lake Baikal and Lake Balkash, the probability of their gradual differentiation from marine types, and of their successive variations as fresh water forms, seems to be associated with no factor of the improbable.

In this consideration due weight must be given to the great influence of Archæan lands upon the subsequent moulding and forming of the continent, whose final systems of drainage, and all the stages of development leading to them, were determined by this early and stable region, which had its representative areas on both sides of the incipient uplift, and at comparatively isolated points over the great central basin; areas around which clustered, throughout the history of continental progress, the geological activities that determined everything.

It seems desirable, in discussing the variations above hinted at, to remember that there must have been a far greater impetus given them, when changes in drainage brought to these creatures the vicissitudes accompanying distribution into bodies of flowing water. Such changes of station, and finally of habitat, were among the last possibilities of continental growth, because it was only in connection with the later grand movements associated with terrestrial evolution, that present systems of drainage become possibilities. It is likewise true, that at no time since any drainage became possible to the continent, in streams large enough to contain a shell fauna, has there been such a complication of circumstances favorable to the local variation of that fauna, and the consequent establishment of varieties as now. For while it is a well determined fact in geology, that with the progress of continental evolution, the complexity of the characters of strata increased, it is also true that each of these new features would become a factor of importance in modifying the character of streams flowing through the land, and would, for this reason, aid in changing the nature of the mollusks inhabiting them; and these facts reach their greatest development in mountain regions, for the following among other causes that may be enumerated.

First, it is in mountainous regions that streams cut their way through strata of the most heterogeneous character, partly owing to the effects of metamorphism and other disturbing causes upon strata that may have been, originally, more homogeneous. *Second*, because even where metamorphic effects may be wanting, the range of formations traversed will be greater through the more extensive erosion. *Third*, because in mountainous regions there is an increase of probability that mineral deposits will fall in the path of streams, which will effect changes in the water, causing abnormal stunting, or extraordinary development of given forms. *Fourth*, because the influx of side streams, bearing the water of mineral springs, will add to these effects.

Fifth, because here we have the maximum of extremes in rate of current, and consequently the maximum of capacity to transport sediments that may act favorably or unfavorably upon the various creatures inhabiting these streams. *Sixth*, because of the probability that these mollusks have been propagated down stream, to the limit of favorable conditions—a limit always determined in the first place by geological causes—and because of the variation in the conditions met in this traverse. *Seventh*, because combined with all these causes is the fact, that all the stages in the development of these creatures are passed in an element thus unstable, amid conditions thus diversified, where the slightest tendency to variation must have the maximum of exciting causes constantly operating to call it into play. If, then, it be admitted that there is in the animal races any capacity for adaptation, and any tendency to variation, life, under such circumstances, would be a continuous development and exercise of these inherent qualities. For mountain regions have been the seat of origin of all drainage, and, no doubt, of the first forms of life inhabiting that drainage.

Now let us examine these probabilities in the light of the actual facts connected with the distribution of certain fresh water-shells.

First, we may consider the circumpolar distribution of certain *Limnæidæ*. These mollusks are essentially *lacustrine*, for while they are distributed into rivers and smaller streams to some extent, their station of fullest development is in lakes the world over.

The genera, *Physa*, *Limnæa* and *Planorbis*, are essentially northern forms, for it is in the cooler regions of the earth that they reach their largest size and greatest differentiation. Distribution southward is accompanied by a stunting of forms, in all cases but that of the subgenus *Bulinus*, of which the *B. aurantium* passes through the American tropics, and is many times the size of its circumpolar northern relative, the well-known *B. hypnorum*. This case stands as the only exception to an otherwise universal rule, in a group of mollusks covering in many described species, and yet one in which the differentiation of forms has led to such interminable varieties, that the most critically accurate of our conchologists hesitate to label them. The careful student of our North American forms, will find these shells more closely allied to their European relatives than any other group of mollusks found on the two continents, unless it be the *Succininæ*, and a few littoral marine species; and as it is not possible to separate the species, *inter se*, upon anatomical distinctions, in the greater number

of cases, it may be regarded as a substantial proof of their high antiquity when taken in consideration with the following facts; first, their universal presence in the lakes of the older geological formations at the north; second, their circumpolar distribution; third, their presence in regions unfavorable to the development of other families of mollusks, as testified by their absence ; fourth, their persistent appearance together, even southward, over regions of elevation. For these reasons, and for others of convenience in this discussion, I shall designate them as Fauna A, and will add this important and distinctly proven statement; that they reach, on our continent, their maximum of size, of differentiation, and the greatest local number of so-called species, in precisely that portion of it having the greater number of lakes, in regions of the oldest land or contiguous to it, and where there is the greatest paucity of other mollusks. This fauna is thus clearly shown to be regional, and the inference is fair that it has a very high antiquity.

Over the same region, both in Europe and America, we have distributed a few species of the *Unionidæ*, mostly represented by the genus *Anodonta*, a lacustrine group, always affecting still waters with muddy bottoms. These forms, with plain surface, and comparatively thin shells, are the predominant types of this family over the whole northern portion of our continent, from Maine to Oregon. It is among these mollusks that there occurs the greatest apparent synonymy, and the systematic zoologist will find himself, in the study of these shells, face to face with the question of varieties in endless and interminable confusion. Nor is this statement an exaggeration, when we remember that European malacologists of greater or less repute have made nearly one hundred synonyms for the *A. cygnea* alone; and that the slightest review of our North American species in the light of the evidence offered by geographical varieties, now well known, must reduce the number of so-called species more than one half ; and many of these varieties continue from eastern New York to Minnesota, and a fewer number southward to the very borders of Mexico, *over all of which area I have traced them!* These shells, for like reasons with the first, I shall designate as Fauna B.

The region occupied by A and B contains very few representatives of the *Strepomatidæ*, or Fauna C. Their geographical range northward was set forth in the first of these papers; and it is a significant fact that the few species of the *Strepomatidæ* occupying this region are those belonging to types that, further south, where the

conditions of variation enumerated in another part of this paper reach their maximum, are so intimately united by varieties as to render their separation into distinct species, in most cases, utterly impossible, as the shells from different localities are so completely blended, that it is no exaggeration to say that fifty per cent. of the described species are the merest synonyms. At the north, even, the difficulty begins; and it vastly increases in the mountainous region further south. This fauna differs essentially from A and B, in that it is not, normally, lacustrine, but fluviatile. A very few species are found in lakes, occasionally; but there is in these shells, an inherent aversion to still water, which characterizes all the genera, leading them to seek rather the rapid parts of rocky streams; and here it is that we meet their greatest diversity of types, and the greatest variety of coloration and ornamentation. This peculiarity of station is so persistent, that no skilled collector ever searches for them in level reaches of deep water, unless in the case of a few species of *Pleurocera*, which affect such localities; but *Io, Angitrema*, *Lithasia*, *Anculosa*, *Schizostoma*, *Goniobasis*, and *Strephobasis*, all genera represented by an infinity of varietal forms, seek always clean, rapidly flowing water, in rocky or gravelly river beds; and these groups are only represented by the genus *Melanopsis*, over the same range in Europe and Asia, and by *Goniobasis* and *Pleurocera* at the north, in America, their grand metropolis; in foreign lands their representatives, also, are confined to a range mostly south of that occupied by A and B. This fauna has a very limited distribution of genera and species west of the Mississippi, a fact easily traced, I think, to true geological causes, some of which are past, and others now in operation.

The shells designated as Ohio River Types in my previous article, I shall call Fauna D. Of its geographical distribution, varieties, and persistent forms, enough was said in that paper; and since it was written, I have received, from the very southwestern borders of Texas, a collection of Uniones gathered at random, which contains nothing but absolutely typical Ohio river species. South of the Ohio, in parallel streams, beginning with Kentucky river and Green river, and continuing to the eastern and southeastern tributaries of the Tennessee, we find, as has already been stated, a group of shells of a distinct facies, requiring no expert knowledge of chonchology to enable one to see that it differs, as a whole, from the Fauna D, with which it is associated. Its southern distribution is co-extensive with that of Fauna C, in all the larger and many of the smaller streams. Here occurs the greater

number of described "species" of the genus *Unio;* for among the forms filched from these prolific streams, malacological enthusiasts have disported themselves as species-makers, until the crying need of our times is an honest, impartial, and thorough review of the whole subject. The approximate boundaries of Fauna E may be placed between the Ohio river on the north, the Tennessee on the south, the Appalachians and the Mississippi. One fact is of curious import here; and it deserves to be put upon record in this discussion, and in this place. In his last edition of his Synopsis of the Family Unionidæ, 1870, which he tells us is his "most important work," Mr. Lea makes the following remarkable statement, the truth of which he had abundant opportunities to verify; "although I have examined critically, and published descriptions of the soft parts of 254 species of this family, and have often dissected 50 to 100 of the same species, I can not see, as yet, any useful division that could satisfy the student or the adept, which can be made by systematic difference in the organic forms of the soft parts." This means, I suppose, that the differences of the soft parts are so small as to afford no safe basis upon which to predicate classification. I may add to this, that the most intimate study of the anatomy of different species of the *Limnæidæ* and *Strepomatidæ*, has convinced me beyond resonable doubt, that specific differences, supposed to be indicated in the shells, do not extend to the animals themselves, so far as these studies go to show. I have now in course of preparation a memoir on this subject, which I hope soon to publish with accurate anatomical illustrations. Here is one of those strange facts, standing at the very threshold of the question of evolution, which finds a parallel in the *Lingula* and the *Rhizopod.*

We may now venture upon a few suggestions, to which these facts give rise. Clearly the oldest shell fauna upon the continent would have naturally inhabited Archæan regions; and as it is altogether likely, from chemical facts associated with the deposit of iron ores, and the presence of graphite in the older rocks of the continent, as pointed out by Prof. Dana and Dr. Hunt, that organic life may have existed to an extent not yet determined by fossils actually discovered as such, I think we do not pass beyond the bounds of probability in assigning to Fauna A a very remote antiquity. From its original *locus*, it has spread to the limit of suitable conditions, a limit undergoing constant variations, perhaps, through the geological ages, but which has been determined by boundaries mainly fixed by true geological causes. Through adaptation this fauna has, in a few cases, overstepped its

primitive barriers, but it remains, as we have seen, true to its original instincts in all its more important phases. It is not probable, as may be suggested by the doubting reader, that this fauna would have been exterminated by the great glacier, which is supposed to have originated in its peculiar haunts, but more likely that the few species having an abnormal southern or southwestern range, received the first impulse of distribution in that direction from the glacial condition; and that with the northward retreat of the glacier they simply resumed their normal habitat, continuing their distribution in that direction in succeeding times to the northern lakes of British America. In case of Fauna B we have evidence that a previous distribution, probably severed, by the same or other causes, has never been fully united in a few cases, as in that of the *M. margaritifera*, occurring in Maine and Oregon, but not between these stations so far as now known. But in most cases, the re-union has been complete. Such remnants as the glacial epoch left, have been equal to the emergency of perpetuating their race over the region desolated by glacial action, and they may thus indicate what are the possibilities of development under determinate conditions. It may be suggested, that as the species of so-called *Strepomatidæ* of the west coast have rather the facies of the tropical Melanians; and as the other associates of the *M. margaritifera* in the waters of Oregon are species not elsewhere found, that this little faunal remnant is an independent one, and I readily agree to all this ; yet there is no doubt of the existence of a Fauna B, nor of its distribution, and the possibility that its present species are the descendants of a geological remnant like those of A. Still more striking is the evidence to be adduced from Fauna C. The region over which this group is distributed may have had some drainage, though perhaps slight, as far back as the epoch of the Cincinnati uplift. It thus may have continued through all the Palæozoic ages thereafter. What wonder, then, that we have here such a diversity of forms, when we remember the mutations through which the continent subsequently passed to the termination of the Palæozoic. Local elevations and submergencies, and the various phenomena associated with the progress of continental development, brought to these creatures a series of vicissitudes that may have left many remnants in favored spots, whose descendants, modified and changed as they are, afford us the multitudinous varieties which this fauna assumes throughout its metropolis.

Indeed, if we could reach the ancestral form of these creatures, we should have another proof of the existence of what Prof. Dana so philo-

sophically called "comprehensive types;" and it is by no means a difficult thing to show abundant evidences of their presence in this heterogeneous host of their modified descendants, as I hope to point out hereafter. Even if this fauna does not antedate the Carboniferous epoch, the station which it has always occupied, for reasons already shown, would have brought a maximum of differentiating causes to bear. Nothing seems clearer to me than the separate origin of D and E. This is indicated by the merest superficial study of the shells, and I confidently expect that future geological explorations, among the western Tertiaries, may bring to light additional evidence upon this subject; and that when the habits and anatomy of these animals have been more thoroughly studied, and when we have a fuller understanding of the relations existing between the living and fossil species of western Europe, and the fossil Tertiary species of southeastern Europe, new light will begin to break in upon the "origin of species" among these protean bivalves; for such work is the special province of geology, and the highest generalization to which the perfection of geological knowledge can lead us. In considering the facts connected with the exploration of the western lake basins, we find the *Unionidæ* to be distributed through the whole series of deposits from the Jurassic to the Tertiary, and well through the latter. In a very philosophical discussion of this subject, Dr. White has shown that there is an intermingling of forms, and an extent of differentiation pointing to remoter origin. But he has, in a foot note on page 620, made the following statement that needs correction. "It is a significant fact that those North American rivers which contain the richest Unione fauna drain Mesozoic and Tertiary regions, while those that drain Paleozoic and Azoic regions have a comparatively meagre Unione fauna." The whole drainage of the Ohio is Palæozoic, or so nearly so that we may call it such. This stream and its tributaries south and southeast are the metropolis of these shells. And it is here that we find the two faunas above indicated most distinctly developed. The rivers draining the Mesozoic and Tertiary regions of the west have a very meagre fauna, both as to species and individuals; and I have already stated, that with the exception of the few *Anodontas* of the northwest, the entire assemblage is composed of Ohio types. Until series of casts of the Ohio river shells are made, and these are carefully compared with the casts of species described from these western localities, we shall not have reached the best conclusion which a study of these fossils will afford us. If we consider the species of the Mesozoic and Tertiary regions

of the south and southwest, we shall find that when we have removed the Ohio types from the lists, very few valid species remain. How absolutely true this is, and how great the synonymy of these shells, I am sure is not the well understood fact in American malacology that it ought to be. There can be little doubt that the distinctively Ohio types, these widely distributed, and so greatly differentiated, antedated any other forms occupying the same region with them. But other groups, during the mutations of the geological ages, left their remnants which have spread over the same area. The persistent species have either less tendency to variation, or the precise circumstances to call out such latent energies have not yet been brought into active account; while other forms, for opposite reasons, present us an infinity of varieties, always easily recognized, and of the derivative character of which no person who has investigated this subject can have any doubt.

In this connection the isolated fauna of the Coosa, to which reference was made in the previous article must not be neglected. This stream flows through a comparatively limited drainage. It contains two genera, *Schizostoma* and *Tulotoma*, represented by thirty species, that have not yet been found outside of it; and this in a region where every stream contains an abundance of *Strepomatidæ*. How easy for a slight geological disturbance to obliterate the record of their existence; how easy to have an isolated remnant of this unique fauna left in the upper reaches of this mountain stream, when a less submergence, than took place in this region during the Tertiary, would exterminate many contemporary species in the lower part of its drainage. In such a case, this isolated remnant, unique and strange, would present us with a problem for consideration like that of the *Unio spinosus*. This single example well represents the principle to which this article points, and shows how readily, in earlier times, when systems of drainage were comparatively limited, and opportunities for the spread of species were correspondingly less, there might have been many cases like that of the Coosa, during the various Epochs, which left remnants of their shell-fauna; and those remnants, which had less tendency to variability, have persisted with comparatively little change; or, possibly, the changes have been in a direction which did not characterize other groups with which they were associated, leaving them distinct. At all events, the faunas are plainly indicated, and in many cases it is not difficult to point out central forms, around which they seem to be clustered. The various other genera of Fresh-Water Shells, found in the western deposits above mentioned, all exhibit a tendency to varie-

ties equal to that of the *Unionidæ*. The species of *Goniobasis* (*?*) *Viviparus*, *Physa*, and *Planorbis*, are all cases in point; but one can not help seeing how closely the three genera last mentioned are related in all these fossil forms to species now living; and it seems that Dr. White's remark, accompanying the description of the *Anodonta propatoris*: "It is not to be denied that its separate specific identity is assumed from its known antiquity, rather than proved by its structure and form," might have been, with still greater significance, written of many of these fossil *Viviparidæ* and *Limnæidæ*. Let this be as it may, I am convinced that the origin of these Tertiary and Cretaceous forms, is to be sought in a Palæozoic progenitor, whose probable starting point was in regions adjacent to the western Archæan. While the species of fresh-water habitat may have persisted since the Carboniferous, in all the region between the Appalachians and the Mississippi, much of that portion of geological time has been fatal to such existence in the region west of the same stream; and though Mr. Tryon speaks of the Mississippi as a barrier to the westward distribution of species, it seems to me that the cause is really to be found in the character of the western tributaries as well; for while the muddy waters of the Mississippi are an effectual barrier, in a general way, accidental transportation or a few cases of actual traverse, that we can not doubt must have taken place, would have furnished abundant materials for spreading the species through our western rivers, if the conditions had been favorable; but they were not favorable, and consequently no such distribution has taken place. Hence it is, that the few species of shells inhabiting those streams, seem to me more likely to be the descendants of ancestry of an old date, and their general correspondence in form to the Ohio type, points to their community of origin. The fauna E is here wanting; nor has it any representative. When we come to the consideration of the down stream distribution of the species east of the Mississippi, we find the *Strepomatidæ*, as represented by their most characteristic genera, and Fauna E of the *Unionidæ*, to have a barrier in that direction. Here they cease, and beyond it, in the Tennessee, Cumberland, etc., we find mainly the Fauna D. Since this fact is general, it becomes one of high significance in this discussion, and stands as a unique evidence in favor of some of the suggestions here made; and it shows, conclusively, that continuous water is not the only condition of molluscan distribution; and that the present station of *Io*, *Goniobasis*, *Anculosa*, etc., in mountain streams, and in the more rapid portions of

these streams, is the result of the presence of conditions to which these creatures are by nature fitted; and while a few species are more cosmopolitan, owing to their greater capacity for adaptation, or to their remote ancestry, the great bulk of Fauna C has its range circumscribed as has here been indicated.

While the evidences upon which the theory of this discussion rests, from the geological and phylogenic aspects of the case, have been thus hurriedly cited, there is yet another argument, resting mainly upon an anatomical basis, which, as above indicated, I hope, after a while to bring out. So little is known of the close relations of these animals from this point of view, that I am of the opinion that the systematic zoologist will look with wonder and surprise upon the almost entire absence of structural likeness in animals, even in such matters as the distribution of the alimentary and circulatory vessels, that may be associated with the widest variation in the character of the shell. Nevertheless, there are cases in both these families, of structural differences as striking as the other facts which have led to this division of our shells into these highly characteristic geological groups; and to these evidences I shall direct attention in a future article.

NEW SPECIES OF FOSSILS AND REMARKS UPON OTHERS FROM THE NIAGARA GROUP OF ILLINOIS.

By S. A. Miller, Esq.

I have recently had the opportunity of examining a very large collection of crinoids belonging to W. C. Egan, Esq., from the quarries at Bridgeport and Cicero, near Chicago, Illinois. It is, probably, the best collection ever made at those quarries, and it has enabled me to re-define and restore several species which, from imperfect specimens, have been classed as synonyms of those described from other places.

The genus *Saccocrinus* was founded upon *S. speciosus*, from the Niagara Group, at Lockport, New York, in 1852, by Prof. Hall. In 1863, he described *S. christyi* from the Niagara Group, at Waldron, Indiana, which is beautifully illustrated in 28th Rep. N. Y. St., Mus. of Nat. Hist., published in 1879. In 1867, in the 20th Rep. he characterized *S. semiradiatus*, from Racine, Wisconsin. In 1875, in Ohio Pal., vol. ii., Hall and Whitfield defined, from the Niagara Group, at Yellow Springs, Ohio, *S. ornatus*, and *S. tennesseensis*. In 1865, Winchell