

THE EVOLUTION OF THE CEPHALO-  
PODA.<sup>1</sup>—II.

THE individual coiled shell of every existing *Nautilus* may be said to pass through the stages of the protoconch, when it is always nearly or quite straight; then through the first of the conch, when it becomes slightly curved; then through a more completely curved period, in which the first whorl of the spiral is completed. After this it continues the spiral, the whorls on the outside touching the exterior of the inner ones, and spreading so rapidly by growth as to begin to envelop them, and, in extreme cases, to completely cover them up.

The natural inference from these facts would be, that there was a similar succession of forms in past times,—the straight in the most remote, the arcuate and the gyroceran in succeeding periods, and the nautilian only in comparatively modern times. This would be a perfectly clear and legitimate mental conception. The structural relations of the adult shells appeared also to demand the same solution, as shown by the researches of Quenstedt, Bronn, and Barrande, and later of Gaudry. Barrande's researches also demonstrated that this idea could not be maintained, and that there were no such serial relations in time, but that the whole series of forms were present in the earliest period, and occurred side by side in each paleozoic formation. This great author's conclusions have had a curious effect upon paleontologists. It has been hastily assumed by some, that the mental conception was more perfect than could be realized in nature; by others, that the imperfection of the recorded succession was an obvious refutation of the doctrine of evolution, and all pursuit of a solution unworthy of serious attention.

Statistically, the logical picture coincides with the observed succession in time. The straight cones predominate in the Silurian and earlier periods; while the loosely coiled are much less numerous, and the close coiled and involute, though present, are extremely rare. The loosely coiled and close coiled gain in numbers in the carboniferous, and the involute are more numerous than in the Silurian; while, in the later times of the Jura, all disappear except the close coiled and the involute, there being a decided predominance of involute shells. Thus we are able, by reversing the record and travelling back to the Silurian, again to see, that antecedent to that period, in the protozoic, there must have been a time when the straight cones or their immediate an-

cestors predominated, to the exclusion of the coiled and perhaps even of the arcuate types or varieties.

The involute shells of the earliest geological times were therefore probably evolved from the straight cones in regular succession; and we may perhaps hope to eventually get the evidence of this succession in the formations. The exact counterpart of our logical picture, as Barrande<sup>1</sup> has truly stated, does not, however, exist in the known geological records of later periods. Judged by the common classification, by the prevalent ideas about the affinities of adult structures, and by the modes of occurrence of fossils in the geological formations, the forms seem to be without law or order in their succession.

But let us imagine, during the paleozoic, a different condition of affairs from what is now the general rule. Let us suppose such a thing possible as the quick evolution of forms and structure, and that in these ancient periods, near their points of origin, animals found the earth comparatively unoccupied, and were not only able, but in fact forced, to migrate in every direction into different habitats, and to make perpetual efforts to readjust their inherited structures to the new requirements demanded by these comparatively unoccupied fields. Food and opportunity would have acted, in such localities, as stimulants to new efforts for the attainment of more perfect adaptation and for changes of structure useful to that end. We can neither imagine the effort to change of habitat and habits, without its cause, the primary physical stimulant, nor the change of structure, except as a result of the direct effort to meet the physical requirements with corresponding or suitable structures.

Let us also compare the changes taking place during the whole of paleozoic time with those known to have occurred in certain isolated cases in more recent times; such, for example, as that of Steinheim, where a single species, finding itself in an unoccupied field, proceeded with unexampled rapidity to fill its requirements by the evolution of new series and many species, all differing from each other, but all referable, by intermediate varieties, to the original form,—in this example, really a single species, the well-known *Planorbis aequi-umbilicatus*.

<sup>1</sup> We regret that space does not permit some account of the author's wonderful book, the *Système silurien de la Bohême*. While opposed to almost every theoretical conclusion and the general arrangement of the facts made by him, we have the strongest feelings of respect and admiration for his powers of observation, the technique of his work and publications, and the surpassing unselfishness of his life, spent in the pursuit of what he deems to be vital truths (see *Science*, Nos. 43, 44).

<sup>1</sup> Concluded from No. 52.

If we admit such possibilities, and then find similar phenomena in the paleozoic epoch, we shall no longer need our first picture, but can construct a far more natural one.

The Nautiloidea will not then present themselves as a simple chain of being, but as they really were, — several distinct stocks, or grand series, and each of these grand series divisible into many smaller lines of genetically connected forms. In the Cambrian, or perhaps earlier, some of these do not have close-coiled forms at all; some of them have: but all, except the most primitive series, which are composed wholly of straight or arcuate forms, have some close-coiled species. These we can often trace directly with the greatest exactness, both by their development and by the gradations of the adult forms, to corresponding species among the straight Orthoceratites.

The series we have described above, from Orthoceras to Goniatites, compares closely with any single genetic series of the Nautiloidea, and shows that this ordinal type arose very suddenly in the protozoic, and evolved true nautilian shells in the Cambrian or earlier.

The Ammonoidea evolved from the nautilian forms of the Cambrian into series, which are structurally much more distinct from each other in the paleozoic than any groups of the same value (i.e., genera) in the succeeding formations, and thus, in different but equally plain characters, teach us that they also had a quicker evolution within that period itself than in the later formations. Either this was the case, or else the Ammonoidea must have been created in full possession of an organization only attained by similar parallel series of congeneric, close-coiled nautiloids, after passing through all the intermediate transformations above described. Here is a curious fact: though taxonomically equal, we cannot compare the order of the Ammonoidea with the whole of the Nautiloidea, but only with a more or less perfect single series of that order. This phenomenon fully accords with the true picture of the genetic relations. The remarkably sudden appearance and fully developed structures of these earlier ammonoids finely illustrates the fan-like character of the evolution of forms from chronological centres of distribution, and the quickness with which they must have spread and filled up the unoccupied habitats.

After the paleozoic, no absolutely new structural modifications are produced; though the complication of the structures is carried so much farther that we are at first apt to imagine that there are several new types of structure in the trias and Jura. We can carry out

this assertion, even into some minute structural characters. Thus the mesozoic ammonoids have, in all forms, a curious little short collar, which arises from the septa, and surrounds the siphon. It seems to be useful simply to close the joint, and perhaps make the connections of this tube more perfect, and exists in no nautiloid at present known. It was supposed from its development, etc., to be confined to the Ammonoidea of periods later than the paleozoic, but has recently been noted by Beyrich in a Goniatites of the carboniferous. We have found in a similar way every distinctive structural peculiarity of the mesozoic Ammonites appearing in some form among the Goniatites of the carboniferous.

The contemplation of the wonderful phenomena presented by these series has finally led the author, not without reluctance, to the conclusion that the phenomena of evolution in the paleozoic were distinct from those of later periods, having taken place with a rapidity paralleled only in later times in unoccupied fields, like Steinheim.<sup>1</sup>

The hypothesis of Wagner, that an unoccupied field is essential for the evolution of new forms, gains immensely in importance, if, as we suppose, it is practical to apply it to the explanation of the phenomena we have observed. Every naturalist must see at once, by his own special studies, that this is the only reasonable explanation of the frequent rapid development of types in new formations, as well as the sudden appearance of so many of the different types of invertebrates in the paleozoic. Newberry's theory of cycles of sedimentation shows that the sudden appearance of types is inexplicable, except upon the supposition that they retired with the sea between each period of deposit, and again returned after long intervals of absence, or perhaps made their appearance for the first time in a given fauna.

With this explanation and that of Wagner the facts we have observed fully coincide, and, we think, amply explain the phenomena, both of sudden appearance in the first deposits of formations, and subsequent quick development in the necessarily unoccupied habitats. The researches of Barrande, Alexander Agassiz, Bigsby, Gaudry, and many others, show us that this must have been especially true of the paleozoic or of the protozoic, if this supposed period is admitted, as compared with subsequent periods.

We find, then, that, in order to make our

<sup>1</sup> Another statement of these facts in the form of a law of evolution is given in the author's 'Genera of fossil cephalopods' (*Proc. Bost. soc. nat. hist.*, xxii. 1884).

logical and generalized picture of exact correspondence between all the changes in the life of a nautilian close-coiled shell and the life of its own group accord with the facts, we must be careful to limit it to groups quickly evolved, and these exclusively paleozoic.

In 1843 Auguste Quenstedt began researches which ought long ago to have led to this solution. He demonstrated by repeated examples, that among diseased types the most extensive changes of form and structure might take place in a single species, and within the narrowest limits of time and surface-distribution. Quenstedt was thus the first to show that in diseased forms the shell had the inherent habit of reversing the process of growth and evolution, and of becoming more and more uncoiled by successive retrograde steps. Von Buch and Quenstedt, master and disciple, and the author independently of either of these predecessors, in three successive researches, have arrived at the identical conclusion, that these uncoiled shells are truly distorted, or, as we may more accurately express it, pathological forms. They are not, however, rare or exceptional, as one might at first suppose, but occur in numbers and in every grade, — from those that differ but little from the normal forms, to those that differ greatly; from those that are exceedingly confined in distribution, to those which lived through greater lengths of time. But in all cases they exhibit degradation, and are expiring types. The author has repeatedly traced series of them, and studied their young, partly in Quenstedt's own collection. In all cases they show us that great changes of form and structure may take place suddenly; and this lesson could have been learned from Quenstedt's work and example as well forty years since as now: and in all species the young are close-coiled, even in some which are arcuate in the later larval, adolescent, and adult stages. Baculites, the extreme form, is straight, and the young still unknown.

When we attempt to resolve these pathological uncoiled series and forms, which show by their close-coiled young that they were descended from close-coiled shells, we find ourselves without comparisons or standards in the early life of the individual. The laws of geratology — that the old age of the individual shows degradation in the same direction as, and with similar changes to, those which take place in successive species or groups of any affiliated pathological series of uncoiled and degraded forms — here come into use, and serve to explain the phenomena. This correspond-

ence is shown in the uncoiling of the whorls, loss of size, the succession in which the ornaments and parts are resorbed or lost, the approximations of the septa, and position of the siphon. It is quite true, as first stated by Quenstedt and also by D'Orbigny, that every shell, when outgrown, shows its approaching death in the close approximation of the last sutures, the smoothness of the shell, the decrease in size, etc.; but, in order to realize that these transformations mean the same thing as those which take place in any series of truly pathological forms, we have to return to the types in which unfavorable surroundings have produced distortions or effects akin to what physicians would term pathological. This frequently happens in small series of Nautiloidea; and, if we confine ourselves to these, we can make very accurate comparisons: or, on the other hand, in the case of the Ammonoidea, we may trace the death of an entire order, and show that it takes place in accordance with the laws of geratology. Such series, among the Nautiloidea, are abundant in the earlier formations; but they have not the general significance of the similar forms among the Ammonoidea, and can be neglected in this article. There are no known cases of degraded series of uncoiled forms among the ammonoids of the earlier or paleozoic periods: they may have occurred, but they must have been excessively rare. In the trias and early Jura, pathological uncoiled forms are rare among ammonoids, but in the middle and upper Jura they increase largely; and finally, in the upper cretaceous they outnumber the normal involute shells, and the whole order ceases to exist. Neumayer has shown, that a similar degradation occurs in all of the normal ammonoids of the cretaceous, and that their sutures are less complicated than those of their immediate ancestors in the Jura. This proves conclusively, that the degradation was general, and affected all forms of Ammonoidea at this time; since the uncoiled forms are not confined to special localities, as in the Jura, but are found in all faunas so far as known. The facts show that some general physical cause acted simultaneously, or nearly so, over the whole of the known area of the world during the cretaceous period, and produced precisely similar effects upon the whole type as had here and there been noticeable only within limited localities and upon single species or small numbers of species during the previous periods. This general cause, whatever it may have been, acted on the type so as to cause the successive generations of the larger part of the shells to become distorted

smaller and more cylindrical in their whorls, smoother, and to lose their complicated foliated sutures. In extreme cases they became again perfectly straight cones, like the orthoceratitic radicals. So much alike are they, that it is quite common for those who are not students of this group to mistake the degraded Baculites for the radical Orthoceras. This decrease in size, increasing smoothness, and uncoiling, is precisely parallel with the similar transformations taking place during old age in the normal involute shells of the Jura, which, when old enough, also depart from the spiral, or tend to straighten out, and always lose their ornaments, decrease in size, and so on.<sup>1</sup>

The universal action of the surroundings, as we now know them, is certainly not exclusively favorable to the continuance of life, and may be wholly more or less unfavorable. It certainly perpetually excites the animal to new and more powerful exertions, and, like perpetual friction, wears out its structures by the efforts which it obliges it to make for the support of the structures in doing work. At first this leads to development, the supply being greater than the demand; but sooner or later, and with unvarying certainty, the demand exceeds the powers of supply, and old age sets in, either prematurely, or at the termination of the usual developmental periods. The remarkable and at present unique example of the Ammonoidea places us in a position where we can see the same process taking place in the whole of a large group, with attendant phenomena similar in every respect to those which we have observed in individual shells of the same order.

In numbers of species and genera, and in the complication of the internal structures and the production of the external ornaments on the shells, the order reaches what appears to be the highest stage of development in the Jura; then retrogression begins, and, steadily gaining, finally affects all forms of the type, and it becomes extinct. Smaller series of the Ammonoidea and Nautiloidea go through the same process in their respective time-limits, and in the same way, but can be compared with the individual much more accurately and closely. It is evident, then, that the comparison of the life of an individual with that of its immediate series or group reaches a high degree of exactitude, and that the observed phenomena of the life of an individual should

enable us to explain, in some measure, the equivalent phenomena of the life of the group; and we are unavoidably led to entertain the expectation that it does explain it. This expectation was actually formulated as a probable law for the whole animal kingdom by Haeckel in the same year (1866) as the author first published on the Tetrabranchiata. We are therefore able to quote this leader in science in support of our weaker knowledge; and also a pupil of his, Wurtemburger, who has announced the same results attained by researches on the Ammonites of the Jura, but, naturally perhaps, omitted to recognize any one but his honored master.

The evidence is very strong, that there is a limit to the progressive complications which may take place in any type, beyond which it can only proceed by reversing the process, and retrograding. At the same time, however, the evidence is equally strong, that there are such things as types which remain comparatively simple, or do not progress to the same degree as others of their own group. Among Nautiloidea and Ammonoidea these are the radical or generator types. We have no case yet of a highly complicated, specialized type, with a long line of descendants traceable to it as the radical, except the retrogressive: but all our examples of radicals are taken from lower, simpler forms; and these radical types are longer-lived, more persistent, and less changeable in time, than their descendants.

We find the radicals of the Nautiloidea living throughout the paleozoic, and perpetually evolving new types in all directions; then this process ceases, and the primary radicals themselves die out. But they leave shells, which are in that stage of progression which I have called the nautilian. These, the more direct descendants of the radicals, become secondary radicals, and generate series having more involute shells. These, in turn, as secondary radicals, exhibit very decidedly a greater chronological distribution than their descendant involute forms, persisting, even to the present day, in *Nautilus umbilicatus*. The same story may be told of the Ammonoidea, but substituting at once the close-coiled shell (the secondary radicals) for the primary radicals of the Nautiloidea, even as far back as the Cambrian. These secondary radicals, greatly modified but still carrying in their simpler organizations and mode of coiling the possibilities of a number of new series, existed by the side of the expiring degraded forms of the cretaceous.

This is the essential element of difference between the life of the whole order and that of

<sup>1</sup> We are aware of the existence of evidence that Ammonites of the normal form, the types of which we have seen, have been described from the lower tertiaries: but there are still doubts about the reputed age of the formations; and, in any case, they only tend to confirm the general trend of the facts.

the individual. We can accurately compare the rise and fall of the individual and its whole cycle of transformations with that of any of the single series or branches of the same stock which become highly specialized and then degenerated; but, when we attempt to go farther, we meet with similar difficulties to those encountered in tracing the progress of types and orders. The radical and persistent types are still present, and teach us, that, as long as they exist sufficiently unchanged, new types are a possibility. We have traced many of these in the two orders, and have found that they change and become more complicated, and that probably a purely persistent or entirely unprogressive type does not exist among the fossil Cephalopoda. The most celebrated example of unchanging persistency has been, and is now supposed to be, the modern *Nautilus*. We think, however, that when our observations are fully published, it will become evident that the similarities of this shell to some of the Cambrian coiled forms — which have caused Barrande and others to suppose that it might be transferred to the Cambrian fauna without creating confusion — belong to the category known to the naturalist as representation; that is, similarities of form, and even of structure, in the adults, but with young having entirely distinct earlier stages of development, and belonging to distinct genetic series. Still, comparative unprogression or persistency is common in all radicals; and they force us to recognize the fact, that the orders could have produced new series, perhaps even in the cretaceous, if it had not been for the direct unfavorable action of the physical changes which then took place, so far as we now know, over the whole earth.

Thus, in making our comparisons between the life of the individual and the life of the group, we cannot say that the causes which produced old age and those which in time produced retrogressive types were identical: we can only say, that they produced similar effects in changing the structures of the individual and of the progressive types, and were therefore unfavorable to the farther development and complication of these types. In their effects they were certainly similar; but in themselves they might have been, and probably were, quite different, agreeing only in belonging to that class of causes which we distinguish as pathological, or those whose nature can be generally summed up as essentially unfavorable to the progress, and even to the existence, of the organization.

In order to understand the meaning of these

evidently degraded structures, we must turn back to our first remarks upon the order. The apertures and forms of the retrogressive shells all show that they were exceptional, that they had neither well-developed arms for crawling nor powerful pipes for swimming; that, in other words, they could not have carried their spires in any of the ordinary ways. Their habitats, therefore, must have been more or less sedentary; and like the sedentary *Gastropoda*, as compared with the locomotive forms, they presented degeneration of the form and structure of their higher and more complicated ancestors. Their habitats did not require the progressive grades of structure, and they dispensed with or lost them; and in many cases this took place very rapidly. This retrogression was in itself unfavorable to a prolonged existence; and the geratologous nature of the changes tells the same story, so that we can attribute their extinction to the unfavorable nature of their new habitats, and also call them pathological types without fear of misrepresenting their true relations to other forms.

We have necessarily avoided even allusions to some of the most important confirmatory facts; but we hope our effort will at least show that the theory advanced is a reasonable one, and that the fossil Cephalopoda are worthy of the attention of even the most enthusiastic of the young disciples of the modern school of embryology. The theories of this school will have to stand tests of which they have now not even a faint idea, and it is to be hoped they will not long neglect the precaution of knowing also the past history of the types they often so incautiously and confidently handle.

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#### *THE MOTION OF WAVES OF COLD IN THE UNITED STATES.*

The chief signal-officer of the army desiring to learn the progress of waves of cold across the United States, an investigation has been undertaken in order to determine the appearance of such waves, their approximate velocity, and general line of advance. It would seem, at first sight, as though the problem might be solved by drawing isotherms (i.e., lines through points at the same temperature) on consecutive days, from simultaneous observations over the whole country. If, then, there were a progressive motion, the study of these lines would show it. It has been found, however, that a cold wave does not travel in a well-defined closed curve; and, more than that, the gradual increase of temperature, as the curves approach