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Discussions about an old problem: the relationships between embryology and evolution*

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In living beings of sexual reproduction, the individual begins its existence in the form of a cellule-egg that comes to be fertilized. This cellule is divided to produce an embryo, then an adult. The succession of embryonic stages that lead the individual from egg to adult is called ontogeny. On the other hand, the temporal succession of the forms that, thanks to paleontology, we consider to be descended from one another is called phylogenesis.

For a long time, naturalists have remarked that comparisons can be made between the succession of species within a lineage and the succession of embryonic stages of a species situated near the end of this lineage, that is, make comparisons between phylogeny and ontogeny. Thus, in the 17th century, Harvey wrote that higher beings, before birth, passed through morphological stages that recall the form of lower beings. These observations have often appeared strange. They are pleasant to all those who sought to surround the phenomenon of evolution with a somewhat mysterious halo.

At the end of the last century, Haeckel was the first to codify these comparisons and give scientific explanations that permitted integrating them without problem into the framework of the mechanics and methods of evolution. Haeckel's conceptions have been discussed and reprised by many authors in the sixty-six years since. It seems useful to us, in light of the most recent embryological data, to try to make a new development on

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these questions. In this article we give the essential ideas of a work in progress that draws up these problems (Michel DELSOL and Henri TINTANT. Provisional title: The relationships between embryology and evolution).

I. THE CONCEPTIONS OF HAECKEL
THE CRITIQUES THAT THEY ADDRESSED

Haeckel divided the embryonic structures of living beings into two categories: palingenetic/regenerative structures and caenogenetic structures.

In most cases, ontogeny—Haeckel said—is only a brief recapitulation of phylogeny. The stages of embryology are a rapid and abridged repetition of the history of the species. For example, the branchial arches that appear in the mammalian embryo reproduce the branchial arches of ancestral fishes. These organs that recall the ancestral state are called palingenetic.

In this perspective, the succession of palingenetic structures can be schematized in the following manner: the embryogenesis of group B, supposedly descended from group A, reproduced, at least partially, the forms of group A before attaining stage B in the course of its embryonic development.

The characters or organs called caenogenetic have a role in assuring the survivial of the embryo: its respiration and nutrition, for example; they disappear with embryonic life. The mammalian placenta, connected to the embryo by the umbilical cord, is this type of caenogenetic organ. In general, these are recent characters (caenogenesis = of recent origin) in the history of the lineage.

It is the study of the succession of palingenetic organs and characters that permits understanding the connections between ontogeny and phylogeny, the processes that connect evolutionary and embryological mechanics and give the images of parallelism that we observe between the movements of phylogenesis and embryogenesis.

In effect, it could be suppose that, if the embryonic development of species B reproduced that of species A from which it descended, it is because the characters that transformed A into B appeared in animal A at a moment in its history in order to make animal B. In these conditions, the formation of animal B must naturally (at least in the general case) pass through the stages of A. The characters *a, a', a"*, formerly adult characters, then will become palingenetic embryonic characters.

Among the authors of Haeckel's time, there was perhaps a mustiness regarding the "mechanism" view of Descartes. At the time they evoked evolution by successive additions, and perhaps unconsciously thought that the animal was a machine to which new pieces were added, stage by stage. Connections between embryology and evolution were explained then as those which could exist between two machines where the more complex was made by additions of pieces to the simpler.

In this perspective, phylogeny recapitulates ontogeny because the mode of evolution is a process of addition of characters. The connection between phylogeny and ontogeny is implied by the process of construction of new species. This connection is irrevocable and obligatory because it depends on an evolutionary mode.

It must have been fairly rapidly perceived that it was necessary to emend the theses of the Jena naturalist; Haeckel's ideas were marked by the conceptions of his times. At the end of the 19th century, the evolutionists enthusiastically believed that it was easy to understand the evolution of the living world. They resolved difficulties with an extraordinary imagination, explaining the neuralgic points of our genealogies with precocious theories that are only today in the field of history. Haeckel himself committed a similar excess several times: he described the first metazoans under the form of a *gastrula*, he was enamoured of limestone sulfate precipitates found at the bottom of the seas and where he believed one moment a synthesis of living matter was seen. At the same time, other authors explained the connection between vertebrates and invertebrates by inversion of a worm; it was believed that the direct ancestral archetype of true vertebrates was seen in *Amphioxus*. It must be said, to excuse the ideas of these authors, that the biologists at the end of the 19th century could not yet imagine the fantastic complexity that our current understandings of the living world have revealed. Therefore it is not amazing that several of their conceptions appear only as simple beginning schemes.

Certain critics were very hard with Haeckel; thus, de Beer wrote in 1929, in the work "Embryology and Evolution" translated by J. Rostand in 1932, that his goal was "to build a more adequate synthesis of our knowledge on the ruins of recapitulationist theory, concerning the relationship between embryology and evolution". De Beer's judgement is, to our eyes, too severe. Without doubt Haeckel had seen the facts only in a summary and too coarse manner. It was desirable that others again take up the comparisons between embryology and phylogeny and try to make a more complete synthesis but not to deny that recapitulationist concepts must form the basis of later work.

One can summarize the critical principals and amendments that must be brought to Haeckel's ideas in three points:

1) It is suggested that recapitulation did not relate to the adult characters of the ancestors but to the characters of the ancestral embryo.

2) It is perceived that addition was not the only mode of evolution, and that as a consequence directly derived recapitulation was not the only type of possible relationship between phylogeny and ontogeny. Thus, neoteny and divergence appear very rapidly as exceptions to the law of recapitulation.

3) Finally, Haeckel's work presented an insolvency that could only be reproached by its author, because it was due simply to the understandings of his time: it wrote the embryological and phylogenetic facts without trying to integrate them into a genetic context. However it is necessary to include certain facts to call upon this discipline.

Therefore we proceed to review systematically the relationships between embryology and evolution.

II. ESSAY OF GENERAL SCHEME OF RELATIONSHIPS BETWEEN ONTOGENY AND PHYLOGENY

To be logical and try to completely buoy up the field of relationships that can exist between phylogenesis and morphogenesis, a systematic analysis of possible cases should be divided into two parts:

— in the first part, one must research the various ways in which new characters become visible in morphogenesis and the relationships of these phenomena with phylogeneses.

— in the second part, it would be necessary to analyse, in the reverse, the manner in which new characters become visible in phylogeneses and the relationships of these novelties with ontogenies.

In fact, a similar subdivision would be fairly artificial, because the notion of phylogenesis is a concept that issues from the study of an alignment of points that together constitute a genealogical lineage. Studying variations of phylogenesis therefore returns to studying variations that could have appeared in individuals that constitute the phylogenetic lineage. As a consequence, to be sure of recovering the ensemble of relationships between phylogeny and ontogeny, it will suffice to study in their ontogenetic aspects the hereditary variations that can be observed in the development of individuals that compose the genealogical lineage and the possibilities of bringing these variations to bear in phylogenetic construction.

A particular point still deserves to be specified before beginning this study. It is advisable to insist on the fact that, in a similar work, each character will be studied in isolation. The characters could in effect evolve independently from one other: neoteny of a single organ is sometimes observed in batrachians.

However, in effecting this analysis, it must never be forgotten that evolution of a character is always more or less linked to that of others. Thus very often, in batrachians, some group of characters become neotenic because they are linked by physiologic relationships that make this common obligatory evolution.

In taking account of the various remarks that we have just made, one can divide into two categories the hereditary modifications that individuals of a lineage attain at some age that it is and as a consequence can modify the direction of phylogenesis:

1) new characters that mark ontogeny of a stable manner

2) new characters that affect only embryogenesis and are not visible in adults.

We proceed to try and see how the acquisition by an individual of one of these two types of new characters could reverberate within phylogenesis.

1. *New characters of a stable manner that the embryo or adult attains. Relationship of these acquisitions with phylogenesis*

Four methods can be considered to exist for a character to be located on a new subject. The three first correspond to elongation of the ontogenetic cycle, the fourth to shortening of the cycle.

a) *appearance of a character in an adult stage: adult variation*

When the appearance or addition of a new character is visible only at the level of the adult stages, the new organism is constructed embryologically like that which preceded it. Some examples of this process are observed in particular for characters corresponding to the appearance of a new behavior (modification of nuptial mating).

It is easily understood that, in this case, in theory, the adult variation modifies the lineage and therefore perturbs phylogenesis, but it will not be visible in the embryo. However, it must not be forgotten that the gene "pool" of individuals reaching an adult variation is necessarily modified; this genotypic variation could thus result in clandestine cytologic modifications in embryonic development.

b) *appearance of a character at the end of embryogenesis: palingenesis or recapitulation of embryonic stages*

When the appearance or addition of new characters occurs at the end of embryogenesis, the new organism B is constructed by addition of characters *b* to characters *a* of the preceding form. It is therefore natural that organism B passes, before being completed, through the stage of organism A that precedes it or at least through the preadult stages of A, because B corresponds to the sum $a + b$. The characters pushed back into the embryo are the palingenetic characters described by Haeckel.

Palingenesis perturbing the embryo and the phylum at the same time, the relationship of the two movements results in parallelism and recapitulation.

It will be noted that there are two types of palingenesis: palingenesis of necessity or true palingenesis and residual palingenesis.

— Palingenesis is necessary when the formation of the organ that appears temporarily in the embryo is used for the formation of the final organ. It is known that in prochordates there exists a dorsal cord in place of the vertebral region. This organ appears in the embryo of all vertebrates that therefore present, in the course of their history, a recollection of the ancestral prochordate. The formation of the dorsal cord seems indispensable for the vertebrate to appear, because the vertebral elements are formed from the cord.

— Palingenesis is residual when an organ is realized without showing any necessity. The formation of residual legs in certain reptiles corresponds to a phenomenon of this type.

Finally, it is noted that palingenetic structures have a tendency to be gradually reduced more and more and become less and less important, as the recapitulated ancestral organ is evidence of a more ancient zoological group. This type of phenomenon is evidently necessary because it would be impossible for ontogeny to faithfully reproduce the past, stage by stage. Shortening of palingenesis is a necessity of nature.

c) *appearance of a character in the course of embryogenesis and maintenance of this character in the adult: divergence*

The appearance of new final characters is realized here in an embryo that has not reached its development; for example, embryonic stage E_4 will become E'_4 and the adult characters that follow will be perturbed by novelties appearing during embryonic construction. It is a subject of new type that is to be born.

Therefore this phenomenon first perturbs the embryo and then the phylum. Modifications of phylogenesis therefore result in perturbations that, in this case, are situated in the course of embryogenesis.

d) *non-appearance of a character at the end of embryogenesis and arrest of development at a stage before the final stage: neoteny*

Neoteny can be considered as characterized essentially by the following facts: "persistence of special organs or provisions in the larvae, non-appearance of special organs or provisions in the adults" (Vachon, 1944). It assists then in the new organism in the promotion of traits in adult stages that must have been embryonic. One can say that, for certain characters, the embryo is no longer developed beyond a defined embryonic stage and in spite of that it acquires the genital glands, that is, the essential character of the adult state.

The most studied phenomena of neoteny have been in the group of amphibians. It is known that in most of the species of this group, the animal passes through a "tadpole" phase in the course of embryonic evolution. After a more or less long period of life, the tadpole metamorphoses and becomes adult. In the axolotl of Mexico and North America, it happens that metamorphosis does not occur. The animal then remains a tadpole its entire life. Nevertheless, the genital organs appear in this animal although it remains an embryo, and it can reproduce. But certain other characters of the adult are never realized; they are lost in some manner. It is evident that the genes corresponding to these lost characters are maintained in the neotenic individual; they are simply genes that no longer enter into action; but it can be obliged to make them. If one treats axolotls of this same age with thyroxine, metamorphisis is produced and the animal thus acquires the form that should have normally been attained some years sooner.

2. Characters that appear in the embryo but are no longer manifested in the adult or temporary embryonic characters. Discussion of the possible relationships of these acquisitions with phylogenesis

Following an analytical scheme analogous to that which we used previously, we could research in what manner new temporary characters are inscribed in the embryos and the relationships of these phenomena with phylogenesis. We will still obligatorily recognize two possible types of temporary embryonic characters: appearances and non-appearances.

However, it would very rapidly be brought to note that these two types are not conveyed by characteristic phenomena as we have been able to obeserve them in the preceding case. On the contrary, certain of these additions or temporary modifications of characters correspond to phenomena that Haeckel described under the name caenogenesis, whereas certain subtractions or modifications represent phenomena that could be collected under the name residual condensations or dyschronies. In summary, observation of facts leads us to disclose a different classification from those which would be derived from simple logical analysis.

Caenogenesis occurs, we recall, when a new character (placenta, for example) appears in an embryo and disappears without traces at the end of embryonic life. The term caenogenesis literaly signifies, we said, "character of new origin". In a work in preparation, Dollander draws attention to this definition and insists on its schematic value: "thus, the annexes of mammals, whatever their variants, reproduce an ancestral organization". This author suggests differentiating the two types of characters by more expressive qualifications: characters corresponding to the organization of the body will be called ontosomatic; characters charged with assuring the protection and life of the embryo will be called embryotrophic.

In principle, an embryotrophic character brings no evolutionary novelty to the adult animal. Caenogenesis represents a mode of evolution that could only provoke morphological transformations that are in the embryos. However, this position is entirely theoretical. It is logical, in effect, to admit that the formation of a placenta or of embryonic organizations that prolong the life of the larva will permit various organs and structures to developed more in the adult, and will modify the selection of mutations that produce new organs in the larva or in the adult.

Furthermore, the appearance of a caenogenetic character demonstrates that the gene "pool" of subjects of the species studied has been changed. This new structure therefore proves that there is a genetic difference between the bearer and its ancestors, in spite of the apparent absence of new morphological characters in the adult.

The notion of residual condensation has already been evoked above. We place in this category the suppression of simple characters or organs due to the fact that those not necessary for the construction of the adult have been eliminated by selection.

Here is a classic example: in *Amphioxus*, the liver is formed from a cul-de-sac emerging in the digestive tube. In vertebrates, the formation of the liver occurs from a cellular mass, that is, it follows a more direct route. Therefore, it seems that the formation of the liver in vertebrates occurs by a condensation of phylogenesis.

One can consider that the phenomena that de Beer called reductions correspond to this type of example. Palingenetic adult structures that are rejected in the embryo in the course of phylogenetic development thus have a tendency to be reduced more and more. We have already said that this condensation is nearly always gradually accentuated as the ancestral recapitulated organ is the evidence of a more ancient zoological group. This type of phenomenon is entirely necessary because it would be impossible for ontogeny to reproduce the past faithfully, stage by stage.

These phenomena are most probably from the accumulations of mutations that, by this process, affect the animal by carrying a coefficient of favorable selection due to the simplification of embryonic development. Thus residual condensation could be considered to represent a particular case of caenogenesis, because its appearance certainly corresponds to a favorable formation in embryonic development.

Finally, there remains studying dyschrony. Dyschrony occurs when two series of characters that evolve in parallel in the embryo of a certain subject no longer evolve in parallel in its descendant.

Here is an example that we borrow from de Beer. In the frog, the heart develops only when the embryo is completely formed. In contrast, the heart appears much earlier in the chicken; in summary, its evolution is accelerated relative to the rest of the organism. In theory, these phenomena concerning the embryo are not echoed in the adult. However, it is easily predicted that, as for caenogenesis, these modifications can reach the adult indirectly and indicate in addition transformations of the relationships between genes.

In nature, the importance of dyschrony is certainly very great. In batrachians, some close species sometimes show very considerable dyschronies of development and can sometimes result in the formation of new genes.

3. The law of recapitulation and paleontology

Embryogenesis and phylogenesis both correspond to the development of a history and can only be understood in a historical perspective. For the first it is a short perspective, directly accessible to the observer, and susceptible to experimentation. The second, in contrast, is developed on an entirely different scale, in a much larger framework that can only be apprehended by the study of the evolution of life and its geological context. There it primarily concerns paleontology.

Only the collaboration of embryologists and paleontologists could permit confronting the data of these two sciences, to compare some results and to establish, in that case, laws that preside over the development of comparative evolution of the individual and the lineage. Haeckel's law of recapitulation, more than all others, reenters this category and necessitates a minute confrontation of the two concerned disciplines.

Specialists who work in isolation risk comitting grave errors. Thus the biologist, when he reconstructs hypothetical phylogeneses by the help of purely theoretical arguments, using only data from the modern world and groups on which paleontology remains mute, risks building a fragile scaffold that is closer to science fiction than to true scientific research.

For the paleontologist, the problem of relationships between embryogenesis and phylogenesis is complex. There exist in effect for him two opposing ways to envision the problem.

The first is objectively from paleontological data, to establish phyletic lineages and their evolution as minutely as possible, relying on stratigraphic data, and then to compare the results thus obtained with those at which the embryologist who studies ontogenetic development in living forms arrives. Only a course of this type permits establishing the relationships between embryogenesis and phylogenesis with certitude, and verifying the veracity of a law like Haeckel's.

But establishment of phylogenies is often poor due to the rarity of fossils and the difficulties of their precise dating. Also, the temptation is great for the paleontologist to consider this law no longer as an *a posteriori* verification but as an *a priori* principle, and to utilize it as a conducting thread, as a principle that permits unravelling the relationships between diverse genera and species and to establish their phyletic relationships. In the course of this century, numerous paleontologists have thus utilized the law of recapitulation as a vertiable dogma to establish, from it, the phylogeny of numerous fossil groups, sometimes in defiance of stratigraphic data. One of the more typical examples of this tendency is given by the works of the great English paleontologist S. S. Buckman, and those of the American A. Hyatt on the evolution of ammonites.

Such a procedure can only be admissible if the theory of recapitulation presented itself to the eyes of the paleontologist as a veritable law, not suffering any exception. But the data from paleontology shows that such an affirmation could not be regarded as proven. If numerous examples confirm for us the reality of certain phenomena of recapitulation, others, nearly as frequent, cannot be explained accordingly and imply an exactly opposite course.

In this case, the new character first appears in earlier stages of ontogenetic development of the individual, then progresses little by little, in the course of generations, towards the adult stages. This process, called proterogenesis by German paleontologist O. Schindewolf, is therefore radically opposed by recapitulation or palingenesis, only under consideration by Haeckel.

Some excellent examples can be furnished by cephalopod evolution, for example in liparoceratids, kosmoceratids, cardioceratids, etc. But they are also found in very different groups: brachiopods, graptolites, that suffice to demonstrate that the law of recapitulation is not considered universal, and would not know, with it alone and without the control of stratigraphy, to furnish a conducting thread for phyletic reconstructions.

The phenomenon of proterogenesis seems to have gone unrecognized by most embryologists who often confounded it, quite wrongly, with neoteny. The explanation of this fact comes without doubt from the unequal distribution of this process among diverse zoological groups. Very frequent in invertebrates, it appears to be absent in vertebrates where we know no certain example. Perhaps the increasing complexity of organisms made certain methods disappear in the course of their evolution that, although frequent in simpler forms of life, are then eliminated in higher forms.

CONCLUSION

From the analysis that we have just given, some fundamental points arise that it seems useful for us to summarize:

— The general study of relationships between embryology and evolution demonstrates that, in one of the described relationships, there is obviously parallelism between the developments of evolution and those of embryogenesis: this is palingenesis.

— This phenomenon, which has been observed for a long time and particularly described by Haeckel, is certainly very frequent. It could perhaps be considered that it is the fundamental phenomenon, and that all the cases studied represent only "failures" of this mechanism. This would be then at least a favorable way to represent the facts.

— If this proposal is admitted, note that, for palingenesis, the fact that it is the fundamental phenomenon does not mean that it is the more frequent phenomenon. The other modes of evolution: adult variation without inscription in embryogenesis, deviation, caenogenesis, dyschrony, are without doubt more frequent than palingenesis (properly so called) but this last remains the "trunk" from which the other phenomena branch.

— The multiplicity of possible relationships between embryology and evolution therefore testifies that there is no single type of connection that defines these relationships, or two—as Haeckel believed—but on the contrary a very great number. This cannot astonish us; nature is only expressed rarely by simple and unique mechanisms.

— Among these various modes of evolution, there are three that merit particular attention: adult variation, divergence, and palingenesis. In effect, as we said above, there is character appearance in these three cases. But, so that evolution is realized, it is necessarily obvious first that new characters appear from time to time in the lineages. The other modes, neoteny and dyschrony, represent only perturbations of that which already exists. If sometimes these perturbations can provoke the manifestation of a novelty, it will be in an indirect manner.

— Finally, it can be asked in what measure the highly theoretical observations that we have just described present an interest for science, and what the problem is that could have led various authors to try, for a century, to understand the play of causes that involve certain parallelisms or certain divergences between the series and stages through which the individual passes and the stages through which its ancestors passed. Said another way, it can be asked for what reasons are biologists interested in reassembling these facts into a general theory.

In fact, this problem takes up the method of scientific research: experiments intended to understand each problem immediately and reflections intended to give a certain coherence to the group of results are always necessary at the same time. Thus the conceptions, in a great part falsified by Haeckel, had the immense merit of bringing to us a first view of certain evolutionary methods.