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Heterodox Concepts in Modern Evolutionary Embryology, 1900-1950

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Review Article

Abstract

Whatever the evolutionary model we adopt, in the case of sexual reproduction, the process has an embryological significance because this is the way to generate individuals and to perpetuate the life. The connection between evolution and embryology is a necessary event. In this evolutionary context, the key question is: how two species are formed from the same biological unit? During the first half of the 20th century embryologists as Richard Goldschmidt, Conrad Waddington, and Walter Garstang answered the question from a heterodox point of view. They introduced new concepts that changed the way to thinking the evolution. This essay analyzes this unorthodox thought and its scientific impact.

Keywords: Epigenetic landscape; Evolution; Embryology; Garstang; Goldschmidt; Heterochrony; Hopeful monster; Mendelian heredity; Recapitulation; Waddington.

Introduction

Taking things to the simplest level, we can say that the fundamental problem of organic evolution knows how a living being is formed. Multi-cellular organisms habitually use sexual reproduction to multiply: the fusion of parental gametes makes up a cell with the potential to develop into another individual. Our analysis will focus on this mode of reproduction. In sexual reproduction, evolution takes place when information regarding morphological changes is integrated into the reproductive mechanism. The connection between evolution and embryology is clear – it is a necessary occurrence. Embryologists swiftly made this connection, back in the 19th century, when the theory of evolution was first formulated. Under this criterion, the question of *how* species evolve is directly linked to embryogenesis. The purpose is to understand how a new species is formed during the morphological sequence occurring in the ovum after fertilisation. In order to achieve this, it became necessary to understand the mechanisms that control the reproductive process.

Supported by compared embryology, the theory of recapitulation, i.e., the conception of considering embryogenesis as a telling of the evolutionary history of a species, exploded, under different titles, during the early 1800s. The theory soon became part of embryological knowledge, but its strongest involvement in the evolutionary debate took place in the 1860s. It is well known that most of the credit belongs to the German zoologist Ernst Haeckel and his book *Generelle Morphologie der Organismen*, published in 1866 [1]. Known as the biogenetic law, Haeckel's theory states that the different embryonic states represent the different adult forms adopted by the species along its evolutionary path. In brief, *ontogeny recapitulates phylogeny.* This statement is as widespread as it is erroneous. Let us take the case of the human species. During its development, the human embryo resembles, successively, a fish, an amphibian, a reptile, a mammal, a primate, until finally adopting the human morphology.

Under recapitulation theory, evolution is a summary of parts, each identifying a specific final product. Let us ask ourselves, how does this happen? Haeckel divided inheritance into two categories. One group contained standard characteristics transmitted by the parents. The second consisted of characteristics acquired by the adult through adaptation to its environment. This was a unique concession to Lamarck. Acquired inheritance was the source of evolutional variability, manifested in the final phase of the embryonic cycle and thus increasing the number of stages. Under evaluation, the argument presents a serious practical problem that did not go unnoticed. The continuous addition of evolutionary stages would result in a physiological distortion of ontogeny, making it unfathomable. The biogenetic law was therefore reformulated. Embryogenesis would no longer constitute an absolute recapitulation, but a condensed repetition of a species' past. By the 20th century there was little doubt as to the falsehood of the theory. Haeckel himself acknowledged having manipulated tests in order to *facilitate* comprehension, by simulating a common evolutionary sequence between the embryos of the different species he had compared [2-4]. Embryology returned to the scientific logic expressed by the biologist Ernst von Baer in the 1820s. A simple, common sense argument: the embryo only resembles members of its own species, and over the course of its

development progresses from a general state to a particular state, from amorphous to specific, gradually acquiring the anatomical characteristics of the informative being contained in the ovum [5]. Embryonic coincidences between different groups are no more than a reflection of their common past. An embryo does not *recapitulate* its past; it partially *repeats* the ontogeny of its ancestors. So, what is the evolutionary significance of reproduction? This is a relevant, necessary and cardinal matter, shaped over the course of the 20th century via genetics and the biology of development.

An early answer to the question was obtained in 1866, although it went unnoticed. This is the notorious pea plant experiment carried out by Gregor Johann Mendel at the Cistercian Abbey in Brno. Over the course of a decade this monk crossbred thousands of plants and examined their fruit. He studied their shape, size, colour and texture in order to explain evolution in a precise context: discovering what biological mechanism enables offspring to inherit parental traits. His hereditary theory laid the foundations for genetics. In his mind, species did not evolve either under the influence of their environment or guided by natural selection. Chance was responsible for mixing parental characteristics during fertilisation. Spontaneously at times, the resulting *genetic combination* would stabilise in the offspring. In this case, descendants would suddenly form a specific, reproductively constant group. Another species would emerge. Plainly speaking, evolution would be the consequence of a singular chromosomic recombination [6].

In 1900, Mendel's laws were rediscovered, and genetics started its unstoppable biological ascent. First there was the formulation of chromosomic theory; then came the notion of genes: the chromosomic unity responsible for phenotypical expression. Using Mendel's model, the Dutch botanist Hugo de Vries, one of the fortunate rediscoverers, wrote *Die mutationstheorie*; two innovative volumes devoted to the origin of species [7,8]. In summary, his mutation theory ventured that evolution did not follow Darwin's principles. Species were not formed via the slow, gradual accumulation of small organic changes, but through the reproductive manifestation of abrupt typological variations, spontaneous, stable, sudden, hereditary changes, known as mutations, that immediately altered the parental typology. This event would be collective and final; occurring in different morphological groups of descendants. Mutation replaced natural selection as the presumed motor behind evolution. It would now be the primary cause.

Only a few years later, convinced by Mendelism, the embryologist Thomas Hunt Morgan, of the University of Columbia, started his experiments with *Drosophila melanogaster*, better known as the fruit fly. This tiny, hairy insect with protruding, vermillion-coloured eyes was to revolutionise genetics. In Morgan's laboratory, flies were not bred by chance. The idea was to explore whether progeny displayed the spontaneous modifications established under the theory. This objective was partly achieved. After a number of years, an individual with white eyes was born. This fly proved the existence of natural mutations, although its evolutionary significance was not as had been expected: it was not a new species of fly. Tens of experimental mutants would appear over the following years. Flies with no wings, or with their wings curled up, stunted or grooved, and flies with brown, chestnut or peach-coloured eyes, are examples of this amazing zoology resulting from genetic manipulation. With this glimpse into the modus operandi of the genome, some of pieces of the morphogenetic puzzle began to fall into place: the chromosome is the material container of the gene, the expression of which regulates embryonic differentiation. Published in 1915, *The Mechanism of Mendelian Heredity* contained the results of this work. The book established the foundations of modern genetics [9].

Under the denomination *synthetic theory* or *modern synthesis*, Neo-Darwinism easily assimilated the pattern of gene variation by applying a well-known recipe: cause and effect [10]. It was thought that evolution was an exact science written in a genetic language. Evolution would have an exclusively genic medium resulting from the expression of small mutations, causing occasional modifications in population typology – the group in which selection takes place. Repeated on a gradual, ongoing and accumulative basis, the phenomenon would explain how species diversify over time via the gradual and selective addition of mutations. Population genetics would characterise Neo-Darwinism for decades.

Hopeful monsters

From 1880 onwards, embryology was a purely experimental discipline that had broken the bounds of descriptive procedure. The mechanics of embryonic development were under investigation. Many questions arose. The main question to be answered was how cellular, tissue, and organic differentiation influenced the construction of the individual. This biological problem focused on discovering what factors determined the transformation of the embryo. Research progressed towards the definition of the event as a chain reaction, meaning that the organisational structure induced in one stage would be a triggering factor for the next, and so on. Next came the concept of the morphogenetic field: the embryo is organised into self-regulating areas, called fields, each acting to create a certain type of anatomy. These fields are correlatively adapted to the embryological stage, governing what take place at all times. This means that the process has the necessary plasticity to reach the relevant organisational level for each successive stage. This was the 1920s, 1930s and 1940s. Adding up all genetic theory, the embryological model was the product of a complicated physiological process of a

genic origin; but the assumed equivalence between the genome and morphology was insufficient to explain to interactive embryonic framework. At this point, upon identifying evolution as a mutational phenomenon, biologists asked themselves, how does genomic change affect ontogeny by tracing out new life? The challenge was to develop a unified theory that could integrate cellular chromosomic information with the embryological process triggered by fertilisation. Richard Goldschmidt, an unorthodox German geneticist residing in the United States, a professor at the University of Berkley from 1936, accepted the challenge. He addressed the issue openly, head on. His theory was published in 1940, in a book called *The Material Basis of Evolution* [11]. This manual contained four hundred pages devoted to the consolidation of a bifocal *embryogenetic* outline, based on the concepts of macro and microevolution. The general hypothesis regarded evolution as an embryological event, with chromosomes as the fundamental ingredient. Two mechanisms would act to re-design populations. One was microevolution, the result of the appearance of micro mutations, identified as morphological alterations in line with the anatomical structure of the species and, therefore, compatible with the existing embryonic schedule. This change would involve the adaptive improvement of a group to a specific region within the distribution area of that species, creating sub-species, breeds or varieties. Simply put, without losing identity, typology is efficiently reshaped in order to inhabit local environments. Micro mutation would be an evolutionary *dead end;* it would constitute a mechanism of specialisation incapable of producing new species.

However, evolution is synonymous with macroevolution. This notion is defined as a genomic reorganisation – called systemic mutation – to a degree that constitutes a new chromosomic pattern; another genetic system. The emergence of a different information system would also lead to a different ontogenic process. This change would be the origin of new organisms belonging to a new evolutionary line, viable provided they find an environmental niche suited to their innovative nature. *The first bird hatched from a reptile's egg*, explained Goldschmidt to illustrate the idea. This was the *hopeful monster:* the embryonic formation of anomalous beings, preadapted to a different environment. Evolution would take place as a succession of evolutionary leaps in disharmony with the gradual-selective pattern established under synthetic theory. Given his rebelliousness and different way of thinking, the German scientist was ignored, condemned, ridiculed and excluded from evolutionist thought [12]. However, the validity of his proposal is being reconsidered as it explains certain evolutionary episodes, for example as a formula for the speciesisation of the botanical group of the orchids.

Epigenetic landscape

In 1924, Hans Spemann, professor of zoology at the University of Friburg, and his student Hilde Mangold, published the results of their experiments with newt embryos, showing embryonic induction; a milestone in developmental biology. It is an easy concept to explain; the difficulty lies in establishing how it happens. Early on in its development, after the stage known as gastrulation, an embryo differentiates an area of tissue that takes control of embryogenesis, determining its future organisation. It is known as the organiser, characterised by its multifunctional validity: when a section of this tissue is grafted onto another embryo, this second organiser generates a secondary embryo using the cellular structure of the recipient. The developmental schedule is executed through chemical signals. Over sixty years would go by before we understood the molecular basis of this mechanism.

Embryonic induction was the path taken by the British naturalist Conrad Hal Waddington as he traced the supposed synthesis between embryology, genetics and evolution. The correct question was: How can the informative rigidity of the genetic code, the conservational nature of the ontogenic system and evolutionary variability be compatible? During the 1930s Waddington investigated the subject in mammals and birds. He carried out some surprising experiments. One of the most famous of these was the transplantation of a rabbit organiser into a chicken embryo, causing the formation of a standard secondary embryo. If nothing else, the inter-special nature of the experiment proved that the signal emitted by the organiser is the same in different species of vertebrates. The response does not depend on the composition of genes, but on their expression. There are of course genetic differences, and molecular similarities, chemical markers that are recognisable to the cellular unit regardless of the origin of the organic matter. This is information regarding the activation of the process, never on the content of the morphological programme, which remains unaffected. Waddington's solution defined the activity of the organiser as a more complex event than a mere response to a signal. Let us simplify. Waddington proposed that the genes in question, known as homeotic genes, have a quantitative effect and act together. The chemical markers resulting from genetic transcription establish concentration gradients, behaving like beacons that channel the spatial distribution of cells and thereby the morphological identity to be constituted subsequently. The outline is known as the *epigenetic landscape*, an intuitive ontogenic scenario where the set of cells is guided by chemical signals towards the different paths that they need to follow. What is the evolutionary purpose of this model? The fundamental intention is to integrate genetics and evolution as elements in a dynamic system, and place them at different operational levels in order to prevent the introduction of evolutionary changes from causing a chromosomic reorganisation incompatible with the viability of the organism. The concept of the *epigenetic landscape* associates the variability of an alteration

of genetic expression with a full or partial inhibition of gene function, causing a different cellular response and leading to a different typology. Simultaneously, this system's unique structure allows it to interact with the external environment, making it viable to inherit acquired characteristics. Conrad Waddington was one of the great 20th century theorists on developmental embryology and evolution. He was an indisputable reference point, even beyond the 1950s. *Organizers and genes*, and *The strategy of the genes*, were fundamental pieces of work in this field [13,14].

Heterochrony

Ontogeny does not recapitulate Phylogeny: it creates it. This statement was made by the British zoologist Walter Garstang. It was published in 1922, in his article *The theory of recapitulation: a critical re-statement of the biogenetic law* [15]. Eight words, just eight, were enough to refute the theory. These words were necessary in order to interpret evolution by applying a revolutionary embryological criterion. Which one? The idea was simple, ingenious, and possible. The idea required a conceptual turnaround to alter the order of things; necessary in order to ensure that the result of reproduction is an end product different to that established in the chromosomes. The strategy consisted of following the path of evolution using the juvenile ontogenic forms. A specialist in marine invertebrates, Garstang detected the evolutionary implications of the approach taken to external sexual reproduction; widespread in this zoological group. Fertilisation takes place in the water. The fertilised egg gives way to a sequential larva transformation that shapes the individual until it becomes an adult. Each stage in this life cycle represents a self-sufficient organic outlie, differentiated from the adult in its anatomical composition and reproductive immaturity. Here we find the heart of the matter. Why? We could categorise the larva stage as a potential *hopeful monster* adapted to the medium of water that, incapable of independent living, continues the routine metamorphosis indicated on the embryonic script. Considering the typological separation found in adults, in order to create a new species it would be sufficient for juveniles to acquire the ability to reproduce prematurely. All this takes place across a time-space alteration. The process is direct, immediate and conservative – it does not require new structures to be created-, decisive characteristics for determining viability. This was the pattern proposed by Walter Garstang: considering the potency of juvenile states for manifesting a new evolutionary line. The conclusion was that *ontogeny creates phylogeny.* Early sexual maturity occurs when there is an alteration in ontogenic synchronism (heterochrony): the development of the gonads is brought forward, allowing incomplete specimens to reproduce – the axolotl is an existing example of this phenomenon. Garstang's model took on full evolutionary significance by investigating the life cycle of the ascidia. This colourful tunicate, tube shaped and fragile-looking, populates the seabed after maturing. However, its young proliferate freely in the ocean, propelled by an unusual caudal appendix. This strange tail bears a dorsal thread known as the notochord. This solid cellular rod resembles an incipient backbone, and disappears upon maturing into adulthood. The notochord is one of the distinctive evolutionary characteristics –synapomorphies– of chordates; a group primarily consisting of vertebrates. This fact led Garstang to identify the evolutional origin of the group as an invertebrate ancestor with a larval development similar to that of the ascidia. At some point, under specific circumstances, the juvenile acquired reproductive ability, maintaining the dorsal chord as a fundamental part of its anatomy. These specimens would be the seed for a successful evolutionary line that went on to adopt thousands of different shapes. With his investigation, Garstang opened a genuine embryological window on evolution, which until that time had been unthinkable [16]. His contemporary British embryologist, Gavin de Beer, took up this opportunity. However, it would be the palaeontologist Stephen Jay Gould who would make the argument an evolutionary benchmark during the last quarter of the 20th century. His work *Ontogeny & phylogeny*, published in 1977, is a classic in biological sciences [17]. Today, this innovative way of thinking makes up a substantial part of evolutionary developmental biology, better known as *evo-devo.*

Conclusion

At this point, it is essential to stress that evolutionary embryology highlights learning about and deconstructing the reproductive process, and understanding how the system changes spontaneously to generate different organisms. The action occurs because of a structurally defined situation, a circumstance that affects the process. Evolution does not have a metaphorical free hand. Our presentation ended in the mid-20th century. The story is not yet complete. The second half of the century presented interesting new developments. Of particular note was the approach developed by the French embryologist Rosine Chandebois in the early 1980s. Her theory is an anti-Darwinist evolutionary proposal, the purpose of which is to build up *a new logic of the living being.* How can this be achieved? By referring to the similarities in comparing the major lines of evolution with the general parameters traced by the developing embryo [18]. But that is not our story to tell today. Finally, we must remember that the solution to the evolutionary puzzle is complex but not unique. There are still many pieces to be discovered. Of the ones we know about, some are in the wrong place, and others we haven't found a place for yet. Patience, tenacity and open-mindedness are the qualities required to progress in the biological process of understanding the *past present future* of life.

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