Development

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DEVELOPMENT.

Development in biology refers to the process of growth and differentiation that is characteristic of living organisms. It describes the continuous changes during the life cycle of individual organisms from the early stage of a single cell until death. *Development* also refers to what is today known as the process of evolution, the transformation of species through time. Other meanings of *development* are connected to economic and psychological processes. The German term *Entwicklung* has the same connotations, especially with respect to the two temporal processes of ontogeny (individual development) and phylogeny (evolutionary development), and its meaning also extends into artistic and literary domains (*Entwicklungsroman*).

Due to the gradual nature of developmental processes and the wide-ranging diversity of organisms (animals, plants, microbes) and modes of reproduction (sexual, asexual), it is not possible to clearly define a unique starting point of development that applies universally to all organisms. Nevertheless, development is a fundamental property of all organisms and one that sets them apart from other physical and chemical systems. In the language of molecular biology, development is the process that translates the sum of the genetic characteristics of an organism (its genotype) into the morphological, physiological, and behavioral features of an individual (its phenotype). Since the 1970s the prevailing interpretation of this process had become increasingly preformistic—the idea that the genotype largely determines the phenotype. With the twenty-first century, however, this view has gradually been replaced by a more interactive, or epigenetic, interpretation of development that sees the individual phenotype as the product of a dynamic interaction between the genotype and the various environments of an organism (cellular, organismal, physical, cultural). These recent positions in developmental biology

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also reflect the long-standing dichotomy of interpretations of development—preformistic and epigenetic—that characterized the scientific and philosophical discussion of the last 2,500 years.

Aristotle on Development

The (human) life cycle and several aspects of development, such as the fertilization of plants, the grafting of fruit trees, and the principle of generation, were already known in antiquity. As with so many other areas of knowledge, it was Aristotle who summarized existing knowledge and by adding his own observations created the first inclusive theory of development. Aristotle expressed his conception of development in *De generatione animalium* (The generation of animals) and in his whole corpus of zoological writings, and development played an integral part in his overall science and philosophy. Aristotle's view of the world was intrinsically dynamic, based on matter and change. Matter is always structured. Form is the realized potential of matter, its entelechy, which is already present within it. In organisms, according to Aristotle, the potential form (entelechy) is gradually realized in the course of development. This dynamic process of development, as well as the resulting organism, requires all four causes of the Aristotelian physics: the material, formal, efficient, and final causes. In embryological development, the female fluid, the menstrual blood, contributes the material cause on which the semen acts, providing the initial stimulus for the dynamic sequence of development. In the course of development the combination of male and female fluids allows the formal and efficient causes to shape the emerging potential of the organism, its telos. This entelechy of the organism, however, has been present from the very beginning as the potential of this particular form of matter (the combination of male and female fluids). In later periods the Aristotelian entelechy has often been identified with the notion of a "soul," but for Aristotle entelechy is not something separate that directs development from the outside, but rather is always already present within the emerging organism as its potential to be realized gradually.

Ideas of Development in the Seventeenth and Eighteenth Centuries: Preformism and Epigenesis

Aristotle's conception of development was shaped by what he could observe—fluids and semen at conception and the gradual emergence of form in the course of development. It is therefore only logical that the next major changes in the philosophical and scientific analysis of development are connected with emerging possibilities of observation during the seventeenth century. One instrument, in particular, played a central role in discussions about development—the microscope. The microscope allowed for the first time analysis of the constitution of those observable fluids at the beginning of development. Looking at semen with his single-lens microscope, Anton van Leeuwenhoek could see structures in the head of the spermatozoa. But what did those structures represent? In the wake of the scientific revolution, a mechanical approach dominated the sciences and medicine. William Harvey had found a mechanical solution to the circulation of blood, and generations of anatomists had analyzed the form and function of the human body in similar terms. In this context of mechanical ideas, Leeuwenhoek's observations took on a specific meaning. For some of his contemporaries, the structures inside the sperm thus represented a smaller, already preformed version of the adult organism, called an "homonculus" by some. Development then was simply a mechanical unfolding and subsequent growth of structures already present at the very beginning in either the sperm or the egg. Others, such as Harvey, continued to advocate the epigenetic position of Aristotle. These epigenesists also claimed that their views only described what they could observe.

Clearly, observations were ambiguous and often fit theory-driven expectations. Preformists were committed to a mechanical and materialistic explanation. They did not want to rely on any form of entelechy or vital force in order to account for development and were also opposed to ideas and reports of spontaneous generation. Epigenesists, on the other hand, were committed to the action of a vital force in nature. They also emphasized the role of observation and pointed out that several facts, such as the existence of hybrids or "monsters," could not easily be explained within the preformist framework. The influence of metaphysical commitments in shaping the interpretation of observations can best be seen in the mid-eighteenth-century debate between Caspar Friedrich Wolf and Charles Bonnet. Both looked at chick embryos at the same stage (twenty-eight hours after fertilization). Both described in detail what they saw—no clearly defined beating heart, for instance. And both arrived at radically different conclusions. For Wolf it was obvious that the heart would only form later due to the agency of a vital force (vis essentialis); Bonnet, on the other hand, concluded that even though he could not see it, the heart must nevertheless already be there.

Metamorphosis and Recapitulation

The eighteenth-century debates about preformism and epigenesis brought development into the spotlight of biological investigations. Ordering the known diversity of life, increasing by the day as a result of European voyages of exploration, was another major concern. For many, especially the Romantic scientists at the turn of the nineteenth century, these two areas of natural history were connected. Did the diversity of nature not arise in the course of development from similar structures? Are the creative principles in nature not the same as in the arts? Pondering these questions on a trip to Italy, the poet-philosopher-scientist Johann Wolfgang von Goethe discovered the principle of metamorphosis and established the foundations of morphology. Specifically, Goethe realized that all the diverse structures of flowering plants are transformations of one basic morphological form, the leaf. Understanding these principles of transformation, or metamorphosis, then allows the scientist or the artist to recreate all existing organic forms, as well as those that could exist but have not yet been realized. This morphological building plan (*Bauplan*) is intrinsically dynamic and developmental; it is a principle that unfolds itself in nature small and large, in the individual and the cosmos. Morphogenesis focused, for Goethe and others, on the emergence of form within a context of change.

Ideas about transformation were soon applied to species as well as individuals. In 1809 Jean-Baptiste de Lamarck published

his theory of evolution, which gave development the additional meaning of the transmutation of species. For Lamarck the transmutation of species was driven by an intrinsic drive toward perfection. In this "escalator theory" of evolution, primitive forms, created spontaneously, pass through increasingly complex stages in the course of subsequent generations. The essence of nature is thus transformation, both in the course of individual development and in the generation of the diversity of life. Lamarck's theory was readily attacked, especially by his colleague George Cuvier, the founder of comparative anatomy. Cuvier had established the most sophisticated classification system of animals of his time, based on the recognition of four distinct types of animals and a strict hierarchy of systematic categories within each of these embranchements. Within this system species were considered immutable, and their relationships were defined by the degree of similarity between them.

Development was one way of explaining this similarity among species. All organisms begin their life as fertilized eggs—Karl Ernst von Baer would discover the mammalian egg in 1827—and the early stages of development also resemble each other more closely than later stages. Summarizing these observations, Johann Friedrich Meckel proposed in 1811 that the embryological stages of advanced organisms represent the adult stages of more primitive organisms. This was the first formulation of the principle of recapitulation, in which development became the causal explanation for the similarity as well as the differences between species. The evolutionary implications were obvious. Defending the clear separation of different systematic groups, Karl Ernst von Baer summarized his opposition to the principle of recapitulation in his developmental laws. He stated that no adult organism is like any embryo of another organism, that each developmental trajectory is unique, but that in each developmental sequence the more general features of the organismal structure appear earlier in development, which explains the close similarities between the early embryos of different species.

Von Baer's authority carried the day, but only briefly. In his theory of evolution as descent with modification, Charles Darwin also relied on embryological evidence, especially when he needed a mechanism that would explain the origin of new variations. Another consequence of the Darwinian theory was that the historical connections between species, their genealogy, immediately suggested an explanation for the similarity between them. The more closely two species are related to each other, the more similar they will be. Homologies, those structures that were considered the same in different organisms, could now be explained as being derived from a common ancestor. The only practical problem was that the genealogical relations between species were not obvious and needed to be inferred based on the similarity between them.

Studying the development of different species offered a way to escape this circularity of reasoning. Ernst Haeckel postulated that ontogeny recapitulates phylogeny, that the developmental sequence of an individual parallels the historical sequence of evolution. For Haeckel development was simultaneously a record of history and an explanation of diversity, as new structures would occur as terminal additions in the developmental process. Development also provided a way to establish homologies; those structures that were derived from the same embryological precursors (anlagen) could be considered to be homologies and used for the reconstruction of phylogenies. Haeckel's ideas, largely discredited today, were extremely influential in the second half of the nineteenth century and led to many proposals about the shape of the "tree of life."

Entwicklungsmechanik and Developmental Genetics

The Haeckel program in evolutionary morphology, with its descriptive outlook and its tendency to speculate about phylogenetic relationships, left many younger scientists dissatisfied. They sought a mechanistic understanding of development, more in tune with the emphasis on experimentation and causal interpretation that characterized sciences like physiology or chemistry. Championed by Wilhelm Roux, this new approach to the study of development dominated late-nineteenth-century biology in Germany and the United States. In detailed and technically demanding experiments, biologists tested the influence of physical and chemical conditions such as gravitation, pressure, temperature, and varying chemical concentrations in the environment on development of select model organisms (mostly amphibians and marine invertebrates) whose free-living embryos were easy to manipulate. This new experimental program in embryology also benefited from the newly founded marine research stations. Many of these experiments were only possible in well-equipped laboratories in close proximity to the diverse biological material of the sea.

The canonical experimental styles in *Entwicklungsmechanik* were the destruction of certain parts of the embryo and the transplantation of specific tissues between and within embryos. Both kinds of experiments disrupted normal development and allowed researchers to discover the effects of certain parts of the embryo. Puncturing one of the two cells in a two-cell-stage frog embryo, Roux found in 1888 that only half an embryo developed. In his mosaic theory of development he then argued that during differentiation the determining factors, which are all present in the fertilized egg, are gradually distributed among the daughter cells. In a similar vein, August Weismann argued in 1892 for the separation of the germ line, which he saw as retaining the full developmental potential and being passed on through the generations, and the soma, those elements of an organism that undergo differentiation. Weismann, too, thought that an unequal distribution of hereditary material accounts for the differentiation of cells during development.

When Hans Driesch repeated Roux's experiment, shaking sea urchin embryos apart during the two-and four-cell stages, he observed the formation of complete, albeit smaller, pluteus larvae. Driesch began to think that development could not be interpreted in strictly mechanical terms. The embryos' demonstrated ability to regulate their own developmental sequence led him to argue that organisms are harmonious equipotential systems and not just complex physico-chemical machines. Organisms as individuals are instead characterized by an irreducible telos, their entelechy, that shows itself in their regulatory abilities. Driesch subsequently embraced a form of neovitalism.

The vast majority of biologists, however, did not accept Driesch's philosophizing but remained committed to experimental

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study of development, mapping cell lineages and investigating fates of transplanted tissues. It was in this context that Hans Spemann and Hilde Mangold found in 1924 that a small region near the dorsal lip transplanted into the ventral side (belly) of a newt embryo could organize a second set of body axes, thus resulting in a "Siamese-twin-like" embryo. They called this specific region of the embryo the organizer, as it was capable of organizing the basic form of the full organism. In addition, researchers demonstrated that interactions between certain tissues such as mesoderm and ectoderm led to the differentiation of phenotypic structures such as the lens of a vertebrate eye, in a phenomenon called induction. The search began for the specific chemical properties of what was assumed to be the material organizer.

It was also clear that ultimately these developmentally active substances would have to be the products of heredity, since the inherited nuclear chromosomes and the genes they presumably carried, together with the material inside the egg, are what is passed on to the next generation. Research programs in developmental and physiological genetics investigated these questions and, after long and painstaking research, could identify specific causal chains, from a gene product to a phenotypic effect. Mutants, such as eye-color mutants of moths and flies, were the preferred experimental systems for this line of research. In 1940 a group headed by the biochemist Adolf Butenandt and the biologist Alfred Kühn were the first to identify and chemically characterize the substance that induced the red-eye phenotype in the moth *Epestia kühniella.*

After World War II, developmental biology gradually transformed itself into developmental genetics, especially after the techniques of molecular biology allowed researchers to study genes in their cellular context. One of the first genetic systems studied molecularly was the so-called lac-operon system, which regulates the expression of a lactose-digesting enzyme inside a bacterial cell. This focus on regulation continued as more and more regulatory networks of genes were found. In the context of molecular biology, development—the growth and differentiation of an organism—had been redefined as a problem of the regulation of gene expression. Aristotle's epigenesis had given way to the mechanistic preformationism of the seventeenth and eighteenth centuries and had come around again to a more sophisticated blend of preformism through heredity and epigenesis through development.

Evolutionary Developmental Biology

During the last decades of the twentieth century, evolutionary developmental biology emerged to reintegrate the two temporal processes within biology, development and evolution. Evolutionary developmental biology (Evo-Devo) is based on the recognition that all genetic changes must be expressed during development in order to produce a phenotype and thus amount to observable evolutionary changes. Development is thus the mechanism that produces the raw material of phenotypic evolution. Phenotypic evolution, in contrast, appears to be highly constrained. Of all the possible forms (the total morphospace), only a small number are actually realized. Furthermore, the diversity of life is organized in a nested hierarchy, whereby millions of species can be subsumed within a few dozen phyla, each characterized by a basic body plan (*Bauplan*). In other words, the many mutational changes of genotypes are translated into a much smaller number of phenotypic variants.

In addition, discoveries since the 1980s have lent further support to the idea that the number of developmental modules (transcription factors, such as Homeobox genes and regulatory networks) is relatively small. Furthermore, these developmental modules have been conserved through millions of years during evolution, in that flatworms, insects, and mammals share a number of regulatory genes. Thus, a limited "genetic toolkit of development" produces the astonishing diversity of life. These findings have serious consequences for the age-old discussions of preformism versus epigenesis. The fact that a small number of genetic elements is responsible for the enormous diversity of life indicates that development is essentially a problem of regulation and the interaction of genetic and environmental factors. In other words, the effects of genes in development are largely context dependent. Whether a specific transcription factor turns on a gene that triggers a cascade leading to the formation of an eye or whether it establishes the gradient for differentiation of the arm, for example, depends on the specific cellular and organismal context. In addition, environmental factors, which can affect developmental plasticity, are increasingly recognized as important. The current conception of development is thus largely epigenetic, within the context of inherited material genes.

Human and Social Dimensions of Development

Interpretations of individual development have also had powerful social impacts, especially as we have learned more about human embryology and reproductive biology. For those who hold the strongest versions of the view that each individual organism begins from unformed material, the emphasis on epigenetic emergence of form suggests that investing in "nurture" will pay off. It is worth investing in parenting that requires time and energy because this can shape the developmental process. In contrast, those who accept the view that the organism has some clear defining point at which it begins as an individual, and that its form or individuality is in some important sense already set, see much less value in investing in trying to shape what develops. Development in these cases is largely a matter of playing out the intrinsic causes. The dominant version of this interpretation maintains, of course, that heredity sets the individual's differentiation and that development is really just a matter of growth.

Though no respectable scientist today would hold either of these extreme interpretations, there are strong preferences depending on whether the researcher is a genetic determinist or a proponent of developmental regulation. Historically, we can find some supporters for almost any interpretation along the range of possibilities. The public's very deeply held views about individual as well as species development make it all the more important that we have a clear understanding of the historical, philosophical, and biological contexts for developmental ideas and that we understand the social implications.

See also Biology ; Evolution ; Life ; Life Cycle ; Science, History of ; Scientific Revolution .

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