Development and evolution

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The disciplines of developmental biology (or embryology) and evolutionary biology have come together twice—once as *evolutionary embryology* in the late nineteenth century and again as *evolutionary developmental biology* (evo-devo, as it is typically known) in the late twentieth century. The current intersections of development and evolution are proving to be of paramount importance for creating a fully integrated theory of biology.

History

Prior to and into the nineteenth century, the word "evolution" had a completely different meaning from its usage today. Then, it was used to describe a particular type of embryonic or larval development—the preformation and unfolding of a more or less fully formed organism from an embryonic or larval stage (for example, a butterfly from a caterpillar, or aphids from the body of an adult female). In fact, Charles Darwin did not use the word "evolution" per se in *On the Origin of Species*, which was published in 1859, although "evolved" was the final word of his book. To reach its present-day definition, the term "evolution" had to undergo a slow transformation from development within a single generation to transformation (transmutation) between generations.

As for the field of developmental biology, in the nineteenth century, embryology (referring to the study of embryonic development) was a progressive field in biology, with researchers describing normal development and then manipulating animal embryos [*experimental* or *physiological embryology* (also known as developmental mechanics)] in search of altered outcomes that would help explain how development occurred. In addition, scientists were looking for similarities and differences in development between species, initially in a comparative context and then in an evolutionary context (as evolutionary embryology, starting in 1859). Late-nineteenth-century evolutionary embryologists such as Ernst Haeckel, Karl Gegenbaur, Francis Balfour, E. Ray Lankester, and others (including Charles Darwin) used comparative embryology to provide evidence for schemes of animal classification, to establish phylogenetic relationships among animals (common descent from a single universal ancestor), and as a major class of evidence for evolution—that is, Darwin's *descent with modification*. During this time period, embryologists observed that, from the earliest stages of development, embryos of diverse species pass through conserved embryonic stages using the same developmental processes of cell division, migration, differentiation, and morphogenesis of cells. It was also observed that the various anatomical structures arise from equivalent (homologous) germ layers. Thus, the foundation was laid for characterizing evolutionary relationships based in part on the similarities and differences in developmental processes.

Currently, experimental embryology continues to flourish through our ability to knock out (inactivate) or overexpress/misexpress (activate) genes, to transplant cells, and to manipulate differentiated cells and transform them into stem cells. Development is thus central to these twenty-first-century studies.

The late twentieth century saw the application of genetics and molecular biology to development and evolution. New molecular evolutionary theories began to emerge describing how genetics influenced life history and phenotypic plasticity [the property of a genotype to produce more than one phenotype: for example, the tadpole and adult frog, or summer and winter forms (morphs) of a single butterfly species]. At the same time, developmental biologists employed molecular biology toward understanding how genes function in the developing organism. Evolution and development emerged as two branches of biology, with most researchers in one field overlooking the progress in the other. On one side, two central pillars of evolution—natural variation and natural selection—have yet to be fully appreciated by the community of developmental biologists. On the other side, gene regulation of developmental processes is often overlooked by evolutionary theorists. In the cases where overlapping collaborations exist, the goal has been to seek and explain ultimate and proximate causes for the origin and diversity of life. As these fields begin to more fully incorporate biological models, the basis for an integrated theory of biology, that is, a twenty-first-century biology, will be created.

Relationship between development and evolution

Because natural selection operates equally on embryonic through adult stages, changes in development can mediate evolution in any life history stage. The apparent constancy of embryonic stages and the seeming lack of variation among individuals of a given embryonic stage in a given species reflect the actions of stabilizing selection (which concentrates features around a norm) and of differential survival (which removes individuals that deviate from that norm so early in development that they do not survive to be studied). Such evolutionary processes explain the conservation, stability, and seeming invariance of development [reflected in conserved embryonic stages and body plans (Baupläne)] in the same way that selection and differential survival and reproduction explain both the maintenance and the transformation of species.

There are a number of major development processes and evolutionary changes that need to be understood more completely in this context. These include the basis for the different body plans of multicellular organisms in the three kingdoms (plants, animals, and fungi); how transformation within and between body plans occurs; and how (or whether) major transitions, such as the origin of the limbs of terrestrial vertebrates from the fins of fish and the origin of flowers in land plants, are associated with the origin of new groups of organisms. The integrated approach to development and evolution known as evo-devo seeks a comprehensive understanding of how mechanisms operating during embryonic development mediate evolutionary change. The fundamental rationale is that no feature (character, trait) of a multicellular organism can change over evolutionary time without modification of development.

The hereditary information (that is, DNA) is transferred from generation to generation as genes, and processes such as methylation (addition of a methyl group), genomic imprinting (a phenomenon whereby one of the two alleles at a gene locus is preferentially expressed depending upon the parent of origin), chromosomal changes, and reduction in chromosome number help to modify gene action. In order for changes (mutations) to enable genetic changes that can influence evolutionary change, the genes controlling development, and therefore developmental processes, must be altered. One key intersection of molecular biology/molecular genetics with development came about through the discovery of a group of key developmental genes (homeotic/homeobox/Hox genes) that act as transcription factors and that are involved in the specification of fundamental animal features, including an anterior-posterior (A-P) axis, bilateral symmetry, and regional (often segmental) organization of body parts/segments/regions. Animals as “different” as insects, arthropods, centipedes, and crustaceans have been found to share a set of homeobox genes that were previously thought to be tied explicitly to the highly derived patterns of segmentation seen in such insects as *Drosophila*. For example, modifications of the expression patterns and of the developmental roles of three homeobox genes (designated as engrailed, distal-less, and orthodenticle) are associated with the origin of the different groups of echinoderms.

Other families of developmental genes (bone morphogenetic proteins, fibroblast growth factors, hedgehog genes) that act as signaling molecules provide the upstream signals that activate critical genetic pathways. Signaling by these molecules ultimately influences all aspects of development, including cell lineage decisions in the developing limbs, kidneys, teeth, heart, and skeleton. Most developmental genes are evolutionarily conserved in their cellular functions. Some have even been shown to act as master regulators of organ development conserved across the animal kingdom. One example is the *Pax-6* gene, which controls eye development in both vertebrates and insects. This was a surprising discovery, considering the morphological disparity between vertebrate and insect eyes.

Gene regulatory networks and the future of evo-devo

The future focus of evo-devo research is likely to center on a field studying the interaction of multiple genes and molecular pathways, referred to as gene regulatory networks. The developing embryo is a coordinated, highly dynamic system requiring rapid changes in cell behavior, all controlled at the molecular level. Therefore, complex molecular networks, where developmental genes and feedback networks regulate specific pathways, are present and are being discovered by scientists throughout the world. Knowledge of a gene network means that the network can be manipulated to generate altered developmental programs and thus altered morphological outcomes. This type of manipulation/experimentation is akin to evolutionary experiments and has been employed in various evo-devo studies, including research programs seeking to discover ancestral larval stages, the universal common ancestor of animals, and the dinosaur ancestor of birds. The placement of gene cascades within the context of specific lineages of cells (for example, muscle-, skeleton-, or heart-forming cells) and specific cell-to-cell or tissue-to-tissue interactions (such as those that regulate feather, limb, kidney, and tooth development) is revealing the hierarchies of interactions required to produce unique attributes of various organisms. Applying this knowledge in an evolutionary context leads to the integration of research to discover the mechanisms behind developmental (ontogenetic) and evolutionary (phylogenetic) transformations. Consequently, evo-devo constitutes one of the most exciting, vigorous, challenging, and cutting-edge sciences of the present day.

See also: ANIMAL EVOLUTION; DEVELOPMENTAL BIOLOGY; DEVELOPMENTAL GENETICS; EMBRYOLOGY; GENE; GENETICS; HOMEOTIC (HOX) GENES; MACROEVOLUTION; MORPHOGENESIS; ORGANIC EVOLUTION; PLANT EVOLUTION.

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