The Changing Role of the Embryo in Evolutionary Thought: Roots of Evo-Devo. By Ron Amundson. xiv + 280 pp. New York. NY: Cambridge University Press. 2005. $75.00 (cloth).

Neo-Darwinism coined a particular picture of evolution: the explanation of adaptation and speciation as the central goals of evolutionary theory, and natural selection as the only directing cause in evolution. Recently, evolutionary developmental biology (evo-devo) became an independent field, pointing out that that there are other important goals of evolutionary biology: the explanation of the origin of morphological novelties and body plans, and an account of evolvability. Neo-Darwinism viewed the study of development as being irrelevant to evolutionary biology, but evo-devo biologists argue that developmental and morphological features rather than natural selection are crucial causal factors in these new types of evolutionary explanations, yielding a more powerful explanatory framework and a broader understanding of the mechanisms of evolution. Apart from contemporary biology, neo-Darwinism also strongly influenced how the *history of biology* has been viewed by biologists, philosophers, and historians. This led to a distorted picture of 19th century biology, and during the last two decades historians of biology have started to correct this view of history. Even though the emergence of evo-devo and recent developments in historical scholarship are largely independent, philosopher of biology Ron Amundson brings these two trends together in this volume. Amundson distinguishes between functionalist and structuralist approaches in the history of biology; the former emphasize the *explanation of adaptation* and the organism-environment relationship, and the latter stress the *explanation of form* and the internal structure and development of individuals. Amundson's central target is what he calls '*Synthesis Historiography*,' i.e., the use of the conceptual framework of neo-Darwinism to interpret the history of biology. The first half of Amundson's book concerns the 19th century and debunks various historical misinterpretations

due to Synthesis Historiography—using a structuralist or evo-devo perspective on history to uncover important historical facts that former approaches have left out. The second half concerns the 20th century, addressing how development dropped out of evolutionary theory, how Synthesis Historiography (SH) emerged in the first place, and discusses the differences between contemporary functionalist and structuralist approaches.

A central element of SH is the distinction between typological thinking and population thinking. It forms the basis of the assumption that pre-Darwinian biologists were typologists or essentialists who explained species fixity based on the idea that species have immutable essences. As Amundson shows in line with recent historical scholarship, this is simply a myth. Species fixism gained acceptance just a century before Darwin, and its original acceptance was scientifically progressive, because naturalists showed that species do not wildly transmute across taxa. As it turns out, species fixity was not explained based on metaphysical ideas such as types or essences, but with recourse to empirical assumptions. Pre-Darwinian, 'idealistic' morphology has also been viewed in the grip of typological thinking. However, the notion of types is actually scientifically legitimate and does not conflict with population thinking. Population thinking is about the variation *within* species, and the notion of a type is about the relation *between* species. Higher taxa, in particular phyla, have a type, but species were not viewed as having a type. The advent of phylogenetic systematics promoted taxa characterized by synapomorphies. This is what pre-Darwinian, 'typological' biology was getting at. SH commentators often regard historical beliefs in continuity between groups as indicators of progressiveness in biological thought, but Amundson makes clear that a crucial step towards evolutionary theory was the recognition of characteristic discontinuities between extant species. The 18th century naturalists usually assumed that the various extant species form a continuous or seamless fabric of nature

and that the taxonomic system was a mere human contrivance, and it was an achievement of early 19th century taxonomy to view the hierarchical structure of taxonomic groups as reflecting real patterns existing in nature. Research in comparative anatomy and embryology supported this view by introducing the homology concept and finding homologies across larger taxa. Morphological relations were viewed as reflecting true relations between biological groups, preparing the way for viewing the hierarchical structure of taxa as reflecting the phylogenetic tree of nature.

SH tended to lump together two different pre-Darwinian traditions based on the notion of typological thinking: natural theology and idealistic morphology. The natural theologians were functionalist, viewing species as independently created by God so as to be perfectly adapted to its ecological niche. However, as Amundson discusses in detail, the idealistic morphologists were structuralists who stressed morphological relations between species and criticized the adaptationist natural theologians for not being able to account for homologies. According to SH, idealistic morphologists viewed morphological types as blueprints in the mind of God. However, some pre-Darwinian morphologists such as Richard Owen clearly expressed evolutionary ideas. In any case, morphological accounts could use a non-phylogenetic notion of a type as a real explanatory concept *without* invoking divine creation by viewing types as reflecting law-like relationships between organismal forms. Amundson points out that it is legitimate that morphologists did not yet have an account of the real (phylogenetic) nature of types, because there are many episodes in the history of science where scientists are justified in invoking a law while still lacking a real understanding of its underlying causal basis. Darwin's main enemies were in fact the creationist natural theologians, and in the *Origin of Species* Darwin explicitly relied on the well-known results of idealistic morphology. The existence of homologies and what

Darwin called the 'Unity of Type' supported his crucial doctrine of common ancestry. Some SH commentators stressed Darwin's ideas of variation and natural selection but ignored the phylogenetic-morphological aspects of Darwin's work or—being puzzled how Darwin could make favorable remarks about the alleged creationist morphologists—blatantly misinterpreted these passages of the *Origin*.

Amundson discusses the influential tradition of 19th century evolutionary morphology (Gegenbaur, Haeckel), which was in the business of establishing phylogenetic trees and studying morphological evolution (such as the origin of tetrapod limbs) based on how morphologies and ontogenies change in the course of phylogeny. Some SH commentators have viewed this as mere description and the telling of historical narratives. Contemporary phylogenetic approaches are more likely to view 19th century morphology as real explanation, and many evo-devo biologists view the tradition of evolutionary morphology as an important forerunner of their approach; extant forms and the origin of morphological novelties are explained based on how ontogenies have changed during phylogeny.

In the 19th century, evolutionary considerations were tightly connected to development. Heredity was viewed as a part of development. In the second part of his book, Amundson describes how the emergence of classical genetics in the 20th century led to a redefinition of 'heredity' so that it referred to the transmission of features but excluded development leading to the split between embryology and genetics, where the latter but not the former became part of the Modern Synthesis. Amundson also examines how the essentialist story about pre-Darwinian biology originated in the late 1950s. It is embarrassing that these historical claims were made without a real study of the history. Apart from the distinction between typological vs. population thinking, neo-Darwinians developed other dichotomies (e.g., proximate vs. ultimate causes).

These conceptual schemes were used both to interpret the history of evolutionary biology in the sense of neo-Darwinism and to argue against contemporary critics of the Modern Synthesis. In the 1980s they came to be used to reject structuralist critiques by arguing that developmental considerations have no bearing on evolutionary theory. Amundson describes these more recent debates. Neo-Darwinians have a 'residual' concept of homology that views homology as the remnants of ancestral features that have not been modified by natural selection. Evo-devo biologists have a 'developmental' concept of homology that views homologues as building blocks of morphological organization that causally figure in development and influence morphological evolution, thereby reviving ideas from 19th century morphology. Neo-Darwinians focus on the explanation of adaptation, viewing populations as the entities that evolve, while evo-devo biologists focus on the explanation of the evolution of form, viewing ontogenies as what evolves. Modern practitioners of evo-devo assume that selectionist and developmental modes of explanations are perfectly compatible. Amundson is in fact impressed by the seeming incommensurability between functionalist and structuralist perspectives, stating that it has yet to be shown that both approaches can really be united.

This volume gives a masterful account and ought to be read by everyone who is interested in evolutionary biology. Amundson reminds us that any contemporary picture of biology and its history should never be taken as complete and unbiased. His discussion also indicates that certain modern debates such as the debate about adaptationism vs. developmental constraints had forerunners (natural theology vs. idealistic morphology), though they occurred in a seemingly different context (such as pre-Darwinian biology). Modern debates are not just about what we take them to be, so that a consideration of the history of biology is relevant for our *current* situation.

INGO BRIGANDT

Department of History and Philosophy of Science

University of Pittsburgh

Pittsburgh, Pennsylvania